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Climate change impacts on Arctic ecosystems and associated climate feedbacks

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Climate change impacts on Arctic ecosystems and associated climate feedbacks

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Climate change impacts on Arctic ecosystems and associated feedbacks

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Climate change is currently reshaping Arctic ecosystems, with highly uncertain future outcomes. In the best-case scenario, warming could lead to the replacement of Arctic ecosystems by more diverse and productive sub-Arctic or temperate ecosystems, which may serve as net carbon sinks. However, recent research indicates that environmental disturbances caused by rapid warming could transform these ecosystems into heavily perturbed and degraded states, resulting in a net release of carbon to the atmosphere. The eventual outcome depends on the scale and pace of environmental changes, as well as the extent of other human disturbances in the region. To navigate these changes, we argue that it is crucial for Arctic nations to collaborate in monitoring and ecosystem-based management while developing policy-relevant pathways and scenarios to guide adaptation in a rapidly changing Arctic.

KEYWORDS

Arctic ocean, borealization, ecosystem perturbation, regime shift, tundra ecosystem

1 Introduction

Since 1979, the Arctic has been warming nearly four times faster than the global average (Rantanen et al., 2022). This cold part of the globe is shaped and characterized by frozen water in the form of sea ice, ice sheets, glaciers, ice on rivers and lakes, permafrost, and snow. However, the Arctic cryosphere is melting at an accelerating rate with profound consequences for the global climate as well as for Arctic nature and people (CAFF, 2013; CAFF, 2017; AMAP, 2017c; AMAP, 2021). In the short term, the changes cause massive ecosystem perturbations which feed back to the climate system with a potential to accelerate local to regional changes in climate and greenhouse gas emissions and affect regional to global-scale climate systems. The resulting impacts on Arctic ecosystem services, livelihoods and wellbeing are accelerating and will have far-reaching consequences for Arctic residents and local communities. Impacts include changes in food security, economic and social wellbeing, cultural preservation, safety, human health, cultural ecosystem services, sense of place, transportation and infrastructure (AMAP, 2017b; AMAP, 2017a; AMAP, 2018).

In this context, the Arctic Council decided to initiate a joint assessment to be conducted by the two Arctic Council working groups; AMAP (Arctic Monitoring Assessment Program) and CAFF (Conservation of Arctic Flora and Fauna) with the over-arching objective to "*assess how climate change affects Arctic ecosystems and feedbacks and inform strategies for adaptation and resiliency*". As a part of this assessment, scientific experts have, in this Special Issue of Frontiers in

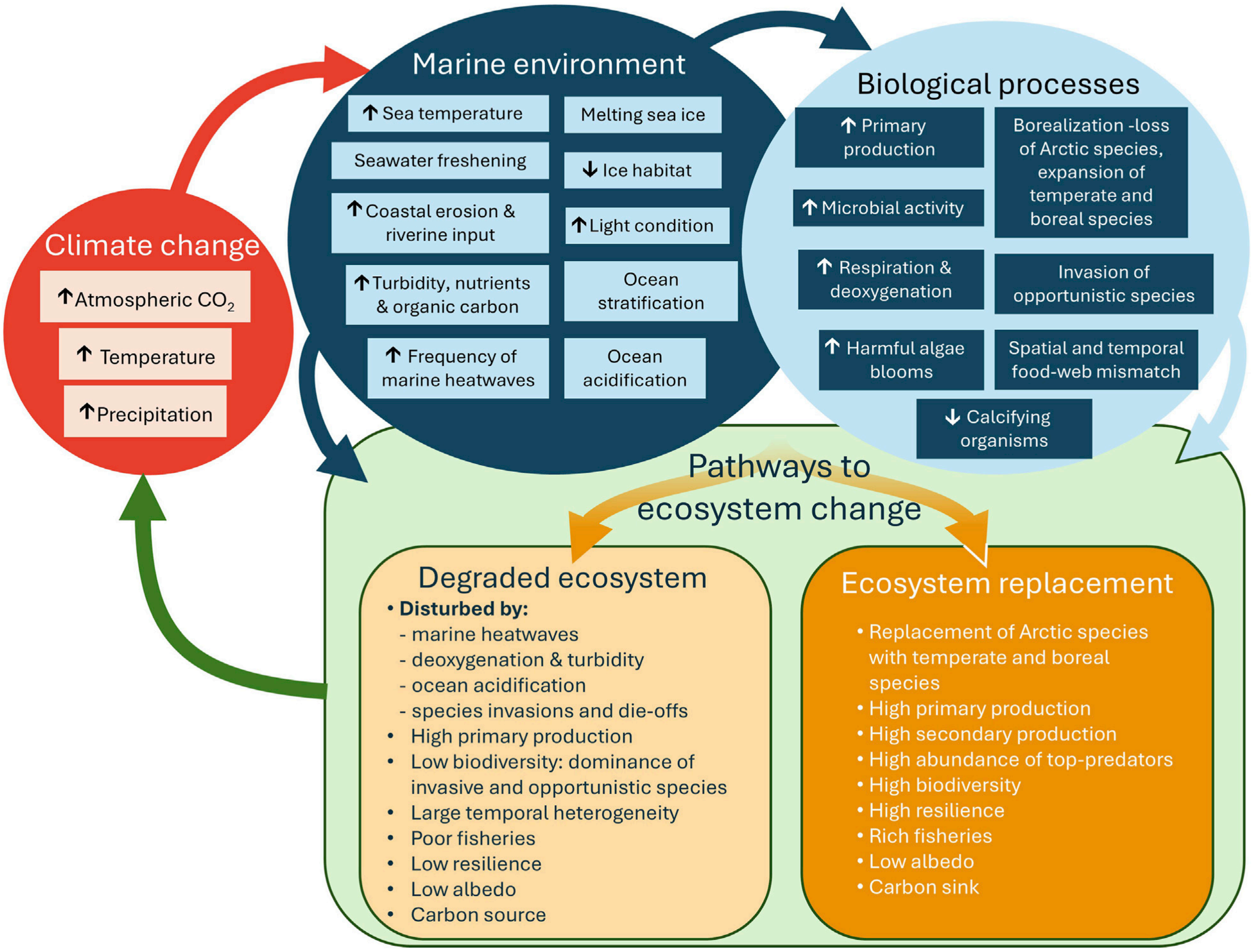

FIGURE 1
Interactions between climate change and Arctic marine ecosystems. Climate change triggers and accelerates a wide range of transformations in the Arctic marine environment (upper left) that subsequently impact various biological processes in the marine ecosystem (upper right). Depending on its initial condition, the rate and extent of the changes, as well as the influence of other human disturbances, the Arctic marine ecosystem may be replaced by a more productive and diverse boreal ecosystem (lower right) or transform into a heavily perturbed and degraded system (lower left). Rapid environmental change coupled with increased human impacts, heighten the chances of a shift toward a degraded ecosystem, whereas a slower pace may favor a more gradual transition to ecosystem replacement. Due to spatial variability in key drivers across the Arctic, trajectories can differ among regions, resulting in ecosystem replacement in some areas and degradation in others. Ultimately, the properties of the new ecosystem, such as albedo and net rate of carbon storage and release, determine how the ecosystem change will feed back to the climate system.

Environmental Science, reviewed the scientific literature to address how the current climatic drivers affect Arctic ecosystems and how these changes feed back to the climate system. The papers include marine, terrestrial and freshwater ecosystems and cover a wide range of climate-induced changes.

Together, the reviews in this Special Issue highlight the rapid and widespread environmental changes unfolding across the Arctic. While a global reduction in fossil fuel emissions could slow these developments and provide valuable time for adaptation, many of the observed changes have already reached -or are approaching -tipping points beyond which they may become irreversible.

In the following, we synthesize the major trends and uncertainties in Arctic marine and terrestrial ecosystems, highlighting the need for coordinated monitoring, future planning and adaptations. In an accompanying editorial synthesis at the end of this Special Issue we summarize current status as portrayed by the papers presented here (Christensen et al., 2025).

2 The Arctic ocean

As sea ice diminishes from the Arctic Ocean, marine algae experience larger ice-free areas and longer growing season (Ardyna and Arrigo, 2020; Attard et al., 2024). Sustained by increased influx of nutrients, net primary production in the Arctic Ocean has increased by 57% from 1998 to 2018 (Lewis et al., 2020). Whether this increase in plant production will contribute to higher production of fish, shellfish, marine mammals and seabirds, as well as increased sequestration and storage of carbon in the bottom sediments is, however, highly uncertain and depend on complex interactions between the climatic drivers and the marine ecosystem (Ardyna and Arrigo, 2020; Oziel et al., 2025) (Figure 1; Table 1).

The rich sub-Arctic marine ecosystems, such as the Barents and Bering Seas support some of the world's richest fisheries, and one scenario under climate warming, is that these rich

TABLE 1 Key climate change-driven processes in Arctic marine ecosystems.

CC process	Description	Ref.
Increased primary production	Melting sea ice increases the area and prolongs the period of favorable light conditions for planktonic and benthic algal growth. Increased production is sustained by larger input of nutrients	1, 2
Seawater freshening	Increased supply of freshwater from melting ice and precipitation stratify the Arctic water masses and reduce the mixing of nutrients and oxygen in the water column	3
Coastal erosion and riverine input	Melting coastal permafrost and increased wave action from an ice-free ocean erode the Arctic coasts. Increased precipitation and melting of permafrost increase the riverine discharge of freshwater and terrigenous materials. About one-third of the Arctic ocean primary production is currently sustained by the input of nutrients from coastal erosion and rivers	4, 5, 6, 7
Increased respiration and deoxygenation	Increased input of terrigenous nutrients, warming and freshening of surface waters increase microbial respiration and remineralization of carbon and nitrogen. The result is deoxygenation, increased turbidity, reduced carbon sequestration and storage, reduced export of organic matter to bottom-dwelling organisms and less production available for higher trophic levels	8
Shift in the plankton community	Warmer and more stratified waters drive a shift in the Arctic plankton community to smaller and less nutritious species, reducing the efficiency of trophic transfer to fish, seabirds and mammals	8, 9, 10
Ocean acidification	Low water temperature and seawater freshening make the Arctic especially vulnerable to ocean acidification. On a basin scale, the Arctic ocean is projected to become undersaturated with respect to aragonite within this century with large potential consequences for calcifying organisms and the marine ecosystem	11, 12, 13
Borealization	Northward expansion of boreal and sub-Arctic species is replacing Arctic and ice-associated species and thereby altering ecosystem function and dynamics	10, 14
Migratory species and food-web mismatch	Many mammals, birds and fish migrate from the south to the Arctic to reproduce and/or feed. Rapid climate change can disrupt the synchrony between interacting species, leading to phenological mismatches in timing or spatial mismatches in distribution. These disruptions can disturb food webs, potentially resulting in population booms due to predator relief, and/or population collapse due to starvation	15, 16, 17
Climatic extremes	Marine heatwaves increase in frequency and intensity with pervasive effects on the marine ecosystem, triggering harmful algae blooms, replacement of important functional groups, and reduced growth and mass mortality of susceptible species	18

References: 1 Ardyna and Arrigo, (2020), 2 Lewis et al. (2020), 3 Kwiatkowski et al. (2020), 4 Nielsen et al. (2022), 5 Feng et al. (2021), 6 Zhang et al. (2021), 7 Terhaar et al. (2021a), 8 Oziel et al. (2025), 9 Mueter et al. (2021), 10 Niemi et al. (2024), 11 Niemi et al. (2021), 12 Terhaar et al. (2021b), 13 Findlay et al. (2025), 14 Husson et al. (2024), 15 Kuletz et al. (2024), 16 Renner and Zohner (2018), 17 Carroll et al. (2024), 18 Pecuchet et al. (2025).

systems simply move north and replace the historically less productive high-Arctic and ice-dominated ecosystems. However, the massive perturbation triggered by warming, ocean acidification and the melting of the Arctic cryosphere is likely to push the marine ecosystem into less stable and undesirable states. In a worst-case scenario, the Arctic marine ecosystems could as a response to these drivers turn into simplified systems dominated by opportunistic algae, high microbial activity, low diversity of plants and animals, turbid waters and expanding low-oxygen areas (see Breitburg et al., 2018; Reusch et al., 2018). This situation mirrors the changes observed in coastal areas world-wide (Breitburg et al., 2018). However, while climate warming, human eutrophication and over-fishing are the culprits in warmer seas, the changes in the Arctic are currently governed by ice-melting, seawater freshening, nutrient input, ocean acidification and warming (Figure 1).

The outcome of the climate-induced changes would depend on the initial state of the ecosystem, the pace and magnitude of the environmental changes, and not least the evolving pressures from emerging human activities in the Arctic, including increased pressures from fishing (Fauchald et al., 2021). To effectively document and understand ongoing changes, coordinated pan-Arctic monitoring and predictive modeling of climatic drivers and marine ecosystem responses are essential. In addition, it is crucial to assess how emerging human activities—such as industrial fishing, shipping, tourism, and the extraction of oil and mineral resources—interact with climate drivers to change the ecosystems. Equally important is the co-creation of scenarios, pathways, and solutions that support a more sustainable future for the Arctic Ocean.

3 Arctic tundra ecosystems

In response to permafrost thaw, shorter periods with snow cover, and warmer summers, the tundra has gradually become greener over the past 40 years (Frost et al., 2025). The Arctic greening serves as a proxy for increased production and biomass of plants, reflecting a shift in vegetation cover, often linked to the expansion of deciduous shrubs. This “borealization” of the terrestrial Arctic ecosystem is occurring alongside a range of ecological disturbances that are expected to intensify in the coming decades, including wildfires (Baltzer et al., 2025), insect outbreaks (Vindstad et al., 2019), and extreme climatic events (Christensen et al., 2021).

The climate induced changes in the tundra ecosystem feed back to the climate system through biotic process such as microbial activity and herbivory (Schmidt et al., 2024). The most significant of these feedbacks is linked to permafrost thaw (Schuur et al., 2022). The Arctic permafrost holds approximately one-third of the world’s soil organic carbon (Schuur et al., 2015). As it thaws, this carbon becomes exposed to microbial decomposition, releasing carbon dioxide and methane into the atmosphere. These greenhouse gas

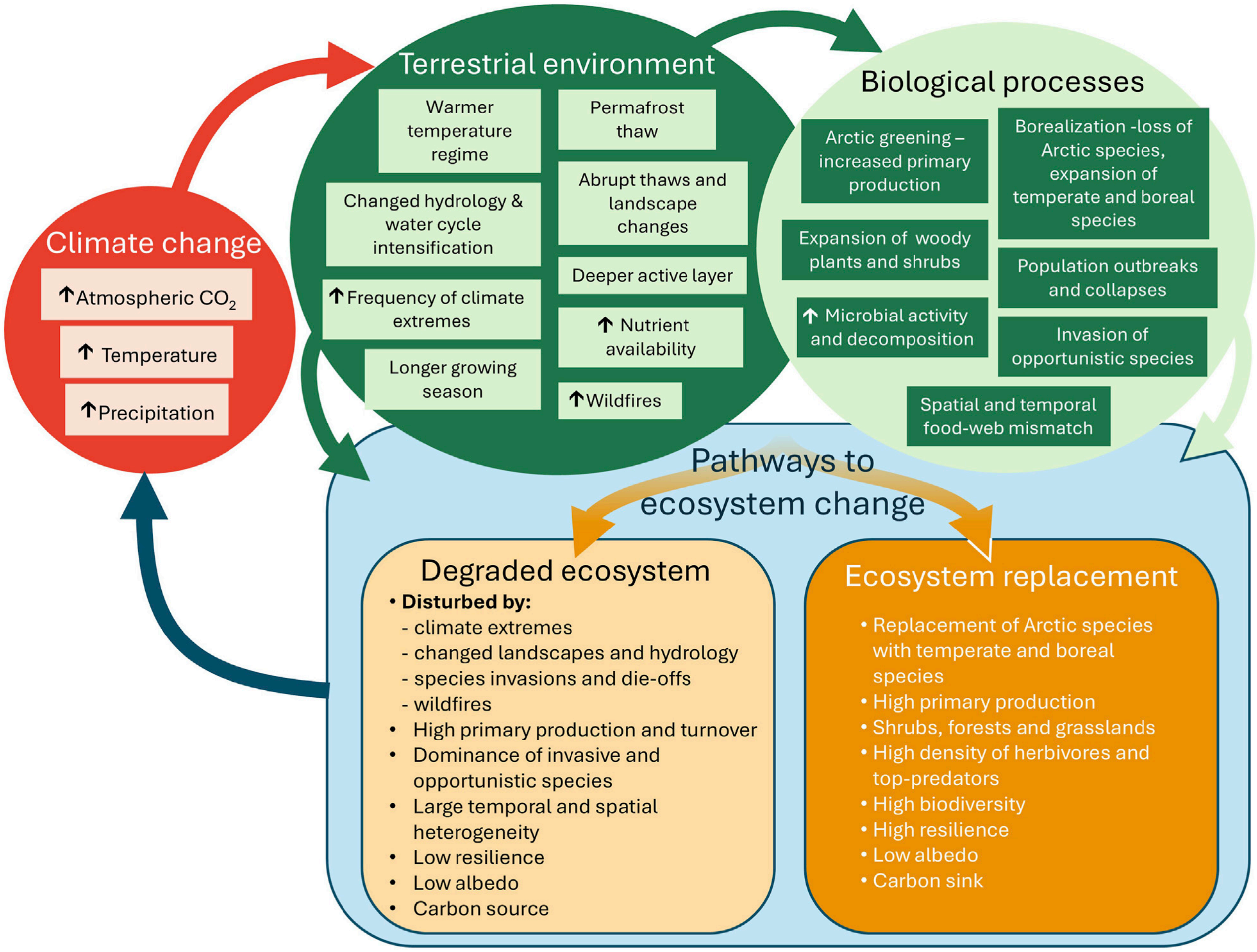

FIGURE 2
Interactions between climate change and Arctic terrestrial ecosystems. Climate change is driving widespread environmental changes in the Arctic (upper left). These alterations initiate complex biological processes (upper right), collectively leading to fundamental shifts in Arctic terrestrial ecosystems. On one hand, Arctic ecosystems may be replaced by more productive and diverse boreal or temperate ecosystems (lower right). On the other hand, disturbances such as changes in fire regimes, climate extremes, landscape and hydrological alterations, and invasive species could cause ecosystems to shift into less desirable states (lower left). The trajectory of these changes depends on the initial condition of the ecosystem, additional human impacts, and the pace of environmental change -ultimately driven by greenhouse gas emissions. Rapid environmental change coupled with increased human impacts, heighten the chances of a shift toward a degraded ecosystem, whereas a slower pace may favor a more gradual transition to ecosystem replacement. Due to spatial variability in key drivers across the Arctic, trajectories can differ among regions, resulting in ecosystem replacement in some areas and degradation in others. Ultimately, the ecosystem's albedo and its net rates of carbon storage and release will influence how these transformations feedback into the climate system.

emissions further accelerate global warming, creating a reinforcing feedback loop. The strength of this climate feedback depends on the magnitude of the emissions, the ratio of methane to carbon dioxide released (Parmentier et al., 2024), and the extent to which these emissions are offset by increased carbon uptake by accumulated plant biomass through Arctic greening (Schuur et al., 2022; See et al., 2024; López-Blanco et al., 2025).

Above the permafrost, the tundra holds a relatively thin and wet active layer, where most microbial and hydrological activity takes place. As the underlying permafrost thaws, the active layer deepens, altering tundra hydrology by promoting the drainage of soil, wetlands, and shallow lakes. These changes in Arctic hydrology could cause atmospheric climate feedback through reduction in cloudiness, which can be in the same order of magnitude as the permafrost carbon feedback (de Vrese et al., 2023; de Vrese et al., 2024). Moreover, the drainage of the tundra causes a shift to more aerobic microbial activity, resulting in reduced methane emissions relative to carbon dioxide (Parmentier et al., 2024). Finally, expanding woody vegetation, drier soils and increased lightning activity are contributing to more frequent, intense, and widespread Arctic wildfires (Kim et al., 2024; Baltzer et al., 2025). Besides having a pervasive effect on the vegetation (Heim et al., 2025), wildfires promote further melting of the permafrost and increase the emission of greenhouse gasses and aerosols.

Feedback loops between the ecosystem and the climate system, lagged ecosystem responses, and massive perturbations from wildfires, changed hydrology, species invasions and a thawing cryosphere will cause abrupt, unexpected and pervasive shifts in Arctic terrestrial ecosystems (Figure 2; Table 2). The magnitude of potential impacts, combined with significant uncertainties, underscores the need for a precautionary approach to development of human

TABLE 2 Key climate change-driven processes in Arctic terrestrial ecosystems.

CC process	Description	Ref.
Permafrost thawing	Permafrost thawing leads to widespread landscape changes, such as ground subsidence, thermokarst development, the formation or draining of wetlands and lakes, and the deepening of the active soil layer. Abrupt thaws occur when local subsidence and changed hydrology expose deeper layers to thaw. As the ice-rich permafrost melts, previously frozen organic carbon is exposed to microbial activity, resulting in the release of CO_2 and methane into the atmosphere	1, 2
Changes in hydrology	Accelerating evaporation, precipitation, ice melting and freshwater runoff intensify and alter the Arctic water cycle, leading to more extreme hydrological events such as floods and droughts, as well as fundamental changes in river regimes, groundwater recharge, and the distribution of lakes and wetlands in Arctic landscapes	3, 4
Arctic greening	Warmer summer temperatures, an extended growing season, and a deeper active soil layer enhance plant growth, leading to increased carbon sequestration and storage in plant tissues. Disturbances such as climate extremes, increased herbivory, wildfires and altered hydrology intermittently disrupt the overall greening trend, resulting in areas of browning	5, 6
Shrub expansion	Arctic greening is associated with a "shrubification" of the tundra, where tall deciduous shrubs expand and replace lichen and moss dominated vegetation. The shift in vegetation cover feeds back to the climate system by enhancing carbon sequestration through plant growth, reducing surface albedo, increasing snow accumulation and soil insulation, and stimulating microbial activity and decomposition	7, 8, 9
Wildfires	Rising temperatures causes longer fire seasons, more ignition from lightning and drier vegetation and soil. Combined with more fire fuels from woody plants and dried peat, the frequency, intensity, and extent of Arctic wildfires are accelerating. Crucially, as permafrost thaws, large areas of carbon-rich soils and peatlands dry out, making them susceptible to prolonged burning. This process releases significant amounts of CO_2 and aerosols into the atmosphere and accelerates permafrost thawing, creating a feedback loop that intensifies the environmental changes. A new fire regime with increased frequency and intensity of wildfires have large implications for biodiversity and ecosystem resilience	10, 11, 12, 13
Dust in the Arctic	Wildfires, loss of snow cover, glacier retreat, permafrost thaw, and rising drought intensity all contribute to increased dust and aerosol production in the Arctic. These particles can be transported over long distances, engaging in complex interactions with both climate and ecosystems, including radiative forcing (positive and negative), cloud formation, albedo and fertilization of aquatic ecosystems	14

References: 1 Schuur et al. (2015), 2 Schuur et al. (2022), 3 AMAP (2017c), 4 AMAP (2021), 5 Frost et al. (2025), 6 Myers-Smith et al., 2020, 7 Mekonnen et al. (2021), 8 Myers-Smith et al. (2011), 9 Schmidt et al. (2024), 10 Descals et al. (2022), 11 Kim et al. (2024), 12 Holloway et al. (2020), 13 Baltzer et al. (2025), 14 Meinander et al. (2025).

activities. Effective policy must be grounded in continuously updated knowledge drawn from coordinated pan-Arctic monitoring and predictive modeling, as well as future scenarios and preferred pathways co-developed by local residents and scientific experts. The spatial heterogeneity across Arctic regions offers valuable opportunities for shared learning, where regional experiences, local and indigenous knowledge, and bottom-up adaptations can inform and strengthen a collective response to ongoing changes.

4 Conclusion

Climate change is driving profound transformations in Arctic marine ecosystems, with increased primary production but growing risks of biodiversity loss and ecosystem instability. While boreal species may expand northward, potentially benefiting fisheries, this shift could disrupt food webs and reduce ecosystem resilience. Ocean acidification, deoxygenation, and harmful algal blooms threaten marine life and carbon storage capacity. Regional outcomes will depend on ecosystem vulnerability, climate dynamics, and human activities such as fishing, shipping and resource extraction. In this regard, cross-sector adaptation planning through ecosystem-based management by national and local governments could play a key role. There is a need for policymakers to prioritize coordinated pan-Arctic monitoring, scenario development, and adaptive and sustainable governance to safeguard the future of the Arctic Ocean.

Arctic terrestrial ecosystems are undergoing rapid and unpredictable transformations due to permafrost thaw, vegetation shifts, and intensifying disturbances such as wildfires and extreme weather. These changes create powerful climate feedbacks, notably through greenhouse gas emissions from thawing permafrost, which risk accelerating global warming. The spatially variable and lagged responses of ecosystems complicate predictions and demand flexible, regionally informed policy approaches. A precautionary stance is essential, supported by coordinated pan-Arctic monitoring, scenario planning, and inclusive co-development with local communities. Policymakers must integrate scientific and indigenous knowledge to guide sustainable Arctic development under growing uncertainty.

To effectively prepare for, navigate, and adapt to these transformations, we argue that the Arctic States, through the Arctic Council, should take the following three actions:

1. Establish coordinated pan-Arctic monitoring and predictive modeling of key climatic drivers, human activities, and their combined impacts on Arctic socio-ecological systems. This action should include:
    - Establish a prioritized list of relevant key parameters to be monitored across the Arctic.
    - Initiate and coordinate monitoring of key parameters by the Arctic States.
    - Initiate and coordinate pan-Arctic predictive modelling of the interactions between climate, human drivers and Arctic ecosystems.
    - Establish a central data repository for data storage and sharing, and an online knowledge hub for dissemination of trends, maps and predictions of key parameters.
2. Co-develop policy relevant pathways and scenarios for a changing Arctic. This action should include activities where:

    - Arctic scientists, policymakers and communities co-develop exploratory scenarios to examine a range of plausible futures based on potential trajectories of climate and economic drivers.
    - Scientists and local and indigenous knowledge holders co-develop desirable goals and possible pathways to reach these goals in normative target seeking scenarios.
3. Promote bottom-up approaches to develop nature-based solutions, ecosystem-based management and ecosystem-based adaptation strategies. This action should include:
    - Local capacity building for ecosystem-based management
    - Facilitate community-based co-development of solutions and actions to enhance resilience of Arctic socio-ecological systems to climate change.

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Conflict of interest

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The changing face of the Arctic: four decades of greening and implications for tundra ecosystems

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Arctic landscapes occupy a nexus of environmental change processes, globally significant soil carbon stores, wildlife populations, and subsistence-based human societies. In response to rapid climate warming, tundra ecosystems are experiencing widespread changes to vegetation and underlying permafrost, coupled with an array of ecological disturbances that are expected to intensify in the future. Declines in the extent of the cryosphere on land (permafrost and seasonal snow) and offshore (sea-ice) raise the question of whether and for how long warmer portions of the Low Arctic will fit established concepts of "what is Arctic," given the influence the cryosphere has historically had on tundra ecosystem structure and function. The era of spaceborne observation of circumpolar tundra greenness, in the form of the Normalized Difference Vegetation Index (NDVI), has entered its fifth decade and provides foundational information concerning ecosystem conditions and responses to climatic trends, variability, ecological disturbance, and successional processes. Here we review the evolving story of Arctic greening, and synthesize long-term spaceborne records of NDVI, climatic data, field observations, and the knowledge base of Arctic residents to place the last four decades of Arctic environmental change in context, and establish expectations and research priorities for the coming decade. Greenness dynamics display high spatio-temporal variability, reflecting complex interactions of climatic warming and variability, landscape history, ecological disturbance, and other factors. Nonetheless, long-term increases in NDVI—commonly known as "the greening of the Arctic"—remain prominent across large areas in all available long-term spaceborne datasets and align with long-term shifts in vegetation structure documented in disparate Arctic regions. Common shifts reported from the Low Arctic, such as shrubification, generally portend declines in floristic diversity, and shifts in fauna that favor boreal forest species. Despite lingering uncertainties regarding trend attribution and sources of interannual variability, the sequence of record-high circumpolar tundra greenness values observed since 2020 provides strong evidence that Arctic tundra ecosystems have entered a state without historic precedent on timescales approaching a millennium.

KEYWORDS

Arctic, tundra, normalized difference vegetation index, greening, remote sensing, climate change

1 Introduction

Arctic tundra ecosystems are experiencing a cascade of interwoven changes to vegetation, permafrost, disturbance regimes, hydrological processes, biogeochemical cycling, and wildlife populations that are linked to a rapidly warming climate (Druckenmiller et al., 2024). The Arctic lies at the forefront of global climate warming due to the strong feedbacks that connect atmospheric processes with declining seasonal snow and ice cover, collectively termed "Arctic amplification" (Serreze and Barry, 2011; Rantanen et al., 2022). Few parts of the Arctic have been spared from profound changes in environmental conditions on land and at sea. In turn, these changes feed back to the global carbon cycle and climate, and impact the Arctic's biodiversity and culturally rich subsistence-based societies.

The Arctic tundra biome spans a broad bioclimatic gradient that includes exceptionally cold, maritime climate regimes in the High Arctic (e.g., mean July air temperature +1.0°C at Krenkel, Franz Josef Land, Russia), to continental Low Arctic environments near the forest-tundra ecotone (e.g., +13.3°C at Bethel, Alaska) (Walker et al., 2005a; Raynolds et al., 2019) (Figure 1). Accompanying this gradient are marked differences in the spatial extent and seasonality of the cryosphere. Permafrost is continuous throughout most of the biome (Brown et al., 2001), but areas rich in ground-ice are experiencing dramatic changes even in the coldest parts of the Arctic and permafrost is becoming increasingly fragmented in southerly locations (Farquharson et al., 2019; Farquharson et al., 2022). Offshore, the extent and duration of seasonal sea ice vary substantially, and high interannual variability in sea-ice extent has become the norm in recent years, with mounting impacts to marine ecosystems (Baker et al., 2020) and coastal communities (Overbeck et al., 2020; Irrgang et al., 2022). Collectively, the responses of tundra ecosystems along bioclimatic gradients provide clues to predict what the future may hold in a warmer, less frozen Arctic.

Superimposed on large-scale changes to the Arctic climate and cryosphere are complex landscape-scale factors, such as tundra wildfires and other disturbances, hydrologic changes, long-term increases in shrub abundance, and shifts in the distribution and abundance of animals (Jones et al., 2011; Tape et al., 2016; Fauchald et al., 2017; Sae-Lim et al., 2019; Steketee et al., 2022; Webb et al., 2022). These factors can amplify, dampen, or mask the influence of large-scale climatic and cryospheric drivers of tundra ecosystem productivity, or "greenness," which has been monitored by satellites since 1982 using the Normalized Difference Vegetation Index (NDVI). NDVI is a foundational, if imperfect, vital sign of the terrestrial Arctic. Decades of spaceborne NDVI observations permit investigation of climatic drivers that are subject to high interannual variability and lag effects, as well as landscape disturbances and extreme weather events. Extensive areas of strong increase and localized decline in greenness are evident in multiple satellite datasets (Park et al., 2016; Phoenix and Bjerke, 2016; Potter and Alexander, 2020; Frost et al., 2024), reflecting interactions of climate change and variability, soils, disturbance, and long-term shifts in vegetation structure (Walker et al., 2009; Melvin, 2019; Myers-Smith et al., 2020; Phoenix et al., 2025).

Since the first reports of "Arctic greening" in the late 1990s and early 2000s (Myneni et al., 1997; Zhou et al., 2001; Jia et al., 2003), the long-term satellite record, available data products, and scientific knowledge concerning Arctic environmental change have expanded substantially (Beamish et al., 2020). However, key knowledge gaps and uncertainties

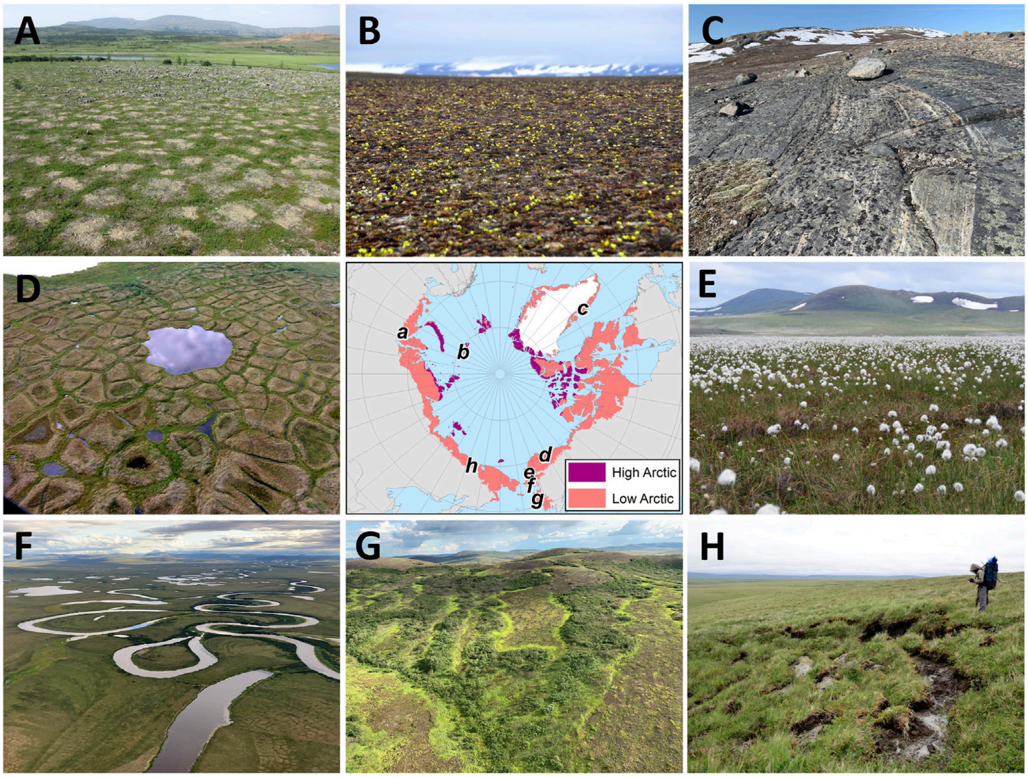

FIGURE 1
Ground and aerial perspectives of heterogeneous Arctic landscapes. Photo locations are shown in the central map: **(A)** Low Arctic tundra in patterned ground landscape, northwestern Siberia; **(B)** High Arctic tundra with discontinuous vegetation, Franz Josef Land, Russia; **(C)** mosaic of vegetation and bedrock in recently deglaciated landscape, southwestern Greenland; **(D)** polygonal tundra with thermokarst pond, North Slope, Alaska; **(E)** moist tussock tundra, northwestern Alaska; **(F)** tundra interspersed with waterbodies, Seward Peninsula, Alaska; **(G)** recently burned tundra with unburned tall shrubs, Andreafsky Hills, Alaska; **(H)** active-layer detachment, Kolyma River drainage, northeastern Siberia. Extents of the Low and High Arctic regions follow (Raynolds et al., 2019). Photos by **(A, C–G)** G. V. Frost, **(B)** D.A. Walker, and **(H)** L. T. Berner.

remain concerning the historical and future state of tundra ecosystems and their connection to the spatiotemporal variability in greening trends, which serve as a proxy for vegetation change. Here we review the evolving phenomenon of Arctic greening, and synthesize a broad, multi-disciplinary information base that includes long-term spaceborne records of NDVI, climate and sea-ice data, field observations, and the knowledge of Arctic researchers and residents to put the last four decades of Arctic environmental change in context, and address scientific questions, knowledge gaps, and critical information needs for the living Arctic over the coming decades.

2 Fundamental concepts, history, issues, and constraints

2.1 Normalized difference vegetation index (NDVI)

Vegetation greenness is an integrative measure of leaf chlorophyll content, leaf area, species composition, and canopy cover and structure. It is thus an essential indicator of tundra ecosystem conditions and responses in a time of rapid environmental change. Numerous spectral vegetation indices exist, all of which exploit the distinctive way in which vegetation absorbs and reflects incoming solar radiation in the visible and near-infrared wavelengths, respectively (Tucker, 1979). Spectral indices apply ratios of reflectance values among bands to help mitigate the effects of sensor calibration, sun-sensor geometry, and topography (Zeng et al., 2022). Here we focus on NDVI because of the long period of record that legacy spaceborne sensors provide (Pinzon and Tucker, 2014). Other spectral vegetation indices include the three-band Enhanced Vegetation Index (EVI; (Huete et al., 2002), other two-band indices such as the Enhanced Vegetation Index 2 (EVI2) (Jiang et al., 2008; Rocha and Shaver, 2009), and derivations of NDVI such as the Near Infrared Reflectance of Vegetation (NIRv) (Badgley et al., 2017), but these lack the period of record of NDVI and their advantages primarily apply in high biomass forest ecosystems.

2.1.1 MaxNDVI

Maximum NDVI (MaxNDVI) is the annual maximum NDVI value observed during the period of peak phytomass in midsummer, typically in late July and early August for the Arctic. MaxNDVI is a strong indicator of aboveground biomass in tundra (Walker et al., 2003; Raynolds et al., 2012), making it particularly responsive to disturbance, successional processes, and long-term changes in vegetation structure. MaxNDVI has a long history of use, and the application of maximum-value compositing is fundamental to the development of operational NDVI products across temporal scales.

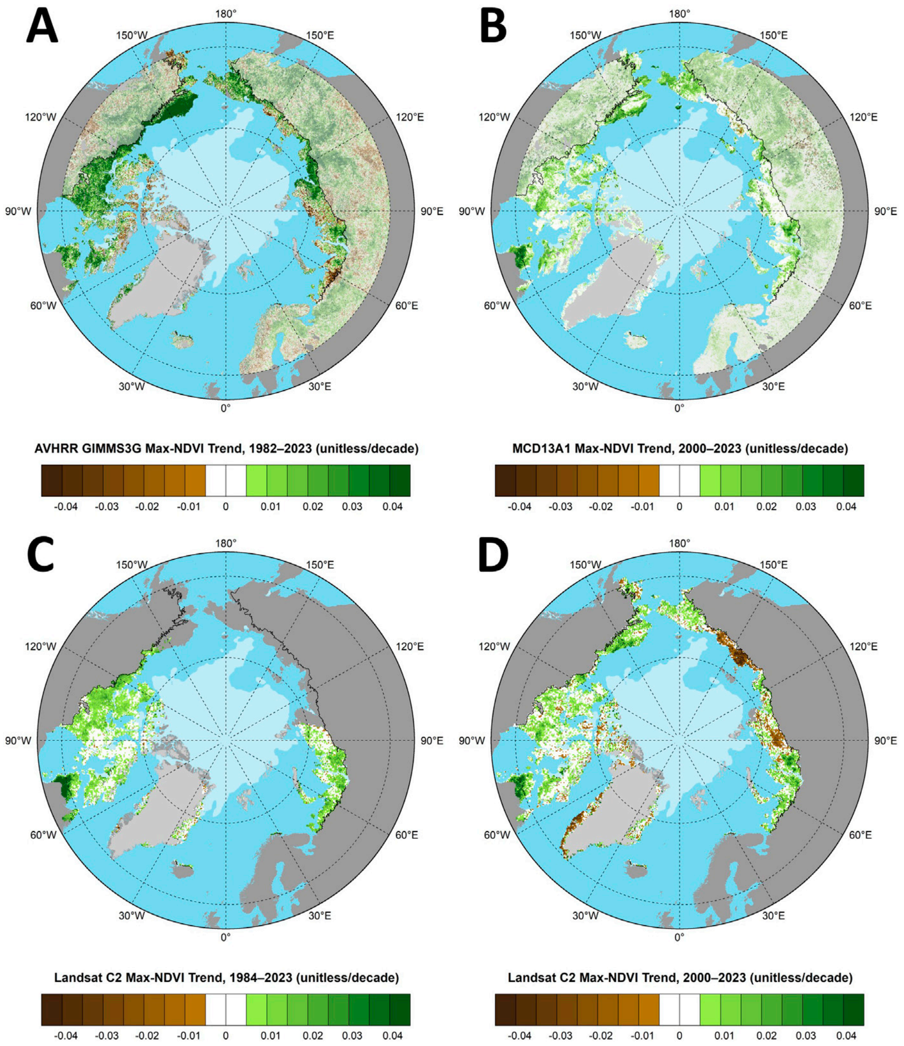

FIGURE 2
Circumpolar MaxNDVI trends from **(A)** GIMMS-3g+ (1982–2023), **(B)** MODIS (2000–2023), and Landsat for **(C)** 1984–2023 (areas with sufficient data density only) and **(D)** 2000–2023. VIIRS trends are not shown due to the short period of record. Trends are shown in muted colors for the boreal forest biome south to 60° N (GIMMS-3g+ and MODIS only). All plots show the mean August 2023 sea-ice extent and the treeline is indicated by a thin black line.

We prepared time series of MaxNDVI through 2023 for the tundra domain of the Circumpolar Arctic Vegetation Map (Raynolds et al., 2019) from four sensors.

1. Advanced Very High Resolution Radiometer (AVHRR), 1982–2023, in the form of the Global Inventory Modeling and Mapping Studies 3 g V1.2 dataset (GIMMS-3g+) with a spatial resolution of 1/12° (~8 km) (Pinzon and Tucker, 2014; Pinzon et al., 2023).
2. Moderate Resolution Imaging Spectroradiometer (MODIS), 2000–2023, combining 16-day NDVI products from the Terra (MOD13A1, v. 6.1) and Aqua (MYD13A1, v. 6.1) satellites (Didan, 2021a; Didan, 2021b) with a spatial resolution of 500 m, hereafter referred to as MCD13A1. Pixels with a SummaryQA value ≥3 (indicating cloudy or otherwise compromised observations) were masked.
3. Landsat Collection 2 data, 1984–2023, derived from the Thematic Mapper, Enhanced Thematic Mapper, and Operational Land Imager sensors at a spatial resolution of 30 m. We use the approach of Berner et al. (2020) and Berner et al. (2023) to randomly for Landsat's coarse (non-daily) temporal resolution. Time series plots are based on annual mean MaxNDVI values at sample pixels with ≥16 observations; observations were sparse in the early part of the record for Alaska and eastern Eurasia, so circumpolar trend analysis is only possible after 2000.
4. Visible Infrared Imaging Radiometer Suite (VIIRS), 2012–2023, using the 16-day VNP13A1 product from the Suomi National Polar-orbiting Partnership (S-NPP) satellite (Didan and Barreto, 2018) with a spatial resolution of 500 m.

All data were masked to exclude permanent ice and water. Spatial trend maps depict linear decadal trends with a significance filter of $p < 0.1$, based on the Pearson's correlation coefficient

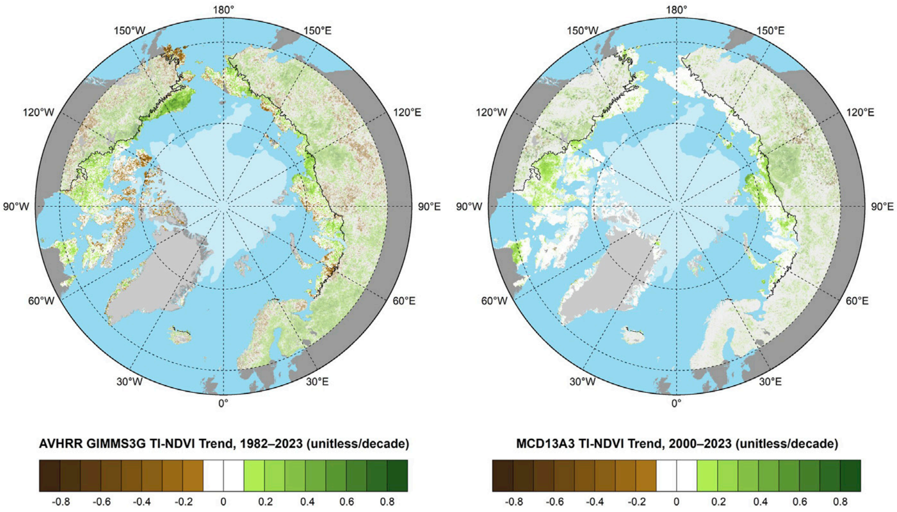

FIGURE 3
Circumpolar TI-NDVI trends from **(A)** GIMMS-3g+ (1982–2023) and **(B)** MODIS (2000–2023). Trends are shown in muted colors for the boreal forest biome south to 60° N. All plots show the mean August 2023 sea-ice extent and the treeline is indicated by a thin black line.

(Figure 2). Further details on MODIS and Landsat time series construction are given in Supplementary Material.

2.1.2 TI-NDVI

Time-integrated NDVI (TI-NDVI) is the sum of maximum NDVI values within set compositing periods during May–September, calculated for datasets with daily temporal resolution (AVHRR and MODIS only); this metric is impractical to calculate from Landsat due to that system's coarse temporal resolution. TI-NDVI has been used since the mid-1980s (Justice et al., 1985; Tucker et al., 1985) and incorporates phenological variations throughout the growing season; therefore, it better represents gross primary production (Tucker and Sellers, 1986) and is typically better correlated with climate variables than MaxNDVI (Bhatt et al., 2010; Bhatt et al., 2021). However, because snow can occur in Arctic environments in any month, variations in TI-NDVI can be expected to reflect interannual variability in seasonal snow cover, primarily in the "shoulder" months of May and September.

We performed trend analysis of TI-NDVI using the spatial and statistical significance filters described above for MaxNDVI (Figure 3). For MODIS, we combined the Terra and Aqua monthly 500 m VI composites (MOD13A3 and MYD13A3 v6.1) to mitigate the imprecise overlap of the twice monthly GIMMS-3g+ and 16-day MODIS compositing periods; we then doubled the resultant values for comparability with GIMMS-3g+. We excluded the 2001 MODIS TI-NDVI value because MODIS Terra was non-functional for part of that summer and MODIS Aqua had not yet launched.

2.2 Seminal reports and early interpretation of Arctic greening

The first reports of Arctic greening emerged in the late 1990s based on the first decade of AVHRR observations (Myneni et al., 1997). Although the earliest reports considered a wide latitudinal band extending well south of the Arctic tundra biome, the modern GIMMS-3g + record shows a series of record or near record-high circumpolar mean MaxNDVI and TI-NDVI values for the Arctic tundra biome beginning in 1987 (Figure 4). This sequence was broken in 1992, concurrent with transient Arctic cooling following the eruption of Mt. Pinatubo the previous year (Lucht et al., 2002); the 1992 record low greenness remains one of the most prominent examples of interannual variability in the GIMMS-3g + record to date. However, four consecutive record-high MaxNDVI values were set during 1997–2000, further strengthening the positive trends reported in early studies (Zhou et al., 2001; Jia et al., 2003). TI-NDVI displayed similar patterns during this period, albeit with a somewhat weaker trend.

In the ensuing years, causal links were drawn connecting the concurrent trends of Arctic greening, increasing land surface temperatures, and declining spring and summer sea-ice extent (Comiso, 2003; Comiso and Nishio, 2008; Bhatt et al., 2010). Shrub expansion quickly emerged as a likely ecological explanation for Arctic greening (Sturm et al., 2001), consistent with predictions from earlier experimental warming studies (Chapin et al., 1995; Michelsen et al., 1996). Beginning in 2006, the U.S. National Oceanic and Atmospheric Administration's Arctic Report Card provided annual synopses of Arctic NDVI trends stemming from the International Polar Year "Greening of the Arctic" initiative. Arctic greening became a prominent theme in several international scientific efforts during the 2010s, including Arctic Council initiatives such as the Circumpolar Arctic Flora and Fauna (CAFF) Arctic Biodiversity Assessment (Meltofte, 2013), and the Arctic Monitoring and Assessment Programme (AMAP) Snow, Water, Ice, and Permafrost in the Arctic (SWIPA) report (AMAP, 2017).

2.3 Enter the 2000s: interannual variability and greening hiatus

By the early 2000s, Arctic greening appeared to enter a period of hiatus after the strong positive trend of preceding decades. This hiatus was particularly evident in the GIMMS-3g + TI-NDVI record

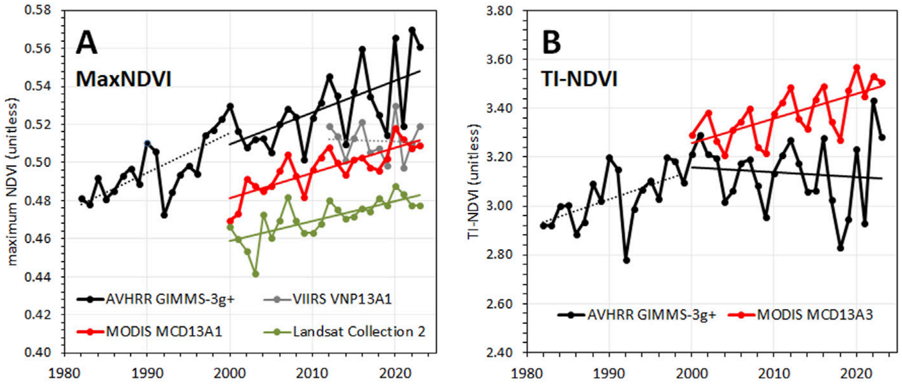

FIGURE 4
Time series of circumpolar mean **(A)** MaxNDVI for GIMMS-3g+, MODIS, Landsat, and VIIRS; and **(B)** TI-NDVI for GIMMS-3g+ and MODIS. Linear trendlines for 2000–2023 are shown as solid lines; trendlines outside this period (GIMMS-3g+ and VIIRS only) are shown as dashed lines. Landsat MaxNDVI prior to 2000 is not shown due to large geographic gaps, and the 2001 MODIS TI-NDVI value is excluded because of data gaps that year.

(Bhatt et al., 2013). Ecologically, a cessation of greening could occur from (1) Arctic vegetation no longer responding to a warming climate, (2) greening being balanced out by the opposite process of "browning" (i.e., declining biomass and productivity), or (3) a combination of these (Phoenix and Bjerke, 2016). If continued long term, a greening hiatus would have considerable implications for Arctic vegetation change, biogeochemical cycling, surface energy balance and permafrost degradation.

Today, the scenario of vegetation not responding may seem unlikely in light of the magnitude of Arctic warming (Rantanen et al., 2022), but a fact often overlooked is that for much of the satellite record, most of the Arctic showed no statistically significant greenness trend; for example, 51% no change versus 39% greening during 1982–2010 (Xu et al., 2013), and 58% no change versus 37% greening during 1985–2016 (Berner et al., 2020) in the GIMMS-3g+ and Landsat records, respectively. While attribution uncertainty and the inherent limitations of NDVI play a role, if about half of the Arctic shows no spectral trend, could mechanisms favoring stability operate more widely to result in a greening hiatus? A key issue is that stability in Arctic ecosystems has been understudied, with literature overwhelmingly focused on greening rather than browning or stability (Callaghan et al., 2021). While this focus on change is understandable, it may bias our understanding of the precursors and causes of stability.

The alternative idea that browning could offset greening, leading to no net change also has some merit. First, while only about 5% of the Arctic exhibits a browning trend (Xu et al., 2013; Berner et al., 2020), many causes of browning are "pulse" disturbance events that are spatially and temporally discrete (Foster et al., 2022), from which vegetation may recover in just a few years (Racine, 1981; Bokhorst et al., 2012; Olofsson et al., 2012; Bret-Harte et al., 2013) and therefore will not be reflected in long-term trend analyses. Nonetheless, these acute browning events could still disrupt the greening signal. Increases in surface water due to thawing permafrost can decrease NDVI values in areas that are otherwise greening (Raynolds and Walker, 2016). In addition, increases in disturbances such as tundra fires (Hu et al., 2015; Zhu et al., 2023), permafrost thaw (Lewkowicz and Way, 2019; Turetsky et al., 2020; Kokelj et al., 2023), climatic extremes (Vikhamar-Schuler et al., 2016; Rietze et al., 2024), and outbreaks of defoliating insects (Vindstad et al., 2022) could directly connect climate warming with browning events and a more muddled greening signal (Phoenix et al., 2025). For instance, multiple disturbance events came together to result in record low productivity in the Nordic Arctic in 2012 (Bjerke et al., 2014).

Regional browning has also been observed from multi-year "press" mechanisms that halted or reversed regional greening for extended periods (Phoenix and Bjerke, 2016). Examples include periods of greater and longer snow cover reducing springtime greenness in Arctic Alaska (Bieniek et al., 2015), and reduced summer warmth over the Eurasian Arctic (Bhatt et al., 2013). Therefore, despite considerable Arctic warming, the 2000s and early 2010s demonstrated that a greening hiatus is ecologically possible. As we now understand, however, Arctic greening did not stop, and while interannual variability is a key feature of Arctic climate change, a greening hiatus has not become the new normal. The stability and browning processes mentioned above are now best described as sources of complexity that operate against the backdrop of the overall Arctic greening trend (Myers-Smith et al., 2020).

2.4 Into the 2020s: record-high tundra greenness

2020 was a benchmark year for Arctic tundra greenness, as record-high circumpolar mean MaxNDVI values were set in all four satellite records (Figure 4), and for TI-NDVI in the MODIS record. These records were concurrent with record-high summer warmth over Arctic lands (see Climatic Drivers of Greening, below). In the years that followed, GIMMS-3g+, MODIS, and Landsat continued to observe a series of record or near-record-high values. For example, the top 3 MaxNDVI values in the 42-year GIMMS-3g + record, 4 of the top 5 values in the 24-year MODIS record, and the top 2 MaxNDVI values in the 24-year circumpolar Landsat record were all recorded during 2020–2023. Interestingly, both GIMMS-3g+ and VIIRS recorded large declines in MaxNDVI from 2020 to 2021, but interannual variability was much lower in the MODIS and

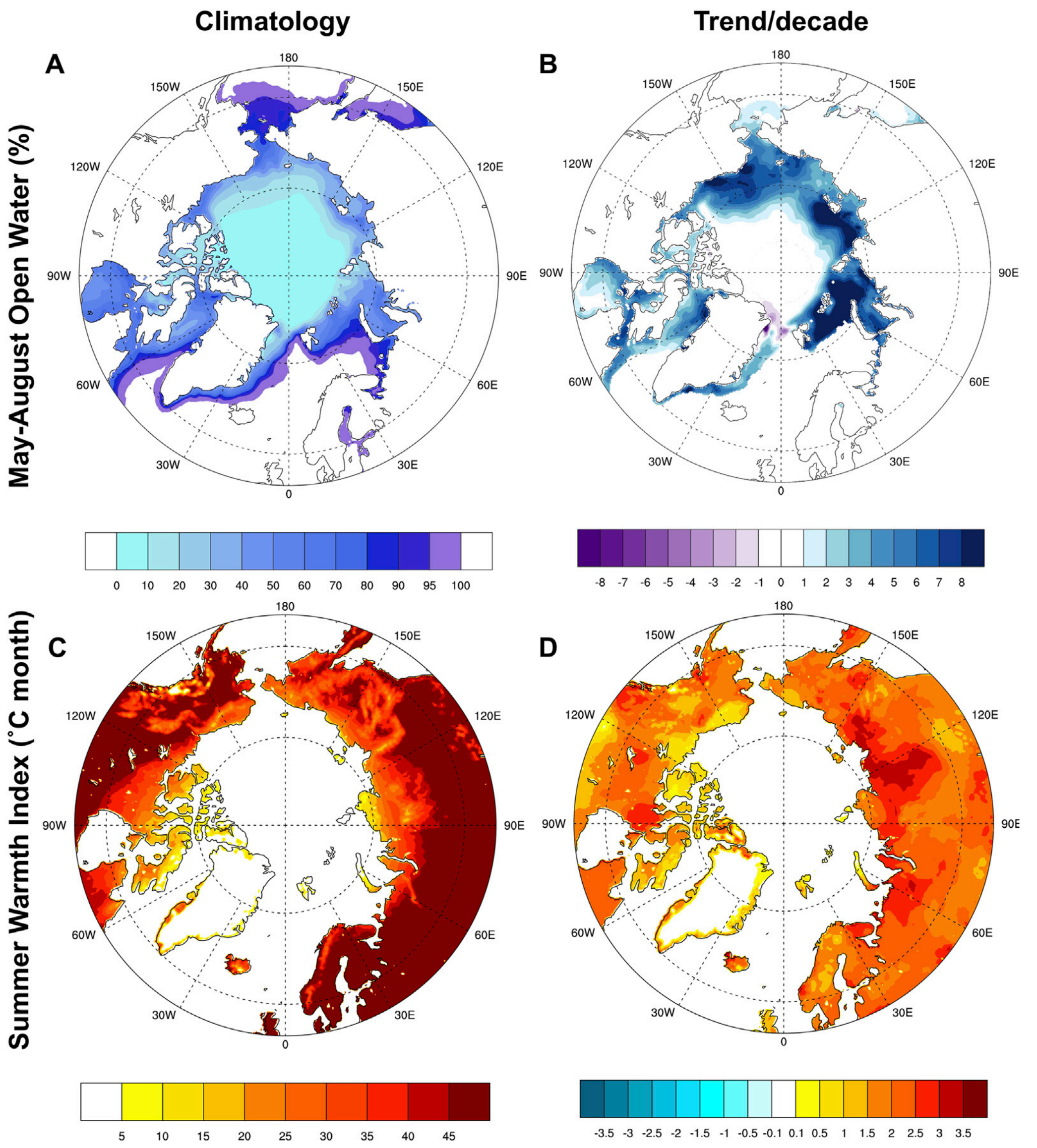

FIGURE 5
Climatology **(A)** and trend **(B)** of average May–August Open Water (% cover) based on passive microwave sea-ice observations, and climatology **(C)** and trend **(D)** of onshore summer Warmth Index based on ERA5 2 m-air temperature, 1982–2023.

Landsat records. On balance, the frequency of exceptionally high greenness values in multiple satellite records provides strong evidence that Arctic peak season live phytomass continues to increase and the greening hiatus has ended.

Long-term records for TI-NDVI present a more confusing picture. While the full 42-year GIMMS-3g + record indicates an overall increasing trend in TI-NDVI of similar magnitude to that recorded by MODIS from 2000 onward, trends over the period of concurrent observation are very different, with GIMMS-3g + indicating weak declines and MODIS indicating strong increases (Figure 4). Although patterns of interannual variability have been qualitatively similar throughout the period of concurrent observations, variability has been much higher in the GIMMS-3g + record, particularly over the last 10 years. Nonetheless, both records indicate that circumpolar TI-NDVI has reached unprecedented highs in the past several years. Like MaxNDVI, the top 2 and top 3 TI-NDVI values in GIMMS-3g+ and MODIS, respectively, were recorded during 2020–2023. Browning and stability remain important, but greening continues, and in light of continued Arctic warming, this seems unlikely to change.

2.5 Large-scale climatic drivers of greening

Long-term spaceborne records of tundra greenness and Arctic surface conditions on land and at sea indicate numerous overarching linkages among tundra greenness, sea-ice, precipitation, cloudiness, and other components of the climate system (Raynolds et al., 2008; Bhatt et al., 2017). Spring sea-ice trends and interannual (Bhatt et al., 2010; Dutrieux et al., 2012) to multi-decadal variability (Hendricks et al., 2023; Polyakov et al., 2023) shape the growing season for Arctic tundra, ~80% of which lies within 100 km of the coast

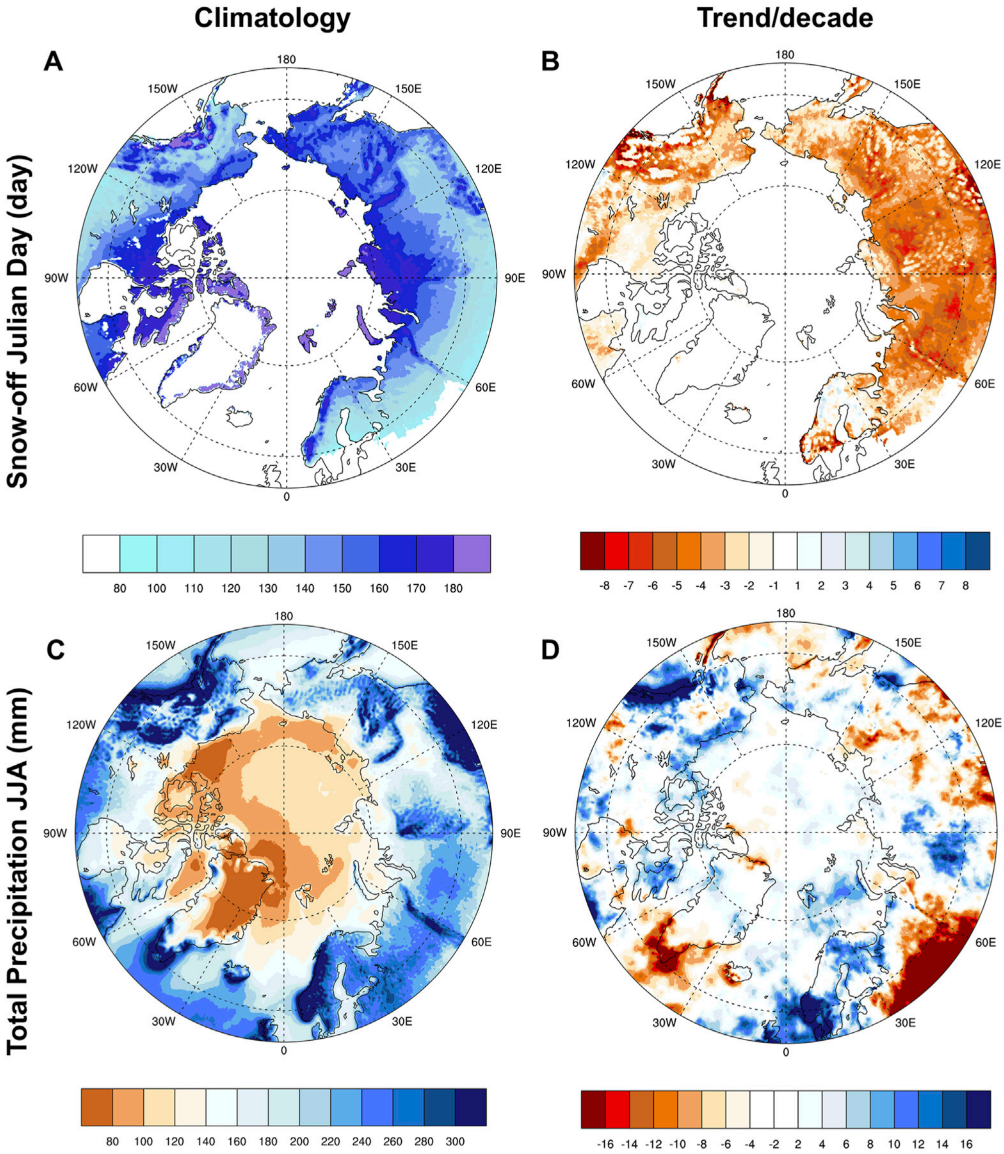

FIGURE 6
Climatology **(A)** and trend **(B)** of snow-off day, defined as the last day of the last 7-day period with any snow between 1 January and 30 June, and climatology **(C)** and trend **(D)** of June–August total precipitation, based on ERA5 reanalysis and climatologies; trends are for 1982–2023.

(Walker et al., 2005b). Extended periods of open water are largely responsible for warming air temperatures along the coasts of the Arctic Ocean that, in turn, promote warmer growing seasons onshore that favor increased greenness (Figure 5). Open water (May–August average cover) and summer Warmth Index (SWI, the sum of average monthly temperatures above freezing) have increased steadily since 1982 and circumpolar mean values have reached record or near-record highs during 2020–2023, concurrent with exceptionally high MaxNDVI and TI-NDVI. These correspondences indicate that, in the big picture, the sensitivity of tundra ecosystems to sea-ice conditions and growing season temperature remains strong. Nonetheless, the correlation between sea-ice variability, NDVI, and field-based metrics of plant productivity has decreased over the last decade as sea ice has retreated farther from the coast, (Buchwal et al., 2020; Bhatt et al., 2021), suggesting that other drivers are becoming more important. The influence of sea ice on vegetation also varies regionally, as it is shaped by local oceanic circulation and landscape-scale drivers (Dutrieux et al., 2012; Yu et al., 2021).

From the climate driver perspective, changes in the hydrological cycle are expected to play an increasing role in tundra greenness dynamics, with precipitation and cloudiness increasing (Liu et al., 2012). As temperature increases and the permafrost active layer thickens, the net result could be increased moisture limitation on plant growth (Haynes et al., 2018). While data on snow and precipitation are less reliable than for sea ice and air temperature, new reanalysis datasets such as the European Centre for Medium-Range Weather Forecasts Reanalysis 5 (ERA5) and GlobSnow (Luojus et al., 2021) provide new opportunities to investigate the changing Arctic

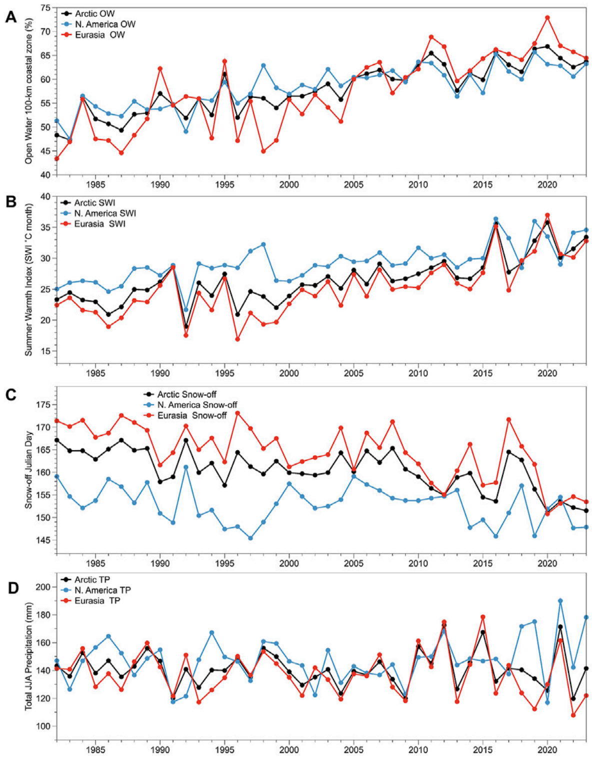

FIGURE 7
Time series of average **(A)** Open Water (%), **(B)** summer Warmth Index (°C month), **(C)** snow-off day (Julian Day), and **(D)** total June–August precipitation (mm), 1982–2023. Plots are based on microwave sea-ice observations and ERA5 reanalysis data.

hydrological cycle. The last day of snow (snowoff, defined as the last day of the last period of ≥7 days with any snow during 1 January–30 June) is climatologically earlier in North America, but the trend towards earlier snowoff is generally stronger in Eurasia (Figures 6A,B). Climatologically, northwesternmost North America and the Barents and Kara Sea coasts of western Eurasia receive the most summer precipitation, while the eastern North American Arctic receives the least (Figure 6C). Arctic summer precipitation trends are very patchy and generally weak, with increasing interannual variability over the last decade (Figure 7). Where present, trends are mostly positive except in southern Greenland and portions of northeastern Siberia (Figure 6D). As a result, impacts of the changing hydrological cycle are highly variable and regional analysis is more likely to reveal relationships with vegetation.

3 Regional variability and interpretation

Although climatic variability and trends are key overarching drivers of Arctic greenness, NDVI dynamics are strongly influenced by the local circumstances of soils, geomorphology, glacial history, permafrost and snow conditions, disturbance history, and other factors (Figure 8). Therefore, regional perspectives are needed to connect spectral trends with salient drivers and manifestations of change.

3.1 Alaska

Alaska's North Slope has stood out as a circumpolar "hotspot" of greening virtually throughout the period of spaceborne NDVI monitoring (Jia et al., 2003), yet the eastern Bering Sea sector in southwestern Alaska is one of the most prominent areas of browning in GIMMS-3g + MaxNDVI and TI-NDVI records (Frost et al., 2021). Relationships between MaxNDVI and summer warmth variations have been different in these regions since 1982 (Supplementary Figure 1). In northern Alaska, greenness and SWI share strong increasing trends, but their patterns of interannual variability differ greatly; in southwestern Alaska, trends are much weaker but interannual variability is similar. These contrasts suggest that their responses to climate change are being modified by regional and landscape-scale factors in different ways. Alaska in general, and northern Alaska in particular possesses a rich history of field-based research due to favorable logistics and the presence of long established field stations (Metcalfe et al., 2018), making it an important region for identifying the ecological manifestations, drivers, and impacts of spectral trends.

Seminal studies of Arctic shrubification—increases in the cover, height, and density of woody plants—were focused on Alaska's North Slope, where retrospective photo comparisons revealed widespread increases in shrub abundance since the mid-20th century (Sturm et al., 2001; Tape et al., 2006). Shrubification soon emerged as one of the most universally recognized mechanisms for greening trends in Alaska and the Low Arctic generally (Myers-Smith et al., 2011), but landscape-scale studies have demonstrated complex patterns of stability and change, with most shrub increase concentrated on or near floodplains (Naito and Cairns, 2011; Naito and Cairns, 2015; Tape et al., 2012; Liljedahl et al., 2020) and in historical tundra fire scars (Jones et al., 2013; Klupar et al., 2021). Findings from western Alaska provide similar conclusions, except that shrubification has also been prominent on hillslopes (Racine et al., 2004; Narita et al., 2015; Salmon et al., 2019; Schore et al., 2023). Retrospective studies of shrubification in Alaska and elsewhere have generally emphasized tall (>~1.5 m) shrubs such as Siberian alder (*Alnus viridis*); however, while tall shrublands are conspicuous in tundra landscapes, their overall spatial extent is limited. In contrast, shrub-tussock tundra is far more extensive in Arctic Alaska, but the lower stature and density of shrubs in this community make it much more difficult to demonstrate cover changes. While field studies indicate that NDVI is more sensitive to changes in the leaf area of shrubs than other plant functional types in tussock tundra (Jespersen et al., 2023), and remote sensing time series strongly point toward widespread increases in deciduous shrub abundance on the North Slope (Macander et al., 2022), repeat-monitoring at long-term plots provides mixed indications of phytomass increase and the plant functional types responsible (Jorgenson J. C. et al., 2015; Pattison et al., 2015; Hobbie et al., 2017). Nonetheless, reports of increasing shrub abundance are virtually ubiquitous in discussions with elders and other indigenous residents in Arctic Alaska (Rearden and Fienup-Riordan, 2014; Fienup-Riordan et al., 2021), and provide a compelling line of evidence that extends the observational period associated with remote sensing-based studies.

Repeated ground measurements of NDVI near Utqiaġvik provide uniquely detailed, albeit local, information that

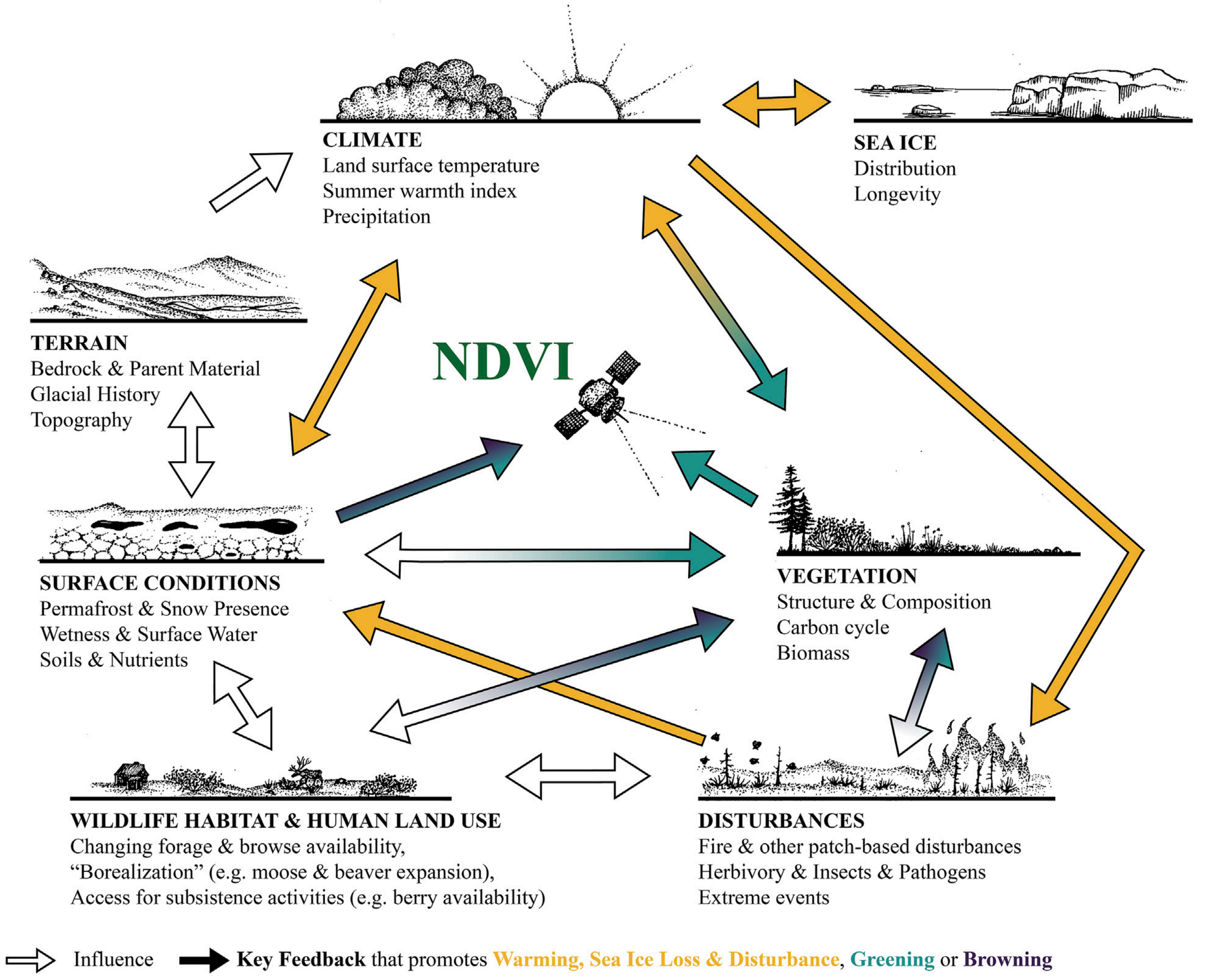

FIGURE 8
Conceptual diagram of interactions among Arctic vegetation, climate, and landscape characteristics and their influence on spaceborne NDVI. Colored arrows indicate key feedbacks that tend to intensify future warming, sea-ice loss, or disturbance (orange); increase tundra productivity (green), or decrease tundra productivity (purple).

implicated changes in herbaceous plant cover at this colder, coastal location (Huemmrich et al., 2023). Transect-based NDVI measurements from circa 2001 and 2022 demonstrated greening linked to increased leaf area in wet sedge tundra, while portions of the transect that exhibited browning had increased standing dead leaf cover in moist graminoid communities. Studies applying handheld NDVI have provided mixed signals concerning the effects of early snowmelt timing and growing season length on tundra productivity, with both positive (Arndt et al., 2019) and negative (Gamon et al., 2013) effects reported.

Ice-wedge degradation has been widely documented in Arctic Alaska in polygonal ground associated with ice-rich permafrost (Jorgenson et al., 2006; Jorgenson et al., 2022; Kanevskiy et al., 2017; Frost et al., 2018a; Jones et al., 2024), where thaw settlement, ponding, and alteration of hydrological pathways produces spatially variable patterns of vegetation mortality, succession, and changes in surface water. Available information indicates this process generally decreases productivity (Lara et al., 2018), though this depends on local circumstances and the time period considered (Raynolds and Walker, 2016); ice-wedge degradation is occurring in many Arctic regions (Liljedahl et al., 2016) and the long-term implications are likely to vary widely (see Current Research Gaps, below). Lake drainage has also been a powerful driver of local greening (Jones et al., 2011; Jones et al., 2020; Nitze et al., 2018), particularly in northwestern Alaska (Nitze et al., 2020), as vegetation colonization and successional changes occur rapidly on newly exposed lacustrine sediments (Chen et al., 2021d). Concurrent beaver expansion in northwestern Alaska promoted pond formation and permafrost degradation (Tape et al., 2018; Tape et al., 2022; Jones et al., 2021; see Long-term Disturbance Effects, below).

3.2 Canada

The Canadian Arctic encompasses diverse tundra ecosystems ranging from productive tall shrublands north of treeline to partially vegetated barrens in the northern polar desert. In contrast to Alaska and Eurasia, the Canadian Arctic predominantly consists of young

(c. 7,000–14,000 years old), postglacial landscapes that were glaciated during the Pleistocene (Margold et al., 2018). MaxNDVI and TI-NDVI trends show considerable variability; MaxNDVI is closely correlated with summer temperature in the Low Arctic, but not in the High Arctic (Supplementary Figure 2). Numerous regional analyses have linked greening patterns with terrain factors including soil moisture, elevation, and surficial geology, and suggest that climate-driven shrub expansion is mediated by the availability of nutrients and mesic soil conditions (Campbell et al., 2021; Chen A. et al., 2021; Seider et al., 2022). Analyses of plot-scale repeat photographs and dendrochronology also point to soil moisture as a key determinant of change (Myers-Smith et al., 2015; Cameron and Lantz, 2016; Bjorkman et al., 2018). Several studies also suggest that spatial heterogeneity is linked to differences in the growth strategies among dominant species (Chen A. et al., 2021; Larking et al., 2021).

Northern Nunavik exhibits some of the strongest greening trends across all sensors; here, repeat photography and field surveys highlight shrubification, especially dwarf birch (*Betula glandulosa*) (Ropars and Boudreau, 2012; Tremblay et al., 2012). Other regional study areas in continental Canada show more variable greenness trends among sensors; however, retrospective image analysis and fieldwork also document increase in dwarf birch (Fraser et al., 2016; Moffat et al., 2016; Andruko et al., 2020; Davis et al., 2021), Siberian alder (Lantz et al., 2013; Cameron and Lantz, 2016; Travers-Smith and Lantz, 2020), willows (*Salix* spp.) (Myers-Smith et al., 2019), and evergreen shrubs such as Labrador tea (*Rhododendron tomentosum*) (Moffat et al., 2016). Field studies suggest that most shrubification has been associated with recruitment (Lantz et al., 2010; Ropars and Boudreau, 2012; Tremblay et al., 2012; Davis et al., 2021), but Bonta et al. (2023) documented change involving vertical expansion and infilling of existing shrub canopies.

NDVI trends vary strongly among all satellite records in the Canadian High Arctic, and few fine-scale investigations exist to help resolve uncertainties (see Current Research Gaps, below). The field studies that do exist highlight a wide range of vegetation responses. These include stability (Bjorkman et al., 2020; Schaefer, 2023); declines in prostrate deciduous shrubs (e.g., *Dryas integrifolia*) and select forbs (e.g., *Bistorta vivipara* and *Saxifraga oppositifolia*) (Schaefer, 2023); and increases in graminoids (Hill and Henry, 2011; Campbell et al., 2021; Schaefer, 2023), forbs (Hill and Henry, 2011; Campbell et al., 2021), shrubs (Hudson and Henry, 2010; Hill and Henry, 2011; Bjorkman et al., 2020; Campbell et al., 2021; Schaefer, 2023), and bryophytes (Hudson and Henry, 2009).

3.3 Greenland

Greenland is the world's largest island, with a vegetated perimeter predominantly consisting of young (<16,000 years old) postglacial landscapes that encircle the Greenland Ice Sheet (Lecavalier et al., 2014). Strong warming has occurred across Greenland's wide summer climate gradient (Mayewski et al., 2014), but MaxNDVI and SWI have been poorly correlated during 1982–2023 (Supplementary Figure 3). Overall, Greenland exhibits greening trends for GIMMS-3g + MaxNDVI since 1982, but trends have been more modest in MODIS and strongly negative in Landsat since 2000. However, studies documenting land cover responses to climate change and ice loss from the Greenland Ice Sheet and surrounding glaciers strongly indicate that vegetation cover has increased in proglacial and periglacial areas since the 1980s. Grimes et al. (2024) determined proglacial land cover changes island-wide using Landsat data over the last three decades, reporting ~28,000 km^2 loss in ice cover, a doubling of vegetation cover, a fourfold increase in wetland cover, more meltwater, less bare bedrock, and increased cover of fine, unconsolidated sediment. These changes were strongly correlated with an increased number of growing degree-days, especially >6°C, since the 1980s; however, the absolute rise in temperature had a minimal direct association with these land cover changes. As in other Arctic regions, warming summer temperatures have been linked to increases in shrub abundance, albeit with substantial time lags (Büntgen et al., 2015). In southwestern Greenland, observed shrub increases appear to be partially linked to changes in human land-use and grazing intensity (Jørgensen et al., 2013). Moth outbreaks have also temporarily reduced plant productivity in southern Greenland (Lund et al., 2017). Long-term field studies at Zackenberg, northeast Greenland have revealed variable, species-specific changes in plant cover despite strong summer warming (Hobbie et al., 2017); the observed changes, coupled with interannual variability in plant phenology, appear to be connected to local soil moisture rather than summer temperature (Westergaard-Nielsen et al., 2017).

3.4 Svalbard

Svalbard also consists primarily of postglacial landscapes and includes extensive areas of High Arctic tundra in close proximity to ice-covered land. The instrumental record at Svalbard Airport indicates temperatures have increased 0.32°C decade^{-1} since 1898, about 3.5 times the global average; after 1991 warming accelerated to 1.7 °C decade^{-1}, over twice the average for the Arctic and seven times the global average (Nordli et al., 2020). Warming over the northern Barents Sea has been even faster due to dramatic sea-ice decline; Isaksen et al. (2022) reported temperature increases of up to 2.7 °C decade^{-1} in northeastern Svalbard. Variations in MaxNDVI have been strongly correlated with increasing summer warmth (Karlsen et al., 2024) (Supplementary Figure 3). In central Svalbard, AVHRR data revealed that MaxNDVI increased 29% during 1986–2015, concurrent with a 59% increase in mean summer temperature (Vickers et al., 2016). However, high interannual variability in greenness in eastern Svalbard is linked to high variability in the timing of sea-ice breakup (Macias-Fauria et al., 2017; Karlsen et al., 2024).

Field measurements of greenness correlate well with MODIS data in Svalbard (Parmentier et al., 2021; Tømmervik and Nilsen, 2023). Regional analysis of MODIS interpolated to daily timescales showed strong correlations with field-based phenological observations, annual productivity, and growing degree days (Karlsen et al., 2018; Karlsen et al., 2022; Karlsen et al., 2024; Karlsen, 2023). Interannual variability in greenness was high, with record-high and intermediate values in 2020 and 2022, respectively, and very low values in 2019 and 2021 (Tømmervik and Nilsen, 2023; Tømmervik et al., 2023).

Historical field plots resurveyed in central Svalbard after up to 85 years revealed increases in graminoids and forbs, consistent with warmer temperatures (Kapfer and Grytnes, 2017). A similar study from central Spitsbergen did not reveal any changes since 1936–1937 that were attributable to climate change (Prach et al., 2010); however, the original surveys were undertaken during an anomalously warm period (Overland and Wang, 2005) and the resurvey was undertaken in 2008, before contemporary warming had started to accelerate.

3.5 Northwestern Siberia

The northwest Siberian Arctic stands out as a circumpolar greening hotspot in all records and long-term GIMMS-3G + MaxNDVI variations have been well correlated with increasing summer warmth in the region (Supplementary Figure 4). At the landscape scale, trend variability has been connected to differences in substrates, which vary in texture, nutrient status, moisture holding capacity, and ground-ice content; sandy uplands tend to support tundra with lower biomass and weak NDVI trends, whereas strong greening trends tend to overlap clayey marine deposits (Walker et al., 2009; Frost et al., 2014; Tassone et al., 2024).

Regional studies again highlight shrubification as a key form of greening. At the level of individual organisms, tundra willow radial growth has been strongly related to summer temperature and NDVI (Forbes et al., 2010). At the landscape scale, shrubification appears to be more closely connected to upland landscapes than in Alaska, but shares similar connections to ecological disturbances. Cryogenic landslides (i.e., active-layer detachments and retrogressive thaw slumps) are common and have been closely studied on the Yamal Peninsula; after initial loss of biomass, these disturbances become focal points of shrubification and greening (Verdonen et al., 2020). In the southernmost Yamal, upland landscapes support widespread mosaics of sorted and non-sorted circles (i.e., frost boils) that provide similar opportunities for rapid alder expansion (Frost et al., 2013) and have been directly linked to pixel-level Landsat greening trends (Frost et al., 2014). All of these disturbance features facilitate shrub recruitment by enhancing nutrient availability (Ukraintseva and Leibman, 2007), snow cover (Leibman et al., 2015), and soil temperatures (Frost et al., 2018b; Loranty et al., 2018a). Indigenous Nenets reindeer herders further corroborate shrubification, reporting increases in the height, density, and abundance of willows in recent decades, with the tallest shrubs now exceeding the antler height of standing reindeer (Forbes and Stammler, 2009). Shrub increase has had some negative impacts on reindeer herding, as animals can disappear from sight and subsequently be lost during migration.

Thermokarst lakes are widespread in northwestern Siberia and seminal studies of lake drainage in permafrost regions documented this process using Landsat data (Smith et al., 2005). On the Yamal Peninsula, there has been a 5.5% net loss in lake area, with most loss occurring in southerly areas with discontinuous permafrost (Nitze et al., 2018). Plant succession is generally very rapid on newly exposed lacustrine sediments; NDVI can reach values comparable to surrounding tundra within a few years after lake drainage (Liu et al., 2023; Von Baeckmann et al., 2024). Young lake basins tend to be floristically diverse, and lush wetlands are regarded by herders as attractive but hazardous grazing areas for reindeer (Laptander et al., 2024).

Reindeer herding has been practiced on the Yamal for centuries, and the distribution and abundance of reindeer has been linked to regional NDVI patterns (Yu et al., 2011). Regional analysis of Sentinel-1/2 and MODIS data suggest that at current densities, reindeer have substantial impacts on ecosystem structure and can potentially counteract shrubification and other climate-induced vegetation shifts (Spiegel et al., 2023). Nonetheless, reindeer browsing appears to have had little impact on tall shrubs on cryogenic landslides, (Skarin et al., 2020), possibly because animals select for young shoots and low shrubs, rather than older, tall shrubs which tend to be less palatable (Thompson and Barboza, 2014).

Oil and gas development has increased dramatically since the 1970s (Kumpula et al., 2011) and the region's industrial footprint is among the highest in the Arctic (Bartsch et al., 2021). Industrialization strongly impacts local greenness, first as extensive off-road vehicle tracks and structures during the exploration phase, followed by proliferation of roads, railways, buildings, and pipeline networks. Although these are relatively small linear features within a vast matrix of tundra, cumulative impacts extend beyond the infrastructure footprint, with impacts to reindeer habitat and movements (Kumpula et al., 2011; Kumpula et al., 2012; Yu et al., 2015).

3.6 Northeastern Siberia

The northeast Siberian Arctic, extending from the Lena River Delta eastward to the Chukchi Peninsula, encompasses a variety of terrain, surficial materials, and climate conditions (Stonevicius et al., 2018), including the Lena River Delta, the Arctic's largest delta. Greenness trends are very mixed (Figure 4) with no net regional trend and no clear relationships between MaxNDVI and summer warmth (Supplementary Figure 4). Northeastern Siberia has received comparatively little scientific attention (Virkkala et al., 2019), but notably, the Yana-Indigirka Lowland in the central part of the region is one of the Arctic's most prominent browning hotpots (Figure 2). The region is underlain by continuous permafrost, including extensive ice-rich, late-Pleistocene Yedoma and Holocene alas (drained pond basin) deposits (Veremeeva et al., 2021; Strauss et al., 2022). These landscapes have recently experienced extensive thermokarst and thermal erosion (Nitze et al., 2018; Veremeeva et al., 2021), which create landforms such as baydzherakhs (residual thermokarst mounds) and alases that support highly productive vegetation. Northeastern Siberia has experienced several extreme climatic events that have likely influenced greenness both directly and indirectly in recent years. Severe heat waves occurred in spring and summer 2019–2021, with associated drought conditions and reduced land surface cooling by vegetation (Rietze et al., 2024), increases in wildfire activity, burned area and atmospheric aerosols, permafrost destabilization, and pest outbreaks (Overland and Wang, 2021; Kharuk et al., 2022; Scholten et al., 2022; Talucci et al., 2022).

The Lena River Delta includes a wide variety of surficial materials and landscape settings, and several regional studies have shown corresponding patterns of variability in greenness trends. Overall, the Lena Delta appears to show increases in MODIS MaxNDVI, concurrent with rising summer temperatures and high variability in snowmelt timing. Early snowmelt was not clearly related to midsummer NDVI, but high June temperatures were (Heim et al., 2022). NDVI trends show strong links to fluvial processes, lake dynamics and permafrost disturbances (Nitze and Grosse, 2016), and floodplain areas in particular support highly dynamic disturbance and successional regimes (Lisovski et al., 2023). Overall, lake drainage events have predominated (Nitze et al., 2018). Landsat data for 2003–2022 also show greening on remnant Yedoma deposits, as well as on central and northern parts of the Lena Delta, but no trend in the eastern delta (Nitze et al., 2024).

The browning hotspot formed by the Yana-Indigirka Lowland is distinctive. Regional analysis of MODIS NDVI indicates an episode of browning during 2010–2020. However, annual drone-based observations after 2014 suggest that this hotspot may reflect exceptionally high interannual variability in moisture and surface water extent resulting from extreme weather events, rather than a long-term trend. The subregion is rich in floodplains and drained lake basins; surface water is typically extensive, but high recent variability in surface water appears to be linked to NDVI variability (Magnússon et al., 2021a). Landsat time series showed lower NDVI in dry summers with little rainfall, but also in summers following extreme snowfall, suggesting that high variability in precipitation may help explain regional browning (Magnússon et al., 2023). Extremely high snowfall in 2016–2018 resulted in large spring floods that plausibly explain widespread browning, including tree mortality at the forest-tundra ecotone (Tei et al., 2020; Magnússon et al., 2021b; Nogovitcyn et al., 2023). Marshes of the Indigirka Delta show browning likely caused by coastal flooding, while browning to the west was attributable to wildfires (Talucci et al., 2022; Nitze et al., 2024). Field studies have also documented shrub mortality and increased aquatic vegetation after ice-wedge degradation (Lashchinskiy et al., 2020; Magnússon et al., 2021), highlighting the influence of soil moisture changes (Ohta et al., 2014; Magnússon et al., 2023).

Further east, the Kolyma River watershed experienced greening across ~20% of its extent from 1982 to 2010; greening was most common in shrublands at higher elevations, where annual productivity was positively correlated with summer air temperatures (Berner et al., 2013). However, more recent time series analyses have shown no substantial trend (MODIS) or even browning (Landsat). These patterns could be partly explained by recent thaw lake expansion; while lake area changed little during 1999–2013, it increased sharply following high precipitation during 2013–2018 (Veremeeva et al., 2021). Similarly, some large floodplains exhibited browning in recent years, likely caused by flooding due to high precipitation.

Chukotka has shown positive MaxNDVI trends across sensors (Figure 2), especially on the Chukchi Peninsula. In central Chukotka, changes in plant aboveground biomass during c. 2002–2017 were modeled by linking field measurements with Landsat satellite data. Plant aboveground biomass widely increased near treeline, particularly with expansion of larch trees and deciduous shrubs. However, few changes were evident in tundra (Shevtsova et al., 2021). Ecosystem models suggest further larch forest densification and expansion into tundra under a warming climate, resulting in loss of tundra-associated biodiversity (Kruse and Herzschuh, 2022; Kruse et al., 2023). However, identified mismatches between NDVI and larch tree density (Loranty et al., 2018b) suggest that relations between larch expansion and NDVI dynamics may be more complex near the treeline. Historical satellite images show increases in both shrub and aquatic vegetation in coastal regions of eastern Chukotka (Lin et al., 2012), and tall shrub expansion in upland landscapes (Frost and Epstein, 2014).

4 Discussion

Retrospective assessment of the now 43-year spaceborne record of tundra greenness provides confidence that the "greening of the Arctic" continues, but many questions persist concerning the last several decades of environmental change and the trajectory of the future Arctic that are relevant to societal efforts to anticipate and adapt to these changes.

4.1 Schools of thought, controversies

There is wide consensus that the Arctic greening trend is quite variable across spatial and temporal scales and many areas show little to no significant change (Berner et al., 2020; Myers-Smith et al., 2020; Callaghan et al., 2021). Nonetheless, the long-term record of Arctic tundra greenness provides compelling evidence that in the big picture, "the greening of the Arctic" is an ongoing phenomenon, with the most unequivocal evidence emerging from MaxNDVI trends across the continental Low Arctic. While long-established connections between Arctic greening and concurrent climatic warming and sea-ice decline endure (Berner et al., 2020; Hendricks et al., 2023), they appear to be waning in some regions (Keenan and Riley, 2018). The greatest uncertainties generally concern trend attribution, scaling issues, drivers of regional variation, the strength of seasonality and phenological change over the full growing season, the role of "pulse" events, and the extent to which spectral metrics in general and NDVI in particular can be used to address emerging science questions.

Some sources of NDVI variability and trends are clear—for example, spatially discrete disturbances such as wildfire interact with predominant trends both through initial vegetation mortality and then by the successional processes that follow. However, interactions among disturbances, topography, and warming can create complex long-term patterns (Rocha et al., 2018; Chen et al., 2021b; Gaglioti et al., 2021). Many other sources of variability remain difficult to parse, and can be obscured by inherent technical limitations of spaceborne monitoring (e.g., low spatial resolution and revisit frequency) and the NDVI metric itself (Huang et al., 2021). Although NDVI's simplicity and long period of record make it integral to Arctic environmental monitoring, it can also oversimplify the complexity of ecosystem dynamics and cannot capture the full scope of changes due to its nonlinear relationship with biomass and resultant saturation effects (Blok et al., 2011; Fraser et al., 2014; Huemmrich et al., 2021). While continued investment and continuity in legacy sensors is crucial, many argue for moving towards more ecologically meaningful metrics, such as solar induced fluorescence (SIF), which is directly linked to leaf chlorophyll concentrations and can potentially serve as an improved proxy for ecosystem gross primary productivity (Cheng, 2024). In addition, the development of hyperspectral sensors and LiDAR capabilities is helping to disentangle heterogenous Arctic ecosystems and explore ecosystem dimensions such as functional traits, biodiversity, and structure (Bjorkman et al., 2018; Thomas et al., 2020; Nelson et al., 2022).

