Title

The ecosystem-climate-human nexus in the Arctic

Authors

Elizabeth Stunz[1,2*], Robert G. Björk[2,3], Anne D. Bjorkman[1,2], Mats P. Björkman[1,2], Martina Angela Caretta[4], Deliang Chen[3], Nils Droste[5], Geerte Fälthammar de Jong[1,2], Paul A. Miller[6,7], Tero Mustonen[8], Wilhelm Osterman[1,2], Louise Rütting[3,10], Henrik G. Smith[7,9], Christine D. Bacon[1,2*]

Author institutions

[1] Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden
[2] Gothenburg Global Biodiversity Centre, Gothenburg, Sweden
[3] Department of Earth Sciences, University of Gothenburg, Gothenburg, Sweden
[4] Department of Human Geography, Lund University, Lund, Sweden
[5] Department of Political Science, Lund University, Lund, Sweden
[6] Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden
[7] Centre for Environmental and Climate Science, Lund University, Lund, Sweden
[8] Snowchange Cooperative, Lehtoi, Finland
[9] Department of Biology, Lund University, Lund, Sweden
[10] Chair of Soil and Plant Systems, Brandenburg Technological University Cottbus-Senftenberg, Germany

*Corresponding authors

Author Emails

Elizabeth Stunz: elizabeth.stunz@bioenv.gu.se
Robert G. Björk: robert.bjork@gu.se
Anne D. Bjorkman: anne.bjorkman@bioenv.gu.se
Mats P. Björkman: mats.bjorkman@bioenv.gu.se
Martina Angela Caretta: martina_angela.caretta@keg.lu.se
Deliang Chen: deliang@gvc.gu.se
Nils Droste: nils.droste@svet.lu.se
Geerte Fälthammar de Jong: geerte.de.jong@bioenv.gu.se
Paul A. Miller: paul.miller@nateko.lu.se
Tero Mustonen: tero@lumi.fi
Wilhelm Osterman: wilhelm.osterman@bioenv.gu.se
Louise Rütting: louise.andresen@gu.se
Henrik G. Smith: henrik.smith@biol.lu.se
Christine D. Bacon: christine.bacon@bioenv.gu.se

Acknowledgements

ES was supported by the Carl Tryggers Foundation Postdoctoral Scholarship (CTS22:2329). RGB was supported by the Swedish Research Council (#2018-04202, #2023-04048). PAM was supported by the Swedish government funded Strategic Research Area ModElling the Regional and Global Earth system, MERGE. TM was supported by the Biodiversa NARROW project. CDB was supported by the Swedish government funded Strategic Research Area Biodiversity and Ecosystem Services in a Changing Climate, BECC, and the Swedish Research Council (#2017-04980, #2022-03927).

Abstract

The Arctic has warmed at nearly four times the global average since 1979, which has intensified the disruption of its biotic and local human communities under ongoing environmental change. Here, we explore the ecosystem-climate-human nexus in the Arctic region. We summarize current knowledge of regional climate change and its impact on ecosystems and their functions, highlight gaps and uncertainties, and explore future outlooks to provide an overview of key areas for ongoing and future research. By detailing how the combination of biodiversity, environmental, and functional changes affect humans, we highlight the necessity of expanding climate change research to better incorporate environmental and social change, and predict ecological response, thereby increasing the resilience of Arctic communities.

Keywords

Biodiversity, Arctic, climate change, human impacts, terrestrial, tundra

Introduction

The Arctic region, which covers 5% of Earth's terrestrial surface (Meltofte et al. 2013), is in crisis. The greatest contemporary changes in both average and year-to-year variability of air temperature are occurring in the Arctic, which has already warmed at nearly four times the global average since 1979 (Rantanen et al. 2022). Climate change is already affecting marine and terrestrial biodiversity in the Arctic by driving changes in species' ranges and modifications of their phenotypes and life cycles across the Tree of Life (e.g. Pecl et al. 2017, Bjorkman et al. 2018, van Beest et al. 2021). Further progression of climate change will cause increased permafrost thaw, retreat of glaciers and ice sheets, and decreased snow cover and sea ice (Intergovernmental Panel on Climate Change [IPCC] 2022), exacerbating these changes (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES] 2019). Arctic permafrost thaw and increased wildfire frequency has disrupted global carbon storage, accelerating the pace of environmental change (McCarty et al. 2020, Witze 2020). Permafrost thaw, extractive industries, and thinning and retreating glaciers and sea ice contribute to reduced land accessibility and loss of territorial rights of local human communities (Kumpula et al. 2011, Hanaček et al. 2022).