Spatial and temporal scaling issues also continue to limit understanding (Melvin, 2019; Myers-Smith et al., 2020; Nelson et al., 2022). Coarse spatial-scale data cannot capture nuanced changes occurring at smaller scales, while high spatial resolution sensors have traditionally suffered from a lack of temporal resolution that limits time series analysis. New very high resolution commercial systems, such as Planet, offer increased temporal and spatial resolution but lack the long-term record of previous sensors and can be cost-prohibitive. In addition, radiometric and other technical differences among legacy sensors introduce inconsistency among records that can never be fully resolved. For example, the GIMMS-3g + record is invaluable for its long period of record, but pixel-level global area coverage data products are derived from systematic sampling of the original observations. Collectively, these issues call for intercomparison of long-term greenness datasets (Beck et al., 2011; Guay et al., 2014; Liu et al., 2024) to "stress test" hypotheses and conclusions based on one dataset by way of corroboration with others, particularly 30-m resolution Landsat data (Berner et al., 2020; Liu et al., 2021). Improved integration of field-based datasets is also badly needed, particularly outside of traditionally well studied areas (Melvin, 2019). At present, this challenge is greatly exacerbated by barriers to access and collaboration in the Eurasian Arctic arising from the Russian invasion of Ukraine. Even before the escalation of Russia's invasion in early 2022, the Russian Arctic was greatly underrepresented in English literature. While the Russian scientific community remains active, the curtailment of cross-border collaboration has undermined efforts to integrate Russian science into circumarctic perspectives of Arctic ecosystem conditions and change (Büntgen and Rees, 2023; Zaika and Lagutina, 2023; López-Blanco et al., 2024; Rees and Büntgen, 2024; Schuur et al., 2024). From the perspective of Arctic greening, these circumstances underscore the critical importance of spaceborne remote sensing and the continuity of long-term circumpolar NDVI datasets. Nonetheless, the cessation of field studies complicates the interpretation of underlying drivers and ecosystem impacts of spectral trends, particularly in regions with idiosyncratic trends such as the Indigirka-Yana Lowland of northeastern Siberia (see Section 3.6, above).

4.2 Current research gaps

There is a sense of surprise regarding some aspects of Arctic change, including the strength and longevity of greening trends, as well as local declines in productivity, the impact of disturbances and extreme events, and the apparent resistance to change in some regions (Phoenix and Bjerke, 2016; Callaghan et al., 2021; Foster et al., 2022). At landscape scales, localized areas with strong trends are often evident that can be attributed to specific processes with high confidence. However, these hotspots are typically interspersed with more subtle trends that are widely distributed across the broader matrix of tundra landscapes that produce the major patterns evident in circumpolar portrayals. Resolution of these uncertainties generally lies at the intersection of coarse-scale time series, high-resolution data, and field observations. Here we highlight several prominent knowledge gaps.

4.2.1 Long-term disturbance effects

Disturbances such as wildfire, permafrost degradation, and extreme weather events have become increasingly prominent, influencing local to regional greenness directly through mortality, defoliation, or stress (Lara et al., 2017; Sundqvist et al., 2019; Post et al., 2021) or indirectly through the modification of surface properties and vegetation succession (Frost et al., 2020; Verdonen et al., 2020; Chen et al., 2021c). Disturbance impacts on spectral trends are widely acknowledged, and different forms of disturbance can have contrasting short- and long-term impacts (Foster et al., 2022; Phoenix et al., 2025). However, the extent to which "today's browning portends tomorrow's greening" in disturbed environments remains an active area of research (Gaglioti et al., 2021; Chen and Lantz, 2024; Chen et al., 2024). Given that many disturbances are expected to intensify, understanding how these will interact with climate-driven greening over the long term is crucial.

Tundra wildfires have emerged as a prominent form of disturbance, particularly in northwestern North America and northeastern Siberia. Combustion of vegetation and organic soil drives abrupt browning of the landscape, but this is followed by intense greening as post-fire succession unfolds (Narita et al., 2015; Chen et al., 2021d), typically resulting in a greener landscape 20–50 years postfire (Rocha et al., 2012; Chen et al., 2021b) and in some cases after more than a century (Jones et al., 2013). The long-term trajectory of postfire vegetation succession determines the magnitude of greening as graminoid-dominated tundra shifts to shrub tundra (Rupp et al., 2000; Racine et al., 2004). Similarly, varied disturbances caused by permafrost degradation initially decrease greenness, but can increase it over long timescales as nutrients, light, and other resources become available to colonizing plants (Lantz et al., 2009; Verdonen et al., 2020). Thermokarst and thermoerosional processes can also trigger catastrophic lake drainage (Nitze et al., 2018; Lara et al., 2021; Jones et al., 2022), in which newly exposed lacustrine sediments support greener landscapes than the surrounding terrain within years (Lantz, 2017; Chen et al., 2021d), an effect that can persist for decades after drainage (Lara et al., 2018; Chen et al., 2023). However, the longevity of this effect appears to be variable across regions (Von Baeckmann et al., 2024).

Biotic disturbances such as herbivory, trampling, and defoliation events can strongly affect local to regional-scale NDVI (Soininen et al., 2021). For example, muskoxen and caribou/reindeer generally decrease greenness by reducing the abundance of deciduous shrubs and overall plant density (Bernes et al., 2015; Sundqvist et al., 2019; Lindén et al., 2021; Spiegel et al., 2023). Small mammals can also influence greenness; Olofsson et al. (2012) linked interannual declines in NDVI with intense defoliation events within experimental plots in northern Sweden. Similar patterns have been observed in northern Alaska, with anomalous phenological patterns in NDVI and other productivity metrics with lemming population booms (Zhang et al., 2023). Nonetheless, links between spaceborne NDVI and rodent herbivory is difficult to detect due to the high spatiotemporal variability (Siewert and Olofsson, 2020) of microtine rodent boom-bust population dynamics (Pitelka and Batzli, 2007).

Human disturbances also influence regional NDVI trends. For example, at least 465 km^2 have been directly affected by infrastructure construction since 2000 along Arctic coastlines, evident as NDVI decline in Landsat time series (Bartsch et al., 2021). Although the initial effects of infrastructure development are obvious, cumulative impacts can affect areas well beyond the footprint of infrastructure and require decades to play out (Raynolds et al., 2014). In addition, disused roads, mining activities, and other infrastructure can support greening (Cameron et al., 2024). With an increasing rate of almost 5% per year, human industrial activity in the Arctic is becoming increasingly important. Finally, atmospheric nitrogen deposition from industrial sources outside the Arctic could play an increasingly significant, but little explored role in altering Arctic nitrogen cycles (Choudhary et al., 2016; Liu et al., 2018).

Rain-on-snow (ROS) and other extreme weather events are known to impact regional NDVI trends, yet the timing, footprint, and long-term impacts of these events remain difficult to predict (Serreze et al., 2021). For example, the effects of ROS vary depending if the snowpack is above or below the vegetation canopy. Although ROS is expected to become more frequent, no clear trends in the frequency of mid-winter events are evident from satellite data in the last two decades. Nonetheless, there have been several high impact events in northwestern Siberia, Alaska, and Svalbard (Bjerke et al., 2017; Bartsch et al., 2023). Delayed sea-ice formation in early winter has been suggested to be linked to severe events documented for the Yamal region (Forbes et al., 2016). However, the progression of individual ROS events there has differed (Bartsch et al., 2023) and impacts in NDVI not reported.

4.2.2 What is really happening in the High Arctic?

The challenges inherent to remote sensing of Arctic ecosystems are widely recognized (Beamish et al., 2020). Nowhere are these challenges more acute than in the High Arctic, where the growing season is shortest, cloud frequency is high (Karlsen et al., 2018), and observations are highly subject to subpixel effects of late-lying snow and surface water (Cooper et al., 2019). NDVI trends recorded by GIMMS-3g+ and MODIS are very dissimilar (Figures 2, 3) and field observations are scarce outside of a few well-studied areas; as a result, there is lingering uncertainty regarding what is really happening in these remote ecosystems. These uncertainties are particularly troubling considering the amplified importance of incremental changes in temperature in these cold ecosystems, and the pace and severity of the resultant changes to permafrost landforms and surface hydrology (Farquharson et al., 2019).

Vegetation tends to be highly discontinuous in High Arctic ecosystems; although NDVI should be highly sensitive to incremental changes in vegetation cover under these circumstances, time series on barren surfaces are often incoherent, and surface reflectance is disproportionately affected by seasonal snow and surface water rather than by the vegetation itself. On balance, available plot-based monitoring studies in the Canadian Arctic Archipelago, Greenland, and Svalbard (see regional highlights sections) call GIMMS-3g + -based long-term browning trends into question and favor the greening signal recorded by MODIS, with long-term increases in graminoid cover being the most common change recorded. Landsat time series for the Antarctic Peninsula, which experiences a climate regime similar to the High Arctic, unequivocally demonstrate recent increases in vegetation cover concurrent with warming (Roland et al., 2024).

4.2.3 Reconciling arctic TI-NDVI and shifts in arctic seasonality

Unlike MaxNDVI, trends in TI-NDVI observed by long-term GIMMS-3g+ and MODIS generally do not agree in magnitude, sign, or regional pattern over the 23-year period of concurrent observation (Figure 3) (Frost et al., 2021). However, qualitative patterns of interannual variability are similar (Figure 4), suggesting that the overall negative trend in GIMMS-3g + TI-NDVI may be an artifact of high noise in this record. Circumpolar mean TI-NDVI values in 2018, 2019, and 2021 are the lowest in the GIMMS-3g + record since the eruption of Mt. Pinatubo, yet are interspersed with some of the highest TI-NDVI values on record. Although increasing climatic variability is a prominent component of Arctic change (Christensen et al., 2021), such extreme interannual fluctuations in circumpolar TI-NDVI are difficult to reconcile.

One possible explanation is that the TI-NDVI metric is highly sensitive to “shoulder season” observations, which are periods when greenness can change very rapidly due to snowmelt, greenup, senescence, and snow-on. In addition, the latter part of the snowfree season (late August–September) coincides with increasing cloudiness and low sun angles in much of the Arctic, complicating trend analysis in the late season regardless of the sensor used (Swanson, 2017). GIMMS-3g+ in particular could be prone to low bias during these periods due to the fact that there is only one sensor. In contrast, MODIS TI-NDVI is derived from two sensors, which provides more opportunities for observation during favorable sky and ground conditions and favors higher values using a maximum-value compositing approach (Bayle et al., 2024). Additional context for TI-NDVI could be gained by comparing patterns of interannual variability using detrended time series from GIMMS-3g+ and MODIS.

4.2.4 Disentangling permafrost thaw, soil nutrient, moisture, and surface water effects

Permafrost is warming and degrading across the Arctic (Biskaborn et al., 2019; Miner et al., 2022; Schuur et al., 2022; 2023; See et al., 2024) with diverse and contrasting effects on plant growth, soil hydrology, surface water, and NDVI (Foster et al., 2022; Heijmans et al., 2022). Deepening of the active layer can improve access to nitrogen and other nutrients, increasing plant productivity (Salmon et al., 2016; Blume-Werry et al., 2019; Heijmans et al., 2022), particularly of deep-rooting taxa with high root plasticity (e.g., tussocks and other graminoids) (Wang et al., 2017). In addition, permafrost disturbances in the Low Arctic often favor recruitment of nitrogen-fixing alder shrubs, which strongly impact local soil nutrient regime (Hiltbrunner et al., 2014). However, deeper active layers may also lower the water table and dry the rooting zone (Heijmans et al., 2022). Collectively, these factors make it difficult to disentangle the effects of active layer deepening on NDVI and plant growth from concurrent air temperature dynamics.

The spatial scale of permafrost degradation has implications for remote sensing of permafrost-mediated NDVI dynamics. Landscape-scale permafrost processes such as thaw lake initiation, expansion and decline, thaw slumping or active layer detachments may be identified in long-term NDVI records and monitored for subsequent development and recovery (Rodenhizer et al., 2024). Local changes such as ice-wedge degradation and formation of smaller thaw ponds or thermo-erosional gullies produce obvious vegetation effects in the field (e.g., "drowning" tussocks and shrubs) that can also be resolved in VHR imagery (Jorgenson M. T. et al., 2015; Magnússon et al., 2021) but not in Sentinel-2 or Landsat imagery. Occurrence of ground-validated, small-scale processes of thaw pond formation and expansion may even be uncorrelated to NDVI dynamics at a spatial resolution larger than a few meters (Magnússon et al., 2023). Hence, linking NDVI records to gradual permafrost degradation processes, and to rapid changes that occur in mosaic landscapes (e.g., polygonal ground), are the most challenging.

Perennial lakes and ponds are widespread in many Arctic landscapes, particularly in coastal plain and deltaic settings. While attempts are made to mask waterbodies from NDVI time series analysis, faithful masking is difficult to perform. High variability and spurious trends may persist due to errors of omission, while important dynamics could be concealed by errors of commission, particularly in warmer Arctic regions that are experiencing systematic declines in lake area, whose drained basins are foci of rapid vegetation development (Nitze et al., 2020; Lindgren et al., 2021; Jones et al., 2022). Finally, systematic spectral trends have been identified in Arctic waterbodies (Kuhn and Butman, 2021), although reports of declining lake greenness are based on different spectral metrics and it is not clear what influence these trends may have on terrestrial NDVI.

4.2.5 Factors promoting stability

Many Arctic regions do not exhibit any statistically significant NDVI trend (Callaghan et al., 2021). While a lack of NDVI trend does not necessarily indicate a lack of change in ground conditions, there are ample plot-based examples of tundra ecosystems that exhibit little or no change over time. Identifying the site factors that confer stability is a pressing need. Several potential factors favoring ecological stability have been proposed (Callaghan et al., 2021). Many Arctic plants have large geographic ranges and are long-lived; these characteristics would seem to require a capacity to survive strong interannual climate variability, and therefore may also favor survival in a warming climate. Second, structural or physiological limitations of cold-adapted Arctic plants may mean that some taxa simply cannot grow more in response to warming; the presence of such species can also preclude seed recruitment of fast-growing, resource acquisitive taxa, including many deciduous shrubs. In addition, many tundra plant communities may lack the capacity to respond to further warming where soil and permafrost conditions do not favor increased access to soil nutrients. Finally, changing trophic webs can also counter the response of vegetation to climate change at regional scales, such as increased herbivore populations arising from the removal of top predators such as wolves (Van Bogaert et al., 2009). Here, greening is being "masked" by browning, given that many disturbance events also increase as a result of the same warming that causes greening (Phoenix and Bjerke et al., 2016). However, only a few of these ideas have been tested and additional research is needed.

4.3 Potential developments

The sunsetting of the MODIS Terra and Aqua satellites makes urgent the integration of VIIRS data to maintain the continuity of this key dataset. In addition, the eighteenth and final AVHRR sensor was launched onboard the MetOp-C satellite in 2018 (Kalluri et al., 2021). Although VIIRS was purposefully designed to serve as a successor to MODIS, the VIIRS circumpolar MaxNDVI record to date is substantially different (Figure 4) and displays relatively high interannual variability that is more comparable to GIMMS-3g+. The release of fully reprocessed VIIRS data products, in the form of VIIRS version 2, is ongoing and will facilitate more robust intercomparison with contemporaneous MODIS collections. In addition, current VIIRS products are derived from a single satellite (Suomi NPP); the incorporation of observations from additional VIIRS platforms could also improve the record‘s comparability to MODIS.

The advancement and proliferation of high-resolution data collection (e.g., UAVs, airborne, and commercial satellite imagery) and big data analysis (e.g., machine learning techniques and artificial intelligence) will help to clarify the actual on-the-ground mechanisms of ecological changes in complex Arctic landscapes. Arctic plant communities typically have diverse plant functional groups such that both vascular (e.g., shrubs, forbs, graminoids) and nonvascular (bryophytes, lichens) lifeforms are prominent, and are experiencing compositional and structural changes (Elmendorf et al., 2012a; Elmendorf et al., 2012b; Bjorkman et al., 2018). Diverse plant communities can show variability in the seasonal timing of leaf emergence, peak productivity and senescence, and diversity in responses to climate drivers on small spatial scales. In tundra ecosystems, this spatio-temporal heterogeneity may be lost when monitoring changes in vegetation indices at resolutions larger than 0.5 × 0.5 m (Assmann et al., 2020). Preserving spatio-temporal dynamics, for instance through the collection of multiple moderate to high resolution satellite, drone or "phenocam" images within a season, can aid in the distinction and monitoring of different Arctic plant communities and their phenological dynamics (Beamish et al., 2017; Westergaard-Nielsen et al., 2017; Karami et al., 2018; Yang et al., 2023). Solar Induced Fluorescence (SIF) is an emerging radiance-based metric of photosynthetic activity and phenology, but the spatio-temporal coverage of SIF datasets remains small.

A key limitation of NDVI is the diminishing sensitivity of the metric as a measure of ecological change in landscapes with high biomass. This limit places bounds on spectral greening, particularly in the Low Arctic, as MaxNDVI values begin to "plateau" in shrubby areas, particularly near the forest-tundra ecotone. Here, current high-resolution spaceborne estimates of vegetation structure can be an important complement to spectral time series, by providing contemporary stratification of landscape vegetation patterns and a means to account for variation in NDVI sensitivity.

The availability of Sentinel-1 and Sentinel-2 at 10-m spatial resolution improves our capability to capture individual disturbance features and thus enhances ability of change attribution. Although data are available only since 2016, they can complement Landsat time series (Runge and Grosse, 2020; Bartsch et al., 2021). The emergence of harmonized Landsat/Sentinel-2 (HLS) data products, which provide much higher spatial resolution with improved temporal resolution, should prove extremely useful for high spatial resolution trend monitoring, especially for challenging regions such as the High Arctic. The quality of these products benefits from very high sidelap of adjacent orbital paths in the Arctic, which increases the effective observation frequency.

The high relevance of direct consequences of environmental change to human livelihoods in the Arctic necessitates improved exchange of information between natural scientists, local people, land managers, and other stakeholders (Bronen et al., 2020). There is increasing recognition of the insights that Indigenous knowledge (IK) can provide in synthesizing a broad base of information regarding Arctic environmental change (Fienup-Riordan et al., 2013; Ksenofontov et al., 2019; Bronen et al., 2020). For example, sharing of IK through the Local Environmental Observer (LEO) network (Mosites et al., 2018) has led to integrated studies (Jones et al., 2023). The shift in concerns among Indigenous communities from industrial impacts to climate-related issues in northwestern Siberia and elsewhere highlights the broader impacts of environmental changes. The involvement of elders is particularly helpful for understanding the drivers, manifestations, and consequences of Arctic greening because their frame of reference can predate the period of record for high-resolution remote sensing, and elder observations can help address uncertainties and disagreement among disparate long-term NDVI and climate datasets through their knowledge of underlying landscape conditions and change (Fienup-Riordan et al., 2021).

4.4 Future trends through the lens of biodiversity and biomass

The concentration of record-high MaxNDVI values in multiple long-term records in recent years, coupled with continued advances in the state of knowledge of key mechanisms provides unequivocal evidence that the “greening of the Arctic” continues and in many cases represents borealization of Low Arctic ecosystems. Given what has been learned from circumpolar monitoring of Arctic tundra greenness since 1982, what are reasonable expectations for the coming decades?

Arctic greening trends in a warming climate have sparked concern that further shrubification and northward expansion of the tundra-taiga ecotone will result in considerable loss of tundra ecosystems and their associated floristic biodiversity (Henry et al., 2022; Kruse et al., 2023). Long-term vegetation compositional records from International Tundra Experiment (ITEX) monitoring sites confirm increases in vascular plant abundance (particularly shrubs and graminoids) and canopy height both under ambient and experimental warming, while bryophyte and lichen cover and diversity decrease, particularly under shrub expansion, lowering overall plant diversity (Henry et al., 2022). Such changes are more evident in warmer, mesic Low Arctic ecosystems, suggesting that Arctic greening resulting from increased cover and stature of woody species could have negative consequences for floristic diversity. In addition, apparent increases in the frequency and extent of tundra fires have particularly detrimental effects on tundra lichens (Jandt et al., 2008; Frost et al., 2020), a key component of floristic diversity and important forage for caribou (Joly et al., 2009). Shifts in Arctic climate and seasonality also directly affect plant phenology, with implications for plant-pollinator interactions and plant reproductive success, particularly in the High Arctic (Prevéy et al., 2019; Collins et al., 2021). Datasets such as ITEX, with three decades of plant community data across the tundra biome, are invaluable for the validation and interpretation of plot- and landscape-level remote sensing products of tundra greenness.

Arctic greening has wide ranging implications for higher trophic levels, including species that are important to subsistence-based Arctic societies (Wheeler et al., 2018). For example, though greening trends may signify increased browse for Arctic ungulates such as caribou and reindeer (e.g., Potravny and Elsakov, 2024), many herds have paradoxically declined as the abundance of plants with strong chemical defenses has increased (Fauchald et al., 2017). Increased canopy height and structural complexity associated with shrubification strongly modify bird habitats, favoring expansion of boreal forest species (mostly songbirds) but at the detriment of tundra-nesting species (largely shorebirds) (Boelman et al., 2015; Munro, 2017; Mizel and Swanson, 2022; Lyons et al., 2024). Greening in northern European tundra has also been linked to increased nest predation risk (Ims et al., 2019).

The Arctic has entered a new climate and cryospheric regime, where historic extremes are becoming the new normal. Although spring and summer sea-ice concentration has long been recognized as a key control of growing season temperatures and tundra greenness (Bhatt et al., 2010), sea-ice extent has approached zero in Arctic marginal seas in several recent years and is expected to decline further in the future (Overland and Wang, 2013). This trend poses two challenges for future projections of tundra vegetation dynamics. The first is simply that spring and summer sea-ice will no longer be a relevant variable for predicting tundra vegetation greenness in parts of the Arctic. Second, the loss of sea ice has profound implications for other climatic variables (e.g., cloudiness, atmospheric moisture), the interactions among them, and their influence on tundra growing conditions (Liu et al., 2012). This shift will affect vegetation dynamics and potentially lead to abrupt transitions in some areas. There is general agreement that greening will continue as an overall trend across the Arctic, but this greening will continue to be complicated by disturbances that may cause localized browning or affect NDVI trends in more complex ways.

Although the relatively subtle “background” greening trends evident across large parts of the Arctic often cannot be interpreted with confidence, other aspects of Arctic change, such as continued sea-ice decline and warming permafrost temperatures, are known with high confidence. The combination of rising atmospheric and ground temperatures portends deepening of permafrost active layer thickness that will, in turn, mobilize heretofore frozen soil nutrients that can support further increases in biomass. In addition, Arctic warming could accelerate decomposition, soil development and associated increases in plant cover and biomass (Doetterl et al., 2021). Although NDVI is inherently tied to aboveground biomass, any changes aboveground are linked proportionately to belowground biomass, and also have implications for soil temperature and biological processes (Mortier et al., 2024). Despite lingering uncertainties regarding trend attribution and sources of interannual variability, the sequence of record-high circumpolar tundra greenness values observed since 2020 provides strong evidence that aboveground live biomass in many Arctic tundra regions is without recent historic precedent. Considering the strength of relationships between tundra productivity, growing season temperature, summer sea-ice extent, and permafrost conditions, aboveground live biomass across much of the Arctic likely exceeds that of any period since well before the era of circumpolar remote sensing. Indeed, given that Arctic air temperatures have generally been colder than today for many centuries (Kaufman et al., 2009), this time period likely extends to nearly a millennium.

Author contributions

GF: Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. UB: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. MM: Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing–review and editing. LB: Data curation, Formal Analysis, Investigation, Methodology, Software, Validation, Visualization, Writing–original draft, Writing–review and editing. DW: Writing–original draft, Writing–review and editing, Conceptualization. MR: Writing–review and editing, Conceptualization. RM: Writing–review and editing, Writing–original draft, Visualization. AB: Writing–original draft, Writing–review and editing. JB: Writing–original draft, Writing–review and editing. HE: Writing–review and editing. BF: Writing–original draft, Writing–review and editing. SG: Writing–review and editing. EH: Writing–review and editing. SK: Writing–review and editing. TK: Writing–original draft, Writing–review and editing. TL: Writing–original draft, Writing–review and editing. ML: Writing–original draft, Writing–review and editing. EL-B: Writing–original draft, Writing–review and editing. PM: Funding acquisition, Writing–review and editing. CN: Writing–review and editing, Funding acquisition. IN: Writing–original draft, Writing–review and editing. KO: Writing–review and editing. TP: Writing–review and editing. GP: Writing–review and editing, Writing–original draft. AR: Writing–review and editing. BR: Writing–review and editing. GS-S: Writing–review and editing, Conceptualization. HT: Writing–review and editing, Writing–original draft. MV: Writing–original draft, Writing–review and editing. AV: Writing–review and editing, Writing–original draft. A-MV: Writing–review and editing. CW: Writing–review and editing.

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Conflict of interest

Authors GF and MM were employed by Alaska Biological Research, Inc. Author AB was employed by b.geos GmbH. Author EH was employed by Global Science & Technology, Inc. Author PM was employed by ADNET Systems, Inc.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Supplementary material

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Impacts of novel wildfire disturbance on landcover and wildlife in boreal North America

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The summer of 2023 was the first time the planet exceeded 1.5 °C above pre-industrial average temperatures and was recognized as the hottest year on record globally. In Canada, this translated to temperatures that were 2.2 °C above average, resulting in a record shattering fire season. Burning conditions were exceptional in many ways including large total burned area and individual fire size, vast swaths of short-interval reburns and severe combustion, fast-moving wildfires, and substantial burning outside of the typical fire season, reflecting climate warming-induced changes in fire regime. While we know how some components of biodiversity in the boreal biome have responded to historic burning, the 2023 fire season highlights that we are rapidly moving into a novel set of burning conditions and that we require better knowledge of how these conditions will alter landcover and the associated wildlife communities. Here, we synthesize our understanding of how changing fire regimes will affect (short- and long-term effects) boreal landscapes and the implications of these changes for terrestrial wildlife using the extreme burning conditions in subarctic forests of the Northwest Territories, Canada in 2023 as a case study. Our goals were to a) evaluate the impacts of the changing fire regime on habitat composition and/or structure in the short- and longer-term; and b) assess the potential responses of terrestrial vertebrates to these changes based on our understanding of their reliance on key aspects of habitat composition and/or structure. We describe impacts of changes in individual aspects of the fire regime on wildlife taxa but, overall, at the landscape level, changes in fire regime are altering the composition and structure of boreal forests, which will drive decreases in taxa requiring mature conifer forest and post-fire structural complexity while favoring early seral species or those that prefer broadleaf forests or open habitats. This review offers us a range of possibilities about the future landcover and northern wildlife communities under changing wildfires, however uncertainties about feedbacks and future conditions of this vast, diverse, and remote landscape present the greatest challenges for forecasting and other supports for adaptation planning.

KEYWORDS

wildlife, novel disturbance regime, boreal wildfire, ecological resilience, state changes, habitat changes

Introduction

The boreal biome comprises ~30% of the global forest area and is one of the most intact forest ecosystems, occupying high latitude, low productivity regions of Canada, Russia and Alaska (Brandt et al., 2013). This vast area contains 30%–40% of terrestrial carbon stocks and more freshwater than any other biome (reviewed in Gauthier et al., 2015). Human population densities are low meaning that ecological processes and natural disturbances operate across broad spatial scales, and the biodiversity of the biome is largely intact, supporting northern livelihoods and a wide range of ecosystem services (reviewed in Turetsky et al., 2017). Large wildfires are the primary natural disturbance in this system and have historically burned every approximately 50–500 years, depending on the region (Coops et al., 2018; de Groot et al., 2013; Johnstone et al., 2010a). Wildfires create heterogeneity at both the landscape level and within individual fire perimeters (Bergeron et al., 2004; Coogan et al., 2021; Johnson et al., 1998; Weir et al., 2000), which promotes biodiversity (Steel et al., 2024; Hekkala et al., 2023). This heterogeneity is owing to variation in fire behaviour and a wide range of factors that impact successional trajectories and maintain a mosaic of successional stages and forest composition (Perera et al., 2009; Perera and Buse, 2014; Day et al., 2020). Wildfires are also well known to influence important ecosystem functions such as biogeochemical cycling (Eckdahl et al., 2023; Eckdahl et al., 2024; Granath et al., 2021; Pellegrini et al., 2018; Walker et al., 2019; Wei et al., 2018), water quality and quantity (Carvalho-Santos et al., 2019; Granath et al., 2021; Robinne et al., 2020; Santos et al., 2015; Smith et al., 2011), and land surface - atmosphere energy exchanges (French et al., 2016; Zhao et al., 2024) among others.

High latitudes are warming approximately four times faster than the global mean rate (Chylek et al., 2022; Rantanen et al., 2022). Trends in precipitation are much less clear with studies reporting small increases which are often non-significant trends (Zhang et al., 2000; Schetselaar et al., 2023). In addition, small streams in the subarctic may be shifting towards a winter-flow dominated hydrological regime where the majority of streamflow occurs in winter rather than after spring snowmelt, reducing surface moisture during the growing season (Spence et al., 2025). Taken together for the growing season, the increase in evapotranspiration is greater than the increase in precipitation meaning that many high latitude regions are experiencing increasing moisture deficits (Mirabel et al., 2023; Wang et al., 2014; Zhang et al., 2019). This has important consequences for fire regimes (i.e., the characteristics of the fires that have occurred over a long period of time, including mean frequency, size, intensity, severity, ignition source, seasonality, type [ground, surface, or crown], and the variation around these means (Whelan, 1995). Warmer, drier conditions increase landscape flammability (Jain et al., 2024; Whitman et al., 2024) and the frequency of extreme fire weather (Wang et al., 2015), increasing fire activity and promoting more extreme burning conditions. Effective fire suppression and removal of Indigenous burning practices have simultaneously acted to lengthen fire return intervals and promote fuel build-up (e.g., Chavardès et al., 2018; Christianson et al., 2022; Parisien et al., 2023a). Coupled with greater amounts and flammability of fuels is an increase in lightning activity owing to increasing convective periods with climate change, meaning greater ignition potential (Veraverbeke et al., 2017).

Due to these changes, we have seen an increase in the average annual area burned in boreal forests over the last several decades (Coops et al., 2018; Soja et al., 2007; Walker et al., 2020). Notably, extreme wildfire years where area burned far exceeds the long-term average are becoming increasingly common and there has been clear attribution to climate change in regions where it has been investigated (Beverly and Schroeder, 2024; Boulanger et al., 2024; Parisien et al., 2023b). The hot, droughty conditions that support large fire years also facilitate other attributes of a more extreme fire regime such as wind events that further increase flammability and carry fire (Tavakol et al., 2020), longer fire seasons including overwinter smouldering (Hanes et al., 2019; Jain et al., 2024; Scholten et al., 2021), burning of parts of the landscape including young forests and peatlands/wetlands that would have historically served as fuel breaks or fire refugia (Kuntzemann et al., 2023; Whitman et al., 2024), and more severe combustion of aboveground biomass and the soil organic layer that serves as a critical carbon sink in the boreal biome and affects post-fire establishment conditions (Walker et al., 2020; 2019; Baltzer et al., 2021). Climate projections for the coming decades suggest that this increasing trend of fire conducive weather will continue (Wang et al., 2020; Wotton et al., 2017). Such changes in fire activity coupled with ongoing warming are expected to alter the successional trajectory of forests with implications for biodiversity and ecosystem function.

The summer of 2023 was the first time that global average summer temperatures exceeded 1.5 °C above pre-industrial average temperatures for 1850–1900. The United Nations Convention on Climate Change's Paris Agreement stipulates that limiting warming to 1.5 °C should be our collective goal as we aim to reduce emissions and slow global warming; a goal that is now considered unachievable without greatly increased ambition and much more rapid implementation (Ou et al., 2021). Global mean summer temperatures of 1.5 °C above pre-industrial levels translated to much greater increases at high latitudes; for example, Canada was, on average, 2.2 °C above pre-industrial levels. During this exceptionally hot and dry summer, out-of-control wildfires burned across Canada leading to a burned area of more than 15 M ha, seven times the 1986–2022 average and more than double the previous record (Jain et al., 2024); this area was comparable to the record breaking 2021 wildfires in Siberia where more than 17 M ha of land burned (Kharuk et al., 2022). Most burning occurred in boreal forests and a range of fire behaviours and outcomes were observed that are novel disturbance conditions relative to historic burning (Jain et al., 2024; Turner and Seidl, 2023). Half of all individual fires were >100 ha and there were >800 "large fires" (>200 ha; Jain et al., 2024). The average number of large fires is 320 (1986–2022) and before 2023 only 1 year on record had >600 large fires (1989; Jain et al., 2024). The fire season started early in the spring and ended late in the fall (Jain et al., 2024) with hundreds of fires continuing to smoulder through winter 2024. Fire spread rate was unprecedented in many areas. For example, the largest fire complex in Canada in 2023 was in the subarctic boreal forests of Northwest Territories (NWT) (Figure 1), which saw a maximum daily growth rate of nearly 100,000 ha (Jain et al., 2024), this is extraordinary when compared to the Canadian average value of 571 ha/day (2001–2021; Barber et al., 2024). The extreme fire weather conditions (Fire Weather Index exceeding the 95th percentile for 1990–2021 at a location; Jain et al., 2024) in many parts of Canada resulted in the reburning of young forests (<20 years since last fire), wetlands, and peatlands that would historically serve as natural fuel breaks (Whitman et al., 2024). Extreme fires have been increasing disproportionately in boreal North America as evidenced by the 2023 fire season, and this is expected to continue with ongoing human-caused climate warming (Cunningham et al., 2024). The 2023 fire season was extraordinary in its early start and late finish. Fires were still burning very actively into the fall with almost 440,000 ha burning across Canada in a single day in September and active fires and fire management well into October (Jain et al., 2024). Effectively, the fire season lasted up to 7 months in some places and in western Canada the fire season practically never ended with more than 150 overwintering or 'zombie' fires smouldering through the winter months in British Columbia, Alberta, and NWT, leading to an early and intense start to the 2024 fire season (Baltzer et al., 2025).

There is mounting evidence that current fire regimes are becoming misaligned with the plant communities inhabiting boreal regions with wide-ranging implications (Baltzer et al., 2021; Johnstone et al., 2016). After wildfire, various biological and structural legacies remain that shape the response of the system to current and future disturbances. These can include seeds and other reproductive structures, woody biomass, and residual organic soils. Many of the changes in fire regime described above have been shown to remove or alter these legacies, with implications for post-fire forest successional trajectory (reviewed in Johnstone et al., 2016). Examples include changes in: forest composition (including recruitment failure) (Baltzer et al., 2021; Burrell et al., 2022; Hayes and Buma, 2021; Johnstone et al., 2016; Whitman E. et al., 2019); mode of ground vegetation recovery with implications for plant community composition (Day et al., 2020; Hollingsworth et al., 2013); microbial community structure and function which affect biogeochemical processes with direct impacts on plant community composition and function (Day et al., 2019; Whitman E.et al., 2019; Eckdahl et al., 2023; Eckdahl et al., 2024); boreal carbon sequestration potential including large carbon emissions and losses of legacy carbon (Veraverbeke et al., 2021; Walker et al., 2019; 2018); and rates of permafrost thaw, which can further amplify vegetation-changes and modify other ecosystem functions (Bill et al., 2023; Gibson et al., 2018; Holloway et al., 2020). Across jurisdictions, there are concerns about the biodiversity and self-sustainability of wildlife populations, including species at risk, given wildfire-induced changes in wildlife habitat. More specifically, for Indigenous communities in northern boreal regions, such wildfire-induced changes affect the diversity, abundance, and access to "country" or subsistence food resources (e.g., wildlife) by altering habitat availability, removing traditional trails, and making land access more dangerous or less predictable (Spring et al., 2019). Understanding and forecasting these changes have been identified as priorities for many northern communities and as such forms the focus of this review.

In this review, we synthesize knowledge of how novel fire regimes are changing North American boreal forests and highlight known and anticipated effects of these changes on landcover (i.e., wildlife habitat) and the terrestrial wildlife that rely on these lands using examples of species that occur in NWT. More specifically, we consider how changes to four components of the fire regime (fire size and area burned; burn severity; short-interval reburning; and longer fire seasons) may impact vegetation structure and composition over the short-term (<10 years post-fire) and longer-term (30–40 years post-fire) and how these changes may differentially affect different groups of wildlife taxa. We use the 2023 burning conditions in NWT as a case study because it was the subarctic boreal region in Canada that was most severely impacted. Furthermore, the 2023 fires in NWT came on the heels of the second largest recorded fire year that occurred in the same area only 9 years earlier, in 2014 [2.85 M ha burned; Walker et al., 2018], leading to effects of compounded extreme fire years. This is not intended to be an exhaustive review of all wildlife taxa but to provide a survey of our understanding of responses across a range of trophic levels and functional groups of the ~300 terrestrial vertebrate taxa in boreal NWT (Working Group on General Status of NWT Species, 2021). Few studies have tackled the impacts of individual components of fire regime on wildlife taxa (e.g., reviewed in Forney and Peacock, 2024; Volkmann and Hodges, 2024) so our goals were to a) evaluate the impacts of these changing components of the fire regime on habitat composition and/or structure in the short- and longer-term; and b) assess the potential responses of terrestrial vertebrates to these changes based on our understanding of their reliance on key aspects of habitat composition and/or structure. We focus predominantly on species of special conservation concern (species at risk, migratory birds, culturally important species) owing to greater availability of information. We did not focus on predators owing to disproportionately fewer studies evaluating predator responses to fire and because the response of predators to fire tends to be an indirect response to prey availability rather than the direct effects of changes in forest composition and structure that we are focused on (reviewed in Forney and Peacock, 2024; Volkmann and Hodges, 2024). We also identify key knowledge gaps to help guide wildlife–wildfire research in NWT and elsewhere in northern Canada. We end with ideas about wildlife–wildfire research and monitoring priorities and how we can best use this knowledge to support adaptation planning in jurisdictions and communities in the boreal forest. Canada's 2023 wildfire season gave us a glimpse of the future in a warming, fierier boreal biome. It is imperative for adaptation planning that we work to understand and forecast these impacts.

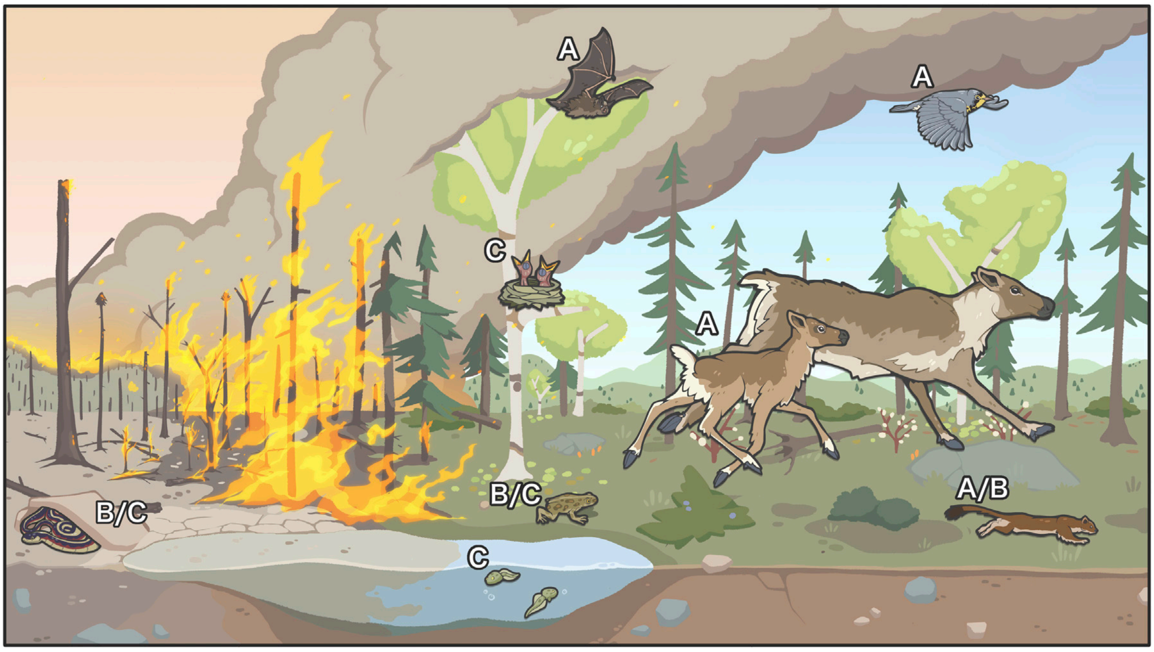

FIGURE 1
Illustration of examples of the acute effects of wildfire on vertebrate wildlife species including **(A)** forcing mobile species to flee: little brown myotis (*Myotis lucifugus*), boreal caribou (*Rangifer tarandus caribou*), Canada warbler (*Cardellina canadensis*), short-tailed weasel (*Mustela erminea*); **(B)** forcing burrowing/denning animals to seek shelter belowground to try to avoid mortality: Red-sided garter snake (*Thamnophis sirtalis parietalis*), short-tailed weasel, western toad (*Anaxyrus boreas*); **(C)** mortality of less mobile species: Red-sided garter snake, western toad, other aquatic species in land-locked water bodies, slow-moving species, nestling birds, *etc.* The species that avoid direct mortality are expected to experience physiological stress because of smoke inhalation, physical exertion, *etc.*

Acute responses to wildfire

The immediate impacts of fire on wildlife populations includes direct mortality, which can be particularly important for small mammals, amphibians, juvenile birds, and reptiles that have limited capacity to flee approaching fire (Figure 1), however there are many unknowns. We will not deal comprehensively with acute fire impacts as these constitute a variety of physiological and behavioural responses beyond the scope of this review (reviewed in Sanderfoot et al., 2022). However, below we will touch briefly on some taxa that face heightened risk of direct mortality from fire in NWT.

Small mammals (mice, voles, shrews, squirrels, and hares) found in NWT forests have co-evolved with wildfire and some species of small mammals (e.g., deer mice [*Peromyscus maniculatus*], voles, and red squirrels [*Tamiasciurus hudsonicus*]) are likely able to survive the immediate impacts of wildfires by using burrows, logs, or crevices under rocks to shelter from passing fires (Banks et al., 2011; Hale et al., 2022; Shaw et al., 2021; Sutherland and Dickman, 1999) or survive within unburned residuals within the fire perimeter (Bond, 2015). Other small mammal species that nest in tree cavities (e.g., northern flying squirrel [*Glaucomys sabrinus*]) and birds nesting on a wide range of substrates may be more susceptible to mortality and loss of young during fires as these aboveground structures are readily consumed. Even though snowshoe hare (*Lepus americanus*) leverets are precocious at birth, they may be particularly susceptible to mortality during a fire event, as they are left unattended in aboveground, shallow, fur-lined bowls and may not be mobile enough to escape a fire (Aldous, 1937; O'Donoghue and Bergman; Rongstad and Tester, 1971). Although it has been suggested that bats could suffer some direct mortality during fires, little is known about the magnitude of this mortality (Loeb and Blakey, 2021). Typically, bats should be capable of leaving their roosts and flying away from an approaching fire although non-volant bat pups may be more susceptible (Dickinson et al., 2010). Similar to small mammals, snakes can take refuge in wetland habitats or belowground (in crevices, hollows, or rodent burrows) which can allow them to survive a fire but does not always provide complete protection (Cross, 2015; Russell et al., 1999; Smith et al., 2001); indeed, high levels of fire-induced mortality have been documented in snake populations (e.g., Erwin and Stasiak, 1979; Lyet et al., 2009). Fires can directly kill many amphibians while they are in terrestrial habitats (e.g., Bailey et al., 2025) and even while they are in burrows or other refuges, especially if the fire is intense (Beranek et al., 2023; Mahony et al., 2022). Combustion of downed woody debris and fires that burn deeper into the soil organic layer and tree root system will likely result in higher immediate mortality of ground-dwelling small mammal, amphibian, and snake species that have lower mobility and typically use protective features (e.g., burrows, hollows in logs) to survive fires *in situ* (Jager et al., 2021). In short, the ability and instinct to flee is a major factor determining whether wildfire will lead to mortality events in a population (reviewed comprehensively in Sanderfoot et al., 2022).

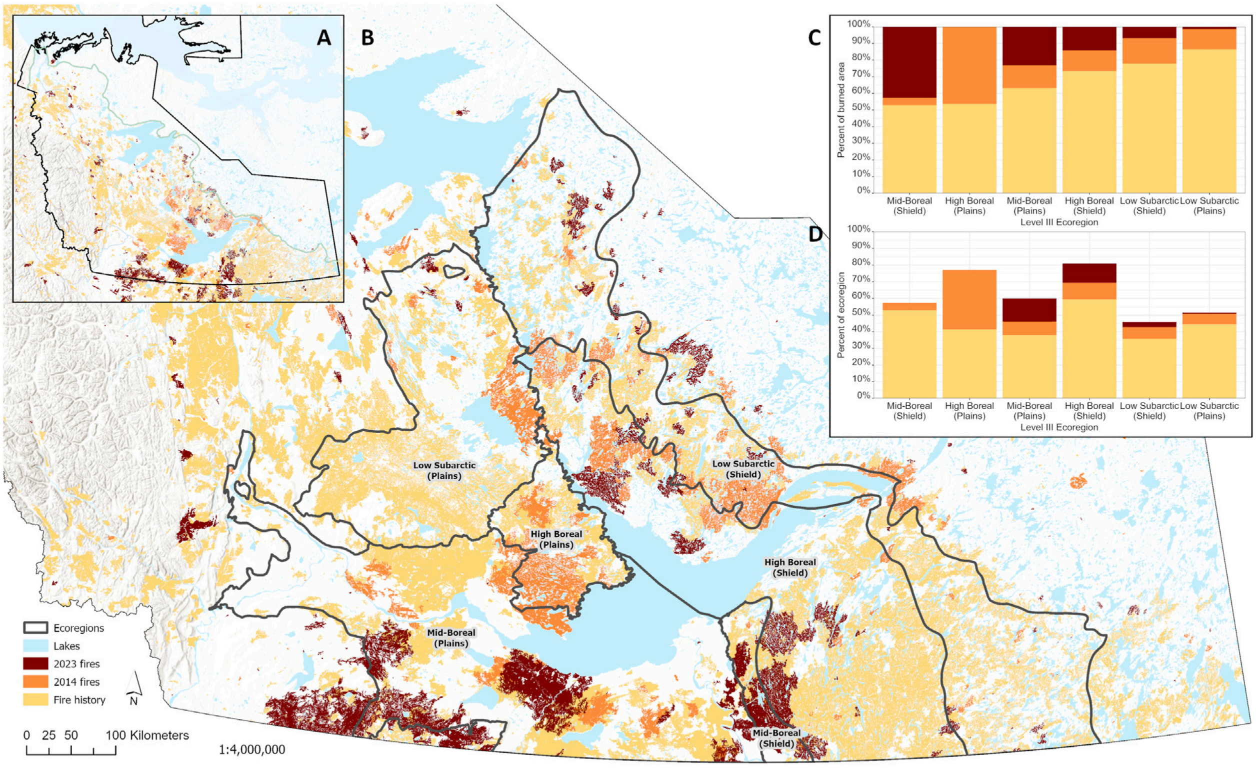

FIGURE 2
Extent of two consecutive mega-fire years (2014, 2023) in the Great Slave Lake region of Northwest Territories (NWT). Fires on a NWT-wide scale **(A)** and within the southern NWT where Level III Ecoregions are also demarcated **(B)**. Ecoregion delineations are from Ecosystem Classification Group (2007 [rev. 2009]; 2008; 2010; 2012). Combined, these fire seasons burned approximately 7 M ha in the same region. The percent contribution of 2014 and 2023 wildfires to total burned area **(C)** and total area of Level III Ecoregions **(D)** is provided.

Area burned and fire size

A key component of any disturbance is its extent. In the case of fire, this includes total area burned in a region as well as the size distribution of individual fires. Both total area burned and individual fire sizes were unprecedented in 2023 (Jain et al., 2024). In NWT alone, more than 4 M ha of forested land burned, almost a third of total burned area in Canada in 2023 (Jain et al., 2024). NWT was also home to the largest fire complex in Canada since the 1950s, exceeding 1 M ha (Jain et al., 2024; Figure 2). This was the largest fire season by far for both Canada and NWT since records began in 1965.

Large boreal wildfires in and of themselves are not necessarily problematic for wildlife. Large fire complexes burn over the course of many days to weeks and across large areas. Consequently, burning conditions vary owing to temporal changes in fire weather and spatial changes in fuel conditions. This means that the fire intensity and spread rate can vary substantially as the fire grows, leading to tremendous heterogeneity in residual vegetation and post-fire vegetation structure within large fire complexes (reviewed in Burton et al., 2008). These variable conditions are thought to emulate pre-suppression fire regimes to which the landscape may be better adapted (reviewed in Stephens et al., 2014). Variation in burn severity within large fire complexes may increase wildlife diversity because greater heterogeneity in the post-fire composition and structure provides a more diverse set of habitat conditions (reviewed in Burton et al., 2008; Jones and Tingley, 2022). Furthermore, large fires tend to have more complex edge structure which has been shown to be important for wildlife (reviewed in Burton et al., 2008). However, much of this will depend on the size, severity, and frequency of burning in these complexes. For example, large, high severity burns (see definition in burn severity section) will promote species that recover rapidly post-fire and can in fact reduce landscape level heterogeneity with associated negative consequences for the diversity of wildlife habitat (reviewed in Steel et al., 2024).

Short-term responses to larger fires

For species that are reliant on mature forest conditions, larger fires have negative short-term effects through reduction in available habitat. In NWT, the two largest fire seasons on record (2014 and 2023; 2.9 M and 4 M ha, respectively; Walker et al., 2018; Jain et al., 2024) impacted the same general region around Great Slave Lake in southern NWT resulting in vast tracts of disturbed forest accumulating across a 9-year period (Figure 2). As the climate warms and dries, we expect such repeated instances of extreme fire years like we have seen in NWT, but the extent of the impact on mature forest specialists is not yet fully known owing to the relative novelty of these large events. For example, boreal caribou (*Rangifer tarandus caribou*) are particularly reliant on mature forests for access to arboreal and terrestrial lichens which are their predominant winter food (Schaefer and Pruitt, 1991; Thompson et al., 2015). Reindeer lichens (*Cladonia* subgenus *Cladina*) are readily consumed by fire and, due to their extremely slow growth rates (~4.9 mm/yr; McMullin and Rapai, 2020), can take several decades to recover to pre-fire biomass found in mature forest stands (McMullin et al., 2011; Silva et al., 2019; Greuel et al., 2021). We expect that increasing occurrence of both larger individual fires and higher total area burned will lead to winter habitat loss (Palm et al., 2022) and could lead to boreal caribou congregating at higher densities in small patches of remaining mature forest during winter. While boreal caribou avoid burns most strongly during winter (Konkolics et al., 2021), they may actually select for recent burns during calving (Silva et al., 2020) or summer (DeMars et al. unpublished data) likely due to the greater availability of protein-rich forage provided by early-successional vegetation that helps female caribou meet the nutritional demands of lactation (Denryter et al., 2017). When boreal caribou do use areas within burns, in all seasons they select areas closer to burn perimeters (Palm et al., 2022). Thus, a very large individual fire event may lead to greater habitat loss for caribou than several smaller fires amounting to an equivalent area due to edge effects (i.e., their avoidance of areas deeper within burns).

Similarly, there are many mature forest specialists in the landbird community that are vulnerable to widespread burning (e.g., Canada Warbler [*Cardellina canadensis*], Brown Creeper [*Certhia americana*], and Evening Grosbeak [*Coccothraustes vespertinus*]; Gillihan and Byers, 2020; Poulin et al., 2020; Reitsma et al., 2020; see also text in short-interval reburn section below). Alternatively, landbird species associated with early seral stages (e.g., Alder Flycatcher [*Empidonax alnorum*] and Dark-eyed Junco [*Junco hyemalis*]) or habitat generalists (e.g., American Robin [*Turdus migratorius*]) would thrive or not show a numerical response to larger fire events (Schieck and Song, 2006). Recently, Lane-Shaw et al. (unpublished data) used predictions from species distribution models for 144 landbird species generated from the Boreal Avian Modelling Center (Stralberg, et al., 2025) to quantify potential changes in abundance of these species breeding in mature forests of NWT following the 2023 fire season. Preliminary results suggest that the most negatively impacted species include the mature forest obligates Rusty Blackbird (*Euphagus Carolinus*), Ruby-crowned Kinglet (*Corthylio Calendula*), Golden-crowned Kinglet (*Regulus Satrapa*), and Bay-Breasted Warbler (*Setophaga Castanea*). For these species, an estimated ~20% of their populations breeding in mature forest experienced lost or altered breeding habitat in NWT. In total, ~59,000 breeding males had habitat in mature forests (>80 years) that burned in 2023 across NWT.

Fire affects foraging opportunities for bats. Recently burned habitat often experiences a "pulse" of higher insect productivity (Lacki et al., 2009; Malison and Baxter, 2010). Fire also changes forest structure by reducing understory vegetation, making flying and foraging easier for bat species that are less tolerant of clutter (Blakey et al., 2019); this can increase activity of bat species such as the little brown myotis (*Myotis lucifugus*) in burned landscapes (Buchalski et al., 2013; Blakey et al., 2019; Low et al., 2024). In contrast, northern myotis (*Myotis septentrionalis*) is more dependent on forest cover (Henderson et al., 2008) and better adapted to foraging in densely vegetated environments (Norberg and Rayner, 1987; Ratcliffe and Dawson, 2003). As such, northern myotis is expected to be more be negatively impacted by larger burned areas compared to the little brown myotis (Blakey et al., 2019; Snider et al., 2013; Bosso et al., 2018; Kotliar et al., 2002; Azeria et al., 2011; Doty et al., 2023).

Despite the potential for widespread mortality of small, ground dwelling mammals during a large fire event, their high reproductive capacity and ability for some individuals to survive the fire *in situ*, means that they can recolonize burned areas relatively quickly (Hale et al., 2022). In boreal North America, deer mice tend to be the most abundant species immediately post-fire, perhaps owing to their omnivorous diet, followed by red-backed voles (*Clethrionomys gapperi*) which may repopulate burns within the first 3 years (Olson et al., 2003; Simon et al., 1998 - reviewed in Fisher and Wilkinson, 2005; Zwolak and Foresman, 2007). Meadow voles (*Microtus pennsylvanicus*) and meadow jumping mice (*Zapus hudsonicus*) may also be more abundant than red-backed voles in the short-term due to their association with grassy cover that may recover quickly post-fire (Fisher and Wilkinson, 2005). Marten (*Martes* spp.) and weasels (*Mustela* spp.), which primarily prey on small mammals, may benefit from edge habitat created by fires that locally increase small mammal populations; however, large homogenous fires may decrease edge habitat and habitat suitability for marten as they avoid areas of low canopy closure and may be reluctant to forage far from the forest edge (Volkman and Hodges, 2024). Red squirrels, conifer seed specialists that are more common in mature forests, may similarly forage within the periphery of recent burns (Fisher, 1999), but are unlikely to recolonize the center of large burns until conifer forests recover.

Reptiles such as red-sided garter snakes (*Thamnophis sirtalis parietalis*) may experience indirect impacts of large boreal wildfires linked to post-fire changes in predator-prey dynamics and habitat suitability (Rochester et al., 2010). As species that rely on habitat structure to avoid predation, they may experience higher predation rates and lower survival in large, recent burns (Doherty et al., 2022; Howey et al., 2016; Russell et al., 1999; Webb and Shine, 2008; Wilgers and Horne, 2007). Reduced cover (i.e., removal of shrubs, woody debris and the litter layer, and opening of the forest canopy) can make it easier for avian predators to detect them (Doherty et al., 2022; Wilgers and Horne, 2007). Reptiles can benefit from the opening of forest canopies or dense shrub thickets that increase surface temperatures (Bury, 2004; Howey et al., 2016; Russell et al., 1999); however, widespread removal of vegetation, leaf litter and woody material can reduce the thermal heterogeneity that they require (Howey et al., 2016; Smith et al., 2001).

There are many impacts of fire on amphibian species, but those most impacted by large fires will likely be those reliant on cool, moist microhabitats and that use ground cover consumed by fire (e.g., leaf litter) (Rochester et al., 2010; Russell et al., 1999), such as the wood frog (*Rana sylvatica*) (Bailey et al., 2025; Constible et al., 2001). Reduced habitat structure, lower soil moisture and more variable soil temperatures in their terrestrial habitats present amphibians with increased risk of overheating, desiccation, and predation, reduced availability of habitat refugia and invertebrate prey, and barriers to movement (Browne et al., 2009; Bury, 2004; Cline and Hunter Jr, 2016; Hossack et al., 2013; Rochester et al., 2010; Russell et al., 1999; Schurbon and Fauth, 2003). Amphibians are also affected by

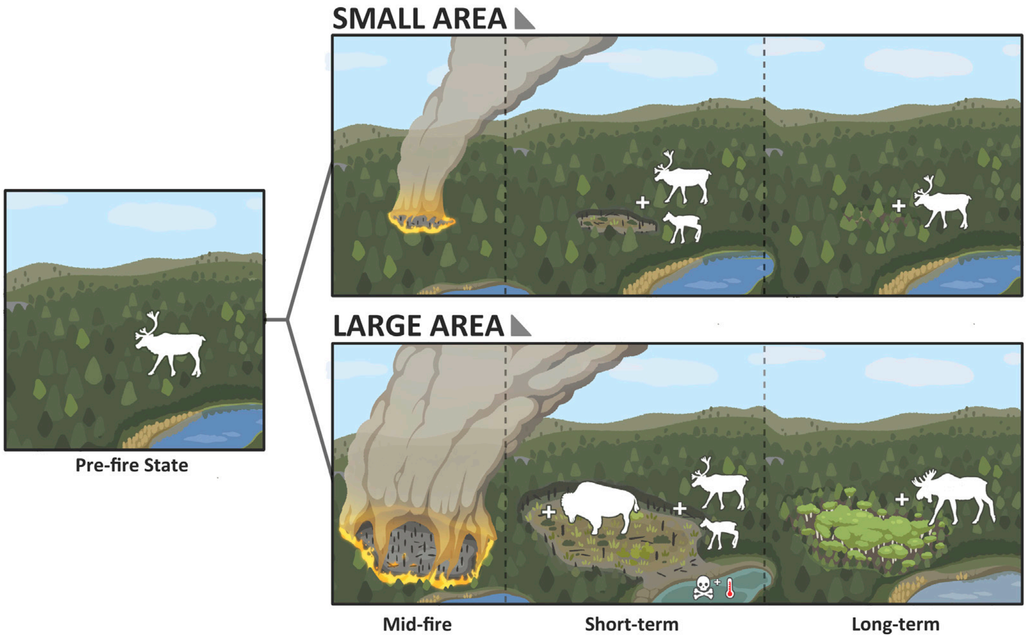

FIGURE 3
Illustration of an example of the effects of burn area on forest succession and some boreal wildlife. Note, plus signs denote habitat selection by the selected large mammal species, not a population response. Smaller burn areas in coniferous forest are more likely to be revegetated by the cones of surrounding trees, thus returning to a structure and composition similar to pre-fire conditions and in a shorter time frame. Larger burns are likely to experience compositional change, favouring long-distance dispersers, such as graminoids and broadleaf deciduous trees (e.g., *Populus tremuloides*). Early successional vegetation post-fire may provide boreal caribou (*Rangifer tarandus caribou*) with improved nutrition during calving. Conifer forest conversion to grass/shrubland or deciduous forest, will favour species including bison (*Bison bison athabascae*) and moose (*Alces alces*), whereas mature conifer forest specialists like boreal caribou will avoid these areas. Larger burn areas may also have profound impacts on adjacent aquatic environments, altering the aquatic species community. For example, large fires may alter water chemistry and thermal conditions of adjacent water bodies more profoundly.

changes to their aquatic habitats post-fire and watersheds that are completely combusted in large burns will see the biggest changes. Reductions in dissolved oxygen seem consistently negative for boreal amphibians whereas other chemical changes have been shown to negatively affect wood frog and boreal chorus frog (*Pseudacris maculata*) abundance but are better tolerated by western toad (*Anaxyrus boreas*; Jager et al., 2021; Browne et al., 2009). Increased solar radiation and contaminants (e.g., wildfire ash) in their aquatic habitats have negative effects on amphibians (Bancroft et al., 2008; Gomez Isaza et al., 2022; McDonald et al., 2018; Muñoz et al., 2019; Xu et al., 2024). Loss of vegetation surrounding wetlands can reduce protection from temperature extremes and predators, with negative effects on amphibian survival (Beranek et al., 2022) and reproductive success (Muñoz et al., 2019). Wetland habitats also experience changes in productivity, water temperature, and hydroperiods that affect amphibians (dos Anjos et al., 2021; Gomez Isaza et al., 2022; Schurbon and Fauth, 2003). However, certain amphibians are more resilient to large fire extents and might even show positive population responses (reviewed by dos Anjos et al., 2021). For example, western toads exhibit rapid tadpole development and are habitat generalists able to reproduce in almost any water body, which facilitates colonization of burned habitat (dos Anjos et al., 2021) but does not necessarily result in longer-term increases (Hossack et al., 2013).

Long-term responses to larger fires

Very large fires can alter post-fire forest composition through their effects on dispersal distances required for establishment. Depending on the pre-fire forest composition and combustion severity of canopy seed sources, soil seedbanks, and below/near-ground budding structures, on-site reproductive sources may be insufficient when distance to an unburned edge is large. This can lead to lagged recovery, post-fire forest compositional changes (e.g., conifer to deciduous), poor recruitment leading to forest structural changes (Girard et al., 2008), or recruitment failure (Johnstone et al., 2010b). For example, white spruce (*Picea glauca*) is a non-serotinous conifer; white spruce stands within a large burn complex may fail to self-replace owing to long distances to the nearest seed source coupled with relatively low dispersal distances of white spruce seeds (Dobbs, 1976). In contrast, trembling aspen (*Populus tremuloides*) seeds can travel as much as 10 km from the nearest seed source (Turner et al., 2003) and aspen produces seed prolifically in the summer following a large wildfire year (J. Baltzer, personal observation; Landhäusser et al., 2019). As such, large burn complexes, especially in conifer dominated areas, may be particularly susceptible to forest compositional change (Johnstone et al., 2010b). Although a few large fire complexes may be beneficial in supporting landscape heterogeneity, where many large fire complexes occur in proximity as has occurred in southern NWT, this change can create challenges. Changes in overstory composition alter the ground vegetation community composition (e.g., Day et al., 2020; Greuel et al., 2021) with implications for wildlife forage availability (Jorgensen et al., 2023) and habitat use (Palm et al., 2022) (Figure 3).

For some wildlife species, changes in forest composition from conifer to deciduous dominance will be beneficial. For example, moose (*Alces alces)* occur throughout boreal North America and consume a variety of forage species including coniferous and deciduous trees and shrubs, graminoids, forbs, and aquatic plants (Joyal and Scherrer, 1978; Jung et al., 2018; Timmermann and McNicol, 1988). However, moose generally prefer deciduous trees and shrubs, notably willow (*Salix* spp.), birch (*Betula* spp.), and poplar (especially trembling aspen) which are commonly a dominant component of moose diet throughout the year (Risenhoover, 1989; Shively et al., 2019). For other wildlife species, such changes will be detrimental. For example, landbird species associated with mature conifer forests, such as Olive-sided Flycatcher (*Contopus cooperi*; Altman and Sallabanks, 2020), Canada Jay (*Perisoreus canadensis*; Strickland and Ouellet, 2020), Boreal Chickadee (*Poecile hudsonicus*; Ficken et al., 2020) and others are expected to decline in abundance as forests transition from conifer to deciduous. Conversion to deciduous forests would also likely be detrimental to boreal caribou as they avoid most age classes of deciduous stands relative to other landcover types from late-fall to late-winter (DeMars et al. unpublished data). However, species associated with mature deciduous or mixedwood forests such as the Warbling Vireo (*Vireo Gilvus*), Magnolia Warbler (*Setophaga Magnolia*), and Ovenbird (*Seiurus Aurocapilla*) will likely thrive for some time (see Short-interval reburning) because of such changes in forest composition (Scheick and Song 2006). Knaggs et al. (unpublished data) showed that, in NWT, early seral stage or habitat generalist species tend to be at a higher probability of occurrence between 3 and 10 years post-fire (e.g., Chipping Sparrow, *Spizella passerina*, White-throated sparrow, *Zonotrichia albicollis*, American Robin) and 11–30 years (e.g., Alder Flycatcher, Lincoln Sparrow, *Melospiza lincolnii,* White-crowned Sparrow, *Zonotrichia leucophrys*), while other species associated more with mature forests started peaking 11–30 (e.g., Hermit Thrush, *Catharus guttatus*), 31–50 (e.g., Swainson's Thrush, *Catharus ustulatus*), or >51 years post-fire (e.g., Yellow-rumped Warbler, *Setophaga coronata*). Other bird species like the Ruffed Grouse (*Bonasa umbellus)* and Willow Ptarmigan (*Lagopus lagopus)* might be more abundant in recent burns due to increase in forage availability (Cringan, 1958; Rusch et al., 2020; Snow, 1996; Weeden, 1963), while Spruce Grouse (*Canachites canadensis)* would be more abundant in mature conifer forests (Cringan, 1958; Ellison, 1975).

While short-term post-fire changes in small mammals communities are fairly well documented (reviewed in Fisher and Wilkinson, 2005), the longer-term implications of larger fires are less clear. The combined effect of fire size and homogeneity of the burn with respect to fire severity is likely a more important driver of longer-term recovery of small mammal populations than fire size alone. Generally speaking, the abundance of small mammals increases with time after fire (Griffiths and Brook, 2014), and the relative abundance of different small mammal species within the community shifts with forest succession (Fisher and Wilkinson, 2005). For example, red-backed voles begin to replace deer mice as the most common species in the small mammal community once shrubby and herbaceous vegetation replaces grasses (Fisher and Wilkinson, 2005). American marten (*Martes americana*) used 21-year-old burns in NWT that had abundant standing snags and deadfall (Latour et al., 1994), suggesting they will make use of recent burns provided there is sufficient residual structure to provide subnivean access to prey and/or shelter. Populations of red squirrels and northern flying squirrels will take longer to recover within large burns as both are reliant on habitat features common to mature conifer forests such an abundant supply of conifer seeds (red squirrels), large live and dead trees used for dens, and as fungal and lichen food sources (flying squirrels) (Fisher and Wilkinson, 2005).

The extent of burns can affect patterns of amphibian occupancy in the longer term, through increased distance to source populations (Bailey et al., 2025; Hossack et al., 2013) and reduced habitat connectivity that impedes movement (Beranek et al., 2022; Cline and Hunter Jr, 2016). These effects would be influenced by heterogeneity and the existence of habitat refugia within large burn perimeters (Mahony et al., 2022; Schurbon and Fauth, 2003). For wood frogs, post-fire breeding persistence in wetlands can be high if unburned habitat is available nearby, but probability of persistence decreases when a greater proportion of the surrounding terrestrial habitat is burned, and it could be several years or decades before wood frogs return to breed in these areas (Bailey et al., 2025). A similar relationship was found for Columbia spotted frogs (*Rana luteiventris)* with effects on occupancy 7–21 years after wildfire (Hossack et al., 2013). Large, intense wildfires can also negatively affect persistence of amphibian species and communities across a broad geographic area and periods of time, and that even species with large populations and/or ranges can be affected (Beranek et al., 2023).

For snakes, habitat refugia (i.e., unburned areas) are important for persistence after fire and re-establishment in the longer term (Robinson et al., 2013; Beaupre and Douglas, 2012). Larger fires could reduce the number and proximity of habitat refugia on the landscape in boreal systems (McKenzie et al., 2004; Mackey et al., 2021), potentially limiting the ability of red-sided garter snakes to recolonize after fire (Santos et al., 2022), especially if large fires simultaneously affect many individuals and/or den sites, a situation that was observed in 2023 (J. Wilson, pers. obs.). Nevertheless, snake populations can persist *in situ* and be resilient to fire (Halstead et al., 2019; Maloney, 2024; Russell et al., 1999; Smith et al., 2001), even large fires (Santos et al., 2021).

In summary, responses to large burn areas or fire sizes vary considerably across taxa. Species reliant on large tracts of mature forest or nearby forest edges will fare poorly in the short- and longer-term as area burned increases and access to these habitats decreases. Many taxa are ambivalent to burned condition *per se* but have forest structural and compositional requirements for protective or thermal cover or other habitat attributes that will determine their response to the fire. Taxa preferring more open habitats or early post-fire vegetation types will fare well in the face of large burns. Longer-term land cover changes associated with large burns (i.e., conifer to broadleaf deciduous) will favour some species and disadvantage others, effectively altering the structure of terrestrial wildlife communities.

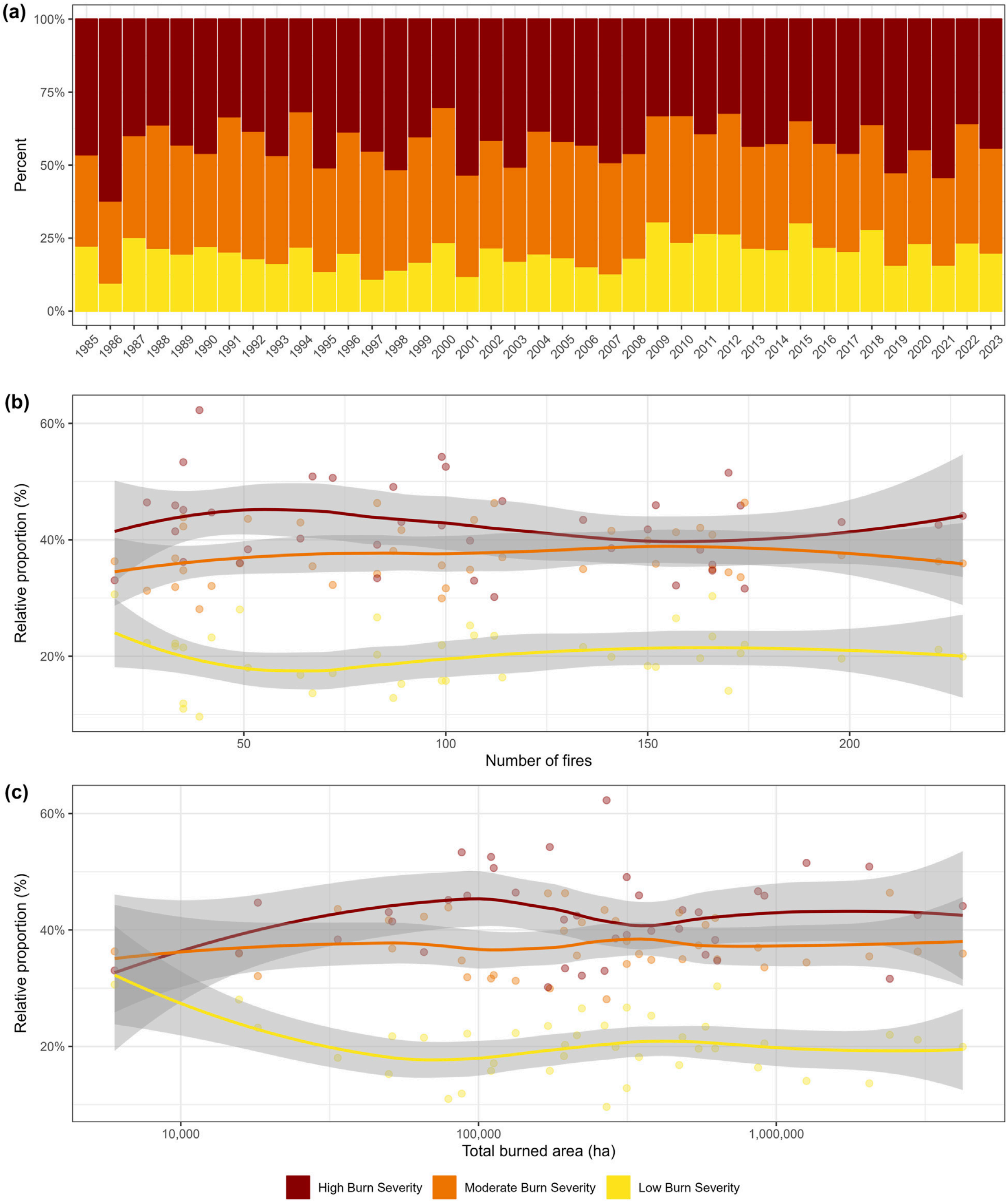

FIGURE 4
Summary of burn severity information for Northwest Territories including the percent of LandSat pixels experiencing high, medium and low severity burning (derived from dNBR thresholds; Hall et al., 2008) through the satellite record **(a)**, as a function of total number of fires **(b)** and as a function of total burned area **(c)**. There are no apparent trends in any of these measures and the statistics are presented in Supplementary Table S2. Methods for determination of dNBR and further details of this categorization are provided in Supplementary Table S1.

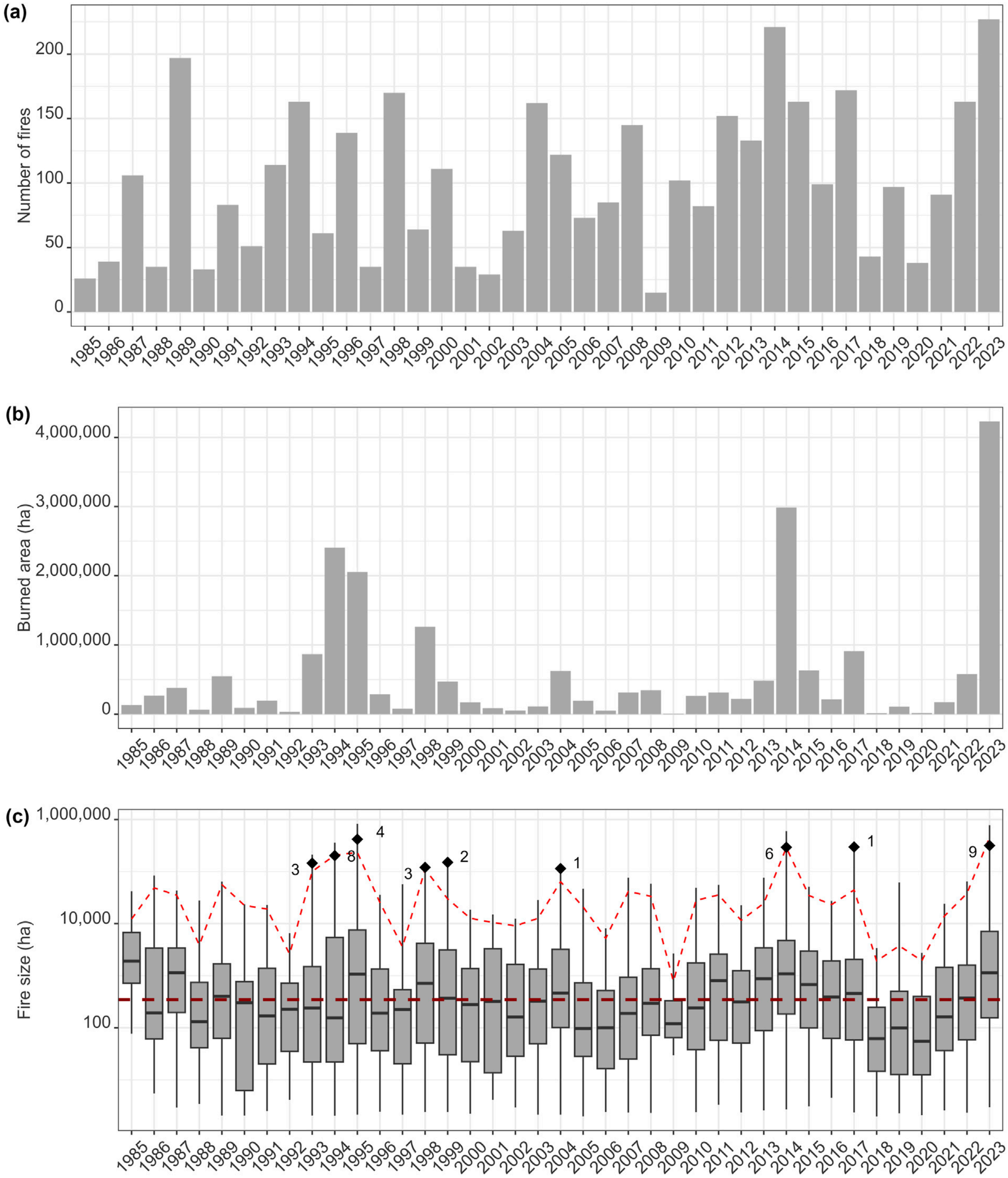

FIGURE 5
A comparison of the total number of fires **(a)**, total burned area **(b)**, and fire size (note the log scale) **(c)** of fire seasons from 1985 onward for the entire Northwest Territories. Note that 2023 had the largest number of fires, largest burned area, and is amongst the top fire years for largest mean fire size. In **(c)** the long-term median (1985–2022; 348 ha) is identified by the horizontal dark red line, whereas the mean area of the five largest fires for each year is indicated by the bright red line. Inset **(c)** also identifies the mean area (shown with solid diamond) and number (adjacent to solid diamond) of exceptionally large fire events, defined by exceeding the long-term mean +3 S.D. The statistics comparing 2023 to the long-term mean (1985–2022) are provided in Supplementary Table S2.

Burn severity

Burn severity characterizes the magnitude of the combustion of both aboveground (vegetation) and belowground (soil) organic matter (Keeley, 2009). Although annual burned area is increasing across the boreal biome with climate warming (Coops et al., 2018; Soja et al., 2007; Walker et al., 2020), the same trend in burn severity, as measured by dNBR (difference Normalized

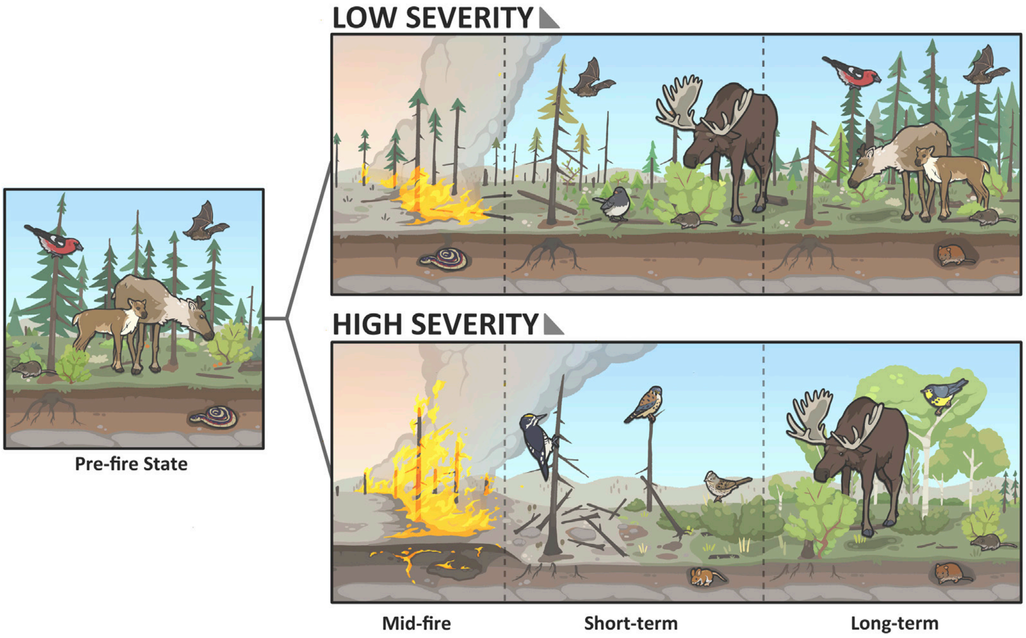

FIGURE 6
Illustration of the effects of high and low burn severity on forest structure and associated boreal species. High severity burns may burn deeper into the ground and completely remove the organic soil layer and more (if not all) of the surface litter, causing direct mortality in burrowing species. High severity burns experience slower forest recovery, and the removal of coniferous seed banks also encourages the replacement of coniferous forest by faster-growing deciduous trees, which will support a different community of boreal species. Low severity; left to Right: Red-sided garter snake (*Thamnophis sirtalis parietalis*), little brown myotis (*Myotis lucifugus*), dark-eyed junco (*Junco hyemalis*), masked shrew (*Sorex cinereus*), moose (*Alces alces*), white-winged crossbill (*Loxia leucoptera*), boreal caribou (*Rangifer tarandus caribou*) red-backed vole (*Clethrionomys gapperi*). High severity; left to right: Black-backed woodpecker (*Picoides arcticus*), American kestrel (*Falco sparverius*), deer mouse (*Peromyscus maniculatus*), Lincoln's sparrow (*Melospiza lincolnii*), moose, Canada warbler (*Cardellina canadensis*), red-backed vole (*Clethrionomys gapperi*), masked shrew.

Burn Ratio; a remotely sensed measure of combustion severity comparing two time points) is not apparent (Guindon et al., 2021). This is consistent for NWT (Figure 4; Supplementary Table S2). Despite 2023 having the largest total area burned and largest total number of fires in recorded history (Figure 5), there is no evidence of elevated dNBR in 2023 compared to previous years and no relationship between annual area burned or number of fires and burn severity as measured by dNBR (Figure 4). As such, we do not expect a proportional increase in the effects of severe fire during large fire years. However, the total area experiencing high burn severity will be greater simply owing to the larger total burned area. Almost 50% of the total burned area experienced severe combustion in 2023 in NWT (Figure 4) meaning that there is nearly 2 M ha of severely burned land that will experience various short-term and longer-term changes. Post-fire NBR (Normalized Burn Ratio; a remotely sensed measure of combustion severity) and dNBR are closely related to canopy combustion severity and can reflect belowground combustion as well although this relationship is less clear (Soverel et al., 2010; Whitman E. et al., 2019). While dNBR demonstrated some potential as predictor for burn depth in a study conducted in the larch forests of Northeast Siberia (Delcourt et al., 2021), Fraser et al. (2017) reported stronger predictions for their char fraction (designed to derive the extent of burning of the surface organic layer) using post-fire NBR. The latter study also indicated how drone-based imagery may assist in clearly defining at fine spatial scales the extent of mineral soil where the entire surface organic layer had been consumed, potentially offering a bridging solution to overcome challenges with predicting the extent of exposed mineral soil directly through satellite imagery (Hudak et al., 2007). Taken together, our understanding of the relationship between satellite-derived metrics such as dNBR and belowground combustion in the boreal forests is still somewhat limited. Additionally, we lack clarity on whether and how dNBR applies to short interval reburns, which limits the inference of these findings and our ability to understand temporal trends in belowground combustion severity.

Short-term effects of more severe burning

More complete belowground combustion (i.e., severe burning of the soil organic layer and tree roots) can result in marked structural changes to the forest with implications for wildlife habitat conditions (Figure 6). Specifically, more severe belowground combustion should accelerate post-fire tree fall because the combustion of tree roots and the organic soil supporting them compromises the structural integrity of the trees. Dead fallen vs dead standing trees alter post-fire regeneration conditions (e.g., *via* shading), fuel structure, decomposition, and wildlife use (Palm et al., 2022; Parker et al., 1984; Parro et al., 2015). For example, increased deadfall in burns, either immediately post-fire or as standing dead trees that fall down over time, is thought to impede movements of boreal caribou (caribou avoid burns from ~11–30 years post-fire; J. Hodson personal communication) and may be one of the mechanisms contributing to their avoidance of burns (Schaefer and Pruitt, 1991; Palm et al., 2022). More severe belowground combustion at the time of fire will accelerate tree fall and may therefore limit access to or movement through burns for a longer period of time and limit access to the protein-rich summer forage that caribou access in new burns. Combustion of roots and soil in 2023 was noticeably greater than in the next largest fire year in NWT (2014) and immediate post-fire tree fall was widespread, which was much less common in the 2014 fire season (J. Baltzer, personal observation).

Severe burning directly impacts wildlife. For example, Knaggs et al. (2020) tested for the effects of fire severity (the first 2 years post-fire) on a community of 42 landbird species nesting in the large 2014 Birch Lake burn complex and surrounding unburned areas in southern NWT. Functional diversity, based on life history traits (foraging and migration strategy and foraging, breeding, and nesting substrate), decreased with increasing fire severity. The same pattern emerged with species richness, but only in peatlands. Unburned peatlands had higher species richness than unburned uplands, but species richness became more similar across habitat types as burn severity increased (Knaggs et al., 2020). Density or occupancy models were generated for 20 species and 86% of them showed significant burn severity effects (positive or negative), sometimes depending on prior vegetation (i.e., uplands vs peatlands). For example, the Olive-sided Flycatcher showed higher densities in recent burns irrespective of fire severity, while the Common Yellowthroat (*Geothlypis trichas*) showed the opposite response. Other species, such as the Black-backed Woodpecker (*Picoides arcticus*) and Three-toed Woodpecker (*P. dorsalis*), benefit from the emergence of nesting substrate and food resources because of large numbers of standing dead trees the first few years post-fire (Knaggs et al., 2020). Clearly there are differences in species responses, and we have insufficient knowledge of the responses of most wildlife to severe burning. Moose may respond negatively in the short-term to burn severity. Post-fire forage availability and burn severity were not strongly related across different soil moisture classes in a <5-year-old fire in north-central British Columbia, and moose used areas of low and medium burn severity more than areas of severe burning (McNay et al., 2021).

There are few published studies evaluating effects of fire severity on boreal small mammals, but studies from temperate forests found that, in the short-term, generalist species like deer mice were more abundant in areas of high burn severity (Culhane et al., 2022; Fontaine and Kennedy, 2012), whereas species dependent on the litter layer such as shrews were most negatively affected (Culhane et al., 2022). Fires that severely burn vegetation cover and seed or berry crops (in tree crowns, seed banks, and live shrubs) had negative impacts on foraging behaviour of specialist small mammals (e.g., voles [*Microtus* sp.] and Albert's squirrel [*Sciurus aberti*]) but less so for generalist species (e.g., mice [*Peromyscus* sp.]) in a study in the southern United States (Morandini et al., 2023). In some cases, small mammal abundance does not differ across fire severity categories, but diversity and hence community structure are reduced after fires (Olson et al., 2003), especially after the most severe fires (Culhane et al., 2022). Terrestrial predators of small mammals like weasels select severe burns, which likely reflects greater availability of their preferred prey (deer mouse and meadow vole) in these areas (Volkman and Hodges, 2024). In contrast, Pacific marten (*Martes caurina*) favor lower severity burns which may reflect their need for areas with more abundant snags and downed woody debris for foraging and higher abundance of primary prey species like red-backed vole and red squirrel (Volkman and Hodges, 2024).

Because high severity burning generally results in greater loss of above- and below-ground biomass (Certini et al., 2021), severely burned areas are likely less suitable for amphibians and snakes owing to reduced cover and drier soil with more variable temperatures (Jager et al., 2021; Constible et al., 2001; Smith et al., 2001). Although lack of cover would typically increase predation risk to snakes, amphibians, and small mammals, it is possible that the risk from avian predators could be lower in severe burns with few or no remaining standing trees (i.e., perches for raptors such as American kestrel [*Falco sparverius*]; Widén, 1994) and substantial downed wood that can serve as protective cover. Changes to aquatic habitat for amphibians (e.g., oxygen levels; water temperature; concentrations of ash, sediment and nutrients; loss of vegetation around wetlands) are also exacerbated with severe fire (Jager et al., 2021; Gomez Isaza et al., 2022; Santos et al., 2022; Beranek et al., 2023).

Although fire can help to create roosting habitat for boreal bats by damaging or killing large trees (e.g., Johnson et al., 2009), these trees must remain standing after fire. Accelerated post-fire tree fall due to severe burning, combined with less residual vegetation (i.e., fewer green islands) in severe burns, would likely result in fewer roosts available on the landscape. Little brown myotis may be less impacted than northern myotis if they have access to alternate roosts (e.g., buildings). While reduction in vegetative clutter in forests can improve foraging opportunities for some bats (e.g., little brown myotis, big brown bat [*Eptesicus fuscus*]; Blakey et al., 2019; Low et al., 2024), severe burning can result in poor foraging habitat that is too open and well-lit for bats to fly (Jung, 2020). The short-term pulses in insect productivity that typically occurs after fire (Lacki et al., 2009; Malison and Baxter, 2010) are less likely to occur, or at least at a lower magnitude, in high severity burns with extensive combustion of above- and below-ground biomass; in fact, insect abundance may actually be lower post-fire (Dole et al., 2023). Few studies on the response of bats to fire have been conducted in the boreal forest where the availability of roost trees on the landscape is limited and bats' foraging opportunities are already constrained by high latitude. However, a large, severe wildfire in Yukon created large patches of homogeneously burned areas that had negative effects on little brown myotis (Jung, 2020). Most importantly, the fire resulted in the nearly complete loss of suitable roost trees: although dead trees (snags) remained in burned uplands, none of them were sufficiently large (≥30 cm diameter at breast height) to meet the roosting requirements of this species (Crampton and Barclay, 1998; Jung et al., 2004). Sites where at least some large standing trees remain are likely very important for the persistence of bats post-fire (Jung, 2020).

Long-term effects of more severe burning

More severe burning increases the likelihood of post-fire forest compositional change (typically conifer to deciduous) and even complete recruitment failure (i.e., forest to non-forest; Johnstone et al., 2016; Whitman E. et al., 2019; Baltzer et al., 2021). Severe canopy combustion can lead to the death or combustion of seeds in aerial cone banks, reducing rates of establishment post-fire (Reid et al., 2023; Splawinski et al., 2019). Likewise, more complete combustion of the soil organic layer alters seedbed conditions by exposing underlying mineral soil, favoring faster growing, broadleaf deciduous taxa over the historically dominant spruce species (Johnstone et al., 2016; Whitman E. et al., 2019; Baltzer et al., 2021). Indeed, modelled projections of these processes demonstrate strong likelihood of landscape level forest compositional changes at high latitudes from conifer to broadleaf deciduous in response to climate warming and increasing fire (Mekonnen et al., 2019; Micheletti et al., 2021). Forest compositional changes or loss attributable to severe combustion can be further compounded by fire in permafrost environments such as those of NWT where fire accelerates thaw. Specifically, burning, but particularly severe burning where there is more complete combustion of the soil organic layer that protects permafrost (i.e., ground perennially at or below 0 °C) drives rapid permafrost thaw (Talucci et al., 2024; Holloway et al., 2020). This can lead to a range of outcomes, but in thaw sensitive landscapes (e.g., permafrost peatlands), both forest compositional changes and net forest loss are possible in response to thaw (e.g., Lara et al., 2016; Baltzer et al., 2014). As described above, a transition from conifer to deciduous may favor moose and lead to habitat losses for mature conifer forest specialists like boreal caribou (Stewart et al., 2023) and squirrels. Boreal bats and other tree-roosting species are associated with large and/or dead trees, therefore recruitment failure because of severe burning that turns forest into non-forest (Johnstone et al., 2016; Whitman E.et al., 2019; Baltzer et al., 2021) would reduce the amount of available habitat. Similar responses are anticipated for the woodpecker community and all other species associated with mature forests. Deep burning also modifies the post-fire soil microbial community with implications for biogeochemical cycling and plant community composition and dynamics, adding complexity to projections of post-fire successional dynamics (Day et al., 2019; Whitman T. et al., 2019; Eckdahl et al., 2023; Eckdahl et al., 2024).

Boreal caribou is a species at risk for which we have a better understanding of long-term impacts of severe burning. During winter, boreal caribou avoid areas of higher burn severity for up to 30 years, whereas in summer they exhibit weak avoidance of high and low severity burn areas (Palm et al., 2022), or even similar selection to unburned forest (A. Kelly, personal communication). Areas selected within burns corresponded to areas with higher percent cover of lichens, and remaining lichen cover within burns was negatively related to burn severity (Palm et al., 2022; Pinno and Errington, 2016), highlighting the importance of variable burn severity and associated post-fire residual vegetation. Negative relationships between winter movement speeds of barren-ground caribou and burn severity have also been found which may indicate greater foraging activity within areas of lower burn severity. However, movement speeds in all burns were still higher than in unburned forests suggesting recent burns were primarily used for movement rather than foraging (Rickbeil et al., 2018). On the other hand, moose may benefit from high severity fires, though this appears to depend on time after fire and time of year. Moose forage biomass was up to three times greater in high severity burns than low severity burns in a 14-year-old fire in Alaska, and moose consumed more forage biomass and a higher proportion of available forage in these high severity burns (Lord and Kielland, 2015). However, areas of lower burn severity may provide a combination of both forage and cover that favors use by moose. For example, in a 20-year old fire in Alaska, moose selected areas of low burn severity in winter, and high burn severity in summer (Brown et al., 2018).

Lower severity burning leads to greater likelihood of self-replacement in conifer stands (Baltzer et al., 2021). Notably, spruce establishes well on thicker residual soil organic layers, which is not the case for faster growing broadleaf deciduous trees or pine (Johnstone et al., 2010a; Baltzer et al., 2021). Lower severity fire also corresponds with a greater frequency of residual vegetation (i.e., "green islands"; Perera et al., 2009), which may enhance landscape connectivity of burned areas, helping to accelerate regeneration, maintain structural diversity, and promote use by species known to avoid wildfires (reviewed in Sommers and Flannigan, 2022). For example, boreal caribou have been shown to use residual patches within burns for calving demonstrating their importance in reducing impacts of fire on this species (Skatter et al., 2017).

Similarly to the short-term effects, many of the longer-term effects of fire on ground-dwelling, less mobile species described earlier (see "Area burned and fire size") will be more pronounced with higher severity burning. Widespread combustion of features that these species use as refugia, like logs, hollow trees or burrows, could slow or prevent the recovery of local populations (Robinson et al., 2013) and potentially reduce their resilience to future fires. Species dependent on cool, moist microhabitats, like wood frogs, may show reduced persistence and time-lagged declines in occupancy, especially where a large proportion of their terrestrial habitat is severely burned (Bailey et al., 2025; Hossack et al., 2013; but see Hunter, 2022). Changes to amphibian breeding wetlands (e.g., productivity, hydroperiod, contaminants) are more dramatic when burning is severe (dos Anjos et al., 2021; Gomez Isaza et al., 2022).

In summary, critical impacts of severe burning in the short term relate to post-fire forest structure that affects landscape permeability, availability of large snags for roosting and foraging, and protective cover from predators and thermal variation. Longer term land cover changes associated with severe burning (i.e., conifer to broadleaf deciduous) will favor some species and disadvantage others, altering the structure of terrestrial wildlife communities in similar ways as large fires but likely more consistently reinforcing forest compositional change than is the case for large fires.