Livelihoods of Indigenous Peoples in the Arctic are based on nomadic herding and informed by millenia of Indigenous Knowledge, and weather instability under climate change is creating novel hurdles that cannot be navigated with previous experience (Shadrin 2021). Environmental change is increasing human access to natural resources in the Arctic, and heavy investments in economic activities including agriculture, maritime trade, natural resource exploration and extraction, immigration, and tourism are expected over the next decades (Barnhart et al. 2016, Constable et al. 2022), creating a high risk of social conflicts (Hanaček et al. 2022). Increased human population sizes and economic activities will introduce new risks associated with extreme weather events and warmer temperatures, such as damage to infrastructure from permafrost thaw. Damage to roads and seasonal pathways can also impact transport options and food accessibility for Indigenous Peoples and cause loss of connectivity between Arctic communities (Constable et al. 2022). Conversion of natural areas into cropland will also impact biodiversity and biogeochemical cycling, and further reduce the areas used for hunting, fishing, gathering, and reindeer (*Rangifer tarandus*) and muskox (*Ovibos moschatus*) pasture, i.e. the basis of society of many Indigenous Peoples (Mustonen and Shadrin 2021, Unc et al. 2021).

The multi-faceted changes in the Arctic will feed back on Earth system processes. Changes in the extent of snow, sea ice, permafrost, and glaciers all contribute to climate regulation at a global scale. Potentially irreversible and rapid non-linear changes of the Earth climate system (such as loss of permafrost and increased melting of the Greenland ice sheet) may occur under intermediate and high global warming scenarios (Peterson et al. 2020). As thinner ice dominates and spring snow cover and summer sea-ice cover decrease, more energy is absorbed at Earth's surface level, influencing the latitudinal temperature gradient and thereby global weather and climate (IPCC 2022). Permafrost thaw will cause drastic carbon sink-source shifts, and impact global climate (Callaghan and Jonasson 1995, Post et al., 2019). Yet, projections of responses to greenhouse gas emission scenarios vary widely, with potential for slow to fast carbon cycle response in Arctic ecosystems (Schuur et al. 2022). Despite spatial variability in Arctic near-surface temperature projections, uncertainty in future socioeconomic pathways and emissions, and inconsistent estimation of future sea ice area and thickness, warming in the Arctic is projected to continue under all scenarios (Cai et al. 2021). While ecosystem response may buffer impacts of disturbance with increased plant community turnover, productivity, and greening, extensive abrupt permafrost thaw and limited plant response could lead to net positive greenhouse gas emissions (Schuur et al. 2022).

Here, we define true tundra areas as High Arctic, Low Arctic, and high elevation northern tundra as Oroarctic, while Subarctic refers to low elevation regions above 55°N and below treeline, following the definitions of the Arctic Climate Impact Assessment (ACIA 2004), Virtanen et al. (2015) and Berner et al. (2024). Canada, the Kingdom of Denmark, Finland, Iceland, Norway, The Russian Federation, Sweden, and the United States are the eight Arctic States (**Figure 1**). Understanding and predicting changes in Arctic biodiversity caused by climate change poses a special problem, due to diverse political and legal priorities, a lack of representative ecological sampling and relatively few research stations across the Arctic (Schmidt et al. 2017a, Metcalfe et al. 2018). An uneven representation of the Arctic's two ecoregions (tundra and boreal forest, respectively) in monitoring programs limits opportunities to inform policy development and protection of Arctic biodiversity. For instance, due to difficulty obtaining data from Russia, exacerbated by the exclusion of Russia from the Arctic Council, data from stations in the Arctic's largest state are inaccessible (López-Blanco et al. 2024, Kasten et al. 2024). Nearly half of the International Network for Terrestrial Research and Monitoring in the Arctic stations occur in the Siberian Subarctic (López-Blanco et al. 2024), and the inaccessibility of this data results in a less comprehensive view of the impacts of climate change on ecosystem function and biodiversity. Further, circumarctic sites of long-term vegetation monitoring are notably limited (**Figure 1**), as only 45 monitoring sites across 32 unique locations (above 63°N) fit this criterion (Bjorkman et al. 2020). A restricted spatial coverage of monitoring stations and access to monitoring station data in the Arctic poses challenges in the understanding of all threats to Arctic biodiversity and ecosystems, as well as actions for conserving biodiversity in the region.

Previous reviews have explored consequences of environmental change in the Arctic in different dimensions, including shifting ecological and trophic relationships (Post et al. 2009), impacts of changing phenology (Ernakovich et al. 2014, Prevéy et al. 2017, Post et al. 2019, Prévey et al. 2019), methane fluxes and shifts in carbon cycles and storage (Callaghan and Jonasson 1995, Post et al. 2019), as well as changes in biodiversity and species abundance (Callaghan and Jonasson 1995, Callaghan et al. 2004, Pecl et al. 2017, Taylor et al. 2020). Multiple studies provide synopses of warming treatment experiments, variability in species response to warming and climate sensitivity, as well as recent findings from long-term biodiversity monitoring programs (Elmendorf et al. 2012, Lehikoinen et al. 2014, Johnson et al. 2015, Taylor et al., 2020, Maes et al. 2024). Although these syntheses provide important summaries of our understanding of biodiversity and environmental change in the Arctic, it is less appreciated how these changes have influenced ecosystem function and how the combination of biodiversity, environmental, and functional changes affect humans.