Short-interval reburning

Young forest stands have historically served as natural fire breaks owing to fuel limitations (Thompson et al., 2017) and less flammable fuel types (Hanes et al., 2020), which has resulted in

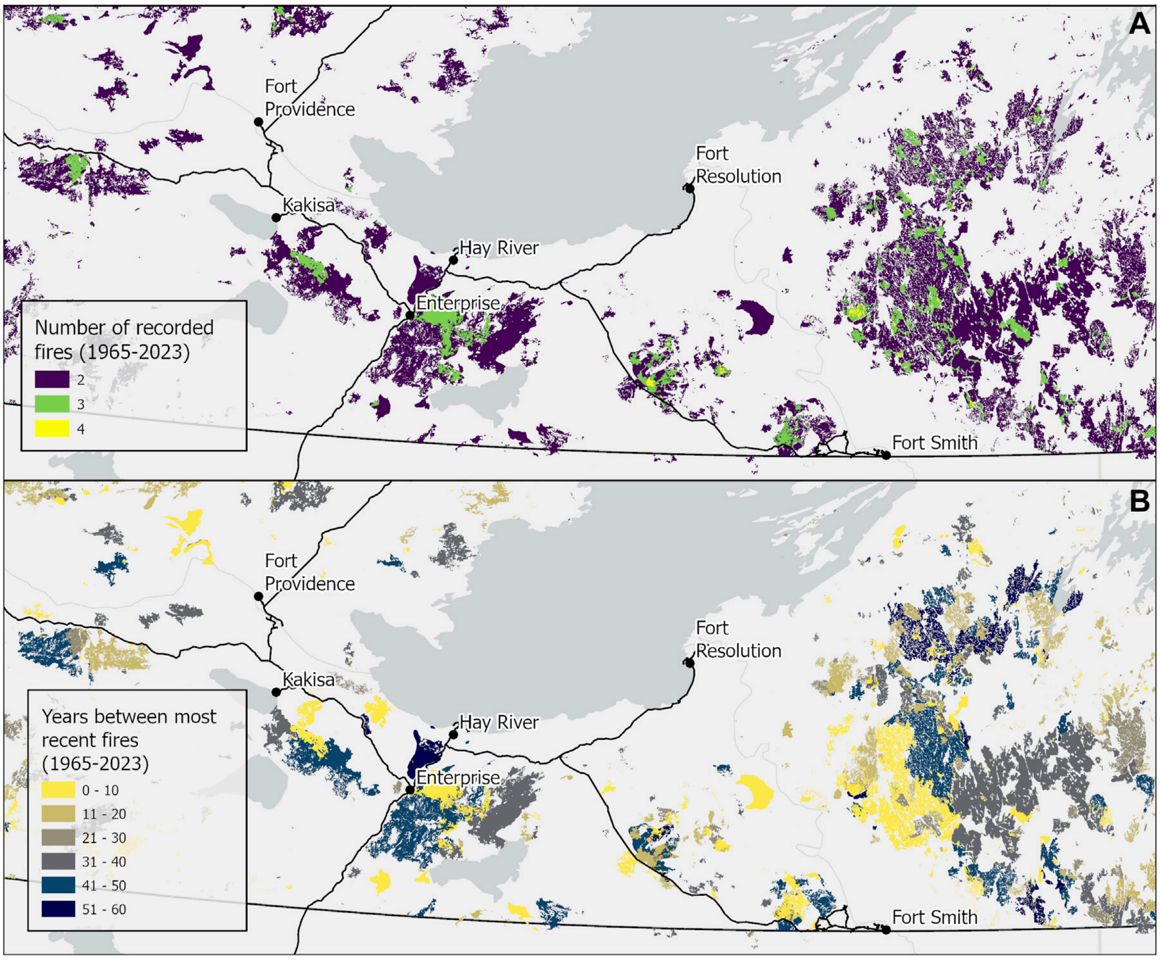

FIGURE 7
Short-interval reburning in the South Slave and Dehcho regions of the Northwest Territories where this was most common in 2023. **(A)** shows the fires in each area since 1965 when the recorded fire history for this region begins. **(B)** shows the fire return interval in the same region where fire return interval is less than 60 years.

strong fire self-regulation on the landscape (Heon et al., 2014; Prichard et al., 2017). Climate drivers are leading to extreme fire weather that reduces this fire self-regulation mechanism (Whitman et al., 2024). This was evident in NWT in 2023 with more than 400,000 ha of forested land experiencing short-interval reburning (i.e., reburning after only 20 years; Figure 7). There is evidence that short-interval reburns (forests younger than 20 years) have been increasing slightly through time from about 2% to 5% of annual burned area in Alaska since the early 1990s (Buma et al., 2022). In contrast, approximately 10% of forest that burned in 2023 in NWT was <20 years old (400K ha short-interval reburn in 4 M ha of total burned area), more than double the reported maximum proportional burned area as was found in Buma et al. (2022). This is in keeping with evidence that short-interval reburning can become much more common during hot, dry fire seasons (Heon et al., 2014; Whitman et al., 2024). In 2023, short-interval reburning occurred across a diversity of landscape positions from treed wetlands to dry upland forests (Figure 8) with implications for forest composition, structure, and function and the wildlife using these lands.

Short-term effects of short-interval reburning

Short-term consequences of short-interval reburning may mirror those of high severity burning for several taxa. These include more complete combustion of material legacies including the soil organic layer (Hoy et al., 2016; Walker et al., 2018; 2019) and standing and downed woody debris (Turner et al., 2019), as well as delayed regrowth of vegetation (Day et al., 2020; Hollingsworth et al., 2013). These changes will create challenging conditions for wildlife species requiring soil moisture, standing trees, vegetation structure, and cover (e.g., amphibians, red-sided garter snake, bats, woodpeckers; Figure 9), with potential impacts on foraging, survival, reproductive success and dispersal (Bailey et al., 2025; Beranek et al., 2023; Bury, 2004; Doherty et al., 2022; Hossack et al., 2013; Howey et al., 2016; Mahony et al., 2022; Muñoz et al., 2019; Rochester et al., 2010; Russell et al., 1999; Schurbon and Fauth, 2003; Webb and Shine, 2008; Wilgers and Horne, 2007; Thomas and Jung, 2019; Jung, 2020; Grindal and Brigham, 1999; Patriquin and Barclay 2003; Henderson and Broders, 2008). Where short-interval reburning is

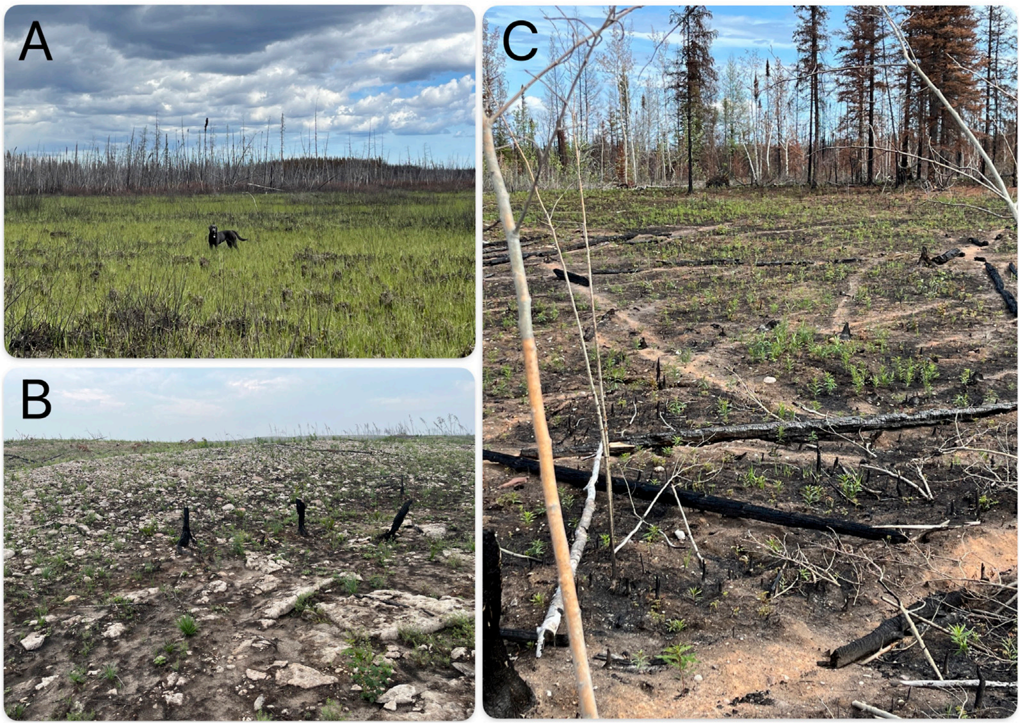

FIGURE 8
Pictures of short-interval reburns from the 2023 wildfires in Northwest Territories taken in summer 2024 demonstrating loss of material legacies. All locations burned in 2014 and reburned in 2023. Examples include **(A)** a treed fen near Kakisa, NWT; **(B)** a dry, upland forest near Fort Smith, NWT; and **(C)** a mesic forest near Hay River, NWT. In **(C)** note the "shadows" of downed stems from the 2014 fires that were combusted during the 2023 fires. Photo credits: J. Baltzer.

low severity, we expect more woody biomass to remain on site, including live trees in many cases and the soil organic layer should be more intact. As such, the short-term consequences of short interval fire will depend strongly on the severity of that fire.

Long-term effects of short-interval reburning

In the longer term, short-interval reburning has a variety of consequences for regeneration. When fires are too close together in time, reproductive structures (cones, rhizomes) are damaged or destroyed causing forest compositional change, commonly conifer to broadleaf deciduous forest, or with multiple short-interval fires, failed regeneration leading to shrub thickets or grassland (Hayes and Buma, 2021; Whitman E. et al., 2019). Short-interval reburning results in more complete combustion of the soil organic layer (Hoy et al., 2016; Walker et al., 2018; 2019), which negatively impacts rhizomatous species and can lead to a shift toward reproduction from off-site seed sources (Day et al., 2020; Hollingsworth et al., 2013), leading to longer vegetation recovery times. These changes may not be unprecedented in the history of this area. Indeed, there is evidence from paleoecological studies that more widespread burning has reduced forest cover dramatically in the past (e.g., Girardin et al., 2024). Whether the type of short interval burning we are seeing today will move the system back toward this state is uncertain but initial reconnaissance in the southern NWT suggests that transitions from forest to prairie or aspen parkland ecosystems may be common in response to short interval reburning in southern NWT (Figures 10a,b). Where short-interval reburning is low severity, there may be many live trees remaining (e.g., Figure 10c) and recovery of ground vegetation may be much more rapid owing to the maintenance of on-site seed sources and intact belowground structures. However, very few data are available for either short or long-term impacts of short interval burning, the variability in its outcomes, or the vegetation conditions that are most likely to support this fire behaviour. This is a major gap in our understanding of changes in fire behaviour.

Forest compositional change, longer recovery time, or failed regeneration due to short-interval reburning would have direct consequences for the wildlife taxa that rely on mature conifer forests. Reduced conifer forest recovery on the landscape would decrease habitat availability for species reliant on that forest type for all or part of their resource requirements. For example, as lichen biomass in NWT forests may take more than 70 years to recover to half that found in late-successional forests (Greuel et al., 2021), decreasing fire return intervals will for the most part lead to a loss of winter habitat for boreal caribou. In contrast, short-interval reburns leading to conversion from conifer to broadleaf deciduous stands may benefit species such as moose that predominantly forage on deciduous browse during winter (Fisher and Wilkinson, 2005; Maier et al., 2005); however, burns in peatlands may not lead to an increase in food availability for moose (DeMars et al., 2019). Similarly, conversion to grasslands associated with recruitment failure may

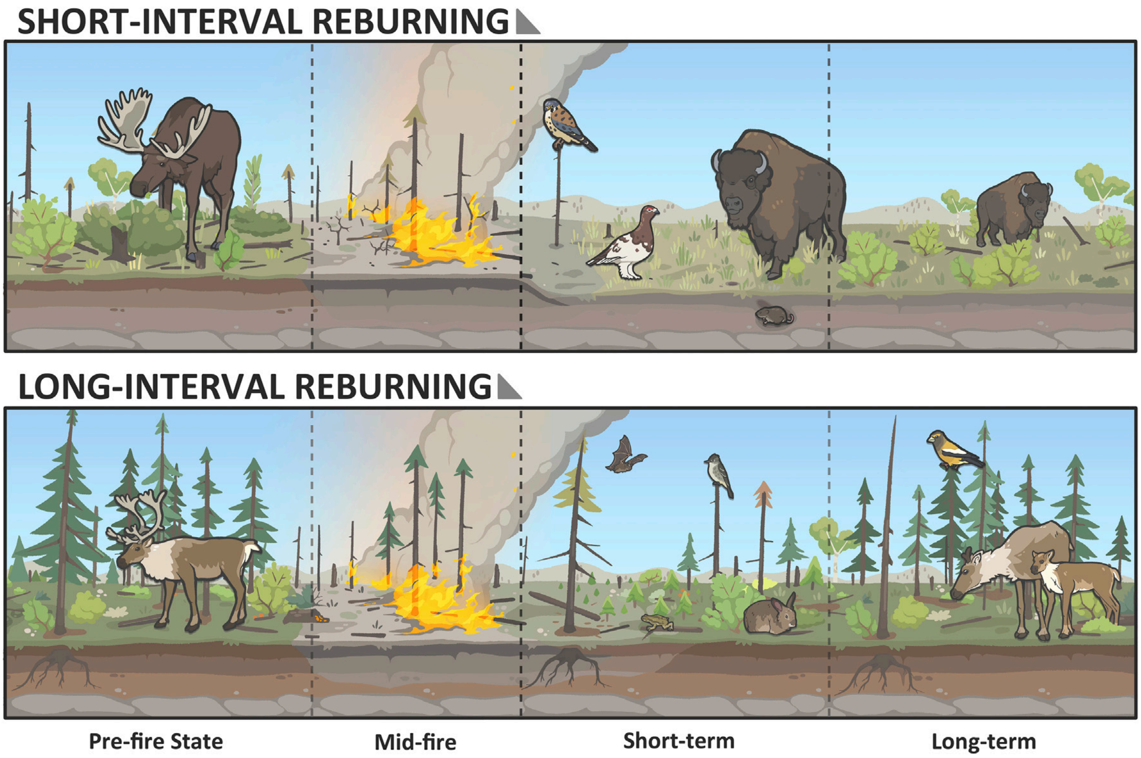

FIGURE 9
Illustration of an example of the effects of the interval between burns on forest structure and associated boreal species. Repeated burns combust trees' reproductive structures (cones, rhizomes) and the soil organic layer and shift the plant community towards grass/shrublands and animal species that occupy them, such as: American kestrel *(Falco sparverius)*, meadow vole (*Microtus pennsylvanicus*), and as shrubby cover regenerates, willow ptarmigan (*Lagopus lagopus*) and wood bison (*Bison bison athabascae*). A longer interval between burns increases the likelihood and speed of recovery to the original plant community and leaves more ground cover/litter and residual standing trees. These trees are vital for perching and foraging for olive-sided flycatcher (*Contopus cooperi*) and roosting for little brown myotis (*Myotis lucifugus*). Species such as boreal chorus frog (*Pseudacris maculata*) and snowshoe hare (*Lepus americanus*) are dependent on the remaining/regenerating cover. Return to coniferous-dominant forest will favour species such as evening grosbeak (*Coccothraustes vespertinus*) and boreal caribou (*Rangifer tarandus caribou*).

benefit wood bison (*Bison bison athabascae*) that prefer to forage on grasses and sedges (Larter and Gates, 1991; Redburn et al., 2008) and meadow voles whose abundance and survival is positively correlated with grass cover (Adler and Wilson, 1989). Black bears (*Ursus americanus*), which are a generalist omnivore species, may also benefit from conversion to grasslands or deciduous vegetation as they tend to consume grasses, forbs and deciduous plants during spring and summer (Mosnier et al., 2008; Romain et al., 2013; Lesmerises et al., 2015; Jorgensen, 2021). Black bears tend to shift towards using younger conifer-dominated stands later in the summer and fall (Tomchuk, 2019), likely reflecting greater availability of berries in these habitats (Nelson et al., 1983; Tomchuk, 2019), and bears may thus benefit from shorter-interval reburns if they increase the prevalence of these stands on the landscape. When short-interval reburning is not stand replacing, fire will remove ground fuels and can leave an open canopy of mature trees, a fire behaviour that commonly occurs in mature jack pine stands (Figure 10c; Stocks, 1989). Anecdotally, many of these stands support high biomass of caribou lichen (J. Baltzer pers. obs.; M. Parisien pers. comm.), which would be beneficial for caribou winter habitat.

Repeat burning can also reduce the quality of habitat conditions in fresh burns by consuming material legacies from the previous fire. Notably, short-interval reburning can lead to the complete combustion of standing and downed woody debris, which reduces protective cover and habitat for a variety of wildlife and modifies the regeneration microenvironment dramatically for plants (Figure 8). For example, although snowshoe hare favour deciduous browse during winter, their need for protective cover (usually provided by conifer forest) might preclude them from benefiting from widespread conversion to deciduous-dominated stands or shrublands (Hutchen and Hodges, 2019). Similarly, lynx (*Lynx canadensis*) avoid travelling through open areas in recent burns and rely on the presence of preferred prey (snowshoe hare) meaning likely avoidance of short-interval reburns (Vanbianchi et al., 2017). Predators that rely on downed woody debris for subnivean access to prey and shelter, such as American marten (Viau et al., 2024), would also likely be negatively impacted.

Landbirds associated with mature forests such as Canada Warbler (*Cardellina canadensis*) (Reitsma et al., 2020) and Evening Grosbeak (*Coccothraustes vespertinus*) (Gillihan and Byers, 2020) are expected to experience important nesting habitat loss in response to shorter fire return intervals. The Olive-sided Flycatcher (*Contopus cooperi)* is an aerial insectivore often

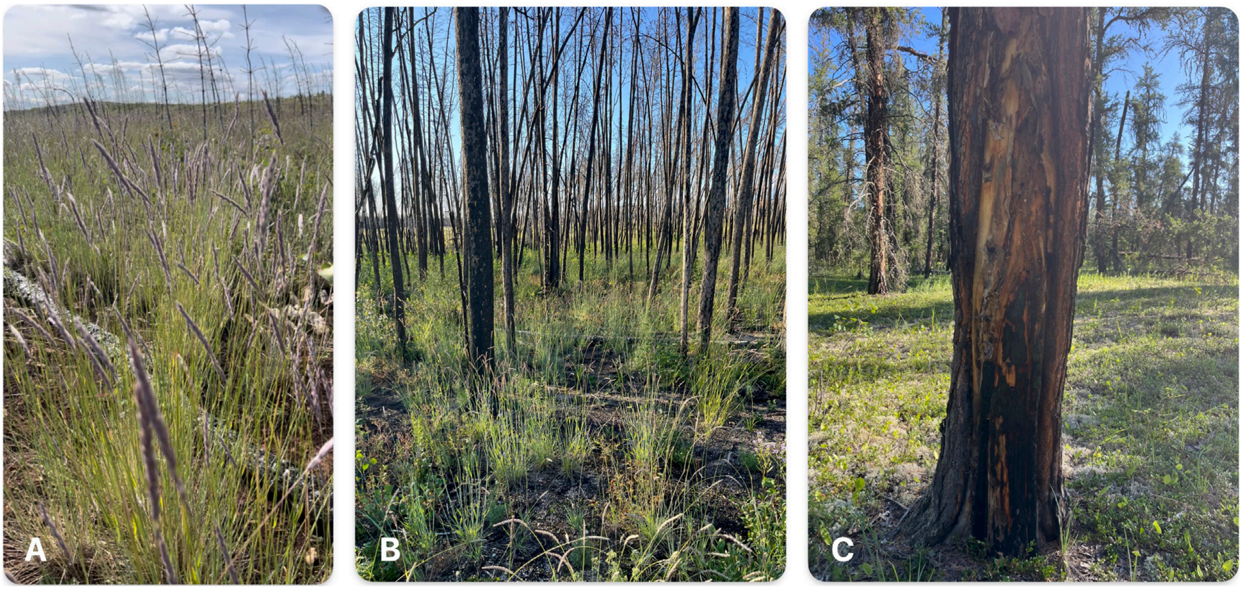

FIGURE 10
Short-interval reburns that occurred in the 2023 fire season near Fort Smith, Northwest Territories. Panels **(A)** and **(B)** depict stands that were forested pre-fire but show little evidence of tree regeneration and appear to be transitioning to grasslands dominated in this case by wild rye (*Elymus innovatus*) though other graminoid taxa can also be common. **(C)** shows a jack pine tree (*Pinus banksiana*) with multiple fire scars indicating repeated low severity (i.e., not stand-replacing) burning. The forest is open with groundcover dominated by caribou lichen (*Cladonia* spp.) and lingonberry (*Vaccinium vitis-idaea*). Photo credits: J. Baltzer.

considered a "fire specialist", but it also thrives at mature coniferous/recent burn ecotones and open mature conifer stands (Altman and Sallabanks, 2020). Thus, the anticipated loss of these edges and adjacent mature stands owing to very large fires and short fire return intervals will likely result in important breeding habitat loss for this species and other species associated with mature forests. For example, the entire woodpecker community will likely also experience important declines owing to loss of standing snags critical for feeding and nesting. Similar responses are anticipated for other species (e.g., bats and northern flying squirrels) using large, mature and dead trees (Senior et al., 2021; Loeb and Blakey, 2021). Similarly, woody debris used by amphibians and reptiles for habitat and refugia (Robinson et al., 2013) may not be available if wildfire occurs too soon after the last fire (Hossack and Pilliod, 2011), and deep accumulations of leaf litter used by amphibians can take years to recover from fire (Schurbon and Fauth, 2003). If more frequent large fires lead to a shift in the age-class distribution of the landscape towards higher prevalence of younger stands, we could see a shift in the boreal small mammal community towards dominance of early-successional or non-forest species like deer mice and meadow voles and lower populations of red squirrels.

In summary, most of the documented impacts of short-interval burning are those of loss of aboveground biomass and conversion of forests from conifer to broadleaf deciduous dominated or to a non-forested state. These changes will drive marked shifts in the wildlife community occupying areas of short-interval fire. However, the impacts, both short and longer term, are mediated by the severity of the fire (see Figure 11) such that low severity, short interval fire may have relatively modest or even beneficial effects in some cases.

Fire season length and timing

Fire season length and timing are changing in multiple ways across Canada and the broader boreal biome. Spring wildfires are increasing in many parts of Canada and are most common when snowmelt is early and/or under fire prone weather conditions (Albert-Green et al., 2013; Hanes et al., 2019; Parisien et al., 2023a). The frequency of overwintering fires is related to annual area burned with very large fire years corresponding with years having greater frequency of overwinter smouldering (Scholten et al., 2021). The 2023 wildfire season was no exception with western North America experiencing unprecedented numbers of overwintering fires (Baltzer et al., 2025). Late season burning is also increasing across boreal North America, a pattern that is particularly pronounced in the west (Kasischke and Turetsky, 2006).

Although there is limited information on how longer-, earlier-, and later-burning fire seasons will impact the boreal biome, there has been some investigation of early and late season fires in other ecosystems which may provide guidance for relevant research directions in boreal forests as fire season length and timing changes. For example, early season fires in grasslands can favor plant species that grow and reproduce later in the season, which could lead to plant community compositional shifts (reviewed in Knapp et al., 2009) with implications for wildlife forage. Potential short-term impacts of early season fires also include overlap in the timing of fire with peak reproductive times in some taxa. For example, wood bison begin calving in April (Jung et al., 2018; Species at Risk Committee, 2016) and most boreal caribou in NWT have their

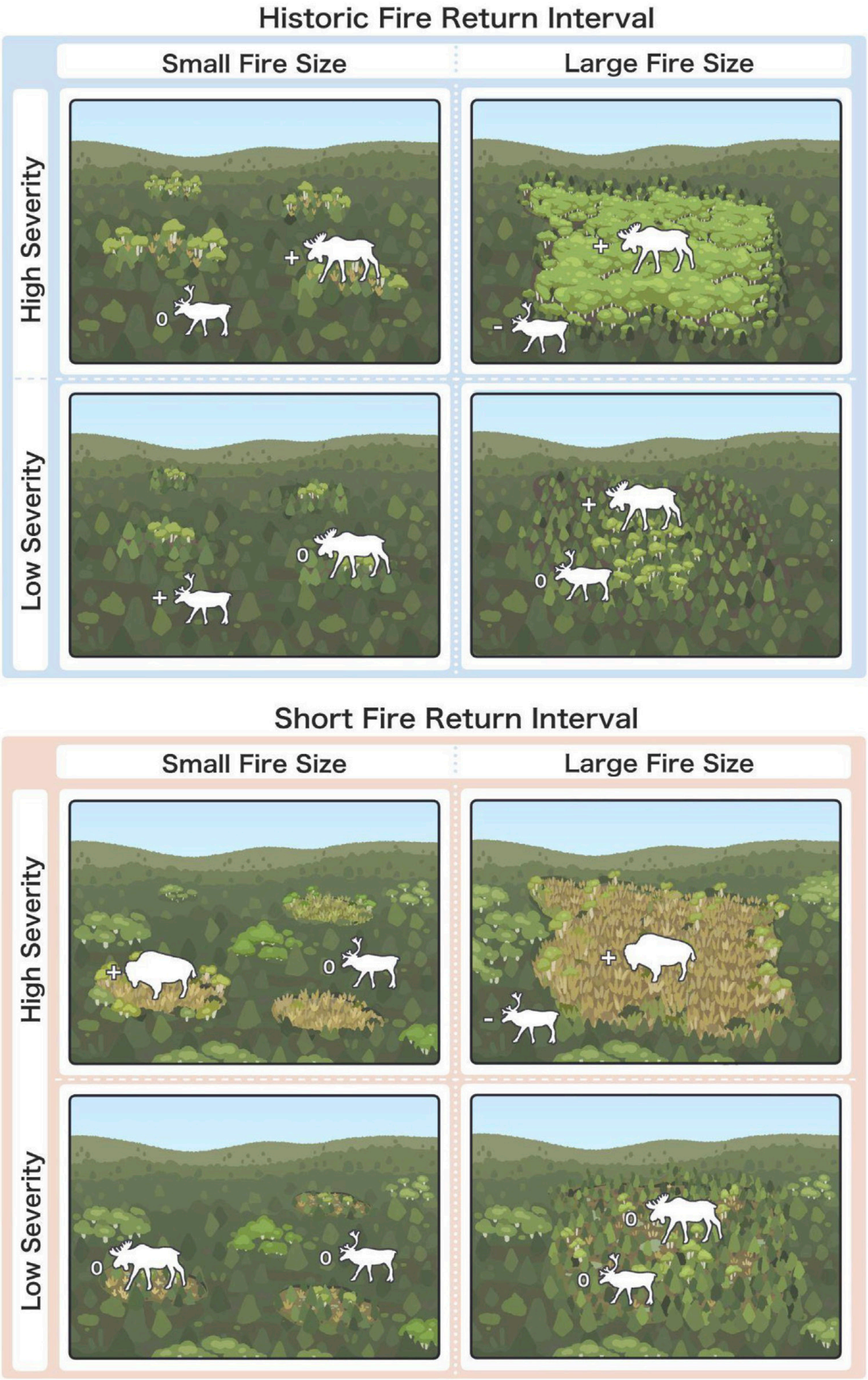

FIGURE 11
Illustration of expected long-term changes in forest landscape composition and patch structure in the NWT under different combinations of burn severity (High vs Low), fire size (Large vs Small), and fire return interval (Historic vs Short). Examples of corresponding changes in abundance (increase (+), decrease (–) or remain unchanged (‘o’)) of large terrestrial mammals - boreal caribou (*Rangifer tarandus caribou*), moose (*Alces alces*) and wood bison (*Bison bison athabascae*). For example, under a fire regime consisting primarily of large, high severity fires that reburn within short intervals (<20 years), we expect to see an increase in the prevalence of grassland and open shrubland habitat, with corresponding increases in wood bison abundance, and decreases in boreal caribou abundance. Under a fire regime consisting primarily of large, high severity fires that reburn at historic intervals (70–100 years), we would expect to see a higher prevalence of deciduous stands, with a corresponding increase in moose abundance and decrease in boreal caribou abundance.

calves during May (Species at Risk Committee, 2022). While caribou calves quickly become mobile after birth, they may be particularly susceptible to mortality from early season fires as they tend to remain at the calving site for about 1 week postpartum (Gustine et al., 2006). Negative impacts can also be expected for resident birds (early breeders) and add physiological stress to arriving migratory birds. However, investigations of fire timing on mobile organisms in other systems suggest that these animals may simply avoid the disturbance (e.g., Murphy et al., 2009). For less mobile or hibernating taxa, early and late season and overwintering fires may have more disruptive effects. Snakes and amphibians may experience higher mortality rates if they encounter wildfire during a season when they are more exposed and vulnerable (Beaupre and Douglas, 2012; Cross, 2015), for example, red-sided garter snakes when migrating between their underground hibernation sites and wetland foraging areas in the spring and fall (Gregory and Stewart, 1975; Larsen, 1987). Wood frogs and boreal chorus frogs overwinter in a dormant state, in shallow micro-sites such as leaf litter, vegetation, or under cover objects such as logs and rocks (MacArthur and Dandy, 1982; Regosin et al., 2003) and would probably be killed if exposed to any out of season fire that overlaps with their dormant period. Certain species' overwintering strategies may offer some protection from the direct impacts of early and late season fires in the boreal forest. Animals overwintering underground (e.g., toads in burrows; red-sided garter snakes in dens; bats in caves or crevices) are likely buffered from the effects of fire at the surface. However, during intense fires, amphibians in underground burrows can still be harmed or killed (Beranek et al., 2023; Mahony et al., 2022), as can snakes (Cross, 2015; González-Fernández et al., 2024; Jordaan et al., 2020; Smith et al., 2001). Hibernating bats respond to fire-related cues such as smoke (Dickinson et al., 2010; Doty et al., 2018) and could experience energetically costly arousals from torpor. Where many individuals overwinter communally together in a single location (e.g., toads, red-sided garter snakes, bats), any harmful effects of fire that do occur have the potential to impact a large part of the population simultaneously (e.g., Shine et al., 2001).

As outlined above, many of the anticipated impacts of out of season fires are acute leading to mortality. The short-term impacts of out-of-season fires will almost certainly relate to their timing and severity. There is the potential for late season fires to burn more deeply owing to complete seasonal thaw and low late season soil moisture (Kasischke and Turetsky, 2006). Impacts of this would presumably be similar to severe burning described above. Spring wildfires occur when the forest, particularly deciduous taxa, have not had a chance to fully rehydrate, providing a ready source of fuel. As such they can be very fast moving and may result in large burn areas (reviewed in Parisien et al., 2023b). The longer-term impacts of changes in fire season length and timing and increased frequency of overwintering fires include changes in forest composition and may favour regeneration of deciduous trees (Baltzer et al., 2025); responses of wildlife taxa to these changes have been elaborated on above. That said, we have little information on the impact of out-of-season fires and effort should be made to understand responses of land cover and associated wildlife to this increasingly important fire behaviour.

Synthesizing impacts and help for planning

Novel wildfire conditions are altering boreal landscapes and ecosystems, creating challenges for northern communities and lifestyles, particularly through impacts on the safety and security of country or subsistence foods and threatening biodiversity and species at risk, with implications for ecosystem functions. Northern communities and governments require information to support adaptation planning in response to these changes. The preceding sections offer us a range of possibilities about the future of wildlife community structure under changing wildfires in northern boreal forests. We have synthesized what we see as likely outcomes to landscape scale changes resulting from changing wildfire based on published studies and experience of the authors in these systems and with the taxa that were considered (see Figure 11 for important large ungulates and Table 1 for a complete list of assessed taxa). However, these possible outcomes are difficult to use directly in planning owing to uncertainties arising from potential feedbacks between fire and landcover conditions as well as insufficient information on the responses of many northern taxa to wildfire. For example, will the increase in high severity burns and decrease in reburn interval cause widespread declines in bats, birds, snakes, small mammals, and boreal caribou because the boreal ecosystem will have widespread conversion to grasslands due to tree regeneration failures? Or will this ecosystem conversion indeed occur, only in a small fraction of the area, resulting in quantitatively modest changes to the wildlife? If these changes are widespread, when would these declines become more important, what might be the population impacts and the implications on the conservation status of different northern wildlife taxa? In the example of short-interval reburn, does this fire behaviour create a positive feedback with areas reburning ever more quickly, or does this lead to an eventual negative feedback with fewer fires by the end of the century owing to fuel limitation (e.g., Marchal et al., 2020) thereby stabilizing observed changes? Given the many outstanding questions reviewed above there is much work to do and we suggest three paths forward for wildlife-wildfire research in northern boreal regions that would help to fill key knowledge gaps and provide information in support of adaptation planning.

The first path is to make better use of existing and ongoing monitoring programs (collar data, cameras, audio recording units (ARUs), small mammal monitoring, studies of land cover change, *etc.*) to understand responses of northern wildlife to fire age, severity, and frequency, and where needed expand monitoring programs. Outside of boreal caribou and, to a lesser extent barren-ground caribou, there is limited information on population responses to wildfire and post-fire habitat selection for other large herbivores, including moose, muskox, and bison, all three of which are important to northern ecosystems and communities. Responses of furbearers, including semi-aquatic furbearers like beaver and muskrat, bears, and other predators were other major gaps. While existing individual-based collaring programs for bison and moose could be leveraged to fill knowledge gaps for these species, filling knowledge gaps for other less well-studied northern boreal species will require expanding research and monitoring initiatives. While there is comparatively better understanding of boreal caribou and barren-ground caribou responses, more work could be done for

TABLE 1 Summary of expected changes in components of the NWT fire regime under climate change, resulting long-term (e.g., next 100 years) likely changes in composition and structure of forests at landscape and stand scales, including implications for wetlands, and examples of expected changes in abundance of terrestrial wildlife species based on our review of literature. Wildlife species for which it was uncertain whether the direction of change would be predominantly negative or positive are not included.

<table>
<tr><td>How is the fire regime expected to change?</td><td colspan="3">• Longer fire season
• Higher total annual area burned
• More large fires
• Larger annual area affected by high severity burns
• More short interval re-burns</td></tr>
<tr><td>What is the long-term expected outcome for vegetation composition and landscape / stand structure?</td><td colspan="3"><i>Landscape-scale</i>
• Lower proportion of late-seral conifer dominated stands
• Lower proportion of older age class forests overall
• Higher proportion of deciduous and mixedwood stands
• Higher proportion of grasslands and shrublands
<i>Stand-scale</i>
• Less downed woody debris and standing deadwood
• More open canopy and understory
• Reduced leaf litter / organic layer accumulation
• Lower soil moisture and higher surface temperatures
<i>Wetlands</i>
• Less residual riparian forests following fire
• Less unburned vegetation/forest connecting wetlands
• Increased water temperature
• Lower dissolved oxygen
• Higher concentrations/loads of ash, sediment and nutrients
• Shorter hydroperiod</td></tr>
<tr><td rowspan="4">How will abundance of different wildlife species change as a consequence at the landscape scale?</td><td>Species group</td><td>Increase</td><td>Decrease</td></tr>
<tr><td>Mammals</td><td>• Deer mouse
• Meadow vole
• Meadow jumping mouse
• Moose
• Weasel sp.
• Wood bison</td><td>• American marten
• Boreal caribou
• Barren-ground caribou
• Little brown myotis
• Lynx
• Northern flying squirrel
• Northern myotis
• Red-backed vole
• Red squirrel
• Shrew sp.
• Snowshoe hare</td></tr>
<tr><td>Birds</td><td>• Alder Flycatcher
• American Robin
• Chipping Sparrow
• Dark-eyed Junco
• Lincoln Sparrow
• Ruffed Grouse
• White-crowned Sparrow
• Willow Ptarmigan
• White-Throated Sparrow</td><td>• American Kestrel
• Bay-breasted Warbler
• Black-backed Woodpecker
• Boreal Chickadee
• Brown Creeper
• Canada Jay
• Canada Warbler
• Common Yellowthroat
• Evening Grosbeak
• Golden-crowned Kinglet
• Hermit Thrush
• Olive-sided Flycatcher
• Ruby-crowned Kinglet
• Rusty Blackbird
• Spruce Grouse
• Swainson's Thrush
• Woodpecker sp.
• Yellow-rumped Warbler</td></tr>
<tr><td>Reptiles / amphibians</td><td></td><td>• Boreal chorus frog
• Red-sided garter snake
• Wood frog</td></tr>
</table>

these species to compare habitat selection/use pre- and post-fire, responses to burn severity and short interval reburns, and on-the-ground work looking at caribou forage resources as a function of fire age and burn severity, tied to collar location data so we are actually sampling places that we know caribou are either selecting or avoiding.

A second path is to take advantage of remote-sensing and other emerging technologies to model and map fire refugia and track broad-scale and, where possible, fine-scale changes in wildlife habitat in near real-time. Northern regions, including the NWT, present a unique opportunity for wildlife-wildfire research given the relatively low human footprint and more limited fire suppression activities, potentially allowing for wildlife responses to wildfire to be more easily parsed out from other anthropogenic impacts. At the same time, the extensive and remote landscapes make *in situ* research and monitoring costly and resource limitations will always result in some species being under-monitored and researched and necessitates the coupling *of in situ* habitat change studies with remotely sensed data products. Given these challenges, ongoing development, ground truthing, and application of remote monitoring tools for measuring habitat and landscape changes in a timely manner will be important. This includes mapping and modeling areas on the landscape that are more resilient to climate change and climate change impacts, including fire refugia.

A third path is to use what is learned and developed in paths one and two to forecast species responses to future wildfire and landscape change. Indeed, making projections i.e., predictions of the future followed by testing, is a valuable means of converting our inferential knowledge to reliable actionable science (Houlahan et al., 2017). One promising pathway for planners and decision makers when facing unprecedented and changing wildfires is offered by the Ecological Forecasting community (Dietze, 2017; Dietze et al., 2018; McIntire et al., 2022). Evidence is mounting that forecasting surprises us by showing that simpler models (e.g., “the null” or “less mechanism”) are better at forecasting than more sophisticated models with more parameters (Barros et al., 2023; Wheeler et al., 2024). Each of the inferences outlined in this review can become part of quantitative forecasting efforts where we can evaluate multiple drivers and direct and indirect effects. For example, there have been initial attempts to build forecasts for these ecosystems with *some* of the processes and species outlined here (e.g., landbirds (Raymundo et al., 2024), and boreal caribou (Stewart et al., 2023)). Further investigations demonstrated that a forecasted increase in area burned caused only a modest forecasted change in landbirds, and that this effect was much smaller than direct climate effects (Micheletti et al., 2023). With this new knowledge, planners can see trade-offs more clearly and prioritize actions now to deal with the changing fire regimes in the context of other environmental changes.

In conclusion, there is an urgent need to improve our understanding of the impacts of the novel burning conditions experienced in 2023 on northern habitats and the associated wildlife communities. Some of the largest unknowns relate to the direct effects of the changing fire regime on wildlife taxa necessitating additional baseline data collection to better understand these impacts. Indeed, aside from some species at risk, long-term monitoring of northern wildlife populations is highly limited, negatively impacting our ability to accurately anticipate the impacts of increasing wildfire or other changes. Implications of climate change and wildfire-mediated boreal vegetation transitions for species range shifts and invasions is another major unknown. The development of ecological forecasting tools to anticipate both landcover changes and associated impacts on wildlife will be essential for informing conservation and management actions. Given the important knowledge gaps and risks associated with all this uncertainty, there is a great need to set wildlife research and monitoring priorities based on contributions of all co-management partners across the NWT and beyond, and to better coordinate resource allocations for more effective co-production of knowledge to inform wildlife conservation in a changing world.

Author contributions

JB: Conceptualization, Writing – original draft, Writing – review and editing. SH: Conceptualization, Writing – original draft, Writing – review and editing. JH: Conceptualization, Writing – original draft, Writing – review and editing. MA: Formal Analysis, Visualization, Writing – review and editing. SC: Visualization, Writing – review and editing. MC: Formal Analysis, Writing – review and editing. EM: Writing – original draft, Writing – review and editing. AM: Conceptualization, Writing – review and editing. ER: Visualization, Writing – review and editing. MT: Conceptualization, Writing – review and editing. JvdS: Formal Analysis, Visualization, Writing – review and editing. JW: Visualization, Writing – review and editing. BW: Conceptualization, Writing – review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Highlighting the role of biota in feedback loops from tundra ecosystems to the atmosphere

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The rapid climatic and environmental changes observed in the Arctic and across the globe in general call for reliable model projections. In recent years our understanding of ongoing and future changes through ecosystem modelling has increased tremendously. Yet, most ecosystem models do not consider many of the feedback loops at play in natural ecosystems. Particularly those influenced by biota, beyond vegetation and to some extent microbes, are often neglected. As a first step towards a better integration of biotic influences into ecosystem models, we provide a broad overview of the various ways biota may influence feedback loops between the high-latitude biosphere and the atmosphere. We focus specifically on three key feedback loops between tundra and atmosphere (carbon dynamics, albedo and permafrost thaw) and the influences of three key ecosystem compartments (vegetation, decomposers and herbivores) on these. The influences of biota on ecosystem feedback loops are multifaceted and may appear patchy in both space and time. However, biota may still play important roles in modulating ecosystem feedback loops, and by including these dynamics into ecosystem models, magnitude, accuracy and credibility of model projections are likely to improve.

KEYWORDS
albedo, arctic, biotic interactions, carbon dynamics, decomposers, herbivores, permafrost, vegetation

1 Introduction

Nowhere else is climate change more apparent than in the Arctic (IPCC, 2021). Because of the long-term and gradual increase in surface air temperatures, loss of snow cover, and permafrost thaw associated with arctic amplification concentrating heat at the poles (Previdi et al., 2021), the arctic biophysical system is now experiencing unprecedented change (Box et al., 2019; Post et al., 2019). In addition to the gradual changes in climate, the Arctic is also experiencing an increase in the intensity, frequency and duration of extreme or erratic events that are directly or indirectly related to weather and climate (Christensen et al., 2021; Descals et al., 2022; Landrum and Holland, 2020; van Beest et al., 2022). The combined impacts of gradual and erratic climate change on the structure and functioning of the biotic components in tundra ecosystems is suspected to have repercussions that extend far beyond the Arctic (Box et al., 2019), not least due to the vast amounts of carbon stored in the circumarctic permafrost region (Palmtag et al., 2022). Over the past few decades, observations and modeling studies have provided compelling evidence that the northernmost regions of the world are experiencing some of the most pronounced and rapid changes in climatic conditions, resulting in pervasive changes to the structure and functioning of the biotic components of the ecosystems. Such changes can in turn influence the magnitude of the feedback loops between the tundra ecosystem and the climate system (Box et al., 2019; Post et al., 2019) that may either amplify or diminish the warming trend. The changes observed in high-latitude ecosystems may therefore have global implications.

Tundra ecosystems are characterized by low productivity, low nutrient availability and low species diversity (Callaghan et al., 2013), yet biotic interactions in the Arctic may still be rather complex (Schmidt et al., 2017). Exposed to the dramatic climatic changes in the northernmost parts of the world, the impacts on tundra ecosystems are numerous, ubiquitous and well-documented, and include changes in phenology (Parmesan, 2007; Roslin et al., 2021; Schmidt et al., 2023), demographic rates (Descamps et al., 2017; Iler et al., 2021; Schmidt et al., 2019) and shifts in distributional ranges (Gilg et al., 2012; Parmesan and Yohe, 2003; van Beest et al., 2023). High-latitude organisms, however, are not only *responding* to the changing climatic conditions: their physical properties, life histories and behaviors are also *influencing* processes of importance to the interplay between the tundra ecosystem and the atmosphere. However, compared to other parameters influencing feedback loops, such as the general global warming and changes in precipitation patterns (Bintanja and Andry, 2017; Rantanen et al., 2022), biotic influences are oftentimes patchier in both space and time. Yet, biotic interactions are still key determinants of how ecosystems respond to climate change (Blois et al., 2013; Post et al., 2023).

In this paper, we highlight the importance of biotic processes in amplifying or diminishing feedback loops between tundra ecosystems and the climate system. In doing so, we hope to guide future climate and ecosystem modelling studies in developing more accurate predictions of potential future trajectories of arctic ecosystems, which are currently hampered by our inability to adequately integrate the bidirectional and highly dynamic interplay between biotic and abiotic ecosystem components (Ripple et al., 2023). We synthesize current knowledge on key feedback loops between tundra ecosystems and the climate system operating in high-latitude regions, focusing on how these may be influenced by biotic processes. Specifically, we target three key feedback loops (albedo, carbon dynamics and permafrost thaw), each representing critical components of the high-latitude system and to its overall dynamics of change. In the following sections, we explore how biotic processes may influence each of these key feedback loops, directly as well as indirectly. By providing a broad overview of these processes, we aim to contribute to a better understanding of the key roles biotic interactions play in shaping tundra ecosystem responses to climatic changes, with particular focus on key processes that feed back to the global climate system.

2 Biotic processes relevant to feedback loops

The interplay between biota and albedo, carbon dynamics, and permafrost thaw in arctic ecosystems has profound implications for the global climate system. In the Arctic, surface reflectivity (i.e., albedo) is particularly important for this dynamic relationship, as diminishing ice and snow cover, as well as shifts in vegetation types towards taller, darker vegetation, contribute to increased absorption of solar radiation and increasing soil temperature, which in turn accelerates permafrost thaw. As the permafrost thaws, organic carbon sequestered over thousands of years becomes accessible to soil organisms. Organic matter decomposition in cold environments responds exponentially to increasing temperatures, hence driving a very effective conversion of soil organic matter to carbon dioxide (CO_2) or methane (CH_4), depending on the oxygen availability to the microbes, which is ultimately released to the atmosphere (García-Palacios et al., 2021; Maes et al., 2024). This creates a positive feedback loop that further amplifies warming. Simultaneously, surface reflectance is influenced by vegetation dynamics such as shifts in vegetation composition and plant phenology, which affects the energy balance directly (albedo, exchange of latent and sensible heat) and indirectly through the exchange of carbon across the soil-plant-atmosphere continuum. Hence, it is evident that biotic influences on ecosystem feedback loops are multifaceted and interlinked and that biotic influences may cascade through the ecosystem. Figure 1 summarizes the main interactions between the three main biotic compartments of the tundra ecosystem (decomposers, vegetation and herbivores) and their influences on the three key feedback loops examined in this paper.

3 Effects of vegetation on climate feedback loops

Arctic vegetation is characterized by low diversity, low stature and low productivity, owing to the generally harsh climatic conditions, short growing seasons and low availability of nutrients (Callaghan et al., 2004). Still, arctic vegetation plays a key role in the sequestration of carbon and forms a key interface between the ecosystem and the climate system (Epstein et al., 2012; Pearson et al., 2013), acting both as a carbon sink (photosynthesis) and as a carbon source (respiration).

3.1 Vegetation and carbon dynamics

During the growing season, the vegetation absorbs atmospheric carbon dioxide and converts it into organic carbon through the dominance of photosynthesis over respiratory losses (Figure 1: process 1). Arctic vegetation encompasses a diverse array of taxa, including mosses, lichens, shrubs, and graminoids, each exhibiting distinct carbon sequestration capacities and mechanisms (Huemmrich et al., 2013). Mosses and lichens, often forming a substantial part of arctic vegetation communities, both in terms of species richness and cover, have relatively low growth rates and biomass compared to vascular plants, such as shrubs and graminoids. As a result, they typically sequester less carbon from the atmosphere through photosynthesis during the main growing season. However, their ability to photosynthesize even at low ambient temperatures (Barták, 2014) and ability to supply themselves with nitrogen directly from the atmosphere (Rousk

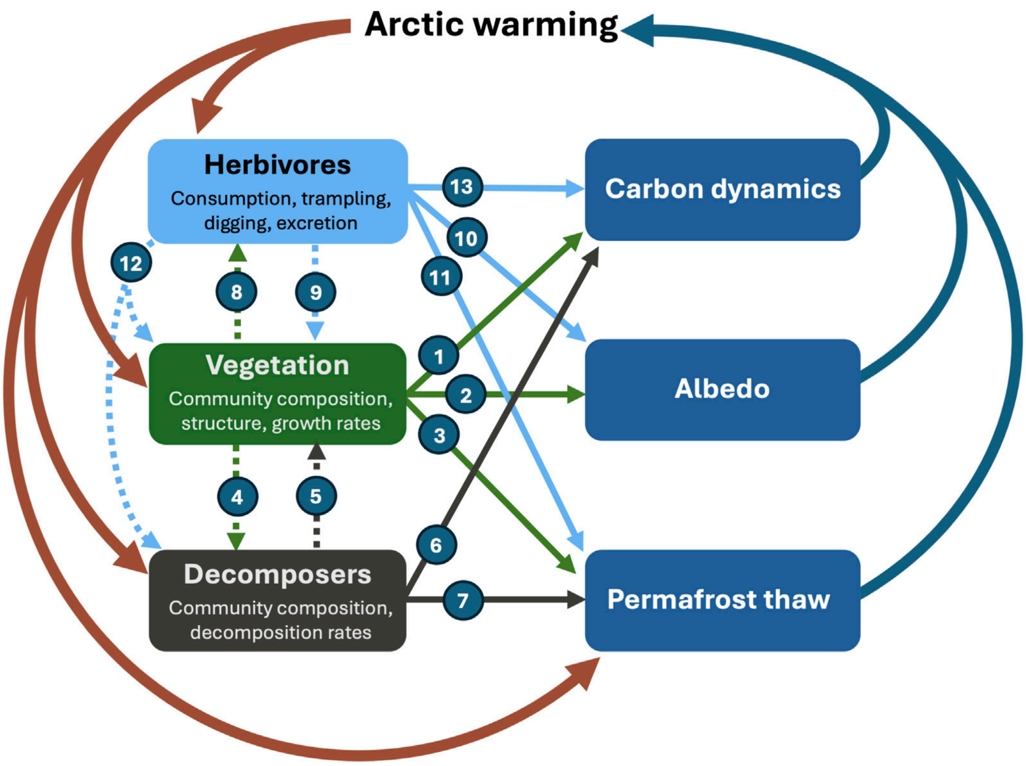

FIGURE 1
Conceptual figure showing the main processes linking the three key biotic components (decomposers, vegetation, herbivores) and the three key feedback loops (carbon dynamics, albedo, permafrost thaw) from the Arctic terrestrial ecosystem to the atmosphere. Full lines indicate direct influences of biota on feedback loops, while dotted lines indicate indirect influences of biota on feedback loops. Main processes include: 1. Vegetation community composition influencing carbon dynamics via photosynthesis and respiration rates; 2. Physical properties of vegetation community composition and structure influencing surface albedo; 3. Vegetation community composition and structure influencing snow-pack insulation capacity regulating soil temperatures and ultimately permafrost thaw; 4. Vegetation community composition influencing litter composition and in turn decomposer community and turn-over rates; 5. Soil community composition and process rates influencing nutrient availability to plants; 6. Decomposer community composition and decomposition rates influencing respiration rates; 7. Decomposer community decomposition rates influencing permafrost thaw; 8. Vegetation community composition influencing herbivore communities; 9. Herbivores influencing vegetation community composition and biomass; 10. Animals influencing surface albedo via trampling, digging and cratering; 11. Animals influencing permafrost thaw via disruption of snow cover and ultimately soil temperatures; 12. Animals influencing nutrient availability to the decomposer community via excretion and carcasses; 13. Herbivores influencing carbon dynamics via enteric methane emissions and respiration.

et al., 2017), suggests that they contribute significantly to the overall carbon balance in the Arctic (Street et al., 2012). Conversely, with their higher growth rates and biomass compared to mosses and lichens (Mekonnen et al., 2021), shrubs have a higher capacity to take-up carbon during the growing season (Andreu-Hayles et al., 2020). Because of the changing climatic conditions and the concomitant environmental changes (Box et al., 2019), shrubs are currently expanding across the Arctic (Myers-Smith et al., 2011), particularly in the low arctic regions (Elmendorf et al., 2012a) and at the boundary between the low and high Arctic (Myers-Smith et al., 2015), where permafrost thaw is most extensive (IPCC, 2021). The expansion of shrubs is oftentimes at the expense of lichens and mosses as well as bare ground (Elmendorf et al., 2012a; Elmendorf et al., 2012b). This may affect the tundra carbon balance by enhancing ecosystem carbon uptake and altering ecosystem respiration (Figure 1: process 1), but also through complex feedback mechanisms involving snowpack dynamics and root-microbe interactions accelerating permafrost degradation (Mekonnen et al., 2021; Parker et al., 2021) (Figure 1: process 3). Overall, vegetation carbon stock has increased with global warming, and is predicted to increase further over the coming decades as warming continues. The increase, sometimes referred to as arctic greening, is however by no means homogeneous in space and time. In fact, significant portions of the Arctic have seen a browning trend (i.e., decrease in productivity) over the last 2 decades (Myers-Smith et al., 2020).

Vegetation change can also fundamentally reshape soil food webs (Figure 1: process 4). As the gatekeeper of carbon entering the system, vegetation composition determines the amount and composition of plant-derived carbon inputs, both through litter and root-exudates (Elmendorf et al., 2012b). As dead plant material constitutes the major component of the energy-base of the decomposer community, changes in plant litter availability and quality alter soil microbial community composition and decomposition rates (Adamczyk et al., 2020; Cleveland et al., 2014; McLaren et al., 2017; Saunders et al., 2023) (Figure 1: process 4). For example, shrub-expansion can increase carbon flows through the decomposer food web to higher trophic levels. This is sometimes referred to as a ‘browning’ of the soil food web (Manlick et al., 2024), and is partly a consequence of the chemical composition and amounts of litter entering the soil. The mere amount of litter is important for the decomposer community composition and energy flows (Adamczyk et al., 2020). An often-overlooked pathway of plant-soil carbon transfer is root exudation, although it can constitute up to half of the soil respiration in arctic ecosystems during the growing season (Parker et al., 2021), and has been estimated to amplify the soil carbon respiration by 12% from permafrost-affected ecosystems (Keuper et al., 2020). While similar dramatic losses of soil carbon have been found as a response to fertilizer-addition (Mack et al., 2004), arctic ecosystems also possess compensatory mechanisms, and over long timespans the carbon lost in one pool may be gained in others. For instance, a study from the Alaskan tundra showed warming resulted in a restructuring of carbon from the upper soil horizon towards the mineral horizon underneath, resulting in no net loss in soil carbon (Sistla et al., 2013). Seeing these two studies together (Sistla et al., 2013; Mack et al., 2004), highlights the importance of accounting for carbon dynamics below the topsoil horizon to establish reliable long-term ecosystem carbon balances to validate models. Further, they highlight the caution needed when making general inferences about a process with multiple interacting knock-on effects, such as global warming, to its single components, e.g., increased nutrient availability (Mack et al., 2004). While studying the pathways separately is important for our mechanistic understanding, Sistla et al. (2013) clearly show that by doing so, we risk missing some important compensatory long-term feedbacks.

3.2 Vegetation and surface albedo

Vegetation change affects the surface energy budget of arctic landscapes through changing surface reflectance because of vegetation penetrating the snow surface and altered snow characteristics (Loranty and Goetz, 2012) (Figure 1: process 2). As compared to snow, vegetation has a much lower albedo, and tall shrubs protruding the snowpack increase the absorption of solar radiation (Sturm et al., 2005). During the snow-free season, surface albedo depends on the community composition of the vegetation (Riedel et al., 2005), the relative abundance of different vegetation types (Oehri et al., 2022) and their phenology (Williamson et al., 2016). However, the contribution of vegetation changes to summer albedo, and ultimately to arctic summer warming, is limited compared to changes in duration of the snow-covered period (Chapin et al., 2005).

Other biologically induced changes in albedo have received less attention, yet they may still have profound effects on the energy balance. For instance, the presence of pigmented algae on ice and snow reduces the albedo markedly and contributes to enhanced melting rates (Hotaling et al., 2021).

3.3 Vegetation and permafrost thaw

Changes in vegetation structure and composition can affect permafrost thaw (Figure 1: process 3) through their influence on surface thermal regimes via shading in summer (Schuuring et al., 2024) and through snow accumulation in winter (Heijmans et al., 2022). For example, tall shrubs tend to accumulate more snow (Sturm et al., 2001), which in turn alters the temperature regime in the soil (Zhang, 2005) and snow depletion patterns, thereby altering permafrost thaw but also plant phenology (Wilcox et al., 2019). Thawing permafrost in itself can influence tundra vegetation change, with gradual permafrost thaw promoting plant growth through increased soil nutrient availability (Keuper et al., 2012). The development of thermokarsts creates landscape deformations and alters ground surface conditions, like soil temperature and moisture or depth of the active layer, promoting shrub growth (Mekonnen et al., 2021). However, in some cases abrupt permafrost thaw may lead to local plant mortality due to increased draining (Osterkamp et al., 2009).

4 Effects of decomposers on climate feedback loops

The main impacts of the decomposer community on climate feedback loops are on the carbon flux (Figure 1: process 6) and to some extent the permafrost thaw feedback loop (Figure 1: process 7), whereas direct impacts on albedo are absent.

4.1 Decomposers and carbon dynamics

The Arctic holds vast amounts of carbon (Hugelius et al., 2014), but also nutrients such as nitrogen (Palmtag et al., 2022), locked in permafrost. During the growing season the thaw of the uppermost parts of the soil, the active layer, allows for biological processes to unfold, including the mineralization of organic matter by decomposers with resulting respiratory carbon dioxide release to the atmosphere. These processes will only be amplified as warming progresses (Maes et al., 2024). As described above, shrubification may fuel the decomposition of old carbon accumulated over millennia by increased root growth expanding the root zone and associated rhizosphere processes into soil layers that were previously free of or poor in active roots. This boost of the rhizosphere microbes can both drive a reduction in soil carbon (Keuper et al., 2020) or restructuring of soil carbon with no net loss (Sistla et al., 2013), depending on the context. Microbes are also essential for the overall nitrogen cycle through nitrogen fixation (Rousk et al., 2018), as well as nitrification and denitrification processes (Crowther et al., 2015; Wang et al., 2020). Thawing permafrost can also increase the water saturation of soils over varying spatiotemporal scales, which can inhibit immediate mineralization of organic matter, but drive an increase in methane emissions (Rößger et al., 2022). Thus overall, nutrient and water availability and their spatiotemporal distributions are key parameters for predicting the land-atmosphere exchange of greenhouse gases as ecosystems continue to warm (See et al., 2024). This results in a feedback of accelerated decomposition of organic matter and release of greenhouse gases to the atmosphere (Altshuler et al., 2019).

Most of the organic matter assimilated by decomposers is respired back to the atmosphere as carbon dioxide relatively fast (Figure 1: process 6). In cold systems, typically only a small fraction of the assimilated carbon is turned into microbial biomass (Hicks et al., 2022). Nonetheless, over long periods over time, this seemingly small fraction is an important source of carbon ending up in association with mineral particles. Mineral-associated organic carbon covers carbon that is chemically protected against decomposers due to adsorption to secondary minerals, e.g., iron-oxides and clay, and physically protected in soil aggregates leading to effective long-term carbon preservation. As chemical weathering rates are slow in cold regions (Brantley et al., 2023), concentrations of secondary minerals, such as clay and iron-oxides, are typically low. Further, the lack of soil engineering meso- and macrofauna, such as earthworms, across large parts of the Arctic (Blume-Werry et al., 2020) leads to limited formation of protective aggregates (Angst et al., 2023; Angst et al., 2024). Consequently, arctic soils are dominated by particulate organic matter relatively vulnerable to perturbations and changing abiotic conditions (García-Palacios et al., 2024). Thus, the observed warming-induced increase in arctic ecosystem respiration (Maes et al., 2024) and soil respiration (García-Palacios et al., 2021) is attributed to the combination of improved kinetics under warming and increased availability of highly decomposable carbon in thawing permafrost (Trumbore, 2009). Functional limitations of the decomposer community can occur when old organic compounds 'exotic' to the present community thaw from the permafrost, yet, the community usually adjusts relatively fast (Monteux et al., 2020). Hence, thawed permafrost carbon is generally quite bioavailable and hence vulnerable to decomposition (García-Palacios et al., 2024; Kuhry et al., 2020).

4.2 Decomposers and permafrost thaw

Decomposer animals and microbes in soils obtain energy by breaking down dead organic matter from, e.g., plant litter (Figure 1: process 4) or animal excreta and carcasses (Figure 1: process 12). Gradually, organic material is broken down into simple organic compounds (e.g., simple sugars, amino acids, etc.) or all the way to inorganic minerals (mineralization). This releases important plant nutrients, including nitrogen, phosphorus, and potassium, to the soil solution, where it is available for plant uptake via roots and/or their symbiotic microbes (Figure 1: process 5). However, the activity of soil microbes produce heat, which in itself may accelerate permafrost degradation further (Hollesen et al., 2015) (Figure 1: process 7), and may even be sufficient to sustain the decomposition process during periods of low ambient temperatures (Khvorostyanov et al., 2008).

5 Effects of herbivores on climate feedback loops

How interactions between animals, plants and soils shape ecosystem ecology, biogeochemical processes and climate feedback loops have long been a subject of interest and dispute. Generally, animals affect elemental cycling via two direct and one indirect pathway: directly through physical disturbance (e.g., trampling, Tuomi et al., 2021), and deposition of waste products like dung and urine (Van Der Wal et al., 2004), and indirectly by restructuring the vegetation community (e.g., by selective feeding, Post et al., 2023; Post et al., 2022). Herbivores can counteract climate-induced changes in the Arctic, such as the release of nutrients (Petit Bon et al., 2023), changes to plant community composition (Post and Pedersen, 2008), and the expansion of woody species and the advancement of the tree line (Christie et al., 2015; Olofsson et al., 2009; Speed et al., 2010), leading to complex interactions. The indirect effects of herbivores on climate feedback loops through vegetation are well established, for example, the climate-effects of reducing shrub expansion into the tundra (reviewed in Olofsson and Post, 2018), but less attention has been given to the direct pathways.

Herbivores depend on plants as a resource (Figure 1: process 8), and one of the main mechanisms through which herbivores influence climate feedback loops is through the removal or damage of plant material while foraging (Tanentzap and Coomes, 2012). Plant consumption not only impacts the plants themselves but also influences plant traits, such as height, cover, biomass and the composition of plant communities (Figure 1: process 9), which in turn affects the carbon dynamics. By selective foraging and by altering the competitive interactions between plant species, herbivores influence the species composition of plant communities. This is for instance seen as a reduction in the abundance of the most palatable plants (Olofsson et al., 2001), or reduced shrub dominance increasing the plant diversity (Post et al., 2023). Nonetheless, in heavily grazed areas, grazing tends to reduce plant species richness, shifting towards a graminoid-dominated vegetation (Ylänne et al., 2018). Hence, tundra ecosystems appear to follow the general predictions of the intermediate grazing hypothesis predicting the highest plant diversities at intermediate grazing pressure. Yet, a recent meta-analysis suggests that a more climate-specific relationship might better catch differences in the grazing-diversity relationship between dry (decreasing) and wet (hump-shaped) areas (Gao and Carmel, 2020). Further, the effects of herbivores on plant communities are not only determined by the grazing intensity but is highly dependent on the functional traits of the herbivore community (Barbero-Palacios et al., 2024; Lundgren et al., 2024).

Herbivores not only impact the organisms they consume, but they also move around biomass, nutrients, seeds and more (Figure 1: process 12). For instance, when herbivores forage in one area and urinate and defecate in another area, nutrients are redistributed around the landscape. In the nutrient-limited Arctic, such translocation of nutrients can be considerable (Mosbacher et al., 2016) and can, at least at the local scale, impact vegetation composition markedly (Van Der Wal et al., 2004). During the process of decomposing the feces, nutrients become available to both soil microbes and plants (Beard et al., 2023) (Figure 1: process 12). Nutrients in urine on the other hand are directly accessible to both the soil microbes (Barthelemy et al., 2024) and the plants (Barthelemy et al., 2018) (Figure 1: process 12). Depending on the size and ecology of the animal, nutrients may be relocated only locally or across large distances. For example, small animals like lemmings, only move short distances and utilize latrine sites (Klein and Bay, 1991), which creates very localized hotspots of nutrients (Roy et al., 2022). Ultimately, when an herbivore dies, the parts of the carcass that are not consumed by predators or scavengers (Johnson-Bice et al., 2023; Schmidt et al., 2022) are decomposed (Figure 1: process 12). Locally, this results in a substantial release of nutrients (Danell et al., 2002). The impact of larger carcasses may last for several years and may increase the nutrient levels in the soil

(Steger, 2023), which in the nutrient-poor arctic tundra leads to increased vegetation surrounding the carcass (Danell et al., 2002) and to changes in the community composition of the vegetation (Steger, 2023). Calving also releases nutrients into the environment and has recently been suggested as an important feedback mechanism for the creation of fertile, revisited calving grounds for reindeer (Ferraro et al., 2024). Nutrient-translocation effects, however, are not limited to herbivores. For instance, the contribution of excreta and prey remains turns Arctic fox den complexes into green islands on the tundra (Johnson-Bice et al., 2023), and marine birds nesting in colonies on land bring in large amounts of "new" nutrients to the terrestrial ecosystem (Otero et al., 2018). The impacts of nutrient additions cascade through the terrestrial food web (González-Bergonzoni et al., 2017), affecting other biotic components (Figure 1: process 12), ultimately influencing climate feedback loops.

Most of our knowledge on the impacts of herbivory in tundra ecosystems refers to vertebrate herbivores, whilst invertebrate herbivory has received far less attention (Barbero-Palacios et al., 2024; Soininen et al., 2021). Invertebrate herbivory at non-outbreak densities, i.e., background herbivory, is widespread across the tundra biome (Barrio et al., 2017; Rheubottom et al., 2019), yet removes only a small proportion of leaf biomass (Kozlov et al., 2015) and its impact on carbon cycling is minor (Kristensen et al., 2020a). However, during population outbreaks invertebrate herbivores can significantly accelerate soil nutrient and carbon cycling resulting in substantial decreases in plant productivity (Kristensen et al., 2020b; Lund et al., 2017). The same is true for, e.g., cyclic populations of small mammals (Roy et al., 2022). Another important aspect to consider regarding the impacts of herbivores on climate feedbacks is that many animals move around and undertake long-distance migrations, carrying along the processes by which they influence the environment (Lundberg and Moberg, 2003; Schmitz et al., 2018). We therefore need a better characterization of the spatial and temporal variability of herbivore impacts to fully understand the changing functional roles of herbivores in arctic ecosystems (Koltz et al., 2022).

5.1 Herbivores and carbon dynamics

The effects of herbivores on vegetation can be substantial (Cahoon et al., 2012; Koltz et al., 2022; Vaisanen et al., 2014) (Figure 1: process 9), ultimately affecting carbon dynamics within the ecosystem through changing carbon stocks and greenhouse gas exchange (Falk et al., 2015; Fischer et al., 2022; Min et al., 2021; Petit Bon et al., 2023) (Figure 1: process 1). However, in addition to the effects mediated by their impacts on other biotic components, herbivores have a direct impact on carbon fluxes through the methane they produce as part of their digestive processes (Clauss et al., 2020). Ruminants, such as reindeer and musk, in particular produce large amounts of methane, thereby releasing carbon directly back to the atmosphere (Figure 1: process 13). In addition, arctic ruminants excrete methane-producing microbes in their feces (Aggerbeck et al., 2022; Andersen-Ranberg et al., 2018; Fritze et al., 2021), which can increase methane production in the soil (Fritze et al., 2021) (Figure 1: process 5).

5.2 Herbivores and surface albedo

Through their impacts on vegetation, herbivores can also contribute to changes in surface albedo (Figure 1: process 10). For example, grazing by reindeer can reduce shrub height and abundance, which increases albedo during the summer (Te Beest et al., 2016). Shorter and sparser vegetation in heavily grazed areas results in delayed snowmelt and increased surface albedo during the snowmelt season (Cohen et al., 2013) (Figure 1: process 2). Higher albedo reduces net energy absorption and the resulting latent and sensible heat fluxes, contributing to a cooling effect. However, herbivore impacts on albedo are mainly detected in areas with high herbivore densities where strong shifts in vegetation from shrub tundra to graminoid tundra have taken place (Te Beest et al., 2016). Heavy grazing by lemmings (Lara et al., 2017) and intense grubbing by geese (Peterson et al., 2013) can lead to the destruction of vegetation cover, exposing bare ground and resulting in lower albedo (Figure 1: process 2) and increased soil temperatures feeding back to enhanced decomposition and permafrost thaw rates.

5.3 Herbivores and permafrost thaw

Herbivores can indirectly influence climate feedback loops in tundra ecosystems through permafrost thaw (Figure 1: process 11). In the snow-covered period, animals may crater through the snowpack to access the vegetation underneath (Beumer et al., 2017; Schaefer and Messier, 1995), thereby reducing snow cover and depth whilst increasing its density (Beer et al., 2020). This reduces the insulative capacity of snow, thereby lowering soil temperatures during the arctic winter (Rixen et al., 2022). Indeed, evidence from Pleistocene Park in Siberia suggests that high densities of herbivores reduce permafrost thaw, by reducing snow depth and keeping soil temperatures low (Beer et al., 2020; Zimov, 2005). During the snow-free season, herbivore-induced changes in plant structure and community composition may also alter the temperature regime in the soil, with direct effects on permafrost thaw (Figure 1: process 3). Most obviously due to the shading-effects of woody vegetation during summers (Kropp et al., 2021), but herbivores can also significantly reduce the depth of the moss layer through trampling (Mosbacher et al., 2019). Both have implications for the temperatures in the soil and microbial activity (Gornall et al., 2007). Trampling can also compact soils, thereby altering the moisture regime in the soil (Tuomi et al., 2021). This in turn may reduce soil respiration and the release of carbon from the soil (Figure 1: process 6). Trampling and digging by animals may in some cases be (locally) pronounced, resulting in the destruction of the vegetation and exposure of bare ground, which in turn may influence several feedback loops. Hence, while animal trampling and digging alone may not directly cause permafrost thaw, they can exacerbate existing environmental factors that lead to thawing soils (Hall and Lamont, 2003).

6 Discussion and concluding remarks

Given the importance of biotic interactions in shaping ecosystem processes and responses (Barbero-Palacios et al., 2024;

Blois et al., 2013; Koltz et al., 2022) and the multifaceted ways by which biota influence ecosystem feedback loops with the climate (this study), accurate predictions of the future trajectories of arctic ecosystems are hampered by our ability to adequately integrate the two-way interplay between biotic and abiotic components into climate and ecosystem models. Over the past decades, significant progress has indeed been made in climate and ecosystem modelling (see, e.g., Eyring et al., 2016; Fisher et al., 2018). Vegetation and microbial communities have long been recognized as an important bridge between the ecosystem and the climate and thus important components in climate and ecosystem models, but other biotic influences on key feedback loops are rarely incorporated into the models (but see Rizzuto et al., 2024). Many of the biotic influences examined in this study may indeed appear patchy in both space and time, yet their role in modulating feedback loops between the tundra ecosystems and the atmosphere can be important, particularly at long timescales. Indeed, the importance of zoogeochemical processes is increasingly documented and recognized (Schmitz et al., 2018), and natural biogeochemical processes are estimated to remove as much as half of anthropogenic carbon emissions across terrestrial and marine ecosystems globally (Schmitz et al., 2023). Inclusion of biotic influences in ecosystem models may therefore improve the accuracy of ecosystem-climate models.

Many of the biotic drivers and processes influencing feedback loops highlighted here can operate on time scales ranging from short (e.g., months or years) to very long (e.g., millennia) and on spatial scales ranging from fine (e.g., km^2) to very large (e.g., continental) (Ripple et al., 2024). As an analogue, arctic climate change generates disturbances that can manifest themselves as ‘press driver’ (i.e., disturbances or stressors that operate over large spatial scales and remain in place for a long time, or slowly increase in pressure) and those that act as ‘pulse driver’ (i.e., sudden and short events that often operate on local spatial scales, though their effects may be long lasting). A press driver can be described as extensive, pervasive, or subtle (e.g., rising mean temperature) and a pulse driver as infrequent, sudden event (rain-on-snow or insect outbreaks) (Ratajczak et al., 2017). The impacts and consequences of large-scale press drivers have historically received most scientific focus, yet the accelerating stress levels associated with increasing frequencies of extreme events in the Arctic may suggest that conventional modelling approaches based on incremental changes in a single long-term stress provide poor estimates of the impact of climate on ecosystems. In developing and evaluating climate and ecosystem models of real-world systems, it is imperative to capture complex feedback networks and feedback loops, as well as the effects of multiple drivers of change operating on different spatiotemporal scales. In fact, a multi-scale integration of press and pulse drivers in feedback network analyses can reveal novel insights into antagonistic or synergistic relationships but also provide more realistic trajectories on potential ecosystem tipping points and/or collapse (Willcock et al., 2023).

As a first step towards a better integration into ecosystem models, we have provided here a broad overview of the many ways in which biota may influence key feedback loops between the ecosystem and the climate system. As a necessary next step, we propose to conduct a thorough meta-analysis on biotic influences on feedback loops in high-latitude ecosystems, focusing specifically on the magnitude and direction of the impact. Understanding the intricate interplay between biota and feedback loops between the tundra and the atmosphere is crucial for understanding and predicting the consequences of climate change in the Arctic and beyond.

Author contributions

NS: Conceptualization, Methodology, Visualization, Writing–original draft, Writing–review and editing. IB: Conceptualization, Methodology, Writing–original draft, Writing–review and editing. JK: Conceptualization, Methodology, Writing–original draft, Writing–review and editing. EL-B: Writing–review and editing. FB: Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Opportunities for improved detection of linked hydroclimate-ecosystem dynamics in Arctic catchments

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Climate warming is transforming Arctic landscapes through changes in the cryosphere and water systems that together contribute to alterations in the structure and function of ecosystems. To better understand these interlinked processes and feedbacks, previous research has recommended studies at the catchment scale that explicitly couple hydroclimatic fluxes and their interactions with the environment. However, using such an approach requires coordinated cross-disciplinary monitoring. In this review, we synthesize knowledge on available monitoring of key hydroclimate and ecosystem indicators to identify opportunities to use a catchment-based approach for improved understanding of climate-ecosystem dynamics in the Arctic. There is overall a small spatial overlap between the coverage of hydroclimate and ecosystem monitoring. *In-situ* monitoring of both climate and hydrological variables is sparse with a northward decline in observation density, while most ecosystem monitoring is focused around accessible regions and near Arctic research stations. As a result, our study shows that only two catchments within the pan-Arctic drainage basin include monitoring of both hydroclimate and ecosystem variables. Although this general spatial mismatch results in a limitation in using a catchment-based approach to study hydroclimate-ecosystem interactions across the Arctic, there are opportunities in some data rich regions. We have identified 32 catchments that include monitoring of all hydroclimate variables. These can be used as a starting point for catchment-based approaches to study climate-ecosystem interactions, and continued improvement of observation methods can further help identify regions with the best potential for downscaling climate model output for future projections. But this requires prioritized coordinated ecological and hydroclimatic monitoring efforts in regions most vulnerable to climate change.

KEYWORDS

Arctic, climate change, climate-ecosystem feedbacks, catchment approach, monitoring

1 Introduction

The Arctic, which encompasses a wide range of different ecoregions, has warmed three to four times faster than the planet as a whole during the period 1979–2022 (AMAP, 2024; Rantanen et al., 2022). The recent warming has triggered substantial changes in the terrestrial cryosphere (e.g., permafrost and snow distributions) and water systems that collectively contribute to transformations of landscapes and alterations in structure and function of ecosystems (AMAP, 2024; AMAP, 2021). Examples of cryosphere and water-driven changes in ecosystems include lake-area reductions (Webb et al., 2022; Karlsson et al., 2015), changing river-lake connectivity, vegetation shifts and conversion between terrestrial and aquatic ecosystems (Karlsson et al., 2011). Permafrost thaw can alter local biological activity through altered hydrology and soil nutrient availability (Natali et al., 2012), leading to, for example, vegetation productivity change through shrubification or “terrestrial greening” (Myers-Smith et al., 2011). Concurrent changes in climate variables and ecosystems can further influence rates and magnitudes of nutrient cycling and export (AMAP, 2021; AMAP, 2017; Bring et al., 2016). These observed changes will likely accelerate with further warming of the Arctic (IPCC, 2021).

Given that many Arctic landscape changes are climatically driven and hydrologically mediated, and they in turn affect climate-related fluxes, it is becoming increasingly important to be able to quantify the spatial extent of these complex interactions. As large-scale observations of individual variables may not be able to capture these complexities, we need an approach where multiple variables can be examined simultaneously. A recommended approach for conducting such studies, is the catchment-based approach (as suggested by, e.g., Wrona et al., 2016; Prowse et al., 2015; Karlsson et al., 2011). The hydrological catchment or drainage basin is a natural topographic and geological unit that can couple terrestrial, freshwater, and nearshore ocean environments and their processes. The approach also allows for a direct consideration of heterogeneity at the landscape scale, as hydrological processes and ecosystem variables are controlled by local catchment characteristics, such as geology, geomorphology, the presence of permafrost, and vegetation cover. A catchment-based approach can advance our understanding of these interrelated fluxes and processes and help answer questions related to how ecosystems in catchments are affected by, and in turn, affect climate change, as well as how they are linked to water flows. However, using a catchment-based approach requires coordinated, cross-disciplinary research and monitoring of climate, hydrological and ecological variables. A critical question to address is if (current) monitoring in the Arctic supports such an approach?

In this review, we synthesize knowledge on available monitoring of key hydroclimatic and ecosystem indicators in Arctic catchments that can be used to assess and project ecosystem responses in a changing Arctic, including: i) what and where hydroclimate and ecosystem variables are being monitored, ii) at what scales these variables are being monitored, including regional (e.g., through remote sensing) or local (*in situ* or ground truth data) scales, and iii) whether the current monitoring network represent the many heterogeneous landscapes of the Arctic. Our aim is to identify opportunities for improved detection, interpretation and projection of linked water-cryosphere-ecosystem dynamics using a catchment-based approach.

2 Hydroclimatic indicators

2.1 Temperature, precipitation, snow cover

Key climate variables that drive climate change impacts on ecosystems include air temperature, precipitation, snow depth and snow water equivalent. The circumpolar network of *in situ* observations is densest for air temperature measurements. For example, the NASA GISSTEMP archive (Lenssen et al., 2019) contains data from stations with continuous, decadal-scale time series, incorporating measurements from 2652 stations in the pan-Arctic drainage basin (PADB, based on the pan-Arctic catchment database, ARCADE; Speetjens et al., 2023), whereof 512 stations are located north of the Arctic Circle (66.5°N) (Supplementary Figure S1). However, the station network remains sparse over large areas, especially Greenland, northern Canada, and Siberia. This sparse network is particularly concerning in regions experiencing rapid climate warming and large variability in orography and surface types. The rapidly warming regions include Svalbard, the northern half of Greenland, the Canadian Arctic Archipelago, mainland Canada north of Hudson Bay, and much of northern Siberia within approximately 500 km of the coastline (Rantanen et al., 2022). The warming patterns include seasonal differences, with generally strongest warming of the terrestrial Arctic in autumn and spring and weakest in winter, when atmospheric warming has mostly occurred in the marine Arctic and Alaska.

Considering the *in situ* network for precipitation measurements, the spatial distribution of station density closely resembles that of temperature stations (compare Supplementary Figures S1a,b), with the lowest densities occurring in the northernmost and coldest regions. However, the overall number of precipitation stations is substantially smaller, comprising 952 stations within the PADB, of which only 127 are located north of the Arctic Circle (Supplementary Figure S1b). The generally low station numbers in the northern parts of the PADB are largely attributable to logistical constraints in these remote regions, but they may also reflect the difficulties of accurately measuring snowfall accurately, which reduces the cost-effectiveness of gauge-based observations. As a result, recent estimates of Arctic precipitation often rely on a combination of atmospheric reanalysis products and both *in situ* and remote sensing data (Becker et al., 2013; Walsh et al., 2023). The observed changes in precipitation underscore the need for a denser observation network, especially in regions with complex terrain. For instance, the east coast of Greenland, where precipitation increased significantly from 1989 to 2016 (Yu and Zhong, 2021), and Svalbard, where wintertime rain has become more frequent (Peeters et al., 2019), are high-priority areas for enhanced monitoring.

Due to wind-driven snow transport, snow depth can vary significantly across small distances, limiting the value of isolated point measurements. Manual snow line measurements, while more representative, require substantial labor. Hence, snowpack mapping in the Arctic is increasingly reliant on satellite remote sensing. Radar and lidar altimetry, such as from CryoSat-2 and ICESat-2, can measure snow depth with a spatial resolution of as high as 100–500 m (Wingham et al., 2006; Markus et al., 2017). Passive microwave sensors (e.g., AMSR2, SMOS) provide snow water equivalent (SWE) data with a spatial resolution of 10–50 km

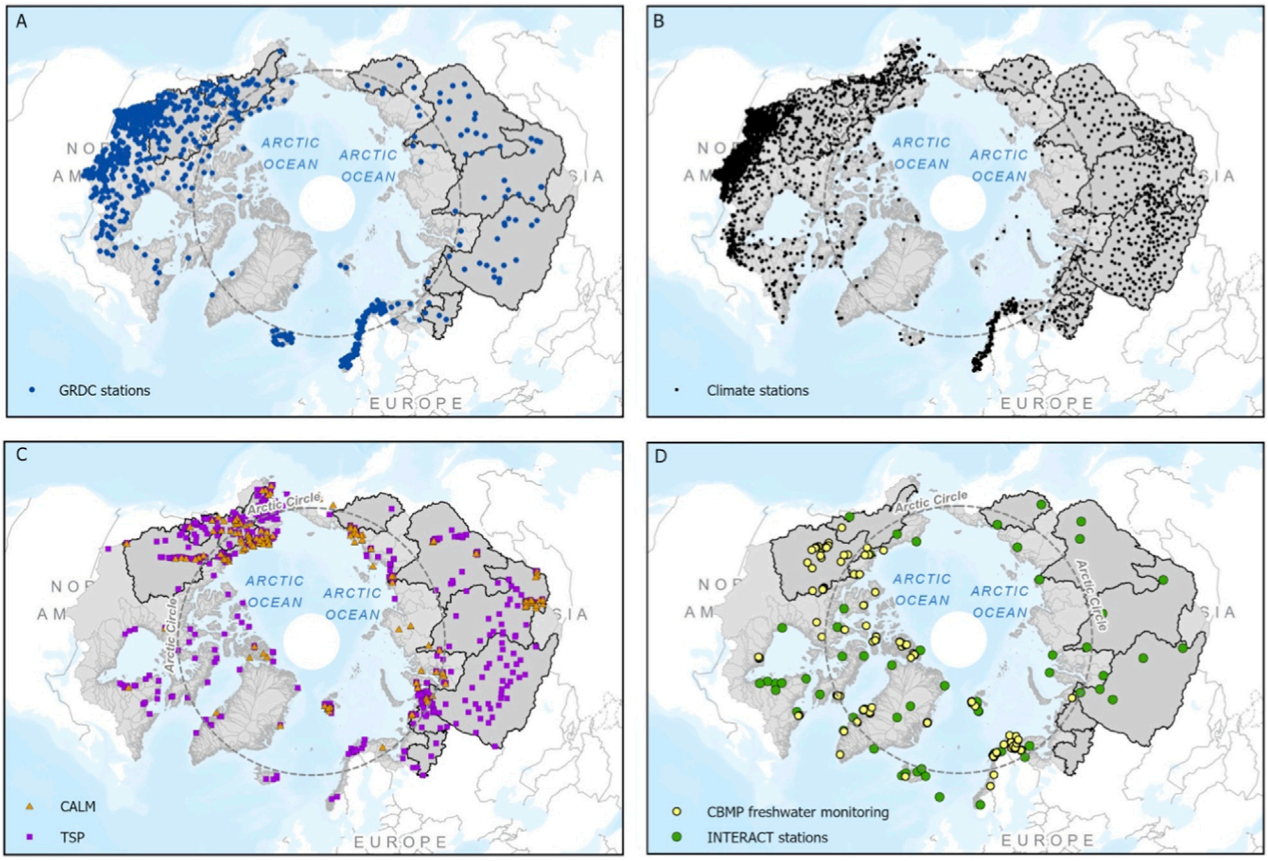

FIGURE 1
In-situ monitoring in the pan-Arctic drainage basin (as defined by the pan-Arctic catchment database, ARCADE; Speetjens et al., 2023) of **(A)** discharge, available from the Global Runoff Data Centre (GRDC) stations catalogue, with an ending date between 2015 and 2024; **(B)** temperature and/or precipitation from national station networks; **(C)** circumpolar active layer monitoring (CALM) sites and thermal state of permafrost (TSP) boreholes from the Global terrestrial network for permafrost (GTN-P) and **(D)** lentic and lotic freshwater environments from the Circumpolar Biodiversity Monitoring Programme, and locations of INTERACT research stations that monitor both climatic and ecosystems variables. The eight largest rivers in the PADB (Yenisei, Lena, Ob, Pechora, Sev. Dvina, Kolyma in Eurasia; Mackenzie, Yukon in North America) are shown with a black outline.

(Kelly, 2009). However, small-scale variations in surface characteristics and snow properties make satellite-based retrievals of snow depth and SWE less reliable over land than over sea ice. Continued surface-based observations are therefore essential to refine remote sensing algorithms for snow depth and SWE, especially in regions with rugged terrain and boreal forest cover. In the future, new tools combining traditional snow lines, drones for near-remote sensing and machine learning techniques could provide further possibilities also in Arctic monitoring to improve snow measurements. Considering *in situ* observations, we see significant potential for stronger collaboration between scientists and Indigenous Peoples and local communities.

2.2 Surface water hydrology

Changes in hydrological conditions, including surface water, both reflect and drive changes in Arctic inland ecosystem functioning by linking abiotic and biotic components. For example, changes in river discharge reflect catchment water balance, including climate, cryosphere and landscape changes of upstream areas, and are in turn related to key ecosystem characteristics and ecological changes. Rivers further link terrestrial and ocean domains. Sustained river discharge monitoring is therefore an important part of the Arctic observation network.

Efforts to monitor river discharge across the Arctic started in the 1930s, with the number of stations and their spatial distribution changing over time (McClelland et al., 2015) (Supplementary Figure S2). However, current hydrological monitoring is limited by large gauging gaps. The number of hydrological gauging stations and monitored areas has decreased since the 1980s (Shiklomanov and Lammers, 2013; Bring and Destouni, 2009), and about one-third of the PADB is currently ungauged (AMAP, 2024). At present, Russia, Canada, United States and the Nordic countries have 69, 546, 59 and 120 (total 794) active river gauging stations, respectively, within the PADB with an ending date between 2015 and 2024 according to the Global Runoff Data Centre (GRDC, 2024) (Figure 1). Note that some of these stations have not always had continuous operation and may have data gaps. Some gauging stations are also only active during the summer months and may therefore have seasonal data gaps. River discharge is often estimated from water stage using rating curves (relationship between measured stage and discharge), which require updates to maintain reliable estimates. Inadequate updates on the measured discharge in downstream gauges (i.e., Russian gauging stations Yenisey at Igarka and Lena at Kusur) has resulted in uncertainties in these water stage estimates (McClelland et al., 2015). The discharge stations are maintained by national water authorities, and discharge data availability varies between these. However, much of this data are also openly available in discharge databases (e.g., Arctic Great Rivers Observatory, Global Runoff Data Centre, R-ArcticNET), although the frequency of updates of these databases also varies depending on the data availability from different countries.

Observed changes in annual river discharge from the eight largest rivers in the Arctic (Eurasia: Yenisei, Lena, Ob, Pechora, Sev. Dvina, Kolyma; North America: Mackenzie, Yukon), covering approximately 70% of the PADB area (Figure 1A), indicates a significant increase of 222 km^3 in total freshwater influx over 1970–2023 (AMAP, 2024). However, it should be noted that the changes in river flow across the PADB are spatially non-uniform. Despite increasing trends in many Arctic rivers, mainly during the last decades, there are also river basins (e.g., in Siberia, Canada and Alaska) that exhibits decreasing annual flows (e.g., Feng et al., 2021; AMAP, 2024) due to, e.g., decreased precipitation and snow accumulation (e.g., Nesterova et al., 2020). Furthermore, a large majority of the northern catchments in the Arctic (along the land-ocean interface) remains ungauged. These nearshore environments transports hydrochemical fluxes that can have significant ecological implications for coastal, and possibly broader, marine environments (Prowse et al., 2015). Combining remote sensing and hydrological modeling that assimilates discharge across the Arctic can provide spatially and temporally flows at all Arctic rivers (Feng et al., 2021), including small rivers in the high Arctic that are missed by current observation networks, and further extend areas that can be used for coupled water-cryosphere-ecosystem studies using a catchment-based approach.

2.3 Groundwater-related variables

Groundwater resources are crucial for human and ecosystem needs in Arctic regions, and is the largest active reservoir in the global hydrological cycle. Movement of groundwater, from land to water bodies and eventually to the sea represents a major source of freshwater, nutrients and carbon for catchment water budget and biogeochemical processes. Groundwater is also important for sustaining certain groundwater dependent ecosystems. Permafrost constrains water pathways and connections during most of the seasons, but the seasonally thawed active layer provides shallow groundwater sources in summer and fall periods even in the high Arctic (O'Connor et al., 2019). Climate change is also already seen as increases in groundwater discharge during winter months in large Arctic river basins (McKenzie et al., 2021).

Groundwater monitoring including depth and quality is primarily conducted in large aquifers used for drinking water supply, as part of environmental monitoring of land use impact, e.g., mining and dams or in experimental research sites. Monitoring is mainly done using traditional water depth measurement methods, and requires drilling, and is only at the point scale thereby limiting good representation of larger spatial variation of groundwater resources. Groundwater is still rarely measured in remote areas, and is currently only measured at research stations and networks, including the International Network for Terrestrial Research and Monitoring in the Arctic (INTERACT). In Arctic monitoring programs, only few sites have groundwater monitoring listed, and a review by Lecher (2017) identified only 16 peer-reviewed studies concerning groundwater discharge in the high Arctic. In regions with seasonally frozen soil, namely, sub-arctic and north boreal regions, although a long tradition of groundwater studies exists, the systematic sharing of monitoring data is lacking. A study by Fan et al. (2013) provided a global estimate for groundwater table level including data from government archives and literature also from northern areas. Their study shows that most groundwater monitoring occurs close to municipal areas, and sharing of groundwater data resources is lacking. Groundwater level is also an important variable for Arctic monitoring and predicting damage to infrastructure (housing, industry, etc.), but local monitoring data is difficult to access or restricted due to critical infrastructure reasons.

For better spatial coverage of groundwater level and dynamics, remote sensing offers some possibilities in Arctic areas. Gravity-based measurements with GRACE and GRACE-FO missions are used to track terrestrial water storages (Richey et al., 2015) and are also separated for groundwater storage parts but only with rather coarse resolution. Interferometric Synthetic Aperture Radar (InSar), used for measuring surface deformation or microwave remote sensing of soil moisture, can provide proxies for groundwater dynamics (Adams et al., 2022). Numerical modelling in 1D-3D can provide additional information but are typically applied to case specific sites and large aquifer types, and usually need good calibration data from measurements. This highlights the importance of monitoring groundwater at ground level in Arctic sites where new groundwater formations, especially shallow ones, are formed after permafrost thawing.

Groundwater has an important role in the carbon cycle (Connolly et al., 2020), but dissolved inorganic carbon (DIC, main carbon fraction in groundwater) transport processes are not systematically monitored in a circum-Arctic context. In a recent study, increase in groundwater DIC concentrations was documented in Sweden (Klaus, 2023), indicating potential climate change impacts to groundwater chemistry in the Arctic. Permafrost thaw promotes shallow groundwater flow and water movement in the active layer and strongly impacts carbon transport possibilities (Serikova et al., 2018). We suggest that several lateral carbon transport components of groundwater, namely, shallow groundwater and soil water quality and transport, should be better included in Arctic monitoring since globally lateral C fluxes have been estimated to be similar in size to the terrestrial C-sink (Le Quéré et al., 2016). Groundwater also has a direct link to ecosystem functions, and thus more systematic monitoring of lateral processes in active layer and groundwater in non-permafrost regions would benefit not only carbon, but also understanding of ecosystem processes.

3 Ecosystem indicators

3.1 Terrestrial ecosystems

The exchange of greenhouse gases (GHG) between terrestrial ecosystems and the atmosphere is largely driven by biological processes of microbial and photosynthesizing nature. These enzymatic processes are constrained by temperature and water availability and interact with other factors (nutrient availability, vegetation composition, topography) and light availability for photosynthesis, which in turn interact with herbivores and other disturbances (Schmidt et al., 2024). Together these are the main controls on the Net Ecosystem Carbon Balance (NECB; López-Blanco et al., 2025) and parameters that can be measured in the field, making NECB an indicator and concept that is particularly well suited for studies at the confined catchment scale. Here it is possible to measure and study all components in the field as well as work with models that can include different levels of the complex ecosystem interactions. The measurements needed within the same catchment for the NECB budgeting include both vertical (atmospheric) and lateral transport of carbon in all its forms (CO2, CH4, DOC, DIC) as well as a good handle on the import/export terms relating to herbivory (grazing, insects, etc.). For longer term assessments there is also an important need for a quantitative understanding of the effects of episodic extreme disturbance such as wildfires and extreme insect outbreaks (Virkkala et al., 2025).

Despite limited productivity, substantial amounts of organic material have accumulated in northern terrestrial ecosystems over the postglacial timescale (Hugelius et al., 2023). These ecosystems have globally significant contributions to the NECB, in particular with respect to CO_2 and CH_4 exchanges, which ultimately can amplify the current (and forecasted) warming (Christensen et al., 2019; Fernández-Martínez et al., 2019; IPCC, 2019; Hugelius et al., 2023; Ramage et al., 2024). Individual components and mechanisms that form part of the NECB are being studied at a number of locations in the Arctic and globally, where interannual variability in climate is used to interpret the responses to predicted future climatic development (AMAP, 2021). This coarse scale approach, however, oftentimes falls short as responses are context-dependent and highly influenced by local conditions. At the catchment scale it is possible to work with a higher resolution of driving parameters and the complete and interlinked NECB and greenhouse gas budgets. Such detailed catchment studies can at the same time be compared along gradients from the southern-to the northernmost parts of the Arctic (López-Blanco et al., 2025).

From a greenhouse gas perspective, catchments may be small, yet their large carbon stores suggest that dynamics represent proxies for processes with global implications. The catchment-scale approach allows for characterizing both latitudinal and temporal aspects of carbon dynamics in Arctic ecosystems. Traditionally, differences are considered to be entirely climate-driven, but this is challenged by the fact that local nutrient availability may be a more important factor in determining carbon flux magnitudes between otherwise comparable ecosystems (López-Blanco et al., 2020). In this concept, lateral movement of water, nutrients and ions in the landscape is critical and often not a well-covered component. Additionally, differences in patterns and intensity of herbivory may be another understudied factor (Väisänen et al., 2014; Metcalfe and Olofsson, 2015; Stark and Ylänne, 2015; Min et al., 2021; Post et al., 2021) influencing and changing the overall NECB (via changes in plant composition, energy balance, nutrient availability, etc., see, e.g., Falk et al., 2015; Mosbacher et al., 2019) and how it responds to climate change. It has also been shown that the ongoing long-term warming may see its most dramatic effects and changes in Arctic ecosystems through local extreme events relating to parameters other than temperature alone such as anomalous precipitation and snow events (Christensen et al., 2021).

Clearly, it is time to challenge existing paradigms using the catchment-scale approach to address questions such as:

1. Local conditions versus large-scale patterns, including herbivory, nutrients, hydrology, snow conditions, and permafrost at the local scale may be the primary controls over NECB and GHG associated ecosystem feedbacks, with underlying large-scale temperature patterns possibly being less important.
2. Extreme events and components, such as heavy rainfall, prolonged drought periods and changes in herbivore (invertebrates as well as vertebrates) activity may exceed the roles of both large-scale temperature patterns and local background conditions in controlling NECB.

Working with such questions in improving our understanding of the NECB as an ecosystem indicator requires a catchment approach.

3.2 Freshwater ecosystems

Lakes and streams are closely linked to their drainage area and reflect changes in runoff patterns and solute concentrations. Freshwater monitoring has normally been designed to associate community samples of different organismic groups (e.g., plankton, benthic invertebrates, fish) to a set of physio-chemical variables that potentially drive ecological change at the local scale. For example, dissolved organic carbon (DOC) is a good indicator of catchment vegetation development (e.g., transition from tundra into boreal forest) and soil processes (e.g., permafrost thaw) in catchments where climate change is the primary driver of change (Huser et al., 2022). Although this historical approach has not normally included climate variables, recent circumpolar assessments of CAFF's (Conservation of Arctic Flora and Fauna; i.e., the biodiversity working group of the Arctic Council) have done this. For example, the Freshwater Circumpolar Biodiversity Monitoring Program (CBMP) analyzed trends in biodiversity variables at the ecozone spatial scale (Culp et al., 2022; Goedkoop et al., 2022). This enabled linkages of freshwater biodiversity and biological processes to climate because terrestrial ecozones are by definition related to catchment and climate attributes (Olson et al., 2001). The temperature regime as well as hydrological connectivity were found to be critical factors that constrain biodiversity and ecological processes in Arctic freshwaters (Laske et al., 2022; Lento et al., 2022; Schartau et al., 2022).

Freshwater monitoring is particularly discontinuous across the Arctic (Lento et al., 2019; Culp et al., 2022) and dependent on accessibility and monitoring traditions in the various countries. For example, the Fennoscandian countries have a long tradition of monitoring the physio-chemical and biological effects of acidification and eutrophication, Iceland and Norway have long monitored fish populations in major rivers, whereas in the vast and remote Arctic regions of Canada, time-series monitoring of baseline conditions is sporadic and instead built largely on the collection of single samples during surveys (Goedkoop et al., 2022). Arctic Council countries have recognized the need for intensified biological monitoring programs that combine remote sensing with on-site monitoring at regional scales, but this approach has not yet been implemented. Such large-scale monitoring that includes remote sensing and local measurement data could resemble the approach undertaken by ArcticGRO (2025). Since 2003 this program has provided essential data on the biogeochemistry and discharge of the largest Arctic rivers, thus providing an integrated measure of the transport of solutes and materials to the Arctic Ocean (e.g., Behnke et al., 2023). Similar monitoring programs, that also include biological variables, exist for smaller Arctic rivers and lakes on a regional scale, such as in northern Fennoscandia, but are lacking on a circumpolar scale. Such approaches, that include both biological and geochemical variables, have the potential to expand to other Arctic countries and explore synergies with existing research and infrastructure hubs such as the Canadian High Arctic Research Station (CHARS) and Zackenberg on Greenland. The inclusion of high-resolution remote sensing data could further improve the monitoring of large-scale ecological change.

Rapid vegetation changes in the Arctic and subarctic, as well as permafrost thawing, can directly impact nutrient inputs delivered from terrestrial to freshwater ecosystems (Wrona et al., 2013). For example, permafrost thaw can cause enrichment with nutrients including nitrogen, phosphorus, and dissolved organic matter (Kokelj et al., 2013; Chin et al., 2016). In contrast, terrestrial vegetation development can lead to increased sequestering of nutrients in soils, thereby leading to oligotrophication of northern freshwater ecosystems (Arvola et al., 2011; Eimers et al., 2009; Huser et al., 2018). Goedkoop et al. (2025) recently demonstrated that long-term sequestration of nitrogen and phosphorus nutrients within terrestrial environments in northern Sweden have led to the oligotrophication of Arctic/alpine lakes. This conclusion was rendered by linking long-term monitoring of subarctic lakes to the greening of landscapes. Similar processes are likely ongoing in other parts of the Arctic, but remain undetected due to the lack of long-term monitoring data. To better define and understand these changes to ecological processes in Arctic freshwaters, intensified monitoring programs that link remote sensing information with regional monitoring are required (Goedkoop et al., 2022).

Culp et al. (2022) and associated papers in this special issue reporting on CAFF-CBMP work demonstrated that existing freshwater monitoring data could be accumulated within terrestrial ecoregions. These regions were described by Olson et al. (2001) and are defined by unique biogeographical features, and can be used to aid broad assessments of hydroclimatic change on freshwater biodiversity at the circumpolar scale (Culp et al., 2022; Lento et al., 2022). Moreover, this approach forms a natural unit for the summarization of geospatial variables associated with global hydrological basin layers (i.e., hydrobasins) that were delineated by Lehner and Grill (2013). The use of ecoregion scale assessment is therefore a promising approach to improve the association of climate variables to freshwater ecological processes, that will also provide improved context for catchment scale observations. Recent work of the Arctic Council's Freshwater CBMP provides proof of this concept as broad latitudinal and circumpolar trends in freshwater diversity across ecoregions could be related to the climate (e.g., Kahlert et al., 2022; Lento et al., 2022). It is imperative that existing databases are utilized to build these broad trends in freshwater biodiversity, with particular emphasis on including long-term monitoring sites such as those at relatively accessible locations (e.g., in northern Fennoscandia) or at isolated sites where necessary infrastructure is in place including Zackenberg in Greenland, CHARS in Canada, and other sites within INTERACT.

4 Opportunities and limitations to track climate-ecosystems interactions using a catchment-based approach

The pan-Arctic drainage basin (PADB) contains around 47,000 river basins and covers an area of more than 20 million km^2 (based on the pan-Arctic catchment database, ARCADE; Speetjens et al., 2023) (Figure 1). To further assess which key hydroclimate and ecosystem variables are being monitored and where in the PADB and to identify opportunities for using a catchment-based approach, we collected georeferenced information of key variables from existing national and international monitoring networks, and (global) databases that include data from monitoring networks (number in parentheses represent number of stations included for each variable). Inclusion of monitoring networks and databases was guided by the FAIR data principles (Findable, Accessible, Interoperable, Reusable) (Wilkinson et al., 2016), and we only included sites and stations that are within the PADB (based on ARCADE). For hydroclimate variables, we collected locations of temperature and precipitation stations (2652 and 952, respectively, 3,604 in total) from national and international networks (Lenssen et al., 2019; Government of Canada, 2025; Razuvaev et al., 1993; USGS, 2025; Norwegian Meteorological Institute, 2025; Finnish Meteorological Institute, 2025), and locations of discharge stations (794) from the GRDC (2024), with an ending date between 2015 and 2024. The reason for choosing 2015 as a lower boundary for the year with latest data available for discharge is that there is at times a delay in reporting from national water authorities to the GRDC. For example, when choosing 2020 as a lower boundary, a majority of the Russian and Norwegian catchments are excluded and some of the northernmost catchments in North America. As permafrost may be the primary control of NECB and an important component in other cryosphere-water-ecosystem interactions, we also included locations of circumpolar active layer monitoring (CALM) sites (191) (GTN-P, 2025a) and thermal state of permafrost (TSP) boreholes (870) (GTN-P, 2025b). For ecosystem variables, we use the freshwater ecosystem (lotic and lentic) monitoring locations (157) from the Conservation of Arctic Flora and Fauna - Circumpolar Biodiversity Monitoring Programme (CBMP freshwater monitoring; Metadata for the CBMP freshwater data is available at the CAFF website https://abds.is/). We also use the locations of the research stations (39) included in the INTERACT network, which have served as platforms for the majority of field-based ecosystem studies in the Arctic (Metcalfe et al., 2018). In total, we included 5,655 hydroclimate and ecosystem monitoring stations (Figure 1).

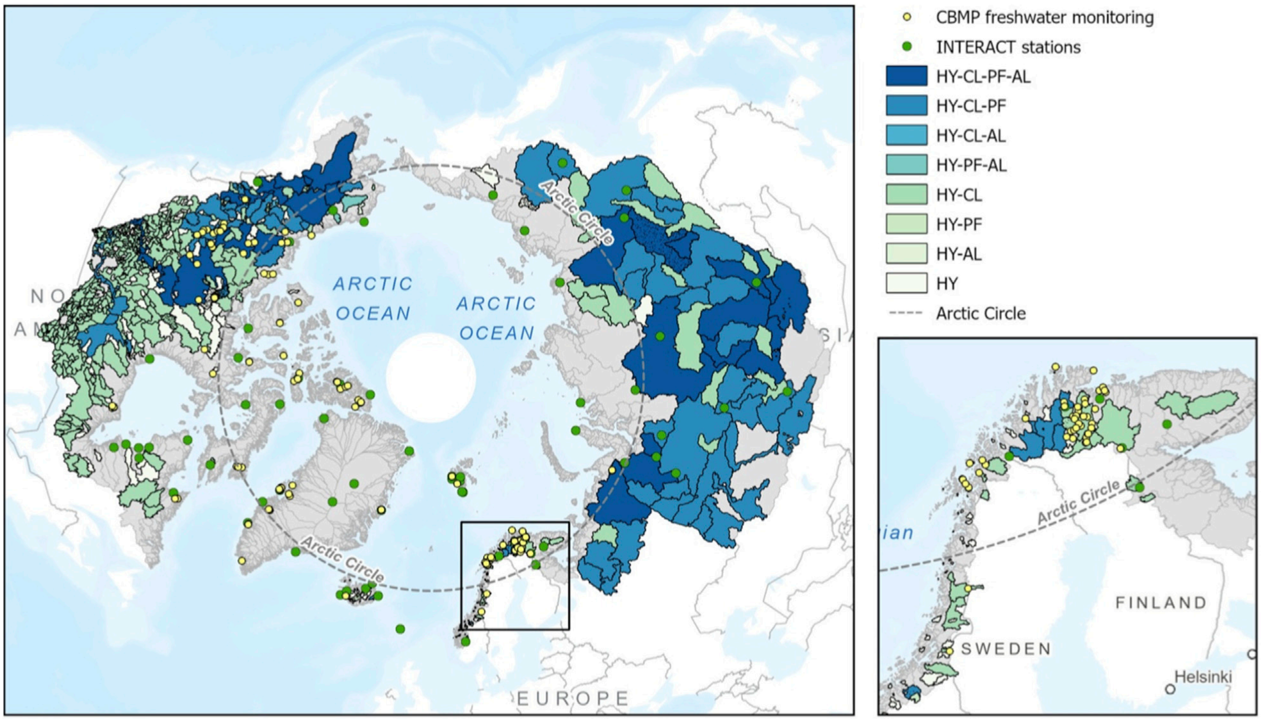

FIGURE 2
Overview of catchments in the PADB that have active discharge monitoring (HY) (as of 2015) and other climate variables that are monitored in the catchments, including temperature and/or precipitation from national station networks (CL) circumpolar active layer monitoring sites (AL) and thermal state of permafrost boreholes (PF). Locations of lentic and lotic freshwater environments from CBMP, and locations of INTERACT research stations. Catchments are ordered in size, from small (on top) to large (bottom). Inset shows data for the northern Fennoscandia.

Note that not all stations may be active today (e.g., some of the GRDC and CBMP freshwater locations) (Figure 1; Supplementary Figure S3), but are included here as they provide (long-term) data that can be used for studying (past) climate change impacts, and guidance where monitoring could potentially be reestablished for comparative studies.

Only a small number of the monitored catchments (539 or 1% of the catchments in the PADB) contain at least one station monitoring climate, permafrost or ecosystem variables, with a median station density of roughly one station per 250 km^2. Although the eight largest catchments include more stations, their densities are much lower, with approximately one station per 1,000–10,000 km^2. The spatial distribution of hydrological, climate and ecosystem observations reviewed here reveals only limited overlap among these monitoring networks. There are only two catchments (Mackenzie and Yukon, the two largest Arctic rivers in North America) that have monitoring of all hydroclimate and ecosystem variables in consideration. This is mainly due to the sparse network of the INTERACT stations, as well as the limited number of CBMP freshwater locations in the Russian part of the PADB. Moreover, although downstream stations in the Mackenzie, Yukon, and the six largest Russian Arctic rivers capture about 70% of PADB discharge, their very large basin sizes (300,000–3,000,000 km^2) and strong spatial heterogeneity limit catchment-based analyses. Smaller catchments and sub-catchments, therefore, provide a more appropriate scale for linking hydroclimatic fluxes with ecosystem processes and local environmental dynamics. In summary, the spatial coverage of hydroclimate, permafrost or ecosystem variables varies across the PADB (Figure 1). For example, as previously noted a large majority of the northern catchments in the Arctic (along the land-ocean interface) remains ungauged (Figure 1A), and other monitored areas have decreased over time (Supplementary Figure S2). The density of temperature and/or precipitation stations from national networks appears to be decreasing with latitude, apart from the Nordic countries (Figure 1B). The network of active layer monitoring is less dense compared to the network of permafrost boreholes, and much of the monitoring of both variables is centered in Alaska (Figure 1C). Regarding the spatial distribution of the CBMP freshwater locations, they are mainly found in North American and Nordic regions, while the INTERACT stations, although few in number, are spread across the Arctic (Figure 1D).

However, some monitoring opportunities exist at catchment or sub-catchment scale that can be used to improve our understanding of linked hydroclimate-cryosphere-ecosystem dynamics. Figure 2 shows catchments (including sub-catchments) with active discharge monitoring (HY; as of 2015) within the PADB together with other active monitoring of climate variables, including temperature and/or precipitation data (CL), permafrost borehole data (PF), and active layer monitoring (AL), as well as the location of CBMP freshwater locations and INTERACT stations. Of the 794 catchments (including sub-catchments) shown in Figure 2, 32 have monitoring of all hydroclimate variables (catchment size ranging from 3,900 Km^2 to 2.95 M km^2) (Supplementary Figure S3). A total of 73 catchments include the combination HY-CL-PF (72) or HY-CL-AL (1) (catchment size ranging from 1980 km^2 to 2.69 M km^2), and 394 catchments include the combination HY-PF-AL (4), HY-CL (381), HY-PF (8), or HY-AL (1) (catchment size ranging from 31 to 293,000 km^2). The remaining catchments (295) only have hydrological (HY) monitoring (catchment size ranging from 1.8 to 93,900 km^2). The spread of catchment sizes appears to be decreasing with decreasing number of monitored hydroclimate variables. Many of the catchments that include three or more hydroclimate variables are, however, located at the lower latitudes, are not near ecosystem monitoring sites, or have areas exceeding 100,000 km^2 and thus unsuitable to study hydroclimate-ecosystem dynamics at landscape scale. Yet some catchments exist, where monitoring of hydroclimate variables overlap with regions of ecosystem variables that can be used to improve detection, interpretation and projection of linked water-cryosphere-ecosystem dynamics using a catchment-based approach. These catchments are located in northern Fennoscandia, Zackenberg in northeastern Greenland, Alaska (US), Yukon, Northwest Territories, British Columbia, Alberta in Canada, and some larger catchments in Russia (Yamalo-Nenets, Altai, Novosibirsk, Sakha, Magadan) (Figure 2).

5 Discussion

In this review, we synthesized knowledge on available monitoring of key hydroclimatic and ecosystem indicators to identify opportunities for improved detection, interpretation and projection of linked water-cryosphere-ecosystem dynamics using a catchment-based approach. In summary, *in situ* monitoring of climate variables (temperature, precipitation and snow cover) remains sparse over large areas (e.g., towards higher latitudes). A similar latitudinal pattern can be seen for surface water (discharge) monitoring, as a majority of northern catchments (along the land-ocean interface) remains ungauged. Groundwater monitoring is even more sparse, with most of its monitoring occurring at research stations and networks. The northward decline in observation density presents a major challenge for two key reasons. First, the rate of climate warming in the terrestrial Arctic intensifies toward the north. Second, the surface topography in the northern coastal and archipelago regions is highly heterogeneous, reducing the spatial representativeness of individual observation stations. To compensate for the limited spatial monitoring of hydroclimate variables, more recent estimates are increasingly reliant on remote sensing data. Current freshwater and terrestrial ecosystem monitoring has poor representation in large parts of the Arctic, and areas with better coverage are often found around relatively accessible locations or near research stations where necessary infrastructure is in place. To improve our understanding of hydroclimate and ecosystem interactions in a continued warming Arctic, we need to prioritize coordinated ecological and hydroclimatic monitoring in regions most vulnerable to climate change.

Overall, there is currently a large spatial mismatch between the coverage of hydroclimate and ecosystem monitoring. This mismatch results in limitations in using a catchment-based approach to study hydroclimate-ecosystem interactions across the PADB, as, i.e., only two catchments have monitoring of all hydroclimate and ecosystem variables considered in this review. However, there are opportunities in some data-rich regions where smaller catchments or sub-catchments have available monitoring of hydroclimate variables, and overlap with regions of ecosystem monitoring. Although these regions do not represent all Arctic heterogeneous landscapes (e.g., due to monitoring biases; López-Blanco et al. 2024), they can be used as a starting point for catchment-based approaches to study climate-ecosystem interactions. Continued improvements in observation methods, including drone mapping of heterogeneous landscapes, advances in satellite remote sensing, and better atmospheric reanalyses with higher horizontal and vertical resolution, including layers in the snow, ground, and lakes, can complement in situ measurements and help fill spatial gaps between observation networks. These advances can also identify regions with the best potential for downscaling climate model outputs to project future linked climate-ecosystem dynamics. Moreover, incorporating multiple knowledge systems, including Indigenous and local knowledge through participatory research and community-based monitoring, can, in addition to scientific information from *in situ* and satellite data, substantially enhance the spatial coverage of observation networks (see, for example, Johnson et al., 2016, and the Atlas of Community-Based Monitoring – https://www.arcticcbm.org).

Author contributions

JM: Writing – original draft, Visualization, Formal Analysis, Conceptualization, Project administration, Investigation, Writing – review and editing. TC: Investigation, Writing – original draft, Writing – review and editing, Conceptualization. JC: Investigation, Writing – original draft, Writing – review and editing. WG: Investigation, Writing – original draft, Writing – review and editing. HM: Investigation, Writing – original draft, Writing – review and editing. NS: Investigation, Writing – original draft, Writing – review and editing. TV: Investigation, Writing – original draft, Writing – review and editing.

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Conflict of interest

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SUPPLEMENTARY FIGURE S1
In-situ monitoring of temperature **(a)** and precipitation **(b)** from national station networks. The eight largest rivers in the PADB (Yenisei, Lena, Ob, Pechora, Sev. Dvina, Kolyma in Eurasia; Mackenzie, Yukon in North America) are shown with a black outline.

SUPPLEMENTARY FIGURE S2
In-situ monitoring of discharge, available from the Global Runoff Data Centre (GRDC) stations catalogue, including latest data available.

SUPPLEMENTARY FIGURE S3
Catchments in the PADB that have monitoring of all hydroclimate variables, including discharge, climate (temperature and/or precipitation), active layer and permafrost.

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Arctic and Subarctic marine heatwaves and their ecological impacts

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The Arctic and Subarctic seas are predicted to become hotspots for marine heatwaves (MHWs). High-latitude marine ecosystems face unique consequences from accelerated warming and sea ice loss, challenging species adapted to cold conditions. We review the literature on MHW characteristics and ecological impacts in the Arctic and Subarctic seas, and contrast MHW characteristics between the Bering Sea and Barents Sea. We uncover the pervasive impacts of MHWs across widely different organism groups, including benthic foundation species, phytoplankton, zooplankton, fish, seabirds, and marine mammals. MHWs in the Arctic marginal seas are especially prevalent in areas experiencing sea ice retreat, such as seasonal sea ice zones, highlighting the complex interplay between MHWs and sea ice dynamics. Overall, few studies have documented the ecological impacts of MHWs on high-latitude ecosystems, with the notable exception of the impacts from the Bering Sea and Chukchi Sea MHWs in 2017–2019. Many Arctic species, with their cold and narrow thermal preferences, appear vulnerable to MHWs, as they might not have access to cold climate refugia, while boreal species appear to benefit from Arctic and Subarctic MHWs. Sessile foundation species, such as kelp and seagrasses, are especially at risk during MHWs, although in the Arctic evidence of MHWs impacts remains limited. Reproductive failure and mass mortality events have been documented for several species in the Pacific Arctic (e.g., seabirds, fish, crabs). MHWs have been observed to have ecosystem-wide repercussions in the northern Bering Sea and Chukchi Sea with shifts in plankton communities affecting the entire food web. The ecological responses to MHWs in the Arctic and Subarctic ecosystems are still not fully understood, highlighting a need for further research to assess the direct and indirect impacts on various taxa and to improve predictive models for better management and conservation strategies. MHWs can also have large consequences for ecosystem services and socio-ecological systems, for example, closures of economically valuable and culturally important fisheries, as seen in Alaska, degradation of traditional ice-hunting practices, and compromised wellbeing of coastal communities. Large and abrupt ecosystem changes following MHWs underscore the urgent need for adaptive management strategies in the face of ongoing climate change.

KEYWORDS

marine heatwave, sea ice, Arctic, Subarctic, marine ecosystem, climate change, extreme events, ecological change

1 Introduction

The Arctic marine ecosystem is characterised by extremely cold temperatures, extreme seasonality, and the presence of permanent and seasonal sea ice. Consequently, the Arctic supports specialised species adapted to these extreme conditions (Gradinger, 2001; Blix, 2005; Castellani et al., 2022). Arctic marine life has evolved to thrive in environments with uniquely prolonged periods of darkness (and light), cold temperatures, salinity variation, and seasonal sea ice cover. However, the Arctic marine ecosystem is changing fast due to anthropogenic climate change. Arctic sea ice is currently at the lowest level since at least 1850, and late summer sea ice loss is unprecedented for at least 1,000 years (IPCC, 2023). Since the late 1970s, Arctic sea ice has decreased in both area and thickness, with a larger area of first-year ice (Stroeve et al., 2012). The Arctic Ocean is expected to become sea ice free in late summer by the end of the 21st century regardless of CO_2 emissions scenarios (Notz and Community, 2020; Jahn et al., 2024). Sea ice is a critical habitat for many Arctic species and its disappearance will transform the Arctic ecosystem. Sea surface temperatures have increased in almost all regions of the Arctic and Subarctic (Figure 1A). Gradual warming of the Arctic Ocean has significantly transformed Arctic marine ecosystems (Mueter and Litzow, 2008; Huntington et al., 2020; Mueter et al., 2021; Husson et al., 2024).

Climate-driven changes are observed throughout the entire food web, from lower trophic levels to top predators. For example, sea ice loss causes an extension of the phytoplankton growing season and alters the timing of the blooms (Kahru et al., 2011; Ardyna et al., 2014; Oziel et al., 2017), while zooplankton populations shift from high to low-lipid content species (Møller and Nielsen, 2020; Kimmel et al., 2023), which can have ramifications for the entire marine food web. Upper trophic levels are also shifting their migration and distribution patterns (Kuletz et al., 2024a), as boreal species become increasingly dominant and compete with Arctic species,

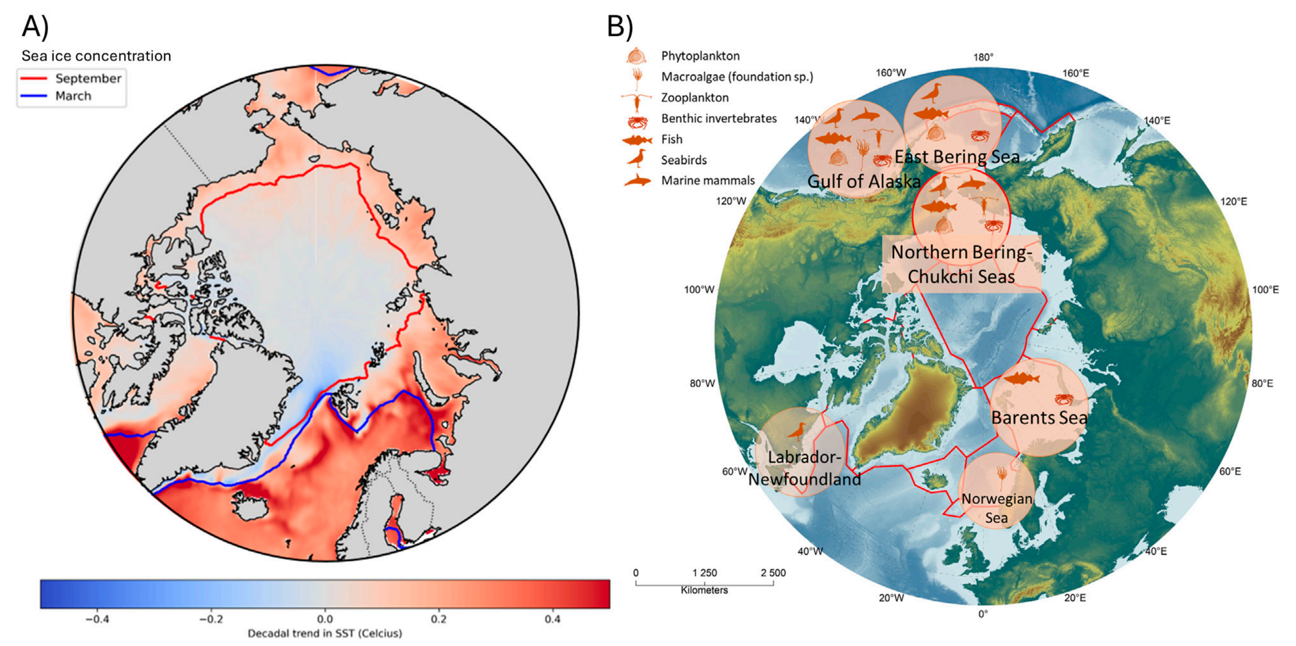

FIGURE 1
(A) Decadal trends in sea surface temperature (SST) calculated using Sen's slope (Sen, 1968) for the Optimally Interpolated SST (OISST) dataset between 1st September 1981 to 31st December 2023. The blue and red line represent the minimum (September) and maximum (March) sea ice extent, respectively, using the climatological mean of the period 1981–2023 and a 15% sea ice concentration cut-off. Multiyear ice, is the area between the North Pole (90˚N) and the red line; first-year ice, the area between the blue and red lines; and open water, the area below the blue line. **(B)** Circumpolar map depicting current knowledge on ecosystem responses to MHWs in the Arctic and Subarctic large marine ecosystems. Symbols represent different taxonomic groups and illustrate where their response to MHWs have been studied in peer-reviewed scientific literature (see references in Supplementary Table S1). The underlying Arctic large marine ecosystem (LME) map was obtained from PAME at https://pame.is/projects/ecosystem-approach/arctic-large-marine-ecosystems-lme-s.

a process known as borealisation (Fossheim et al., 2015; Mueter et al., 2021; Stafford et al., 2022; von Biela et al., 2023; Husson et al., 2024).

In addition to being a hotspot of decadal warming, the Arctic Ocean is also predicted to be a future marine heatwave (MHW) hotspot (IPCC, 2023). MHWs are periods where ocean temperatures substantially exceed historical norms in a given region, with durations ranging from several days to in some cases, years (Hobday et al., 2016). These events have varying spatial scales, spanning from just a few to many thousands of km (Sen Gupta et al., 2020; Oliver et al., 2021). Whilst some studies define MHWs by biological impacts, such as the threshold for coral bleaching (Pearce and Feng, 2013), they are most commonly defined when anomalies in sea surface temperature (SST) surpass their local 90th percentile threshold for at least five consecutive days or longer (Hobday et al., 2016). The category of a MHW is then assigned based on how much temperatures exceed the local climatology, ranging from moderate to extreme in intensity (Hobday et al., 2018).

MHWs are complex and highly multifaceted events, making it challenging to identify the underlying drivers of their onset, duration, and dissipation (Frölicher and Laufkötter, 2018; Holbrook et al., 2020). Localised factors such as temperature fluxes between the atmosphere and the ocean, or horizontal heat transport such as from Ekman advection, contribute to the onset and duration of MHWs (Holbrook et al., 2020). Over larger scales, MHWs are attributed to a combination of hydrodynamic and atmospheric forcings, as well as global-scale teleconnections (Holbrook et al., 2020). El Niño Southern Oscillation (ENSO), and the Atlantic Multidecadal Oscillation (AMO), have been shown to contribute towards some of the largest MHWs (Pearce and Feng, 2013; Holbrook et al., 2020; Ren and Liu, 2021). Some of the most notable MHWs, such as the northeastern Pacific "Blob" (the 2014–2016 MHW) have been linked to ENSO (Bond et al., 2015; Di Lorenzo and Mantua, 2016), while shifts in atmospheric jet streams contributed to MHWs in the Atlantic (Chen et al., 2014; Gawarkiewicz et al., 2019). ENSO has been one of the most prominent causes of MHWs globally, associated with warming events in the Pacific, the Atlantic, and the Southern Ocean. In addition to these physical drivers, human-induced global warming has contributed directly to many of the most intense MHWs (Laufkötter et al., 2020).

On a global scale, the frequency and duration of MHWs has increased, with their occurrence nearly doubling over the last century (Frölicher and Laufkötter, 2018; Oliver et al., 2018). Earth system model simulations have indicated that nearly 90% of MHWs have been attributed to anthropogenic warming, which is likely to increase with greater greenhouse gas emissions (Frölicher et al., 2018; Laufkötter et al., 2020). By the end of the century MHWs are expected to become more severe in their frequency, length, and intensity (Frölicher et al., 2018; Plecha and Soares, 2020). The number of MHWs are projected to increase significantly, with a global rise at the end of the century of 2–9 times under the low CO_2 emissions scenarios, up to 3–15 times under the very high CO_2 emissions scenario, with the largest changes projected for the Arctic and tropical oceans (IPCC, 2023). These prolonged periods of anomalously high SST will likely have large and lasting consequences for marine ecosystems (Arimitsu et al., 2021; Suryan et al., 2021).

While long-term ocean warming gradually reshapes the distribution of marine life and ecosystem structures, functions, and associated services (Vergés et al., 2014; Pecl et al., 2017), a single MHW can have large and long-lasting consequences on the whole ecosystem (Smale et al., 2019; Wernberg, 2021; Smith K. E. et al., 2023). MHWs can lead to the displacement of marine life at a much larger geographic scale compared with gradual, long-term, warming (Jacox et al., 2020). MHWs in tropical and temperate regions have been linked with depletion of kelp forests (Wernberg et al., 2019; Smith K. E. et al., 2023), extensive loss of seagrass (Strydom et al., 2020), bleaching of coral reefs (Hughes et al., 2017), harmful algal blooms, and mass mortality of fish, seabirds, and marine mammals (Roberts et al., 2019; Gabriele et al., 2022; Jones et al., 2023).

The ecological impacts of MHWs on high-latitude ecosystems are just beginning to emerge. Here, we review the current knowledge of MHW characteristics in the Arctic and Subarctic seas, by discussing the unique features of MHWs in these regions, notably their interactions with sea ice. We then calculate and compare the temporal trends of MHWs metrics in the Bering Sea and Barents Sea, two major Arctic gateways and transition regions between Subarctic and Arctic conditions. Next, we reviewed documented impacts of MHWs on Arctic and Subarctic marine ecosystems across trophic levels and functional groups (Figure 1B, a summary table of which and how taxonomic groups have been documented to respond to MHWs can be found in Supplementary Table S1). The ecological impacts of MHWs in Arctic and Subarctic marine ecosystems are being increasingly documented. Throughout the review, we especially draw on studies linked to the Bering Sea and Chukchi Sea MHWs in 2017–2019 (Box 1), and to a lesser extent to the 2014–2016 MHW event (the "Blob") in the northeast Pacific as well as some global model studies. We also discuss the social and economic implications of MHWs, notably their impacts on commercial and subsistence harvest opportunities and disruption of traditional livelihoods in the Arctic. Finally, we discuss how more adaptive management options could help the social-ecological system become more resilient to MHWs, as well as highlights current knowledge gaps and research needs.

Box 1 Case study: ecosystem-wide impacts of the 2017–2019 MHW in the northern Bering and Chukchi seas

The northern Bering Sea and Chukchi Sea experienced a series of MHW events during 2017–2019 (Baker et al., 2020; Kuletz et al., 2024b (Supplementary Appendix 1A) (Figure 3F). The winters of 2017/2018 and 2018/2019 had extremely low sea ice extent, and the Bering Sea cold pool, the area where near bottom water is less than 2°C on the Bering Sea shelf, disappeared in the summers of 2018 and 2019. This extreme event triggered complex responses throughout the marine food web in the northern Bering Sea and Chukchi Sea, impacting the entire ecosystem from primary production, zooplankton, fish populations, seabirds, and marine mammals (Figure 4). Reduced ice cover and warmer seas altered thermal, light, and stratification conditions, influencing the timing and extent of phytoplankton blooms. In 2018, while the phytoplankton bloom was delayed in the southern Bering Sea, and significantly lower than usual in the northern Bering Sea, the ice-associated bloom occurred early and was extensive (Duffy-Anderson et al., 2019). Cases of harmful algal blooms arose which could impact UTLs (Walsh et al., 2018), such as occurred in the northern Bering and

(Continued on following page)

Box 1 (*Continued*) Case study: ecosystem-wide impacts of the 2017–2019 MHW in the northern Bering and Chukchi seas

Chukchi seas, where seabird die-offs were associated with toxic algae blooms (Van Hemert et al., 2020). In the Chukchi Sea, changes in zooplankton and benthic populations were observed, with copepods (*Calanus glacialis/marshallae*) and epibenthos having much lower abundance compared to previous years (Huntington et al., 2020).

In the Bering Sea, during the MHW a shift in the zooplankton community was observed, with an increase in small, low-lipid copepods and a decrease in large, high-lipid copepods (Duffy-Anderson et al., 2019). Young fish also seem to have responded to the MHW, with a large increase in the abundances in 2017 of juvenile pink salmon, juvenile walleye pollock, and age-0 polar cod, although with overall low energy content for the latter (Huntington et al., 2020; Copeman et al., 2022; Levine et al., 2023). The effects of the warm period extended to higher trophic levels. With the lack of the cold pool in the Bering Sea in 2018, adult walleye pollock, Pacific cod, and northern rock sole biomass increased in the northeastern Bering Sea, likely due to northward expansion (Stevenson and Lauth, 2019), whereas the snow crab population collapsed as a result of reduced habitat and increased competition, which led to mass mortality events, likely due to starvation (Szuwalski et al., 2023). Seabird populations also experienced mass mortality events, such as puffins in 2017 (Jones et al., 2019), and murres, fulmars (*Fulmarus glacialis*), and shearwaters in the Bering Sea in 2018 (Duffy-Anderson et al., 2019; Jones et al., 2023). Changes in seabird distribution were observed with notably an increase in short-tailed shearwater densities in the Chukchi Sea (Kuletz et al., 2024b), and breeding success was low for seabirds in the Bering Sea (Romano et al., 2020; Will et al., 2020a). The ecosystem changes also affected marine mammals. Bowhead whales were sighted earlier than usual in northern Alaska, and their wintering patterns shifted to the Chukchi Sea (Huntington et al., 2020). Spotted seal pups were found in poorer condition, and a significant increase in seal carcasses, particularly in the northern Bering and southern Chukchi seas, was observed (Huntington et al., 2020). The MHW in the northern Bering and Chukchi seas has had consequences on all trophic levels, which ultimately can impact ecosystem structure and functioning. The MHWs can have direct and indirect effects on the populations, yet which effect dominates remains unknown and will vary across trophic levels, with food web mediated effects likely affecting UTLs. Huntington et al. (2020) suggests that observed changes in the composition and abundance of zooplankton towards lower-lipid species, along with an increased competition due to a higher biomass of predator fish, might have caused the observed mass mortality of seabirds and seals. While the northern Bering and Chukchi seas have shown signs of transition towards a Subarctic ecosystem in response to ocean warming, the ecosystem response to the 2017–2019 MHW events may be preludes to future changes.

2 Specificity of marine heatwaves in the Arctic and Subarctic

The intensity, duration, and frequency of MHWs have increased in the Arctic Ocean and its marginal seas (Carvalho et al., 2021; Golubeva et al., 2021; Huang et al., 2021). Between 2007 and 2021, 11 MHWs occurred with peak anomalies up to 4°C (Barkhordarian et al., 2024). These MHWs coincide with significant declines in Arctic sea ice (relative Arctic sea ice extent anomalies), notably in 2007, 2012, and 2020, with the 2020 event being the most severe in terms of intensity and duration (Barkhordarian et al., 2024). Between 1982 and 2020, the frequency and duration of MHWs in the Barents Sea significantly increased, with more than half of the MHW days having occurred between 2011 and 2020, and the most intense event in 2016 (Mohamed et al., 2022b). Similarly, in the Bering Sea, Carvalho et al. (2021) showed that in the period 1990–2019 the number of MHWs days increased, with the last decade (2010–2019) having the largest number of MHWs and MHW days. The increased trends of MHWs in the Arctic are closely associated with the long-term decrease in sea ice concentration and increase in surface air temperature (Huang et al., 2021; Barkhordarian et al., 2024).

2.1 Drivers of MHWs in the Arctic

In the Arctic Ocean, MHW dynamics are unique due to the complex links between the ocean, sea ice, and atmosphere (Hu et al., 2020; Barkhordarian et al., 2024). To date, relatively few studies have analysed the drivers of MHW onset and decay in the Arctic. The Arctic Ocean is relatively isolated from the rest of the global ocean, except for inflow shelfs such as the Barents and Bering Seas (Carmack et al., 2015). Consequently, the primary driver of MHWs in the Arctic is heat exchange between the atmosphere and the ocean, mainly through radiative fluxes (Hu et al., 2020; Richaud et al., 2024). The advection of oceanic heat plays a more important role in the inflow regions (Richaud et al., 2024). In general, Arctic MHWs dissipate through bottom heat fluxes, in spring and summer, and through surface fluxes in autumn, but there is spatial heterogeneity in the driving heat fluxes (Richaud et al., 2024). As such, common drivers of Arctic MHWs are similar to more temperate regions.

A unique feature of the Arctic is the presence of sea ice, which influences the occurrence and intensity of surface MHWs in complex ways. By reflecting large parts of incoming solar radiation, and through heat uptake and release during melting and freezing, the presence of sea ice keeps surface ocean temperatures close to the freezing point and temperature variability low (Carton et al., 2015). MHWs therefore mainly occur in open water or partially ice-covered waters (Hu et al., 2020; Huang et al., 2021), and the frequency and intensity of MHWs are inversely correlated to the sea ice cover (Carvalho et al., 2021; Golubeva et al., 2021; Mohamed et al., 2022b; Barkhordarian et al., 2024). Sea ice is thought to influence MHWs in two ways. First, sea ice melt in spring exposes the surface ocean to more solar heating, which can create or enhance MHWs (Barkhordarian et al., 2024; Richaud et al., 2024). Second, released freshwater from sea ice melt shoals the surface mixed layer, which can accelerate the heating by surface fluxes. Through this process, the presence of sea ice in seasonally ice-covered waters can potentially amplify the intensity and duration of MHWs (Hu et al., 2020; Richaud et al., 2024).

Recently, Zhang et al. (2024) investigated the main factors influencing Arctic MHWs from 1982 to 2020 in different ice cover regions, including multiyear ice, seasonal or first-year ice, and open water (Figure 1A). They found that the MHWs in the MYI region are mainly influenced by freshwater dilution processes such as sea ice concentration, precipitation and salinity of the mixed layer. In the FYI region, MHWs were influenced by surface air temperature and total heat flux mainly through thermodynamic processes, and the 500-hPa geopotential height also influences MHWs mainly through large-scale atmospheric circulation. MHWs in the OPW region were associated with sea ice, 850-hPa geopotential height, and meridional wind components, suggesting that MHWs in this region are correlated with atmospheric processes and wind fields. Generally, MHWs in shallow water regions (e.g., Barents Sea and North Sea) are coupled with the atmosphere (Mohamed et al., 2023; 2022b). However, MHWs occurred more frequently in the Barents Sea than in the North Sea. This could be due to Arctic amplification (Screen and Simmonds, 2010).

Because of the strong control of sea ice on surface temperatures, the recent decline in Arctic sea ice cover strongly contributed to the increased occurrence and intensity of Arctic MHWs (Mohamed et al., 2022b; Barkhordarian et al., 2024). First, sea ice loss plays a key role in Arctic amplification (Screen and Simmonds, 2010), leading to more extreme warming of the Arctic Ocean compared to the global oceans (Shu et al., 2022). Second, sea ice loss exposes regions with a low temperature variability to strong temperature increase, which can facilitate the occurrence of MHWs (Frölicher et al., 2018; Huang et al., 2021). Changes in the timing of Arctic MHWs are also influenced by changes in sea ice phenology. Huang et al. (2021) found a strong extension of MHW conditions during autumn, which is caused by the stronger trend in later sea ice advances compared to the trend in earlier sea ice retreats. In addition, the more severe Arctic MHWs occurr predominantly in regions with first-year ice, driven by ocean stratification (Zhang et al., 2024). As the extent of first-year ice increases in the Arctic, MHWs are expected to become more frequent and intense (Hu et al., 2020).

Defining MHWs from satellite observations of SST poses challenges in polar environments due to interannual variability in sea ice cover, limiting the number of open-water days from year to year. In a circumpolar study of MHWs in the Arctic, Huang et al. (2021) used the under-ice SSTs in areas of seasonal ice cover, allowing for long-term assessments of MHWs in historically ice-covered regions. Sea ice acts as a physical barrier to the atmosphere, thereby limiting atmospheric forcings on the ocean, and as such, both statistical (Huang et al., 2021) and mechanistic (Banzon et al., 2020) approaches can be used to estimate under-ice SST. Furthermore, because of the low temperature variability, defining MHWs in sea ice covered regions can be challenging, because the MHW threshold is very close to the climatological average. For example, regions permanently ice-covered in winter experience MHW conditions due to long-term upper-ocean freshening, which raises the freezing point of water (Richaud et al., 2024).

2.2 Characteristics of MHWs in the Subarctic marginal seas: example of the Bering and Barents seas

In this section, we compare the trends of SST anomalies (SSTA) and MHW characteristics in the two main pathways to the Arctic Ocean (i.e., the Barents Sea and the Bering Sea) by reviewing and extending the results of Carvalho et al. (2021) and Mohamed et al. (2022b). Following Hobday et al. (2016), daily SST data from the NOAA Optimum Interpolation SST (OISST) V2.1 product (Reynolds et al., 2007) were used to detect MHW events in these two regions over the period 1982–2022 (41 years). MHWs are "prolonged periods of anomalously warm water in which the SST exceeds the 90th percentile of the 30-year local mean for five consecutive days or longer" (Hobday et al., 2016). Here, we consider all the criteria of Hobday et al. (2016), including the SST baseline climatology, which should be based on at least 30 years, and if two consecutive MHW events occur with gaps of 2 days or less, they are considered as a single event. The climatological mean and the 90th percentile threshold are thus calculated based on the entire period (1982–2022). We compare trends in SSTA and MHWs metrics frequency (MHW events/decade) and total duration (number of days). The SSTA is calculated by subtracting the corresponding monthly climatology value from the observed SST value for each calendar month in the dataset.

In the Barents Sea, there was high spatial variability in SSTA with the highest SSTA trends in the regions affected by the accumulation of warm Atlantic water (Skagseth et al., 2020). Specifically, in the southeastern part of the Barents Sea and the Storfjorden Trough, SSTA trends were greatest, while the lowest SSTA trend was observed in the northern part of the Barents Sea and the Storbanken region (Figure 2A). Non-significant SSTA trends were found over the north and east of Svalbard, south of Franz Joseph Land, and on Spitsbergen Bank (Figure 2A), which were mainly influenced by the sea ice in these regions. For the Bering Sea, significant ($p < 0.05$) SSTA trends were observed over the entire region (Figure 2B), with a few exceptions that showed non-significant trends.

The highest SSTA trend was observed in the western Bering Sea, while the lowest trends were found in the eastern Bering Sea (Figure 3B). The highest SSTA values in the Barents Sea were observed in 2013 and 2016, which were associated with a strong positive phase of the East Atlantic Pattern (EAP), while the lowest values were recorded in 1982 and 1998 (Figure 3A). In the Bering Sea, the highest SSTA values were observed in 2003 and between 2014 and 2020, while the lowest anomalies were recorded in 1999 and 2012 (Figure 3B). It is noteworthy that the SSTA in the two basins showed opposing fluctuations (i.e., anti-correlated positive and negative anomalies) in 1997, 2003, 2012, and 2019. The overall temporal trends of SSTA were 0.31 ± 0.11 and 0.24°C ± 0.09°C/decade for the Barents Sea and Bering Sea, respectively (Figures 3A, B; Table 1).

Statistically significant trends in MHW frequency and total number of days were observed in most areas of the Barents and Bering seas (Figures 2C–F). In the Barents Sea, the strongest trend in both MHW frequency and total number of MHW days was observed in southwestern Svalbard and the southern part of the Barents Sea (Figures 2C, E), i.e., in the regions affected by the inflow of warm Atlantic water. These patterns were broadly consistent with SST trends (Figures 1B, 2A), confirming the role of long-term warming in the formation of MHWs. The lowest trends in MHW frequency and total number of days are found in the south-western part and northern part of the Barents Sea. The low trends in these regions could be due to lower SST variability (Mohamed et al., 2022a), as the southwestern region is influenced by warm Atlantic water, while the northern regions are mainly influenced by cold Arctic water. An increase in the trend of MHW frequency was observed for most of the Bering Sea, excluding the Alaskan coast (Figure 2D). The largest MHW frequency trends (up to 1.8 events/decade) were observed in the western Bering Sea and along the Russian coasts, while the lowest MHW frequency trends were observed in the eastern Bering Sea and the Bering Strait (Figure 2D). The MHW days showed significant trends over the Bering Sea (Figure 2F). The highest MHW days trends (up to 28 days/decade) were observed in the central Bering

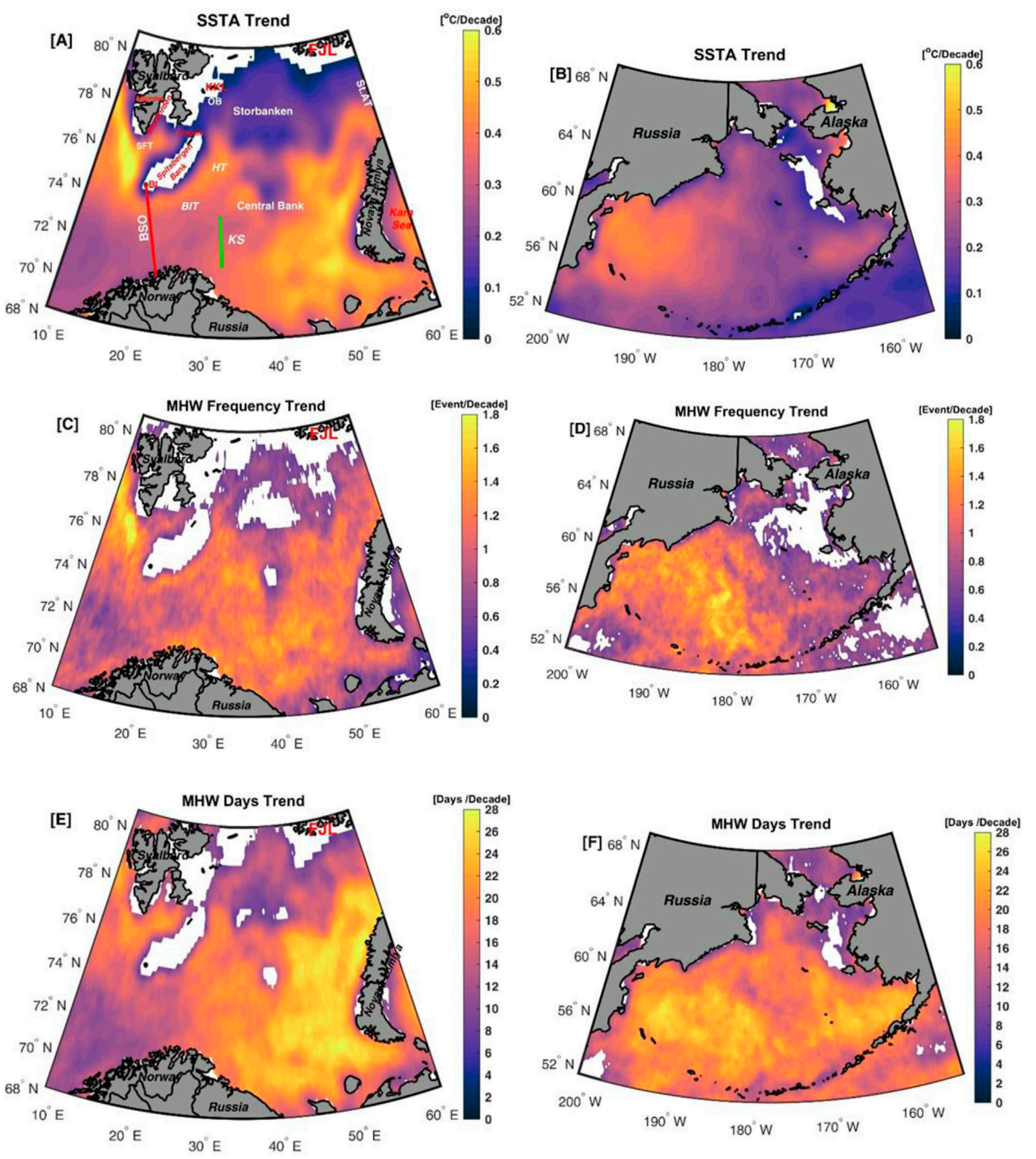

FIGURE 2
Trend maps for **(A, B)** sea surface temperature anomalies (°C/decade), **(C, D)** MHW frequency (events/decade), **(E, F)** MHW days (days/decade) between 1982 and 2022 for the two pathways to the Arctic Ocean - the Barents Sea (left column) and the Bering Sea (right column). The white regions indicate that the trend is non-significant ($p > 0.05$) at a 95% confidence interval. The abbreviations in panel **(A)** refer to the Barents Sea Opening (BSO), Hopen Trench (HT), Bear Island Trough (BIT), Bear Island (BI), Storfjorden Trough (SFT), Franz Joseph Land (FJL), Kong Karls Land (KKL), Olga Basin (OB), and the St. Anna Trough (St.AT). The Kola Section (KS) is marked with a straight green line.

Sea, while the lowest MHW days trends were found in the northern Bering Sea and the Bering Strait (Figure 2D).

A temperature shift was observed in the Barents Sea after 2004, which was associated with an increase in MHW events from 1 event per year to >3 events per year compared to the period before 2004 (Mohamed et al., 2022a; 2022b). The highest annual MHW frequency (>5 events/year) and total days (>100 days/year) were observed in 2012, 2013, and 2016

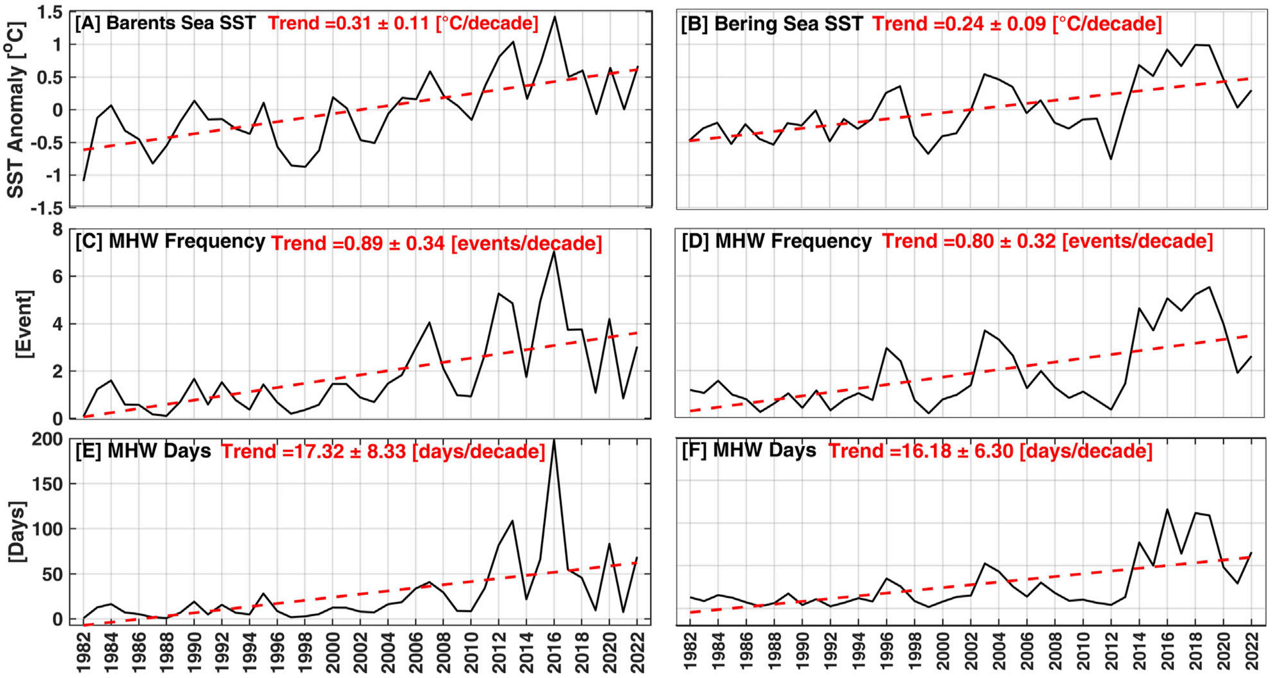

FIGURE 3
Temporal annual variability and trends for **(A, B)** sea surface temperature anomalies (°C/decade), **(C, D)** MHW frequency (events/decade), **(E, F)** MHW days (days/decade) between 1982 and 2022 for the two pathways to the Arctic Ocean: the Barents Sea (left column) and the Bering Sea (right column). The red dashed lines represent the best-fit linear curves of the SST and MHW characteristics. Note that the trend values are also displayed at the top of each subgraph.

TABLE 1 Summary of the long-term trend in SST (°C/decade), MHW frequency (events/decade), and MHW days (days/decade) for the Barents Sea and Bering Sea between 1982 and 2022.

Region	SST	MHW frequency	MHW days
Barents Sea	0.31 ± 0.11	0.89 ± 0.34	17.32 ± 8.32
Bering Sea	0.24 ± 0.09	0.80 ± 0.32	16.18 ± 6.30

(Figures 3C–E), which were also the warmest years in the Barents Sea (Figure 3A). Sea ice duration in the Barents Sea in these warm years was <80 days/year (Mohamed et al., 2022a), which is considered a favourable condition for the MHWs and increases the probability of their occurrence. In the Bering Sea, the highest annual MHW frequency (>3 events/year) and total days (>40 days/year) were observed in 2003, and between 2014 and 2020 (Figures 3D, F). The occurrence of a MHW in the Bering Sea is highly correlated with the reduction of the sea ice concentration in the Chukchi Sea and the increase in the Alaskan air temperature (Carvalho et al., 2021). The average trends of MHW frequency and total days in the Barents Sea (Bering Sea) were 0.89 ± 0.34 (0.80 ± 0.32) events/decade and 17.32 ± 8.32 (16.18 ± 6.30) days/decade, respectively. The year 2016 stands alone with a record of 7 (5) events and 200 (110) MHW days in the Barents Sea (Bering Sea) (Figures 3C–F). In general, an increase in MHW frequency and total days were observed in both the Barents and Bering seas during the study period. The distribution of frequencies and total days followed similar temporal distributions of SST, indicating the role of Arctic amplification in the generation of MHWs. This suggests that the MHW metrics might be very different in these Subarctic regions if the MHWs were detected by removing the SSTs trend instead of using a fixed baseline.

One of the longest-lasting and most impactful MHW events in the northeast Pacific is known as the warm "Blob" that occurred in 2014–2016, while in the Bering Sea, multiple MHWs occurred in 2017–2019, as shown by SSTA (Figure 2B). The "Blob" was mainly caused by a persistent high-pressure system that led to a reduction in winds and heat exchange between the ocean and the atmosphere. This led to an accumulation of warm water in this region, causing ocean temperatures to reach record-breaking levels. The SST associated with the "Blob" was exceptionally high; in some regions, the SSTA was about 3°C–6°C above average (Gentemann et al., 2017).

3 Ecological responses to MHWs

The impacts of MHWs are superimposed on substantial climate-driven changes occurring across Arctic marine ecosystems. The Arctic is warming at a rate that is four times faster than the global average (Rantanen et al., 2022), which has significantly altered the Arctic and Subarctic marine ecosystems through the reduction in sea ice thickness and extent, warming sea temperatures, increased freshening and stratification, and higher turbidity due to melting land ice and run-off (Meredith et al., 2019). These climate-driven changes impact the entire food web, from the lower trophic level to top predators (Wassmann et al., 2011; Husson et al., 2024). For pelagic species in the western Arctic Ocean, increased stratification reduces nutrient supply (Polyakov et al., 2020; Zhuang et al., 2021), which appears to favour smaller phytoplankton types over larger diatoms, such as in the Beaufort Sea (Li et al., 2009) and Chukchi Sea (Neeley et al., 2018), and can cause harmful algal blooms (Anderson et al., 2022). Modelling studies also indicate that future climate change in the Arctic might favour phytoplankton species adapted to mid-latitude environments, such as coccolithophores, leading to a potential shift in planktonic ecosystems (Manizza et al., 2010; Neukermans et al., 2018). Additionally, sea ice loss affects the timing of phytoplankton blooms, extending the growing season (Manizza et al., 2023), while the delayed freeze-up of Arctic sea ice has also triggered a new and unprecedented novel fall bloom (Ardyna et al., 2014). Changes in sea ice cover and ocean warming also impact zooplankton populations, for example, large, high-lipid copepods tend to decline while smaller copepods with lower lipid content tend to increase in number and range, such as occurred in the Bering Sea (Kimmel et al., 2023) and Western Greenland (Møller and Nielsen, 2020). The population changes from high to low-lipid content has large ramifications for the marine food web. Reduced Arctic sea ice also increases the light reaching the sea floor in some areas, which can increase benthic primary production. This is driving increases in biomass and depth extent of macroalgal forests, seagrass meadows, and microalgal mats along some Arctic coastlines (Krause-Jensen et al., 2019; Attard et al., 2024). Yet, long-term data on these changes remains rare, and the impacts of sea ice loss are likely offset by increased turbidity from melting ice in other areas (Bonsell and Dunton, 2018; Filbee-Dexter et al., 2019). Upper trophic levels in the Arctic are also responding to long-term warming and sea ice retreat by altering their distributions, migration patterns, and phenology (Stafford et al., 2022; Husson et al., 2024; Kuletz et al., 2024a), and there is evidence of changes in their feeding, reproductive success, and survival (Mueter and Litzow, 2008; Fossheim et al., 2015; Stevenson and Lauth, 2019; Mueter et al., 2021; Renner et al., 2024).

The ecological response to MHWs can vary significantly based on the duration and intensity of the event (Joyce et al., 2024). Short and high-intensity MHWs are expected to cause acute stress, potentially increasing mortality, especially for sessile species (Smith K. E. et al., 2023; Garrabou et al., 2022). Longer, but not especially more intense, MHWs might in contrast alter the fitness of the organisms, such as altering their feeding, growth and reproduction, and ultimately lead to changes in mortality rates (Piatt et al., 2020). Long-lasting MHWs can also cause a distributional shift of species, impacting ecological communities and food webs. A global model study showed that while short MHWs might result in moderate biomass reduction, especially in the polar biomes, longer MHWs might cause larger ecosystem impacts, which would take longer to recover in polar systems than in temperate or tropical systems (Guibourd de Luzinais et al., 2024). We review below observed and modelled MHW' ecological impact studies. We acknowledge that MHWs can have differentiated impacts on the ecosystems based on their characteristics, such as their duration, but in this review, we do not explicitly separate the ecological impacts based on the MHW characteristics, nor disentangle the effects of a MHW event from long-term warming.

3.1 Phytoplankton

Changes in upper-ocean stratification in the Arctic are directly attributed to MHW events, through increased warming and buoyancy to the top layers of the water column (Hu et al., 2020; Richaud et al., 2024). This change in stratification may consequently impact the availability of nutrients and light available to phytoplankton, thus altering the species composition of the planktonic ecosystem. During the recent MHWs in the subpolar North Pacific Ocean, several studies have shown shifts in phytoplankton functional groups (Suryan et al., 2021; Wyatt et al., 2022; Arteaga and Rousseaux, 2023; Strom, 2023). The 2014–2016 MHWs in the Gulf of Alaska (GoA) caused a shift in the phytoplankton communities through a reduction in surface biomass and shift from large to smaller cells (Suryan et al., 2021; Strom, 2023). Modelling studies in the GoA agree with observations and showed that the warm “Blob” in 2014 caused the occurrence of a phytoplankton shift, with dinoflagellates being favoured at the expense of diatoms due to the reduction in silicate availability caused by increased stratification (Wyatt et al., 2022; Arteaga and Rousseaux, 2023). Similarly, MHWs in the polar waters of the southern hemisphere caused a shift from cryptophyceae to nano-phytoflagellates and other heterotrophic groups (Latorre et al., 2023).

Studies on both long-term effects and on MHW events are aligned with previous literature on phytoplankton succession being driven by nutrients and turbulence (Margalef, 1978). Anthropogenic climate change in the Arctic and Subarctic regions has been transforming the physical and chemical habitat of planktonic organisms and thus driving ecological shifts. As these regions warm and become more stratified, smaller phytoplankton tend to dominate in calm, low nutrient environments, whereas larger phytoplankton succeed in areas of higher turbulence and greater nutrient concentrations (Ardyna and Arrigo, 2020). The modelling results focusing on MHW events, and those with projections into a future warmer climate, tend to converge on the response of the phytoplankton assemblages responding to large thermal perturbations, from the lower atmosphere to the upper ocean (Ardyna and Arrigo, 2020; Henson et al., 2021).

MHW events, and ocean warming more generally, can affect the bloom phenology. For example, in the Bering Sea, during years of intense warming (2017–2019) and low sea ice coverage, the phytoplankton bloom phenology markedly changed, with an increased importance of winds at controlling their seasonal timing and onset (Nielsen et al., 2024). Furthermore, MHWs can be associated with other extreme events such as acidification and de-oxygenation throughout the water column, as modelled in the GoA (Hauri et al., 2024). These compound extreme events could impact planktonic organisms in multiple ways, such as shifting from diatoms to nanophytoplankton (Hare et al., 2007), a decrease in taxonomic diversity (Hoppe et al., 2018), and competition changes within and between phytoplankton functional groups (Dutkiewicz et al., 2015). Shifts in phytoplankton composition can be furthered by consecutive MHW events. For example, coastal Arctic phytoplankton exposed to repeated heatwave conditions in incubation experiments revealed that both cool and warm phases of consecutive MHWs can have long-term impacts on phytoplankton physiology and composition (Wolf et al., 2024). Ultimately, additional studies are needed to determine the consequences of the co-occurrence of MHWs and ocean acidification on phytoplankton community composition.

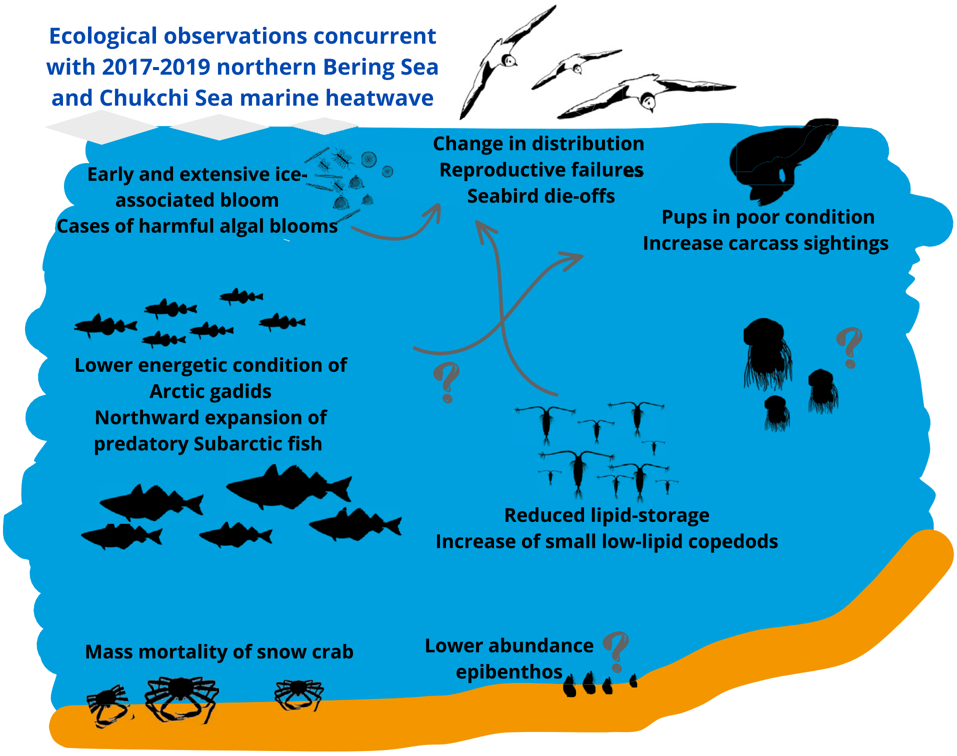

FIGURE 4
Schematic representation of ecological observations attributed to the 2017–2019 MHWs in the northern Bering Sea and the Chukchi Sea. The question marks indicate that there remain large knowledge gaps on the ecological response to MHWs in this Arctic LME (e.g., the response of the pelagic and benthic invertebrates and the indirect, food web mediated effects).

The response of the phytoplankton to MHWs in the global ocean varies with latitude (Noh et al., 2022). Chlorophyll responses to MHW switch from negative to positive in both hemispheres around the 40°–50° latitude bands (subpolar regions), the areas where the strongest meridional gradient in nitrate concentration exists (Noh et al., 2022). In these response-changing regions, the latitudinal contrast of the chlorophyll response is starker in the warm season rather than in the cold season due to the shallower climatological mixed layer. The Noh et al. (2022) study highlights that the phytoplankton responses to MHWs highly depend on the upper-ocean interactions between phytoplankton and the mixed-layer that ultimately impacts the light and nutrient availability. Similarly, the magnitude of phytoplankton blooms during a MHW occurrence depends on background nutrient concentration (Hayashida et al., 2020). Considering that model projections suggest a poleward expansion of the nutrient-poor waters in the future, we would expect the development of weaker phytoplankton blooms during MHWs in the coming decades. However, their future model projections do not show a great impact on the Arctic and Subarctic oceans, where phytoplankton blooms during MHWs are expected to remain strong.

3.2 Zooplankton

Changes in the composition of phytoplankton could affect zooplankton assemblages, both directly (impacting their metabolism) and indirectly (changing their food source and trophic interactions). The impact of MHWs on Arctic zooplankton communities is still sparsely studied, but some observations from the “Blob” allow us to draw some general understanding of zooplankton response. In the northern California Current, there was an observed increase in the species richness of copepods but an overall decrease in the biomass of both copepods and euphausiids (krill) (Peterson et al., 2017), while other studies observed a decrease in euphausiid biomass concomitant with the “Blob” in the California Current (Cavole et al., 2016; Lavaniegos et al., 2019). In the GoA, a decline of euphausiids in the walleye pollock (*Gadus chalcogrammus*) diet during 2015 points to a potential negative impact of the MHW on euphausiid populations (Rogers et al., 2021), but contrasting observations reflect that the euphausiid response was not clear (Batten et al., 2022). Generally, warm-water associated zooplankton appeared to have increased during the MHW event in the GoA (Suryan et al., 2021; Batten et al., 2022), while the cool-water associated zooplankton community did not show any evident response (Suryan et al., 2021). Consistent with the observed impacts of long-term warming, MHWs are expected to impact the zooplankton communities by switching the dominance of high-lipid, cold-associated copepods towards low-lipid, warm-associated copepods, as observed in the Bering Sea (Duffy-Anderson et al., 2019). Being at the base of the food web, lower zooplankton food quality (i.e., low-lipid organisms), can have repercussions on the rest of the food web, such as resulting in a decrease in fish larvae and juvenile survival, and ultimately increased mortality of upper trophic levels (Figure 4, Box 1).

Jellyfish distributional response to warming temperatures has been examined in the Bering Sea (Brodeur et al., 2008; Decker et al., 2023), but linkages to MHWs in the Arctic have not been studied. Summer trawl surveys in the eastern Bering Sea of jellyfish biomass from 1975 to 2005 showed an increase in jellyfish biomass throughout the 1990s. Starting in the 2000s, warmer temperatures co-occurred with a peak in jellyfish biomass, which then stabilized throughout the rest of the study period. On the other hand, a hindcast model for the Eastern Bering Sea from 1985 to 2017 observed no significant increases in jellyfish biomass in warmer years, which may be evidence of jellyfish adaptation to ecosystem shifts (Decker et al., 2023). These long-term observations and models indicate the sensitivity of jellyfish biomass to thermal regime changes, underscoring the need to understand MHWs impacts on jellyfish populations, as changes in jellyfish biomass can significantly impact the Subarctic ecosystems, particularly affecting zooplankton and fish communities through direct predation and competition (Brodeur et al., 2002).

3.3 Benthic species

Sessile foundation species provide ecosystem structure and function, through the establishment of a physical framework that supports other species (Wernberg et al., 2024). For example, Arctic kelp species, which are large brown seaweeds occurring throughout Arctic coastal waters, provide habitat and food for many ecologically and commercially important species, due to their high standing biomass, productivity, and physical habitat structure (Filbee-Dexter et al., 2019; Lavoie et al., 2024). Changes in the composition and abundance of sessile foundation species may severely degrade the health and resilience of marine systems to other stressors (Thomson et al., 2015). These sessile species are particularly vulnerable to MHWs due to their inability to escape, making them more sensitive compared to mobile species such as fish (Smale et al., 2019). Although sessile organisms can acclimate to tolerate slightly warmer conditions (Staehr and Wernberg, 2009; Staehr and Borum, 2011), temperatures above a certain optimum will affect performance negatively, for example, through reduced growth and reproduction, while exposure to temperatures near the upper level of tolerance lead to enhanced mortality. Severe heat stress occurring under a MHW may thus lead to reduced fitness, local extinctions, and eventually, to large-scale changes in range distribution.

Only a few studies have documented the ecological effects of MHWs on Arctic sessile foundation species, however studies from other areas indicate negative effects at all levels (species, communities, ecosystems) with some effects persisting long after the MHW event. MHWs are most damaging at the warm range edges of species, because they push the local temperatures across thermal thresholds for mortality (Smale et al., 2019; Filbee-Dexter et al., 2020). In the Arctic, most foundation species are at their cool range edges and therefore may not yet be vulnerable to MHWs. This is particularly true for Arctic macrophytes, which have only recently recolonized the Arctic after it reopened following the last ice age. These plants are therefore near their cool range edges and experience water temperatures well below their thermal maxima (Bringloe et al., 2022). Climate-driven increased water temperature and decreased sea ice cover can therefore benefit foundation species in the Arctic. For example, persistent losses in sea ice cover along Arctic coastlines are expected to expand habitats for macroalgae and seagrass (Attard et al., 2024), although there is yet little evidence of these impacts (Krause-Jensen et al., 2020).

An analysis of the vulnerability of seagrass to MHWs across their global distribution, using empirically- or experimentally determined seagrass upper thermal limits, found that seagrass growing in boreal and Subarctic regions will not cross their thermal limits within the next 200 years, making direct mortality from a MHW unlikely (Marbà et al., 2022). Similarly, kelps are often living below their thermal optima in the Arctic. This lack of vulnerability is supported by a laboratory study of MHW impacts on two kelp species (*Agarum clathratum* and *Saccharina latissima*) at their cold range limit in Greenland. The study found no impact of higher temperature during a simulated MHW on the species, and showed that warmer temperatures mitigated (to some extent) the impact of low light stress (Niedzwiedz et al., 2024). Yet, in some regions of the Subarctic, kelps are near their thermal maxima and can be susceptible to summer MHW events. An example of a dominance shift following a MHW is the observed decline in macroalgal foundation species in the northern GoA following the “Blob,” which caused a region-wide shift in rocky intertidal habitats from a state dominated by autotroph-macroalgal (*Fucus distichus)* to a heterotroph-filter-feeder dominated state (Weitzman et al., 2021). Other examples of vulnerable kelps could include the Arctic endemic kelp *Laminaria solidungula*, which is range restricted to 6°C summer temperatures, although it can tolerate up to 16°C for up to 2 weeks (Roleda, 2016).

Seagrasses generally display a wide temperature tolerance range with the ability to acclimate making them capable of dominating the sublittoral soft bottom zone of climatic zones extending from tropical to arctic conditions (Staehr and Borum, 2011 and references therein). While seagrasses generally display a capacity for range shifts, some slow growing species are less tolerant and capable of acclimating to sudden temperature elevations, potentially causing negative local impacts of MHWs for seagrasses living near their upper temperature tolerance limits. Evidence of such negative local impacts on seagrasses has so far not been found in Arctic waters. Overall, the impact of MHWs on the sessile foundation species adds to other important human related pressures, such as overgrazing from sea-urchins (stimulated by overfishing of top-predators), coastal eutrophication, and physical disturbance from human activities like sediment extraction and bottom trawling. Reducing these pressures is therefore crucial for enhancing coastal ecosystem resilience to MHW impacts (Wernberg et al., 2024).

High-latitude marine ecosystems are characterized by relatively high benthic biomass, with the Bering Sea and the Chukchi Sea being notable “hotspots” of benthic biomass (Wei et al., 2010; Grebmeier et al., 2015). Despite this, the impact of MHWs on high-latitude benthic invertebrates has generally been little studied. One significant exception is the documented mass die-offs of snow crab (*Chionoecetes opilio*) in the Bering Sea between 2018 and 2021 (Figure 4, Box 1), making it one of the largest observations of the negative ecological effects of MHWs (Szuwalski et al., 2023). A combination of increased crab densities due to reduced habitats, through the disappearance of water masses lower than 2°C on the sea floor (i.e., the “cold pool”), and increased caloric demands due to the heatwave, likely resulted in the starvation of up to 10 billion snow crabs (Szuwalski et al., 2023). Prior to this MHW event, the snow crab population was assessed to be at historically high abundance, with a large recruitment of immature crabs. Other negative impacts of MWHs on benthic invertebrate communities were observed in the southeastern Chukchi Sea, where the epibenthic biomass declined in 2017 following multiple warm years (Huntington et al., 2020). In the GoA, contrasting trends in benthic invertebrate populations were observed after the onset of the "Blob," with sea star abundance generally declining while mussels, a prey of sea stars, generally increased (Suryan et al., 2021). In the Barents Sea, benthic monitoring in a Svalbard fjord showed that benthic invertebrate's abundance and richness declined sharply after a MHW event in 2006, but the benthic community appeared to recover after several colder years, pointing towards some potential resilience of benthic communities (Jordà-Molina et al., 2023).

3.4 Fish

Fish responses to MHWs in the Arctic and Subarctic ecosystems are also relatively unknown, whereas many studies from non-Arctic regions have documented MHW impacts on fish. Notable exceptions are the 2014–2016 northeastern Pacific "Blob" and the Bering Sea and Chukchi Sea MHWs in 2017–2019, which had profound and cascading impacts on fish populations in the North Pacific. In the GoA, forage fish species such as Pacific capelin (*Mallotus catervarius*), Pacific sand lance (*Ammodytes personatus*), and Pacific herring (*Clupea pallasii*) experienced historically low abundance and decreased body conditions due to the MHW (i.e., lower quality prey for top predators) (Biela et al., 2019; Arimitsu et al., 2021; Robinson et al., 2023). The polar cod (*Boreogadus saida*), another crucial forage fish, also experienced large declines in nutritional value due to the MHW in the Chukchi Sea (Copeman et al., 2022). These changes in the body conditions of fish can have ramifications for energy transfer to top predators. Additionally, the "Blob" had large impacts on fish early life stages, such as the walleye pollock in the GoA. Record-low levels of pollock larvae were observed in 2015, and their summer survival rates were significantly reduced, resulting in very low abundances of juvenile pollock (Rogers et al., 2021). Not only the extreme temperature, but multiple factors such as low-saline conditions, low zooplankton density, and poor body condition of age-0 pollock, contributed to the juvenile pollock declines (Rogers et al., 2021), illustrating the complex direct and indirect interactions influencing fish responses to climate warming. In the northern Bering and Chukchi seas, a large influx of juvenile walleye pollock and increase in the abundances of juvenile pink salmon (*Oncorhyncus gorbuscha*) and age-0 polar cod were concomitant to the 2017–2019 MHW (Huntington et al., 2020; Levine et al., 2023) (Box 1).

MHWs can cause demographic responses in fish populations, influencing recruitment success, growth patterns, and natural mortality (Box 1). For example, in the GoA, MHWs induced changes in the phenology and growth of Pacific cod (*Gadus macrocephalus*) juveniles, causing earlier hatching and faster growth (Almeida et al., 2024). The biomass of adult Pacific cod in the GoA, which sustains an important commercial fishery, had severely declined in 2017 following the MHW (Barbeaux et al., 2020). The decline was most likely due to increased metabolic demand combined with lower prey availability, but also reduced survival of recruits and loss of suitable spawning habitat (Barbeaux et al., 2020; Laurel and Rogers, 2020). Fish thermal tolerance range is often the smallest during early-life stages, e.g., eggs and larvae, which are highly sensitive to temperature variations (Dahlke et al., 2020). If a MHW coincides with the distribution of critical life stages (in space and time), it can result in high mortality; for instance, walleye pollock in the GoA experienced significant early-life stage mortality (i.e., recruitment failure) during the "Blob" (Rogers et al., 2021). Analyses of species' thermal niches can inform on species vulnerability to MHWs, for example, in the Pacific Arctic, juvenile polar cod are more likely to suffer from increased temperatures during MHWs compared to other gadids such as saffron cod (*Eleginus gracilis*), walleye pollock, and Pacific cod, due to negative impacts of warm temperature on their activity, growth, and survival at a lower temperature threshold (16°C; Laurel et al., 2016).

A behavioural response of fish to abnormal sea temperatures is to move to more suitable areas, for example, by moving to climatic refugia and/or following their thermal niche (Jacox et al., 2020; Alabia et al., 2021). These displacements can cause large changes in the composition of the fish assemblages (abundance, biomass, and diversity), but in many instances these changes appear to be short-term. For example, the "Blob" in the northern California Current led to large but short-term changes in fish species abundances in eelgrass meadows, with the fish assemblage quickly returning to baseline levels (Robinson et al., 2022). In the northern Bering Sea, spatial distributions of several commercially important fish species shifted during the warm summer of 2017, with increased biomass of walleye pollock, Pacific cod, and northern rock sole (*Lepidopsetta polyxystra*) in the northeastern Bering Sea (Stevenson and Lauth, 2019). In the Barents Sea, community-level redistributions were apparent during MHWs, but they appeared to affect different fish species and groups, and long-term effects were not evident (Husson et al., 2022). In accordance, a large-scale analysis of demersal fish communities across Europe and North America, including the Subarctic Barents Sea and Bering Sea did not find significant impacts of MHWs on the fish biomass, abundance, and biodiversity (Fredston et al., 2023). Still, MHWs could facilitate the northward range expansion of Subarctic fish species into the Arctic. This is exemplified by walleye pollock, which extended its northern range into the southern and central parts of the Chukchi Sea during the 2017–2019 MHW events (Levine et al., 2023).

Global simulation models indicate that MHWs in exclusive economic zones could lead to a 6% drop in maximum commercial fish catch potential, affecting 77% of exploited fishes and invertebrates (Cheung et al., 2021). However, negative impacts from MHWs in Subarctic regions are expected to be on average smaller than for the temperate and tropical regions (Cheung et al., 2021). These global models also highlight that MHWs can cause a substantial and rapid biomass decrease and shifts in fish distribution, with a projected doubling of MHW-related effects on major commercial fish species by 2050 (Cheung and Frölicher, 2020).

3.5 Upper trophic levels: seabirds and marine mammals

Upper trophic level (UTL), homeothermic vertebrates like seabirds (here, defined as all birds that use the marine environment), and marine mammals generally show a delayed response to MHW events, due to their trophic distance from primary productivity and lower trophic levels, longer life spans, and high mobility (Burger and Piatt, 1990; Johns et al., 2022; Orgeret et al., 2022). In addition, at least for marine mammals, their large bodies and capacity for energy storage via fat reserves buffer interruptions to the food web. However, the thick blubber of some Arctic cetaceans, like narwhals (*Monodon monoceros*) and bowhead whales (*Balaena mysticetus*), may reduce their ability to dissipate heat. Narwhals, in particular, have limited physiological flexibility to adjust their swimming or diving behaviour to thermoregulate if water temperatures become extreme (Chambault et al., 2020). Given evidence that the distributional range of Arctic marine mammals is temperature driven, MHW events could have potentially direct negative impacts on these species. There have been multiple examples of the delayed response of seabirds and marine mammals to MHWs, ranging from weeks to years (Gulland et al., 2022; Jones et al., 2023; Welch et al., 2023; Renner et al., 2024). Most of these examples are from non-Arctic regions, but have included Subarctic marine species that use the Arctic for some portions of their life cycles.

Although UTL animals may show longer-term impacts or delayed responses to MHWs, there are more immediate direct and indirect effects. Physiological responses to intense heat, i.e., heat stress, can occur in the water and on land. For instance, the high atmospheric temperatures that typically accompany MHWs can cause heat stress for seabirds incubating eggs or attending chicks on open cliff nests (Cook et al., 2020). MHWs can result in toxic algae blooms and diseases that directly affect UTLs. In the northern Bering and Chukchi seas, seabird die-offs were associated with toxic algae blooms (Van Hemert et al., 2020), and in the northern Bering Sea, avian influenza was detected in murres (*Uria spp*) during the 2018 heatwave (Will et al., 2020b). In the Canadian Arctic, avian cholera outbreaks increased with climate change, threatening populations of northern common eiders (*Somateria mollissima borealis*) (Iverson, 2015). The first recorded mortality of a polar bear (*Ursus maritimus*) from avian influenza occurred in the winter of 2024; the bear was likely infected by scavenging on infected marine birds, which has broad conservation and health issues for mammalian species, including humans (Ward, 2024).

High marine mammal mortality has been documented during extended warm periods, including humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) following the 2014–2016 GoA MHW (Gabriele et al., 2022). However, the spatio-temporal dispersal of observations makes it difficult to link their deaths to specific MHWs (Albouy et al., 2020; Gabriele et al., 2022). For marine mammals, reduced survival can be a long-term impact from MHWs, including reduced abundance and low calf production (Suryan et al., 2021; Gabriele et al., 2022).

Variation in impacts can vary even within a broad ecological region, such as documented for endangered Steller's sea lions (*Eumetopias jubatus*) during and after the GoA MHW (Hastings et al., 2023). Indirect impacts of MHWs on UTLs include changes in the prey field and/or foraging habitat. Following the GoA MHW, changes in distribution by humpback whales and their prey resulted in higher entanglement of whales in fishing gear farther south, due to greater temporal and spatial overlap of whales and fisheries (Santora et al., 2020). A specifically Arctic example is that, as sea ice retreats during exceptionally warm years, forage fish like polar cod move farther offshore or into waters too deep for diving seabirds [e.g., black guillemots (*Cepphus grylle*); Divoky et al., 2021].

In the northern GoA, the 2014–2016 MHW reduced the abundance of three important forage fish species, which impacted UTL consumers during the MHW (Arimitsu et al., 2021), and for years afterward (Suryan et al., 2021), with long-term demographic consequences (Schoen et al., 2022). Demographic impacts were also documented for common murres (*Uria aalge*) in the North Atlantic, with evidence that the behavioural flexibility of murres in response to higher SSTs was not sufficient to ameliorate immediate and long-term negative impacts on reproductive success (Wanless et al., 2023). Some seabirds, such as black-legged kittiwakes (*Rissa tridactyla*) in the GoA, altered foraging behaviour and searched a wider area for prey to feed chicks. However, this species experienced widespread breeding failure in the GoA, which continued for 5 years after the MHW (Osborne et al., 2020). In contrast, benthic-feeding sea ducks did not show evidence of negative impacts from MHW conditions in the northern GoA, illustrating the importance of considering trophic interactions when predicting resilience to anomalous conditions (Robinson et al., 2023).

MHW effects on prey species, such as reduced size and nutrient content of zooplankton (Kimmel et al., 2023), were detrimental for planktivorous seabirds nesting in the northern Bering Sea (Will et al., 2020a). Indeed, an ecosystem model suggested that loss of high-lipid Arctic copepod species may have the greatest impact on UTLs, including forage fish, planktivorous seabirds and a variety of marine mammals (Gillie et al., 2024). Forage fish also had reduced size-at-age and lower fat content following the extremely warm period (with multiple MHW events) in the Bering Sea during 2017–2019 (Copeman et al., 2022). These changes in prey were associated with unusual seabird die-offs and breeding failures (Romano et al., 2020; Will et al., 2020a; Kaler and Kuletz, 2022; Jones et al., 2023). The 2017–2019 MHW events in the northern Bering and Chukchi seas also facilitated a massive influx of juvenile walleye pollock into the Chukchi Sea (Levine et al., 2023), which, along with changes in other prey species and foraging conditions, influenced the distribution of planktivorous and piscivorous seabirds there (Kuletz et al., 2020; 2024b) (Box 1).

The timing of prey availability in the Arctic is critical to UTLs, particularly those that attempt to raise young (i.e., many seabirds, walrus, and seals) or must obtain adequate food for long migrations, e.g., shearwaters *Ardenna* sp., and large cetaceans (Kuletz et al., 2024a). In one cross-taxa modelling exercise focused on the eastern North Pacific, Welch et al. (2023) found that top predators could vary widely in their response to MHWs, with some species benefiting from newly available suitable habitat, while others faced reduced habitat, and in some cases, species-specific responses varied between MHW events. Coastal UTL species, and more southerly species, showed the greatest spatial displacement during MHW events (Welch et al., 2023).

Most UTLs can "buffer" against short-term ecosystem perturbations via moving from impacted areas, behavioural flexibility, or switching to alternative prey (Sinclair et al., 2008; Jones et al., 2023 and references therein; Woehler and Hobday, 2023). However, mass mortality events of seabirds and marine mammals are often associated with MHWs (or a series of brief MHW events) in Arctic and Subarctic regions, indicating significant and long-term impacts to the ecosystem that overrode the behavioural flexibility of UTLs (Jones et al., 2023). Examples include tufted puffins (*Fratercula cirrhata*) and crested auklets (*Aethia cristatella*) in the Bering Sea in 2017 (Jones et al., 2019), and murres and shearwaters in the same region in 2018 (Duffy-Anderson et al., 2019; Romano et al., 2020). In the North Atlantic, northern gannets (*Morus bassanus*) starved during the 2012 MHW off Newfoundland (Montevecchi et al., 2021). Seabird mortality during the GoA MHW, originally estimated at 3 million seabirds, primarily common murres (Piatt et al., 2020; Jones et al., 2023) is now estimated to have claimed 4 million common murres, half of the Alaskan population, and the largest seabird mortality event on record (Renner et al., 2024). Notably, 5 of the 13 colonies monitored for this study are located in the southeastern Bering Sea, reflecting impacts to populations that overwinter in the GoA but breed elsewhere.

Animals often redistribute in response to MHWs, e.g., chick-rearing kittiwakes foraged over a wider area in the northern GoA (Osborne et al., 2020), and short-tailed shearwaters (*Ardenna tenuirostris*) spread across the Chukchi Shelf in 2017 and 2019; the latter was concurrent with the invection of warm Bering Sea water there, and the lack of concentrations of euphausiids (Kuletz et al., 2024b). For long-distance migrants like the shearwaters, MHW conditions may result in longer, more wide-spread foraging trips (Yamamoto et al., 2015) and be reflected in later arrival at southern hemisphere breeding areas and low breeding success (Glencross et al., 2021). While some Subarctic breeding animals may adjust to warm conditions by foraging farther north (e.g., thick-billed murres *Uria lomvia*, and short-tailed shearwaters (Kuletz et al., 2020), those that reside in the Arctic year-round do not have that option. For example, following the warm conditions in the northern Bering and Chukchi seas, ice-seals like spotted seal (*Phoca largha*) had high mortality and their pups were in poor condition (Huntington et al., 2020).

4 Discussion

4.1 Social, economic, and cultural impacts on Arctic and Subarctic communities

The multifaceted MHW impacts outlined above have had substantial social and economic impacts across fishing and coastal communities, subsistence-based communities, and diverse marine users. MHWs reverberate across the spectrum of human wellbeing, which is defined as the state when basic needs are met and individuals and communities can pursue their goals and enjoy a satisfactory quality of life (Breslow et al., 2016). Social scientists have identified the numerous dimensions of human wellbeing tied to marine ecosystems, including mental and physical health, social connections to place and people, intergenerational knowledge transfer, cultural and spiritual practices (Breslow et al., 2016). The following two paragraphs describe overarching effects of MHWs on human dimensions, while the final three paragraphs detail the impacts specifically on the social, economic, and cultural systems of Arctic and Subarctic communities.

MHW impacts on commercial and subsistence fisheries such as fish stock downturns, harvest restrictions, closures, and shifts in fishery timing have been particularly detrimental for communities. Direct economic impacts of these changes have been estimated at hundreds of millions of US dollars for a single fishery (Smith et al., 2021; Szuwalski et al., 2023). Not all impacts have been adverse, with some species responding positively with range extensions and increasing abundance from favorable conditions (Smith et al., 2021; Free et al., 2023). Yet, even these seemingly positive impacts have been associated with intensified conflicts across multiple political boundaries (Pershing et al., 2018; Szymkowiak and Steinkruger, 2023).

MHWs have also disrupted traditional ways of life and subsistence lifestyles across the world as ecological changes have altered the marine food web upon which indigenous coastal communities rely. Fisheries downturns associated with MHWs have included critical subsistence and cultural keystone species, undermining multi-generational connections to these resources and food security (Falardeau et al., 2022; Free et al., 2023). Mass mortality events of seabirds and marine mammals associated with MHWs have also undermined subsistence harvests with profound food security implications for indigenous communities (Young et al., 2014; Naves, 2018; Siddon et al., 2020). Large-scale harmful algal bloom events associated with MHWs have increased safety hazards associated with paralytic shellfish poisoning in shellfish, hindering traditional shellfish gathering practices and eliminating this critical food source for indigenous peoples (Kourantidou et al., 2022). Kelp mortality from MHWs has undermined traditional knowledge and spiritual values for indigenous communities that have utilised kelp for thousands of years in numerous cultural practices (Smith K. E. et al., 2023). Subsistence harvest practices have also been affected by altered migratory patterns and timing of seabirds and marine mammals, and their accessibility to hunters due to sea ice loss (Kuletz et al., 2024a and references therein).

In the Arctic and Subarctic, MHWs have been increasing in frequency and extent, disrupting coastal socio-ecological systems grounded in marine resource access and use. The "Blob" drove unprecedented fisheries downturns in the GoA across both groundfish and salmon fisheries, which were exacerbated by the return of MHW conditions in 2019 (Barbeaux et al., 2020; Free et al., 2023). From 2015 to 2017, the Pacific cod fishery in the region experienced a 70% decline, and after multiple years of increases in harvest restrictions, the fishery closed in 2020 due to concerns over the sustainability of the resource (Barbeaux et al., 2020; Laurel and Rogers, 2020; Peterson Williams et al., 2022). Starting in 2016, the region also experienced disasters across several different salmon species and runs, attributed to poor oceanographic conditions (Bellquist et al., 2021). Rapid and repeated declines in multiple fisheries over a 5-year timespan precipitated an exodus of participants from these fisheries and created uncertainty and stress in fishing communities (Suryan et al., 2021; Abelman et al., 2023). Although sablefish had an unprecedented recruitment class following the heatwave, the tremendous influx of small fish into the commercial fishery disrupted the market and led to substantial declines in prices (Szymkowiak and Rhodes-Reese, 2020). At the same time, fishermen's attempts at exploiting the increased abundance of warm water species in the region to buffer declining revenues were largely unsuccessful due to conservation concerns over traditional target species (Szymkowiak et al., 2024). The MHW also precipitated increased polarization of viewpoints about fisheries allocations and enhancements amongst fisheries stakeholders in the face of declining abundance, signifying the impact of these abrupt changes on social conflict in the region (Szymkowiak and Steinkruger, 2023).

In addition to disruptions in fisheries, the "Blob" created tremendous upheaval across diverse marine user groups. Large-scale die offs of seabirds in the GoA disrupted traditional seabird harvest (Piatt et al., 2020). The warm waters precipitated the largest harmful algal bloom on record, with paralytic shellfish poisoning events and oyster farm closures in Kachemak Bay near Homer, Alaska (Walsh et al., 2018). Increased harmful algal blooms and paralytic shellfish poisoning generated food safety concerns throughout Alaska, disrupting shellfish gathering for commercial and subsistence harvesters (Walsh et al., 2018). The MHW also resulted in declines in cetaceans (see Section 3.5), which had adverse impacts on the marine tourism industry in the region (Suryan et al., 2021).

The socio-ecological systems that depend on the Bering and Chukchi seas have also experienced unprecedented disruptions in the years following the 2017–2019 MHWs in the region. Warm water temperature and declines in the extent and duration of sea ice cover prevented traditional ice-based harvesting of marine resources, i.e., fish, crabs, seals, and whales (Walsh et al., 2018). Access issues were compounded by seabird and marine mammal die offs in the region and downturns in availability of these resources due to breeding failures and changes in migratory patterns (Walsh et al., 2018; Siddon et al., 2020; Kuletz et al., 2024a). HAB events and associated food safety concerns also extended to the Bering Strait region at this time (Walsh et al., 2018; Siddon et al., 2020).

Reductions in lipid-rich prey, due to warmer waters in the region, also precipitated steep declines in chum salmon (*Oncorhynchus keta*) run sizes, leading to closures of the commercial and subsistence fisheries in western Alaska (Farley et al., 2024). This exacerbated ongoing Chinook salmon (*Oncorhynchus tshawytscha*) run failures in the region, which are critical for the cultural fabric and spirituality of the indigenous people in the region (Carothers et al., 2021), and food security issues (Farley et al., 2024). In addition to impacts on salmon, the MHWs in the Bering and Chukchi seas led to large scale shifts in fisheries resources in the region. There were substantial northward migrations of highly valuable commercial fish populations – Pacific cod and walleye pollock – associated with the MHW (Duffy-Anderson et al., 2019; Siddon et al., 2020; Levine et al., 2023). In response, fishing fleets experienced longer travel times between fishing grounds and ports and the shift triggered long-term considerations about the potential need to shift stock assessment survey grounds, fisheries management boundaries, and processing capacity to meet the shifting spatial distribution of the resources (Siddon et al., 2020). The mass mortality of the Bering Sea snow crab led to the closure of the fishery for the first time in history for the 2022–2023 season, causing the largely indigenous, island community of St. Paul, which relies heavily on revenue from processing crab and servicing the crab fishing fleet, to declare a cultural, economic, and social emergency (Szuwalski et al., 2023).

4.2 Adaptive management and mitigation of impacts from MHWs

Arctic and Subarctic fisheries are feeling the impact of MHWs due to the ecological disturbances affecting harvested marine populations (Barbeaux et al., 2020; Szuwalski et al., 2023; Farley et al., 2024). Considering the expected increase in the frequency of MHWs, there is a need to transition towards adaptive management of marine resources (Free et al., 2023). Adaptive resource management, a more flexible decision-making process, involves managing natural resources while simultaneously learning from outcomes and adapting strategies based on new information and changing conditions (Allen et al., 2011; Williams and Brown, 2014). By enhancing flexible harvest strategies and quick responses it can better mitigate and adapt to the impact of MHWs on socio-ecological systems (Caputi et al., 2016; 2019). The socio-economic consequences and management decisions following the two extreme MHWs in Australia in 2010–2011 and the northeast Pacific in 2014–2016, provided useful lessons about the management of fisheries following MHWs (Caputi et al., 2019; Free et al., 2023). Caputi et al. (2019) highlighted the importance of adaptive fisheries management to protect ecological populations that suffered recruitment failures due to MHWs, suggesting that early identification of temperature hot spots and abundance changes as well as flexible harvest strategies, can allow for a quick response, to minimize the effect of fishing on reduced commercial populations. Fisheries catch data from Alaskan fishing communities revealed that diversifying resource portfolios and adapting to changing fishing opportunities can help mitigate economic instability during major ecological and/or economic disruption (Cline et al., 2017). This emphasizes the importance of maintaining diverse economic options to strengthen the resilience of the socio-ecological systems to extreme events (Cline et al., 2017).