The preceding sections highlight the entwinement of climate change, ecosystem functions, and human livelihoods in the Arctic, advocating for a nexus approach to understand their interconnectedness. This approach emphasizes the importance of identifying opportunities to mitigate threats, minimize trade-offs, and foster synergies (Liu et al. 2018). Here, we identify major knowledge gaps in our understanding of the nexus between climate, humans, and ecosystems in the Arctic region. We first identify what has been observed and is known about climate change and environmental change in the Arctic. We then outline knowledge gaps and uncertainties that scientists acknowledge. Many uncertainties are acknowledged that cannot be properly quantified; such deep uncertainties represent voids in our understanding as to how climate, humans, and ecosystems in the Arctic will respond. Finally, we detail future outlooks for the Arctic and consequential directions for future research. Due to the critical situation in the Arctic, our goal is not only to review these topics, but provide an overview of key areas of current and future research, creating a roadmap of the Arctic nexus.

1. Climate change

1.1 Tipping points, feedbacks, and carbon dynamics

Arctic summers are now the warmest they have been in 2,000 years, and air temperatures are expected to increase by 3°C (SSP1-2.6) to 12°C (SSP5-8.5) by 2081-2100 (Lee et al. 2021), with warming projected to be stronger over the Arctic Ocean than over land (e.g. ~5.9°C over the Arctic Ocean vs. ~4.6°C over Arctic land under the intermediate SSP2-4.5 scenario; Cai et al. 2021). Warming in the Arctic could lead to modification of multiple cryosphere and biosphere elements resulting in tipping points, or critical thresholds that once surpassed can qualitatively alter a system, often irreversibly (Lenton et al. 2008). Many uncertainties in climate projections associated with feedbacks from sea ice, ocean, and atmosphere interactions remain, as models are unable to consistently incorporate local feedbacks or simulate changes in spatial patterning of sea ice loss (Cai et al. 2021). One critical issue is how the Earth climate system will be impacted when elements like the Atlantic Meridional Overturning Circulation (AMOC) reach tipping points (van Westen et al. 2024). The AMOC is an integral component of ocean thermohaline circulation and North Atlantic climate regulation. Freshening of the North Atlantic Ocean by Arctic freshwater sources, notably from melting of the Greenland ice sheet, Canadian Arctic Archipelago glaciers, and Arctic sea ice, is influencing convection in the Labrador Sea and likely weakening the AMOC (Yang et al. 2016). The complexity of the AMOC system has led to widely opposing estimates of timing and degree of AMOC collapse, with some studies predicting a weakening and recovery after temperature stabilization of 1.5°C to 3°C of global warming (Jackson and Wood 2018, Sigmond et al. 2020) and others forecasting a potential full collapse as early as mid-century (Ditlevsen and Ditlevsen 2023, van Westen et al. 2024).

Global warming is expected to reach 1.5°C by the 2030s, even with drastic emission reductions (Lee et al. 2021). Exceeding the 1.5°C threshold potentially means a 3°C warmer Arctic, a shift of the Subarctic northwards, increased melt of the Greenland ice sheets, widespread permafrost thaw, and frequent loss of Arctic summer sea ice (Scheffer et al. 2012, Schuur et al. 2015, Hoegh-Guldberg et al. 2018, Armstrong McKay et al. 2022). Regardless of the emission scenario, recent projections have shown that the Arctic will be sea ice-free in September as early as the 2030s-2050s (Kim et al. 2023). Furthermore, if global air temperatures warm to 2°C, Arctic temperatures could increase by 4-8°C or more in some regions. This could lead to substantial areas of permafrost degradation, which would seriously impact hydrology, ecosystems, and building and road infrastructure (Kokelj and Jorgenson 2013, Chadburn et al. 2017, Biskaborn et al. 2019). Abrupt permafrost thaw, potentially leading to permafrost collapse, could impact global temperatures, especially if deeper carbon-rich permafrost (Yedoma deposits) are exposed (Schurr et al. 2015, Armstrong McKay et al. 2022). Permafrost thaw and subsequent surface water redistribution, leading to either drier or wetter conditions, can impact ecosystem carbon dynamics irreparably (Jorgenson 2013, Schuur et al. 2022).

Phenological shifts such as earlier green-up and delayed senescence (Treharne et al. 2020) may influence biogeochemical processes (e.g. carbon sequestration and photosynthesis), and physical attributes (e.g. water balance and the surface energy balance) (Peñuelas et al. 2009) with direct and indirect climate feedback. At the biogeochemical level, increased carbon dioxide uptake from a longer period of photosynthetic activity would reduce warming from greenhouse gases by decreasing atmospheric carbon dioxide (Schuur et al. 2022), while increased temperatures and plant productivity increases ecosystem respiration rates (Maes et al. 2024). Increased plant activity and species composition change could also lead to changes in the strength and type of the emission of biogenic volatile organic compounds (such as terpenoids), which could enhance or counteract global warming due to aerosol formation (Peñuelas et al. 2009, Tang et al. 2023). For instance, a cooling effect could be expected where evergreen conifers expand their ranges into the High Arctic and monoterpene emissions increase, while a warming feedback is expected where broad-leaved deciduous trees replace evergreens and monoterpene emissions decrease (Tang et al. 2023). The degree to which soil organic matter decomposition in permafrost may enhance global warming is uncertain and influenced by local conditions of soil saturation, freeze and thaw cycles (especially duration and soil layer depth of thaw), and movement of labile organic matter through the soil profile (Walz et al. 2017).

Record high permafrost temperatures have already been recorded at multiple long-term monitoring sites (boreholes down to ~10-20m depth) around the Arctic (Biskaborn et al. 2019). As permafrost thaws, hydrological modifications become more common and the soil organic carbon stored for millenia becomes available for microbes to degrade. The amount of carbon in permafrost soils is estimated to be nearly double that of the atmosphere (Hugelius et al. 2014). Even partial loss of this carbon through microbial degradation as carbon dioxide and methane, can lead to drastic increases of greenhouse gases in the atmosphere (IPCC 2019, 2022). High emission scenarios (i.e. RCP 8.5) estimate a potential release of 5 to 15% of the carbon pool in Arctic permafrost by 2100, a feedback that would influence climate change on a similar scale as a major land-use change such as deforestation (Schuur et al. 2022). Carbon budgets limiting warming to 1.5°C need to be reduced to account for permafrost thaw, with further reduction to maintain temperature stabilization (Rogelj et al. 2018). Up to 5,300 teragrams of carbon from methane release and 240,000 teragrams of carbon from carbon dioxide from permafrost thaw may occur during the 21st century, but the timing and amount of greenhouse gases released from permafrost soils are still highly uncertain (Canadell et al. 2021). If climate mitigation goals (e.g. the Paris Agreement on climate change, the Kyoto Protocol) are achieved then northern peatlands may remain net carbon dioxide sinks, but under RCP 8.5 increased carbon dioxide and methane emissions could augment warming by 0.21°C by 2300 (Qiu et al. 2022). Soil methane uptake can also reduce carbon release, as Arctic wetland net methane emissions predicted for 2100 increased only by 18% (29 to 35 teragrams of methane a year) after incorporating methane-oxidizing bacteria and methanogens dynamics (Oh et al. 2020). Yet, as atmospheric carbon dioxide concentration increases, a smaller fraction of atmospheric carbon will be stored in Arctic terrestrial and oceanic sinks as these sinks become saturated (Canadell et al. 2021).

1.2 Changes in Arctic weather, wildfire frequency, and browning events

Increases in winter precipitation and mean summer temperature are predicted under climate change in the Arctic (Leffler et al. 2016). Despite projected increases in precipitation over high latitudes, soil moisture shows high regional variability across warming levels, with both drier and wetter soils projected due to the influence of evapotranspiration and future regional permafrost conditions (Bring et al. 2016, Wrona et al. 2016). Fluctuations in terrestrial precipitation, evaporation, and soil moisture in the Arctic have contributed to increased tundra wildfire frequency, magnitude, and severity due to unprecedented drought, extreme weather events, and earlier snowmelt (Bokhorst et al. 2011, Wrona et al. 2016). The Arctic region is also experiencing increasingly extreme fire seasons, with recent large-scale fires across Alaska and Siberia (McCarty et al. 2021). Fires in the northern latitudes are driven by climate and fuel conditions, lightning, and human activity (McCarty et al. 2021). Wildfire seasons, particularly in tundra regions of Alaska, northwest Canada, and Siberia, have been significantly correlated to summer heatwave activity (Thoman et al. 2023, Hegedűs et al. 2024). While the majority of global wildfires are intentionally or accidentally set by humans, lightning is the predominant cause of burning in Arctic regions (Veraverbeke et al. 2017). Lightning is also projected to become twice as frequent in the Arctic tundra than in the Subarctic, increasing by about 150% by 2100 (Chen et al. 2021a).

Warmer winters with both snow and rain, and more extreme weather events are expected (Walsh et al. 2020, Henry et al. 2022). However, the scarcity of controlled winter field experiments in the Arctic that manipulate single factors limits understanding of the impacts of warmer weather conditions and severe events (Bokhorst et al. 2023). Extreme winter warming events, ‘frost drought’, and rain-on-snow events which cause an ice layer at the surface of, within, or below the snowpack, may lead to destruction of living plant biomass, and result in browning events (reviewed by Phoenix et al. 2024). Extreme winter warming events can also have severe consequences for large mammals and small animals that live under the snow. For instance, a severe rain-on-snow event in the Canadian Arctic Islands region killed ca. 20,000 muskoxen as they could not access food sources (Putkonen et al. 2009). Similar findings have been reported for reindeer both on Svalbard (Kohler and Aanes 2004) and Western Siberia (Forbes et al. 2016). Earlier snowmelt has been associated with spring phenology advancements of many organismal groups, and while thinner snowpack often increases mortality in plants via frost drought; impacts on animals are not as consistent or clear (Slatyer et al. 2022). Winter warming can result in a thinner snowpack, earlier snowmelt and earlier flowering, which can lead to increased exposure to freezing spring conditions and decreased flower abundance, as found for *Cassiope tetragona* and *Salix arctica* in High Arctic Greenland (Wheeler et al. 2015). If flowering continues to occur earlier, plants will likely be exposed to freezing temperatures more often, which may further reduce flower production and negatively impact plant survival (Wheeler et al. 2015). Yet, the response of different plant species to earlier snowmelt varies widely, and it often takes multiple years of consistent earlier snowmelt for a response to become evident (Frei and HSenry 2021). Landscape heterogeneity and microclimate variables are also important to consider in terms of their potential influence on snow accumulation and snowmelt timing on phenological shifts.