As species' distributions shift with warming or in temporary response to MHWs (Kuletz et al., 2024a), changes in monitoring design and fisheries management boundaries might be needed (Siddon et al., 2020; Free et al., 2023). Early detection of ecological impacts through monitoring of fish and invertebrates' early-life stages and abundance would require increasing monitoring efforts, which although desirable might not be possible due to the economic costs of scientific surveys. Yet, monitoring programs could be modified to increase knowledge of the system response and identify early-warning signals by increasing the use of alternative monitoring sources, such as eDNA and fishery-dependent data (Borgman et al., 2022; Free et al., 2023). For example, eDNA sampling could be sampled by ships-of-opportunity and thereby help expand spatial and temporal coverage and reduce costs (Valsecchi et al., 2021). This approach could be especially useful in the Arctic, due to its remoteness and limited seasonal accessibility. In addition, early identification of SST anomalies through satellite monitoring can provide an early warning of MHWs occurrence (Hobday et al., 2016). This can inform of potential socio-ecological disturbances and thus trigger adaptive management strategies. Improved SST forecasts can also be used for short-term predictive models to inform dynamic management measures, such as adjusting harvest guidelines and reducing fisheries bycatch (Holsman et al., 2019). In Arctic coastal regions, which harbor critical habitats like kelp forests, monitoring of sea temperatures should be supplemented with continuous *in situ* observations (Borgman et al., 2022). There is thus a need for increased funding and support for the development and implementation of advanced detection and monitoring technologies, such as satellite monitoring for early detection of SST anomalies, eDNA sampling for ecological monitoring and *in-situ* observations.

Additionally, expanding Marine Protected Areas (MPAs) and effectively enforcing them, particularly by covering climate refugia, could significantly enhance the resilience of Arctic marine ecosystems to climate-induced stressors (Ainsworth et al., 2020; Queirós et al., 2021). MPAs, restricting some to all human activities within a defined area, are often seen as a key tool to protect marine biodiversity and build ecosystem resilience. While MPAs have had successes in terms of restoring biodiversity due to the relaxation of human pressures (e.g., of no-take MPAs; Sala and Giakoumi, 2018), the performance of MPAs to limit the ecosystem effects of uncontrollable external stressors and extreme events (e.g., storms or temperature rise) is less obvious. In the Arctic, the multi-level impacts of sea ice loss could prove particularly challenging in terms of applying MPAs to mitigate detrimental effects. Evidence suggests that MPAs, compared to unprotected sites, may provide refuge and contribute to the resilience of fish communities during MHWs by, e.g., dampening the loss of trophic diversity and accelerating the recovery of taxonomic diversity (Ziegler et al., 2023; Benedetti-Cecchi et al., 2024). Yet, the potential of MPAs as a tool to mitigate the impacts of MHWs on ecological communities is still unclear (Freedman et al., 2020; Smith J. G. et al., 2023), indicating the need for further research to better understand the role of area-based protection in mitigating climate impacts. In addition, the efficacy of MPAs can be compromised by inadequate enforcement or design, for example, by not spatially covering climate refugia. Climate refugia are areas that remain relatively detached from climate change impacts, which could provide important sanctuaries for vulnerable Arctic species during extreme events like MHWs. The Arctic currently has several MPAs; as of 2020, over 5% of the Arctic's marine areas had some level of protection (CAFF/PAME, 2022). This coverage fell short of the 2020 Aichi Biodiversity Target 11 of 10% marine protection and is far from the 2030 target 3 of the Kunming-Montreal Global Biodiversity Framework of 30% of ecologically representative and effective protection and management of global marine areas. In addition to MPAs, other regulations and spatial restrictions can play important roles in protecting marine biodiversity, such as the Central Arctic Ocean (CAO) fisheries agreement, which is a 16-year ban of commercial fishing in the CAO. Finally, international collaborations should be strengthened to designate Other Effective Conservation Measures (OECMs) and identify vulnerable marine ecosystems, supporting global efforts towards achieving the biodiversity targets set for 2030 (CAFF/PAME, 2022).

4.3 Conclusion and future research needs

The intensity, duration, and frequency of MHWs have increased in the Arctic Ocean and its marginal seas. Significant progress has been made in understanding the onset and dynamics of MHWs, as well as in improving the forecasting of MHW events globally. In the Arctic and Subarctic marine ecosystems, MHW dynamics are unique due to the interplay between sea ice, ocean, and atmospheric dynamics, where declining sea ice amplifies MHW occurrence, duration, and intensity by exposing open water to solar heating and reducing temperature variability. Subarctic marginal seas like the Barents and Bering seas experience high spatial variability in MHW frequency and duration due to regional influences such as warm Atlantic water inflow, Arctic amplification, and sea ice retreat.

While Arctic MHWs appear to be primarily driven by atmospheric heat fluxes and oceanic heat advection in inflow regions, there remain substantial knowledge gaps regarding the subsurface mechanism of MHWs, compound events, the potential impacts on marine ecosystems and fisheries, and the predictability and forecasting of MHWs in the Arctic regions. Also, identifying MHWs in the Arctic based on satellite observations of SST include challenges due to the sea ice cover limiting the number of open-water days, and, definning relevant. Defining relevant MHW threshold is difficult in the Arctic regions due to the low sea temperature variability which causes the MHW threshold to be very close to the climatology. This highlights the need for further research to understand better the detection and mechanisms of MHWs in the polar regions, such as increased knowledge about subsurface mechanisms, the effect on the MHW identifications of removing the SSTs trend instead of using a fixed baseline, and more generally the limitations of applying MHWs detection methods developed in non-polar regions to the Arctic.

Many Arctic species have narrow thermal preferences, making them especially vulnerable to MHWs, as many are already at, or near their upper thermal limits. The limited behavioural flexibility caused by extreme photoperiods further exacerbates the risks for these species. MHWs can thus be disastrous for Arctic species that are losing large parts of their suitable habitats and might not be able to find and move to suitable colder areas to avoid extreme heat. Sessile species, such as benthic foundation species like kelp and seagrass, are likely more vulnerable to MHWs in contrast to mobile species (Smale et al., 2019), but in the Arctic, many of these sessile species are distributed at the cold end of their thermal range and evidence of MHWs impacts there remains limited. In addition, by affecting the stratification of the upper ocean, MHWs can influence nutrient and light availability for phytoplankton, thereby altering their community composition and size. MHWs can also cause shifts in the lipid content of zooplankton communities (from high- to low-lipid species). Changes in the planktonic system can have repercussions throughout Arctic and Subarctic food webs, and ultimately impact UTLs (Gillie et al., 2024). Fish, seabirds, and marine mammals in the Arctic and Subarctic regions exhibit varied responses to MHWs. Demographic responses through decline in body condition, increased mortality rates and recruitment failures were documented. Distributional shifts of UTL animals during and after MHWs were also observed. UTL animals may exhibit longer-term impacts (Renner et al., 2024) or delayed responses to MHWs (e.g., black-legged kittiwakes following the GoA MHW; Schoen et al., 2022), but current assessments focus mainly on short-term impacts, leaving a knowledge gap regarding the long-term or population-level effects of MHW events on UTL species.

Future research is needed to assess the comprehensive ecological impacts of MHWs, particularly how variations in their duration and frequency affect Arctic ecosystems. In addition, current observational studies often focus on short-term impacts. However, there is a critical need for long-term or population-level studies to understand the enduring effects of MHWs on the resilience of Arctic species. To investigate how MHWs duration influence the ecological responses of Arctic species, both field-based observations and laboratory-controlled experiments are needed (Joyce et al., 2024). Experimental studies are valuable for isolating the impacts of specific MHW characteristics (e.g., intensity, duration, frequency), and their combined effects, on marine species adaptation and resilience. Experimental settings could also be useful in distinguishing the ecological effects of MHWs from the impacts of long-term warming. Additionally, shifts in the planktonic Arctic ecosystem due to climate change are expected to significantly impact the functioning of both the carbon export and the biological carbon pump, affecting CO_2 uptake in these waters (Manizza et al., 2010). Predictive models incorporating all these processes are needed to correctly represent the response of the ocean carbon cycle of Arctic regions in relationship with the potential carbon-climate feedback. More generally, as anthropogenic activities and their associated pressures continue to rise in the Arctic, it is essential to evaluate how MHWs interact with other climatic variables and human-induced stressors, and to understand their cumulative impact on marine biodiversity.

Currently, 15% of the world's marine fish are caught in the Arctic and Subarctic, mostly in the southern Arctic inflow shelves, while the interior shelves and Central Arctic Ocean mainly support subsistence catches (Zeller et al., 2011; 2016; Mueter, 2022). Arctic fisheries, both commercial and subsistence, are undergoing significant changes in response to a northward shift in the distribution of commercial fish and shellfish species such as mackerel, cod, haddock, and capelin (Haug et al., 2017). Diminishing sea ice and warmer conditions gave opportunities for increasing fishing activities, especially trawling, in previously ice-covered Arctic shelf areas (Fauchald et al., 2021). The northward expansion of trawling is posing environmental concerns for these relatively commercially unexploited marine ecosystems. Arctic coastal states need to take stronger measures to regulate and manage the growing fishing pressure, to protect vulnerable Arctic shelf ecosystems from potential negative impacts (Christiansen et al., 2014; Fauchald et al., 2021; Mueter, 2022). In addition to fishing, other extractive human activities such as oil and gas exploration and extraction, and deep-sea mining, as well as shipping activities, might take advantage of the retreating sea ice to expand poleward in the future, increasing the risk of the vulnerable Arctic marine ecosystems to these cumulative pressures.

The summary for policymakers of the IPCC sixth report concludes "*human activities, principally through emissions of greenhouse gases, have unequivocally caused global warming, with global surface temperature reaching 1.1°C above 1850–1900 in 2011–2020. Global greenhouse gas emissions have continued to increase, with unequal historical and ongoing contributions arising from unsustainable energy use, land use and land-use change, lifestyles and patterns of consumption and production across regions, between and within countries, and among individuals (high confidence)*" (IPCC, 2023). As long as the greenhouse-gas emissions (GHG) from human industrial activities continue to rise, the ocean will keep getting warmer by absorbing the excess heat, and thus extreme heat events such as MHWs will occur. Attribution analysis indicates that GHG forcing is a necessary condition for the observed extreme MHWs in the Arctic, and there is a high probability that such intense MHWs would not have occurred if it were not for the GHG forcing (Barkhordarian et al., 2024). IPPC sixth report also states that "*adaptation options that are feasible and effective today will become constrained and less effective with increasing global warming*" (IPCC, 2023). While adapting and transforming our societies, governance and management systems are necessary to face the already existential threat of MHWs to Arctic ecosystems and livelihood, reducing global GHG emissions remains our best chance to safeguard a liveable planet for all and reduce human suffering and ecological collapse.

Author contributions

LP: Conceptualization, Project administration, Visualization, Writing–original draft, Writing–review and editing. BM: Conceptualization, Formal Analysis, Visualization, Writing–original draft, Writing–review and editing. AH: Conceptualization, Formal Analysis, Visualization, Writing–original draft, Writing–review and editing. AA-A: Writing–original draft, Writing–review and editing. JD: Writing–original draft, Writing–review and editing. KF-D: Writing–original draft, Writing–review and editing. KK: Writing–original draft, Writing–review and editing. KL: Writing–original draft, Writing–review and editing. MM: Writing–original draft, Writing–review and editing. CM: Writing–original draft, Writing–review and editing. PS: Writing–original draft, Writing–review and editing. MS: Writing–original draft, Writing–review and editing. TW: Writing–review and editing, Writing–original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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A review of climate change impacts on migration patterns of marine vertebrates in Arctic and Subarctic ecosystems

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Climate change is impacting marine ecosystems throughout the circumpolar Arctic, altering seasonal habitats and the food bases for fishes, seabirds, and marine mammals. Arctic and Subarctic regions provide resources for resident species and for species that migrate to the north from more southerly regions. Changes in northerly latitudes thus impact endemic as well as non-endemic animals. Herein, we review what is known about climate-driven changes in the migration patterns of Arctic and Subarctic marine vertebrates, including: 1) Arctic residents with seasonal movements – those fishes, seabirds, and marine mammals that complete their entire life cycle within the Arctic but exhibit seasonal movements; 2) Breeding migrants – many seabirds enter the Arctic to breed and subsequently migrate south in the fall; and 3) Summer visitors for feeding – certain species of boreal fishes, seabirds and marine mammals arrive during the northern summer to feed on abundant prey though they breed elsewhere. Migratory movements are often driven by the timing and extent of sea ice, which defines suitable habitat for some animals and limits access to open water and prey for others. Longer open-water seasons, warmer ocean temperatures, and stronger winds have resulted in earlier production blooms in spring and often, extended open-ocean plankton blooms into late summer, resulting in altered prey types and distributions. A common thread among taxa is that shifts in distribution and timing of migrating animals indicate they are traveling farther north, or shifting longitudinally, and migrations are occurring over longer seasonal time frames. Species performing multiple lifetime migrations or long-distance migrants may need to adjust migration timing or routing iteratively to match changes in marine productivity. Altered animal distributions or phenology, and reduced sea ice, affects access to animals that are critical nutritional, economical, and cultural components of Indigenous people's lives in the Arctic. Ongoing changes challenge the resilience and adaptability of Arctic people and ecosystems, and will require adaptive research and management approaches.

KEYWORDS

Arctic, distributional shift, fish migrations, marine mammal migrations, phenology, sea-ice loss, seabird migrations, subsistence harvest

1 Introduction

Animal migrations have evolved in response to spatial and temporal changes in resource availability (Newton, 2008; Milner-Gulland et al., 2011; Evans and Bearhop, 2022). In the Arctic, much of the marine-based prey that support upper trophic level taxa are only available during the brief Arctic summer and fall. Animals that remain in the Arctic year-round often conduct seasonal movements within Arctic areas (Alerstam et al., 2007; Pettitt-Wade et al., 2021), while Subarctic and temperate animals that depend on the Arctic's summer production period migrate north as sea ice retreats and return south as winter advances and darkness and low temperatures prevail (Berge et al., 2015a). Migration strategies depend on reasonable levels of ecosystem predictability to ensure timely access to prey for replenishment of energy stores and for breeding success. Among migratory species, the ability to adjust to spatial and temporal variability in resources varies along a continuum from narrow to flexible (Corkeron and Conner, 1999; Evans and Bearhop, 2022). However, climate change is altering marine systems such that resources and other environmental conditions are becoming more unpredictable in space and time (UNEP/CMS, 2006; Robinson et al., 2009; Gilg et al., 2012). This unpredictability is a current and future challenge for marine vertebrates that rely on migration to or within the Arctic to maximize their survival and reproductive success. Indigenous communities that rely on animal harvests are also impacted (Huntington et al., 2016; Hauser et al., 2021).

As climate change alters the timing and spatial distribution of resources, animals may need to alter their phenologies and migratory routes or staging areas. Changes in their traditional patterns and altered resource bases are likely to result in expending more energy searching for food and issues with finding adequate prey densities to support large-bodied animals (Bauer et al., 2008; Howard et al., 2018). Concurrently, other species may gain access to more direct routes, and more or higher-quality food over a longer season, reducing individual energetic expenditures of migration. Climate change induced impacts to migration can therefore affect reproductive success and overwintering survival, with repercussions to entire populations (Harrison et al., 2011). Ultimately, ecosystems will be impacted, as some fish species that are being negatively affected by climate change constitute key species in Arctic marine food webs, upon which many of the top trophic feeders depend (Welch et al., 1992; Hop and Gjøsæter, 2013). As upper trophic level consumers, predatory fishes, seabirds, and marine mammals serve as sentinels of ecosystem health (Moore et al., 2014; Sydeman et al., 2015; Moore and Kuletz, 2019). These three animal groups also constitute important food resources to people who rely on Arctic marine ecosystems for subsistence and many species serve as cultural cornerstones (Guyot et al., 2006; Huntington et al., 2013; 2016).

Migratory animals have significant impacts upon the marine ecosystems to which they migrate, serving as prey, predators, contributors to, and cyclers of, nutrients (Bauer and Hoye, 2014). Because animal migrations cross national boundaries, the United Nations established a global treaty on the Conservation of Migratory Species of Wild Animals (UNEP-WCMC, 2024), which defines a migratory species as: "The entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries." While this definition overlooks migratory movements that only occur within national boundaries, it does recognize the impact of climate change on animal migrations, and the need to address how current and future environmental changes will impact animals that rely on migration strategies to maintain their populations.

The timing and extent of sea-ice retreat is a primary driver of Arctic marine systems, and in spring it affects water-column characteristics, phenology and spatial extent of primary production, and consequently, abundance of lower trophic organisms, species composition, and nutritional quality (Gaston et al., 2009; Daase et al., 2013; Leu et al., 2015; Stige et al., 2019). The decline in area, thickness, and seasonal duration of sea ice within the last 20 years has greatly altered Arctic ecosystems, and these declining trends in sea ice will continue as northern latitude air and water temperatures increase (Barber et al., 2015; Hunt et al., 2016; Meredith et al., 2019; IPCC et al., 2023). With warmer conditions, early sea-ice melt in spring has resulted in earlier spring blooms, increased chlorophyll, and higher zooplankton biomass that experiences higher turnover, albeit of smaller, low-nutrient prey species, from zooplankton to fishes (Österblom et al., 2008; Hop and Gjøsæter, 2013; Renaud et al., 2018; Møller and Nielsen, 2020; Copeman et al., 2022). Such changes also affect competition among species at different trophic levels (Bogstad et al., 2015; Stige et al., 2018). Subsequently, the distribution of zooplankton, pelagic and benthic invertebrates, and forage fishes affect the upper trophic level vertebrates that migrate to or within the Arctic, including annual (e.g., seabirds and marine mammals) and life-cycle stages (e.g., anadromous fishes).

Most migration to the Arctic occurs latitudinally, in the extreme, from the Antarctic to the Arctic (Egevang et al., 2010), but migration also occurs longitudinally across the circumpolar realm (Alerstam and Gudmundsson, 1999; Alerstam et al., 2007). Migratory patterns can be influenced by the presence or absence of ice and impacts vary across taxa (McKeon et al., 2016; Briscoe et al., 2017; Clairbaux et al., 2019). Migration patterns of nearshore foragers and anadromous fishes could also be affected by changes in riverine and coastal systems, as freshwater runoff, thawing terrestrial permafrost, retreating glaciers, increased sedimentation, and lack of shore-fast ice alter the coastal domains (Carmack et al., 2015). Likewise, populations that rely on transport by surface currents for successful migration may be affected by changes in ocean circulation patterns (Frederiksen et al., 2016; Eriksen et al., 2020).

The forms of migration vary widely within and among taxa. Resident species may spend most or all of their life cycle within Subarctic or Arctic areas but exhibit regular movements within those areas. Such patterns are exhibited by some species of anadromous and marine fishes (Pettitt-Wade et al., 2021), certain marine mammals (Von Duyke et al., 2020; Shuert et al., 2023; Storrie et al., 2023) and at least three species of seabirds (Divoky et al., 2016; Gilg et al., 2016a; b; Frederiksen et al., 2021). Breeding migrants include some seabird species that migrate from the Subarctic and elsewhere to breed in the Arctic. Non-breeding migrants arrive during summer and fall only to feed in the Arctic. Among these species, some arrive as post-breeders from the Subarctic or nearby temperate realms, including species of seabirds (Kuletz et al., 2015; Gaston et al., 2017; Piatt et al., 2021) and migrant baleen whales (Storrie et al., 2018; Moore et al., 2022). This pattern also includes some marine fishes that migrate seasonally to the Arctic, e.g., capelin (*Mallotus villosus*) and several gadid species (Haug et al., 2017; Mueter et al., 2021). A few avian species are long-distance migrants from the Southern Hemisphere and travel to the Subarctic and Arctic only to feed and increase body reserves (Kuletz et al., 2015; Yamamoto et al., 2015; Nishizawa et al., 2017). Regardless of origin or strategy, animals need to match the phenology of their movements to the availability of food resources, which can be particularly critical for species that move to the Arctic to breed (Klaassen, 2003). For example, most seabirds are highly philopatric to colony breeding sites (Hamer et al., 2001), and for certain anadromous fishes, migration to freshwater breeding sites may be site-specific and rather inflexible (Hendry and Sterns, 2004).

Migratory strategies of animals can range from extreme “income migrants” (also known as a “fly-and-forage” strategy) to “capital migrants” (Evans and Bearhop, 2022). Income migrants forage as they move towards their migration endpoint, with little or no physiological alteration to prepare for migration and rely on multiple ecosystems for replenishment while *en route*. At the opposite extreme are capital migrants, individuals that must store adequate reserves for the entire journey, often undergoing physiological alterations to conserve energy until they reach their endpoint (Evans and Bearhop, 2022). For capital migrants, the timing of movements is critical and depends on the availability of food and suitable environmental conditions immediately upon arrival. As our knowledge regarding foraging patterns of migrants increases, it appears that most animals fall somewhere along this continuum, and some may even alter their strategies at different stages of their migratory journey (e.g., Lydersen et al., 2020). Our goal was to review available scientific literature to provide a synthesis of information on the impact of climate change on migratory Arctic marine vertebrates (fishes, seabirds, and marine mammals), and thereby inform decision-makers about these conservation challenges.

2 Methods

2.1 Spatial and temporal scope

For our review we primarily considered the marine and associated freshwater inflows across the circumpolar Arctic as defined by the Arctic Council’s Conservation of Arctic Flora and Fauna (CAFF) boundaries, which includes Arctic and Subarctic waters (Figure 1; https://caff.is/work/projects/arctic-biodiversity-data-service/). The Arctic Ocean incorporates an area of approximately 14,060,000 km^2, with most of its waters north of 66° N latitude, but including some Subarctic regions generally north of 60° N. The Arctic coastline within this region is ~45,390 km, although the CAFF boundary incorporates regions farther south. In the Pacific Arctic, the Subarctic includes the entire Bering Sea and portions of the northwestern Gulf of Alaska shelf. In the Atlantic Arctic, the boundary includes Hudson Bay, the Labrador Sea, and waters off southern Iceland and northern Norway (Figure 1). Because many of the migratory animals we review herein spend portions of their life cycle south of these boundaries, we also refer to areas outside our primary study area as appropriate. Our temporal scope emphasizes changes that have occurred in animal migration reported in publications over the last two decades.

In the High Arctic, the deep (mean of ~3,000 m) Central Arctic Ocean (~3.3 million km^2) borders five of seven Arctic Marine Areas (AMAs) as defined by the Circumpolar Marine Biodiversity Monitoring Program (CAFF, 2017). The Arctic Ocean is bordered by six countries, with the largest basins adjacent to Russia (Eurasian Basin) and Canada (Amerasian Basin). Warm, saline water flows from lower latitudes into the Arctic via two major “gateways.” In the Pacific, the narrow (~82 km wide) and shallow (90 m) Bering Strait has inflow from the Bering Sea, with the nutrient-rich Anadyr Current on the west and the warmer, fresher Alaska Coastal Current on the east, merging with Bering Shelf Water through Bering Strait and diverging across the shallow (~80 m) Chukchi Shelf (Weingartner et al., 1999). The Chukchi shelf slope is also influenced by the eastward-flowing deep Atlantic water of the Arctic Basin and the westward-flowing Beaufort Gyre. The Atlantic gateway is the wide (~450 km) and deep (5,500 m) Fram Strait, with the relatively warm West Spitsbergen Current as the primary inflow. It continues eastwards along the shelf north of Svalbard as the Atlantic Water Boundary Current (Renner et al., 2018) into the Nansen Basin of the Arctic Ocean. The Fram Strait is also a primary outflow on the west side of the Atlantic with the colder and fresher East Greenland Current (Karpouzoglou et al., 2024). Large river systems drain into the Arctic Ocean from multiple points, especially the large Russian rivers, resulting in fresher, cooler waters near coastal areas, which influence coastal currents (Feng et al., 2021).

Throughout the circumpolar Arctic and Subarctic, seasonal and long-term sea ice have been important structural components of marine ecosystems, which have been changing dramatically in recent decades (Taylor et al., 2022; IPCC et al., 2023). Historically, seasonal sea-ice formation expanded from November to March. On the Pacific side, sea ice could extend south across the central Bering Sea shelf and retract in late spring, and the Bering Strait would not be ice-free until June (Stabeno and Bell, 2019). As seasonal sea ice retreated, a layer of cool, fresh water influenced

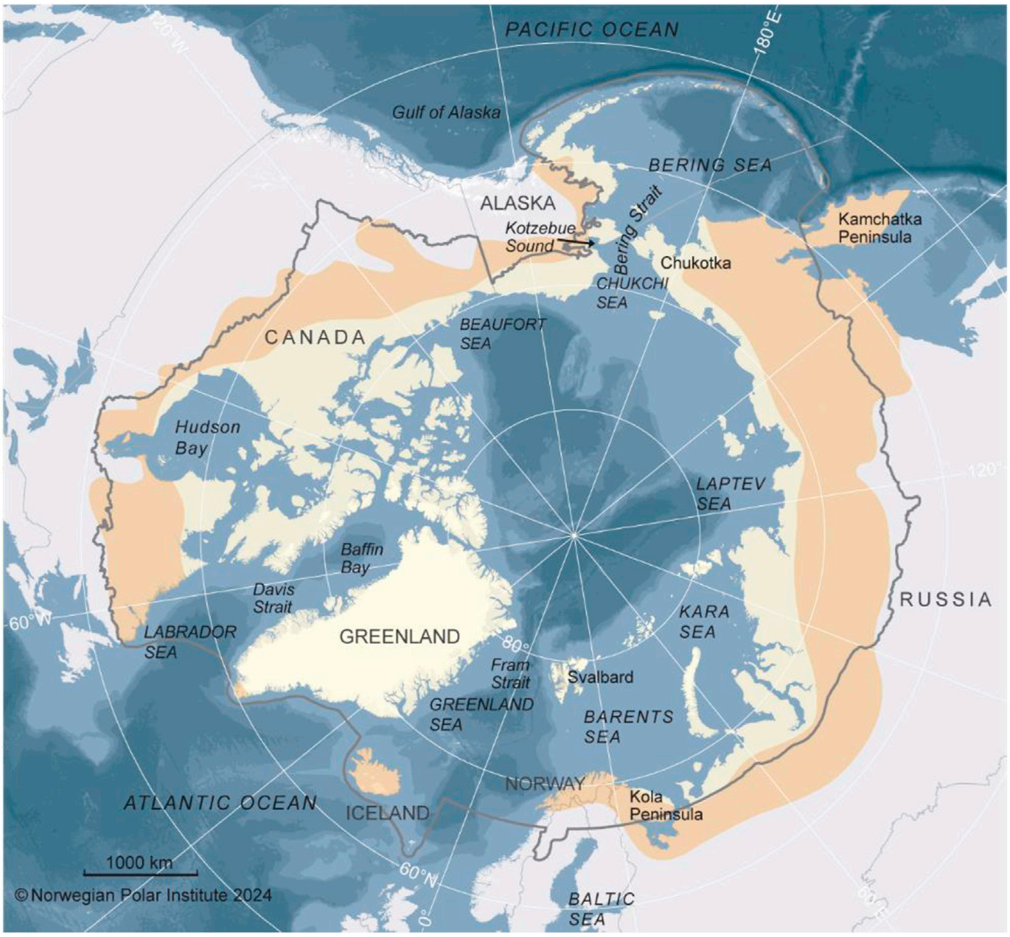

FIGURE 1
The Circumpolar study region, showing the CAFF boundaries, which include Arctic (pale yellow shading) and Subarctic (light brown shading) regions.

water masses, currents, and productivity (Lin et al., 2019; Danielson et al., 2020). The Atlantic Arctic is changing more rapidly than any other Arctic area. The region is heavily influenced by mixed Atlantic Water entering the Barents Sea from the south in two currents–one that goes eastward into the southern Barents Sea and one that flows north along the west coast of Svalbard (Ingvaldsen et al., 2021). The volume and temperature of these currents have changed over recent decades, altering sea-ice conditions at high latitudes dramatically (Efstathiou et al., 2022; Isaksen et al., 2022; Polyakov et al., 2023). In recent decades, sea-ice loss has drastically altered the physical and biological properties of Arctic marine systems (Fossheim et al., 2015; Descamps et al., 2017; Baker et al., 2020; Danielson et al., 2020). The open water season in the gateway areas currently extends from May to December (Stabeno and Bell, 2019; Efstathiou et al., 2022; Isaksen et al., 2022; Urbanski and Litwicka, 2022).

2.2 Review process

Our review of Arctic marine ecology as related to migration includes fishes, seabirds, and marine mammals, with expert representation from both the Pacific and Atlantic Arctic sectors. We included sources published in scientific journals, books, and publicly accessible agency reports. We relied on the expertise of the team and used internet search engines, including Google Scholar and Web of Science to survey the literature. Key words searched included taxa-specific names, plus combinations of: climate change, Arctic, migration, global warming impacts, timing of migrations, distributional shift, phenology, and movement patterns.

3 Results

3.1 Anadromous and marine fishes

3.1.1 Life histories and migrations

The migration of fishes is typically a “migration triangle,” as they move seasonally or in life stages among nursery, feeding, and spawning grounds (Harden-Jones, 1968). In Arctic and Subarctic regions, migratory fishes consist of two general types: anadromous and strictly marine. Anadromous fishes hatch in fresh water, migrate to the ocean, and return to reproduce in freshwater; individuals of some species perform multiple seasonal migrations during their lives (Hendry et al., 2004). In contrast, strictly marine fishes complete their entire life cycle in the ocean. Marine migrations, the focus of this review (i.e., freshwater stages of anadromous fishes are not considered), are influenced by a myriad of factors, including water temperature, ice phenology, ice extent, wind direction, and primary and secondary production. Changes in these factors can cause changes in timing and spatial extent of fish migrations. Because of their different life histories and migratory patterns, and their relative importance to subsistence (predominantly anadromous) versus commercial fisheries (predominantly marine) in the north, we address anadromous and marine fishes separately.

The most abundant anadromous fishes in the Arctic are from the sub-family Salmoninae (Pacific salmon species *Oncorhynchus* spp., Atlantic salmon and sea trout *Salmo* spp., and various char *Salvelinus* spp.) and members of the Coregoninae (whitefishes and ciscoes *Coregonus* spp.) (Reist et al., 2006). They contribute to a variety of fisheries, including subsistence, commercial, and recreational in North America and Eurasia (e.g., Falardeau et al., 2022). Collectively, salmonids exhibit a great diversity in life-history characteristics including semelparous (single) or iteroparous (multiple) reproductive cycles in a lifetime, facultative or obligatory migration, partial migration, and phenotypic plasticity (Hendry and Sterns, 2004). Species that have received relatively more attention on how climate change may affect migration are Atlantic salmon (*Salmo salar*), Arctic char (*Salvelinus alpinus*), and brown trout (*Salmo trutta*), while coregonines and endemic populations of Pacific salmon north of the Bering Strait have received less research attention.

Marine fish in the Arctic consist of two main categories with respect to migratory behavior: Arctic resident species and boreal species. Arctic residents comprise a diverse fish community living in environments characterized by low temperatures and strong seasonality in photoperiod and sea-ice cover. They typically have limited migrations within Arctic waters, as they move between spawning, feeding, and overwintering areas. Most Arctic marine species are small (<35 cm) benthic forms, dominated by sculpins (Cottoidea), eelpouts (Zoarcidae), and snailfishes (Liparidae), that typically have large demersal eggs and benthic larvae or short pelagic larval phases. Thus, they generally have poor dispersal potentials and their seasonal migrations are local, often between shallow and deeper waters (Brand and Fischer, 2016). However, there are exceptions, such as the Greenland shark (*Somniosus microcephalus*), which can reach a length of 5.5 m (Lynghammar et al., 2024). Boreal species' main centers of distributions occur farther south and they undertake seasonal migrations to the Arctic to feed, typically arriving in early summer and leaving before freeze-up (Lynghammar et al., 2024). Such migrants include both pelagic and demersal species. The migration timing of Arctic marine fish is closely linked to seasonal changes in the environment, particularly temperature and sea-ice conditions, and varies among species based on their specific life history traits and ecological requirements. However, for marine fish there is no information on temporal changes in migration. Most data are based on trawling, typically performed annually rather than seasonally, which reveals information on changes in distribution over time rather than migration timing (e.g., Fossheim et al., 2015; Frainer et al., 2017; Levine et al., 2023). Distributions are generally shifting farther north with warming conditions, and this is more apparent for pelagic species than for demersal species; the latter tend to tolerate a wider range of thermal conditions (Baker, 2021).

3.1.2 Phenology of migration for anadromous fishes

Among iteroparous anadromous fishes, several factors affect the timing of seasonal migration, including ocean temperatures and in some cases, ice cover. Marine habitats in Arctic North America and eastern Eurasia are ice covered during winter, unlike areas affected by the North Atlantic Current that keep the northern coasts of Iceland and Norway ice-free year-round. Sea ice forms when seawater (35 ppt) freezes at −1.8°C, and while doing so, ejects colder briny water from the ice. Anadromous fishes are not known to contain antifreeze compounds (e.g., glycoproteins), and are thus generally limited to occupying water temperatures >−0.7°C (Cheng, 2009). Therefore, sea ice and cold water act as barriers to the movements of anadromous fishes. Increased air temperatures in the Arctic have induced earlier spring ice melt, which can determine when fish undertake their marine feeding migration to take advantage of seasonal ocean productivity (Cooley et al., 2020; Falardeau et al., 2022). Similarly, ice formation in the fall is now occurring later, resulting in a longer ice-free season and increased sea surface temperatures (SST). As many anadromous fish species' movements are governed by by ice cover and water temperature (Bond and Quinn, 2013), some have responded by shifting their migration timing earlier in the spring (Kovach et al., 2013; Dempson et al., 2017) and later in the fall. Migration of char species is associated with ice presence, and some species can move below the ice in the ocean during winter and spring (Hammer et al., 2022; Smith et al., 2022), but spring coastal movements are limited by ice and are also influenced by marine temperatures (Hollins et al., 2022). Dolly Varden (*Salvelinus malma*) enter the ocean after land-fast ice has broken up and its marine dispersal is limited by sea-ice extent in summer (Gallagher et al., 2021).

3.1.3 Distributional shifts in anadromous fishes

Marine water temperatures influence the spatial distribution of anadromous salmonids during summer months (Mulder et al., 2020; Gallagher et al., 2021; Rikardsen et al., 2021; Nordli et al., 2023). In Arctic North America, the cold-adapted species Arctic char and Dolly Varden are surface oriented, typically occupying depths <5 m, and prefer temperatures between approximately 2°C and 8°C (Courtney et al., 2016; Harris et al., 2020; Mulder et al., 2020). Both species track their preferred isopleths in the ocean, which can shift spatially interannually, altering their marine distribution from year to year (Jensen et al., 2014; Harris et al., 2020; Gallagher et al., 2021). For example, Dolly Varden often occupy nearshore habitats in years with cooler SSTs but use more offshore areas in years with warmer SSTs (Gallagher et al., 2021). Additionally, SSTs impact estuarine use by Arctic char, as these habitats are typically occupied when the ocean is relatively cold, thus warming temperatures could decrease movement into estuaries (Harris et al., 2020). Increased water temperatures and higher productivity are thought to be related to the increasingly northward extent of migration in Subarctic and temperate species, such as observed for Pacific salmon species (Dunmall et al., 2013).

Other factors influencing the spatial extent of anadromous fish migrations include oceanographic fronts that typically have relatively high primary and secondary productivity. For example, an oceanographic front with high productivity, where the warm North Atlantic Current intersects with cold polar waters of the

Northeast Atlantic Arctic, is an important feeding area for Atlantic salmon (Rikardsen et al., 2021). Similarly, Dolly Varden feed at a front in the Chukchi Sea where euphausiid abundance is high (Courtney et al., 2016). As conditions in the Arctic change, frontal boundaries may move (Lu et al., 2015), which will impact location, duration, and energetic costs of migration (Rikardsen et al., 2021). Finally, prevailing wind direction may affect juvenile fish migration. For example, the intensified strength of easterly winds in the western parts of the North American Arctic (Falardeau et al., 2023), may improve juvenile Arctic cisco (*Coregonus autumnalis*) dispersal towards nursery and feeding areas favorable for recruitment (Fechhelm et al., 2007; Zimmerman et al., 2013).

3.1.4 Ontogenetic and seasonal migrations of Arctic marine fishes

The few relatively large demersal species in the Arctic that extend to the Subarctic include flatfishes, such as Greenland halibut (*Reinhardtius hippoglossiodes*), Arctic skate (*Amblyraja hyperborea*) and the Greenland shark. Most flounders undertake ontogenetic migrations, moving to deeper water as they grow (Bassi et al., 2024). Older fish also move seasonally into fjords and shallow waters during the ice-free season, and into deeper water during winter (Barkley et al., 2018). In the North Atlantic, the population structure of Greenland halibut is complex, with three main components that have different migratory patterns (Vihtakari et al., 2022). In the Northeast Atlantic, the spawning area extends from Vesterålen (68° 41′N, 15° 24′E), Norway, north to Bear Island (74° 30′N, 19° 00′E). The pelagic eggs and larvae drift northward with the West Spitsbergen Current and pelagic juveniles occur north of Svalbard and in the Arctic Ocean (Ingvaldsen et al., 2023).

Arctic skates occur from moderate depths (300 m) to the lower continental slopes (2,500 m). Tagging studies indicate that their migration routes are relatively limited, generally within 30–40 km of capture sites at Baffin Island (Peklova et al., 2014). The Atlantic is the most important dispersal route for skates into the Arctic Ocean, whereas on the Pacific side, the cold bottom water in the Bering Strait restricts their dispersal into the Arctic (Lynghammar et al., 2012). Climate warming and reduction of the Bering Sea "Cold Pool" thermal barrier (bottom water ~ −1.5°C), could facilitate increased migration of skates and other fishes from the Bering Sea through the Bering Strait into the Arctic Ocean (Mueter et al., 2021).

In contrast to skates and other benthic fishes in the Arctic, the demersal Greenland shark is the most migratory elasmobranch in the Arctic, undertaking movements that are similar in extent to the Arctic whales. The Greenland shark is capable of long-distance migrations exceeding 1,000 km, and often conducts excursions between inshore and offshore waters (Campana et al., 2015; Edwards et al., 2022). Greenland sharks typically occur in coastal fjords during ice-free periods to feed (McMeans et al., 2013) and they move offshore during the period of ice reformation (November to July). On the other side of the Arctic Ocean, the Pacific sleeper shark (*Somnious pacificus*) ranges from the Bering Sea throughout the deep waters in the Pacific and into the Southern Ocean (Yano et al., 2004), and this fish also undertakes seasonal migrations from onshore to offshore waters. Little is known about how climate warming will affect these sharks, except when they occur in shallower coastal waters to feed and can then be caught and outfitted with biotelemetry instruments (Lydersen et al., 2016).

Arctic pelagic fishes include the Arctic cod (*Boreogadus saida*) and the polar cod (*Arctogadus glacialis*), both of which are important forage fishes for Arctic and Subarctic predators (e.g., Welch et al., 1992, 1993; Pettitt-Wade et al., 2021). On the Pacific side, the saffron cod (*Eleginus gracilis*) is abundant in the western Arctic, where it plays a significant role in food webs (e.g., Crawford et al., 2015). It is more demersal than Arctic and polar cod and it has a more southerly and nearshore distribution (De Robertis et al., 2017). Seasonal movements by Arctic cod are typically inshore/shallow during summer and are associated with juvenile development, adult feeding, and pre-spawning schooling, whereas movements to deeper areas are linked to spawning and overwintering below sea ice (Hop et al., 1997; Geoffroy et al., 2011; Benoit et al., 2014; Bouchard et al., 2016). Adult polar cod may perform long seasonal movements (<200 km) within the Arctic (Kessel et al., 2017). In the eastern Barents Sea, polar cod migrate northward in May-June, following the ice edge, with the largest fish moving first (Aune et al., 2021). In the Chukchi Sea, seasonal differences in Arctic cod abundance suggest that their migration between nursery grounds as juveniles, feeding grounds as subadults, and spawning grounds as adults, is linked to ice cover and seasonal production patterns (Forster et al., 2020). Polar cod also move between inshore and offshore areas in relation to spawning, feeding, and juvenile development, respectively (Bouchard et al., 2016; Pettitt-Wade et al., 2021). Saffron cod have different seasonal movements since they migrate inshore to spawn during winter and offshore to feed during summer (Logerwell et al., 2015). This seasonal offshore movement allows them to access abundant food resources in deeper waters. The impacts of reduced sea ice on these life stage migratory movements are largely unknown.

3.1.5 Seasonal movements of boreal fish species into the Arctic

Several boreal fish species migrate seasonally to the Arctic to feed on abundant and lipid-rich prey. In the Atlantic, the main species are capelin, Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*). Capelin juveniles and sub-adults undertake feeding migrations along the east coast of Greenland and in the eastern Fram Strait and in the Barents Sea over to the slopes of the Arctic Ocean (Carscadden et al., 2013). Their northern distributions overlap with Arctic cod and they compete for some of the same zooplankton food sources (Hop and Gjøsæter, 2013; McNicholl et al., 2018).

Atlantic cod perform feeding migrations to Svalbard and the northern Barents Sea to the slopes of the Arctic Ocean, where they feed on capelin, Arctic cod, and other species (Haug et al., 2017). Such migrations are part of their life history, after pelagic eggs are released at spawning sites in northern Norway and larvae drift into the Barents Sea via the Norwegian Coastal Current (Ottersen et al., 2014). Juveniles and sub-adults disperse in the feeding areas, which include the Barents Sea as well as the shelf west and north of Svalbard to the slope of the Arctic Ocean. Adults perform annual spawning migrations to the Norwegian coast in March and subsequently migrate northwards after spawning. An increasing cod stock represents more prey for marine mammals, but also competes for some of the same food sources (Bogstad et al., 2015). The more demersal haddock migrate northwards to areas also used by Atlantic cod, particularly on the western and northern coasts of Svalbard and adjacent slopes, where they predominately feed on benthos rather than fish (Landa et al., 2014).

In the Pacific, the reduced Bering Sea "Cold Pool" has facilitated the dispersal of juvenile walleye pollock (*Gadus chalcogrammus*) from the Bering Sea into the Chukchi Sea (Eisner et al., 2020; Grüss et al., 2021; Levine et al., 2023). This has created a migratory pattern for walleye pollock, from a source population in the northern Bering Sea, with larvae and juveniles advected into the Chukchi Sea with presumed return migration (Levine et al., 2023). However, some individuals migrate across the Arctic Ocean to the North Atlantic (Orlov et al., 2021). The same process has brought Pacific cod (*Gadus macrocephalus*) into the northern Bering Sea, and although juveniles have passed through the Bering Strait they are unlikely to survive beyond age-1 because of poor growth conditions for this species in the Chukchi Sea (Cooper et al., 2023).

Mackerel (*Scomber scombrus*) and Atlantic bluefin tuna (*Thunnus thynnus)* can occasionally undertake migrations to the Arctic from their more typical southern ranges, with respective spawning areas in the eastern North Atlantic and in the Mediterranean Sea (Mackenzie et al., 2014; Berge et al., 2015b). These expansions involve longer seasonal migrations to feeding areas, since their southern spawning areas have not changed. If ocean warming facilitates more efficient predatory fishes to move into the Arctic, this could cause cascading top-down effects on marine food webs.

3.2 Seabirds

3.2.1 Seabird life history patterns in circumpolar regions

For this review, we use the term "seabirds" to encompass species that spend most of their lives at sea and return to land to nest and raise young (families Procellariidae, Phalacrocoracidae, Laridae, Alcidae), as well as other marine-feeding birds that spend more time in terrestrial or freshwater habitats, and do not typically nest in colonies (families Anatidae, Gaviidae, Stercoraridae, and phalaropes [Scolopacidae]). In general, seabirds are highly mobile and have evolved to find food in a dynamic environment, with a wide range of life history traits among species. Approximately 64 seabird species use the Arctic, ~30 of which breed only within the CAFF boundaries of the Arctic (Irons et al., 2015). Seabirds are highly philopatric to their nesting sites, becoming central place foragers while raising chicks, and are free-ranging the rest of the year. Some seabird species and most sea ducks and phalaropes stage in marine areas prior to post-breeding migration, and then typically use a "fly and forage" strategy (e.g., red phalaropes (*Phalaropus fulicarius*) (Saalfeld et al., 2024) and track areas with high prey densities (e.g., little auks (*Alle alle*) (Amélineau et al., 2018). Other species nest far south of our study area (e.g., *Ardenna* shearwaters) or in Subarctic regions (e.g., *Aethia* auklets), but migrate seasonally to the Arctic where they can forage opportunistically during their post-breeding periods.

Seabirds that breed in the Arctic display an array of migratory patterns, ranging from movements within an ocean basin to species that migrate between the Arctic and Antarctic (Arctic terns, *Sterna paradisaea*). Foraging behavior and diets include surface foragers and divers, zooplanktivores, piscivores, benthivores, and omnivores. It is thus difficult to generalize regarding climate change impacts on seabirds, and indeed, the variability in foraging and migratory patterns guarantees that different responses are exhibited across families and species (Cairns, 1987; Piatt et al., 2007; Woehler and Hobday, 2024).

Most seabirds cannot store large amounts of body fat and thus require close synchronization of seasonal life phases with environmental cues. In general, photoperiod is the most important cue for avian species to initiate migratory movements, breeding, and molting (Coppack and Pulido, 2004, and citations therein). Given the Arctic's brief summer season and seasonal extremes in daylight, temperature, open water access, and subsequent prey availability, the spatio-temporal match between a seabird and its prey is critical. Although they are highly mobile, seabirds often depend on concentrated, high densities of prey for efficient foraging (Russell et al., 1999; Jahncke et al., 2005), particularly when feeding chicks (Møller et al., 2018), and prey must be near the surface or at least within species-specific diving depth range (Benoit-Bird et al., 2013).

A few seabird species rely directly on ice-associated fauna. The Mandt's black guillemot (*Cepphus grylle mandtii*) in the Pacific Arctic (Divoky et al., 2016) and the ivory gull (*Pagophila eburnean*) (Spencer et al., 2014) and Ross's gull (*Rhodostethia rosea*) in the Atlantic Arctic (Gilg et al., 2016b) are closely tied to sea ice year-round, often following the marginal ice zone. Ivory gulls also forage on sea ice, scavenging on the remains from polar bear (*Ursus maritimus*) or polar fox (*Vulpes lagopus*) kills (Karnovsky et al., 2009). The red-legged kittiwake (*Rissa brevirostris*), which nests on islands in the central Bering Sea, shows a strong association with sea ice-influenced waters during the winter (Orben et al., 2015a). As their current primary habitat disappears, such pagophilic species will be forced to adapt their migratory patterns in the future, if they are to survive (Spencer et al., 2014; see Case Study No.1).

3.2.2 Evidence of changes in migration routes

Few seabird surveys have been conducted in the High Arctic and little is known about the extent to which seabirds rely on cross-Arctic routes for migration between breeding and overwintering areas. However, satellite tracking of individual birds and studies utilizing tracking radar have found that such routes do exist. Alerstam et al. (2007) documented Arctic Ocean migrations that were estimated to include over 2 million birds–comprised primarily of shorebird species, but also including terns (sub-family Sternidae) and skuas (*Stercorarius*). Reduced sea ice could facilitate increases in cross-Arctic migration (Clairbaux et al., 2019). For income migrants (that depend on feeding *en route*, i.e., most seabirds), more open water increases potential access to prey, making such transits possible (McKeon et al., 2016; Briscoe et al., 2017). At least a portion of one population of black-legged kittiwake (*Rissa tridactyla*) has been documented to travel over the Arctic from a colony in the Barents Region to overwintering sites in the Chukchi and Bering seas, and more cross-Arctic migrations of kittiwakes could occur as sea ice declines (Ezhov et al., 2021).

We lack long-term studies that can detect changes to migratory movements of most Arctic seabird species, but tagging studies indicate extensive cross-Arctic and ice-associated migrations that could be impacted by changes to this habitat. Ivory gulls that nest in the Atlantic Arctic migrate to the Bering Sea during their non-breeding season (Gilg et al., 2010), and Ross's gulls conduct cross-Arctic migrations in and among the Russian, Alaskan, and Canadian Arctic regions (Maftei et al., 2015; Gilg et al., 2016b), with most of the estimated world population moving westward past northern Alaska during October-November (Maftei et al., 2014). One four-decade study that combined distribution modeling and tracking data for thick-billed murres (*Uria lomvia*) in the Hudson Bay region, found that the greatest shift in distribution (westward and to recently ice-free waters) occurred during the fall migration period (Patterson et al., 2021).

Long-term monitoring via at-sea surveys can be used to examine seabird response to anomalously warm or ice-free conditions, perhaps a prelude to a warmer Arctic. One long-term pattern in the Pacific Arctic suggests that with longer open water seasons and increased zooplankton productivity, planktivorous seabirds have shifted post-breeding movements northward. In the eastern Chukchi Sea, zooplankton feeders such as *Aethia* auklets and short-tailed shearwaters (*Ardenna tenuirostris*) were more abundant in offshore waters during the 2000s than the local-nesting, fish-eating seabirds (alcids and larids), which had predominated in offshore waters during 1974–1995 (Gall et al., 2017). In fact, short-tailed shearwaters have gradually shifted their migratory route northward since ca. 2014 (Kuletz et al., 2020). Because the auklets and shearwaters do not nest in the region, their influx reflects a shift in their post-breeding migration, to forage on newly abundant late summer resources. However, this shift has not been a linear response to the warming Arctic; during a recent, anomalously warm period (2017–2019), substantially fewer auklets migrated into the Chukchi Sea in late summer and fall, and shearwaters altered their distribution across the Chukchi Shelf (Kuletz et al., 2024; Case Study No. 2).

Based on both satellite-tagged birds and at-sea surveys, some seabird species that nest in temperate and Subarctic regions migrate to Arctic waters for brief periods (weeks) after their breeding periods. In the North Pacific, ancient murrelets (*Synthliboramphus antiquus*) that breed on islands in British Columbia and the Aleutian Archipelago migrate to the northern Bering and Chukchi seas (Day et al., 2013; Gaston et al., 2017). Kittlitz's murrelets (*Brachyramphus brevirostris*) nest in Subarctic coastal areas of the northern Gulf of Alaska and migrate to the Arctic post-breeding (Day et al., 2013; Piatt et al., 2021). While abundance in the Arctic for both of these (primarily piscivorous) small alcid species have varied interannually, the long-term trend shows increasing numbers during late summer and fall in the northern Bering and Chukchi seas (Day et al., 2013; Kuletz et al., 2020). These species return south in the late fall when the hours of darkness increase and formation of sea ice begins (currently, October-November).

The philopatry shown by most seabird species to their traditional breeding sites limits shifts in colony formation as a rapid response to environmental change. However, northward expansions of seabird species are occurring and shifts in migrations northward to new feeding areas during the non-breeding portion of their life cycles have occurred with climate warming. For example, models based on at-sea surveys revealed that the three albatross species (*Phoebastria*) that spend portions of their non-breeding season in the Gulf of Alaska and Bering Sea have increased in numbers and two of those species have shifted their center of distribution northward in the Bering Sea (Kuletz et al., 2014). These changes indicate new migratory and overwintering patterns because the albatrosses breed on islands in the tropical North Pacific. The locally-breeding northern fulmar (*Fulmarus glacialis*) has also shown a northward shift in its center of distribution in the Bering Sea (Renner et al., 2013), but there is so far no evidence of a shift in breeding distribution. However, in the Atlantic Arctic, a northward shift in breeding has been documented with the establishment of northern gannets (*Morus bassanus*) on the northernmost coasts of Norway and Russia, and as far north as the Bear Island (in 2011), a major northward extension of their breeding distribution. These new colonies in the Arctic are associated with the northward movement of the gannet's prey species, such as herring (*Clupea harengus*) and mackerel, as the Barents Sea is warming (Barrett et al., 2017).

3.2.3 Evidence of changes in stop-over and wintering areas

Migration strategies include the locations of stop-over, staging, and over-wintering areas (Baurer et al., 2008; Newton, 2008), and observations indicate that these portions of the migratory cycle are also undergoing climate-related changes. For example, Steller's eiders (*Polysticta stelleri*) have shifted their main wintering areas from the Baltic Sea to the White Sea, as the latter has become increasingly ice-free in winter (Aarvak et al., 2013).

Documented shifts in the distribution of molting spectacled eiders (*Somateria fischeri*) in the Bering Sea between the 1990's and ca. 2010 could not be correlated with shifts in the distribution of benthic prey or other environmental variables (Sexson et al., 2016). Although the eiders did not change their wintering areas in response to changes in ice conditions, eider survival rates were lowest at either extreme in ice conditions (i.e., having no ice for resting, or lack of open water for foraging) (Christie et al., 2018). In the northern Gulf of Alaska, benthic feeding sea ducks seem to be more resilient to changes in environmental conditions than pelagic-feeding seabirds, highlighting the importance of considering trophic interactions when modeling responses to climate change (Cushing et al., 2018; Robinson et al., 2024).

Some species exhibit long stopovers, sometimes for molting, prior to movements to overwintering sites (Mosbech et al., 2006; Frederiksen et al., 2012; Fort et al., 2013). For example, red-legged kittiwakes leave their central Bering Sea island colonies and move to the western Bering Sea in the fall, before relocating to the southwestern Bering Sea near Kamchatka and Japan in late winter (Drummond et al., 2021). Migration patterns can differ between closely related species (e.g., kittiwakes, Orben et al., 2015a; murres, Takahashi et al., 2021; and puffins, Shoji et al., 2023), and between sexes (e.g., murres, Mosbech et al., 2006; Frederiksen et al., 2016; Huffeldt et al., 2024; Ross's gulls, Gilg et al., 2016b). Both tagging studies and at-sea surveys indicate that interannual variability in spatial distribution during migration is common (e.g., short-tailed shearwaters, Yamamoto et al., 2015; black-legged kittiwakes, Orben et al., 2015b; red phalaropes, Saalfeld et al., 2024). Thick-billed murres in Hudson Bay, Canada, have adjusted timing of departure in fall and arrival in spring as the open-water season has become extended by nearly 3 weeks, and modeling indicates that overwintering sites have shifted

211 km west and 50 km north per decade (Patterson et al., 2021). Behavioral flexibility during the non-breeding season suggests that while changes in sea ice may be a key feature in the High Arctic and can influence actively migrating seabirds, birds may not alter use of overwintering areas in Subarctic regions based solely on ice conditions (e.g., red-legged kittiwakes in the Bering Sea; Orben et al., 2018).

3.2.4 Energetic aspects of climate related changes in migration

Pre-breeding and post-breeding migrations by seabirds often include the need to replenish fat reserves lost during winter or breeding, respectively, or to fuel molting (Markones et al., 2010; Fort et al., 2013). These energetic needs require most seabirds to be "income migrants," taking advantage of concentrations of prey along their migratory paths. However, short-tailed shearwaters make few foraging stops when migrating from the Arctic back to their Australian breeding grounds (Woehler and Hobday, 2024), and the energetic costs of extending the Arctic portion of their non-breeding route (Kuletz et al., 2020; 2024) could have implications for their survival and reproductive success (Glencross et al., 2021).

3.3 Marine mammals

The Arctic marine mammal community consists of 11 resident Arctic endemic species and ca. 25 seasonally-resident species that migrate into Arctic waters to take advantage of seasonally productive foraging opportunities during the open-water period. Climate change is impacting endemic Arctic marine mammals via both direct alterations to their habitats and indirectly via ecosystem change, as well as changing patterns of human activity (e.g., Kovacs and Lydersen, 2008; Kovacs et al., 2011; 2012; 2021; Gilg et al., 2012; George et al., 2015; Laidre et al., 2015; Descamps et al., 2017; Halliday et al., 2022). Many seasonal migrants are benefitting from longer open-water seasons and are tracking northward shifts of their prey species. Northward shifts in range to track optimal environmental conditions are a predicted response to climate change for Arctic marine mammals, which are highly mobile, large animals (Gilg et al., 2012). The ongoing climate changes are influencing movement patterns on both large and small scales.

3.3.1 Shifts in phenology of Arctic endemic species

Variability in the timing of migration, induced by global warming, has been recorded for many marine mammal species, including Arctic endemics. Most populations of bowhead whales (*Balaena mysticetus*) migrate from key foraging areas, where they have access to seasonally abundant zooplankton prey during the polar summer and fall, to habitats used for mating in winter and calving in spring. Migration timing is linked to the northward sea-ice retreat in spring and the southward sea-ice expansion in the fall for most populations of bowhead whales (but see Lydersen et al., 2012). In recent years, variability in timing of migration has been linked to variability in the timing of the open water season (Druckenmiller et al., 2018). Phenological changes with both earlier migration in the spring (Noongwook et al., 2007; Huntington et al., 2021; Szesciorka and Stafford, 2023) and later migrations in fall (Stafford et al., 2021; Szesciorka et al., 2024) have been documented in recent decades in the Pacific Arctic, where acoustical time-series data extend over decades and multi-generational Indigenous Knowledge has been documented. Sea surface temperatures have been suggested as one potential cue triggering (or delaying) migration (Tsjuii et al., 2021), along with changes in sea-ice concentrations (Ferguson et al., 2010). Some individual bowheads have ceased migration entirely, remaining in their summering grounds in the Amundsen Gulf and in the eastern Beaufort Sea (Insley et al., 2021; Diogou et al., 2023) and in Cumberland Sound (Fortune et al., 2020), although this pattern may have existed undetected prior to telemetry studies.

Many populations of beluga whales (*Delphinapterus leucas*) undertake cyclical annual migrations, moving between summering grounds and offshore wintering areas, which are often within drift-ice areas or near ice edges. Large beluga whale populations that occupy High Arctic areas tend to migrate greater distances relative to small populations, which have relatively localized regional movements (Luque and Ferguson, 2009; McGuire et al., 2020; Lydersen and Kovacs, 2021). Tagging data from 1998 to 2002 and 2007–2012 indicated that during the latter period (which had less sea ice and a later freeze-up), Chukchi Sea beluga whales delayed fall migration by 2 to >4 weeks (Hauser et al., 2017).

Most narwhal (*Monodon monoceros*) populations aggregate in predictable coastal areas during summer and then migrate to ice-covered areas offshore before the onset of heavy ice formation. Kenyon et al. (2018) and Shuert et al. (2022) documented significant delays in the timing of fall migrations using tracking data that extend over two decades in the Canadian Arctic; these time frames match climate-driven rates of sea-ice loss for the region.

Few long-term tracking studies exist for Arctic endemic seals, although some species undertake extensive migrations. The Atlantic drift-ice seals, harp seals (*Pagophilus groenlandicus)* and hooded seals (*Cystophora cristata*), breed in spring in southern parts of their ranges, but migrate northward to molt and to forage throughout the summer in Arctic waters, before returning south again in fall (see Vacquié-Garcia et al., 2024). Hooded seals have undergone significant changes in phenology of their movements, with earlier departures north and delayed departures southward (see Case Study No. 3), resulting in an extended period of Arctic residency. Summer foraging migrations of ringed seals (*Pusa hispida*) to preferred sea-ice concentrations start at similar times compared to the past, but now require longer travel distances compared to decades ago (Freitas et al., 2008; Lone et al., 2019; Ogloff et al., 2021).

Most Pacific walruses (*Odobenus rosmarus divergens*) follow seasonal migration patterns between southern wintering areas and northern summering areas. Sea-ice changes in the Pacific Arctic have resulted in changes in the phenology of migration, with walruses arriving earlier and staying later in their Chukchi Sea summering areas during 2008–2011, compared to past decades, until they return south to the Bering Sea following the expansion of winter sea ice (Jay et al., 2012).

Female polar bears generally migrate between foraging areas on offshore sea ice during summer and denning areas on land for the winter, and landfast sea ice is an important spring foraging area for mothers with young-of-the-year cubs (Rode et al., 2015). However, there are exceptions to these patterns, e.g., denning occurs on the sea ice in the Beaufort Sea, and a proportion of the Barents Sea polar bear population remains ashore year-round (Aars et al., 2017; Rode et al., 2022). It is likely that some immature or adult male bears remain in offshore habitats year-round, but tracking data is lacking for these groups of bears. Reductions in sea ice are resulting in phenological changes to the movement patterns of bears, with some moving onto land earlier in the fall and departing later in the spring (Rode et al., 2015; Escajeda et al., 2018; Laidre et al., 2018; Atwood et al., 2021).

3.3.2 Shifts in phenology of seasonal migrants

Based on passive acoustic monitoring (2012–2019), gray whales (*Eschrichtius robustus*) have shown little change in spring arrival timing in the Pacific Arctic, but they have been departing the northern Bering Sea and southern Chukchi Sea earlier each year since 2016; it is uncertain whether this is a major phenological change or whether it is simply an east-west range shift away from the recorder sites (Moore et al., 2022). Other seasonal migrant cetaceans, including blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), minke (*B. acutorostrata*), sperm (*Physeter macrocephalus*), and killer whales (*Orcina orca*) arrive earlier to high latitudes, and depart later in the northeast Atlantic Arctic (Storrie et al., 2018; Bengtsson et al., 2022; Stafford et al., 2022; 2024). Some species (e.g., fin whales) that were summer residents in the past are currently detected acoustically at high latitudes year-round (Ahonen et al., 2021). Killer whales have extended their season of residence both in the Canadian High Arctic and in the Pacific Arctic (Higdon et al., 2014; Stafford, 2019), indicative of expanded migratory routes and timing, with evidence that some killer whales traveled to the Arctic from tropical waters (Matthews et al., 2020; 2024).

3.3.3 Shifts in distribution of Arctic endemic species

Bowhead whales in the Bering-Chukchi-Beaufort region have wintered farther north into the Chukchi Sea during 2018 and 2019, away from their typical winter home range in the western Bering Sea, which was devoid of sea ice those years (Citta et al., 2023). Aerial survey data indicate a westward shift (closer to Point Barrow) during fall migration of bowheads during 1997–2014, compared to 1982–1996, which corresponds to a shift closer to shore with more open water in recent years (Druckenmiller et al., 2018). In West Greenland, bowhead whale movements away from traditional summering areas in Disko Bay have occurred with the animals shifting southward, tracking SST patterns, with the whales specifically targeting a narrow range of temperatures, between −0.5°C and 2°C (Chambault et al., 2018).

Shifting of migratory pathways to reach new areas has been documented for narwhals that formerly resided in Eclipse Sound in the eastern Canadian Arctic, but now travel to Admiralty Inlet and Prince Regent Inlet (Kenyon et al., 2018). High levels of human disturbance associated with heavy vessel traffic servicing an industrial mine (Witting, 2023), as well as killer whale predation, have been suggested as the principle causes of this change (Lefort et al., 2020). Influx of warm Atlantic water (with associated boreal prey) has changed the coastal distribution of belugas on the west side of Svalbard. Previously, belugas in this area foraged on Arctic cod almost exclusively at tidewater glacier fronts and migrated between such areas along the coastlines (Lydersen et al., 2001; 2014; Vacquié-Garcia et al., 2018). However, they now spend much more time away from shore in the fjords, occupying different water masses, presumably to feed on small boreal fish species (Hamilton et al., 2019). In contrast, belugas in the Pacific Arctic have not significantly shifted their habitats despite loss of sea-ice cover during 1990–2014 (Hauser et al., 2018a).

Changes in sea-ice distribution (mainly, summer sea-ice edges occurring farther north) have resulted in much longer migrations for ringed seals in the Barents Region, as well as changes in their foraging behavior (Hamilton et al., 2015). Young animals must travel farther north to reach sea ice and adult ringed seals that stay in coastal areas around Svalbard now have very restricted movement patterns compared to a few decades ago, with small home ranges, where they show increased foraging effort (Hamilton et al., 2016; 2019).

Previously, when sea ice remained throughout the year over the shallow shelf of the Pacific Arctic, female walruses and young animals remained year-round near the sea ice, which serves as a haul-out platform. With the retreat of the sea ice northward over the deep Arctic Ocean, females and young now move to land-based haul-out sites along the coasts of Alaska and Russia between feeding trips, where male walruses also gather (Jay et al., 2012). Disturbances at these mixed-sex, high-density haul-outs have resulted in increased calf mortality from stampedes, at levels that can negatively impact population demographics (Udevitz et al., 2012).

Polar bear migrations have tracked sea-ice reduction in some parts of the species' range. In Svalbard, bears no longer migrate south to islands (e.g., Hopen Island) that were previously key sites for denning, because sea ice no longer forms this far south in the late fall-early winter (Andersen et al., 2012). Female bears leave the coastal sea ice in early summer and travel on shore, feeding at ground nesting bird colonies along the west coast (Hamilton et al., 2017; Bengtsson et al., 2021). Olson et al. (2017) have documented a trend toward less denning on sea ice and more denning on land for the polar bear population in the southern Beaufort Sea. In this region, declines in sea ice have resulted in divergent movement patterns, with most of the subpopulation remaining on sea ice during summer, though some animals remain on land. The bears on ice have increased their home range sizes and migrate longer distances, while bears on land exhibit vastly smaller (88% less) annual utilization distributions (Pagano et al., 2021). Similarly, the Chukchi Sea polar bears are moving onto land for longer time periods due to reduced sea-ice cover (Rode et al., 2015; 2022). In Baffin Bay in the 1990s, summer offshore sea ice allowed polar bears to move widely, but its disappearance in the 2000s led to reduced movement rates (Laidre et al., 2018). During this time, adult females favored lower sea-ice concentrations when it provided access to the continental shelf and delayed den entry accounting for shorter denning durations (Escajeda et al., 2018). In Hudson Bay, polar bears are spending more time on sea ice that is distributed farther north than in the past (Miller et al., 2022), with their migrations to and from coastal areas being tightly coupled to sea-ice concentrations and fragmentation (Biddlecombe et al., 2021). Migrations involve significantly more swimming time for polar bears in areas where sea ice has declined, which has energetic implications for individuals (Pilfold et al., 2017).

3.3.4 Shifts in distribution of seasonal migrants

Northward shifts in migration endpoints (seasonal distributions) for many migratory cetaceans including blue, fin, humpback, minke, killer, and sperm whales have been documented over recent decades (Brower et al., 2018; Storrie et al., 2018; Stafford, 2019; Stafford et al., 2022; Lydersen et al., 2020; Ahonen et al., 2021; Bengtsson et al., 2022; Heide-Jørgensen et al., 2022; Pöyhönen et al., 2024). The Nunavummiut, Inuit residents of Nunavut, have observed an increase in killer whales in Nunavut waters associated with reductions in sea ice and changing movement patterns of other marine mammals that killer whales prey upon (Higdon et al., 2014). Increasing presence of sperm whales and northern bottlenose whales (*Hyperoodon ampullatus*) has been observed in Baffin Bay, coincident with the longer open-water season and expanded northward migratory routes (Posdaljian et al., 2022; Davidson et al., 2023). Harbor porpoises (*Phocoena phocoena*) have been detected in mid-winter in Kotzebue Sound in the Chukchi Sea, which likely reflects a recent northward extension of their migration patterns (Whiting et al., 2020).

4 Discussion

The decline in area, thickness, and seasonal duration of sea ice within the last 20 years has greatly altered the Arctic ecosystem, and this trajectory is predicted to continue as northern-latitude temperatures increase (Barber et al., 2015; Hunt et al., 2016; Ballinger and Overland, 2022; IPCC et al., 2023), due to anthropogenic carbon emissions (Kumar et al., 2020; Carvalho et al., 2021). The biological importance of the marginal ice zone (MIZ), or ice edge, to Arctic vertebrates has long been recognized (Divoky, 1977; Bradstreet and Cross, 1982; Hunt et al., 1996; Stirling, 1997). For many Arctic upper trophic level animals, their migratory timing and distribution track the MIZ because the mix of open water and ice-associated primary productivity support prey from invertebrates to forage fishes, and from benthic to pelagic food webs (Bradstreet and Cross, 1982; Kędra et al., 2015; Axler et al., 2023). As the MIZ has retreated earlier in spring and moved farther north (Perrette et al., 2011), it has potential to impact migratory movements at multiple trophic levels. Although we lack historic data on the migration patterns of many Arctic species, there is mounting evidence that the rapid changes occurring in the Arctic, particularly during spring through fall, have already resulted in changes in marine vertebrate migrations.

Climate change continues to alter open water patterns, sea-ice habitat and associated prey, timing of prey availability, and accessibility of foraging and travel routes. Changes in the temporal and spatial characteristics of habitat and prey in these circumpolar regions will alter species composition, biodiversity, and food web characteristics. The reduction in sea ice will also influence human activities, with increases in vessel traffic, oil, gas, and mining exploration and extraction, and coastal construction being likely in many areas, introducing artificial light sources, ocean noise, and risks of collisions that can impact migratory behaviors of some species (Reeves et al., 2014; Ivanova et al., 2020; Gjerdrum et al., 2021; Burt et al., 2023; Witting, 2023).

Sea-ice cover influences basic marine productivity (Arrigo et al., 2008) and access to prey (Benoit et al., 2010), and therefore affects both temporal and spatial aspects of migration. However, because of the extreme seasonal patterns of daylight in the Arctic, the temporal boundaries on primary and secondary production likely restrain the effectiveness of phenological responses of marine vertebrates to environmental change, especially for species that breed in the Arctic. Adaptation will thus often require alterations in spatial patterns of migration. The extent to which upper trophic level taxa can adjust their phenologies, habitat use, prey type, and spatial distribution will determine their resilience to ecosystem changes brought about by climate change. Where data are available, the emerging pattern among Arctic vertebrates is to change both spatial routing and temporal duration of migrations.

4.1 Influence of ecological barriers and bridges on migratory routes and ecosystems

Sea-ice losses remove an “ecological barrier” for some marine animals, as more open water creates “ecological bridges” across the Arctic, with more access to prey and travel corridors (Heide-Jørgensen et al., 2011; McKeon et al., 2016; Briscoe et al., 2017). Less ice in the Central Arctic Ocean will also open up new and energetically favorable migration routes for birds (Clairbaux et al., 2019). Shifting ranges northward to track optimal environmental conditions is a predicted response to climate change for Arctic animals, particularly for highly mobile, large-bodied marine mammals (Gilg et al., 2012). Consequently, changes in migratory patterns functionally result in shifts in ranges for these animals. Northward shifts by invertebrates and fish are also likely to play a role in changes in other marine animal distributions, although predation, competition, anthropogenic noise, and other human activities might limit geographic adjustments for some species (Gilg et al., 2012; Reeves et al., 2014; Blackwell et al., 2015; Matthews et al., 2020a; ; 2020b; Halliday et al., 2022).

Northward expansions of Subarctic and temperate marine vertebrates in response to global changes (referred to as borealization, or Atlantification and Pacification), are difficult to separate from changes in migration, and in some cases may just be a matter of semantics. Clearly, migratory pathways have shifted northward or otherwise changed to track favorable habitats (e.g., glacial fjords, or shoals that entrap ice during summer), which effectively becomes a range expansion or contraction. Ectothermic fishes are particularly responsive to temperature, and warmer water temperatures have led to northward expansions of both anadromous and marine species (Dunmall et al., 2024; Haug et al., 2017; Baker, 2021). Warm phases and marine heatwaves can facilitate northward excursions by species such as juvenile Chinook salmon (*Oncorhynchus tshawytscha*) that have moved north in the Bering Sea (Murphy et al., 2017) or sub-adult Chinook salmon from the Pacific Northwest occurring in the Bering Sea (Guthrie et al., 2021). The massive and unprecedented influx of juvenile walleye pollock and Pacific cod into the Chukchi Sea during the 2017–2019 warm phase precipitated ecosystem-wide impacts (Ballinger and Overland, 2022; Cooper et al., 2023; Levine et al., 2023; Kuletz et al., 2024; Case Study No. 2). Conceivably, such shifts in seasonal migratory patterns and accompanying ecosystem impacts, could become permanent.

The retraction of sea ice also removes essential habitat for some animals and intensifies spatial overlap of species. For example, declines in landfast ice in fjords and along Arctic coasts have increased seasonal mixes of Arctic and Subarctic fish species (Watt et al., 2016; Vihtakari et al., 2018), as well as avian and mammalian species (Higdon et al., 2014; Madsen et al., 2019; Stafford et al., 2022). Ice concentration, wind speed, and wind direction can interact to affect migratory movements; for example, polar bears in Hudson Bay move onto land when wind conditions and temperatures result in early seasonal ice breakup (Bohart et al., 2021). In the western Beaufort Sea, bowhead whales and beluga aggregate where and when favorable wind and current conditions tend to concentrate euphausiids and fish (Ashjian et al., 2010; Okkonen et al., 2011; Stafford et al., 2013). Under similar conditions, aggregations are seen for bowhead whales at Arctic hotspots in Russia, Canada, and Greenland (Citta et al., 2015; Banas et al., 2021). In the Chukchi Sea, such episodic conditions can create hotspots of foraging for seabirds and marine mammals during the late summer and fall migration period (Kuletz et al., 2015), which may influence timing and spatial patterns of migration.

Recently documented overlaps due to new migratory movements indicate disruptions in food webs and altered predator-prey relationships, such as the competition for prey between Atlantic cod and marine mammals in the Barents Sea (Bogstad et al., 2015). Increased numbers of Subarctic species can result in greater competition (e.g., diet overlap), potentially causing declines in endemic populations and affecting ecosystem structure, as postulated for Arctic cod in the Atlantic Arctic, where Subarctic fish species have encroached (Renaud et al., 2012; Christiansen, 2017). While new prey species may be available to predators, the nutrient quality vs capture effort may not be comparable. For example, Subarctic fishes often contain less lipids than Arctic species, or can be an unpredictable food source due to variable abundance, reducing their energetic value to – or predictability for – seabirds and marine mammals (Österblom et al., 2008; Gaston et al., 2009; Hop and Gjøsæter, 2013; Descamps and Strøm, 2021).

While Subarctic species are expanding their distributions by altering migratory routes, the distributional ranges of some Arctic species are contracting northward to areas more influenced by sea ice, or to cold deep waters along slopes or basins of fjords (Huserbråten et al., 2019; Bonnet-Lebrun et al., 2021). As Subarctic fish species expand into the Arctic, mainly driven by increasing water temperatures and declining sea-ice distribution (Mueter et al., 2021), there is evidence of ecosystem impacts (Falk-Petersen et al., 2007; Eriksen et al., 2017). Arctic endemic fish species may reach limits in spatial adaptability when moving between breeding and non-breeding areas. The distance to summer Arctic feeding areas may limit the effectiveness of migratory adaptations, due to longer transits and new predators. For example, models for Barents Sea capelin indicate that their populations will shift east and north in summer as ocean temperatures increase, and their spawning areas could potentially also change from the Norwegian coast to include Arctic islands (Huse and Ellingsen, 2008). Increasing distances to northern ice edges are likely to become energetically limiting for some marine mammals (e.g., Freitas et al., 2008; Lydersen et al., 2014). Likewise, for seabirds that migrate to the Arctic for post-breeding replenishment, the additional distance to prey fields that have moved farther north (Kuletz et al., 2024) may no longer be energetically beneficial for those birds. When summer ice edges occur north of the shelf seas, over deep Arctic Basin waters, low productivity because of limited nutrients affects the abundance of prey species and, thus, will likely limit the northward range expansion of predators.

4.2 Timing of migratory movements and energetic implications

The cues that trigger migratory movements may vary in importance among taxa, and will affect different aspects of their life histories. Ectothermic fishes are more directly impacted by changes in water temperatures, and larval and juvenile stages are subject to passive "migratory" movements, and thus show a rapid, and sometimes dramatic response to altered environmental conditions (Langangen et al., 2016). Fish species that perform multiple lifetime migrations may be particularly vulnerable, given the multiple times they must contend with various stressors to time their migration to match pulses of marine production during spring-summer. Some endothermic long-distance migrants, such as shearwaters, may face similar issues matching movements with prey availability as they navigate between hemispheres. Shearwaters may act more as capital migrants while in the Arctic and Subarctic, by storing fat reserves for long southerly transits with minimal foraging (Woehler and Hobday, 2024). However, large die offs of shearwaters have been observed in Alaska during marine heatwave events (Baduini et al., 2001; Jones et al., 2023), suggesting that this migratory strategy may not be adequate with continued warming of northern oceans. Alternatively, animals that are restricted to a specific type of habitat during migration, or that can only move within a small area, may face even greater impacts from alterations of that habitat due to climate change.

Seabirds are highly mobile, but their breeding season restrictions mean that the greatest shift in timing and habitat use for them are the migratory periods immediately before and after breeding. Tracking data suggest that for some species, overwintering areas can generally be consistent among years (Orben et al., 2015b), although other studies indicate that individuals show flexibility and variability (Guilford et al., 2011). Photoperiod appears to be the critical element for timing of migratory movements for seabirds, even if migratory routes vary, and this may be how mated pairs that migrate and winter apart are able to synchronize their returns to the nest site (e.g., thick-billed murres, Huffeldt et al., 2024). These evolutionary-scale relationships will be strained by the rapid changes in the Arctic environment.

Many marine mammals, which can rely on body fat reserves due to their large body size, have adjusted to changing conditions by arriving earlier and remaining longer in their summer Arctic foraging areas (Hauser et al., 2017; Szesciorka et al., 2024). Some species have individuals that currently remain in High Arctic areas year-round (Insley et al., 2021), thereby increasing opportunities for exchange among populations (Heide-Jørgenson et al., 2011; Ahonen et al., 2021; Diogou et al., 2023). Changes in Arctic marine mammal migratory routes indicate a primarily northward shift to track suitable oceanographic conditions, ice-edge upwelling areas, or preferred prey (Storrie et al., 2018; Bengtsson et al., 2021; 2022; Citta et al., 2023). Reduced sea-ice conditions have apparently created a "boom time" for large whales in the Pacific Arctic in newly exposed areas (Moore, 2016). However, several Unusual Mortality Events among ice-dependent species of marine mammals in the Pacific Arctic have been linked to reductions in sea ice (Barratclough et al., 2023), highlighting variable results for different species in response to changes in a single driver.

4.3 Social and ecological impacts

Increases in ship traffic and other human activities have already been observed in the Arctic, with anticipated effects on movements of some fishes (e.g., Arctic cod, Ivanova et al., 2020), seabirds (Merkel and Johansen, 2011; Gjerdrum et al., 2021) and marine mammals (Reeves et al., 2014; Hauser et al., 2018b; Silber and Adams, 2019; Halliday et al., 2021). Another risk for endemic Arctic species is the possibility of novel pathogens arriving via Subarctic species spending more time in the Arctic (Greer et al., 2008; Barratclough et al., 2023).

For most Arctic, and many Subarctic species, limited historic and current data make forecasts regarding changes in migratory phenology and routes challenging. Changes that have occurred also impact the quality of species' monitoring; for example, new wintering areas may be more remote than traditional sites already monitored (e.g., Fox et al., 2019), or new migration routes and stopovers are not yet discovered. Establishing monitoring programs that are adaptable to such changes will require planning for such contingencies and working with people that live in the Arctic (Kochanowicz et al., 2021; Hauser et al., 2023; Clairbaux et al., 2024).

Ongoing climate changes challenge the resilience and adaptability of Arctic people and ecosystems and will require a close coupling of adaptive monitoring and research, with ecosystem-based management of human activities at all levels, including those involved with Indigenous harvest practices (see Case Study No. 4), as recommended by the Arctic Council (Siron et al., 2008; https://pame.is/projects/ecosystem-approach). In nearshore Arctic areas, earlier ice break-up and warming air and SST impact food security and traditional cultural practices that rely on availability and access to migratory marine vertebrates (ICC-Alaska, 2015; Regehr et al., 2017; Falardeau and Bennett, 2020; Ford et al., 2021; Hauser et al., 2021; Falardeau et al., 2022; Ovitz et al., 2024). Indigenous Peoples have been adapting to changing conditions since time immemorial, yet rapid climate-driven changes require adoption of new strategies. Indigenous Knowledge and perspectives in decision-making contribute to interpretation of observed changes in animal migration and equitable solutions to Arctic change (Wong et al., 2020; Hauser et al., 2021; Yua et al., 2022). Additionally, Indigenous Knowledge provides information on long-term changes, including changes in migration phenology or evidence of population fluctuations (Mallory et al., 2003; Moore and Hauser, 2019; Clairbaux et al., 2024).

4.4 Conclusion

Unpredictability in Arctic physical and biological conditions is a key current and future challenge for marine vertebrates that rely on migration for survival and reproductive success. Fish species may respond more directly and quickly to physical changes, but many fish species are more limited in mobility than seabirds and marine mammals. Seabirds are highly mobile, but may be more restrained by photoperiod, and less able to use a capital migratory strategy because of their relatively small body sizes, thus temporal and spatial changes to prey could impede their adaptability. Marine mammals have altered their timing and spatial migratory patterns, but prey availability and new predation regimes (i.e., new and longer presence of top predators) may limit the effectiveness of altering migratory patterns. Increased human activity levels in previously ice-covered areas will also influence Arctic ecosystems, while altered animal migration routes and loss of sea ice that facilitated hunting impact Indigenous communities. Monitoring Arctic populations of fishes, seabirds, and marine mammals will require adaptive practices to track shifts in timing and distribution of these important ecosystem components. Habitat declines for ice-dependent Arctic species is a serious threat to global biodiversity, and collaboration among stakeholders is imperative to address these challenges effectively.

5 Case Studies

5.1 Case Study No.1. Ivory gull: an ice-dependent seabird

The ivory gull is probably the most Arctic of all marine birds. It is tightly linked to sea ice habitats throughout the year, where it feeds on a variety of prey ranging from marine invertebrates to seal carcasses (Gilg et al., 2016b; Spencer et al., 2016; Dumas et al., 2022). Ivory gull breeding colonies are located in the High Arctic in Canada, Greenland, and in the High Arctic archipelagos of Svalbard (Norway) and Franz Josef Land (Russia). Tracking studies and observations have shown that the main wintering areas are along ice edges in the Davis Strait and the Bering Sea (Gilg et al., 2010; Spencer et al., 2014; Frederiksen et al., 2021). Notably, ivory gulls consistently migrate along ice edges to areas south of the Arctic Circle, and overwinter where daylight remains available in mid-winter. This pattern is consistent with visual foragers that depend on sufficient light to feed. Winter sea ice is projected to retract northwards, and little ice is expected to occur south of the Arctic Circle in mid-winter by the late 21st century, particularly in the Bering Sea (DeRepentigny et al., 2020; Dörr et al., 2021). The available tracking data are insufficient to demonstrate changes in the timing or pathways of ivory gull migrations, but given the species' close link to ice-edge habitats and the observed and expected changes in this habitat, changes are likely occurring. The retreat of the marginal ice zone favoured by the ivory gull will impact its migratory pathways, and most of the non-breeding habitat of the ivory gull is projected to disappear. Unless the ivory gull can alter its migratory patterns, such changes in the ice habitat it uses for migration and overwintering, combined with the impact of receding summer sea ice near breeding colonies, puts this iconic species at high risk of decline and possible extinction before the end of the century.

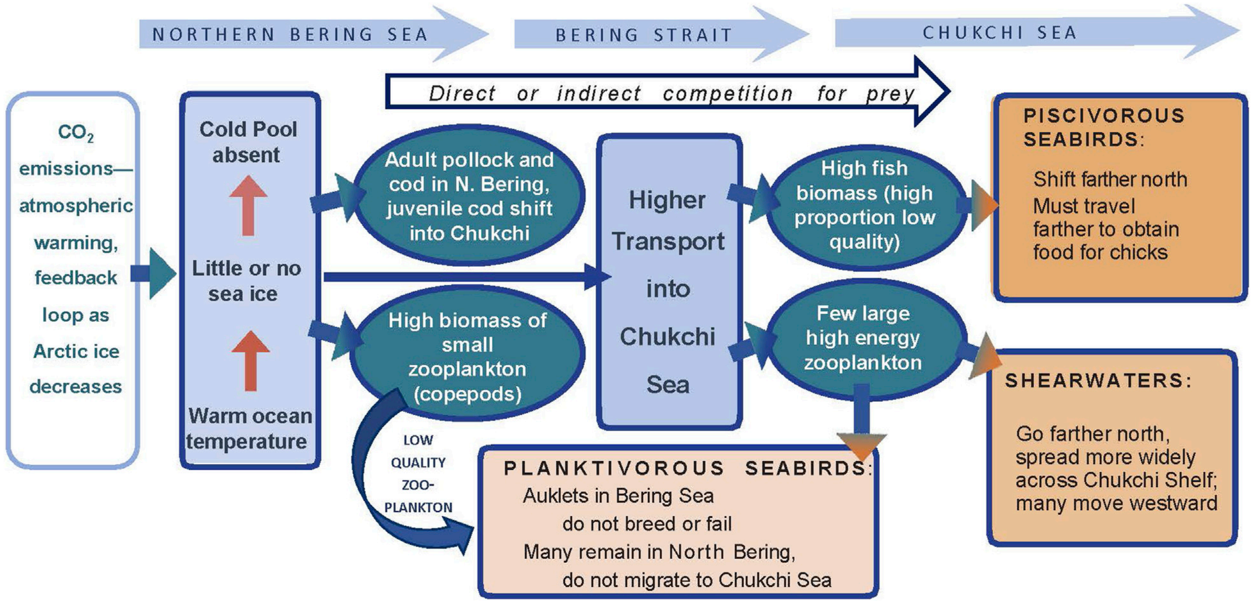

FIGURE 2
A conceptual model showing the physical drivers and changes in the Chukchi Sea ecosystem during a period characterized by marine heatwaves (2017–2019) and impacts to seabirds. Modified from Figure 12 in Kuletz et al. (2024).

5.2 Case Study No. 2. Seabirds respond to changes in the Chukchi Sea

In the eastern Chukchi Sea of the Pacific Arctic, reduced sea ice and warmer ocean temperatures have led to longer open-water seasons, higher zooplankton abundance and increases in boreal fish species (Mueter et al., 2021). These changes have led to changes in the offshore avian community during the post-breeding period, when seabirds must replenish body reserves and prepare for winter and migrations south. Piscivorous seabirds that nest along the southern Chukchi Sea coast used to be the most abundant seabirds in offshore waters during summers (1970s–1980s), but ship-based surveys during 2007–2012 found that planktivorous seabirds had become more abundant offshore (Gall et al., 2017). The offshore increase in planktivores was primarily due to abundance increases for two species of *Aethia* auklets, which feed on copepods and small euphausiids, and short-tailed shearwaters, which feed on larger euphausiids and small fish; both groups migrate through the Bering Strait into the Chukchi Sea to forage on abundant prey in late summer (Kuletz et al., 2015; Gall et al., 2017). Auklets and other alcids conduct such post-breeding northward migrations from breeding sites in the Bering Sea or even the Gulf of Alaska (Kuletz et al., 2024 and references therein). For the shearwaters, the Chukchi Sea is the northernmost extent of their seasonal migration from Australian breeding grounds (Yamamoto et al., 2015).

Continued warming of the Pacific Arctic may further alter seabird migratory patterns. During a recent period (2017–2019) with multiple marine heatwave events, the Chukchi Sea had high biomass of small zooplankton, but low abundance of large nutrient-rich copepods and euphausiids (Spear et al., 2019; Kim et al., 2020). Concurrently, fish abundance was elevated, including an unprecedented movement of age-0 walleye pollock into the region (Levine et al., 2023). The lack of a thermal barrier deep in the Subarctic Bering Sea known as the "Cold Pool" allowed adult pollock to shift northward and spawn near the Bering Strait, where warmer conditions led to increased advection through the strait and facilitated juvenile pollock movement into the Chukchi Sea (Baker et al., 2020; Levine et al., 2023; Figure 2). The pollock may have provided new prey to piscivorous birds but could also have competed for zooplankton with planktivorous seabirds and other forage fishes. Concurrently, abundance of the more omnivorous short-tailed shearwater increased greatly, but they were distributed across the shallow Chukchi Shelf (Kuletz et al., 2024) rather than in previously identified hotspots (Kuletz et al., 2015). In contrast, only low numbers of auklets, which experienced breeding failures in the northern Bering Sea (Will et al., 2020), traveled to the Chukchi Sea in 2019 (Kuletz et al., 2024). For highly mobile animals like seabirds, rapid changes in migratory patterns may be possible, but there are likely energetic costs incurred in traveling farther or for longer periods.

5.3 Case Study No. 3. Climate change impacts on hooded seal migration patterns

Hooded seals are Arctic endemic, drift-ice breeding, true seals that migrate between traditional pupping areas in southern parts of their range and traditional molting sites farther north, before dispersing over vast areas where they forage during summer and fall, mostly in High Arctic waters of the North Atlantic (Andersen et al., 2009; Vacquié-Garcia et al., 2017). Climate warming has resulted in increased ocean temperatures and marked reductions in sea-ice thickness, extent, and seasonal duration across the hooded seals' North Atlantic/Arctic range over the past three decades, with Atlantification of both physical and biological conditions (Kovacs et al., 2021). Few long-term data series are

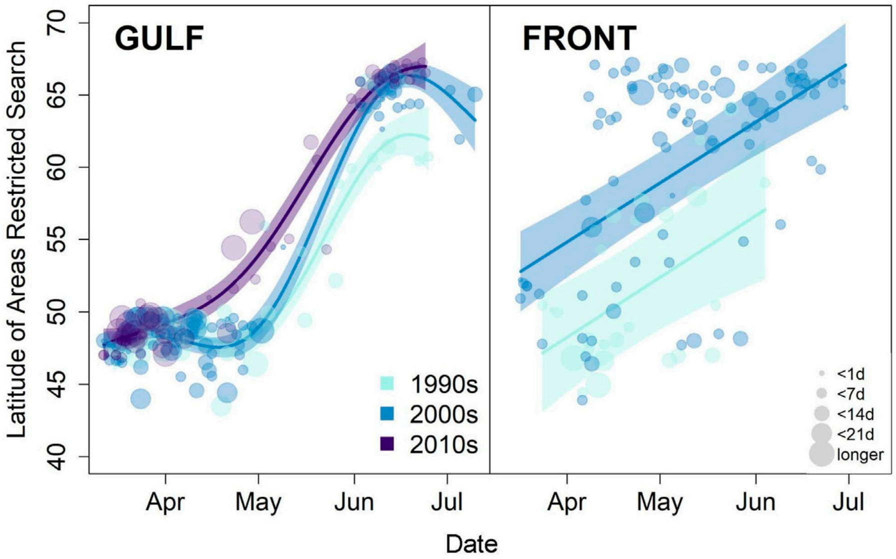

FIGURE 3
Foraging areas (identified along tracks by Areas Restricted Search [ARS] in hierarchical switching state-space models) for hooded seals, with respect to latitude and date, from the Gulf of St Lawrence (GULF) and the FRONT north of Newfoundland, over three decades (in colors). The size of the circles represents durations of ARSs. Solid lines and shaded areas represent the fitted estimates and their respective confidence intervals (From Vacquié-Garcia et al., 2024). Results showed earlier and more northerly locations over time (decades).

available for marine mammals that allow for exploration of how such changes influence animals' migration patterns, but a unique 30 years-long tracking data set for hooded seals from the Northwest Atlantic allowed Vacquié-Garcia et al. (2024) to explore movement patterns in the context of climate change. They found that hooded seals from two breeding areas off the east coast of Canada targeted different environmental conditions. However, each breeding group has remained faithful in their selection of the same oceanographic conditions for their foraging activities over the whole of the study period. Despite different temperature, sea-ice concentration, depth, and salinity preferences, both populations had shifted the phenology of their migration–leaving breeding areas earlier–and also shifted their migratory endpoints to places farther north (Figure 3), to access similar oceanographic characteristics across the decades covered in the study. This northward shift is likely to continue into the future, but the limits to adaptive capacity of hooded seals with respect to the loss of traditional breeding and molting sites are unknown. Hooded seals are already experiencing markedly increased rates of polar bear predation off the east coast of Greenland, where the drift ice now occurs very close to shore compared to decades ago (McKinney et al., 2013), which has become a driver to negative populations trends for Greenland Sea hooded seals (Øigård et al., 2014).

5.4 Case Study No. 4. Arctic changes impact subsistence harvests by Indigenous Peoples

Lifestyles of Indigenous coastal communities in Arctic North America, Greenland, and eastern Eurasia are closely associated with seasonal sea ice. The ability of these communities to engage in the traditional harvests on which they rely are being heavily impacted by a warming environment, largely because of changes to the spatiotemporal patterns of migratory marine mammals, seabirds, and anadromous fishes (Badjeck et al., 2010; Brewster et al., 2016; ICC-Alaska, 2015; Savo et al., 2017; Huntington et al., 2020). In western Arctic North America, Inuit harvests of seals and anadromous fishes have been impacted by climate change (Hauser et al., 2021; Falardeau et al., 2022).

Many migratory marine mammal species are fundamental to the nutritional, spiritual, and cultural aspects of Indigenous life in coastal Arctic Alaska communities (Huntington et al., 2017). These animals are dependent on sea ice and ocean conditions, and wind and weather conditions can impact the ability of hunters to safely harvest bowhead whales and walruses during the seasonal periods in which they are available (Hansen et al., 2013; Huntington et al., 2013). In Northwest Alaska, an interdisciplinary team of researchers worked with an Iñupiaq Elder Advisory Council to understand how bearded seal harvest phenology was changing relative to changing environmental conditions (Hauser et al., 2021). Bearded seals ("ugruk" in Iñupiaq), migrate into the region during spring sea ice break-up, relying on ice floes for resting between foraging bouts. This study found that the duration of harvests declined significantly as break-up shifted earlier (Figure 4); this was determined by integrating harvest records, Indigenous Knowledge on conditions impacting bearded seal spring habitat and accessibility of seals to hunters, and remotely-sensed sea-ice data. Indigenous hunters have so far been able to compensate for decreased harvesting periods by changing how they searched for and hunted seals.