While Arctic vegetation is expected to increase carbon storage through treeline expansion northward, increased photosynthesis, water use efficiency, unknowns such as drought occurrence, changes in land use, nitrogen availability, limits to migration rates, and wildfire prevalence could diminish carbon sink capacity (Canadell et al. 2021, Chen et al. 2021b, Gustafson et al. 2021). Further, decreased albedo from forest encroachment into tundra is expected to increase the rate of global warming due to positive biogeochemical feedbacks to the earth-atmosphere energy balance (Zhang et al. 2013). Shrub expansion constitutes one of the most noticeable climate-driven changes in tundra vegetation (Sturm et al. 2001, Elmendorf et al. 2012, Bjorkman et al. 2018, Vowles and Björk 2019), and landscape attributes could influence the direction of vegetation state transition (Chen et al. 2021b). For instance, in dry tundra, climate change and increased wildfire frequency could promote Arctic shrub expansion, whereas, in wet tundra, wildfires could counteract the climate-driven shrub expansion (Chen et al. 2021b). However, there remains high uncertainty regarding how multiple stressors (e.g. combination of climatic drivers and increased fires frequencies) will impact Arctic ecosystems. Will these stressors be additive, counteractive, or even drive Arctic ecosystems to alternative states?

2. Human activity

2.1 Vulnerability of humans in the Arctic

The Arctic region is home to almost four million people, of which 10% are Indigenous Peoples (Johnson et al. 2015, IPCC 2019, Constable et al. 2022). Population density and economic activity vary significantly across the eight Arctic States (**Figure 1**), ranging from large areas with no human settlements or industry, either on- and off-shore, to areas with larger cities and significant economic activities (European Environment Agency 2017).

Climate change increases the vulnerability of Arctic Indigenous communities by modifying resource availability and mobility within and between communities. Humans in the Arctic are highly vulnerable due to their dependency on limited natural resources (e.g. fish, reindeer, game birds, wild plants), which are sensitive to climate change (Meredith et al. 2019, Mustonen and Shadrin 2021, Fedewa et al. 2020, Jørgensen et al. 2019). For instance, the productivity and phenology of Pacific and Atlantic salmon (*Oncorhynchus* spp., *Salmo salar*) in freshwater and coastal areas in Alaska, Norway, and Finland have been altered due to warming and algal blooms (Brattland and Mustonen 2018, Cline et al. 2019, Mustonen et al. 2021). Declines in reindeer abundance and habitat (Vors and Boyce 2009), have led to the categorization of reindeer as vulnerable on the IUCN Red List of Threatened Species (Gunn 2016). Road, harbor, and water treatment infrastructures are negatively impacted by climate-induced flooding, thawing permafrost, erosion, and sea level rise (Ford et al. 2021, Mustonen and Shadrin 2021). Less ice coverage has also allowed for increased shipping, growth in marine trade, tourism, and mineral and oil resource extraction, all which may lead to increased nitrogen deposition and pollution (Stephen 2018, Ford et al. 2021, Parmesan et al. 2022). Beyond physical risks for these local human communities, there is a risk for heightened political tensions playing out at the expense of vulnerable and marginalized communities that have historically had little to no voice in their governance (Dawson et al. 2018, Drewniak et al. 2018). Climate change can effectively erase important locations and traditions which keep Indigenous communities alive and united, and provide them a source of income through hunting and fishing tourism, for example (Fenger-Nielsen et al. 2020, Jensen 2020).