Climate change effects on fisheries for Arctic char and Dolly Varden during the open water season, and their quality as a food source for Inuit people, raise concerns pertaining to altered marine habitat use, diet changes affecting flesh quality, exposure to contaminants, and interactions with non-endemic species (Tran

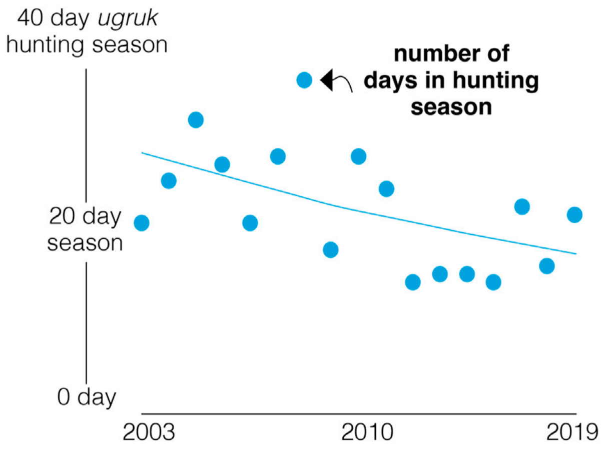

FIGURE 4
The length of the hunting season (2003–2019) for bearded seal (ugruk) by Iñupiaq harvesters in northwest Alaska. Over this period, the length of the harvest season has declined significantly, due to early start and end dates in correlation with earlier sea ice break-up. The hunting season now ends in mid-June rather than early July. Modified from Figure 2 in Hauser et al. (2021).

et al., 2019; Chila et al., 2022; Harris et al., 2022; Bolduc et al., 2024; Pearce et al., 2024). Arctic char might become harder to harvest in shore-based gill net fisheries during summer, as the char follows preferred cooler temperatures to deeper areas farther from shore (Harris et al., 2022). Nearshore habitat-use and marine spatial distribution of Dolly Varden are influenced by SST and ice conditions (Gallagher et al., 2021). The increasing loss of coastal ice during summer has impacted Dolly Varden harvests as the presence of drifting ice improves catches of fish (Brewster et al., 2016; WMAC and Aklavik HTC, 2018). Additionally, increased frequency and strength of wind and wave activity impedes the travel to coastal fishing camps and also the ability to deploy gill nets, which is further exacerbated by coastal erosion (Brewster et al., 2016; Kokelj et al., 2021; Pearce et al., 2024). The challenges posed by changes in fish habitat use, accessibility to fishing locations, and long-term changes in the fish community composition in the western Arctic (Brewster et al., 2016; Priest et al., 2022; von Biela et al., 2023) require harvesters to adjust fishing practices, which will have social and economic consequences for Indigenous communities.

Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Publisher's note

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Borealization impacts shelf ecosystems across the Arctic

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Climate change is rapidly modifying biodiversity across the Arctic, driving a shift from Arctic to more boreal ecosystem characteristics. This phenomenon, known as borealization, is mainly described for certain functional groups along sub-Arctic inflow shelves (Barents and Chukchi Seas). In this review, we evaluate the spatial extent of such alterations across the Arctic, as well as their effects on ecosystem-level processes and risks. Along the inflow shelves, borealization is driven by long-term strengthened inflow of increasingly warm waters from the south and punctuated by advection and low sea ice extreme events. A growing body of literature also points to an emerging borealization of the other Arctic shelf ecosystems, through a “spillover” effect, as local changes in environmental conditions enable movement or transport of new species from inflow shelves. These modifications are leading to changes across functional groups, although many uncertainties remain regarding under-sampled groups, such as microbes, and technical challenges of consistent, regular monitoring across regions. There is also clear consensus that borealization is affecting phenology, species composition, community traits, population structure and essential habitats, species interactions, and ecosystem resilience. Non-dynamic environmental factors, such as depth and photoperiod, are thought to limit the complete borealization of the system, and may lead to intermediate, “hybrid” ecosystems in the future. We expect current borders of Arctic and boreal ecosystems to progress further northward and ultimately reach an equilibrium state with seasonal borealization. Risks to the system are difficult to estimate, as adaptive capacities of species are poorly understood. However, ice-associated species are clearly most at risk, although some might find temporary refuge in areas with a slower rate of change. We discuss the likely character of future Arctic ecosystems and highlight the uncertainties. Those changes have implications for local communities and the potential to support Blue Growth in the Arctic. Addressing these issues is necessary to assess the full scale of Arctic climate impacts and support human mitigation and adaptation strategies.

KEYWORDS

Climate change, Arctic, biodiversity, ecosystem functioning, species distribution, Blue Growth

1 Introduction

Global redistributions of marine species under climate change are leading to unprecedented changes in biodiversity worldwide (Pinsky et al., 2013; Poloczanska et al., 2016). These redistributions are largely driven by populations following their thermal preferences (Burrows et al., 2019), leading to long-term poleward or depth displacements of species with lower thermal affinities. At mid-latitudes, poleward shifts of fish species have led to the progressive declines of cold-affinity boreal species in favour of warm-affinity Lusitanian species (Dulvy et al., 2008; Hofstede et al., 2010; Engelhard et al., 2011). At higher latitudes, regions that border the Arctic and receive the inflows from lower latitude Atlantic- and Pacific-influenced waters are the ultimate gateways of the poleward displacements of boreal species to the Arctic. Beyond these frontiers is the Arctic, with its strong seasonal light variability, and harsh environmental and living conditions, to which resident communities are well-adapted.

Climate change and Arctic amplification are responsible for warming rates in this region nearly 4 times faster than the rest of the world (Rantanen et al., 2022), and are causing structural changes across the Arctic ecosystems. Global projections suggest increasing biomass of commercial species coming from lower latitudes and thriving in increasingly productive, warmer, and ice-free ecosystems (Lam et al., 2016; Lotze et al., 2019; Tai et al., 2019). However, these projections vary strongly both in magnitude and direction among models (Bryndum-Buchholz et al., 2019). In addition, the strong seasonality in solar radiation will remain in the north due to the Earth inclination on its axis that could limit boreal species' northward progress and survival (Kaartvedt, 2008). A large body of literature reports evidence of such northward shifts into the Arctic by boreal species of many functional groups, driven by local habitat modifications and advection of warm water and associated species from lower latitudes (Polyakov et al., 2020a; Brandt et al., 2023), a phenomenon called "borealization" (Fossheim et al., 2015). Arctic shelves and basins vary strongly with regard to hydrological, geochemical and biological functioning (Carmack and Wassmann, 2006). However, they are also strongly connected through large scale atmospheric, sympagic and oceanic circulation patterns (Carmack and Wassmann, 2006; Wassmann et al., 2020). Understanding the possible temporal and geographical extent of this borealization initially observed at inflow shelves, the risk posed to Arctic species and ecosystem functioning, and the consequences for the dependent local human inhabitants, are essential to facilitate planning for an adaptive, equitable management of Arctic and sub-Arctic ecosystems, and for the conservation of biodiversity.

Borealization of Arctic and sub-Arctic regions can be defined as a process by which ecosystems that were historically characterised as Arctic are progressively or transitively acquiring features typical of more southern, boreal ecosystems (Polyakov et al., 2020a). Sea surface temperatures in Arctic marine ecosystems are typically near or at the freezing point year-round (in the central Arctic Ocean) or seasonally (mostly on the shelves). In the central Arctic Ocean, the stratification is strong throughout the year with a cold, fresh Arctic water mass laying on top of the warmer and saltier Atlantic water mass. The overlaying fresher Arctic water mass contributes to high local sea-ice production.

Arctic and sub-Arctic ecosystems display very distinct communities and functions tuned to local conditions. In first-year ice areas, at the edge of the central Arctic Ocean and in seasonally ice-covered shelf regions, remineralized and recycled nutrients are used by ice-algae that can lead to a strong under-ice bloom (Arrigo et al., 2012; Assmy et al., 2017), followed by a stronger pelagic bloom dominated by diatoms when the ice is melting (Ardyna and Arrigo, 2020). There is greater diatom diversity in the sea-ice compared to the water column, where diversity differs by region with intermediate levels in the Canadian Arctic Archipelago and Pacific Arctic, and lower diversity in the Russian inner shelf seas, Hudson Bay and the Central Arctic Basin (CAFF, 2017). Microbial diversity (about ~2000 taxa for pelagic and sympagic eukaryotes, Poulin et al., 2011) includes endemic microbial populations that have evolved to thrive under the extreme ice-influenced local conditions (Lovejoy et al., 2006; Lovejoy et al., 2007; Verde et al., 2016; van Leeuwe et al., 2018; Dorrell et al., 2023). Phytoplankton especially are able to survive prolonged dark periods that limit photosynthesis (Kvernvik et al., 2018; Lacour et al., 2019; van de Poll et al., 2020), using flexible strategies such as mixotrophy or overwintering as metabolically quiescent cells or as cysts (Stoecker and Lavrentyev, 2018). Some Arctic bacteria also use normally recalcitrant sources of organic carbon, including terrestrial organic matter from the large rivers that continue to flow into the Arctic even during winter (Colatriano et al., 2018).

Zooplankton are the primary link between the primary producers and higher trophic levels in Arctic and sub-Arctic marine food-webs. Some 300–400 zooplankton species occur in the Arctic water column (Kosobokova et al., 2011). Hyperiid amphipods and large, lipid-rich mesozooplankton, such as *Calanus glacialis* and *Calanus hyperboreus* play a crucial trophic role in the Arctic ecosystem (Søreide et al., 2010; Kohlbach et al., 2016; Brown et al., 2017). Gelatinous zooplankton, including hydrozoans (e.g., *Aglanta digitale*), are also ubiquitous in the Arctic pelagic niche (Kosobokova et al., 2011), and in the central Arctic basins, the gelatinous zooplankton appears to be more abundant than pelagic fishes (Ingvaldsen et al., 2023). The pan-Arctic hosts over 5,000 metazoan species, including 229 fish species (Bluhm et al., 2011b; Mecklenburg et al., 2011). Benthic communities sometimes rely strongly on the sympagic-benthic coupling driven by sinking sea ice algae to the bottom after they bloom and at ice breakup (Koch et al., 2020; Cautain et al., 2022). Arctic demersal and benthic fish communities are mainly composed of species such as sculpins (Cottidae), snailfish (Liparidae), eelpouts (Zoarcidae) and eelblennies (Lumpenidae), but the benthos is typically dominated by invertebrates including many benthic polychaetes and other worms, molluscs, arthropods and echinoderms. In contrast, the pelagic compartment is less diverse. Polar cod (*Boreogadus saida*) sometimes represents more than 95% of the fish species abundance (Geoffroy et al., 2023), while ice cod (*Arctogadus glacialis*), saffron cod (*Eleginus gracilis*), capelin (*Mallotus villosus*) and Arctic sand lance (*Ammodytes hexapterus*) are less abundant. Mesopelagic species are scarce in the deep basins. Glacier lanternfish (*Benthosema glaciale*), armhook squid (*Gonatus fabricii*), and even single individuals of Atlantic cod (*Gadus morhua*) are also present in the pelagic, but in low densities (Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023).

Typically, offshore boreal ecosystems exhibit contrasting characteristics, with warmer, saltier, and less stratified waters, higher phytoplanktonic primary production, smaller mesozooplankton species and abundant krill and pelagic amphipods in the North Atlantic compared to Arctic ecosystems (e.g., Dalpadado et al., 2003; Dalpadado et al., 2014; Weydmann et al., 2014). Similar gradients exist in the Pacific-Arctic but zooplankton communities on the extensive shallow inflow shelves are dominated by neritic species (Questel et al., 2013; Hunt et al., 2014; Ershova et al., 2015). The boreal pelagic niche is more diverse than the Arctic one, including a more prominent mesopelagic compartment in deeper water hosting, among the fishes, abundant myctophidae and stomiidae (Sameoto, 1989; Byrkjedal et al., 2004). Boreal and Arctic communities of demersal fish and benthic invertebrates differ in terms of traits such as temperature tolerance windows (Aune et al., 2018; Jørgensen et al., 2022; Logerwell et al., 2022), longevity (Ravelo et al., 2017), and age-at-maturity. Boreal fish include many mobile generalists of large size, such as Atlantic cod (*Gadus morhua*), Pacific cod (*G. macrocephalus*) and walleye pollock (*G. chalcogrammus*). This higher generalism implies a higher trophic redundancy, but also connectivity (i.e., feeding link richness) in the trophic network (Livingston and Tjelmeland, 2000; Kortsch et al., 2019). One of the key questions posed by the occurring process of borealization is whether this process can ultimately lead to a complete transformation of Arctic shelf ecosystems into boreal ones (replacement scenario), or to a hybrid version of both ecosystems (hybridization scenario, "cocktail"), and what the consequences for overall ecosystem functioning may be.

We review the existing knowledge on the mechanisms driving borealization and compile the evidence of borealization across ecosystem compartments in the marine Arctic. Our objectives are 1) to explore the spatial and temporal extent of borealization across the Arctic shelves, 2) to explore its extent across functional groups and consequences for ecosystem functioning, 3) to discuss the degree of transformation of Arctic ecosystems into boreal ones, now and in the future, 4) to discuss consequences for societies and management.

2 The environmental context of borealization across the pan-Arctic

The Arctic climate is driven by large scale processes within, and interactions between, the atmosphere, the cryosphere and the ocean (Timmermans and Marshall, 2020). Powerful local feedback processes associated with the air-sea-ice system amplify warming and sea-ice loss (Serreze and Barry, 2011; Ivanov et al., 2016; Polyakov et al., 2020b; Previdi et al., 2021). The recent decades have shown accelerated atmospheric and oceanic warming caused by a combination of global, regional and local drivers (Polyakov et al., 2020a; Shu et al., 2021; Isaksen et al., 2022; Smedsrud et al., 2022). Numerous studies have reported the many transformations of the entire Arctic system, including the intensification of hydrological cycles (increased precipitation and river discharge), glacier and sea ice melting and thinning, and modal shifts in atmosphere altering ocean circulation patterns (Greene et al., 2008; Wood et al., 2015; Box et al., 2019; Huntington et al., 2020; Polyakov et al., 2023). Extreme seasonal ice or temperature conditions have become more frequent (Hinzman et al., 2005; Dörr et al., 2021, Pécuchet et al., 2024). The current warming appears to have peaked between 2012 and 2018 for most of the Arctic (Danielson et al., 2020; Ingvaldsen et al., 2021), accompanied by record low sea ice cover (Stabeno and Bell, 2019). Nevertheless, the years post 2018 are a temporary reprieve, and the Arctic climate is projected to continue to warm as a result of increasing levels of atmospheric carbon dioxide (Pörtner et al., 2019).

Regional differences in climate change footprint across the Arctic can mostly be explained by the different hydrologic and geographic contexts of the sub-Arctic areas (Figure 1). These can be separated into four categories: the *inflow shelves* (Bering and Chukchi seas on the Pacific side, Barents Sea on the Atlantic side, west Greenland shelf), the *outflow shelves* (Canadian Arctic Archipelago, Western Baffin Bay, Eastern Greenland Shelf), the *interior shelves* (Kara, Laptev and Siberian Seas) and the *Arctic basins* (Carmack and Wassmann, 2006; Wassmann et al., 2020). Sea ice loss in the Barents and Bering inflow shelves are strongest during winter (Figure 2). This is a direct effect of warmer or stronger advection of sub-Arctic waters into the Arctic (Onarheim et al., 2018; Woodgate, 2018), and causes an increase in the extent of thermal habitat associated with boreal ecosystems throughout the year. Year-long suitable conditions favours the gradual borealization of the inflow shelf ecosystems, which can occur due to advection from the sub-Arctic seas and along the flow into the basins (Polyakov et al., 2020a). The Chukchi Sea and interior shelves, as well as the Canadian Arctic Archipelago, on the other hand, show strong sea ice loss during summer (Figure 2), but are strongly connected to neighbouring shelves through currents (Figure 1). Progressing borealization on to the interior shelves could occur through planktonic species advected through lateral basin-shelf or inter-shelf exchanges when sea ice loss and warming is sufficient (Nelson et al., 2014), and through mobile boreal shelf species reaching their northernmost depth habitat at the inflow shelves, thereby expanding their distribution to nearby shelves.

We used Sea Surface Temperature (SST) data to support our general comparison of the upper ocean warming experienced by Arctic shelves in the past century. We note that as these data are based on surface waters, they are interlinked with the loss of sea ice

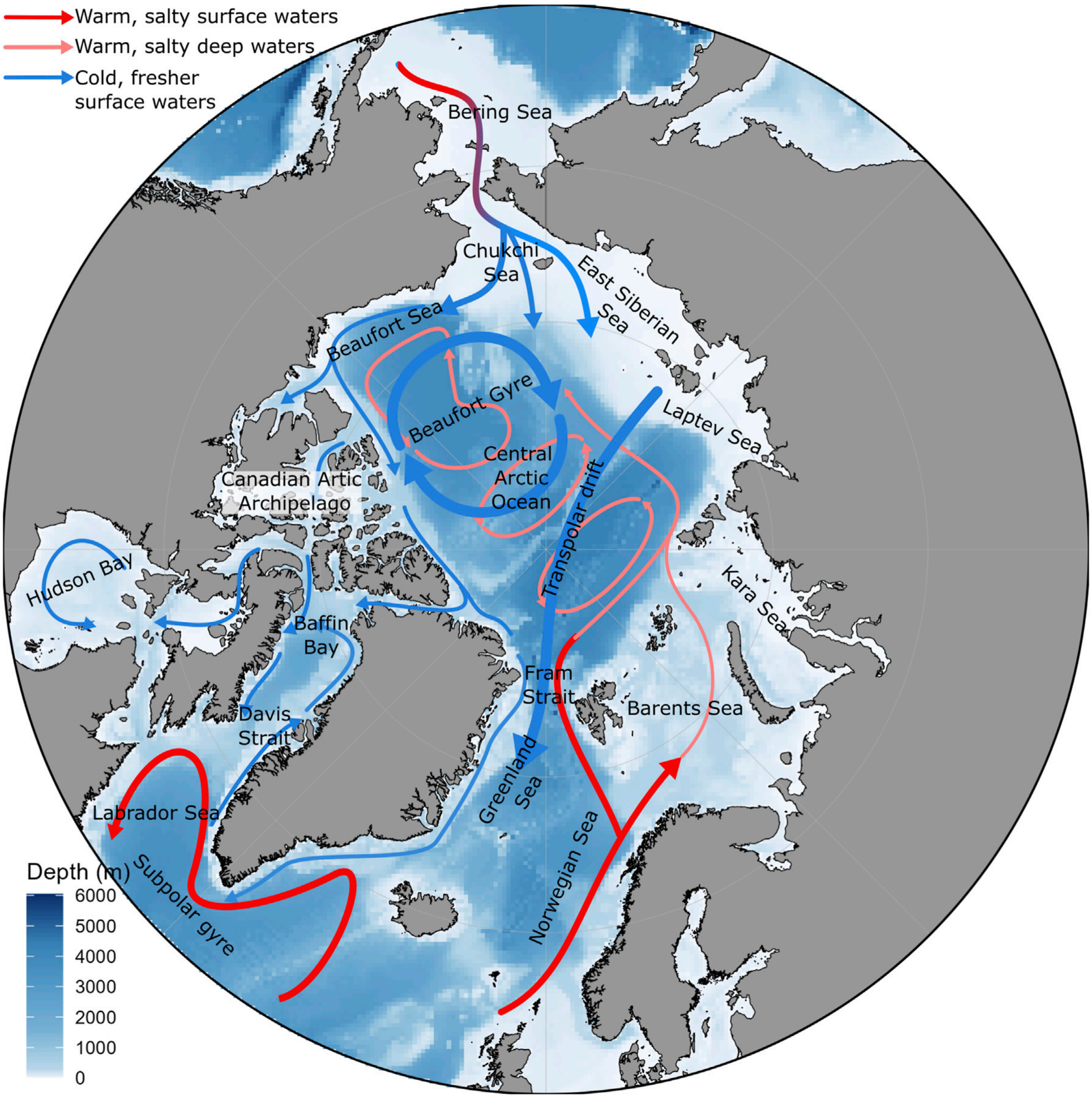

FIGURE 1
Main arctic and sub-arctic oceanic currents. Adapted from Anderson and Macdonald (2015), Armitage et al. (2017), and Constantin and Johnson (2023).

and may not be representative of changes at depth. The NOAA Extended Reconstructed SST V5 (ERSSTv5; Huang et al., 2017) is a global monthly SST analysis from 1854 to the present derived from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) data with missing data filled in by statistical methods. The data are available on a 2° × 2° (latitude-longitude) grid globally, but here were restricted to latitudes north of 50°N (see coverage in Figure 3). Several analyses were performed with this dataset. To illustrate the regional differences in warming rates, linear trends were calculated on the annual summer (July-September) temperatures for each pixel of the dataset for the period 1950–2023 (Figure 3) and averaged by regions (Table 1). Regions were defined following the Arctic Ocean and Adjacent Seas (AOAS) from the Conservation of Arctic Flora and Fauna (CAFF). Monthly SSTs averaged over the same regions for each year also highlight the warming trends and the increasing length of the open water season over time (Figure 4). Finally, decadal anomalies of summer SSTs (in °C) were calculated. For this analysis, the annual time series of summer mean SST for each region was built by averaging monthly values between July and September for a given year. Anomalies were calculated for each year by subtracting the long-term summer average over 1900–2000, before computing averages of the annual anomalies for each 10-year periods (1955–1964, 1965–1974, until 2015–2024). Decadal anomalies are illustrated per region (Figure 5), and values are provided for the last decade (Table 1).

Summer surface waters of the Arctic Ocean have been warming unevenly over the last seven decades (Figure 3). The warming trends are in relatively close correspondence with the sea ice loss trends (Figure 2). When averaged by region, greatest warming trends are

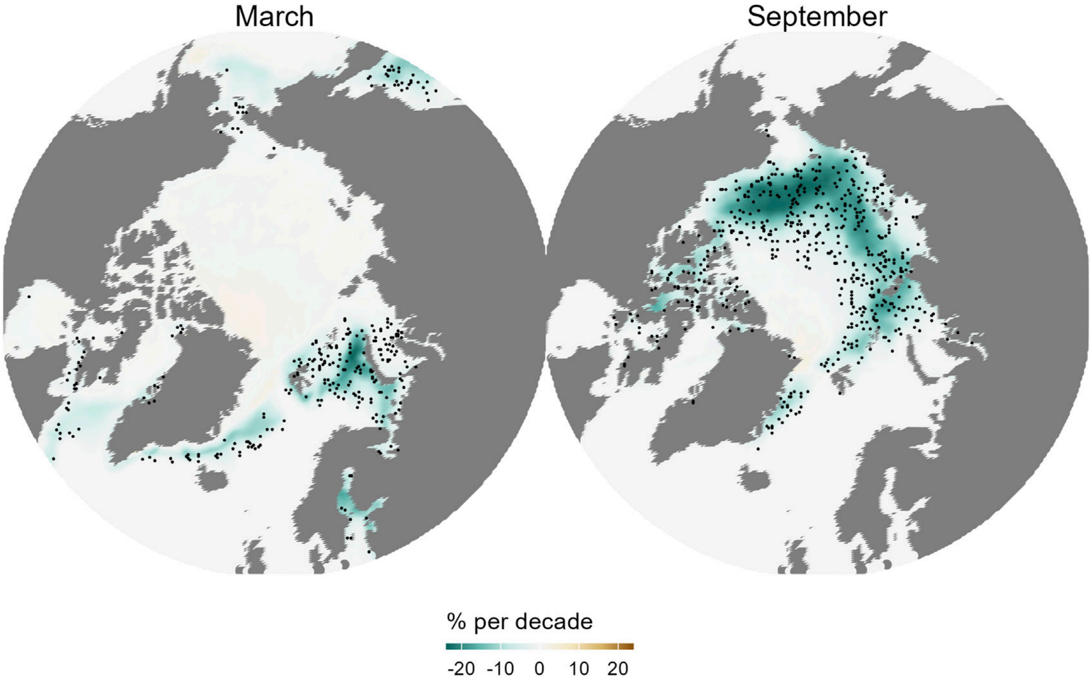

FIGURE 2
From copernicus climate indicators for sea-ice (https://climate.copernicus.eu/climate-indicators/sea-ice). Linear trends in sea ice concentration during 1979–2023 (% per decade) for March and September. Dots indicate areas where the trends are statistically significant. Credit: ECMWF, copernicus climate change service (C3S) C3S/ECMWF/EUMETSAT/MET Norway.

found in the northernmost regions of the Russian (Kara, Laptev and Siberian seas), Alaskan (Chukchi Sea) and Canadian Arctic coasts (Beaufort Sea and the Canadian Arctic Archipelago, Table 1). Those regions are mainly outflow shelves and interior shelves. Outflow shelves such as the East Greenland and the Canadian Arctic Archipelago also show signs of significant decrease in multi-year ice and relocation of different ice types (Sou and Flato, 2009; Michel et al., 2015). In contrast, interior shelves experience the effects of changing Arctic coasts, such as massive erosion in non-lithified coasts, and of run-off of freshwater and organic and inorganic materials contained in it (e.g., Williams and Carmack, 2015; Irrgang et al., 2022). The central Arctic basin north of Greenland and the Canadian Arctic Archipelago did not show large trends in SST due the quasi-permanent sea ice cover.

These warming trends in surface waters are, in some regions, associated with both warming and a longer ice-free summer season (deeper tones of yellow and widening of the white lines towards the top of the panels, Figure 4). The regions with the more moderate surface warming trends are generally those not exhibiting full sea ice cover for any month of the year (regions without white lines in Figure 4). Longer-term trends in summer SST anomalies (Figure 5) confirm earlier studies revealing that the warming of the Arctic started in most of the region in the second half of the 20th century, with an overall acceleration in the last three decades (Bengtsson et al., 2004; Matishov et al., 2012; Shu et al., 2021; Isaksen et al., 2022). The Canadian Arctic (Beaufort Sea, Canadian Arctic Archipelago and the Hudson Bay Complex) as well as the Greenland and Kara seas exhibited the largest SST increases in the last decade (2015–2024) compared to the long-term average (Table 1).

Compared to other regions, inflow shelves experienced slower warming trends in the summer (Figure 3; Table 1). However, this observation changes when studying other seasons. The Chukchi Sea, in autumn, and the Barents Sea, in winter, displayed the largest warming rates of air temperature in the Arctic since the 1980’s (Koenigk et al., 2020). Arctic waters cool to the freezing point prior to ice formation in autumn; warmer waters thus transfer more heat from the ocean to the atmosphere during the fall process of oceanic heat loss (Danielson et al., 2020). The Chukchi and Barents Seas are under the dual influence of the Arctic and the lower latitude systems that drive very strong inter- and intra-annual variability, with seasonal sea-ice cover, changes in temperature and important contrasts in seasonal light regime. These seas are the main gateways to borealization (Polyakov et al., 2020a). In the hydrosphere, their systems have evolved toward something less Arctic, and more similar to lower latitudes in the northern Pacific and the Atlantic, two phenomena referred as “Pacification” and “Atlantification”, respectively (Polyakov et al., 2017; Danielson et al., 2020; Ingvaldsen et al., 2021). Both are driven by anomalous advection of warmer Pacific and Atlantic water (Woodgate et al., 2010; Woodgate, 2018; Ingvaldsen et al., 2021; Smedsrud et al., 2022), leading to higher ocean heat transport into the shelf ecosystems and the Arctic (Xu et al., 2024). Consequently, average temperatures in both systems are increasing, at a rate of +0.04°C/year since 1980 in the Bering Strait and on the Chukchi Sea shelf (Danielson et al., 2020), and +0.05°C/year since 2000 in the Barents Sea (Ingvaldsen et al., 2021). The inflow shelf changes are also characterised by the loss of sea ice extent, increased open water season duration and faster transitions (Frey et al., 2015; Danielson et al., 2017; Onarheim et al., 2018; Dalpadado et al., 2020).

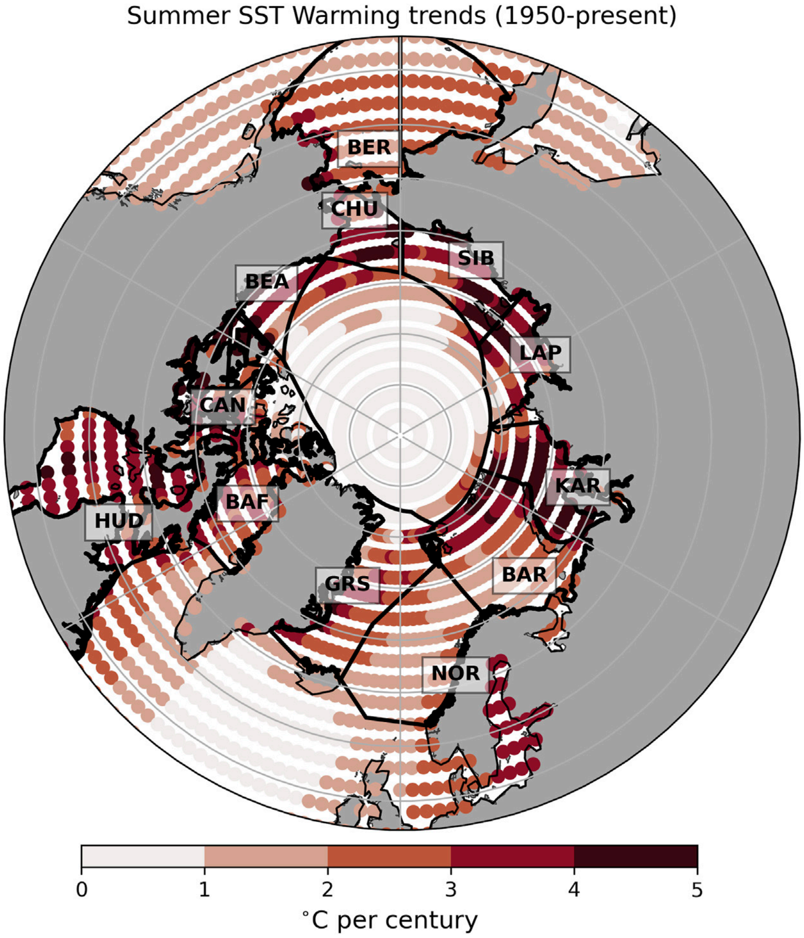

FIGURE 3
Map of summer (July-September average) SST warming trends (in °C per century) between 1950 and 2024 for each pixel (2° × 2° latitude-longitude) derived from ERSSTv5. The Arctic Ocean and adjacent Arctic seas (AOAS) regions, drawn here in black, were used for further regional analyses. These regions are (counterclockwise from top): Bering Sea (BER), Chukchi Sea (CHU), Beaufort Sea (BEA), Canadian Arctic Archipelago (CAN), Hudson Bay Complex (HUD), Baffin Bay (BAF), Greenland Sea (GRS), Norwegian Sea (NOR), Barents Sea (BAR), Kara Sea (KAR), Laptev Sea (LAP) and Siberian Sea (SIB).

3 Evidence of borealization across the Arctic and impact on the functioning of ecosystems

3.1 Changes in the environment affect Arctic biogeochemistry and microbial communities

Climate driven changes in atmospheric, ice and oceanic conditions are likely resulting in shifts in the biogeochemical processes and microbial communities at pan-Arctic scales. However, a comprehensive understanding of regional trends and potential disparities among regions is hampered by the scarcity of long-term datasets of observed or modelled conditions (CAFF, 2017; Juranek, 2022). A set of studies describing the different hydrographic functioning and ecosystem production have revealed a wide variety of properties and pathways in the carbon cycle across the Arctic (Dunton et al., 2006; Grebmeier et al., 2006; Hirche et al., 2006; Hop et al., 2006; Michel et al., 2006; Rysgaard and Nielsen, 2006; Schmid et al., 2006; Tremblay et al., 2006; Wassmann et al., 2006a). These carbon cycles vary in efficiency depending on the processes transforming organic matter into nutrients (carbon mineralisation), and nutrients into organic matter (primary productivity). Productivity on the Arctic shelves is generally considered to be limited by the concentrations of available nitrogen compounds, especially in the Pacific Arctic (Mills et al., 2018; Ko et al., 2020), rather than by irradiance limitation from sea-ice and photoperiod (Tremblay and Gagnon, 2009; Tremblay et al., 2015). Most of the nutrient supply is advected through inflow shelves (Le Fouest et al., 2013b; Torres-Valdés et al., 2013; Tremblay et al., 2015). River inputs into sub-Arctic inner shelves may also be an important local source of nutrients and organic matter from land (Dittmar and Kattner, 2003; Dunton et al., 2006; Carmack et al., 2016), and estimates suggest terrestrial sources with coastal erosion, contribute to 28%–51% of net primary productivity in the Arctic Ocean via the Transpolar Drift (Le Fouest et al., 2013a; Terhaar et al., 2021), but see contrasting results in Le Fouest et al. (2013a).

At the pan-Arctic scale, rising temperatures and prolonged open water seasons have driven substantial increases (>50% over two

TABLE 1 SST mean trends (in °C per century) averaged over 1950–2023 for each of the Arctic Ocean and Adjacent Seas (AOAS) regions defined in Figure 3. The 6 regions with trends larger than 3°C per century are in bold. For SST anomalies during the last decade (2015–2024) compared to the 1900–2000 period, the 5 regions with anomalies larger than +2°C are in bold.

AOAS region	Mean trend (°C per century)	2015–2024 anomaly (°C)
Bering Sea	+2.3	+1.6
Chukchi Sea	**+3.7**	+1.8
Beaufort Sea	**+3.2**	**+2.6**
Canadian Arctic Archipelago	+2.3	**+2.5**
Hudson Bay Complex	**+3.4**	**+2.6**
Baffin Bay	+2.7	+1.9
Greenland Sea	+2.3	**+2.6**
Norwegian Sea	+1.9	+1.9
Barents Sea	+2.9	+1.3
Kara Sea	**+4.0**	**+2.3**
Laptev Sea	**+3.2**	+1.2
Siberian Sea	**+3.8**	+1.3

decades) in sub-Arctic primary productivity, with earlier and extended blooms of pelagic phytoplankton (Arrigo et al., 2008; Kahru et al., 2011; Kahru et al., 2016; Hill et al., 2013; Hill et al., 2018; Ardyna et al., 2014; Arrigo and van Dijken, 2015). In addition, the decrease in multi-year ice and increase in first-year ice extent are driving a temporary increase in ice-algae habitat (Lim et al., 2022). Production increased in most regions but with varying magnitude (Arrigo and van Dijken, 2015). The Barents Sea was the area that experienced the highest increase in primary production over the last two decades (Dalpadado et al., 2020; Lewis et al., 2020). Primary production has also increased in spatial extent in the Bering Sea during warm years (Nielsen et al., 2024). The Canadian Arctic Archipelago, Baffin Bay and the eastern Greenland shelf display an altered functioning, with changes in productivity spatial-temporal patterns (Michel et al., 2015; Blais et al., 2017; Mayot et al., 2020). Data are scarce for other shelves, but short term studies also revealed interannual variation in production and particulate organic carbon export between years with varying sea ice cover (Lalande et al., 2009; Bienhold et al., 2022).

In recent years, ice dynamics and water temperature no longer suffice to explain increases in primary production on inflow shelves (Lewis et al., 2020). It has been hypothesised that the increased transport of deep Atlantic waters into the Arctic might have increased dissolved inorganic nitrogen (DIN) supply, favouring higher primary production in downstream regions (Henley et al., 2020; Lewis et al., 2020). However, despite increasingly northward Atlantic water flow and subsequent increased vertical mixing, multiple studies point to a long-term decrease in nutrients across most of the pan-Arctic, with the exception of the pan-Arctic slope (Oziel et al., 2022). Oxygen and nutrients seem to have decreased within the halocline of the Eastern and Western Eurasian Basin (Polyakov et al., 2020a). Similarly, there has been a decline in nitrate concentrations in the Atlantic water inflow into the Barents Sea between 1990–2010 (Oziel et al., 2017), and no long-term (35 years) trend in nutrients from Atlantic water flowing into the Arctic north of Svalbard (Duarte et al., 2021). In the Chukchi and Beaufort seas, only oxygen concentration has increased (Polyakov et al., 2020a), while nitrate and phosphate concentrations have decreased by 79% and 29% respectively (Zhuang et al., 2021). This was hypothesised to result from the joint effect of decreased vertical mixing following the strengthened stratification due to the loss of multi-year sea ice, and the increased consumption by primary producers (Zhuang et al., 2021). At interior and outflow shelves, nitrogen discharge from river outputs is usually quickly utilised, for example, through efficient denitrification in the Laptev Sea (Sanders et al., 2022; Tuerena et al., 2022), and nitrate and other dissolved inorganic nutrient fluxes from land seem to have declined (Tank et al., 2023). Lack of observations currently greatly limits our understanding of nutrient transport and budgets (Torres-Valdés et al., 2016).

Changes in primary production can also be linked to changes in phytoplankton communities. Phytoplankton communities affect carbon flux attenuation and production regimes (Ardyna et al., 2011; Wiedmann et al., 2020), and vary with environmental conditions across all Arctic shelves and basins (Ardyna et al., 2011; Min Joo et al., 2012; Lee et al., 2019; Ibarbalz et al., 2023). For example, small algae, more efficient at assimilating nutrients and thus potentially more competitive compared to local larger species, have been observed in higher quantities in the Canada Basin and coastal Canadian Arctic Ocean (Li et al., 2009; Blais et al., 2017), and in the Atlantic water masses west of Svalbard (Lalande et al., 2013). In the Beaufort Sea, microbial communities have transitioned towards taxa characteristic of oligotrophic environments (Comeau et al., 2011). In addition, strong advection at inflow shelves has driven the northward shift of temperate species of coccolithophores (Winter et al., 2014; Neukermans et al., 2018; Oziel et al., 2020). In contrast, there is no evidence of temporal changes in microbial community composition or biomass in the North Water (northern Baffin Bay) or the Laptev Sea (Freyria et al., 2021; Bienhold et al., 2022). In the rest of the Arctic, time series are scarcer, but microbial communities, including phytoplankton, have

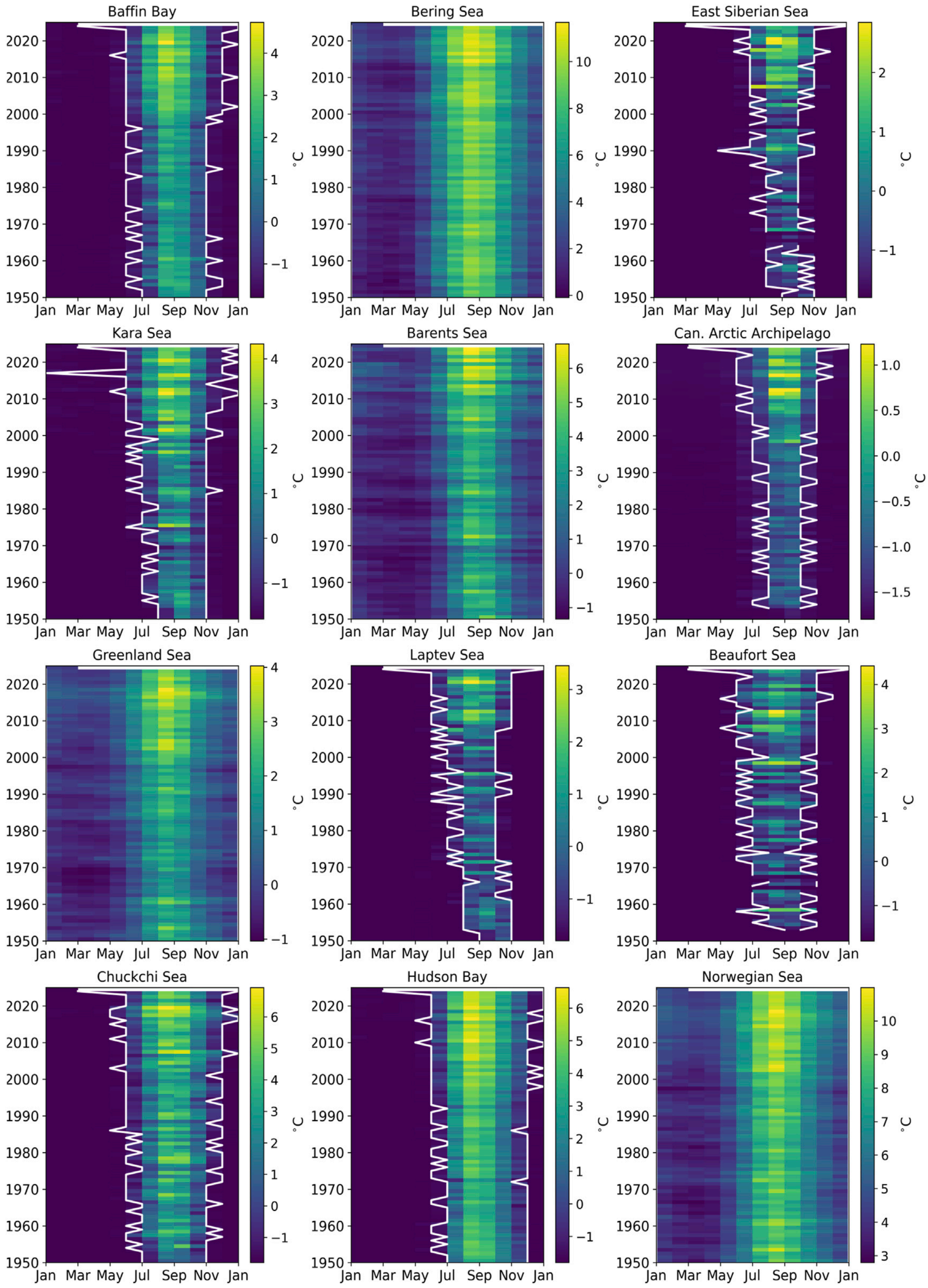

FIGURE 4
SST annual cycles between 1950 and present for each of the regions of the arctic identified in Figure 3. For each year (vertical axis), the averaged SST is plotted for each month on the horizontal axis. Months with a 100% ice cover are at a fixed value of –1.8°C (dark blue). This allows us to plot the opening and closure of the open water period defined here as the first and last month with average temperatures above –1.8°C (white lines). Note that the colour bar scale is different for each subplot.

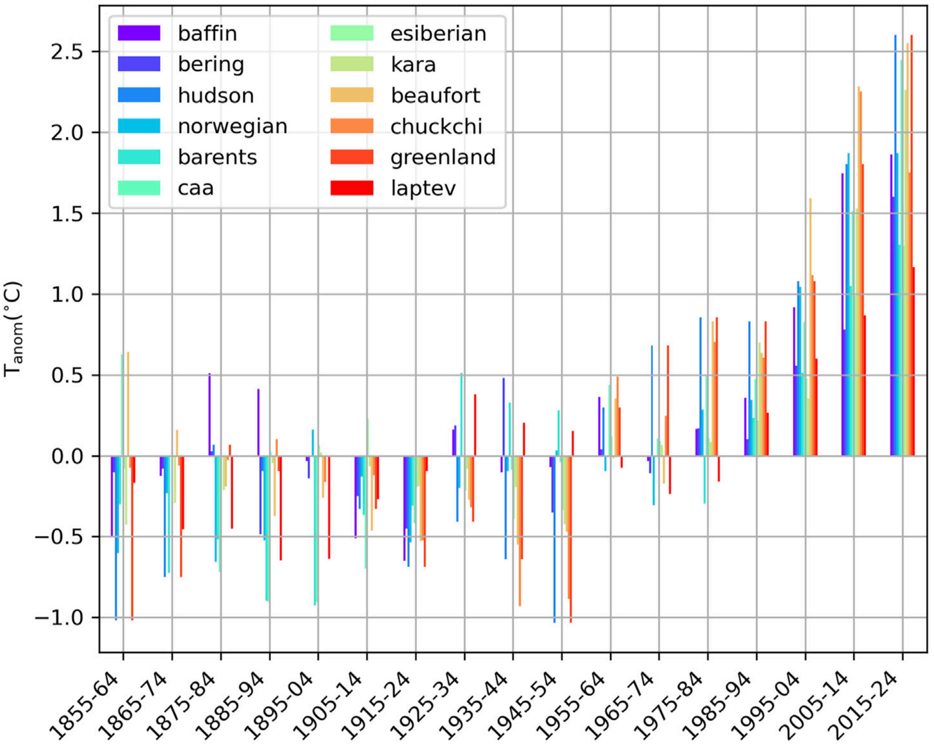

FIGURE 5
Decadal summer (July-September) SST anomalies referenced to the period 1900–2000 for each of the regions in Figure 3.

been characterised by recent studies, setting baselines for the investigation of climate impacts (Demidov et al., 2021; Polyakova et al., 2021; Sukhanova et al., 2021; Liu et al., 2023; Bezzubova et al., 2024). Shifts in microbial communities are likely to drive changes in trophic functioning, affecting the diets, phenology and development of grazing species (Søreide et al., 2010; Daase et al., 2011). Changes in planktonic communities and new environmental conditions can cause harmful algal blooms (HAB), which have direct impacts on the food-webs and human consumption (Okolodkov, 2005; Bruhn et al., 2021). Cases of HAB have been noticeably increasing northward in recent years, with many reports from the Pacific Arctic in particular (Anderson et al., 2021; Anderson et al., 2022; Einarsson et al., 2022; Fachon et al., 2024), with important impacts on top predators, including humans (Hendrix et al., 2021; Lefebvre et al., 2022; Van Hemert et al., 2022).

3.2 Altered habitats and feeding conditions affect pelagic systems

Changes in the environment and in primary productivity (species composition, spatial and temporal patterns) are propagating through the food web, driving the borealization of the pelagic compartments. Indeed, environmental changes trigger contrasting responses of the boreal and Arctic pelagic communities, due to their strong differences in biogeography, life history strategies and functions. For example, many zooplankton communities dominate successively across seasons and regions, varying in their ecological niches and functional traits (Questel et al., 2013; Balazy et al., 2018; Kimmel et al., 2018; Kimmel et al., 2023; Mańko et al., 2020; Mańko et al., 2022; Hop et al., 2021; Darnis et al., 2022; Mazanowski et al., 2023; Van Engeland et al., 2023; Wold et al., 2023). Large, lipid-rich Arctic copepod species such as *C. glacialis* and *C. hyperboreus* can utilise allochthonous production, and survive low productivity periods owing to their large lipid reserves (Hunt et al., 2014; Hirche et al., 2024). Arctic species thus tend to dominate the biomass in late summer/autumn during years with low advection and late sea ice retreat (Kimmel et al., 2018; Spear et al., 2020). However, Arctic zooplankton have a slower increase in respiration rate with rising temperatures compared to their Atlantic counterparts, which implies that, although they might be resilient to warming, Atlantic zooplankton may become more competitive under such conditions (Kaiser et al., 2022). In contrast, boreal species typically consist of smaller zooplankton with less reserves. Along the continental slope of the Atlantic Water inflow, high concentrations of *C. finmarchicus* prevail (Bluhm et al., 2020). Differing traits of Arctic and boreal zooplankton might be adaptative of their respective environment (Renaud et al., 2018), and a shift from lipid-rich Arctic to more boreal communities might not have strong impacts on plankton-feeders as boreal zooplankton occur in larger numbers, over a longer period of time, and have a faster life cycle. However, reduced abundances of lipid-rich *C. glacialis* on the Bering Sea shelf have been associated with poor energetic condition and reduced survival of young walleye pollock (Heintz et al., 2013).

Warm water advection and sea-ice retreat are major determinant of zooplankton community dominance across the Arctic (Ershova et al., 2015; Kimmel et al., 2018; Kimmel et al., 2023; Spear et al., 2019; Abe et al., 2020; Dalpadado et al., 2020; Drits et al., 2023; Ramondenc et al., 2023). Krill, gelatinous zooplankton, ichthyoplankton and young-of-the-year pelagic fish also display different life history strategies and habitat preferences and respond strongly to varying advection regimes (Eriksen and Dalpadado, 2011; Eriksen et al., 2015; Eriksen et al., 2020; Oviatt et al., 2015; Benkort et al., 2019; Deary et al., 2021; Skjoldal et al., 2022). Adult pelagic fish are often less directly affected by variations in environmental conditions. Boreal mobile pelagic fish can relocate to follow the production and expand into newly suitable habitats, thus propagating the borealization of the lower trophic levels up the food chain, although other important factors such as recruitment and availability of suitable spawning habitat also have a strong impact on population spatial-temporal dynamics (Hollowed et al., 2013b; Eriksen et al., 2017). In contrast, some Arctic species such as polar cod are very dependent on ice to complete their life cycle, and loss of sea-ice thus drives a loss of essential habitats for those species (David et al., 2016; Huserbråten et al., 2019; Gjøsæter et al., 2020; Marsh and Mueter, 2020; Deary et al., 2021; Geoffroy et al., 2023).

Long-term borealization has thus been reported on for many pelagic compartments. Shifts from lipid-rich Arctic zooplankton to communities of smaller individuals are of concern in western Greenland (Møller and Nielsen, 2020), the Bering sea (Kimmel et al., 2018; Kimmel et al., 2023), the Chukchi Sea (Abe et al., 2020; Spear et al., 2020; Ershova et al., 2021; Mueter et al., 2021a), Labrador, eastern Greenland and the Barents Sea (Trudnowska et al., 2012; Weydmann et al., 2014; Eriksen, 2016; Eriksen et al., 2017; Freer et al., 2022), and the Fram Strait, main gateway of Atlantic inflow into the Arctic (Gluchowska et al., 2017). Subtle changes in species composition may also be underway within neritic species complexes (Ershova et al., 2015). Krill is also shifting in species composition from Arctic to temperate in the Barents Sea (Eriksen and Dalpadado, 2011; Orlova et al., 2015; Eriksen, 2016), Svalbard, and Bering Sea (Hunt et al., 2016). Lack of long time series hampers our ability to detect changes in zooplankton community composition on the other shelves. Similarly, boreal gelatinous species are thought to also extend northward on the inflow shelves (Brodeur et al., 2002; Brodeur et al., 2008; Eisner et al., 2014; Eriksen et al., 2017; Geoffroy et al., 2018). But drivers of their abundance may be complex (Decker et al., 2023) and historical data and from other shelves are limited, making temporal and regional comparisons difficult.

Further up in the food web, the geographical retreat of polar cod due to the loss of sea-ice is often concomitant with the northward expansion of more southern species, such as capelin, saffron cod or walleye pollock in the Atlantic or Pacific Arctic (Hop and Gjøsæter, 2013; Stige et al., 2019; Wildes et al., 2022; Levine et al., 2023; von Biela et al., 2023). Increased abundance of more southern fish species, such as capelin and Pacific sand lance, are also observed at interior and outflow shelves: in the Canadian Arctic Archipelago (Falardeau et al., 2017), in the Hudson Bay (Gaston et al., 2003), and northern Baffin Bay (Ulrich and Tallman, 2021). While mesopelagic fish have been suggested to be limited in their northward expansion because of the light conditions (Ljungström et al., 2021; Langbehn et al., 2022) or a combination of both light and temperature (Chawarski et al., 2022), studies based on observations rather than modelling have partially challenged the light hypothesis by reporting mesopelagic sound scattering layers partly formed of boreal fish species (e.g., glacier lanternfish *Benthosema glaciale* and juvenile redfish) in the high Arctic (Knutsen et al., 2017; Geoffroy et al., 2019; Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023). Moreover, studies looking at both temperature and latitude (a proxy for irradiance) have concluded that temperature fronts might also contribute to hindering the northward range expansion of mesopelagic fish (Chawarski et al., 2022). Data are more limited for the inner shelves of the Kara, Laptev and East Siberian seas, but those ecosystems are often relatively poor in pelagic fish (Hirche et al., 2006; Schmid et al., 2006).

Pelagic borealization is affecting populations and ecosystem functioning. Changes in zooplankton development and community succession along the seasons have been linked to pelagic fish diet and biomass trends (Orlova et al., 2010; Dalpadado et al., 2024), propagating climate effects to upper trophic levels. They also affect first year juvenile fish survival, mainly walleye pollock and polar cod, as lipid-rich species associated with autumn blooms during cold years are a critical source of reserve for the juvenile fish before the winter (Kimmel et al., 2018; Kimmel et al., 2023; Bouchard and Fortier, 2020; Dupont et al., 2020), and as prey size impacts that of its visual predators, as shown by bioenergetic and behavioural modelling studies (Ljungström et al., 2020). In contrast, the sustained advection of krill in the Barents, Chukchi and western Beaufort seas is altering trophic controls and stabilising predator populations (Berline et al., 2008; Eriksen and Dalpadado, 2011; Orlova et al., 2013; Ashjian et al., 2021). Increasing co-occurrence of polar cod with other species such as capelin or Pacific sand lance would lead to more competition for food at inflow and interior shelves, with negative consequences for both species (Orlova et al., 2010; Falardeau et al., 2014; McNicholl et al., 2016; McNicholl et al., 2018; Pedro et al., 2020). Changes in dominant forage fish and zooplankton prey have altered marine mammals' and seabirds' migration patterns and diet across the pan-Arctic, sometimes leading to lower growth rate for chicks or altered demography (Provencher et al., 2012; Chambellant et al., 2013; Gaston and Elliott, 2014; Falardeau et al., 2017; Gall et al., 2017; Balazy et al., 2018; Kuletz et al., 2020; de la Vega et al., 2021; Merkel et al., 2021; Ulrich and Tallman, 2021; Descamps et al., 2022; Moore et al., 2022).

3.3 Changes in benthic demersal systems

Many studies have reported changes in benthic (mostly invertebrates) and demersal (mostly fish) ecosystems across Arctic and sub-Arctic shelves. Signals of borealization are stronger on inflow shelves, where shifts in demersal fish communities have been widely reported, such as in the Barents Sea (Fossheim et al., 2015; Bergstad et al., 2018; Spotowitz et al., 2022), in western Greenland (Post et al., 2021), as well as the northern Bering Sea and, to a lesser extent, the Chukchi Sea (Mueter et al., 2021a; Zhang et al., 2022). An emerging pattern from recent studies is that borealization of inflow regions seems to impact neighbouring areas by spillover effect. In eastern Greenland (Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b), demersal communities across depths have rapidly reorganised in response to climate change, in particular between 350 and 1000m depth. Specifically, studies have found that Atlantic cod, beaked redfish and deep-sea shrimps (*Pandalus borealis*) observed on the northeast Greenland shelf originated from the Barents Sea populations (Christiansen et al., 2016; Andrews et al., 2019). In addition, across the Siberian Arctic (Kara Sea, Laptev Sea, East Siberian Sea), North Atlantic species have expanded eastward while North Pacific species have expanded westward (Orlov and Volvenko, 2024).

Borealization in inflow shelves has also been documented for benthic communities, although responses are lagged with regard to climatic signals (Grebmeier, 2012; Jørgensen et al., 2019; Waga et al., 2020; Zakharov et al., 2020; Calvet et al., 2024). Interestingly, the borealization of benthic communities does not necessarily lead to an increase in productivity or biomass (Zakharov et al., 2020 for the Barents Sea; but see Krause-Jensen et al., 2020, for pan-Arctic increases in seaweeds). In contrast, unchanged community biogeography could suggest resilient communities in the Laptev Sea (Kokarev et al., 2017), and to some degree in the Bering and Chukchi Seas, over several decades (Grebmeier et al., 2015a but see Grebmeier et al., 2006; Huntington et al., 2020, for biomass declines). The lack of repeated surveys hinders our ability to evaluate the degree of borealization of benthic communities, especially on interior and outflow shelves, but bycatch data from commercial or scientific bottom trawls can serve as a baseline for future assessments (Jørgensen et al., 2022), and the Distributed Biological Observatory in the Pacific Arctic provides time series for macro- and megabenthic fauna (Grebmeier et al., 2015b; Grebmeier et al., 2018).

At smaller scales, some studies have revealed the borealization of some coastal zones across the Arctic, as suggested by an increase in boreal fish species in lagoons on the Beaufort Sea (von Biela et al., 2023), and by increased macroalgal cover (Krause-Jensen et al., 2020), abundance of boreal species and coincident shifts in benthic invertebrate communities in Svalbard fjords and near Franz Josef Land (Kortsch et al., 2012; Węsławski et al., 2018; Al-Habahbeh et al., 2020; Dvoretsky and Dvoretsky, 2024). However, the degree of borealization of benthic communities in Atlantic Arctic fjords might depend on the bathymetric features of the coastline, such as fjord sills and the interannual strength of the Atlantic Water inflow (Beuchel et al., 2006; Renaud et al., 2007; Jordà-Molina et al., 2023). A more important driver of major changes in Arctic coastal ecosystems and landscapes could instead be the melting marine terminating glaciers (Lydersen et al., 2014; Meire et al., 2017; Williams et al., 2021; Kavan and Strzelecki, 2023). Some sub-Arctic coastal regions do not display any particular response to climate change. For example, western Greenland intertidal ecosystems do not vary with latitude, which would suggest resilience to climate change, based on space-for-time substitution (Thyrring et al., 2021), and in the Baydaratskaya Bay, Kara Sea, benthic communities were unchanged until 2013, and only seemingly impacted by other local anthropogenic impacts since then (Azovsky and Kokarev, 2019).

As in the pelagic systems, demersal and benthic borealization appears to be mainly driven by changes in suitable habitats and prey distribution induced by climate change. Rates of response to environmental changes are often lagged and species-specific (Alabia et al., 2018). At the inflow shelves, the main drivers are the fluctuating extent of colder and warmer water masses and timing of ice retreat. This has been shown in the northern Bering Sea and Chukchi Sea, for both demersal and benthic communities (Grebmeier, 2012; Nishio et al., 2020; Zhang et al., 2022), and in the Barents Sea (Ingvaldsen et al., 2021; Nascimento et al., 2023). In addition to expanding suitable warmer habitats, advected waters transport demersal and benthic early life stages. Variations in water mass extent across interannual to decadal scales have been linked to the varying abundance of advected ichthyoplankton species, leading to variation in dominance regime of fish larvae in the Eastern Chukchi Sea (Randall et al., 2019; Axler et al., 2023), and in the Barents Sea (Eriksen et al., 2015; Eriksen et al., 2017). These fluctuations in water mass inflows are linked to large-scale circulation patterns, such as the sub-polar gyre in the northern Atlantic in western Greenland (Post et al., 2021), or the Arctic dipole in other inflow shelves (Polyakov et al., 2023). While warm conditions are maintained at inflow shelves and neighbouring regions are gradually warming due to local changes in the environment, mobile populations such as fish are likely able to further expand beyond inflow shelves (Andrews et al., 2019; Orlov and Volvenko, 2024), but demersal Arctic fish species living on the edge of the shelves cannot move north as they run out of shelf (Wassmann et al., 2006b; Fossheim et al., 2015). The northward expansion of less mobile boreal benthos is likely more dependent on the dispersion of the larval phase (Ershova et al., 2019; Meyer-Kaiser et al., 2022), although those will may not settle successfully (Wassmann et al., 2015; Ershova et al., 2019; Descôteaux et al., 2022).

Shifts in species distribution can drive changes in both pelagic and benthic-demersal life cycles, oceanic seascapes, population structures and interspecific interactions. In the Chukchi Sea, increasing number of boreal pre-spawning, spawning and post-spawning walleye pollock have been observed in recent years (Emelin et al., 2022). This could indicate an expansion of their spawning location or range but does not necessarily correlate with juvenile survival. Survival of the early life stages depends on species capacity to take advantage of available food and to resist harsh winter conditions. Polar cod, adapted to Arctic conditions, have a unique fat storage strategy, from diatoms and *Calanus* origin, that enables it to thrive in cold ice-covered region (Copeman et al., 2022). In contrast, juvenile walleye pollock have better condition in the southern than in the northern Chukchi Sea (Copeman et al., 2022), which suggests that they are not yet adapted to colder northern conditions. In the Barents Sea, climate induced changes in temperature and food availability also drive trends in 0-group fish lengths (Skjoldal et al., 2022) and distribution (Eriksen et al., 2017). Apart from their lipid storage strategy, differences in spawning timing between species is likely a key driver of their successful survival during the Polar Night. Indeed, winter surveys around Svalbard show that the spring spawning strategy of boreal fish, which contrasts with winter-spawning Arctic and arcto-boreal species, might lead to a temporal mismatch between their planktonophagous larvae and zooplanktonic blooms (Berge et al., 2015; Geoffroy and Priou, 2020). Large incoming boreal fish are often generalists which are thus able to feed on boreal as well as Arctic prey. This was shown by the diet composition of walleye pollock in the northern Chukchi Sea, where Arctic copepods, euphausids and polar cod were observed in their stomach content (Benzik et al., 2022). Walleye pollock also consume other incoming species, such as Pacific sand lance, whose abundance has been increasing with the decline of sea-ice (Baker et al., 2022). Similarly, in the Barents Sea, ctenophore species, which might benefit from warmer conditions in the region, and snow crab (*Chionoectes opilio*), which overlaps increasingly with Northeast Arctic cod as these expand north-eastward, increased in frequency in Northeast Arctic cod diets (Eriksen et al., 2018; Holt et al., 2021). However, there is no sign that polar cod are increasing in Northeast Arctic cod's diets (Holt et al., 2019).

3.4 Ecosystem-level impacts of borealization

3.4.1 Biological and functional diversity across compartments

Understanding the degree of borealization of Arctic ecosystems necessitates knowledge on biological diversity of native and incoming communities. Efforts to catalogue species across the pan-Arctic are still ongoing (Renaud et al., 2006; Bluhm et al., 2011b; Bluhm et al., 2011a; Kosobokova et al., 2011; Poulin et al., 2011; Lin et al., 2014; Jørgensen et al., 2022). The Central Arctic Ocean can be divided in two main regions with distinct biodiversity: the Eurasian and American regions (Alfaro-Lucas et al., 2023). There is relatively little difference in species composition between the central Arctic Ocean basins (Bluhm et al., 2015; Alfaro-Lucas et al., 2023), yet substantial variation among benthic habitats within the basins (Ramirez-Llodra et al., 2023). However, some ecological compartments and regions are still largely under studied (CAFF, 2017; Alfaro-Lucas et al., 2023). Where long time series are available, studies highlight the strong impact of borealization on biodiversity. Species distribution ensemble models applied to 69 apex- and mesopredators revealed varying trends in species richness across the pan-Arctic over the last two decades (Alabia et al., 2023). The authors suggested that species richness has been increasing overall in the Arctic, in line with large range shifts, especially from large mobile apex predators, but more strongly in interior and outflow shelves than inflow shelves. In the Barents Sea, an 8-year study showed a steady increase in species richness and biodiversity indices, especially within the advected waters (Prokopchuk and Trofimov, 2019). A study on shorter time scales in the Chukchi Sea revealed contrasting responses of functional group diversity between warm and cooler years: during a warm year, diversity increased among zooplankton and fish communities, decreased for bacteria, protists, epibenthos and seabirds, and did not vary significantly for macrobenthos, relative to a colder year (Mueter et al., 2021a).

The documented changes in Arctic biodiversity bring about functional reconfigurations with implications for ecosystem function and vulnerability (Ingvaldsen et al., 2021). Many boreal species differ from Arctic ones in terms of functional characteristics, as exemplified by fish and copepods (e.g., Aune et al., 2018). Boreal fish species are often large, and predatory, with a generalist diet, whereas Arctic fish are rather small benthivores like sculpins (Frainer et al., 2017; Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b). In East Greenland, the incoming boreal functional traits do not compensate for the loss of Arctic traits, which leads to a decrease in functional diversity across depths (Emblemsvåg et al., 2022a). In contrast, in the Barents Sea, functional diversity increases with the northward shift of functionally-rich boreal communities (Frainer et al., 2021), but this situation might be transitory as predation and competition between newly co-occurring boreal and Arctic species might lead to the decline of Arctic species (Pecuchet et al., 2020). The alteration in functional diversity is correlated with a change in dominance of different life history strategies, including an expansion of so-called "periodic" species, which have a greater adaptive capacity owing to higher reproductive output, broader diet, and migratory behaviour (Bernardo et al., 2024). Higher functional diversity is thought to increase adaptive capacity and affect ecosystem stability and resilience to perturbations. However, these studies have so far been limited to fish communities, and a pan-Arctic overview is lacking.

3.4.2 Impacts on apex predators

Changes in environmental conditions in the Arctic also affect seabirds and marine mammals, which are often emblematic and/or Red-listed and are thus also an important component of biodiversity, despite low species richness compared to smaller groups. For example, seabirds colonies are experiencing changes in densities and species composition around the Svalbard Archipelago (Descamps and Strøm, 2021), and in the northern Bering Sea and eastern Chukchi Sea (Kuletz et al., 2020). Similarly, changes in marine mammals are observed with changes in habitat conditions: killer whales are increasingly observed in the Chukchi Sea and elsewhere as sea-ice retreats (Ferguson et al., 2010; Stafford, 2019), in East Greenland an increase in the abundance of several boreal cetaceans (humpback, fin, killer, and pilot whales and dolphins) has been seen as summer sea ice has disappeared and water temperatures have increased (Heide-Jørgensen et al., 2023), while narwhals seem to distribute preferentially where temperatures are colder, and might abandon their warmer habitats of Mideast and Southeast Greenland (Chambault et al., 2020; Heide-Jørgensen et al., 2023). Sea surface temperatures are also linked to seasonal displacements of bowhead whales in Baffin Bay (Chambault et al., 2018). With sea ice decline, polar bears are pushed to more frequent long-distance swimming (Pilfold et al., 2017). Gray whales, associated with warmer waters, occur more frequently in the Chukchi Sea to feed on abundant prey when ice conditions allow. However, recent warm events have been associated with unusual mortality events in gray whales (Stewart et al., 2023), suggesting that increased availability of prey in newly ice-free areas was insufficient to compensate for decreasing prey availability in more southern feeding areas. Concomitant displacements have been observed for Arctic ice-associated species, with poorer body condition and population status (Kovacs et al., 2011; Laidre et al., 2015). Environmental changes and prey behaviour are also altering migration patterns and timing of marine mammal species (Kuletz et al., 2024).

Changes in distribution of lower trophic level communities affect the diet of many apex predators, modifying trophic interactions and food webs (de la Vega et al., 2021). Spatial or compositional shifts in epibenthic invertebrate communities in the Bering and Chukchi Sea could affect prey species of benthivorous marine mammals like Pacific walrus and bearded seals, which are important subsistence resources for Alaska Native communities (Richman and Lovvorn, 2003; Logerwell et al., 2022), as well as benthivorous seabirds like the endangered Steller's eiders (Richman and Lovvorn, 2003). However, current latitudinal and regional variability in ringed seals and beluga diets would suggest that those species could adapt to changes in prey (Yurkowski et al., 2016a). For polar bears, some individuals are more opportunistic than others, and those that specialise on seals are most sensitive to climate change impacts (Thiemann et al., 2008). Apart from changes in diet and habitat loss, Arctic top predators will likely face an increasing number of anthropogenic pressures, such as increased noise and pollution from shipping, plastic pollution, increasing disease and parasite occurrence, (Kovacs and Lydersen, 2008; Merkel et al., 2021). Top predators have been shown to sometimes adapt to the change in diet (e.g., Yurkowski et al., 2016b; Vihtakari et al., 2018; Sauser et al., 2023), although not always successfully, as changes in prey quality, notably fat content, would affect species fitness (e.g., Descamps et al., 2022; Anderson et al., 2023; Sauser et al., 2023). The decline of iconic marine mammals in the Arctic is a major conservation concern, with implications for biodiversity and cultural ecosystem services in the Arctic.

3.4.3 Food-web impacts

Apex- and mesopredator incoming boreal species establish new feeding links in Arctic marine ecosystems, thereby reorganising food-webs, leading to increased food-web connectance and decreased modularity, which is associated with low resilience (Kortsch et al., 2015; Blanchet et al., 2019; Pecuchet et al., 2020; Jordán et al., 2024). A core function of Arctic food webs that is affected by borealization is the sympagic-pelagic-benthic carbon coupling through the sinking of ice-algae when ice melts. This function is particularly important for benthic biomass and biodiversity (Boetius et al., 2013; Kędra et al., 2015; Hansen et al., 2020). Indeed, several studies have shown the strong reliance of megabenthic communities to this coupling in the Barents Sea, northeast Greenland shelf (Cautain et al., 2022; Cautain et al., 2024), on Siberian shelves (Schmid et al., 2006; Lalande et al., 2009), in the Northern Bering Sea and Chukchi Sea (Koch et al., 2020), in Baffin Bay (Yunda-Guarin et al., 2020) and in the Canadian high-Arctic (Yurkowski et al., 2020). The anticipated - though poorly documented (see Zhulay et al., 2023 for the Chukchi Borderland) - decline in benthic-pelagic coupling has important implications for ecosystem functioning (Niemi et al., 2024). Food web and ecosystem models can explore the consequences of declining sea ice and new trophic interactions in an integrative approach. In the Beaufort Sea, the shelf and slope ecosystem with strong riverine influence and changes in salinity has likely driven lower diversity and changes in biomass, consumption and trophic levels of marine mammals and fish, including Arctic key species (Sora et al., 2024). In the Barents Sea, multiple pressures have caused changes in the food-web over time, but an ecosystem model suggests that increased productivity fuelled the food web through bottom-up effects after the 1990's (Pedersen et al., 2021). In Baffin Bay, an ecosystem model revealed that polar cod is a key component of the food-web structures (Pedro et al., 2023). An exploration of past dynamics could reveal the impacts of changes in the polar cod stock on the ecosystem.

4 Discussion

4.1 Spatial extent of borealization: the "spillover" effect

Local changes in environmental conditions, driven by alterations in large scale circulation patterns and fluid (water, air) masses properties, are reported across the pan-Arctic. The strongest impacts seem to affect the inflow shelves, where high connectivity to very different systems result in a high interannual variability and sensitivity to external forcings. Borealization has thus progressed more rapidly on these shelves, affecting all trophic levels (Csapó et al., 2021). Ecosystems inflow shelves are currently transitioning towards a more boreal functioning but retain some Arctic characteristics. The potential degree of borealization in the future is discussed below. A new emerging signal, as revealed by many recent studies reviewed here, is that interior and outflow shelves are also experiencing borealization through climate-induced modifications of local environmental conditions (sea-ice cover, river runoff, temperature) that render habitat suitable for species that are transported or actively relocate there (Figure 6).

However, the extent of this "spillover" effect of borealization across space, time and functional groups is uncertain, due to several knowledge and data gaps. Indeed, a recent biodiversity assessment for the whole Arctic domain has highlighted the lack of data for the Siberian seas (Kara, Laptev, East Siberian seas) and the Canadian Arctic (Canadian Arctic Archipelago, Beaufort Sea, Hudson and Baffin Bay, Alfaro-Lucas et al., 2023). In addition, for all shelves and for the Arctic basins, data are largely restricted to the summer and autumn seasons, with recent but limited knowledge on winter and polar night processes (Berge et al., 2015; Berge et al., 2020; Gerland et al., 2019), and transition periods between ice-free and ice-covered seasons (Shogren et al., 2020). More seasonal and spatial coverage, including land-sea connectivity at more extensive spatial scales than currently conducted, are important for understanding physical processes such as sea ice loss, water freshening, nutrient and carbon cycles (Brown et al., 2020; Shogren et al., 2020; Timmermans and Marshall, 2020), as well as biological processes (Berge et al., 2015; Geoffroy and Priou, 2020). Deployment of dedicated autonomous technologies are often suggested to fill this data gap. In addition, approaches such as participatory modelling tools have a strong potential to fill the knowledge gaps around e.g., winter processes, using local ecological knowledge (Pedro et al., 2023). A more comprehensive overview and monitoring of Arctic ecosystem borealization would also necessitate the allocation of research resources to characterise and better understand processes of relatively understudied compartments such as microbial communities, epibenthos and infauna (CAFF, 2017).

4.2 Through the spyglass: a boreal Arctic in the future?

Predicting the extent to which Arctic borealization will continue in the future across ecosystem compartments is a priority that has received much attention from the scientific community. Climatic scenarios from the coupled model intercomparison project (CMIP) suggest various trajectories for future Arctic climatic and

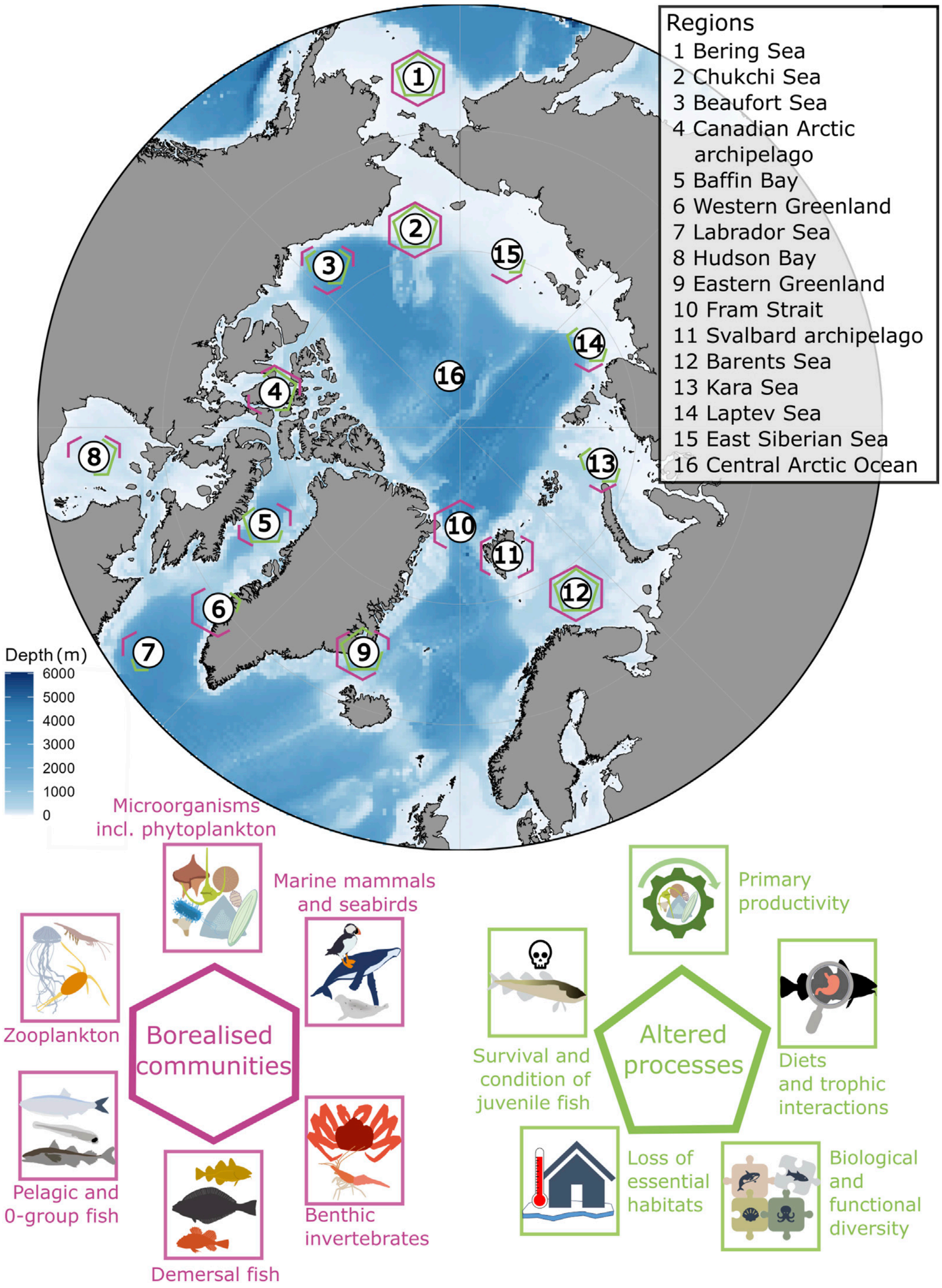

FIGURE 6
Map of evidence of borealization of communities and ecosystem processes across regions. Regions that are indicated are based on the naming used in the literature cited in the main text.

oceanographic conditions, but all scenarios display similar trajectories until the 2040s. The Artic will likely continue to warm at a faster rate than mid-latitude systems. Arctic amplification could continue under a low emission scenario, where ice albedo feedback would maintain the phenomenon, but it would be less prominent in a high-emission scenario (Ono et al., 2022). The increase in heat transport from the Atlantic and the Pacific will likely continue and progress poleward through the Bering Strait and the Barents Sea (Drinkwater et al., 2021; Dörr et al., 2024). All shelves will become ice free in the summer, irrespective of the climatic scenario, and the Barents Sea could become ice free in winter by the end of the century (Årthun et al., 2021). Expanding open water areas and increasing precipitation will contribute to large and rapid changes in hydrological cycles (McCrystall et al., 2021). Increased river runoffs should increase stratification and subsurface warming in the central Arctic Ocean (Nummelin et al., 2016).

It is challenging to assess the degree of borealization of biogeochemical processes and microbial communities at pan-Arctic scales. Primary production is arguably the microbial process that has received most attention in the literature, and numerous studies suggest an evolution towards a more boreal functioning in the future (Ardyna and Arrigo, 2020; Noh et al., 2024). The Pacific and Atlantic inflow shelves will likely experience the strongest increase in primary productivity, although this is more uncertain for the western Barents Sea, where oceanographic models project variable directions and magnitudes of change depending on how stratification processes are represented (Mueter et al., 2021b; Mousing et al., 2023). However, increasing cloud cover (Bélanger et al., 2013) and strong seasonality in light conditions at higher latitudes are likely to limit the transition towards a completely boreal phenology, and primary production should retain some characteristics of an Arctic system, which would lead to arctic-boreal hybrid functioning. Yool et al. (2015) projected that, by 2,100, despite an increase in productivity driven by the loss of sea ice, the Arctic will not be more productive than the Atlantic, with both systems entering a low nutrient regime. In contrast, the Pacific, richer in nutrients, might experience a longer rise in productivity (Yool et al., 2015). However, the trajectory of nutrient limitation remains a significant knowledge gap, leaving predictions of Arctic productivity in the future uncertain (Slagstad et al., 2015; Mueter et al., 2021b; Mousing et al., 2023). While observational data on other microbial processes across the pan-Arctic remain limited, experimental studies offer valuable insights into potential shifts in crucial microbial functions. For example, temperature variations might influence bacterial metabolic rates, phytoplankton community structure and chlorophyll a concentrations and, consequently, carbon cycling (Kritzberg et al., 2010).

The climate driven environmental changes will continue to trigger distributional shifts and changes in biodiversity across functional groups and Arctic regions. These shifts are quantitatively explored based on species distribution models fitted to species' current thermal preferences. Ensemble modelling predicts an increase in phytoplankton species richness all over the globe under the highest warming scenario, by the end of the century, except in the Arctic, where no trend is expected (Benedetti et al., 2021). Other projections with similar time horizons suggest that poleward shifts in zooplankton distribution could continue at a pace of 8.7 km/decade, accompanied by a change in seasonal occurrence peak up to 13 days earlier, a high species turnover, and a northward shift of many boreal gelatinous zooplankton, sometimes only into sub-polar regions (Villarino et al., 2015; Benedetti et al., 2021; Pantiukhin et al., 2023; Pantiukhin et al., 2024; Cheung et al., 2015) also predicted a northward range expansion for Pacific pelagic fish species of 30.1 ± 2.34 (S.E.) km decade^{-1}. However, regional predictions for Canadian waters predict a decline in biomass in both the Pacific and Atlantic sides (Bryndum-Buchholz et al., 2020). In contrast, projections under a high emission scenario reveal an increase in total forage fish biomass in Hudson Bay, but with decreasing fish size and a shift from lipid rich polar cod to smaller boreal fish (Florko et al., 2021). Overall, responses to climate change are likely region-specific, as well as species specific and are thus challenging to predict (Mueter and Litzow, 2008; Alabia et al., 2018; Husson et al., 2020; Calvet et al., 2024). The impact of climate change on benthic habitats may depend on the spatial scale of the projection. In the Bering and Chukchi seas, the habitat of many assemblages of epibenthic invertebrates is predicted to be reduced by 50% by 2050 and almost 100% by 2,100, with the exception of eurythermal species such as the basket star *Gorgonocephalus cf. arcticus* (Logerwell et al., 2022). At the pan-Arctic scale, however, habitat change for benthic species might be limited in the future (Renaud et al., 2019). Habitat loss should mainly affect currently cold and aragonite-oversaturated areas such as northern Barents Sea and east Greenland Sea (Renaud et al., 2019), and cold-stenothermal species such as gastropods and bivalve mussels *Musculus* spp. in the Bering and Chukchi Sea, leading to large losses of biodiversity locally (Logerwell et al., 2022). At the ecosystem-level, long-term projections using species distribution ensemble models suggest an increase in species richness and functional redundancy poleward with an increase in predatory taxa that will threaten Arctic species and decrease the modularity of Arctic food webs in the Bering and Chukchi seas (Alabia et al., 2020). It is predicted that the co-occurrence of boreal and arctic fish species in borealized regions will vary from 1 year to the other, with more Arctic species in cold years and more boreal species in warm years (Geoffroy et al., 2023), as seen in the Labrador and Bering seas (Marsh and Mueter, 2020).

The poleward progression of communities could lead to many changes in seascapes, with shifts in essential habitat localisation and altered connectivity, leading to declining stocks and a potential increase in population mixing and hybridization by the end of the century. Habitat forming species such as macroalgae are likely to continue their colonisation of coastal Arctic regions, with more of the Canada, Greenland and Svalbard coasts becoming suitable habitats due to less ice cover for three important macroalgae species by 2,100 (Jueterbock et al., 2013). In contrast, in the soft-sediment dominated Beaufort Sea, kelp production has been shown to be limited by wind speed that resuspends river and coastal sediments and limits light penetration to the seabed (Bonsell and Dunton, 2018). This is likely to affect nursery and feeding habitats, although their variations are only partially understood and might be affected by multiple factors. Along the Norwegian coast, Northeast Arctic cod spawning locations have been fluctuating with a northward trend, seemingly under the effect of population demography, while the effect of climatic factors is uncertain (Höffle et al., 2014; Opdal and Jørgensen, 2015). Similarly, spawning locations of Northeast Arctic haddock (*Melanogrammus aeglefinus*) are likely driven by density dependence, rather than temperature (Langangen et al., 2018). Finally, predation by boreal species has been shown to influence capelin's spawning area (Olsen et al., 2024). It is thus challenging to model future locations of spawning sites. Nevertheless, modelling studies based on thermal preferences and bottlenecks of species early life stages can give a first estimate. Capelin is anticipated to shift spawning north-eastward in the Barents Sea (Huse and Ellingsen, 2008). For Northeast Arctic cod, further northward shifts in spawning sites could affect juveniles' survival and increase their sensitivity to spawning timing (Endo et al., 2024).

Population mixing will likely increase and would probably occur via the Northeast and Northwest Passages (Vermeij and Roopnarine, 2008; Kelly et al., 2010; Wisz et al., 2015). This has likely already started, as suggested by the first observations of interoceanic dispersals (e.g., a Pacific diatom in the Atlantic waters, Reid et al., 2007). The Greenland halibut Pacific and Atlantic populations, with so far limited genetic mixing (Orlova et al., 2019), are now increasingly interacting along the Eurasian Arctic, suggesting that a potential reunification of those populations is possible in the future (Orlov and Volvenko, 2024).

To summarize, all climatic scenarios point to a profound transformation of the Arctic oceanic functioning. Under those conditions, many species will shift, but not all, and not all the way into the Arctic Basin, where conditions will remain harsh. Ecosystems' primary productivity, biodiversity, functioning and food webs will be altered. All this suggests that Arctic marine ecosystems might not entirely transform into a boreal functioning, but rather stabilize in a hybrid state between Arctic and boreal ecosystem at a latitudinal limit north of the current one, with transient borealization during warmer periods.

4.3 Into the fog: uncertainties and key questions

Large uncertainties and bias surround projected trajectories for the Arctic and sub-Arctic ecosystems. Arctic Ocean circulation is complex, with numerous feedback and potentially tipping processes among and between the cryosphere, hydrosphere and atmosphere, and several possible future evolutions depending on climate change intensity (Lannuzel et al., 2020; Timmermans and Marshall, 2020). The most recent version of the Coupled Model Intercomparison Project (CMIP6) has persistent bias on Arctic water masses representations, inherited from the previous version, which necessitate major improvements, notably by using higher model resolutions (Khosravi et al., 2022). For example, other studies showed that heat transport from lower latitudes might be underestimated by model with too coarse spatial resolution (Xu et al., 2024).

Projections of community shifts in the future are also associated with considerable uncertainties, although hard to estimate and thus rarely mentioned in the studies. The potential for further borealization of the ecosystem depends on species habitat preferences, the location and connectivity of their essential habitats (spawning, nursery, feeding grounds), and their capacity to acclimatise and then adapt to new abiotic and biotic conditions. Projecting species future habitats using species distribution models is a first approach to anticipating species movement. However, those models are often based on strong assumptions, such as environmental niche stability, and are built around limited number of environmental covariables, ignoring the impact of population dynamics and interspecific interactions on species distributions. Among environmental variables, factors that do not vary over time are not always included. Indeed, while temperature, salinity or oxygen, which will be affected by future climate change, can be used as time-varying predictors of most fish species' suitable habitats, poleward displacement might be limited by non-dynamic factors such as depth, light regimes, or seabed type. Considering a species' traits and life cycle can help estimate the likelihood of that species to shift northward. Using this approach, it is assumed that cod and haddock have reached their northern limit at the shelf break of the Barents Sea and minke whale or harp seals will likely follow the ice edge, while other species, such as capelin, redfish or snow crab will likely be able to expand further into the Arctic (Hollowed et al., 2013b; Hollowed et al., 2013a; Haug et al., 2017; Mullowney et al., 2023).

When conditions in the Arctic are limiting, species that will not be able to shift their distribution will have to acclimate, then adapt, or die (Hoffmann and Parsons, 1990), and this will impact the pace and extent of borealization across regions and functional groups. Adaptation to environmental stress manifests itself mainly via two mechanisms: the species plasticity (capacity of a genotype to express different phenotypes under varying environmental stress), and the selection, on evolutionary scales, of certain phenotypes. Species phenotypic plasticity includes, among others, behavioural flexibility and physiological tolerance, both of which are challenging to observe in natural environments (Beever et al., 2017) and manifest differently across a species' range (Donelson et al., 2019). Plasticity can be a way to cope temporarily with environmental stress, but can also hinder adaptation in some cases (Fox et al., 2019). It is thus important to assess species adaptive capacity to understand species responses to climate change and support conservation and management efforts (Hoffmann and Sgrò, 2011). This can be done by considering the species fundamental adaptive capacity, characterised via its functional traits such as longevity, mobility, and dispersal capacity (Beever et al., 2016). Such approaches, along with experiments on species thermal adaptivity, are often suggested as potential improvements to species distribution models (Drost et al., 2014; Drost et al., 2016; Logerwell et al., 2022). Evolutionary models could integrate that information and incorporate interspecific interactions to further explore possible trajectories of co-evolution for Arctic marine systems.

Finally, lasting borealization, emerging from species completing their life cycle, implies that environmental conditions are suitable for all life stages (Wassmann et al., 2015), of which early life stages and spawning adults are often the bottlenecks (Dahlke et al., 2020). Several species have been suggested to be able to complete their life cycle in areas where it was previously not observed, for example, the boreal capelin in Hudson Bay (Gaston and Elliott, 2014), the copepod *C. finmarchicus* and the Atlantic hyperiid amphipod *Themisto compressa* at the Fram Strait, with the latter two species much poorer in lipid than their Arctic counterparts (Kraft et al., 2013; Tarling et al., 2022). Connectivity between the habitats and along dispersal routes is thus a key consideration when projecting population shifts and species range shifts. Knowledge on thermal preferences of early life stages enabled modellers to estimate changes in spawning sites for cod and polar cod under various gas emission scenarios (Dahlke et al., 2020; Sanders et al., 2022). Results of these studies all suggest a deterioration of the current spawning sites for both species under high emission scenarios, and more limited impacts for low emission scenarios. In addition, some local conditions such as depth may act as barriers to dispersal of fish species across the pan-Arctic (Bouchard et al., 2018).

4.4 Risks and vulnerability of borealized socio-ecological systems

Despite some uncertainties and knowledge gaps, there is a clear consensus on the ongoing borealization of Arctic ecosystems, and its likely continuation in the future. Arctic endemic communities and ecosystems are most at risk, if they are unable to adapt to the multiple environmental stressors or to compete with new incoming species (Kędra et al., 2015). Sympagic species or species with a strong link to the ice, through their diet or life cycle, are particularly at risk (Kohlbach et al., 2016), while some may survive in the pelagic zone (Kunisch et al., 2020). The ice association is well documented for example, for polar cod. In the Chukchi Sea, its body condition appears to be lower during warm years, suggesting that the region is warming beyond the species' thermal limits (Copeman et al., 2022). With sea ice loss, polar cod will lose its spawning habitat (Huserbråten et al., 2019), and new incoming species could outcompete it (Mueter et al., 2016). However, some studies suggest that competition for food might be limited at least for early life stages, through niche partitioning (Falardeau et al., 2014; Bouchard et al., 2022). Moreover, in the Canadian Arctic Archipelago and Central Arctic Ocean, the relaxation of the most extreme conditions with climate change could benefit polar cod, at least in the short term (Bouchard et al., 2017; Steiner et al., 2019; Geoffroy et al., 2023). There, larval survival of polar cod increases in years with earlier ice-breakup and warmer sea surface temperatures (Bouchard et al., 2017).

With sea-ice loss and increased open water area, carbon sinking and ocean acidification are likely to increase (Lannuzel et al., 2020; Terhaar et al., 2020; Qi et al., 2022), adding to the effect of warming to affect species habitats and distributions. The extent of the impacts of ocean acidification on marine populations is still not well understood. Experimental studies show that acidification affect coastal phytoplankton species growth, colony length and chain length, although the effect vary across species (Thoisen et al., 2015). In addition, increased acidification could lower phytoplankton growth rates and amplify the decrease in primary production with warming (Coello-Camba et al., 2014), and alter microbial community composition (Brussaard et al., 2013; Sugie et al., 2020). Finally, acidification can lead to the dissolution of Arctic benthic invertebrate shells (Comeau et al., 2009; Niemi et al., 2021) and, in combination with warming temperatures, increased consumption by Arctic brittle stars (Wood et al., 2011). However, some Arctic bivalves are more resilient to decreasing pH (Goethel et al., 2017).

In addition to those climate-driven pressures, Arctic ecosystems will experience increasing pressures from many other anthropogenic sources. Microplastic contamination is already affecting benthic organisms in the Chukchi Sea and other areas of the Arctic through local sources and transport (Fang et al., 2018; Bergmann et al., 2022). New ice-free conditions along the shelves and seasonally in the Central Arctic Ocean would allow Arctic shipping year-round starting in the 2070s (Min et al., 2022), leading to increased concentrations in pollutants (Svavarsson et al., 2021). This increase in shipping would also be prompted by industrial opportunities newly accessible in a future seasonally ice-free Arctic, such as mineral, oil and gas extraction, of fishing. Indeed, large global models project a high potential for Blue Economy in the Arctic, with potential for new fisheries, owing to increased local productivity and incoming new stocks (Cheung et al., 2015). However, the latest FAO report stresses the high risk associated with potential fishing in the Arctic due to very high uncertainties around the future biomass projections associated with the two main Earth system models used to force the simulations (Tittensor et al., 2021; Blanchard and Novaglio, 2024). In addition, climate is not the only factor affecting Arctic fisheries, and complex cross-scale, cross-domain (ecology, society, economy) processes can greatly affect the future of pan-Arctic fisheries (Niiranen et al., 2018). The potential growth of biomass of commercial stocks thus call for new management approaches (Christiansen et al., 2014; McBride et al., 2014) and careful consideration of potential new fishing opportunities. For example, a study investigating the potential for a fishery on walleye pollock that are expanding into the western Chukchi Sea highlight strong uncertainties around the amount of biomass entering the region, the state of the stock, and the possibility of harvesting considering the harsh local fishing conditions (Maznikova et al., 2023). Such complex systems are challenging to apprehend, and models are often a key tool to anticipate future changes. To date, few models explore regional ecosystem response to potential effects of climate change scenarios on ecosystem services and human wellbeing, with or without considering other human pressures such as fisheries. The few projections that have been completed anticipate a decrease in fish biomass or high uncertainties in biomass trajectories, thus challenging the hypothesis of a future Blue Growth in the Arctic (Bryndum-Buchholz et al., 2020; Whitehouse et al., 2021).

In the meantime, some traditional local fisheries are threatened by ecosystem changes. For example, the winter ice fishery on Greenland Halibut (*Reinhardtius hippoglossoides*) is now being threatened by the progressive loss of sea ice (Hussey et al., 2017). Fishermen in Greenland are shifting their traditional fishing practices in response to changes in ice cover, and are observing new species (Schiøtt et al., 2022). Local ecological knowledge, including knowledge from Indigenous communities whose livelihoods and cultures are tightly linked to Arctic ecosystems, is increasingly highlighted as a most valuable tool to face future challenges and apply an adaptive strategy to the fast changing Arctic (Riedlinger and Berkes, 2001; Schwoerer et al., 2021). Local fishermen and hunters have detailed knowledge on seasonal and spatial scales that are rarely covered by any scientific survey, and are highly useful to combine with scientific knowledge and data do detect changes in Arctic ecosystems and threats to traditional livelihoods (Chila et al., 2022; Falardeau et al., 2022; Bouchard et al., 2023; Dunmall et al., 2024). Better inclusion of this rich source of information could be done through community-based monitoring and co-construction of scenarios to directly inform management (Nilsson et al., 2021; Falardeau et al., 2022). Indeed, balancing ecosystem and livelihood conservation and the increasing economic interests in the Arctic necessitate consideration of the whole socio-ecological system, but a holistic, interdisciplinary and systematic approach is currently lacking to properly picture the complexity of the Arctic socio-ecological system and the pressures that affect it (Falardeau and Bennett, 2020; Eerkes-Medrano and Huntington, 2021). Identified gaps include for example: the heterogenous knowledge base across the Arctic, limited research on cumulative impacts of climate change with other anthropogenic pressures, a lack of knowledge on some feedbacks between ecosystem services and human well-being, and a lack of projection into the future for human systems (Falardeau and Bennett, 2020). Considering the local and global importance of

Arctic climatic and biological processes, urgent mitigation and adaptive actions are needed (Overland et al., 2019).

Author contributions

BH: Conceptualization, Writing–original draft, Writing–review and editing. BB: Writing–review and editing. FC: Conceptualization, Formal Analysis, Writing–review and editing. SD: Conceptualization, Writing–review and editing. EE: Writing–review and editing. MF: Writing–review and editing. MG: Writing–review and editing. RH: Writing–review and editing. RBI: Conceptualization, Writing–review and editing. LJ: Writing–review and editing. CL: Writing–review and editing. LM: Writing–review and editing. FM: Writing–review and editing. RP: Writing–review and editing. MW: Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Ice algae contributions to the benthos during a time of sea ice change: a review of supply, coupling, and fate

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The polymer-facilitated flux of ice algae on Arctic shelves can initiate benthic activity and growth after the nutritionally constrained winter period. Lipid-rich ice algae are readily consumed by benthos and those entering the sediment can benefit deposit feeders. Ice algae assimilated by benthic organisms cascade up multiple trophic levels within the benthic sub-web, re-entering the pelagic sub web through habitat coupling species. Pelagic predators can have significant ice-algal carbon signals obtained from the benthic compartment. Sympagic-pelagic-benthic coupling on Arctic shelves is expected to weaken with ongoing sea-ice change. This review discusses the phenology, quantity, and quality of ice-algal contributions to coupling, linked to thinning snow and ice cover including multi-year ice replacement. Predicting future coupling between marine sub-webs requires focused research that considers trophic markers of multiple carbon sources.

KEYWORDS

sea ice, ice algae, Arctic change, benthos, sympagic-pelagic-benthic coupling

1 Introduction

Sympagic-pelagic-benthic (SPB) coupling has a key role in the functioning of pelagic and benthic compartments of Arctic marine ecosystems including the trophic interactions of species (i.e., sub-web) within each compartment (Søreide et al., 2013; Wassmann et al., 2020; Amiraux et al., 2023a). This coupling can support the benthic sub-web for two reasons: i) the vertical export of Arctic primary production is highly pulsative, which can limit degradation processes within the pelagic zone, and ii), over >50% of the Arctic marine area consists of shallow Arctic shelves (e.g., <200 m) where coupling occurs more direct than in deep areas. On the Arctic shelves, ice algae grow attached to and within all ice types, first year (FYI) and multi-year ice (MYI) as well as land fast and pack ice. Sympagic production rapidly transitions from a heterotrophic to a diatom-dominated autotrophic community following the end of the polar night (Mundy and Meiners, 2021; Marquardt et al., 2023). Under scenarios of Arctic environmental change, the export of ice algae to the benthos is expected to be less efficient as a greater proportion of organic matter is predicted to be retained within the water column thereby weakening SPB coupling (Wassmann et al., 2011).

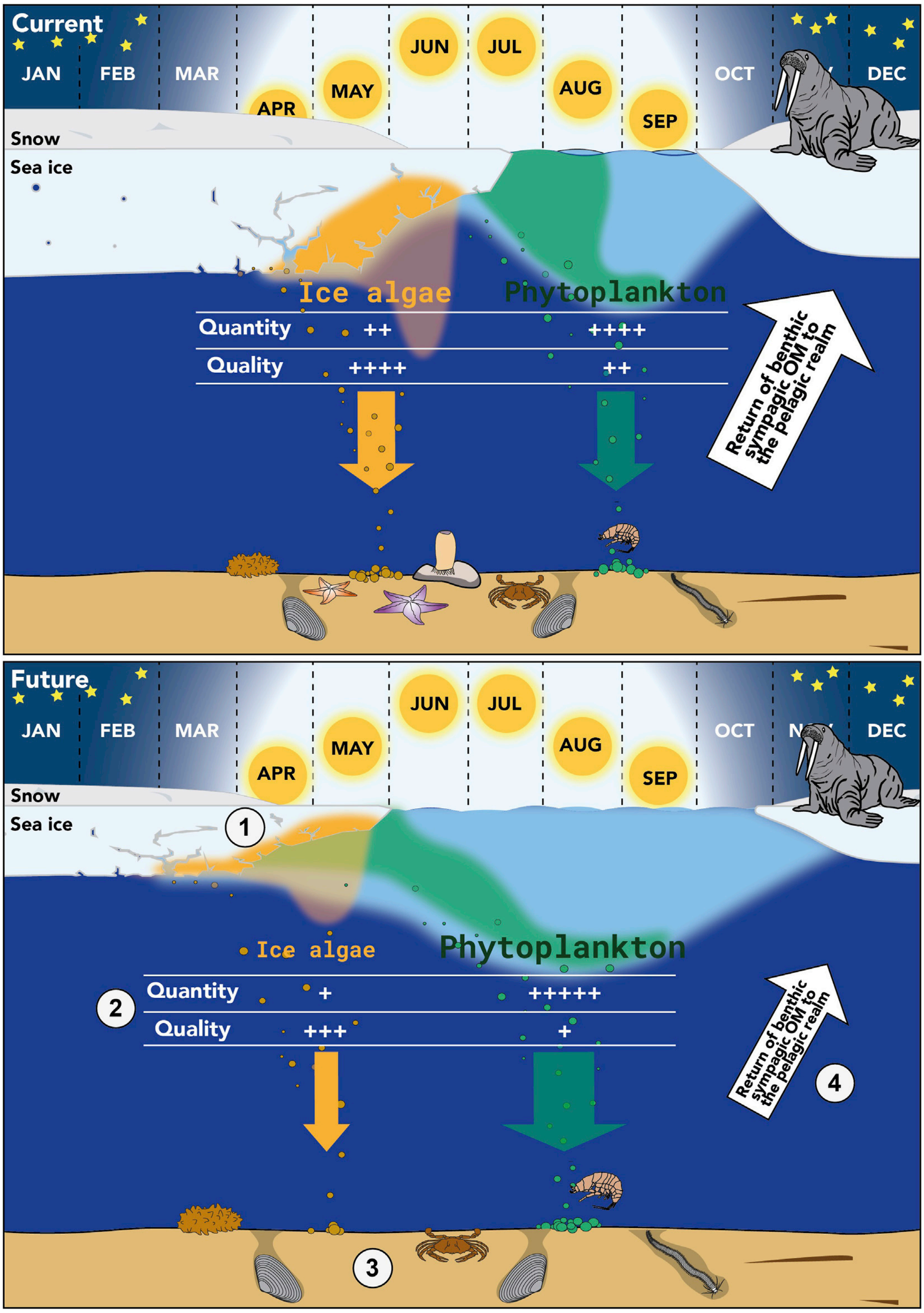
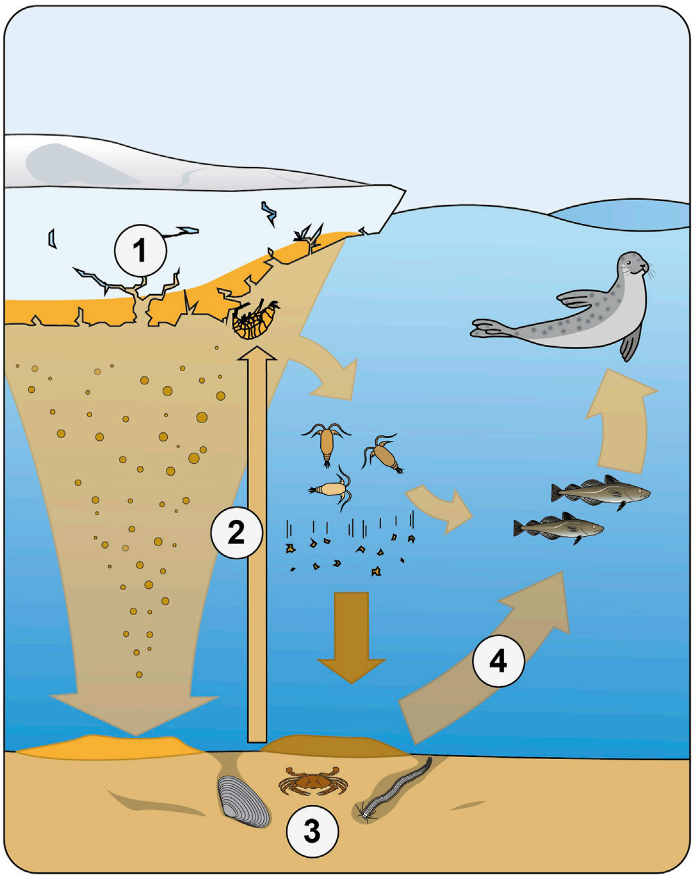


FIGURE 1
In this scenario, future conditions are driven by thinning snow and ice cover that allows light conditions suitable for ice algal and under-ice primary production to occur earlier in the year. Orange and green shading represent ice algal and phytoplankton, respectively, in the euphotic zone (light-blue shading). Numbering is related to the following expected mechanisms of change: 1) increased light availability early in the spring allows for potential co-occurrence of ice algal and under-ice phytoplankton blooms with diminished strength of the spring ice-edge phytoplankton bloom, 2) truncated ice algal bloom could reduce supply (quantity) relative to phytoplankton, and fresher/warmer surface waters could increase algal degradation in the water column reducing the quality of the downward flux, 3) different food sources altering community structure and function, and 4) overall weakened connection between benthic and pelagic food webs due to altered benthic structure.



Processes of priority focus

1. *Sea ice*

Quantification of ice algae's contribution to annual net primary production, incorporating temporal and spatial variability in ice algae production of carbon, EPS, and molecules of nutritional quality (e.g., lipids, carotenoids, AFP). This requires a good understanding of the effect of environemental conditions (e.g. light, temperature, salinity, nutrient, pH) on shaping ice algae community phenology, production and degradation.

2. *Water column*

Quantification of pelagic retention vs export pathways (such as aggregates, colloidal matter aggregation, fecal pellets, and animal migrations), contingent upon characteristics of ice algae production (e.g., quantity, quality, composition). This involves examining the succession of export pathways, fluxes of molecules, and their subsequent participation in organic matter degradation.

3. *Benthos*

Characterizing each ice algae export pathway's contribution to the benthic sub-web structure and carbon storage involves assessing their impact on carbon and nutritional quality molecules upon arrival in sediments, as well as their retention and utilization throughout the year. Understanding benthic organisms' adaptability to diverse food sources (sympagic, phytoplankton, benthic algae and terrestrial inputs) and their resilience to environmental changes, including shifts in biomass, taxonomic, and functional diversity, remains a crucial goal.

4. *Bentho-pelagic connection*

Constrain the intensity of fluxes of C and nutritional molecules from the benthos back to the pelagic sub-web, including how it impacts both pelagic and benthic sub-webs structuration and dynamics. This includes identifying the relative contribution of the different carbon sources including sympagic, phytoplankton, benthic algae (micro- and macro) as well as terrestrial inputs that support pelagic predators through benthic deposition.

FIGURE 2
Conceptual diagram depicting ice algal processes requiring investigation to understand both the present and future significance of ice algae in SPB coupling. Research needs are provided for the sea ice, water column and benthos compartments as well as the re-entry of ice algae to the pelagic compartment (benthos-pelagic connection).

Herein, we present recent (primarily post 2010) assessments of ice algae supply and current insights into the benthic use of ice algae in a time of sea ice change (Figure 1). We acknowledge the importance of ice algae for pelagic diets, including for key species of copepods (Kohlbach et al., 2016; Kohlbach et al., 2021; Koch et al., 2023) and pelagic higher trophic levels such as certain seals (Kunisch et al., 2021; Carlyle et al., 2022) and polar bears (Brown et al., 2018). In this review, we primarily focus on the contributions of ice algae to the benthic sub-web, and the less frequently considered reintroduction of ice algal-derived organic carbon back into the pelagic sub-web. There are significant changes occurring in the Central Arctic Ocean in regards to sea ice and productivity, however, for the purpose of this review, we have chosen to focus on the highly productive shelf seas of the Arctic where there is relatively strong SPB coupling and sea-ice dynamics are shifting rapidly.

2 Ice algae supply – dynamics in the ice and pelagic compartments

2.1 Sea-ice compartment

Ice algae represent a variable and relatively low contribution to total annual net primary production (phytoplankton + ice algae) on productive Arctic shelves in recent periods of sea-ice change (1%–26%, Legendre et al., 1992; Payne et al., 2021). However, the contribution of ice algae to total primary production on Arctic shelves can be significantly higher early in the season when the ice algal bloom occurs prior to an under-ice or spring phytoplankton bloom (e.g., Gradinger, 2009; Hegseth and von Quillfeldt, 2022). From this early season perspective, ice algae can be the primary source of energy for pelagic and benthic consumers and their associated predators (e.g., nearshore amphipods and benthic juvenile polychaetes) (Gradinger and Bluhm, 2010; McConnell et al., 2012; Pitusi et al., 2023). Overall, the relative contribution of ice algal production remains poorly constrained as it cannot be remotely assessed at meaningful seasonal and spatial scales (Lalande et al., 2019; Figure 2).

In the sea ice, ice algae are highly concentrated in the bottom 3–10 cm at the ice-water interface and are easily accessible for ice-associated grazers. During the bloom period the ice algal community consists of diatom-dominated assemblages rich in cellular levels of long chain polyunsaturated fatty acids (LC-PUFA) and antioxidant carotenoids (Harwood, 2019; Amiraux et al., 2021a; Amiraux et al., 2022). Ice algal cell quality is sustained by physiological and metabolic adaptations that maintain favorable micro-environments for growth in the ice

(Boetius et al., 2015), and through the release of exopolymeric substances (EPS: polysaccharides released by ice algae that accumulate as gels around the cells, Krembs et al., 2002; Riedel et al., 2006) that limit abiotic and biotic degradation of the ice algae. The contribution of ice algae to pelagic and benthic sub-webs may, hence, be best represented by measurements of both biomass and diatom composition, rather than production alone (Lalande et al., 2021).

The quantity of ice algae produced in and released from the ice is expected to increase on Arctic shelves with sea-ice change (Leu et al., 2015; Tedesco et al., 2019; Wassmann et al., 2020). Two climate-related processes, driven by the same mechanism are mainly responsible for that. First, replacement of MYI by FYI, and second, an increase in the number of ice algae growing days. Both processes are mechanistically driven by improved light transmission due to thinner snow-on-ice cover and thinner ice (Lim et al., 2022; Figure 1) that facilitates, a) increased growth of ice algae where previously there was expected light limitation, and b) an earlier start of ice algae growth. Light transmittance represents the amount of photosynthetically active radiation (PAR) reaching ice algae after considering the amount of incoming solar radiation as influenced by atmospheric attenuation and Arctic seasonality (i.e., photoperiod), and loss factors related to different snow and ice properties. Very low light transmission (i.e., 0.014%; Lange et al., 2017, or 0.17 μmol photons m^{-2} s^{-1}; Hancke et al., 2018) is required for ice algal growth, highlighting their value as a carbon source beyond when phytoplankton are capable of growth.

2.1.1 Multi-year ice replacement

Seasonal and spatial studies of sympagic communities (Leu et al., 2015; Mundy and Meiners, 2021) and modelling of sympagic primary production under climate change scenarios (e.g., Tedesco et al., 2012; Tedesco et al., 2019; Wassmann et al., 2020; Payne et al., 2021) all indicate increased ice algae supply with MYI replacement and eventual complete MYI loss. This shift has already taken place in many locations including the Chukchi Sea shelf (Payne et al., 2021), currently exceeding ice algae lost due to overall decreases in sea ice extent (Lannunzel et al., 2020; Lim et al., 2022). However, comparative field measurements from the Lincoln Sea shelf found similar ice algal biomass, nutritional quality, and net community production at the bottommost layer of MYI and FYI on Arctic shelves (Lange et al., 2015; Kohlbach et al., 2020; Campbell et al., 2022a) such that on the last remaining MYI-dominated shelf region, the Lincoln Sea, MYI replacement may result in little to no future increase in ice algae supply (Lange et al., 2017; Lange et al., 2019; Campbell et al., 2022b) and controlling factors other than light transmission may be highly relevant in this Arctic shelf region. The extent to which ice algal supply increases requires further research. For example, the photophysiology of ice-algal species could result in a shift in ice-algal community composition, resulting in decreased ice algal quality, rather than increased supply with MYI replacement on the Lincoln Sea shelf (Campbell et al., 2022a; Figure 2).

In pack ice with increasing dominance of FYI, ice algal supply could be affected by increased variability of snow cover on FYI relative to MYI (Lange et al., 2019) as well as increased wind-driven formation of ridges or infiltration layers (Fernández-Méndez et al., 2018; Granskog et al., 2020). Increased wind-driven lead formation has been hypothesized to favor ice algal supply from new ice. However, colonizing species (i.e., inoculum), potentially originating from a dwindling MYI source (Olsen et al., 2017), may not be available for new ice production, or the species that are available may not photoacclimate to the high-light conditions of the new ice (Kauko et al., 2017; Kauko et al., 2019; Campbell et al., 2022a).

2.1.2 Increased growing days

The duration (i.e., number of growing days) of ice algae production is a critical factor to understand variability in the quantity and timing of ice algal supply for SPB coupling (e.g., Beaufort Sea shelf, Dezutter et al., 2019; Dezutter et al., 2021; Nadaï et al., 2021, Chukchi Sea shelf, Selz et al., 2018). This duration varies over geographical scales and relates to sea ice decline. It also relates to snow cover as illustrated in pack ice of the Chukchi Sea shelf where ice algal growth started in mid-May and a growth duration of 70 days was recorded under low snow cover (0.02 m). Nearby, in contrast, growth was delayed by 4 weeks and the magnitude of the ice algal bloom was lower and shortened under high snow cover (0.4 m; Hill et al., 2022). These observations support expectations for a longer growth period and consequently higher ice algal biomass as the Arctic ice snow pack becomes thinner reducing light limitation early in the spring (Wassmann et al., 2020). Currently, however, increased ice algae supply due to overall earlier/longer growing season is not strongly apparent. Between 1985 and 2018, days suitable for ice algal growth (see Lim et al., 2022 for details) are estimated to have increased by ≤ 2.5 days decade^{-1} for the Chukchi, Beaufort and Kara seas, and decreased by < 2 days decade^{-1} for the Barents Sea and Baffin Bay. In the Barents, a shallow seasonally ice-covered shelf sea, any benefits of thinning ice and snow allowing for earlier ice algal growth may have already been erased by early snow or ice melt that precedes or truncates the ice algal bloom (Leu et al., 2015; Onarheim and Årthun, 2017).

If increased light transmission allows for a longer ice algal growth period, nutrient limitation could be an increasingly limiting factor for ice algal supply and quality (Hill et al., 2022). Gravity drainage during ice growth, turbulent diffusion (Duarte et al., 2022; Hill et al., 2022), and forced convection from tides in coastal regions (e.g., Kitikmeot Sea, Dalman et al., 2019) could contribute to relieving nutrient limitation thereby supporting higher ice algal supply for SPB coupling. The resuspension of remineralized nutrients induced by strong tidal mixing could also reduce nutrient limitation in surface waters of the shallow Siberian shelf (Lalande et al., 2014).

Increasing light and heat transmission will also affect ice algal growth at the scale of brine channels. The warming Arctic air (Rantanen et al., 2022) and subsequent warming of snow and ice will change bulk ice properties (e.g., brine volume and bulk salinity; Wang et al., 2020; Wang et al., 2023) altering connections between brine channels and the distribution of habitable space within the sea ice (Leu et al., 2015; Mundy and Meiners, 2021). For example, in land fast FYI of western Baffin Oziel et al. (2019) detected unexpected homogenous vertical profiles of ice brine, potentially due to an early warming and episodic snow melt event that altered brine volume for the rest of the season. Episodic and seasonal warming could thus affect both habitable space and drive earlier termination of the ice algal bloom (Mundy and Meiners, 2021).

2.2 Pelagic compartment

The release of ice algae into the pelagic compartment can typically be detected from February to July on Arctic shelves (Juul-Pedersen et al., 2008; Lalande et al., 2020; Dezutter et al., 2021; Bodur et al., 2023). Peak periods of release and the eventual complete sloughing of ice algae coincide with snow and ice melt (Oziel et al., 2019; Lim et al., 2022; Figure 1A). With continued Arctic change, it is possible that the number of flux events, prior to complete sloughing, could increase due to temperature fluctuations that lead to intermittent snow melt events (e.g., as observed by Oziel et al., 2019 in western Baffin Bay). SPB coupling is expected to weaken due to shorter periods of intense flux (e.g., on Pacific Arctic shelves, Lalande et al., 2021) and increased recycling of material during flux (Fadeev et al., 2021; Koch et al., 2020a; Dybwad et al., 2022; Figure 1B). However, on Arctic shelves where seasonal, and in particular, land fast ice persist, the strength of SPB coupling has not currently been diminished (Kohlbach et al., 2019; Cautain, et al., 2022).

The flux of intact and repackaged (e.g., fecal pellets) ice algae to the seafloor is mediated by herbivorous meiofauna within the sea ice, grazers immediately under the ice that can access ice algal cells within the bottom ice skeletal layer, and further grazing within the epipelagic and deep waters. These grazers can use the lipid-rich ice algae to help fill their polar-night depleted lipid stores and synthesize membranes composed of polar lipids (Leu et al., 2011; Kunisch et al., 2023). Grazing impact by under-ice/pelagic herbivorous fauna is higher than by sea-ice meiofauna (Kohlbach et al., 2016; Gradinger and Bluhm, 2020; Ehrlich et al., 2021). Coupling to pelagic grazers rather than directly to the benthos is dependent on zooplankton abundance at the time of ice algae release (i.e., potential mismatches, Dezutter et al., 2019; Nadaï et al., 2021) and zooplankton species composition (Ehrlich et al., 2020). Pelagic zooplankton can include meroplankton (i.e., planktonic early life stages of benthic invertebrates) such that sympagic support of benthic species is not limited to processes occurring in the benthic compartment. Meroplankton in the water column can graze on ice algae, benefiting the benthos during these critical early benthic life stages (Stübner et al., 2016; Dezutter et al., 2019).

From multi-year studies with variable sea-ice conditions, it is clear that under-ice and pelagic grazers can take advantage of early ice melt and ice algal release, supporting earlier development of copepod nauplii (Søreide et al., 2010; Søreide et al., 2013; Dezutter et al., 2021). Consequently, for an early ice algae release to successfully bypass pelagic grazers, the timing must extend beyond the natural reproductive and feeding plasticity of the pelagic grazers. It is expected that access to ice algae will continue to influence copepods as a trophic nexus for Arctic food web function (Renaud et al., 2018; Ershova et al., 2021), as pulses of both ice algal and phytoplankton production are critical for zooplankton growth and reproduction (Søreide et al., 2010; Kohlbach et al., 2022; Koch et al., 2023).

When ice algae arrive at the seafloor it is generally of higher quality relative to the phytoplankton flux (McMahon et al., 2006; Figure 1A). The pulsative, rapid, flux of ice algae and associated exopolymeric substances at the time of snow or ice melt (Amiraux et al., 2021a; Salter et al., 2023) can evade grazers (Fadeev et al., 2021; Nadaï et al., 2021) and limit degradation processes within the pelagic zone. Consequently, this material provides substantial nutritional contributions to the Arctic benthic sub-web (Juul-Pedersen et al., 2008; Kohlbach et al., 2019; Yunda-Guarin et al., 2020; Amiraux et al., 2021b). The polymer-facilitated sinking of ice algae beyond the euphotic zone limits abiotic (light-induced) degradation of their cellular compounds. Additionally, the presence of exopolymeric substances around ice algae restricts remineralization by bacteria whose remineralization efficiencies are higher than bacteria in the sea ice compartment (Amiraux et al., 2017; Amiraux et al., 2021b; Rontani et al., 2022).

3 Fate of ice algae in the benthic compartment

3.1 Ice algae use in the benthic compartment

The deposition of ice algae during ice melt allows for the intake of carbon that initiates benthic growth and reproduction after the nutritionally constrained winter period (North et al., 2014). Individual diatom cells, ice-algal aggregates, and ice algae in zooplankton fecal pellets that enter the benthic sub-web during the ice algal bloom can invoke rapid benthic feeding responses due to the early accessibility, concentrated deposition, and the high quality of the ice algal material (Renaud et al., 2007; Amiraux et al., 2021a).

During the ice-covered spring on Arctic shelf areas that have long periods of land fast ice coverage, sea ice-derived carbon can contribute a substantial portion (e.g., >75%,) of the benthic carbon pool in both invertebrates and sediments (Kohlbach et al., 2019; Yunda-Guarin et al., 2020). The high quality of ice algae means they are readily consumed and assimilated by the Arctic benthos (McMahon et al., 2006; Amiraux et al., 2021a). Yet, Arctic shelves can have sedimentary stores of sea-ice carbon created during peak ice algal flux (Koch et al., 2023). Although there is limited information about ice algal storage in sediments of Arctic shelves (Figure 2), sediment samples from the southeast Beaufort Sea shelf indicate the presences of ice associated carbon within the upper 70 mm of sediment, with sedimentation rates of ca. 1 mm y^{-1}. This indicates that burrowing infauna could have year-round access to sea-ice carbon deposited from the last century (Koch et al., 2023). The quality of this ice algal source requires further study.

The responsiveness of benthic organisms to ice algae varies, even among taxa with similar feeding behaviors. Amiraux et al. (2021a) showed that, despite both bivalves, *Serripes groenlandicus* and *Mya truncate*, being slow-moving burrowing suspension feeders, their responsiveness to settling primary production differs due to their distinct bioturbation affinities. Unlike *M. truncata*, which induces diffusive mixing bioturbation (Lacoste et al., 2018) and is expected to ingest a variable and non-negligible quantity of buried organic matter, *S. groenlandicus* solely consumes settling organic matter and exhibits a high responsiveness to these inputs. Therefore, since *S. groenlandicus* enables monitoring of SPB coupling, it is regarded as a sentinel of this process (Amiraux et al., 2021a).

Differences in the strength of ice algal signals exist between benthic feeding types as suspension feeders are less reliant on ice algae than deposit feeders (both surface and subsurface; Koch et al., 2020b), likely because the latter can use sediment that may be a reservoir of ice algae material throughout the year. Benthic detritivores can also benefit from utilizing sediments with stores of ice algal material (Amiraux et al., 2021b; Rontani et al., 2022). However, this benefit applies almost exclusively to ice algae exported in aggregate form during peak periods of flux that allow for sequestration/burial. The quality of ice algae exported in fecal pellet form undergoes significant reduction due to grazing and the presence of bacteria from zooplankton, rather than from sea ice, which can effectively degrade the fecal pellet material during sinking (Burot et al., 2021).

3.2 Re-entry of ice algae from the benthic to the pelagic compartment

On Arctic shelves, pelagic and benthic sub-webs share similar structures and complexities, encompassing three to five trophic levels and featuring their respective top predators (Iken et al., 2010; Stasko et al., 2018; Amiraux et al., 2023a). Therefore, the sympagic carbon assimilated by lower trophic level benthic organisms, including deposit or filter feeders, can cascade up multiple trophic levels within the benthic sub-web (Yurkowski et al., 2020; Koch et al., 2021; Amiraux et al., 2023b).

Pelagic and benthic sub-webs are closely linked through habitat coupling species. These species serve as bridges between compartments, facilitating the transfer of organic carbon, including sympagic material, from benthic to pelagic organisms and vice versa. Habitat couplings arises from mobile, opportunistic species (Baustian et al., 2014), which in the Arctic include, but are not limited to, walrus feeding on benthic bivalves (Fisher and Stewart, 1997; Ray et al., 2006; Mann et al., 2020), grey whales feeding primarily on benthic prey in the Arctic (Stewart et al., 2023), the Arctic finned octopods, shorthorn sculpin and Greenland halibut (demersal fish) feeding on both benthic and pelagic prey (Giraldo et al., 2018; Landry et al., 2018; Golikov et al., 2023), as well as numerous mobile invertebrates such as cumaceans and amphipods. Sympagic carbon that moves through the benthic sub-web can re-enter the pelagic sub-web at various trophic levels, ultimately reaching pelagic apex predators. Evidence for this was given by Amiraux et al. (2023a) who demonstrated that the relatively high dependence of Arctic marine mammals (53% ± 22% of body carbon) on sympagic carbon in the coastal area of Southampton Island (Hudson Bay, Nunavut) results from their direct or indirect (trophic cascade) use of sympagic carbon from the benthic compartment.

This re-entry of ice algae to the pelagic sub-web can vary over time and latitude. For example, despite a sea ice decline of 18% in both mid- and high-latitudes Canadian Arctic shelves (Foxe Basin and Jones Sound, respectively) from 1982 to 2016, Yurkowski et al. (2020) found that walrus sympagic carbon presence, resulting from a benthivorous diet, remained high (e.g., 89%–98%) at high latitudes but had decreased by 75% at mid-latitudes. For these walrus, ice algae dependency has already weakened at the lower latitudes such that further ice decline, reducing ice algal supply, could have a greater impact on the high latitude walrus. Decoupling from ice algae is not necessarily detrimental for higher trophics relying on the benthic compartment for their diet due to adaptability facilitated by flexible habitat use or migration.

4 Future perspectives for the benthic sub-web

Ice algae currently contribute to the growth and reproduction of species in the pelagic and benthic sub-webs. Therefore, it is reasonable to expect that any decline or shift in ice algae supply, including shifts in quality, could induce a restructuring of Arctic food webs (Moore and Stabeno, 2015). This restructuring will be driven by directional regulations within the Arctic marine ecosystem. Variations in ice algae supply will exert an influence on the benthic sub-web through a bottom-up regulatory process. This influence will propagate upward, impacting the benthic top-down controls, potentially initiating trophic feedback within the pelagic realm. Although not yet documented, less ice algae within the benthic sub web could ultimately impact benthic predators (e.g., sea stars, Amiraux et al., 2023b), thereby reducing predation pressure on benthic prey that support pelagic predators (i.e., bivalves for walrus, Yurkowski et al., 2020).

Arctic fauna can rely on multiple carbon sources including ice algae, phytoplankton, benthic algae and terrestrial inputs (Bell et al., 2016; Gaillard et al., 2017; Harris et al., 2018). Omnivory and trophic plasticity contribute to the stability of a food web in the event of changing food supply (Bridier et al., 2021; Yunda-Guarin et al., 2022; Yunda-Guarin et al., 2023). Therefore, while not all benthic species may react equally (Bridier et al., 2023), it is probable that many species will be able to adapt to changing ice algal supply and organic matter quality. The Arctic's complex food webs highlight the adaptability of Arctic benthic species to diverse food sources that are supplied in abundance (Wei et al., 2020). However, sea ice change and the potential decrease in SPB coupling efficiency (Zhulay et al., 2023), will inevitably change the composition of food sources, potentially impacting benthic community functioning, including endemic species (Figure 1B). These assumptions are supported by Yunda-Guarin et al. (2023), showing that a diversity of food resources facilitate the development of epibenthic communities characterized by a more complex structure (more trophic levels) and higher interconnectedness (larger individual niche size) compared to trophic structures based on lower food diversity. The extent to which benthic biodiversity and/or biomass responds to changing food source diversity and shifting predator-prey interactions in different regions of Arctic shelves requires further, mechanistic study (Figure 2).

5 Conclusion

The impact of global warming on ice algae supply has already been observed in many Arctic regions, and future changes in ice-algal production will be closely linked to snow cover and ice thickness. These factors influence the availability of light for ice algal growth, affecting the onset and duration of the bloom, community composition, succession, degradation from both abiotic (light-induced, autoxidative) and biotic (bacterial mineralization, zooplankton grazing) processes and ultimately nutritional quality of the ice algae. Consequently, the quantitative and qualitative contribution of ice algae to SPB coupling has and will be altered. Whether and how this anticipated loss for the benthos gets compensated for is rather unclear, though recent work suggest that other carbon sources such as microphytobenthos, macroalgae and terrestrial carbon may play increasing roles on Arctic shelves (Krause-Jensen et al., 2020; Attard et al., 2024).

Given the pivotal role of light as an abiotic driver of SPB coupling, there is a current imperative for research focused on identifying changes in ice algae production, degradation, and quality in response to light-driven phenology (Figure 2). This involves examining morphological aspects like algal cell size and shape, as well as physiological traits such as exopolymer production. These characteristics are influenced by microalgal phenology and contribute to the sinking of algal material out of the euphotic zone. Additionally, the export pathways should be better constrained through a deeper understanding of the contribution of ice algae export from aggregates, fecal pellets, migrations and heteroaggregation of the colloidal fraction (Figure 2). Furthermore, exploring lipid content throughout ice algal succession, including variations in type and quantity, and examining how both abiotic and biotic processes influence these contents, is crucial in determining the flux of high-quality organic matter to the benthic environment.

In the benthic compartment, a primary focus should center on understanding the spatial and temporal variability of ice algal contribution compared to other carbon sources (Figure 2). This understanding could be advanced by studies of species acting as sentinels for the SPB coupling, along with a comprehensive investigation of their trophic links. Moreover, it is imperative to improve quantification of how changes in ice algae, encompassing both quantity and quality, will impact the trophic structure and functioning of the benthic sub-web and, consequently, extend back to the pelagic sub-web. We suggest that the resolution of such a challenge should rely on a multitude of trophic markers (e.g., fatty acids, highly branched isoprenoids, stable isotopes) and approaches (e.g., quantification of ice algae-derived carbon, isotopic niche and redundancy) as well as using integrating models (e.g., Bayesian models) to comprehensively assess the current and future contribution of ice algae and alternate carbon sources to the Arctic marine ecosystems.

Author contributions

AN: Conceptualization, Data curation, Funding acquisition, Project administration, Writing–original draft, Writing–review and editing. BB: Conceptualization, Writing–review and editing. TJ-P: Writing–original draft, Writing–review and editing. DK: Writing–review and editing. MR: Writing–review and editing. DS: Writing–review and editing. RA: Conceptualization, Visualization, Writing–original draft, Writing–review and editing.

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Dust in the Arctic: a brief review of feedbacks and interactions between climate change, aeolian dust and ecosystems

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Climatic feedbacks and ecosystem impacts related to dust in the Arctic include direct radiative forcing (absorption and scattering), indirect radiative forcing (via clouds and cryosphere), semi-direct effects of dust on meteorological parameters, effects on atmospheric chemistry, as well as impacts on terrestrial, marine, freshwater, and cryospheric ecosystems. This review discusses our recent understanding on dust emissions and their long-range transport routes, deposition, and ecosystem effects in the Arctic. Furthermore, it demonstrates feedback mechanisms and interactions between climate change, atmospheric dust, and Arctic ecosystems.

KEYWORDS

dust, climate, arctic, ecosystem, atmosphere

1 Introduction

During the last 4 decades, the warming in the Arctic has been nearly four times faster than the overall warming in the rest of the Earth (Rantanen et al., 2022), a phenomenon called Arctic amplification (AA) (Ghatak and Miller, 2013; Gong et al., 2017; Gaston, 2020; Rantanen et al., 2022). There are several Arctic-specific feedback processes (Arnold et al., 2016), which are both a consequence and a driver of the observed AA (e.g., Dai et al., 2019; Serreze et al., 2009). However, warming is not homogeneous across the Arctic, but instead dependent on scale, location and season (Westergaard-Nielsen et al., 2018; You et al., 2021). For example, in Greenland, warming has been largest in the west (Abermann et al., 2023), yet many weather stations along the Greenlandic coast show no clear trend in increasing surface temperatures (Cappelen et al., 2021). On a regional scale, areas in the Eurasian sector of the Arctic Ocean have warmed even up to seven times as fast as the globe (Rantanen et al., 2022).

The United Nations (UN) General Assembles and the UN Coalition to Combat Desertification (UNCCD) (UNEP, 2016; UNCCD, 2022) reiterated that the global frequency, intensity, and duration of Sand and Dust Storms (SDS) have increased in

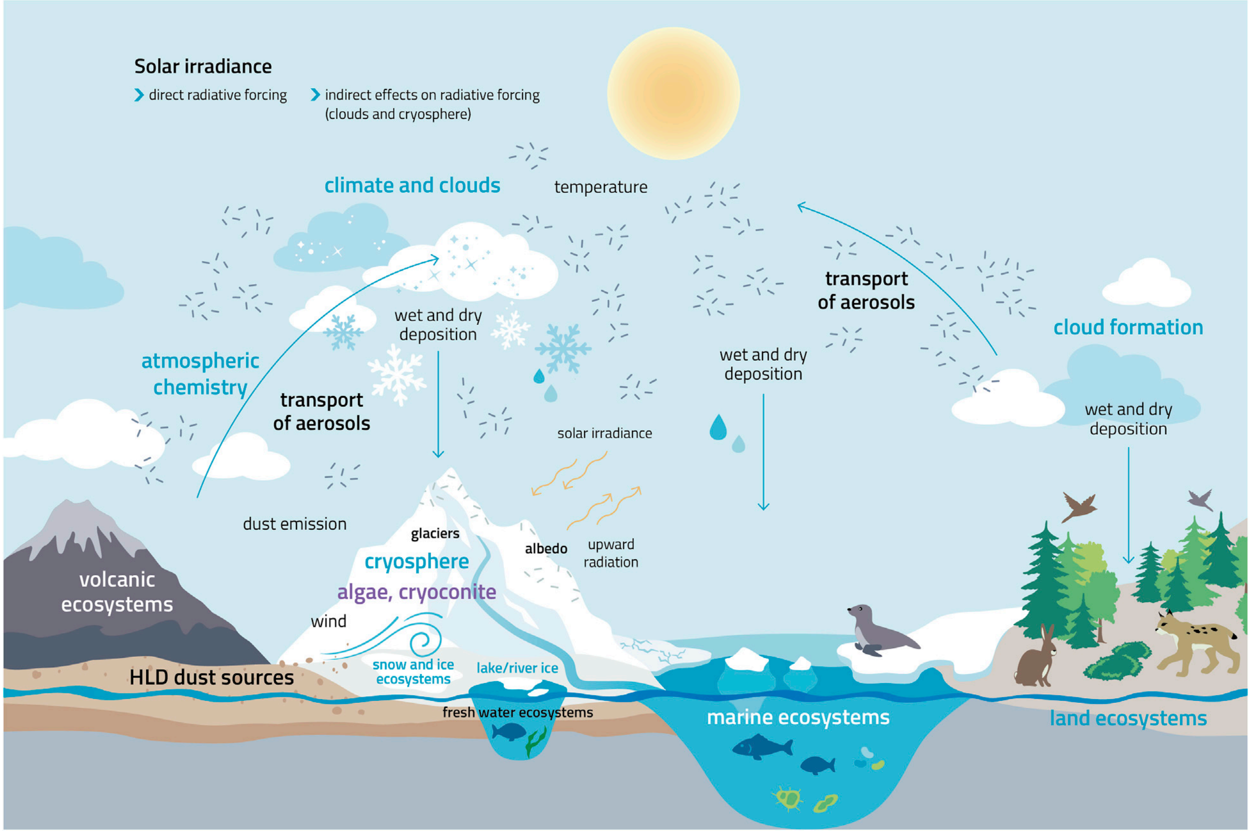

FIGURE 1
Climate and ecosystem related interactions of aeolian dust in the Arctic. These include direct radiative forcing (absorption and scattering), indirect radiative forcing (clouds and cryosphere), and effects on atmospheric chemistry and on terrestrial, marine, fresh water, and cryospheric ecosystems. In addition, semi-direct effects of dust on meteorological parameters (e.g., atmospheric pressure, temperature profile and cloudiness) affect the radiative balance in the atmosphere. Dust deposition can supply ecosystems with macro and micronutrients, acid-neutralizing capacity, heavy metals, microbes and other biota, synthetic materials, and light-absorbing particles.

the last decade and that SDS have natural and human causes that can be exacerbated by desertification, land degradation, drought, biodiversity loss, and climate change. UNCCD and FAO (2024) also highlighted that emerging SDS source areas have been associated with the warming of the Arctic and high latitude regions, the seasonal or permanent drying of inland waters and river deltas, or are following large-scale deforestation and wildfires, or even the ploughing of a single field. Loss of snow cover, retreat of glaciers, and increase in drought intensity due to climate change can lead to surface conditions that increase the likelihood of creation, continuation and expansion of SDS source areas.

Aeolian dust refers to particles that originate from the Earth's surface and are light enough to be suspended by wind and turbulence in the atmosphere, carried by the wind for significant distances, but heavy enough to be deposited by sedimentation. Additionally to air quality impacts, dust affects both weather and climate, but is also driven by those: dust life cycle, i.e., emissions, atmospheric transport, and deposition, are dependent on soil properties, weather and climatic conditions. Long-range transport (LRT) of dust to the Arctic and impacts of high-latitude and Arctic dust emissions is an emerging topic, also recognized as an important climate driver in the Polar Regions (IPCC, 2019; AMAP Arctic climate change update 2021; IPCC, 2021; IPCC, 2023). Each component of the dust cycle is influenced by natural processes (e.g., desertification, permafrost thaw, glacier melt and retreating snow-covered surfaces in general) and anthropogenic activities (e.g., degradation of agricultural and eroded lands, deforestation, construction, mining, and landfills). The dust cycle facilitates the exchange of particles among Earth's major systems, e.g., atmosphere, lithosphere, hydrosphere, cryosphere, and biosphere, enabling dust to traverse ecosystems. A well-known example is Saharan dust fertilizing Amazonia by providing annually about 22,000 tonnes of phosphorus and other nutrients for the area (Yu et al., 2015). Even Greenland's ice-free areas have long been identified as locally important dust sources (Hobbs, 1942; Wientjes et al., 2011; Bullard and Mockford, 2018).

Aeolian dust, depending on the disciplinary context, can refer to all primary emitted particles to the atmosphere from the Earth's surface, or only to the inorganic (mineral) fraction of dust. Dust can also contain organic (e.g., soil organic matter, bacteria, fungi, fungi, algae, pollens, spores, insect and plant fragments), synthetic substances (e.g., fertilizers and microplastics), and adsorbed nutrients and heavy metals. During the transport of dust particles in the atmosphere, they can also undergo chemical and physical transformations, whereas labile fractions of nutrients and metals can be found within the organic fractions (Brahney et al., 2024). For clarity, dust is defined here as a terrestrial sediment, sized <100 µm which is transported in aeolian suspension.

We focus here on interactions between climate, the life-cycle of dust, and ecosystems (flora and fauna), in the northern high-latitudes ≥50°N and Arctic ≥60°N (Figure 1). Climate and ecosystem relevant feedbacks include direct radiative forcing (absorption and scattering) and indirect radiative forcing (modified cloud properties through seeding cloud droplets and ice crystals) and any kind of dust impact by dry and wet deposition on snow- and ice-covered surfaces. Atmospheric chemistry is affected since dust can serve as a sink for radiatively important atmospheric trace gases. Terrestrial, marine, freshwater, and cryospheric ecosystems can show increased productivity and carbon uptake through deposition of dust delivering nutrients like iron and phosphorus. Scattering of solar shortwave (SW) radiation cools the climate, whereas SW absorption warms the climate. Both the scattering and absorption of terrestrial longwave (LW) radiation warm the climate as both decrease the transparency of the atmosphere to terrestrial LW radiation (Kok et al., 2023). The semi-direct effect (Hansen et al., 1997) represents the thermodynamic effect of dust, absorbing solar radiation, on meteorological parameters (e.g., atmospheric pressure, temperature profile and cloudiness) which in turn affects the radiative balance in the atmosphere. It tends to increase the static stability of the atmospheric boundary layer and suppress convection and cloud formation, so as a result allows more solar radiation to penetrate to the surface and counteracts the direct effect.

Dust provides a positive radiative forcing on the order of a few tens of Wm-2 at the top of the atmosphere through the shortwave and longwave scattering and absorption, and the albedo decreases of snow and ice surfaces. High-latitude dust contributes significantly to this forcing, especially during summer and autumn (Kylling et al., 2018; Markowicz et al., 2022). High-latitude emissions thus lead to highly effective regional climate forcing (Kylling et al., 2018). In contrast, high-latitude dust constitutes a negative forcing on the order of a few tenths of Wm-2 due to depletion of the liquid water path and change of cloud phase of lower level mixed-phase clouds (Shi et al., 2022; Kawai et al., 2023). Clouds at high latitudes frequently persist in a supercooled state (Murray et al., 2021). *In-situ* observations and models have shown that HLD serving as a highly potential INP converts cloud droplets to ice crystals, leading to dramatic reduction of a cloud's liquid water content while reducing its albedo and exposing the surface underneath. Increased downward longwave radiation results in positive climate feedback. HLD has been shown to be highly effective biogenic ice-nucleating material while dust from the most prominent low latitudes is abiotic (Tobo et al., 2019; Meinander et al., 2022). During transport, dust scatters and absorbs SW and LW radiation, modifies cloud properties, mixes with other aerosols and serves as a sink for radiatively important atmospheric trace gases (Kok et al., 2023; Mahowald, 2011). When deposited, dust darkens snow and ice and stimulates ecosystem productivity and carbon dioxide drawdown through the delivery of iron and phosphorus. These mechanisms both cool and warm the climate system, the net effect of which is uncertain and accordingly, the sign and magnitude of radiative perturbations arising from increases in dust since the pre-industrial era are also uncertain. This means that it is unknown whether global dust changes have enhanced or opposed anthropogenic warming (Kok et al., 2023).

2 Dust sources

The Earth's largest and most persistent dust sources are known to locate in the Northern Hemisphere, mainly in a broad "dust belt" that extends from the west coast of North Africa, over the Middle East, Central and South Asia, to China (Prospero et al., 2002). A new dust source area appeared recently at the bottom of the Aral Sea that dried out during the last 50 years (Chen et al., 2022). Dust from low latitudes also reaches the Arctic through atmospheric transport. There are, however, important large dust sources also in the Southern Hemisphere, located in Australia, Africa and South America. Dust emission sources located at the northern high latitudes have been added to the discussion more recently (Bullard et al., 2016; Meinander et al., 2022), where the term for northern "high latitude dust" (HLD) has been defined to consider high latitudes as areas ≥50°N (Bullard et al., 2016). "Arctic dust," in turn, has been used for dust emissions from latitudes ≥60°N (e.g., Meinander et al., 2022; Matsui et al., 2024). Moreover, Meinander et al. (2022) have recently presented evidence for a "northern HLD belt", defined as the area north of 50° N, with a "transitional HLD-source area" extending at latitudes 50°–58° N in Eurasia and 50°–55° N in Canada and a "cold HLD-source area" including areas north of 60° N in Eurasia and north of 58° N in Canada, with currently "no dust source" area between the HLD and low-latitude dust (LLD) belt, except for British Columbia.

Bullard et al. (2016) have estimated that high-latitude sources cover >500,000 km^2. Meinander et al. (2022), in turn, presented source intensity (SI) values, which show the potential of soil surfaces to act as sources for dust scaled to values from 0 to 1 concerning globally most productive sources, using the Global Sand and Dust Storms Source Base Map (G-SDS-SBM, Vukovic, 2019). They estimate that northern high-latitude land areas with higher (SI ≥ 0.5), very high (SI ≥ 0.7), and the highest potential (SI ≥ 0.9) for dust emission cover >1,670 000 km^2, >560,000 km^2, and >240,000 km^2, respectively. In the Arctic HLD region (≥60° N), in turn, land area with SI ≥ 0.5 is 5.5% (1,035 059 km^2), area with SI ≥ 0.7 is 2.3% (440,804 km^2), and area with SI ≥ 0.9 is 1.1% (208,701 km^2). Hence, the estimates from Bullard et al. (2016) agree with the estimate of Meinander et al. (2022) of very high potential area for dust emissions, both estimating an area of >500,000 km^2.

Typical high latitude dust emissions originate from ice-proximal areas, including glacier forefields and riverbeds, glacial lake areas, sandy beaches and deserts, and large old pumice areas around volcanoes (Bullard and Austin, 2011; Bullard and Mockford, 2018; van Soest et al., 2022; Bullard et al., 2023; Baddock et a. 2024). For example, a recent study showed that dust emissions occur in the High Arctic desert environment of Peary Land, NE Greenland, indicating that aeolian dust emissions are likely a ubiquitous phenomenon along the majority of proglacial river systems draining the Greenland Ice Sheet (Baddock et al., 2024). In the northern high latitudes, Iceland has been identified as the most active source for dust emissions (Bullard et al., 2016; Meinander et al., 2022). When ice and snow melt or permafrost thaws as a consequence of warming, new land areas will be revealed, and these appear as potential new dust emission sources (Meinander et al., 2022).

3 Dust emissions and timing

There has been great interest in understanding the role of aeolian dust emissions in climate by modulating solar radiation and cloud properties (e.g., Barr et al., 2023). Bullard et al. (2016) estimated that HLD sources emit at least 80–100 Tg yr−1 of dust to the atmosphere (~5% of the global dust budget), which they expect to increase under future climate change scenarios. Other model results by Groot Zwaaftink et al. (2016) and Meinander et al. (2022) indicate that Arctic dust emissions amount to roughly 1%–3% of global dust emissions. In addition, it has been estimated that 1.5–31 Tg of dust aerosols are transported from lower latitudes to the Arctic region (Böö, 2023). Moreover, dust emissions have increased in the Arctic during 1981–2020 according to model simulations by Matsui et al. (2024).

The northern hemisphere dust emission rates vary in response to environmental conditions, such as seasonal variation in wind shear, soil moisture content, snow cover and temperature, where, e.g., snow cover can decline dust emissions (Bullard et al., 2016; Di Biagio et al., 2018; Meinander et al., 2022). However, Arctic winter storms and snow-dust storms occur in Iceland (Dagsson-Waldhauserova et al., 2015; Dagsson-Waldhauserova et al., 2019). In 1949–2011, Iceland had on average 34–135 dust days per year (days per year in Iceland with conventionally used synoptic codes for dust observations) with the highest frequency in winter and spring in the southern parts of Iceland, and in May-October in the Northeast Iceland (Dagsson-Waldhauserova et al., 2013; 2014). Similar frequencies as in the NE Iceland have been reported from Alaska and Greenland (Crusius et al., 2011; Bullard et al., 2023). The long-term seasonal variations of local dust storms in Iceland during 1949–2011 (Dagsson-Waldhauserova et al., 2014), reveal that in southern Iceland March, April and May are the months where dust events have been most frequent, while in NE Iceland they occur mainly in summer and early autumn (May–September).

4 Dust transport paths

East Asia and Africa are important sources of dust observed at higher latitudes in the Arctic, as confirmed by analysis of ice cores, aerosol samples, satellite observations and numerical modeling (e.g., Groot Zwaaftink et al., 2016; Đorđević et al., 2019). Dust has been suggested to travel more than 20,000 km from a Chinese origin to the French Alps (Grousset et al., 2003), and over 5,000 km from Africa to Finland with water vapor transport as the driving force (Meinander et al., 2023). In fact, during the last 4 decades, 78% of atmospheric rivers occurring over northwest Africa have been associated with extreme dust events over Europe (Francis et al., 2022). LRT dust in Finland has been found to originate from the Sahara, Aral-Caspian and Middle East (Varga et al., 2023). Records of LRT dust reaching Finland during 1980–2022 (Varga et al., 2023), reveal that March, April and May are the months where dust events have been most frequent. Saharan dust transport across the eastern side of the North Atlantic Ocean towards the Arctic, associated with ice melt over the deposition area in Greenland, was reported by Francis et al. (2018).

Dust from high latitudes is often transported over shorter distances in the Arctic (Groot Zwaaftink et al., 2016), but it can also reach lower latitudes (Crusius et al., 2011; Cvetkovic et al., 2022). In Svalbard, dust emissions from a proglacial river plain (Adventdalen) indicate the presence of a highly emissive source for sediments in such environments (Rasmussen et al., 2023). Iceland receives long-range transported Saharan dust once or twice a year on average (Varga et al., 2021), while local Icelandic dust has been collected, e.g., in Svalbard (Moroni et al., 2018). Long-term model simulations have confirmed large amounts of Icelandic dust transport to the ocean, but also to Greenland, Svalbard and Europe (Groot Zwaaftink et al., 2017). Svalbard, in turn, has been reported to receive LRT dust mostly from Africa, Asia and Eurasia (Groot Zwaaftink et al., 2016; Di Mauro et al., 2023).

5 Dust deposition and impacts on ecosystems

5.1 Deposition

Aeolian dust is deposited on soils, lakes, streams, seas and oceans, on ice and snow, as well as on vegetation, across the Arctic region (Bowen and Vincent, 2021). Ecosystem implications are highly dependent on the dust amounts and specific particle properties, e.g., mineral composition (Baldo et al., 2020; Varga et al., 2021) and nutrient concentrations (Arnalds et al., 2014) and timing of deposition. For wet and dry dust deposition, the ecosystem effects may vary depending on the location, season and geographical scale (e.g., Meinander et al., 2022; 2023). With increasing altitude, contributions from remote sources, especially Africa and Asia, are increasing and LRT dust therefore becomes more important for dust loads in the Arctic (Groot Zwaaftink et al., 2016). Kavan et al. (2024), in turn, have reported a correlation between dust deposition and the altitude of sampled dust in Svalbard stating that with higher altitude lower deposition amounts were found, implying a high probability for LRT.

For global dust emissions and their Arctic deposition, Meinander et al. (2022) calculated that when total annual global dust emissions for <30 µm particles are 3,000 Mt (megatonnes), then deposition on Arctic snow is 7.6 Mt, on Arctic Sea ice 4.7 Mt and on Arctic Sea surface 21 Mt. In comparison, Arctic dust with a total emission of 30 Mt has 4 Mt deposition on Arctic snow, 3 Mt on Arctic sea ice, and 12 Mt on Arctic Sea surface. Simulations by Groot Zwaaftink et al. (2016) on the other hand, indicated that over 83% of dust deposited on Arctic sea ice originates from HLD sources, since due to limited convection, larger particle sizes and enhanced efficiency of removal, dust emitted in these source regions is mostly deposited closer to the source. Also, for coarse particles, one could expect an increasing contribution from nearby sources. Moreover, Icelandic top sediments show coarser particle size distributions compared to the high dust-emitting crusts from mid-latitude arid regions (González-Romero et al., 2024).

5.2 Dust contributions to ecosystems

Dust can affect the ecosystems through numerous mechanisms, for example,:

1. *Dust as a light absorbing particle in cryospheric ecosystems.* Dust can impact via an "ice-albedo feedback", which increases cryospheric melt and the effective snow grain size as a result of a darker (low albedo) surface, and may shorten the melt period and influence water availability (Painter et al., 2012; Meinander et al., 2013; Skiles et al., 2018; Boy et al., 2019). In contrast, insulation and prevention of snow and ice from melting is observed with a sufficiently thick layer of particles (Wittmann et al., 2016). Natural debris flows have also prevented large ice masses from melting in Iceland (Ben-Yehoshua et al., 2020; Kavan et al., 2024). The cryosphere also includes cryoconite (Di Mauro et al., 2017), a mixture of mineral and organic material covering glacial ice, playing important roles in biogeochemical cycles and lowering the albedo of a glacier surface formed by dust, small rock particles, soot, and microbes (Piotr et al., 2022).
2. *Dust as a nutrient and factor affecting atmospheric carbon dioxide fixation.* Dust can supply macro- and micronutrients to marine (Gaston, 2020; Meinander et al., 2022), freshwater (Scholz and Brahney, 2022), and terrestrial ecosystems (Aciego et al., 2017; Ponette-González et al., 2018). Dust can enrich surface soils with a wide range of nutrients (P, K, Mg, Na, Ca, Fe, Cu, Mn and Mo) and some elements have an indirect effect on the availability of other elements (McTainsh and Strong, 2006). HLD of volcanic origin, e.g., from Iceland and Alaska, is rich in bioavailable iron with significantly higher solubility (up to 30%) than the typical low latitude dust with low pH (Baldo et al., 2020). This can impact primary productivity and nitrogen fixation in the North Atlantic and Pacific Oceans and lead to additional carbon uptake. Iron deposition on the ocean can be higher around Iceland than west of Africa (Arnalds et al., 2014). Impacts of phosphorus minerals on ice algal blooms have also been documented (McCutcheon et al., 2021). The highest dust deposition rates in Iceland have been found in the areas with the highest densities of bird nests (Gunnarsson et al., 2015).
3. *Dust is a factor affecting acidity.* Dust has been found to contribute to the alkalization of precipitation pH (Grider et al., 2023), and to altering the surface water pH, depending on the chemical composition (Brahney et al., 2024).
4. *Dust as a distributor of biota.* Dust can deliver microorganisms (Dastrup et al., 2018), microfauna (Rivas Jr et al., 2018) and organic material (Field et al., 2010) to the recipient ecosystems. Diatoms and organic material can be transported during snow-dust storms in Iceland (Dagsson-Waldhauserova et al., 2015).
5. *Dust as a provider of toxins.* Dust can bring toxins to the ecosystems (Fubini and Fenoglio, 2007).
6. *Dust as a contributor for soil formation.* Dust can be an important contributor to pedogenesis, i.e., the phenomenon leading to soil formation (Munroe et al., 2024).
7. *Dust as a modifier of atmospheric radiation, clouds and precipitation.* Dust aerosols absorb and scatter solar irradiance (Kok et al., 2023) and act as cloud condensation nuclei (CCN) and ice nucleating particles (INPs) (Creamean et al., 2022; Barr et al., 2023; Kok et al., 2023) having a direct and indirect effect on Arctic climate. Varga et al. (2023) found that during 1980–2022 all winter LRT dust events reaching Finland were associated with freezing rain. Indirect ecosystem effects of dust in the Arctic ecosystems include impacts on the availability of light and water (atmospheric radiation, cloud formation and precipitation).

Anderson et al. (2017) have stated that dust input to soils and lakes may have substantial ecological impacts in Greenland, while in Iceland, deforestation of large native woodlands by Vikings only up to 120 years after the settlement led to almost total elimination of forests (Aradottir and Arnalds, 2001). Final ecosystem collapse occurred with the arrival of colder climate and massive erosion where the vegetated ecosystem was turned into desert, existing until today in large parts of Iceland and forming a large source of high-latitude dust.

6 Discussion and future perspectives

This brief review examines feedback and interactions between climate change, dust life-cycle, and ecosystems in northern high-latitudes and the Arctic. The multiple mechanisms related to dust emissions, transport and deposition both cool and warm the climate system, with an uncertain net effect. Dust plays a significant role in terrestrial and aquatic ecosystems, e.g., by providing nutrients, and with impacts on the availability of light and water. Due to Arctic warming, HLD dust emissions can be expected to increase. For example, Matsui et al. (2024) found that the globally simulated dust emission flux in the Arctic (>60°N) increased by 20% from 1981 to 1990 to 2011–2020.

Reanalysis data sets, which combine modeling and remote sensing data, estimate that 1.5–31 Tg of dust aerosols are transported from lower latitudes to the Arctic region (Böö, 2023). The contributions of LLD and HLD complicates the interpretation of how much different sources contribute to the dust loadings and corresponding temporal and spatial deposition patterns. Another challenge is that low latitude dust source emissions of road and agricultural dust is barely characterized at all (Kristensson et al., 2024).

In future research, cross-sectional networking of atmospheric high latitude dust experts (measurement, modeling and remote sensing communities) with soil and cryospheric experts should be utilized for identification of current and future dust source locations and particle properties (on the ground, when windlifted, during transport and when deposited). Optical properties of various dust types need to be investigated to estimate their climatic significance. For example, for dark Icelandic dust, the imaginary part of the complex refractive index (i.e., absorption properties) at 660–950 nm has been found 2–8 times higher than most of the northern Africa and eastern Asia dust samples (Baldo et al., 2023), and dust deposition amounts in the Arctic have been estimated larger in terms of mass than those of BC (Meinander et al., 2022), and the absorption potential of Icelandic dust similar to BC (Peltoniemi et al., 2015).

In the future, dust emissions from northern soils are expected to increase, e.g., due to increase of bare ground as a result of glacier retreat, permafrost thaw and melt of snow- and ice-covered surfaces. There is an urgent need also for a better understanding (e.g., Matsui et al., 2024; Romanello et al., 2024) of the complex counterbalancing feedbacks related to Arctic dust, e.g., shortwave and longwave cloud radiative effects (CREs), induced by the increase in temperature (temperature feedback) and by the increase in dust emission flux and atmospheric burden (emission feedback). For example, Matsui et al. (2024) found that an increase in dust emission weakened the sensitivity of ice nucleation in Arctic lower tropospheric clouds to warming by 40%, as compared to the case without Arctic dust emission increase.

Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Vulnerability of Arctic-Boreal methane emissions to climate change

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The rapid warming of the Arctic-Boreal region has led to the concern that large amounts of methane may be released to the atmosphere from its carbon-rich soils, as well as subsea permafrost, amplifying climate change. In this review, we assess the various sources and sinks of methane from northern high latitudes, in particular those that may be enhanced by permafrost thaw. The largest terrestrial sources of the Arctic-Boreal region are its numerous wetlands, lakes, rivers and streams. However, fires, geological seeps and glacial margins can be locally strong emitters. In addition, dry upland soils are an important sink of atmospheric methane. We estimate that the net emission of all these landforms and point sources may be as much as 48.7 [13.3–86.9] Tg CH_4 yr^{-1}. The Arctic Ocean is also a net source of methane to the atmosphere, in particular its shallow shelves, but we assess that the marine environment emits a fraction of what is released from the terrestrial domain: 4.9 [0.4–19.4] Tg CH_4 yr^{-1}. While it appears unlikely that emissions from the ocean surface to the atmosphere are increasing, now or in the foreseeable future, evidence points towards a modest increase from terrestrial sources over the past decades, in particular wetlands and possibly lakes. The influence of permafrost thaw on future methane emissions may be strongest through associated changes in the hydrology of the landscape rather than the availability of previously frozen carbon. Although high latitude methane sources are not yet acting as a strong climate feedback, they might play an increasingly important role in the net greenhouse gas balance of the Arctic-Boreal region with continued climate change.

KEYWORDS

methane, permafrost, wetlands, lakes, gas hydrates, arctic ocean, Arctic-Boreal region

1 Introduction

The sweeping landscapes of the Arctic-Boreal region harbor a wide diversity of environments that are sources of methane to the atmosphere, including numerous wetlands and lakes, as well as ocean sediments. These sources are influenced by the presence of permafrost, and as the climate warms this perennially frozen ground may thaw. The soils of the permafrost region contain more than twice the amount of carbon present in the atmosphere, and if only a fraction of this is released as methane it could act as a significant feedback on the global climate (Schuur et al., 2022). Permafrost thaw may also impact surface wetness, altering the environmental conditions for methane formation (Nauta et al., 2014), or it might alter transport pathways up to the surface when the

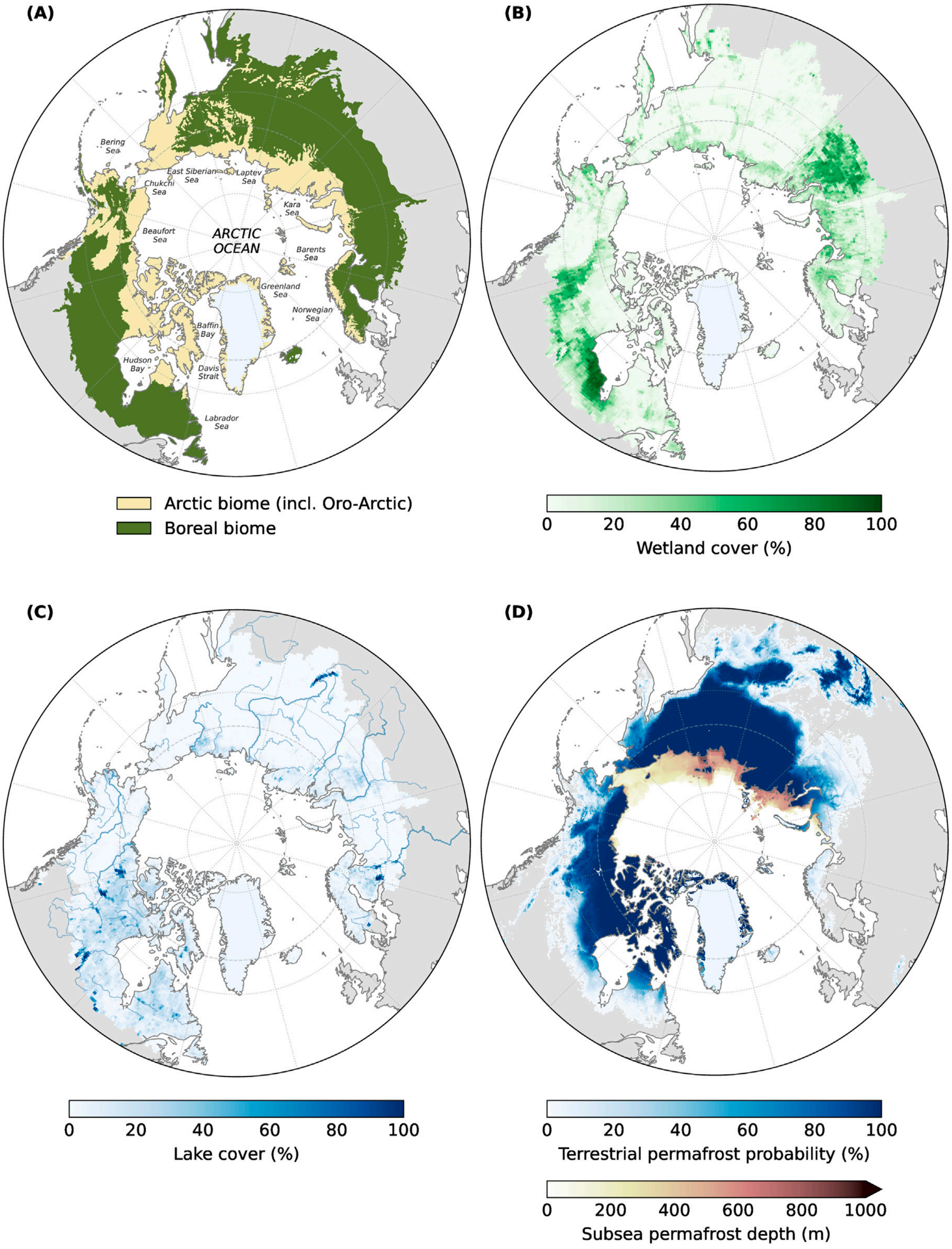

FIGURE 1
Ecoregions, wetlands, lakes and permafrost extent of the Arctic-Boreal region. **(A)** Spatial extent of the Arctic-Boreal region, showing the (Oro-) Arctic (yellow) and Boreal (green) terrestrial biomes, as well as the Arctic Ocean and its marginal seas. The Arctic Circle is depicted as a dashed line. **(B)** Wetland cover in the Arctic-Boreal region **(C)** lake cover and major rivers in the Arctic-Boreal region. **(D)** Extent of terrestrial permafrost (blue) and subsea permafrost (orange). The Arctic and Boreal biome extents are from Dinerstein et al. (2017). Wetland and lake cover are from the BAWLD dataset (Olefeldt et al., 2021). Terrestrial and subsea permafrost data are from Obu et al. (2019) and Overduin et al. (2019), respectively.

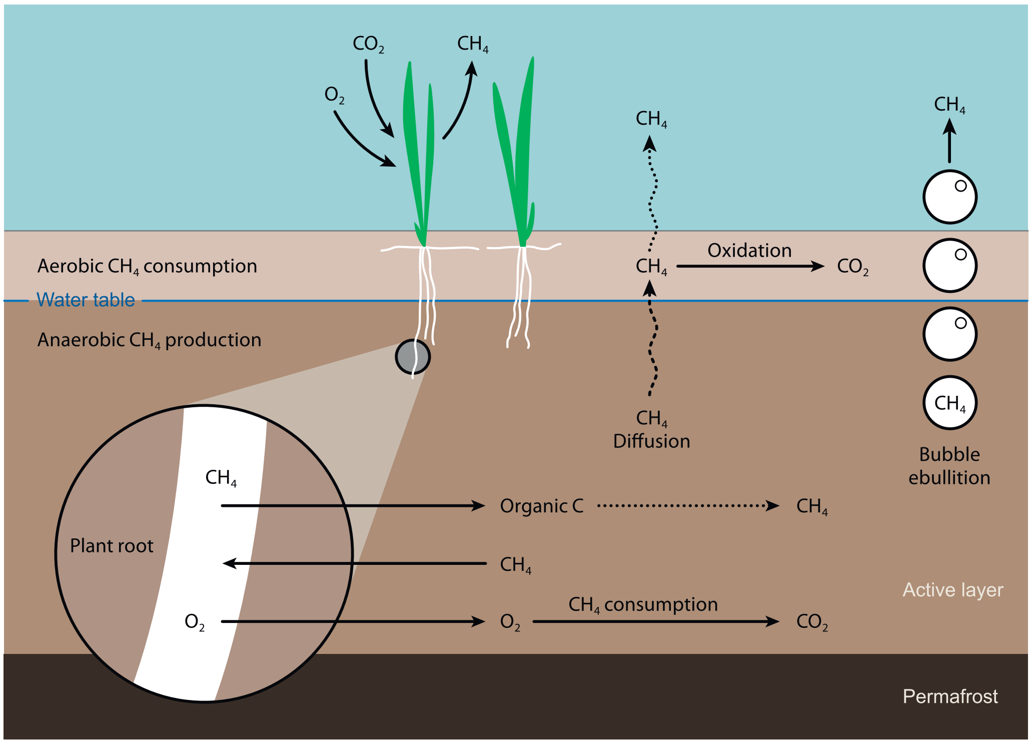

FIGURE 2
Pathways of methane emissions in wetland soils, and the role of vascular plants. Permafrost is shown for illustrative purposes. When it thaws, and the active layer deepens, it may act as an additional carbon source or alter surface hydrology. Episodic bursts of methane may also occur when the active layer refreezes in winter. Otherwise, the mechanisms shown here are similar in non-permafrost wetlands. Adapted from Joabsson et al. (1999) and AMAP (2015).

permafrost no longer acts as an impervious barrier (Walter Anthony et al., 2012). Most high latitude methane sources are microbial in origin, and global warming will increase this metabolic activity (Yvon-Durocher et al., 2014). Since methane is a potent greenhouse gas (AMAP, 2022), subsequent increases in emissions may pose a significant challenge to society (Hope and Schaefer, 2015).

These concerns have motivated extensive research efforts over the past decades to understand the processes underlying terrestrial and marine methane emissions from the high latitudes, and how they are associated with permafrost thaw. However, whether high-latitude methane emissions will increase in the future, and with what magnitude, remains highly uncertain. Many of these uncertainties arise from temporal and spatial omissions in current monitoring efforts (Peltola et al., 2019; Pallandt et al., 2022). Arctic landscapes are highly heterogeneous, complicating accurate monitoring, upscaling efforts and process modeling. In addition, the consumption of atmospheric methane by dry soils is also temperature-dependent (Voigt et al., 2023), which may counteract increased emissions elsewhere (Watts et al., 2014).

While acknowledging that CO$_2$ emissions are also an important part of the permafrost carbon feedback (Treat et al., 2024), this review restricts itself to methane by providing a broad overview of the current state of knowledge on sources, as well as sinks, in the Arctic-Boreal region. In this paper, we follow the terrestrial biome definitions from Dinerstein et al. (2017), which means that the terrestrial Arctic includes the treeless tundra of northern highlands (i.e., the oro-Arctic; Virtanen et al., 2015), while the boreal region is defined by areas predominantly covered by boreal forest or taiga (Figure 1A). In addition, we consider the Arctic Ocean and its marginal seas. A unique aspect of this paper is that it assesses sources in both the terrestrial and marine domain, including wetlands, lakes, gas hydrates and subsea permafrost, since all may potentially contribute to a rise in methane emissions from the high latitudes. We focus on how our understanding of these sources has evolved over the last decades, in the context of two assessments by the Arctic Monitoring and Assessment Programme (AMAP, 2015; 2022), to act as a guidance on this complex topic.

2 Natural sources and sinks of methane in the Arctic-Boreal region

2.1 Terrestrial environment

2.1.1 Wetlands

Early global atmospheric studies identified wetlands as a major natural source of methane to the atmosphere (Ehhalt, 1974). The early overall emission numbers (140–280 Tg CH$_4$ yr^{-1}) are still within the uncertainty range for the overall estimates of wetland-emitted methane in the most recent budgets (Christensen, 2014; Saunois et al., 2020). Although these global emissions are dominated by tropical wetlands, with a share of about 65% (Saunois et al., 2020), they hold a substantial contribution from northern wetlands including wet tundra and surrounding environments. The overarching background for these substantial emissions is the waterlogged nature of organic soils in the Arctic, which host stable anaerobic environments with optimal conditions for methanogenic activity (Figures 1B, 2).

These anaerobic conditions are found below the water table, where methane is produced from soil organic matter by methanogens that exclusively belong to the archaea domain (Ferry, 1999). Methane production is the final step in the degradation of organic matter, which methanogens most commonly do by reducing CO_2 with H_2 or by reducing the methyl group of acetate into methane (Thauer et al., 2008). If a water table drops below the surface, the top part of the soil becomes aerated and methane may be oxidized by a diverse group of bacteria – aerobic methanotrophs – when it diffuses upwards (Dean et al., 2018), as illustrated in Figure 2. However, oxidation can be avoided if this zone is bypassed through plant roots or by ebullition (Christensen et al., 2003; Ström et al., 2003). Ebullition, the fast upward movement of bubbles, happens too quickly for significant oxidation to occur in the top part of the soil, which is why it can be an important fraction of total emissions (Strack et al., 2005).

The role of plants in the production and transport of methane is more complex: many wet-tolerant plant species, such as sedges and rushes, contain a spongy tissue called aerenchyma which facilitates the transport of ambient air between the shoots and the roots (Figure 2). While this allows for the downward transfer of oxygen, it also provides a fast conduit for methane to travel upwards, while root exudates can act as additional substrate for methanogenesis (Ström et al., 2005).

Both of the microbial processes that produce and consume methane – methanogenesis and methanotrophy – are temperature dependent, and the position of the water table determines their relative importance (Olefeldt et al., 2013). Lower water tables increase the amount of oxygen in the soil, providing a larger habitat for methanotrophs, which is why this reduces net emissions – even if higher temperatures stimulate the activity of both methanogens and methanotrophs (White et al., 2023). Compared to tropical wetlands, influenced heavily by seasonality of flooding, wet northern source areas tend to be more stable in their extent (Yuan et al., 2024). Many factors, such as nutrients, plant species composition, soil carbon content, topography and hydrology, will modulate the size of the emissions, but a stable non-tidal natural wetland will under normal circumstances always be a source of atmospheric methane. In contrast, dry tundra is typically a sink for atmospheric methane (Voigt et al., 2023).

2.1.2 Point sources and disturbances

In a landscape perspective, the constantly emitting wet soil environments are surrounded by and intermixed with uplands, glaciers, lakes and rivers – all with their distinct and in some cases very different methane flux characteristics. Consequently, large temporal and spatial uncertainties exist in overall composite landscape emission estimates and new observations of unexpected fluxes remain possible. Recently, glacial outflow of methane has been identified as a hitherto unknown source of atmospheric methane in the terrestrial domain (Christiansen and Jørgensen, 2018; Lamarche-Gagnon et al., 2019). This emission source may be quite common for glaciers (Sapper et al., 2023), although its relative contribution to the Arctic-Boreal methane budget appears minor since it is restricted to the marginal areas of glaciers and ice sheets.

Another interesting phenomenon is the discovery of new crater-like formations, tens of meters wide and deep, in Siberian Russia – notably on the Yamal Peninsula (Bogoyavlensky et al., 2020). These features have been suggested to be the result of explosive degassing events, or cryovolcanism, although the exact mechanism remains under debate (Buldovicz et al., 2018; Bogoyavlensky et al., 2020; Hellevang et al., 2023). Due to the high methane concentrations measured in these craters, combined with their dramatic and sudden appearance in the landscape, they have attracted much media attention. Currently, however, these do not seem to be a significant new source of methane to the atmosphere, given their thus far limited extent, combined with the observation that they may revert to somewhat ordinary lakes a few years after formation (Chuvilin et al., 2020). Still, significant amounts of methane trapped within and beneath permafrost – e.g., from subsurface fossil hydrocarbon reservoirs – can be released to the atmosphere through geological seeps that form along faults, joints, fractures or open system pingos (Walter Anthony et al., 2012; Hodson et al., 2019).

Disturbances such as wildfires, thermokarst and animal activity may also impact the methane budget of the Arctic-Boreal region. Smoldering combustion of biomass increases the amount of methane emitted by fire relative to CO_2, when compared to flaming combustion. This slow burning process is common in boreal forests with carbon-rich organic soils (Wiggins et al., 2021), and they can persist throughout the winter, flaring up again in spring (Scholten et al., 2021). Boreal fires have been increasing in the past decades due to more frequent lightning and longer fire seasons (Veraverbeke et al., 2017), while projections show that fires may become more common in arctic tundra as well (Chen et al., 2021). These fires have a direct impact on permafrost thaw, through increases in soil temperatures and active layer depth, while climate change is expected to alter post-fire recovery (Holloway et al., 2020). While dwarfed by carbon losses in the form of CO_2, postfire impacts on methane emissions may be negligible to a slight increase in uptake, if soil temperatures increase and soil moisture declines (Ribeiro-Kumara et al., 2020).

Disturbances other than fire primarily alter methane emissions by transforming the hydrology of the landscape, such as surface subsidence from abrupt permafrost thaw (Christensen et al., 2004; Turetsky et al., 2020). Animal activity may also influence methane emissions, in particular the migration of beavers into the Arctic which construct dams that increase the number and size of beaver ponds (Tape et al., 2022), turning terrestrial environments into aquatic methane sources (Whitfield et al., 2015).

2.2 Freshwater systems

Freshwater systems (lakes, ponds, rivers, and streams) are abundant in the Arctic (Figure 1C), and subject to strong seasonal

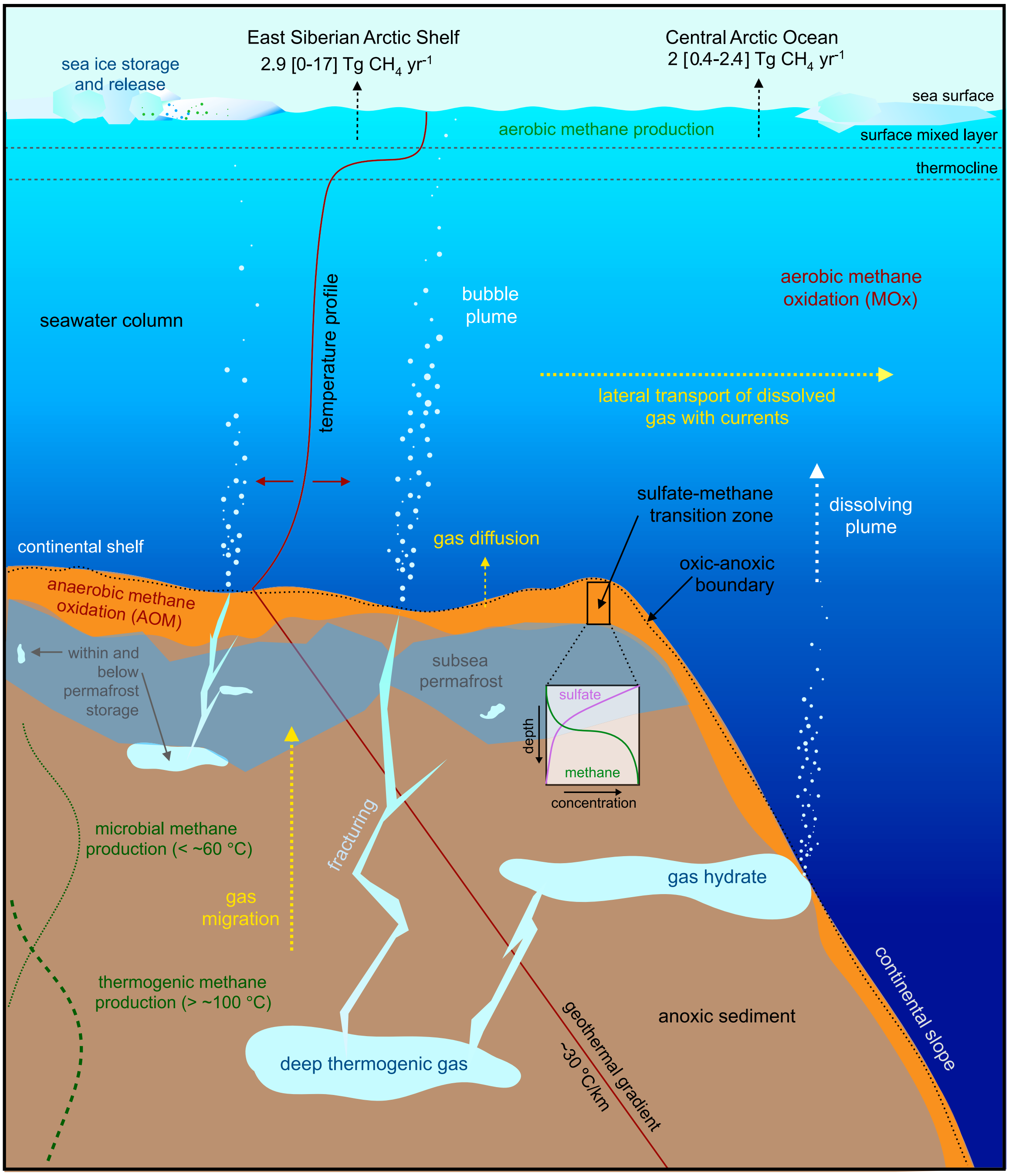

FIGURE 3
Typical areas of methane production, oxidation and migration within the ocean and its sediments. Emission estimates for the East Siberian Arctic Shelf (ESAS) and the Central Arctic Ocean are from Table 1. Figure is not drawn to scale.

variability in their methane emissions due to freeze-thaw cycles. The microbial production of methane in lakes and ponds is similar to that in wetlands, and follows the same upward pathways, but there's a larger relative contribution of ebullition to the emission to the atmosphere since diffusive methane fluxes can be anaerobically oxidized in surface waters and lake sediments (Walter et al., 2008a; Martinez-Cruz et al., 2018). Besides ebullition and turbulent dispersion, substantial emissions can also occur via transport through vascular plants in very shallow lakes (Bastviken et al., 2023).

Since harsh winter weather makes fieldwork demanding, there are few observations during winter, a similar gap in observational coverage as for wetlands (Kuhn et al., 2021). Although formerly thought to be mostly inert during the ice-covered or winter season, it is now well-known that methane is actively produced and destroyed in under-ice conditions, with rapid release of stored methane at spring thaw/ice-melt (Jammet et al., 2015). The dynamic nature of these systems, combined with the fact that current freshwater studies are taking place in a dynamic Arctic already experiencing the effects of climate change (Bruhwiler et al., 2021), complicates interpretation of observations when extrapolating to the Arctic as a whole.

2.3 Marine environment

2.3.1 Gas hydrates and subsea permafrost

Not so long ago, marine emissions of methane to the atmosphere were thought to be globally almost negligible and irrelevant to recent atmospheric methane increases (Reeburgh, 2007). This point of view was reasonable, as sulfate-rich seawater in sediments – in addition to ocean water itself – are hostile to methane, rapidly dissolving any methane in small bubbles, and then readily oxidizing it once dissolved (AMAP, 2015). Seafloor vents of methane and widespread production in the oxic surface layer of the ocean, while scientifically interesting, were not seen as systems changing with a warming climate. In the Arctic seas, early measurements supported this view (Kvenvolden et al., 1993), although it was unknown how these deposits would respond to present-day climate change (Kvenvolden, 1993). The tremendous amount of methane thought to be stored in ocean sediments in the form of hydrates (Hester and Brewer, 2009; Ruppel and Kessler, 2017) signifies the vast potential of the marine environment to emit large amounts of this greenhouse gas.

The production, consumption and transport of methane differs significantly between the terrestrial and marine environment (compare Figures 2, 3). Some similarity exists on the production side, since methanogens can also produce methane in ocean sediments (Garcia et al., 2000), but the environmental conditions are different: depending on the local geothermal gradient, microbial methane production occurs in the top ocean sediment, down to a depth of 1 to 2 km, at an optimum of 35°C–40°C and with an ultimate limit of 60°C (Judd, 2004). Thermogenic processes may occur deeper down in the ocean sediment, when temperatures exceed 110°C (Milkov, 2005). This may be as far down as 4 to 5 km, and depends on the presence of organic matter deposits such as coal beds (Judd, 2004). In addition, abiogenic methane formation can occur through metamorphic processes such as serpentinization, which is commonly associated with hydrothermal vents and faults in the oceanic crust, degassing of mafic magmas and cooling of mafic igneous rocks (Etiope and Sherwood Lollar, 2013).

When methane of any source origin migrates up towards the sea floor, it can be captured in gas hydrates – crystalline compounds that are stable under the high pressure from the overlying water and sediment column, and at low temperatures (Buffett, 2000). The range of depths with sufficiently high pressure and low temperatures are referred to as the gas hydrate stability zone (GHSZ). Globally, the GHSZ starts at ocean depths of 300–500 m, with the shallowest depths found in colder waters such as those of the Arctic (Kvenvolden, 1988). Commonly, such regions include the outer continental margins, slopes and rises (Kvenvolden, 1993), but also areas of permafrost, both onshore and offshore (Kvenvolden, 1988), where depths may be as shallow as 200 m, although the total amount of gas hydrates remains highly uncertain (Ruppel, 2015). Isotopic analyses indicate that the majority of the hydrate deposits on Earth contain biogenic methane (Archer, 2007), but hydrate formation may theoretically sequester methane from various origins (Rajan et al., 2013).

Besides hydrates, the shallow ocean shelves of the Arctic Ocean have known large petroleum systems (Cramer and Franke, 2005), and subsea permafrost that contains large amounts of frozen organic material laid down when sea level was lower in previous ice ages, leaving the land exposed (Romanovskii et al., 2000). The majority of subsea permafrost is found on the East Siberian Arctic Shelf (ESAS; consisting of the Laptev, East Siberian, and in most definitions, the Chukchi Sea), as shown in Figure 1D. The potential of methane originating from marine sediments to reach the atmosphere in these areas has somewhat shifted views on the marine environment within the global methane budget over the past two decades.

Still, the ultimate source of emissions from the shallow ocean shelves has been controversial. Methane could conceivably be sourced from eroded organics from thawing permafrost onshore, thawing submerged permafrost, surface seawater methane sources, sub-seafloor transport of methane-rich terrestrial freshwater (Charkin et al., 2017), or deep thermogenic (petroleum-associated) sources. The existence of extensive petroleum sources in the ESAS (Cramer and Franke, 2005), however, is not enough to imply an emission of methane to the atmosphere. For instance, while old thermogenic methane is present at depth on the petroleum-rich Beaufort Shelf, this does not reach the surface and atmosphere in substantial quantities even at depths as shallow as 30 m (Sparrow et al., 2018). A study of $\delta^{14}C$ in methane and stable methane isotopologues from water samples collected near a large gas seep in the outer Laptev Sea has also pointed to a deep thermogenic source (Steinbach et al., 2021).

Despite large potential sources, loss processes in the sediment – including anaerobic oxidation – limit present-day methane releases to the ocean water (Overduin et al., 2015; Stranne et al., 2019), and ultimately the atmosphere. Sulfate-dependent anaerobic oxidation of methane can occur near the ocean floor by anaerobic methanotrophic archaea, commonly referred to as the sulfate-methane transition zone (Knittel and Boetius, 2009). In areas with high production or hydrate dissociation, this transition zone may be bypassed, and methane bubbles can escape the seafloor through gas seeps, entering the water column. Some work has suggested that at high seafloor warming rates (>0.01°C yr^{-1}) – well within the range of some projections for the coming century – the efficiency of these biological methane "filters" cannot keep pace with overpressure-induced hydraulic fracturing of the sediment as methane hydrates decompose, and substantial methane is released to the water column (Stranne et al., 2022).

2.3.2 Water column and ocean surface

It is clear that some methane from seafloor gas seeps reaches the atmosphere via bubble transport (Leifer and Patro, 2002), although the total amount escaping via this pathway is controversial. Whether methane emitted from the sea floor reaches the atmosphere depends on the rate of dissolution of methane from these bubbles into the ocean water (Rehder et al., 2009), and the amount of aerobic methane oxidation (Steinle et al., 2015). The importance of these processes depend on water depth since the probability for methane dissolving into and microbially oxidizing in the ocean water (Valentine et al., 2001), before reaching the atmosphere, has greater probability with increasing depth. For example, despite widespread venting along the continental margin near Svalbard

(Sahling et al., 2014), a very minor fraction (0.07%) was estimated to reach the atmosphere (Mau et al., 2017), since 70% of observed bubble emissions occurred at depths of 120 m or greater. However, in shallow seas the water column depth is more amenable to mixing dissolved or bubble methane out of the water and into the atmosphere (McGinnis et al., 2006), and the Arctic Ocean has extensive shelf seas that are relatively shallow (Jakobsson, 2002).

In the central Arctic Ocean, deep water prevents seafloor sources from reaching the atmosphere. Under-ice methane production, and its connection with the more general “marine methane paradox” of methane production in oxygenated surface waters remains somewhat unclear, although Damm et al. (2010) proposed a model wherein phosphate-poor Pacific-origin seawater led to more near-surface methane production than in Atlantic-derived, phosphate-rich seawater. Methane production in oxic surface waters may be more prevalent than previously believed (Bižić et al., 2020) and this provides a likely additional source of methane from the marine environment in the Arctic. The scale of this process in the Arctic marine environment, and how much it contributes to the atmosphere, remains to be quantified.

Sea ice has been proposed as a modulator of the emission of methane from surface sources (Kvenvolden et al., 1993; Damm et al., 2015), and polynya openings may be a source of methane emissions even during winter (Damm et al., 2007). Aircraft and in-situ measurements demonstrated methane emissions from ice leads in the deep Arctic Ocean (Kort et al., 2012; Silyakova et al., 2022), areas which should not be easily influenced by seafloor methane sources – although the Transpolar Drift seems to move some dissolved methane from shallow shelf seas to the central Arctic Ocean (Damm et al., 2018). The discovery of methane supersaturations under sea ice in the ESAS (Shakhova et al., 2010) and in the Canadian Arctic (Kitidis et al., 2010) support the idea of wintertime accumulation and later release of methane.

3 Methane budget of the northern high latitudes

3.1 Challenges in upscaling fluxes

The upscaling of methane fluxes from plot level measurements to the entire Arctic-Boreal region is a challenging task. Periglacial landscapes exhibit a high degree of microtopography, which results in a surface where dry and wet ecosystems are alternating. Subsequently, methane emissions vary strongly across short distances (see e.g., Parmentier et al., 2011). Assessing the areal extent of wetlands is key to upscaling terrestrial methane emissions, but these ecosystems remain poorly mapped, leading to significant uncertainty in upscaled fluxes (Petrescu et al., 2010; Peltola et al., 2019). The need for spatial detail to achieve landscape emission estimates is further emphasized by the fact that the aerial extent of small lakes and ponds is poorly-constrained, which may lead to a double-counting of emissions that inflates budget estimates (Thornton et al., 2016b). Marine methane emissions can also be highly localized, leading to budget estimates that may vary up to an order of magnitude (Shakhova et al., 2014; Berchet et al., 2016; Thornton et al., 2020). In the following, we give an overview of the various methane budget estimates that have been made across the Arctic-Boreal region, using bottom-up methods such as extrapolations from site-data and process models, as well as the top-down method of inverse modeling constrained by atmospheric data (see e.g., Saunois et al., 2020).

3.2 Terrestrial methane emissions

3.2.1 A short history of upscaling techniques

From a ground-based measurement perspective, extrapolated northern wetland emission estimates have for a long time been lying between 20 and 100 Tg CH_4 yr^{-1}. Sebacher et al. (1986) estimated 45–106 Tg CH_4 yr^{-1} for Arctic and Boreal wetlands, Crill et al. (1988) estimated 72 Tg CH_4 yr^{-1} for undrained peatlands north of 40° N, Whalen et al., 1992 estimated 42 ± 26 Tg CH_4 yr^{-1} for wet meadow and tussock shrub tundra based on measurements, and Christensen (1993) estimated 18–30 Tg CH_4 yr^{-1} for global tundra based on measurements from comparable habitats on the North Slope of Alaska. Reviewing the literature available at the time, Bartlett and Harriss (1993) estimated a mean emission from wetlands north of 45° N of 38 Tg CH_4 yr^{-1} – a value not far from the early estimates of 42–45 Tg CH_4 yr^{-1} using inverse modeling for the northern hemisphere to derive a total emission estimate (Chen and Prinn, 2006).

These early, mostly ground-based, extrapolation-based estimates have been found to be mostly at the higher end of the ranges that emerged once dynamic process models capable of simulating methane emissions became available. Historically, these models focused on wetlands, since they represent the largest source of methane in the Arctic-Boreal region, but also because models can draw on a longer and more extensive record of observations for testing and validation. One of the earliest modeling attempts to establish a budget for northern wetlands modified a vegetation model by allocating a fixed fraction of heterotrophic respiration to methane production (Christensen et al., 1996). This built upon the assumptions that methane production generally scales with NPP and that forested and open wetlands each showed a narrow range of CH_4/CO_2 ratios. This study estimated that wetlands north of 50° N emitted 20 ± 13 Tg CH_4 yr^{-1}. Surprisingly, this was comparable to the 21.8 Tg CH_4 yr^{-1} estimated by a more process-based study released in the same year, that modeled methane production in relation to soil and vegetation carbon pools, temperature and the position of the water table (Cao et al., 1996). Nonetheless, both of these estimates were lower than the ~35 Tg CH_4 yr^{-1} that atmospheric inversions and extrapolations from flux measurements indicated at the time (Christensen et al., 1996).

The representation of methane production and consumption in these early model implementations was relatively basic, which reduced their usefulness to predict changing methane emissions under a future climate (Bruhwiler et al., 2021). Since then, models have been introduced that simulate both the production and consumption of methane as temperature sensitive processes, while accounting for diffusion, and bypassing of the oxic layer through aerenchyma and ebullition (Walter and Heimann, 2000). This class of models continues to be expanded by including numerous processes, with some recent advances focusing on the consumption of atmospheric methane in soils (Oh et al., 2020),

TABLE 1 Recent budget estimates of terrestrial, freshwater, and marine methane emissions to the atmosphere in the Arctic-Boreal region. Estimates are given with either confidence intervals (in brackets) or standard deviations as in the original studies. Where necessary, values were converted from Tg CH_4-C yr^{-1} to Tg CH_4 yr^{-1}. The estimates from Saunois et al. (2020) were extracted by Bruhwiler et al. (2021) and Yuan et al. (2024) for top-down and bottom-up methods respectively. We also extracted wetland emissions for the Arctic-Boreal region from the raw data presented in Peltola et al. (2019) and the lake emissions in Liu and Zhuang (2023). The 2 Tg yr^{-1} for Kort et al. (2012) is estimated by extending emissions for a year and scaling them to the area they surveyed.

Source	Method	Tg CH_4 yr^{-1}	Study
Wetlands			
Wetlands >50° N	Process model (1)	38.82 ± 3.03	Oh et al. (2020)
Wetlands >50° N	Atmospheric inversions (11)	33.6	Saunois et al. (2020), Bruhwiler et al. (2021)
Arctic-Boreal region	Upscaled flux measurements	26 [25.2–27]	Peltola et al. (2019), This study
Arctic-Boreal region	Process models (13)	16.4 ± 0.7	Saunois et al. (2020), Yuan et al. (2024)
Arctic-Boreal region	Process model	35	Watts et al. (2023)
Arctic-Boreal Region	Upscaled flux measurements	20.3 ± 0.94	Yuan et al. (2024)
Arctic-Boreal permafrost region	Upscaled flux measurements	34.1 [19.6–48.5]	Ramage et al. (2024)
Lentic systems (lakes and ponds)			
Lakes and ponds >50° N	Upscaled flux measurements	16.5 ± 9.2	Wik et al. (2016b)
Lakes and ponds >50° N	Upscaled flux measurements	13.8–17.7	Matthews et al. (2020)
Lakes and ponds >54° N	Upscaled flux measurements	13.4	Bastviken et al. (2011)
Arctic-Boreal region	Process model	8.0 ± 1.2	Liu and Zhuang (2023), This study
Arctic-Boreal permafrost region	Upscaled flux measurements	9.5 [3.9–13.6]	Ramage et al. (2024)
Lotic systems (rivers and streams)			
Rivers and streams >50° N	Upscaled flux measurements	2.4	Rocher-Ros et al. (2023)
Rivers and streams >54° N	Upscaled flux measurements	7.5	Stanley et al. (2016)
Rivers and streams >54° N	Upscaled flux measurements	0.3	Bastviken et al. (2011)
Arctic-Boreal permafrost region	Upscaled flux measurements	3.1 [2.1–3.9]	Ramage et al. (2024)
Upland soils			
Mineral soils >50° N	Process model (1)	−9.52 ± 0.59	Oh et al. (2020)
Boreal forest soils	Upscaled flux measurements	−1.5 [-2.9–0]	Ramage et al. (2024)
Other terrestrial sources			
Fires (Boreal and Tundra)	Satellite-derived upscaling	2.4 [1.9–2.8]	Ramage et al. (2024)
Geological emissions	Observation-based upscaling	2 [1.6–2.4]	Ramage et al. (2024)
Subsea permafrost			
ESAS	Upscaled diffusive fluxes and ebullition measurements	17	Shakhova et al. (2014)
ESAS	Upscaled diffusive fluxes	2.9	Thornton et al. (2016b)
ESAS	Upscaled eddy covariance flux measurements	3.02	Thornton et al. (2020)
ESAS	Regional atmospheric inversion	0–4.5	Berchet et al. (2016)
ESAS	Regional atmospheric inversion	0.58 ± 0.47	Tohjima et al. (2020)
Central Arctic Ocean			
Arctic Ocean + Beaufort and Chukchi Seas (<82° N)	Upscaled airborne flux measurements	2	Kort et al. (2012)
Arctic Ocean (excluding shelf regions)	Upscaled diffusive flux measurements	0.95 [0.36–2.35]	Lorenson et al. (2016)
Arctic Ocean (seas >60° N, ESAS excluded)	Regional atmospheric inversion	2 [1.7–2.2]	Tohjima et al. (2020)

microbial dynamics to improve temperature sensitivity and observed hysteresis (Chadburn et al., 2020) and coupled iron-redox cycling (Sulman et al., 2022).