Arctic Indigenous communities are facing multiple cascading and compounded risks, which creates an existential threat for these communities (Constable et al. 2022). Food insecurity in the Arctic is expected to increase, partly due to rising sea water temperature, influencing subsistence fish species to migrate (e.g. the brown trout (*S. trutta*) in Russia) and invasive marine species to expand their ranges (e.g. mackerel (*Scomber scombrus*) in Iceland) (Astthorsson et al. 2012, Pecl et al. 2017, Huntington et al. 2020, Mustonen et al. 2021). Other factors, such as global shifts in phytoplankton distribution and abundance in response to increased ocean temperature, acidity, and stratification also contribute to subsistence fish distribution patterns (Hoegh-Guldberg and Bruno 2010). Direct exposure to climate-induced hazards, coupled with food insecurity and an increasing rate of waterborne and vector-borne diseases (such as gastroenteritis and tularemia), and environmental contamination are projected to worsen the health of humans in the Arctic (Waits et al. 2018, Grigorieva 2024). For example, Arctic populations, Inuit in particular, have been exposed to elevated levels of mercury (Basu et al. 2022), which pose serious health effects. Exposure pathways are mainly through diet (Basu et al. 2022, Donaldson et al. 2010), and while concentrations of chemicals (like lead and mercury) have been declining in some areas of the Arctic, contaminants like selenium have been reported for the first time (Gibson et al. 2016, Abass et al. 2018). Estimated mercury release from permafrost thaw has been projected to increase mercury concentrations in the Yukon River, Canada by 14% to 50% by 2100, depending on the emission scenario (Schaefer et al. 2020). Most emerging disease outbreaks in the Arctic over the last 30 years have been vector-borne or zoonotic, both of which are indirectly affected by climate (Ruscio et al. 2015). As temperatures increase and permafrost thaws, factors such as renewed pathogen activity, increased pathogen survival, and vector range expansion increase transmission risk (Waits et al. 2018, Mohite et al. 2023). Due to decreases in water quantity and quality, associated with water treatment failures, water rationing, and the absence of indoor plumbing, an increase in waterborne disease outbreaks have been reported, including new, emerging waterborne pathogens (Thomas et al. 2016, Harper et al. 2020, Mustonen and Shadrin 2021). Increasing temperatures and precipitation are predicted to have the strongest impacts on promoting the spread of pathogens (Raheem 2018).

The loss of archeological sites, cultural sites, and cultural practices, such as ice-fishing and reindeer herding due to ice thaw, represents a major risk, and potentially an existential one, for the heritage and identity of Indigenous communities (Raheem 2018, Nicu and Fatorić 2023). Mental health and well-being of these communities are also at stake due to indirect exposure to risks heightened by climate change, such as loss of cultural heritage, place-based knowledge, and livelihoods (Cunsolo Willox et al. 2015, Harper et al. 2020). These health impacts are and will be unequally distributed among populations depending on age and gender (Kowalczewski and Klein 2018, Feodoroff 2021). Primary knowledge gaps of humans in the Arctic regard adaptation to climate change and how impacts from global markets will influence human-natural systems interactions (e.g. subsistence harvesting, increased transport and tourism, and natural resource development projects) (Kapsar et al. 2022). These interactions are complex and reliant on cooperation from the local to global level to be sustainable as climate change progresses. For instance, in many rural Indigenous communities of Alaska, subsistence harvest accounts for over 50% of the local diet (Fall 2016). The traditional practice of subsistence harvest is essential for cultural wellbeing and depends on healthy ecosystems and populations to continue sustainably. If subsistence harvest, and therefore food security, is compromised, an increase in migration from rural to urban areas is likely, which could lead to environmental degradation and impacts on local biodiversity as urban centers grow (Kapsar et al. 2022).

2.2 Adaptation in local Arctic human communities

Knowledge is still limited regarding how Indigenous communities have changed their practices and habits to match changing climate and environments. Adaptation in Arctic communities has mostly been behavioral and reactive, with few examples of transformational adaptation that, for instance, consider the concerns of Indigenous communities and integrate their solutions in a long-term and potentially more sustainable way (Canosa et al. 2020). The Alaska Native Tribal Health Consortium, a local environmental observation platform, is an example of transformational adaptation that is used for sharing information on environmental impacts and local human community health effects (Berner et al. 2016). In fact, climate change appears not to be explicitly included in planning and design in many sectors (Canosa et al. 2020), due to the limited participation of Indigenous communities in decision-making bodies, a manifestation of colonialism and historical inequities and injustices (Ford et al. 2021). The integration of local Arctic residents' knowledge and involvement in the framework, design, and production of human-natural system research is essential to create effective policy in a changing Arctic (Kapsar et al. 2022). Additionally, while certain adaptation practices may work in the present, they may result in maladaptive behavior in the future. For instance, due to reduced caribou availability, Inuit in the Northwest Territories of Canada have relied more on muskox for food, as well as income through guided hunts. This adaptation has led to a decrease in the population size and health of muskox (Fawcett et al. 2018). Evidence of successful adaptation, maladaptation, and limits to adaptation are still scarce, and represent major knowledge gaps which need to be investigated to understand where, how, and if participatory governance has included climate change impacts in planning to reduce exposure and risk to local populations.