Despite the large focus on adding process detail, it remains challenging to accurately parameterize these processes in models due to a lack of data across most of the Arctic-Boreal region, in particular across Siberia (Kuhn et al., 2021) – combined with the high spatial and temporal variability of observations as opposed to the coarse resolutions used by models (Treat et al., 2018b). Recent advances in machine learning help to disentangle this complexity, and by combining numerous data sources, from satellites, reanalysis products and land cover classes, Peltola et al. (2019) used a random forest technique to upscale site level observations to all wetlands north of 45° N. Estimates for that area ranged from 31 to 38 Tg CH_4 yr^{-1}, depending on the prescribed wetland map, with an average of 26 [25.2–27] Tg CH_4 yr^{-1} for the Arctic-Boreal region alone (Table 1).

3.2.2 Uncertainties related to wetland extent

A lack of knowledge on the total surface area of wetlands, and where they are located, have been a major obstacle to achieving accurate budgets for the entire terrestrial Arctic-Boreal region. It is telling, despite valuable attempts, that the global wetland map presented in the seminal paper by Matthews and Fung (1987) was still in use several decades later (see e.g., McGuire et al., 2012). This was mostly due to a lack of alternatives that were proven to perform substantially better in the Arctic (Petrescu et al., 2010). However, static wetland maps are potentially problematic to assess temporal trends in methane emissions since there is no guarantee that wetland extent will remain the same in a changing climate. Poulter et al. (2017), therefore, leveraged remote sensing data of surface inundation to vary the extent of wetlands depending on the presence of surface water, which resulted in the Wetland Area and Dynamics for Methane Modeling (WAD2M) wetland area dataset (Zhang et al., 2021).

WAD2M is a significant advance to represent seasonally varying wetlands in e.g., the tropics, but this approach may be less applicable to the Arctic where wetland area is less dynamic, while methane emissions can continue when water levels are well below the surface (Olefeldt et al., 2013). In addition, these remote-sensing based products effectively switch off in winter, even though cold season emissions can be up to half of the yearly budget (Treat et al., 2018a). This may explain why an ensemble of models by the Global Carbon Project that used WAD2M led to the relatively low estimate of 9 (2–18) Tg CH_4 yr^{-1} north of 60° N (Saunois et al., 2020), with a median of 16.7 Tg CH_4 yr^{-1} across the whole Arctic-Boreal region (Yuan et al., 2024). By upscaling flux measurements across the same region with machine learning, Yuan et al. (2024) estimated a slightly higher emission of 20.3 ± 0.9 Tg CH_4 yr^{-1} while using WAD2M. In contrast, a previous estimate by the Global Carbon Project, with many of the same models used by Saunois et al. (2020), came to a much higher central estimate of 35 (21–47) Tg CH_4 yr^{-1} across the smaller area of Arctic tundra alone (McGuire et al., 2012). Then again, this estimate is probably too high compared to observations since the same study also estimated a budget of 15 (0–29) Tg CH_4 yr^{-1} based on an upscaling of flux measurements alone.

An additional reason for the low estimates by studies that use WAD2M is that the areal extent of lakes and ponds was subtracted from the wetland extent to avoid the double counting of emissions from wetlands and aquatic systems (Thornton et al., 2016b). While it is important to address this bias, the areal extent of wetlands and open water was determined independently, leaving the total extent of methane emitting landforms poorly constrained. To resolve these issues, Olefeldt et al. (2021) developed The Boreal–Arctic Wetland and Lake Dataset (BAWLD) that accounts for the distribution and abundance of wetland, lake, and river classes within the same framework (Figures 1B, C). Each land class in the dataset has distinct methane emissions (Kuhn et al., 2021), including different types of wetlands (i.e., bogs, fens, marshes and wet tundra), but also dry ecosystems (e.g., dry tundra, bare rock). By defining them simultaneously, as a fraction of the total surface area of each grid cell, biases from overlaps between classes – i.e., double counting – are avoided.

While still a static mapping product, this approach may be more relevant for determining high-latitude methane budgets, since it accounts better for unique high-latitude ecosystems, such as permafrost bogs and tundra wetlands, while being specifically designed to estimate methane emissions. Moreover, WAD2M exhibits no trend in Arctic-Boreal wetland extent from 2002 to 2021 (Yuan et al., 2024), which shows that a static map remains suitable to estimate historical Arctic-Boreal methane budgets. Using the BAWLD dataset to categorize and upscale flux observations, Ramage et al. (2024) estimated that all natural sources of the Arctic-Boreal permafrost region combined are emitting 51.1 (29.1–71.2) Tg CH_4 yr^{-1}, of which about two-thirds was emitted by terrestrial ecosystems (35.6 Tg CH_4 yr^{-1}), a quarter by inland waters (12.5 Tg CH_4 yr^{-1}), and the remainder by fires (2.4 Tg CH_4 yr^{-1}) and geological sources (2 Tg CH_4 yr^{-1}).

3.2.3 Gaps in temporal and spatial coverage

Apart from the challenge of accurately assessing the spatial extents of methane-emitting landscapes, dry upland soils can take up atmospheric methane, where it is oxidized by methanotrophs (Whalen et al., 1992). This may lower regional estimates (>50° N) of net methane emissions by as much as −9.5 Tg CH_4 yr^{-1} when included in models (Oh et al., 2020) – although observation-based upscaling suggests that this sink may be as little as −1.5 Tg (−2.9–0) CH_4 yr^{-1} (Ramage et al., 2024). Still, these areas are often overlooked in observational studies (Jørgensen et al., 2014), despite the fact that this methane sink will also increase with rising temperatures (Voigt et al., 2023), compensating for emissions elsewhere. Recently, it was also proposed that microbially mediated drawdown of methane on and in trees may reduce boreal emissions slightly, by −0.055 Tg CH_4 yr^{-1} (Gauci et al., 2024).

Apart from these oversights in the uptake of methane, the winter period is under-sampled, even though the cold season may account for up to half of annual emissions (Treat et al., 2018a). Short-lived pulses caused by freeze-thaw actions can contribute significantly to cold season emissions, but observations remain sparse (Mastepanov et al., 2013; Pirk et al., 2015; Raz-Yaseef et al., 2017). Improved mapping of Arctic-Boreal landscapes and year-round monitoring remain necessary to better constrain budget estimates.

3.2.4 Atmospheric constraints

In addition to above-mentioned bottom-up methods, atmospheric inversion models are useful tools to determine top-down budget estimates across large regions (Bruhwiler et al., 2021). The 11 inversions included in a comparison by the Global Carbon Project estimated a mean emission from wetlands north of 50° N of 33.6 Tg CH_4 yr^{-1} (Saunois et al., 2020; Bruhwiler et al., 2021). These atmospheric flux inversions use statistical optimization and atmospheric transport models to estimate fluxes that are in optimal agreement with both a prior estimate (initial guess) and observations of atmospheric methane concentrations. The prior is typically a bottom-up method, such as a process model or statistically upscaled fluxes of wetland emissions, as well as inventories of anthropogenic emissions from fossil fuels and agriculture. In regions with little data coverage, atmospheric transport can become a large source of uncertainty, which may lead to model-data mismatch errors (Bruhwiler et al., 2021). Moreover, inversions rely on their prior, which means that uncertainties in bottom-up methods, e.g., the wetland extent or poor cold season data coverage, also affect budget estimates from inversions.

Atmospheric inversions are highly useful to determine the total methane budget, since they are constrained by atmospheric concentrations, but a caveat is that they struggle to distinguish between anthropogenic sources, wetlands and lakes unless their priors are strongly separated spatially (Bruhwiler et al., 2014). Inversions provide an overview of the size and trends of all emissions, but they are limited in the amount of information they can provide on individual sources, even though they are an important constraint on the combined amount of these individual sources.

3.3 Freshwater methane emissions

3.3.1 Observation-based and modeled lake emissions

Lakes have long been recognized to be a substantial source of methane to the atmosphere, but estimates are typically below those of wetlands. Bastviken et al. (2011) estimated a total emission north of 54° N of 13.4 Tg CH_4 yr^{-1}, with just 6.8 Tg CH_4 yr^{-1} north of 66° N. Wik et al. (2016b) boosted the prominence of lakes in the Arctic, deriving a pan-Arctic estimate of 16.5 ± 9.2 Tg CH_4 yr^{-1} of methane from lakes and ponds. However, the aforementioned problems of overlapping and conflation of small, shallow lakes and ponds with wetlands, and lake-wetland interface zones, continued to be a challenge (Thornton et al., 2016b). In addition, ebullition from lakes is the most difficult to quantify, due to its episodic and often stochastic nature. Approaches have included ice-bubble surveys on frozen lakes (Walter Anthony et al., 2010; Wik et al., 2011), bubble traps (e.g., Wik et al., 2013), and synthetic aperture radar surveys of frozen lake surfaces (Walter et al., 2008b; Engram et al., 2020). The high temporal variability of ebullition, combined with the difficulty and expense of long-term lake ebullition sampling in the Arctic, has likely led to many studies underestimating lake methane emissions (Wik et al., 2016a).

While the estimate by Wik et al. (2016b) put Arctic lakes' methane emissions at a similar magnitude to that of wetlands, recent estimates using newly available databases are again lower. Matthews et al. (2020) estimate 13.8–17.7 Tg CH_4 yr^{-1} for lakes <5000 km^2 north of 50° N, while Ramage et al. (2024) estimated just 9.5 (3.9–13.6) Tg CH_4 yr^{-1} for lakes in the Arctic-Boreal permafrost region. Meanwhile, model implementations of lake methane emissions are dwarfed by the work on wetlands, but a recent attempt by Tan and Zhuang (2015) estimated a budget of 11.9 (7.1–17.3) Tg CH_4 yr^{-1} for lakes north of 60° N, not too dissimilar from the observation-based upscaling. An updated version of the same model estimated an emission of 14.76 ± 0.44 Tg CH_4 yr^{-1} for all lakes north of 45° N (Liu and Zhuang, 2023), of which 8.0 ± 1.2 Tg CH_4 yr^{-1} originated from lakes in the Arctic-Boreal region.

3.3.2 Gaps in temporal and spatial coverage

As with wetlands, local hydrology is a key regulator of carbon cycling and methane emissions in lake landscapes. Terrestrially produced methane can be transported from wetlands' active layer into lakes via groundwater flow (Paytan et al., 2015). Large numbers of Arctic lakes are in thermokarst environments, and are often quite shallow, making them more vulnerable to heating and increased permafrost thaw, below and around the lakes, under climate warming (Walter et al., 2006). The net contribution of small lakes and thaw ponds has proven difficult to determine; such lakes are numerous and rich in dissolved organic carbon (DOC) and methane (Langer et al., 2015). High-resolution airborne hyperspectral mapping of water bodies also confirmed a strong relation between methane emissions and the distance to standing water (Elder et al., 2020). However, a study of lakes in the West Siberian Lowlands (a well-known major terrestrial wetland methane source) found only a minimal contribution to total methane from the small thaw lakes within this landscape (Polishchuk et al., 2018). On the other hand, lakes in carbon-rich Yedoma sediments have been found to be highly productive, and methane can be produced year-round if a thaw bulb has been established in lake sediments, despite low mean annual air temperatures (Walter et al., 2007).

Similar to wetlands, it has become more recognized in recent years that the so-called edge seasons – spring and autumn – are major, and variable, contributors to total annual methane emissions depending on lake ice-out and freeze-up conditions. Additionally, these edge seasons are expected to experience the most dramatic warming changes in the future, as ice-free seasons of lakes are extended. Year-round eddy covariance observations have demonstrated that lake spring methane efflux is variable between years (Jammet et al., 2017), and is lower in years with less snowmelt (Jansen et al., 2019). Spring contributions to annual emissions vary hugely interannually, 4%–74% of total annual emissions (Denfeld et al., 2018), and are driven by sub-ice and in-ice methane buildup overwinter (Juutinen et al., 2009; Wik et al., 2011; Walter Anthony and Anthony, 2013). Although the spring emission was once thought to be a single large burst or pulse at ice-out and lake overturn (mixing of the entire water column), recent measurements have shown more variability (Denfeld et al., 2015).

3.3.3 Rivers and streams

Compared to wetlands and lakes, little data exists on methane emissions from rivers and streams in the Arctic-Boreal region. A compilation of measurements from freshwater fluvial systems suggests an emission of 7.5 Tg CH_4 yr^{-1} from these systems alone, north of 66° N (Stanley et al., 2016; Thornton et al., 2016b) – 25x higher than an earlier estimate of 0.3 Tg CH_4 yr^{-1} (Bastviken et al., 2011). A recent global estimate of riverine methane emissions falls in between these two estimates, at 2.4 Tg CH_4 yr^{-1} for the area North of 50° N (Rocher-Ros et al., 2023). This is about the same fraction of global emissions from fluvial systems (17% vs. 15%)

as temperate and subtropical regions (30°–50° N), despite being ice covered for a large part of the year. A rather similar estimate of 3.1 (2.1–3.9) Tg CH_4 yr^{-1} was derived by Ramage et al. (2024) for the rivers of the Arctic-Boreal permafrost region. Although there remains a high uncertainty to these numbers, the influence of large freshwater fluvial systems on coastal marine methane cannot be understated, as large increases in dissolved methane in surface waters are frequently observed near major river outlets (Shakhova et al., 2010; Bussmann, 2013; Kohnert et al., 2017).

3.4 Marine methane emissions

The past decade has seen a wide variety of estimates of present-day methane emissions from the Arctic Ocean, and considerable uncertainty remains about the net emissions from the surface waters from the Arctic Ocean proper, and how that may change in the future. Interest has continued to be focused on shallow shelf areas of the Arctic Seas, especially the ESAS. Emissions are, in some areas, enhanced by direct bubble transport from the sediment to the atmosphere, and resupply to surface waters by dissolving bubbles.

Early studies from the ESAS estimated fluxes as high as 8 to 17 Tg CH_4 yr^{-1} (Shakhova et al., 2010; Shakhova et al., 2014). A global modelling study by Warwick et al. (2016), indicated that Arctic wetland emissions would have to be overestimated to accommodate such large emissions from the ocean. Atmospheric measurements of methane concentrations and isotopic signatures also show that Arctic methane emissions are dominated by wetlands and not the ocean (Fisher et al., 2011; Thonat et al., 2017). Several follow-up studies show that ESAS emissions had been overestimated in the early studies. Berchet et al. (2016) used a regional inverse model and suggested a range of 0–4.5 Tg CH_4 yr^{-1}. Thornton et al. (2016a) used surface water and atmospheric measurements in the central ESAS to suggest 2.9 Tg yr^{-1} from the ESAS region, drastically lower than the earlier estimate of 17 Tg yr^{-1} (Shakhova et al., 2014). An eddy-covariance based study (Thornton et al., 2020), estimated 3.02 Tg yr^{-1} for the ESAS, even though emission “hotspots” above seafloor gas seeps reached emission rates of >600 mg m^{-2} d^{-1} – roughly an order of magnitude higher than onshore sources. The apparent spatial rarity of these large emissions seems to limit their regional-scale influence.

Measurements in other regions of the Arctic have to date revealed much smaller methane emissions to the atmosphere than in the ESAS. Notably, emissions from the North American Arctic have been estimated to be as low as 0.009 [0.002–0.023] Tg CH_4 yr^{-1} (Fenwick et al., 2017; Manning et al., 2022; Vogt et al., 2023). Rivers appear to be a significant contributor to marine methane in the nearshore Canadian Arctic, in particular during spring ice melt (Manning et al., 2020). In the waters near Svalbard, where extensive seepage from gas hydrates has been documented (Westbrook et al., 2009; Sahling et al., 2014), it appears that very little enters the atmosphere, with budget estimates ranging from 0.0015 to 0.06 Tg CH_4 yr^{-1} (Graves et al., 2015; Lund Myhre et al., 2016; Mau et al., 2017). In this area, it was demonstrated that carbon dioxide uptake from the atmosphere above active seafloor methane seeps resulted in a net negative radiative forcing despite some methane reaching the atmosphere (Pohlman et al., 2017). For the Central Arctic Ocean, methane emissions are relatively small compared to terrestrial sources (Lorenson et al., 2016; Silyakova et al., 2022; Prytherch et al., 2024), and budget estimates range from 0.36 to 2.35 Tg CH_4 yr^{-1} (Kort et al., 2012; Lorenson et al., 2016; Tohjima et al., 2020).

4 Discussion

4.1 Future trajectories under continued climate change and permafrost thaw

4.1.1 Terrestrial emission trends

Whether northern wetlands will become a significantly larger source of methane to the atmosphere remains highly uncertain, and this will depend on the relative change in temperature and surface hydrology. From a temperature perspective, it would be expected that methane emissions will increase with continued climate change, since this will raise the activity of methanogens (Yvon-Durocher et al., 2014). In principle, this will also raise the activity of methanotrophs (Voigt et al., 2023), but model simulations show that this increasing sink capacity can compensate for, but will not outpace, increases in methane production (Oh et al., 2016). However, if the permafrost region becomes drier, and the total extent of wetlands decreases, methane emissions could stay the same or even decline. The direction in which the hydrology of the permafrost region will develop with climate change remains the largest wildcard in the Arctic-Boreal methane budget.

The recent past may provide some hints about the trajectory that high latitude methane emissions are on. The longest eddy covariance record of methane emissions, from the Samoylov research station in the Lena delta, showed that June-July emissions had increased by 1.9% ± 0.7% yr^{-1} since 2004 due to earlier snowmelt and higher temperatures (Rößger et al., 2022). However, emissions were not statistically different in August and September. This may be related to drier conditions in late summer when active layer depths are deeper, making surface drainage more effective, suggesting that methane emissions can be sensitive to the seasonality in warming trends – as was previously shown for CO_2 (Helbig et al., 2022). Similarly, Yuan et al. (2024) showed in their upscaling of fluxes across the Arctic-Boreal region that the strongest increases in emissions occurred in June and July, but not late summer, and that the annual total had increased by ~9% (~1.7 Tg CH_4 yr^{-1}) from 2002 to 2021.

Model ensembles have generally struggled to show similar increases in annual emissions (McGuire et al., 2012; Saunois et al., 2017), but this may be related to a high variability in simulated flux magnitude among models, as well as a high interannual variability (Ito et al., 2023). Despite generally underestimating emissions, the models of the Global Carbon Project appear to show a slight increase in cold season emissions (Ito et al., 2023). It is also possible that such increases are restricted to smaller regions. Parmentier et al. (2015) combined three process models to show that warming along the Arctic Ocean, related to the sea ice albedo effect, can lead to an amplification of methane emissions from near-coastal wetlands in autumn and early winter. This may be one of the reasons why atmospheric inversion models show an average increase of ~3 Tg CH_4 yr^{-1} from 2000 to 2018 in high latitude emissions (>60° N) while emissions remained unchanged further south (50°–60° N) despite significant year-to-year variation (Bruhwiler et al., 2021).

While recent studies point to a modest increase in methane emissions, the question is whether this is due to microbes processing ancient permafrost carbon that has recently thawed, or whether this is due to a general intensification of the carbon cycle. The latter would provide larger amounts of fresh substrate, e.g., in the form of root exudates, that can be readily transformed to methane. A study from thawing permafrost peatlands in northern Canada suggested that the former is likely, with less than 10% of methane fluxes being derived from previously frozen carbon (Cooper et al., 2017).

Furthermore, a meta-analysis of methane fluxes across the Arctic-Boreal region has shown that thermokarst sites had higher emissions than adjacent intact permafrost sites, which was attributed to differences in temperature (Olefeldt et al., 2013). Given comparable environmental conditions, however, there was no statistical difference between thermokarst sites and permafrost-free sites. This suggests that changes in methane emissions are more closely related to changes in hydrology, vegetation composition and temperature following permafrost thaw rather than the availability of ancient permafrost carbon (Olefeldt et al., 2013; Cooper et al., 2017). Still, thermokarst significantly changes the hydrology of the landscape, and it has been suggested that abrupt thaw may be responsible for as much as 30.9 (19.7–41.9) Tg CH_4 yr^{-1} of terrestrial methane emissions (Ramage et al., 2024) – although this estimate may be inflated by double counting.

4.1.2 Freshwater emission trends

A growing body of evidence points towards an increase of lake methane emissions with climate change. Ever larger lake site-specific datasets have allowed detailed analyses of how different regulators, such as wind shear and temperature, control methane emissions over short and long timescales (e.g., Jansen et al., 2019). In addition, it has been proposed that ebullition is controlled by the energy input to lakes (Wik et al., 2014) as well as temperature and lake productivity (DelSontro et al., 2016). Shallow lakes in permafrost regions appear more vulnerable to warming (Arp et al., 2016) and longer ice-free seasons increase the solar energy input to all lakes (Wik et al., 2014; Thornton et al., 2015). Overall, longer and warmer ice-free seasons raise microbial methane production, which seems to prime lakes to be a sustained methane source under warming (Wik et al., 2018) – a prediction not confined to the Arctic (see e.g., Guo et al., 2020; Zhu et al., 2020).

Increased production of methane can originate from both ancient permafrost carbon and modern carbon pools. Dean et al. (2020) showed through an analysis of carbon isotope compositions that emissions from inland waters in the East Siberian Arctic were primarily (>80%) driven by the decomposition of contemporary carbon, although sites with active permafrost thaw saw contributions of ancient carbon above 50%. Since both old and recent carbon inputs can act as a source of methane, and given the general rise in temperature, it is likely that the per-unit area emissions of freshwater systems will go up with climate change.

Even though the direction appears clear, the magnitude of this change remains poorly quantified. Tan and Zhuang (2015) used a process-based model to estimate that methane emissions from lakes north of 60° N will increase by 10.3 and 16.2 Tg CH_4 yr^{-1} by the end of the 21st century under a low or high warming scenario, respectively (Representative Concentration Pathways 2.6 and 8.5). However, as with wetlands, local hydrology will play an important role in these trajectories. Arctic lakes can be highly dynamic, and both increases and decreases in lake size have been observed with remote sensing in the past (Smith et al., 2005; Carroll et al., 2011). If lake drainage reduces the number and total extent of lakes, this can ultimately limit the amount of methane emitted from lakes and ponds (van Huissteden et al., 2011). Finally, whether emissions from fluvial systems will go up depends much on the quantity and lability of the inflow of carbon from terrestrial environments, and lakes and ponds (Vonk et al., 2015).

4.1.3 Marine emission trends

For decades, the concept of large-scale release of methane from subsea methane hydrate (also known as clathrate) sources, directly to the atmosphere in rapid cataclysmic events, has been seen as a potential climate tipping point (e.g., Nisbet, 1990; Dickens, 2003; 2011). Hydrates are present beneath the Arctic continental shelves, and can be exposed on some Arctic continental slopes (Westbrook et al., 2009). However, due to the aforementioned processes that destroy methane in the ocean water, the scale of hydrate emissions reaching the atmosphere appears to be relatively insignificant (James et al., 2016; Mau et al., 2017). Also, previous modelling work suggested that methane releases from hydrates under a warmer climate will most likely be a slow process, over timescales of centuries or millennia (Archer, 2015; Kretschmer et al., 2015).

Nonetheless, uncertainties remain with respect to hydrate stabilities and rapid transport through sediments under certain circumstances (Stranne et al., 2016; 2017). The storage of hydrates has been modulated over glacial-interglacial cycles by the presence of massive ice sheets in the Arctic, and associated glacial rebound, which alter the location of the hydrate stability zone (Portnov et al., 2016; Wallmann et al., 2018). Internal cyclical behavior of gas hydrates may make them more vulnerable to climate perturbations, triggering mechanical sediment failures such as the formation of pipes, chimneys or pockmarks (Gupta et al., 2023). Also, long-distance migration of methane through permeable sediments may be the cause of methane venting at shallower depths, beyond the marine limit of gas hydrates (Davies et al., 2024). This highlights that significant uncertainty still exists regarding the dynamics of methane release from gas hydrates to ocean waters.

Changes are occurring more quickly on the shallow shelves of the Arctic Ocean, where thaw rates of 1–15 cm yr^{-1} have been observed near the coast of the Laptev and East Siberian Seas (Overduin et al., 2007). While this thawing of previously frozen permafrost can lead to methane release, this gas still has to traverse the top sediment before entering the water column. Overduin et al. (2015) showed that methane concentrations in the top ~25 m of overlying unfrozen sediment were much lower than in the ice-bonded permafrost below, which was due to rapid anaerobic oxidation of methane long before reaching the seabed. Observed methane emissions in this region are not derived from degrading permafrost, but they must originate from deeper sources (e.g., thermogenic or gas hydrates), possibly released along fault lines (Nicolsky et al., 2012). These deeper sources are unlikely to be influenced by contemporary climate change since the warming

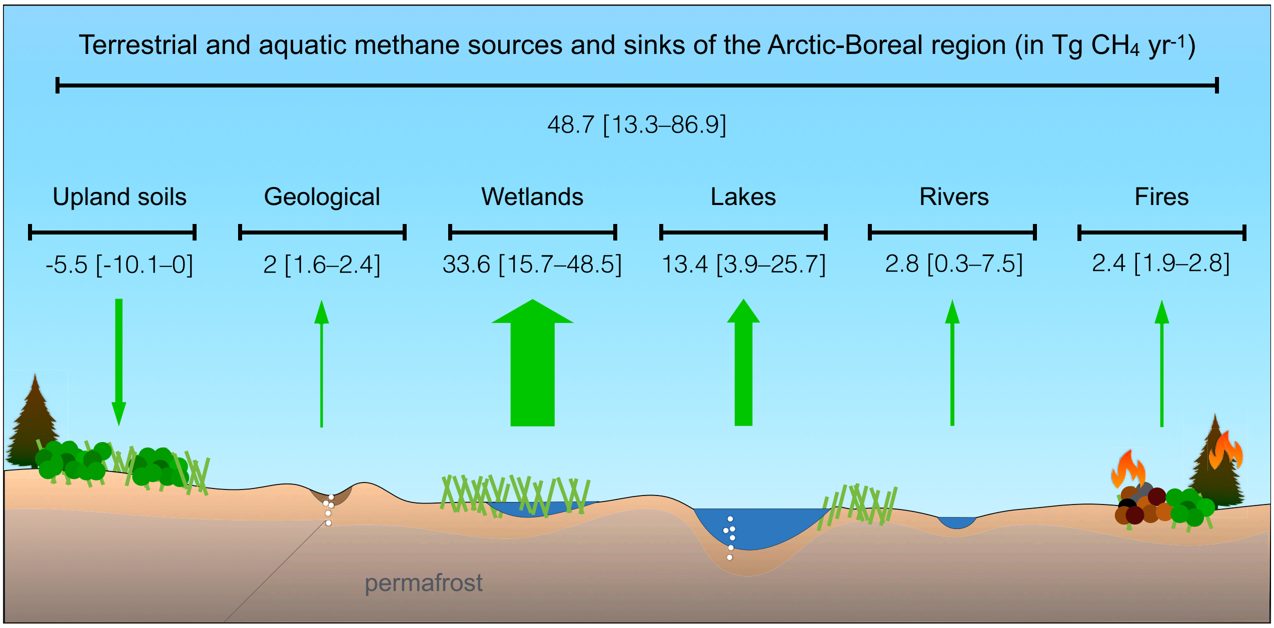

FIGURE 4
Terrestrial and freshwater methane sources and sinks, and their estimated sizes in Tg CH_4 yr^{-1}. Confidence intervals are given in brackets. Green arrows indicate the direction and relative size of each flux. See Table 1 for individual source estimates.

signal takes up to a millennium to reach the depths of the gas hydrate stability zone in subsea permafrost (Dmitrenko et al., 2011).

This indicates that marine methane emissions to the atmosphere are unlikely to significantly increase in magnitude in the near future despite a recent estimate that subsea permafrost contains about double the amount of carbon stored in terrestrial permafrost (Miesner et al., 2023). However, the same study also showed that the large permafrost shelf carbon pool is largely insensitive to thaw, strongly limiting the availability of permafrost carbon and the potential for it to be released to the atmosphere as methane. Still, environmental changes in the Arctic Ocean do matter for the regional methane budget since reductions in sea-ice coverage will increase atmospheric warming due to the sea ice-albedo effect (Screen et al., 2012). This warming extends to the land, which will likely raise terrestrial methane emissions and also affect the CO_2 balance (Parmentier et al., 2013).

4.2 Methane vs. CO_2 emissions

While this study focuses on methane, it is important to note that changes in the surface hydrology of the high latitudes will also have serious consequences for the exchange of CO_2. The decomposition of soil organic matter in wetlands is generally slowed down due to high water tables and low oxygen content. This means that wetlands are typically a source of methane but a sink of CO_2, while dry ecosystems are typically a sink of methane but do not build up equally large soil carbon pools (Treat et al., 2024). If, however, wet ecosystems become drier and soil organic matter is exposed to oxygen, this would lead to a release of CO_2 emissions instead of methane (Schuur et al., 2022). Alternatively, thermokarst can lead to a transformation from dry to wet tundra, leading to a large increase in landscape scale methane emissions, while releasing soil carbon into the aquatic domain in the process (Christensen et al., 2004). These strong links with hydrology emphasize that the exchanges of methane and CO_2 do not happen in isolation, but rather that they are two sides of the same coin.

Combined, the terrestrial ecosystems of the Arctic-Boreal region are most likely a sink of CO_2 (Bruhwiler et al., 2021; Virkkala et al., 2021), but this may be largely offset by CO_2 emissions from inland waters and fires. By accounting for this, Ramage et al. (2024) concluded that it is possible that the combined terrestrial and freshwater systems of the Arctic-Boreal permafrost region are near carbon neutral, emitting 12 (−606.4–661.4) Tg C yr^{-1} on a CO_2 basis alone (Ramage et al., 2024). Still, this estimate comes with a very high uncertainty, and excludes the Arctic Ocean, which is a strong sink of CO_2 (Parmentier et al., 2017), while emitting much less methane to the atmosphere than the land due to efficient oxidation in ocean waters. Nonetheless, if methane is released in large enough amounts from the sea floor, this will enhance ocean acidification, impact marine biogeochemistry and negatively affect calcifying organisms (Biastoch et al., 2011; Boudreau et al., 2015). In the terrestrial domain, the future direction of the CO_2 balance will strongly depend on whether enhanced vegetation growth can or cannot compensate for enhanced soil carbon loss from respiration and increases in disturbances such as fires, thermokarst and extreme weather events (Treat et al., 2024).

5 Conclusion

Over the past decade, longer observational records, more detailed process models, better mapping of wetlands and lakes, and novel upscaling techniques with machine learning have all been tremendously important to improve budget estimates of high latitude methane sources. Table 1; Figure 4 summarize recent budget estimates that predominantly cover the Arctic-Boreal region. Surveyed regions were broadly similar but varied from a simple latitudinal cutoff to the whole Arctic-Boreal region. We extracted data for the Arctic-Boreal region where possible and based our central estimates on medians to minimize biases due to outliers.

Collectively, these studies indicate that the wetlands of the Arctic-Boreal region are emitting 33.6 [15.7–48.5] Tg CH_4 yr^{-1}, followed by lakes and ponds emitting 13.4 [3.9–25.7] Tg CH_4 yr^{-1}. Of the smaller sources, rivers and streams emit 2.8 [0.3–7.5] Tg CH_4 yr^{-1}, fires may add 2.4 [1.9–2.8] Tg CH_4 yr^{-1} and geological emissions about 2 [1.6–2.4] Tg CH_4 yr^{-1}. However, upland soils may compensate somewhat for these emissions by taking up as much as −5.5 [−10.1–0] Tg CH_4 yr^{-1}. Together, this sums up to a total methane budget for the terrestrial Arctic-Boreal region of 48.7 [13.3–86.9] Tg CH_4 yr^{-1}, which is roughly a quarter of all global natural emissions as estimated by inversions (Saunois et al., 2020). In addition, the East Siberian Arctic Shelf may release 2.9 [0–17] Tg CH_4 yr^{-1} while the rest of the Arctic Ocean is estimated to emit 2 [0.4–2.4] Tg CH_4 yr^{-1}, adding up to a total of 4.9 [0.4–19.4] Tg CH_4 yr^{-1} for the whole Arctic marine environment.

Arctic-Boreal methane sources are diverse and dynamic in nature, with a high interannual variability. For a long time, this has made it difficult to separate the signal from the noise when identifying trends. However, recent studies constrained by observations indicate that high latitude methane sources from wetlands have slightly increased over the first two decades of this century by about 1.7–3 Tg CH_4 yr^{-1} (Bruhwiler et al., 2021; Yuan et al., 2024). This increase appears to be due to higher temperatures in early summer, leading to earlier snowmelt and a general higher activity of methanogens. At the moment, however, the observational record remains too sparse to quantify how sources other than wetlands have responded to climate warming.

In a global context, this increase is modest, representing roughly 5%–10% of the recent growth in methane emissions attributed to natural sources worldwide (Nisbet et al., 2023) – albeit with high uncertainty. Natural contributions to the recent rise in atmospheric methane are strongly influenced by tropical wetlands, with the permafrost region contributing to, but not clearly dominating, these changes. Moreover, anthropogenic reductions in methane emissions have the potential to compensate for such natural increases (Christensen et al., 2019), although natural feedbacks will make it more difficult to achieve the goals set out by the Paris agreement (Schuur et al., 2022).

Going forward, a large release of methane from the Arctic-Boreal region remains probable, despite relatively minor emission changes in the recent past. Future trajectories remain highly uncertain and difficult to predict, while the Arctic-Boreal region continues to warm more rapidly than the rest of the world. Wetland methane emissions are highly sensitive to the local hydrology, which means that shifts in the extent of wetlands and inland waters will strongly impact future methane emissions – on top of what can be expected from increased microbial activity following warming. There remains a distinct likelihood that methane emissions from the Arctic-Boreal region will show substantial growth – becoming a more dominant component of the global methane budget.

The evidence presented here appears to point towards a modest rise in methane emissions from the Arctic-Boreal region since the start of the century. At the same time, it is uncertain whether the region as a whole is a net sink or source of CO_2 – when accounting for lateral flows and disturbances. Given the stronger global warming potential of methane compared to CO_2, a change in methane emissions can be an important factor in whether permafrost thaw will lead to a strong positive climate feedback. A continued focus on expansion of monitoring, improvement in process understanding, and added detail in the modeling of vegetation dynamics, microbial processes, geomorphology, and hydrology of high-latitude landscapes will be crucial to determine how climate change will continue to alter methane emissions from the Arctic-Boreal region in the future.

Author contributions

F-JP: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing. BT: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing–original draft, Writing–review and editing. AS: Writing–original draft, Writing–review and editing. TC: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Validation, Writing–original draft, Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The net ecosystem carbon balance (NECB) at catchment scales in the Arctic

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The Net Ecosystem Carbon Balance (NECB) is a crucial metric for understanding integrated carbon dynamics in Arctic and boreal regions, which are vital to the global carbon cycle. These areas are associated with significant uncertainties and rapid climate change, potentially leading to unpredictable alterations in carbon dynamics. This mini-review examines key components of NECB, including carbon sequestration, methane emissions, lateral carbon transport, herbivore interactions, and disturbances, while integrating insights from recent permafrost region greenhouse gas budget syntheses. We emphasize the need for a holistic approach to quantify the NECB, incorporating all components and their uncertainties. The review highlights recent methodological advances in flux measurements, including improvements in eddy covariance and automatic chamber techniques, as well as progress in modeling approaches and data assimilation. Key research priorities are identified, such as improving the representation of inland waters in process-based models, expanding monitoring networks, and enhancing integration of long-term field observations with modeling approaches. These efforts are essential for accurately quantifying current and future greenhouse gas budgets in rapidly changing northern landscapes, ultimately informing more effective climate change mitigation strategies and ecosystem management practices. The review aligns with the goals of the Arctic Monitoring and Assessment Program (AMAP) and Conservation of Arctic Flora and Fauna (CAFF), providing important insights for policymakers, researchers, and stakeholders working to understand and protect these sensitive ecosystems.

KEYWORDS

net ecosystem carbon balance, high Arctic, boreal zone, permafrost region, carbon sequestration, methane emissions, lateral transport, herbivore interactions

1 Importance of understanding NECB in high arctic and northern boreal catchments

The delicate balance of carbon (C) exchange within ecosystems, particularly in Arctic and northern boreal catchments, holds significant implications for understanding and mitigating the impacts of climate change. The Net Ecosystem Carbon Balance (NECB) considers all carbon fluxes, including both vertical net exchange of C between ecosystems and the atmosphere and lateral C transfer downstream. The NECB integrates processes such as photosynthesis and autotrophic and heterotrophic respiration (López-Blanco et al., 2019; See et al., 2024), methane emissions (McNicol et al., 2023; Parmentier et al., 2024; Yuan et al., 2024), and lateral C transport (Rocher-Ros et al., 2019; Casas-Ruiz et al., 2023). Only few studies so far have included all components (Roulet et al., 2007; Nilsson et al., 2008; Juutinen et al., 2013; Pumpanen et al., 2014). Most often land-atmosphere exchanges, lateral dissolved organic C (DOC) fluxes, and their links to hydrological pathways or the impacts of grazing and environmental disturbances are studied in isolation. Addressing all flux components, i.e., compiling NECB, provides a comprehensive measure of an ecosystem's capacity at the landscape level to act as either a C sink or a source. This is essential for evaluating ecosystem health—referring to its resilience and functional stability—and its role in climate regulation (Schuur et al., 2015).

Understanding the regulation of all flux components is pivotal now when the Arctic and boreal ecosystems are undergoing some of the fastest warming on the planet, with temperatures increasing three to four times faster than the global average (AMAP, 2022; Rantanen et al., 2022). Recent climate models project Arctic temperature increases of 3°C–4°C by mid-century, far outpacing global averages due to Arctic amplification (Box et al., 2019). This phenomenon, driven by feedback mechanisms such as albedo changes from sea ice and snow loss, shifts in atmospheric and oceanic circulation, and variations in cloud cover and water vapor, has profound implications for C cycling in these regions (Serreze and Barry, 2011).

Arctic amplification alters precipitation patterns and form (Bintanja and Andry, 2017; Bintanja et al., 2020), disrupts permafrost stability (Koven et al., 2011; Turetsky et al., 2020), and accelerates greenhouse gas (GHG) emissions (Natali et al., 2019; Hugelius et al., 2024; Ramage et al., 2024). While extended growing seasons may enhance plant productivity, increased soil respiration can counteract these gains by releasing stored C (Natali et al., 2019). The overall intensification of biogeochemical activities in soil and water bodies further amplifies this dynamic. Moreover, permafrost destabilization risks releasing vast amounts of stored C, altering hydrological regimes and affecting CO_2 and CH_4 emissions and lateral C transport (Schuur et al., 2009; Vonk et al., 2023). Additionally, warming increases the likelihood of extreme events (Walsh et al., 2020), such as droughts or heavy precipitation, which can exacerbate ecosystem instability and further disrupt C and water cycles (Frank et al., 2015).

The NECB in Arctic-boreal systems plays a central role in global climate change projections due to the enormous C stocks stored in these regions and their sensitivity to warming (McGuire et al., 2009; Schuur et al., 2015). Permafrost regions store approximately 1,000 ± 200 Pg of organic C within the upper 3 m (Hugelius et al., 2014; Mishra et al., 2021; Palmtag et al., 2022)—almost double the C present in the atmosphere. Understanding the NECB responses to warming is crucial for predicting potential carbon-climate feedbacks, which can significantly impact global climate trajectories (Vonk and Gustafsson, 2013; Turetsky et al., 2020). These feedback effects represent a significant challenge for maintaining the stability of the Earth's climate system (Vonk and Gustafsson, 2013; Schuur et al., 2015; Turetsky et al., 2020).

Recent studies (Hugelius et al., 2024; Ramage et al., 2024) have underscored the critical role of permafrost regions in the global C cycle, providing pan-Arctic insights into GHG dynamics from 2000 to 2020. For example, GHG flux upscaling estimates indicate the permafrost region is a net CO_2 sink but a significant source of CH_4 and N_2O emissions (Ramage et al., 2024). Modeling approaches reveal a weak CO_2 sink and substantial CH_4 and N_2O emissions, with a net warming effect over short timescales (20 years) but a neutral effect over 100 years (Hugelius et al., 2024). These findings highlight substantial uncertainties and mismatches between field observations and models, emphasizing the need for localized investigations to better understand site-specific dynamics and interactions affecting NECB across diverse Arctic ecosystems. Watts et al. (2023) estimated the terrestrial domain of Arctic-Boreal zone be a C sink as a whole, but if accounting the aquatic ecosystems, the sink decreased notably and there were substantial differences in the C sink strength across the boreal-arctic domain.

2 Components contributing to the NECB

Understanding the components of the NECB is key to comprehending how Arctic and boreal ecosystems operate and adapt to environmental changes. These components encompass net ecosystem CO_2 exchange, methane emissions, lateral C transport, interactions with herbivores, and ecosystem disturbances. Below, we delve into each component in detail to explore their individual and collective roles in shaping NECB.

2.1 Net ecosystem exchange (NEE) of CO_2

NEE is the balance between gross primary production (GPP) and ecosystem respiration (ER), and both are fundamental components of the NECB. GPP represents the total CO_2 assimilated by plants through photosynthesis, while ER encompasses the release of CO_2 from organisms and decaying matter, including both autotrophic (plant) and heterotrophic (microbial) respiration (López-Blanco et al., 2019). The balance between these two processes determines whether an ecosystem acts as an atmospheric CO_2 sink or source (McGuire et al., 2009; See et al., 2024).

In Arctic regions, GPP is typically constrained by short growing seasons, low temperatures, snow cover, and limited nutrient availability (Chapin III et al., 2000). However, climate change alters these limitations, potentially enhancing GPP by extending the growing season, increasing temperatures in air, soil and water bodies, and augmenting nutrient availability through permafrost thaw (Natali et al., 2015; López-Blanco et al., 2020). Studies have shown that GPP in tundra ecosystems is highly sensitive to temperature fluctuations and can significantly influence NECB (Euskirchen et al., 2006). Longer-term changes in plant community composition, such as shrub expansion, can alter photosynthetic rates and GPP across different landscapes (Myers-Smith et al., 2011; Bjorkman et al., 2018). The NEE is highly sensitive to annual variations in water table levels and temperature. For instance, dry summers or periods with atmospheric drought can shift peatlands, typically net CO_2 sinks, into net CO_2 sources, primarily due to reductions in GPP (Alm et al., 1999; Aurela et al., 2007; Rinne et al., 2020). Historically, peatlands have functioned as C sinks in most years, facilitating peat accumulation over time, which has cooled the climate due to the stored C (Frolking and Roulet, 2007).

In high latitudes, ER, on the other hand, is expected to increase with warming temperatures, potentially offsetting gains in GPP (Schuur et al., 2009; Commane et al., 2017). Soil respiration, a major component of ER, is particularly sensitive to temperature changes in permafrost regions (Bond-Lamberty and Thomson, 2010). Recent research has highlighted the importance of winter respiration, which can significantly contribute to annual C budgets (Natali et al., 2019). Helbig et al. (2022) analyzed multiyear eddy covariance data from boreal-Arctic peatland sites and found that warm anomalies increased CO_2 uptake relative to average conditions when warming occurred in early summer, whereas late-summer warming resulted in increased CO_2 release. These anomalies were linked to earlier vegetation development during early summer and typically lower water levels in late summer, possibly suppressing GPP and increasing ER.

The Arctic-boreal zone exhibits substantial variability in CO_2 fluxes, with observed annual NEE ranging from −27.9 g C m^{-2} yr^{-1} (net CO_2 uptake) to net release of CO_2 in certain years. Seasonal dynamics are pronounced, with monthly GPP varying from −2 to −516 g C m^{-2} and ER from 0 to 550 g C m^{-2} (Virkkala et al., 2022; See et al., 2024). Notably, more than 30% of the region functions as a net CO_2 source, and when fire emissions are included, the permafrost region approaches a net zero CO_2 balance, highlighting the critical role of fire in shaping regional C dynamics (Virkkala et al., 2025). The complex interplay between GPP and ER under changing climate conditions underscores the need for continued monitoring and improved modeling of these processes to accurately predict future C dynamics in Arctic-boreal ecosystems (Virkkala et al., 2022). Respiratory outputs (particularly heterotrophic respiration), and C turnover and decomposition processes remain highly uncertain and poorly constrained in models (Carvalhais et al., 2014; López-Blanco et al., 2019). Precipitation and soil moisture have been highlighted as the key drivers of heterotrophic respiration interannual variability (Yao et al., 2021; Guenet et al., 2024). Such uncertainties ultimately propagate over the rate and magnitude of C accumulation.

2.2 Methane emissions (CH_4)

CH_4 emissions play a crucial role in the NECB of Arctic-boreal ecosystems, particularly in wetlands and peatlands, and areas affected by permafrost thaw. Methane is produced by microbes under anaerobic conditions and has a much higher global warming potential than CO_2 over short time scales (Turetsky et al., 2014; Kuhn et al., 2021). Even without considering the global warming potential, methane emissions in wet ecosystems also form a significant component of the mass transfer of C and may account for 20% of the total C turnover (Christensen et al., 2007). In many, if not all, wetlands CH_4-C losses decrease substantially the C gain of NEE (Juutinen et al., 2013; Rinne et al., 2020). Recent studies have shown that methane emissions in the Arctic are higher than previously estimated, especially during the cold season (Zona et al., 2016). Treat et al. (2018a) estimated that methane emissions from freshwater bodies (observationally measured) contribute 4%–17% of the total annual methane emissions for the circumpolar Arctic region, corresponding to 6.1 ± 1.5 Tg CH_4/year north of 40° latitude. This is also the case in results obtained from ecosystems models for which the calibration is mainly driven by growing season datasets and for which cold season processes may be missing or may not be well accounted for (Ito et al., 2023). CH_4 emissions from lakes and streams are crucial components to consider in the boreal-Arctic region, especially as part of catchment-scale assessments. Some studies even identify freshwater bodies as the largest CH_4 source in the boreal-Arctic area (Wik et al., 2016).

Arctic-boreal wetlands, including peatlands, are significant sources of methane, with emissions modulated by warming and vegetation activity. Wetlands emit in the order of 48.7 (13.3–86.9) Tg CH_4 yr^{-1}, while freshwater systems contribute approximately 12.5 Tg CH_4 yr^{-1} (Parmentier et al., 2024). These emissions are influenced by temperature, vegetation activity, and permafrost thaw. For instance, a recent study found that temperature explains 52.3% of the increasing CH_4 emission trend, followed by GPP (40.7%) (Yuan et al., 2024). Thawing permafrost can lead to the formation of thermokarst lakes and extend wetland areas, potentially releasing large amounts of previously frozen organic matter and increasing methane production (Treat et al., 2018b; Turetsky et al., 2020; Parmentier et al., 2024).

The spatial and temporal variability of methane emissions across Arctic-boreal landscapes presents significant challenges for accurate quantification and prediction. Recent efforts, such as the BAWLD-CH_4 dataset, have advanced our understanding of methane flux patterns across diverse boreal and Arctic ecosystems (Kuhn et al., 2021). However, uncertainties remain, particularly regarding the fate of methane in the water column and its transport through soil, surface runoff and snow (Saunois et al., 2020). For instance, non-growing seasons, particularly in autumn and spring, remain difficult periods for maintaining continuous methane flux measurements (Jentzsch et al., 2024). Vegetation composition and the presence or absence of specific vascular plant species also significantly influence methane emissions, making the impacts of climate change on future vegetation composition a critical area for further study (AMAP, 2015). Uncertainties surrounding lateral methane transport from wet tundra and peatlands are compounded by limited understanding of dissolved methane dynamics—how much is oxidized versus emitted from streams and ponds (Oh et al., 2020). These processes, currently underrepresented in ecosystem models, demand further investigation across diverse Arctic landscapes. Challenges persist in both experimental and observational approaches to accurately measure methane emissions on an annual scale in the context of NECB. Addressing these gaps is essential for improving the parameterizations used in process models. Ultimately, enhancing our understanding of methane dynamics is key to accurately assessing the greenhouse gas budget of Arctic-boreal regions and predicting their feedback to global climate change (Hugelius et al., 2024).

2.3 Lateral C transport

Lateral C transport, the movement of DOC, particulate organic C (POC), and dissolved inorganic C (DIC), plays a crucial role in the Arctic-boreal C balance, yet it remains underrepresented in NECB assessments (Dean et al., 2020). Carbon moves from terrestrial ecosystems to aquatic systems via groundwater leaching, runoff, streams, and rivers, contributing to substantial C losses from terrestrial ecosystems, influencing both local and regional C budgets (Tank et al., 2012; Tank et al., 2018; Vonk et al., 2023). A significant portion of this C is either emitted as CO_2 and CH_4 from freshwater systems or transported to the ocean, with global fluxes estimated at 5.1 Pg C yr^{-1}—of which 0.9–1.3 Pg C yr^{-1} reaches the ocean, 2.1–2.9 Pg C yr^{-1} is released as CO_2, and 0.6–1.5 Pg C yr^{-1} is buried in sediments (Tank et al., 2018). Globally, lateral C fluxes have been estimated to be comparable to the terrestrial CO_2 sink, approximately 3.1 Pg C yr^{-1} (Le Quéré et al., 2016), ranging from 1.1 Pg C yr^{-1} to 5.1 Pg of C yr^{-1} (Drake et al., 2018). In Arctic-boreal ecosystems, studies suggest that lateral C fluxes represent 0.2%–1.4% of the terrestrial C stock, depending on the region and landscape characteristics (Martens et al., 2022), and nearly 20% of the net terrestrial C uptake (Kling et al., 1991).

Recent high-resolution studies have revealed complex seasonal and interannual variations in DOC transport processes in subarctic headwater catchments (Croghan et al., 2024) and indicated complex variations between C sources at the landscape level. Climate change is altering these transport mechanisms, with spring snowmelt floods and summer/autumn storm events becoming increasingly important for DOC export (Rawlins and Karmalkar, 2024), and also winter runoff in southern Arctic sites. The thawing of permafrost is expected to enhance the mobilization and transport of previously frozen organic matter, potentially leading to increased DOC and DIC fluxes to aquatic systems (Vonk and Gustafsson, 2013).

The fate of this laterally transported C is crucial for understanding its impact on the global C cycle. While some of the C may be deposited in sediments or transported to the ocean, a significant portion can be evaded directly to the atmosphere or processed within inland waters, leading to CO_2 and CH_4 emissions (Casas-Ruiz et al., 2023; Mustonen et al., 2024). Recent research has highlighted that small watersheds and water bodies including streams, ponds and lakes may play a disproportionate role in Arctic land-ocean fluxes, emphasizing the need for better representation of these systems in C budget assessments (Vonk et al., 2023). However, the lack of watershed-scale studies across Arctic limit our ability to identify the main controlling factors and key locations at the landscape level.

Integrating aquatic C fluxes and the ecosystem-atmosphere exchange of C remain a challenge due to the high spatial and temporal variability of these processes. Improved monitoring networks including high-resolution sensors, coupled with advanced modeling approaches, are necessary to better constrain estimates of lateral C transport and its contribution to NECB in Arctic-boreal ecosystems (Rocher-Ros et al., 2019; Olefeldt et al., 2021).

2.4 Herbivore interactions

The role of herbivores in C cycling within high-latitude ecosystems has gained increasing recognition in recent years (Schmitz et al., 2014). Both large herbivores, such as reindeer/caribou (Ylänne et al., 2018), muskox (Falk et al., 2015) and small mammals (Tuomi et al., 2019), significantly influence C cycling in Arctic and boreal ecosystems through grazing, trampling, and nutrient deposition (Koltz et al., 2022), also during the snowy seasons. Their trampling and cratering in search of food under the snow can damage the vegetation, potentially hindering treeline expansion (Heggenes et al., 2017). Additionally, tree girdling caused by reindeer rubbing against young trees ("buck rub") can further inhibit forest regeneration (Roturier and Bergsten, 2006). Their interactions can alter vegetation dynamics, soil properties, hydrology, energy balances, and C and nutrient cycling, ultimately affecting the NECB (Ylänne et al., 2015; Schmitz et al., 2023; Schmidt et al., 2024). In the Arctic, grazing and trampling activities compact snow reducing insulation, which consequently prevents permafrost thawing, thereby reducing CH_4 emissions. For example, increasing herbivore densities in Arctic regions could protect up to 80% of the Yedoma permafrost domain, which stores around 500 Gt of organic C (Schmitz et al., 2023). However, herbivory can also have mixed effects on C dynamics, with some studies showing reductions in C uptake by 15%–70% due to changes in plant community composition and ecosystem respiration rates (Schmitz et al., 2018).

Large herbivores are known to influence plant community structure, often reducing shrub and moss abundance and promoting graminoid-dominated vegetation (Olofsson et al., 2009), or reducing overall plant biomass (Olofsson et al., 2014). This shift can have cascading effects on ecosystem processes, including C sequestration, soil respiration (Väisänen et al., 2014), and methane emissions (Falk et al., 2015), as well as on ecosystem energy balance via changes in, e.g., evapotranspiration (Zimov et al., 1995), albedo (te Beest et al., 2016), soil thermal regimes, and thaw depth (Windirsch et al., 2022). Recent studies have highlighted the substantial impacts of herbivores on C fluxes and stocks; for example, muskox and lemming herbivory can reduce net CO_2 uptake in the short term, though vegetation often recovers quickly (Falk et al., 2015; Plein et al., 2022), while different types of large animals can increase the C storage in permafrost soils (Zimov, 2005; Windirsch et al., 2022). Further research is needed however to disentangle whether increased C content results from reduced decomposition or higher C input. Herbivory-induced changes in plant communities not only impact NECB directly but also indirectly through various belowground alterations, such as changes in the quantity and quality of litter (Francini et al., 2014) and soil organic matter (Väisänen et al., 2015). Additionally, herbivores can induce shifts in soil faunal (Sørensen et al., 2009) and microbial communities (Ahonen et al., 2021). Herbivores also influence their environment through the redistribution of nutrients, contributing to local fertilization (Van Der Wal et al., 2004) and physical disturbances, such as trampling (Mosbacher et al., 2019).

The overall strength and direction of herbivore effects on NECB can vary spatially and temporally, influenced by factors such as herbivore traits and density, plant community composition, and climate conditions (Schmitz and Leroux, 2020). Understanding these complex herbivore-ecosystem interactions is essential for accurately assessing and predicting C dynamics in rapidly changing Arctic and boreal regions (Koltz et al., 2022).

2.5 Disturbances

Disturbances can significantly impact the NECB of tundra and boreal ecosystems (Foster et al., 2022) by altering C storage and fluxes (Phoenix and Bjerke, 2016). Climate change is intensifying various disturbance regimes in the Arctic, including extreme weather events (Christensen et al., 2020; van Beest et al., 2022), thermokarst formation (Lewkowicz and Way, 2019; Turetsky et al., 2020), wildfires (Mack et al., 2011; Byrne et al., 2024), and insect outbreaks (Heliasz et al., 2011; Lund et al., 2017).

These natural disturbances, combined with anthropogenic activities like resource extraction (mining, land use and settlements) and infrastructure development (Raynolds et al., 2014), are reshaping tundra landscapes and C dynamics. Extreme weather events disrupt vegetation growth and soil processes (Phoenix and Bjerke, 2016), while thermokarst formation mobilizes frozen soil C (Turetsky et al., 2020). Increasingly frequent wildfires consume surface vegetation and alter post-fire succession (Mack et al., 2011), and expanding insect outbreaks can reduce productivity and increase shrub and tree mortality (Heliasz et al., 2011; López-Blanco et al., 2017; Lund et al., 2017). The northward expansion of beavers into Arctic tundra ecosystems is emerging as a significant disturbance regime, profoundly altering hydrological patterns, accelerating permafrost thawing and enhancing methane emissions (Tape et al., 2022; Clark et al., 2023). The complex interplay between these disturbances creates feedbacks that amplify climate change impacts in tundra and boreal ecosystems (Raynolds et al., 2014; Phoenix and Bjerke, 2016), highlighting the need for comprehensive monitoring and modeling of Arctic C balance.

Understanding and quantifying these components together provides a comprehensive view of the key ecosystem processes influencing NECB in Arctic and boreal ecosystems. Future research should focus on integrating these components to better predict ecosystem responses to ongoing climate change.

3 Methodological advances

Recent years have seen significant advancements in our understanding of high-latitude C dynamics, driven by improvements in both observational techniques and modeling approaches. These advances have enhanced our ability to understand, quantify, and predict NECB in Arctic and boreal ecosystems.

3.1 Eddy covariance flux measurements

Eddy covariance (EC) has become the gold standard for measuring ecosystem-scale greenhouse gas fluxes (Baldocchi, 2003), and recent years have seen significant advancements in this technique. High-frequency open-path and closed-path gas analyzers have improved, allowing for more precise measurements of CO_2, CH_4, and H_2O fluxes (Burba, 2013). The development of low-power, low-maintenance EC systems has enabled year-round measurements in remote Arctic and boreal locations, addressing critical data gaps during the non-growing season (Oechel et al., 2014). Additionally, novel approaches such as the use of unmanned aerial vehicles (UAVs) equipped with miniaturized EC systems (Bolek et al., 2024) or connected with high-resolution portable GHG analysers (Scheller et al., 2022) have emerged, allowing for spatial mapping of fluxes and concentration hot spots over heterogeneous landscapes.

Recent studies have also focused on improving flux gap-filling and partitioning methods. Vekuri et al. (2023) have recently shown that the commonly used marginal distribution sampling (MDS) method produces significant systematic error for data sets collected from northern (>60°N) sites, and should be replaced by machine learning methods which avoid this error. The partitioning methods, which are typically used after gap-filling the NEE time series, separate NEE into its component fluxes of GPP and ER. There are novel machine learning approaches that have been developed to improve the accuracy of flux partitioning, particularly in Arctic ecosystems where traditional methods may fall short (Tramontana et al., 2020). Furthermore, advances in CH_4 isotope measurement techniques have provided new insights into the sources and sinks of C in these ecosystems, revealing significant spatial variations in $\delta^{13}C\text{-}CH_4$ values and highlighting the importance of substrate availability for methanogenesis in driving CH_4 emissions patterns (Rinne et al., 2022).

3.2 Automatic chambers flux measurements

Automatic chamber systems have become increasingly important for measuring GHG fluxes in Arctic-boreal ecosystems, particularly during the challenging non-growing season (Koskinen et al., 2014) and in aquatic systems (Thanh Duc et al., 2020). These systems allow for continuous, high-frequency measurements of CO_2 and CH_4 fluxes, providing crucial data on temporal and spatial variability (Pirk et al., 2017; Natali et al., 2019), also documenting surprising seasonal dynamics and episodic events (Mastepanov et al., 2008). Recent advancements in automatic chamber design have improved their reliability in harsh Arctic conditions, with better insulation and heating systems to prevent snow and ice accumulation (Mastepanov et al., 2013; Korkiakoski et al., 2017).

Multi-chamber systems have been developed to capture spatial heterogeneity in flux patterns, especially important in ecosystems with high microtopographic variability (Mastepanov et al., 2013; Pirk et al., 2017). Additionally, the integration of soil temperature and moisture sensors within chamber systems has enhanced our understanding of the environmental drivers of flux variability (Göckede et al., 2019). These systems can now be coupled with real-time gas analyzers, allowing for immediate data processing and quality control (Korkiakoski et al., 2020). This advancement enables researchers to obtain and analyze high-quality greenhouse gas flux data in near real-time, improving the efficiency and accuracy of field measurements in Arctic and boreal ecosystems.

3.3 Lateral C transport measurements

Lateral transport of C, with particular focus on understanding the speciation of the C pool, has gained attention as a crucial component of the NECB in Arctic-boreal systems (Tank et al., 2018). Recent methodological advances have improved our ability to quantify these fluxes. High-frequency *in situ* sensors for DOC and POC using optical sensors have been deployed in river systems, allowing for continuous monitoring of C export from terrestrial to aquatic ecosystems (Shogren et al., 2021; Rawlins and Karmalkar, 2024). Coupling high-frequency dissolved C concentrations with discharge (e.g., concentration-discharge relationships) provides a tool to identify processes that control C export (Gómez-Gener et al., 2021; Speir et al., 2024). To understand the fate of this C export, there is a need to couple these measurements with *in-situ* aquatic flux measurements, especially given the spatial variability of these fluxes (Bretz et al., 2021).

Tracer techniques, using both stable and radioactive isotopes, have been refined to better understand the sources and ages of water and laterally transported C. These methods have revealed the importance of old C mobilisation from thawing permafrost in lateral fluxes (Serikova et al., 2018), novel approaches combining hydrological measurements with C concentration data have improved estimates of annual C export, particularly during the critical spring freshet period (Beel et al., 2021). Further, recent studies using ^{222}Rn have provided estimations of methane transport in groundwater (Olid et al., 2022).

There has been a recent call for more spatially resolute sampling to identify landscape control points that influence lateral C transport and, consequently, emissions from land-water systems (Bernhardt et al., 2017). To accurately scale these fluxes to the catchment level, it is essential to account for both the landscape features that supply C to freshwater systems (e.g., wetlands, thaw slumps) and *in-situ* controls such as gas transfer velocity (Kokelj et al., 2013; Rocher-Ros et al., 2019; Shogren et al., 2019).

3.4 Exclosure experiments to understand the herbivory component

Fences that either exclude or enclose herbivores are an essential tool for quantifying the impact of herbivory on NECB in Arctic-boreal ecosystems. Long-term exclosure studies, spanning several decades to over a century, have provided valuable insights into the cumulative effects of herbivores on vegetation structure, soil C stocks, and greenhouse gas fluxes (Ylänne et al., 2018). Moreover, exclosure designs that selectively exclude different herbivore guilds (e.g., large, small mammals, and geese) help the disentanglement of their specific impacts (Köster et al., 2017; Petit Bon et al., 2023), which is particularly relevant in the context of shifting tundra herbivory communities (Barbero-Palacios et al., 2024).

The integration of flux measurement techniques with exclosure and enclosure experiments has significantly improved our understanding of herbivory effects on C cycling. For instance, portable flux chambers have been used to compare CO_2 and CH_4 fluxes inside and outside exclosures, revealing how herbivores influence both primary productivity and soil respiration (Cahoon et al., 2012; Lara et al., 2017; Silfver et al., 2020), and how plant abundance, phenology, and nitrogen dynamics change (Mosbacher et al., 2019). Some studies have combined exclosures with manipulative experiments (e.g., warming, fertilization) to investigate how herbivory interacts with other environmental changes to affect NECB (Sjögersten et al., 2012; Väisänen et al., 2014), and to provide crucial data on potential feedbacks between climate change and herbivore impacts on C cycling (Post et al., 2021).

3.5 Long-term monitoring networks and data-model synthesis efforts

Long-term monitoring networks have become increasingly crucial for understanding the complex dynamics of Arctic-boreal C cycling. The FLUXNET network, for example, and its regional counterparts (e.g., ICOS in Europe, AmeriFlux and NEON in North America), has been instrumental to provide continuous, multi-year datasets of C, water, and energy fluxes from numerous sites in high-latitude regions (Pastorello et al., 2020). Specifically, the FLUXNET-CH_4 community network has greatly enhanced our understanding of methane dynamics in wetland ecosystems across the Arctic-boreal zone (Knox et al., 2019). The Greenland Ecosystem Monitoring (GEM) program (Christensen et al., 2017), established in 1995, provides a unique integrated and interdisciplinary approach to understanding Arctic ecosystems and climate change effects, by measuring a wide range of cross-cutting variables across a catchment scale, from glaciers to marine systems within a 20 km range. GEM serves as example of coordinated observational data gathering across meteorological, hydrological, terrestrial and limnic ecosystem domains in a confined catchment area providing the opportunity for true data-based NECB budgeting (Figure 1). This may in turn serve as pivotal data for NECB model calibration and validation.

These networks not only provide essential data for understanding current C dynamics but also serve as early warning systems for detecting ecosystem changes. For instance, the International Tundra Experiment (ITEX) network (Henry et al., 2022), established in the early 1990s, continues to provide valuable long-term data on the impacts of experimental warming on tundra vegetation and associated C fluxes (Bjorkman et al., 2018). Likewise, the Back to the Future project reveals multi-decadal changes in vegetation and soil C stocks (Callaghan et al., 2011).

In-situ GHG budget synthesis efforts have been instrumental in integrating diverse datasets to derive comprehensive insights across the pan-Arctic region. For example, the recent second phase of the Regional Carbon Cycle Assessment and Processes project (RECCAP2) (Ciais et al., 2022) has specifically focused on the permafrost region (Hugelius et al., 2024; Ramage et al., 2024), synthesizing multiple lines of evidence to deliver thorough assessments of current C dynamics in these critical areas. This budgeting initiative includes three extensive compilations of

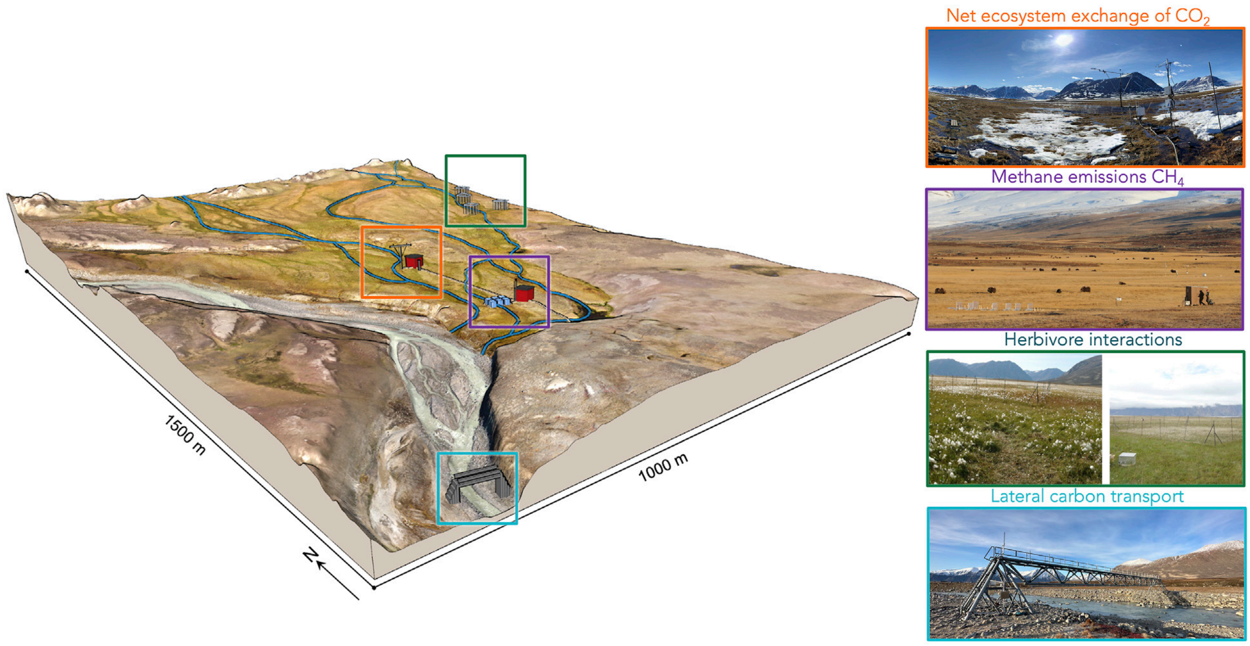

FIGURE 1
Integrated assessment of Net Ecosystem Carbon Balance (NECB) components (Sections 2.1–4) in the Rylekærene fen, Zackenberg, East Greenland. The 3D terrain representation, viewed from the southwest corner, illustrates the spatial distribution and measurement approaches for key C flux processes: net ecosystem CO_2 exchange (orange box, measured via eddy covariance towers), methane emissions (purple box, quantified through automatic chambers), herbivore-vegetation interactions (green box, studied using exclosure experiments), and lateral C transport (blue box, monitored via river discharge and DOC measurements). This landscape-scale integration enables comprehensive NECB modeling and assessment of ecosystem responses to environmental changes. The map has been edited for illustrative purposes, combining hand-drawn features with enhancements using GIS and photo-editing software. It is based on original image mosaics from Greenland Ecosystem Monitoring (2014 and 2020). The topography is vertically exaggerated by a factor of 5, and the locations of buildings and instruments have been modified for presentation purposes. The stream network is simplified for clarity. Picture acknowledgements, from top to bottom: Efrén López-Blanco, Lars Holst Hansen, Falk et al. (2015) from Fig. 3, Efrén López-Blanco.

GHG flux datasets for CO_2 (Virkkala et al., 2022), CH_4 (Kuhn et al., 2021), and nitrous oxide, N_2O (Voigt et al., 2020), all derived from valuable *in-situ* observations. These collective efforts have not only advanced our understanding of existing C cycling patterns but have also underscored the numerous unresolved uncertainties that persist in this field.

3.6 Modeling approaches and data assimilation

Since the 1970s, Earth System Models (ESM) have been used to study the NECB by accounting for biophysical processes. However, it is only in the 2000s that these models began to incorportate the full complexity of the C cycle and its interactions with the other biophysical components (Fisher and Koven, 2020). Since then, significant progress has been made in modeling approaches and data assimilation techniques to improve Arctic-boreal C cycling representation. The development of more sophisticated ESM that incorporate permafrost dynamics, coupled carbon-nitrogen cycles, and improved representations of Arctic vegetation has enhanced our ability to project future changes in the NECB. Specifically, ESM have been refined to explicitly represent key processes specific to high-latitude ecosystems, such as permafrost dynamics (Guimberteau et al., 2018; Chaudhary et al., 2020), snow insulation effects (Wang et al., 2013; Pongracz et al., 2021; Charbit et al., 2024), *Sphagnum* dominated peatland ecosystems (Qiu et al., 2022), vegetation shifts (van den Hurk et al., 2016) and lateral transfer of C from land to rivers (Bowring et al., 2019; Bowring et al., 2020). The incorporation of microbial dynamics and soil organic matter decomposition models has improved simulations of soil C responses to warming (Huang et al., 2021).

Data assimilation techniques have evolved to better integrate diverse observational datasets with model simulations and ultimately allowing for better constraints on regional and pan-Arctic C budgets. For example, the Carbon data model Framework (CARDAMOM) (López-Blanco et al., 2019; Hugelius et al., 2024) or the Carbon Cycle Data Assimilation System (CCDAS) (Kemp et al., 2014; Scholze et al., 2019) now incorporate a wide range of observations, including atmospheric CO_2 concentrations, satellite-derived vegetation indices, soil organic C, plant biomass, burned area, and forest loss to provide more accurate estimates of C fluxes, stocks, and transit times and quantify their uncertainties.

Moreover, machine learning approaches, such as neural networks and random forests, have been increasingly used to upscale site-level flux measurements to regional and pan-Arctic scales, providing new insights into spatial patterns and drivers of C fluxes (Väisänen et al., 2014; Peltola et al., 2019; Virkkala et al., 2021; Yao et al., 2021; McNicol et al., 2023; Nelson et al., 2024).

Additionally, the development of benchmarking systems that use multiple observational constraints has enhanced our ability to evaluate and improve Earth System Models for high-latitude regions (Collier et al., 2018; Hou et al., 2023).

In situ data are also crucial for the calibration and validation of process-based models (Le Noë et al., 2023). Specifics of Arctic regions promoted sensitivity model analysis studies assessing models' capacity in simulating Arctic ecosystems (Dantec-Nédélec et al., 2017; Pongracz et al., 2021). Today, more and more models are employing harmonized monitoring databases with statistical optimisation approaches such Bayesian methods and history matching (Salmon et al., 2022; Bacour et al., 2023; McNeall et al., 2024), among others, to calibrate model parameters at regional or global scales and to pinpoint model weaknesses. Additionally, *in situ* data synthesis and meta-analysis are guiding modellers to assess model development priority that aims to reduce model uncertainty or to enhance physical process representation.

4 Remaining uncertainties

Despite the recent advancements in our understanding of C cycling dynamics, significant uncertainties persist, particularly in permafrost regions. The release of CO_2, CH_4, and N_2O, and also lateral DOC transport from thawing permafrost represents a critical yet poorly constrained component of the global C budget. Climate change hydrologically activates different layers of Arctic soils, potentially triggering new C processes. The recently published permafrost RECCAP2 update, following an initial budgeting effort (McGuire et al., 2012), aimed to address these uncertainties by synthesizing two decades of observations and modeling efforts (Hugelius et al., 2024; Ramage et al., 2024). Insights from RECCAP2 highlight the complexity of permafrost region GHG dynamics and underscore the need for improved monitoring and modeling approaches to accurately quantify their contribution to atmospheric GHG concentrations. Two important take-home messages have been found: First, there are large discrepancies between bottom-up and top-down estimates (Hugelius et al., 2024) - Bottom-up approaches (data-driven upscaling and process-based models) generally estimate higher land-to-atmosphere fluxes for all GHGs compared to top-down approaches (atmospheric inversions). This points to fundamental differences in methodologies that need to be reconciled. From a modeling perspective, priorities for future research include improved representation of inland water ecosystems including rivers, lakes, reservoirs and materials lateral transfer, and disturbances like fire dynamics and abrupt permafrost thaw in process-based models, and the compilation of process-based model ensembles for CH_4 and N_2O (Hugelius et al., 2024). The increased complexity of models, driven by the explicit representation of processes, is both challenging and essential to accurately capture the spatial heterogeneity and temporal dynamics of NECB. Second, there is a need for more and better well-distributed *in-situ* data coverage - there are significant gaps in spatial and temporal coverage of *in situ* GHG measurements, especially for winter and shoulder seasons (Ramage et al., 2024). On a related note, the ongoing geopolitical conflict and war between Russia and Ukraine have severely deteriorated our ability to study and understand not only current but also future pan-Arctic changes (López-Blanco et al., 2024).

The northward advancement of the tree- (Harsch et al., 2009) and shrub- (Myers-Smith and Hik, 2018) lines in the boreal-Arctic transition zone represents two significant ecological processes driven by climate warming, with implications for vegetation composition, surface albedo, and C dynamics. These shifts can enhance aboveground C storage but may also reduce surface albedo, as darker canopies replace tundra vegetation, thereby amplifying regional warming through feedback mechanisms (Sturm et al., 2005; Bjorkman et al., 2018; Schmidt et al., 2024). However, the advancement of tree and shrub lines is neither uniform nor as rapid as anticipated (Myers-Smith et al., 2011; Rees et al., 2020), due to local factors such as nutrient availability, soil conditions, and herbivory, which further modulate these processes. For example, nitrogen limitation in Arctic soils has been shown to constrain tree growth despite warming (Körner and Paulsen, 2004). Moreover, shifts in vegetation composition can alter soil organic C dynamics and decomposition rates, influencing net C balance (Natali et al., 2019). Herbivory also plays a significant role by altering vegetation structure and soil properties; for example, reindeer grazing can reduce shrub density and limit C uptake, further effecting ecosystem C storage (Koltz et al., 2022).

At a local-to-regional scale, addressing these uncertainties will require expanded and comparable long-term monitoring measurements, continued data synthesis efforts for CO_2, CH_4 and N_2O (e.g., , improved resolution in upscaling techniques (Ramage et al., 2024), and ultimately advancing integration between field observations, remote sensing data, and numerical models to more effectively constrain previously unconstrained ecosystem processes (Hugelius et al., 2024). Reducing these uncertainties is critical for accurately quantifying the contemporary and future GHG budgets of the permafrost region.

5 Future perspective

This paper highlights the critical importance of Arctic and boreal ecosystems in the global C cycle and their vulnerability to rapid climate change. Our review of the key NECB components, methodological advances, and remaining uncertainties, emphasizes the critical need to address and quantify uncertainties in GHG budgeting for permafrost regions and provides several key insights for future research and policy directions:

1. Integrated monitoring approaches: There is a pressing need for more comprehensive, year-round monitoring networks that integrate multiple NECB components, including CO_2 and CH_4 fluxes, lateral C transport, and disturbance impacts. Long-term, catchment-scale studies like the one flagged in Zackenberg Valley offer valuable models for future research efforts.
2. Focus on understudied components: Greater attention should be given to quantifying and understanding the roles of winter fluxes, lateral transport of C, disturbance regimes, and herbivore interactions in the NECB of Arctic-boreal

ecosystems. This will likely help reduce discrepancies between bottom-up and top-down GHG estimates.

3. Advancing methodologies: Reducing uncertainties in NECB assessments requires the adoption of state-of-the-art technologies and methods. For example, this includes deploying high-resolution GHG analyzers that can operate in extreme Arctic winters and remote areas with limited power supply, using high-resolution remote sensing tools to improve upscaling capabilities, and integrating isotopic/radioactive tracing techniques to better understand the sources and ages of transported C. Additionally, heavily data-constrained modeling approaches and innovative field experiments are crucial to quantifying and disentangling the individual processes shaping the Arctic-boreal C budget.
4. Interdisciplinary collaboration: Addressing the complex challenges of Arctic C cycling requires increased collaboration across disciplines, including ecology, biogeochemistry, hydrology, and climate science and across approaches, including measurements, remote sensing and modeling. This interdisciplinary approach is essential for developing a holistic understanding of NECB dynamics.
5. Policy and collaboration frameworks: Strengthening NECB research within the context of the Arctic Council, integrating the AMAP and CAFF agendas, is vital. This includes fostering collaboration between local data-model initiatives and pan-Arctic networks, encouraging the development of holistic, site-specific programs with broader regional relevance, and aligning these efforts with international climate goals.

By addressing these key areas, researchers can significantly enhance our ability to predict and mitigate the impacts of climate change on Arctic and boreal C cycles. This improved understanding will be crucial for informing effective climate policy, ecosystem management strategies, and global climate change mitigation efforts in these rapidly changing northern landscapes.

Author contributions

EL-B: Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review and editing. MV: Writing – review and editing, Investigation, Resources. ES: Writing – review and editing, Investigation, Resources. CJ: Writing – review and editing, Investigation, Resources. NS: Writing – review and editing, Investigation, Resources. HM: Writing – review and editing, Investigation, Resources. AL: Writing – review and editing, Investigation, Resources. SJ: Writing – review and editing, Investigation, Resources. JS: Visualization, Writing – review and editing, Investigation, Resources. TC: Conceptualization, Writing – review and editing, Investigation, Resources.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Editorial: Climate change impacts on arctic ecosystems and associated climate feedbacks

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Editorial on the Research Topic
Climate change impacts on arctic ecosystems and associated climate feedbacks

1 Introduction

The Arctic region, a pivotal component of the Earth's climate system, is experiencing rapid and unprecedented changes driven by climate change (Meredith et al.).

The Arctic Council has, through its report to Ministers in 2019, acknowledged that climate change will affect ecosystems and ecosystem services and that this is key to human livelihoods in the Arctic. As a follow up on this the Arctic Council, through its working groups *Arctic Monitoring and Assessment Programme* (AMAP) and *Conservation of Arctic Flora and Fauna* (CAFF), decided to initiate an assessment and a process with a focus on how climate change affects Arctic ecosystems and feedbacks and inform strategies for adaptation and resiliency. Forming part of this assessment process this Research Topic investigated the complex dynamics of Arctic ecosystems, focusing on marine, terrestrial, and atmosphere-ecosystem interactions. As sea ice diminishes and temperatures increase, the equilibrium of these ecosystems is disrupted, resulting in significant alterations in biodiversity, species distribution, and ecological processes. This Research Topic of studies elucidates the critical role of ice algae in marine food webs, the intricate feedback loops between tundra ecosystems and the climate, and the importance of methane emissions in global climate feedback mechanisms. By addressing key knowledge gaps and emphasizing the necessity for adaptive management strategies, this Research Topic provides a comprehensive understanding of the challenges and opportunities confronting Arctic ecosystems in the context of a rapidly changing environment.

2 Findings

2.1 Marine

The role of the productivity of Arctic marine ecosystems is crucial. Here ice algae play an important role and particularly in their contributions to both benthic and pelagic food webs amidst changing sea ice conditions (Niemi et al.). Ice algae serve as a high-quality carbon source for benthic organisms, especially during the ice melt period, which triggers benthic growth and reproduction. Further research is needed to understand the dynamics of ice algae production, degradation, and their interactions with other carbon sources to fully grasp their impact on ecosystem functioning. Importantly, more research is needed to understand the consequences of climate induced changes in sea-ice dynamics for ice algae supply and the sympagic-benthic-pelagic coupling.

Pecuchet et al.reviews the increasing frequency, intensity, and duration of marine heatwaves (MHWs) in the Arctic and Subarctic regions, highlighting their unique dynamics influenced by sea ice and ocean-atmospheric interactions. Sea ice loss and narrow thermal niches of high-arctic organisms make the Arctic marginal seas highly exposed and vulnerable to MHWs. The ecological impacts of MHWs are significant and include shifts in species distribution, declines in marine life, and alterations in food webs. It emphasizes the need for long-term studies to understand the cumulative effects of MHWs and their interactions with other climate variables and human activities (Pecuchet et al.) and calls for adaptive management strategies to enhance ecosystem resilience against MHWs.

Climate change impacts the migratory patterns of Arctic marine vertebrates, including fishes, seabirds, and marine mammals, by altering resource availability and ecosystem dynamics due to declining sea ice, more open water patterns as well as changing ocean conditions (Kuletz et al.). These changes affect the timing and spatial extent of the northward migration during summer with consequences for the endemic Arctic ecosystems. The reduction of sea ice will also influence human activities with increase in vessel traffic, oil, gas and mining exploration and extractions, etc., that can affect spatial distributions and migratory patterns of endemic Arctic species, including species of importance to local and indigenous communities and lifestyle. Conservation strategies are therefore necessary to address these challenges, with particular attention to the implications for indigenous communities reliant on these species.

In Arctic and Subarctic ecosystems, climate change-induced migration patterns of marine vertebrates highlight the phenomenon of borealization discussed in a further paper in this Research Topic (Husson et al.), where Arctic ecosystems acquire characteristics typical of southern boreal ecosystems. Species redistribution driven by thermal preferences leads to significant changes in biodiversity and ecosystem functioning. Adaptive management strategies are essential to address the ecological and socio-economic consequences of these changes, especially for local human communities dependent on these ecosystems.

2.2 Terrestrial and freshwater

Biotic interactions play a critical role in shaping feedback loops between tundra ecosystems and the climate system, especially in the context of rapid Arctic climate change. Schmidt et al.identify key feedback loops between climate and tundra ecosystems as albedo, carbon dynamics, and permafrost thaw and how vegetation, decomposers and herbivores significantly influence these processes. Current ecosystem models often neglect these biotic influences, leading to inaccurate predictions of ecosystem responses to climate change. A comprehensive understanding of these interactions is essential for improving the accuracy of climate and ecosystem models.

Significant environmental changes are occurring in Arctic landscapes, particularly concerning soil carbon dynamics and vegetation greenness. Frost et al. discuss how climatic variability and Indigenous knowledge are crucial in understanding these changes, emphasizing the importance of integrating local insights with scientific data. Trends in Time-Integrated NDVI (TI-NDVI) and MaxNDVI indicate a shift towards increased plant productivity and greening in the Arctic, despite interannual variability. The impacts of permafrost thaw on plant growth and soil hydrology further underscore the complexity of these interactions.

The unprecedented summer of 2023, marking the first time global temperatures exceeded 1.5 °C, underscores the urgent need to understand also the implications of extreme fire regimes on biodiversity and ecosystem functions (Baltzer et al.). Changing fire regimes affect the ecological resistance and resilience of boreal ecosystems, with pyrodiversity and post-fire residual vegetation playing important roles. While large boreal wildfires can enhance biodiversity through varied burn severity, they also pose risks of compositional changes and recruitment failures in forest ecosystems.

Mård et al. presents a spatial analysis showing there is a small spatial overlap between hydroclimate and ecosystem monitoring. *In-situ* monitoring of climate and hydrological variables is in general sparse, especially at higher latitudes. The catchment-based approach is recommended for studying hydroclimate-ecosystem interactions, but its application is limited due to the spatial mismatch in monitoring data. Some regions with dense monitoring networks can serve as starting points for catchment-based studies, such as northern Fennoscandia, Greenland, Alaska, and parts of Canada and Russia (Mård et al.).

2.3 Atmosphere-ecosystem interactions

Methane emissions from the Arctic-Boreal region, encompassing both terrestrial and marine sources such as wetlands, lakes, and permafrost, play a significant role in global climate feedback mechanisms. Anaerobic conditions in organic soils, particularly in waterlogged environments, facilitate methanogenesis. Parmentier et al. discuss the uncertainties surrounding future methane emissions due to climate change and the complex interactions between various environmental factors. Disturbances like wildfires and animal activity also impact methane dynamics, highlighting the need for a comprehensive understanding of methane sources and sinks.

Interactions between climate change, aeolian dust, and Arctic ecosystems are crucial, with dust playing a significant role in ecological processes. Meinander et al. show how dust can transport microorganisms, nutrients, and toxins, affecting soil formation and ecosystem health. The frequency and intensity of Sand and Dust Storms (SDS) have increased due to climate change, exacerbating desertification and land degradation. Feedback mechanisms related to dust emissions and their long-range transport impact atmospheric chemistry and ecosystem dynamics.

Arctic and boreal ecosystems play a critical role in the global carbon cycle and are highly vulnerable to climate change. Reducing uncertainties in Net Ecosystem Carbon Balance (NECB) assessments through advanced methodologies and technologies is essential (López-Blanco et al.). Understanding carbon cycling patterns, particularly in relation to permafrost thaw and greenhouse gas dynamics, is crucial. Discrepancies between bottom-up and top-down greenhouse gas estimates highlight the need for improved modeling approaches. Enhanced research is necessary to accurately quantify greenhouse gas budgets in permafrost regions. Catchment scale studies are highly appropriate for such studies as also discussed by Mård et al.

3 Gaps

3.1 Marine

There are significant knowledge and data gaps regarding the spatial and temporal extent of borealization across the Arctic, particularly in the Siberian seas and Canadian Arctic regions. Limited data availability is noted for winter and polar night processes, as well as transition periods between ice-free and ice-covered seasons. The understanding of microbial communities, epibenthos, and infauna is underdeveloped, necessitating more research resources to characterize these ecosystem components. The adaptive capacities of species to climate change and their phenotypic plasticity remain poorly understood, impacting predictions of species responses.

Amid climate change, there is limited understanding of how altered spatial organization and migratory patterns in Arctic shelf and pelagic ecosystems affect predator-prey relationships, inter and intra specific competition and food web dynamics. The impacts of increased human activity in previously ice-covered areas on Arctic ecosystems remain underexplored. The adaptability of Arctic marine vertebrates to unpredictable physical and biological conditions is not fully understood, necessitating further research.

There are substantial knowledge gaps regarding the subsurface mechanisms of marine heatwaves (MHWs) in Arctic regions. The predictability and forecasting of MHWs in the Arctic remain poorly understood. Challenges exist in identifying MHWs due to sea ice cover limiting open-water days. Defining relevant MHW thresholds is difficult due to low sea temperature variability. Further research is needed on the detection and mechanisms of MHWs in polar regions. The ecological impacts of MHWs on various taxa are still not fully understood. There is a need to improve predictive models for better management and conservation strategies.

Focused research is needed to predict future coupling between marine sub-webs, considering trophic markers of multiple carbon sources due to ongoing sea-ice change. The extent to which ice algal supply increases with multi-year ice replacement requires further investigation, particularly regarding the photophysiology of ice-algal species. The impact of variations in ice algae supply on benthic biodiversity and biomass, as well as the responses to changing food source diversity and predator-prey interactions, necessitates mechanistic studies. Understanding the influence of light-driven phenology on ice algae production, degradation, and quality is critical.

3.2 Terrestrial and freshwater

There is a significant research gap in the integration of biotic influences into climate and ecosystem models, particularly regarding feedback loops between tundra ecosystems and the atmosphere. A thorough meta-analysis on biotic influences on feedback loops in high-latitude ecosystems is needed, focusing on the magnitude and direction of impacts. Many biotic influences appear patchy in space and time, hindering a comprehensive understanding of their roles in ecosystem responses to climate change. Capturing complex feedback networks and interactions between biotic and abiotic components in future modeling efforts is essential.

The strength and longevity of greening trends, local declines in productivity, and the impact of disturbances and extreme events remain uncertain. Key knowledge gaps and uncertainties persist concerning the historical and future state of tundra ecosystems and their connection to spatiotemporal variability in greening trends. Improved integration of field-based datasets, particularly outside traditionally well-studied areas, is needed, currently hindered by access and collaboration barriers. Understanding how intensifying disturbances will interact with climate-driven greening over the long term is crucial.

Key knowledge gaps regarding the direct effects of changing fire regimes on wildlife taxa necessitate additional baseline data collection to better understand these impacts. There is an urgent need to improve understanding of the impacts of burning conditions experienced in 2023 on northern habitats and associated wildlife communities. The complexities between climate, wildfire, and vegetation, as well as their direct and indirect effects, require further exploration to inform conservation and management actions. Developing ecological forecasting tools to anticipate land cover changes and their impacts on wildlife is essential.

There is a significant lack of *in-situ* monitoring stations for key hydroclimate variables like precipitation and snow cover, particularly in remote and northern areas. Groundwater monitoring is primarily conducted near research stations and municipal areas, with limited data sharing and representation of larger spatial variations. Ecosystem monitoring is concentrated around accessible regions and research stations, leading to potential biases in understanding Arctic ecosystems.

3.3 Atmosphere-ecosystem interactions

There is a significant lack of knowledge regarding the total surface area and location of wetlands, which hampers accurate methane budget assessments in the Arctic-Boreal region. This has led to reliance on outdated wetland maps. Further, temporal data gaps, particularly in winter, are problematic as they may account for up to half of annual emissions. The heterogeneous nature of Arctic landscapes complicates current monitoring efforts, making upscaling and process modeling challenging.

The temperature-dependent consumption of atmospheric methane by dry soils adds further uncertainty to emission estimates.

A better understanding of the complex counterbalancing feedback related to Arctic dust is needed, particularly how increased dust emissions affect climate interactions. There is a lack of characterization of low latitude dust source emissions, such as road and agricultural dust, complicating the interpretation of dust loadings. Future research should focus on the optical properties of various dust types compared to black carbon to estimate their climatic significance. Cross-sectional networking among atmospheric dust experts and soil and cryospheric experts is essential for identifying current and future dust source locations and particle properties.

Significant gaps exist in the spatial and temporal coverage of *in-situ* greenhouse gas (GHG) measurements, particularly during winter and shoulder seasons. At the catchment scale uncertainties surrounding lateral methane transport from wet tundra, lakes and peatlands are compounded by a limited understanding of dissolved methane dynamics, necessitating further investigation. The roles of winter fluxes, lateral transport of carbon, disturbance regimes, and herbivore interactions in the Net Ecosystem Carbon Balance (NECB) of Arctic-boreal ecosystems require greater attention to reduce discrepancies in GHG estimates.

4 Suggested future research foci

The papers in this Research Topic have outlined both specific and broader recommendations for future research. In the policy brief that introduced the Research Topic, a number of action points were identified (Fauchald et al.). Here these action points are merged with foci identified in the individual papers. These foci should advance the overarching theme of fostering further efforts at the intersection of biodiversity, ecosystem studies, and cumulative climate feedbacks. The suggestions include:

- To further quantify changes in ice algae and assess impacts on trophic structures and phenology effects.
- To investigate benthic species adaptability to changing food sources and long-term climate impacts on migratory patterns.
- To develop monitoring programs for shifting migratory routes, new wintering areas, and interactions during migrations, as part of a coordinated pan-Arctic monitoring effort.
- To work on the detection, mechanisms, and effects of marine heatwaves (MHWs) on species resilience and interactions with stressors.
- To improve predictive models for ocean carbon cycle, borealization extent, nutrient limitations, and integrate biotic interactions and feedback loops.
- To improve predictive models for changes in migration patterns and distribution of species of importance for local and indigenous communities as well as species of socioeconomic and cultural importance.
- To adapt monitoring to ecosystem components of local community importance and study socio-economic consequences of ecological transformations, including capacity building for ecosystem-based management.
- To prioritize coordinated ecological and hydroclimatic monitoring in regions most vulnerable to climate change to improve spatial coverage and data quality, supported by a central data repository and online knowledge hub.
- To utilize advances in satellite remote sensing, drones, and machine learning to enhance monitoring capabilities and fill spatial gaps.
- To focus on smaller catchments or sub-catchments with available monitoring data to improve detection, interpretation, and projection of linked hydroclimate-ecosystem dynamics.
- To foster cross-disciplinary research efforts to better understand the complex interactions between climate, cryosphere, water, and ecosystems in the Arctic.
- To investigate relationships between vegetation changes, soil food webs, carbon dynamics, and greening trends.
- To advance novel sensor capabilities and integrated monitoring approaches for GHG budgeting and flux measurements.
- To further understand the impacts of dust emissions and develop forecasting tools for fire regimes and climate change impacts.
- To co-develop policy-relevant pathways and scenarios with scientists, policymakers, and Indigenous knowledge holders to explore plausible futures and desirable goals for Arctic socio-ecological systems.
- To promote bottom-up approaches for nature-based solutions and ecosystem-based adaptation strategies through community-based co-development of actions to enhance resilience.

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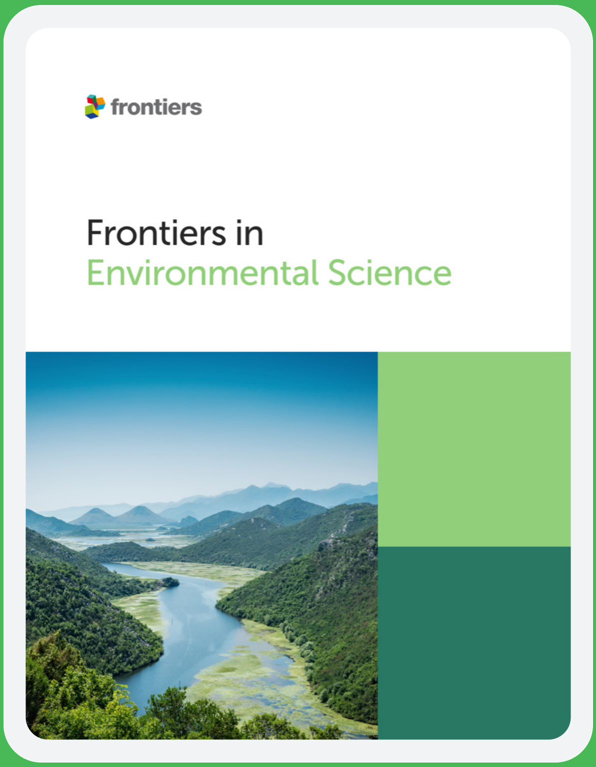

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