3. Ecosystem evolution

3.1 Evolution of the Arctic

The biogeography of the Arctic regions has influenced the ecological and evolutionary trajectories of its biotic communities. The macrofossil record indicates that the Arctic tundra became a recognizable biotic community at the end of the Neogene (the Pliocene) into the early Pleistocene (ca. 3-2 Ma; Bennike and Böcher 1990, Matthews and Ovenden 1990, Murray 1995), as cooling cycles and continental glaciation shifted the tundra from continuous forest to treeless landscapes (Repenning and Brouwers 1992, Murray 1995). Molecular data suggests that the Arctic flora assembled from dispersal events as old as 10 mya, with dispersal increasing over time as a function of climate and peaking at 1.0-0.7 mya (Zhang et al. 2023). A relatively homogenous tundra flora persisted until the Last Glacial Maximum (~20 kya), when increases in temperature and precipitation led to higher plant diversity as herbaceous and woody communities emerged during the early to mid-Holocene (MacDonald et al. 2000, Wang et al. 2021). Currently, the Arctic flora includes 2,218 vascular species (Elven et al. 2011), and Low Arctic areas are generally situated within larger landmasses like the American and Eurasian continents. In contrast, most of the landmass in High Arctic regions above 70°N feature numerous large archipelagos. This geographical distinction holds implications for the susceptibility of ecosystems to novel species introductions and the pace of species turnover. However, there is a lack of studies exploring how the biogeographical patterns impact current biotic community change.

Changes in phenology, such as the timing of vegetation green-up (or leaf emergence), and abundance are commonly used indicators of species and ecosystem response to climate change, due to their responsiveness to warming and wide-ranging impacts on ecological processes (Peñuelas et al. 2009). Earlier green-up trends across the Arctic have been well-supported with long-term ecological research plot observations, remote sensing, and warming treatments (Bjorkman et al. 2020, Jenkins et al. 2020, Collins et al. 2021). Yet, vegetation green-up and abundance response is often not detectable, is species- and/or site-specific, or dependent on specific temperature windows (Myers-Smith et al. 2015, Bjorkman et al. 2020, Scharn et al. 2021), thus often making species response over time difficult to predict. Arctic animals that can respond phenologically, such as modifying the timing of breeding events or migration, may have an advantage under climate change (Gilg et al. 2012). For instance, a colony of the Arctic seabird, Mandt's black guillemot (*Cepphus grylle mandtii*), advanced its egg lay date by nearly eight days between 1976 and 2017 on the northern coast of Alaska (Sauve et al. 2019). Interestingly, long-distance migrant Arctic shorebird birds, such as the Western sandpiper (*Calidris mauri*) and Red Phalarope (*Phalaropus fulicarius*), have shown greater phenological response to spring green-up than short- and medium-distance migrants (Tavera et al. 2024).

Due to warming and environmental modification at northern range limits, many Arctic species are expanding their ranges northward and/or to higher elevations. Continued northward expansion of generalist Arctic bird species and increases in herbivorous Arctic bird taxa will likely further degrade habitat quality, cause vegetation loss, and potentially induce trophic cascades (Davey et al. 2013, Smith et al. 2020). Arctic species and genotypes at the northern edge of their ranges are especially at risk of extirpation when further poleward and/or higher elevation range expansion is not possible. In the Swedish Scandes mountain birch (*Betula pubescens* ssp. *tortuosa*) saplings were found ca. 400m higher than the species' uppermost limit in 1955 (Kullman 2002), though stunted growth of birch saplings above treeline suggest that tundra plant communities are not yet shifting to birch forest (Scharn et al. 2022). Non-Arctic species are also expanding their ranges northward. Range expansion of the red fox (*Vulpes vulpes*) into the southern range limit of the arctic fox (*V. lagopus*) is linked to increased food availability with a resulting retreat of the arctic fox populations from Low Arctic habitat due to climate warming (Killengreen et al. 2007). Additionally, more humans and infrastructure correlate with higher density of red fox populations and increased human activity in the Arctic will likely promote further encroachment of the red fox into arctic fox habitat and further retreat its population (Elmhagen et al. 2017, Kapsar et al. 2022).

3.2 Genetic attributes and plastic response of Arctic species

Most Arctic plant and animal species are characterized by low genetic diversity (Mcgraw 1995, Gilg et al. 2012). Range contractions risk further decreasing genetic diversity, within and across populations, due to evolutionary processes like genetic drift and reduced gene flow (Ellstrand and Elam 1993, Rubidge et al. 2012). Reduced genetic diversity of High Arctic plants and animals has been attributed to genetic bottlenecks and repeated loss of habitat due to range contractions during warmer interglacial periods (Alsos et al. 2002, Gilg et al. 2012, Birkeland et al. 2017, Stojak and Jędrzejewska 2022). Global-scale population genetic data shows that while plants in taiga and tundra ecosystems support relatively low genetic diversity, it tends to be higher in refugial populations and lower in more recently deglaciated areas, which has been attributed to persistence in glacial refugia, demographic processes, and glacial and post-glacial range contractions and expansions (Stenström et al. 2001, Taberlet et al. 2012, Eidesen et al. 2013). Ancient DNA, microfossil, and pollen records from sediment samples have been used to examine shifts in plant communities over the past 24,000 years in the Polar Ural Mountains (Clarke et al. 2020) as well as support the persistence of Arctic species in refugia (Alsos et al. 2016, 2020). Refugia from the early (1.0 to 1.6 mya) to late Pleistocene in Alaska, Russia, Europe, and Greenland were recently identified for a widespread Arctic plant, the Arctic Bell-Heather (*Cassiope tetragona*; Elphinstone et al. 2024). Areas within the Beringian region, such as eastern Russia and western Alaska, as well as locations within British Columbia, Europe, and Greenland, remained mostly unglaciated during Pleistocene glacial cycles and served as refugia for many Arctic plant and animal species (Abbott and Brochmann 2003, Alsos et al. 2005, Elphinstone et al. 2024).

Arctic species with small effective population sizes, long life cycles, and narrow distribution ranges are at a particular disadvantage in the warming Arctic (Hamrick and Godt 1996, Gilg et al. 2012). Wind-pollinated Arctic plants with wide geographical ranges are generally expected to retain higher genetic diversity as compared to animal-pollinated species, selfing species, and species with narrow geographical ranges (Hamrick and Godt 1996, Alsos et al. 2012). The primary pollination and dispersal mechanism, wind, may not be sufficient to overcome the negative consequences of range contractions since it does not guarantee that populations will be able to mate or establish over long distances. Low levels of seed germination and seedling recruitment are common in Arctic plant species (Bliss 1958), and low seedling survival in addition to dense forest canopy reducing population connectivity can inhibit establishment and range expansion of plants in the Arctic. For instance, treeline has been shown to be a barrier to gene flow between ecotypes of the tussock cottongrass (*Eriophorum vaginatum*) found south and north of the Brooks Range in Alaska (Stunz et al. 2022), and white spruce (*Picea glauca*) north of the Brooks Range demonstrates treeline advance in the region (Dial et al. 2022). Advancement of trees, and specifically the advancement of the forest-tundra ecotone, may fragment open tundra and further exacerbate landscape resistance, limiting gene flow for some Arctic plant species (Stunz et al. 2022). Long-distance dispersal with higher seed germination rates and establishment under climate change is expected for some species, especially wind-pollinated and wind-dispersed trees (Hamrick and Godt 1996). Additionally, more open water in the Arctic Ocean leads to more southerly winter winds which can facilitate seed and pollen dispersal further northward, above treeline (Dial et al. 2022). Increased open water can lead to a deeper snowpack, which can protect juvenile trees from severe winter winds, and snowmelt can alleviate soil moisture limitations during the growing season (Dial et al. 2022). Multiple animal species utilize the forest-tundra ecotone for shelter, breeding, and foraging (e.g. passerine and wader bird species that breed in peatlands; Järvinen et al. 1987), and structural changes in forest habitat could strongly alter the distribution of animal species as well.

Major knowledge gaps remain regarding the potential of certain species and/or genotypes to expand their ranges and experience an increase or decrease in establishment success in a warming Arctic (Alsos et al. 2002). Increased encroachment of red fox into Low Arctic areas of Siberia may lead to further population fragmentation and inbreeding of Scandinavian arctic fox genotypes by limiting connectivity of Siberian and Scandinavian arctic fox subpopulations (Elmhagen et al. 2017, Cockerill et al. 2022). The Arctic is rich in polyploid plant species, and some polyploids may be able to expand their ranges due to their increased genetic variability, especially if they are long-distance dispersers or derived from multiple colonizations (Brochmann et al. 2004, Meimberg et al. 2009, Mata et al. 2023). Species like grayleaf willow (*Salix glauca*) and dwarf birch (*Betula nana*) have been shown to have narrower distributions, low rates of seed germination, and increased clonal reproduction near northern range limits and during periods of climate cooling (e.g. 4 kya-2.5 kya; Birks 1991, Alsos et al. 2002). As more extreme weather events increase and climate fluctuations occur in a warming Arctic, the frequency of sexual reproduction, especially in thermophilous species like the grayleaf willow and dwarf birch, is expected to increase as well (Alsos et al. 2002). Increased sexual reproduction leading to higher adaptation potential of aggressive shrub species could have major implications for ecosystem functioning and biodiversity in the Arctic as their abundance increases in Subarctic and Arctic areas (Tape et al. 2006, Berner et al. 2018). If range expansion of polyploids and higher rates of sexual reproduction under climate change leads to increased genetic variability of Arctic plant species (Alsos et al. 2002, Brochmann et al. 2004), the survival, abundance, and adaptation of these plants and the composition of their associated arthropod communities may also be altered (Colella et al. 2020).

Phenotypic plasticity is common in Arctic plants and allows species to produce different phenotypes under modified environmental conditions, allowing for direct response and potential resilience to environmental change (Bret-Harte et al. 2001, Deslippe and Simard 2011, Dobbert et al. 2021). While the long lifespan of many Arctic species suggests limited evolutionary potential to evolve fast enough under rapid environmental change, plasticity, increased mutation rate, and increased sexual reproduction (with subsequent seed germination and seedling establishment) may promote adaptation and persistence of some species (Colella et al. 2020). For instance, the developmentally plastic dwarf birch can shade out plants like the tussock cottongrass, a species that has a disproportionate impact on ecosystem function due to enhanced nutrient cycling and deep rooting that increases active soil layer depth (Chapin and Shaver 1985, Curasi et al. 2022), which could lead to drastic modifications in ecosystem and biotic community structure, both aboveground and belowground (Keuschnig et al. 2022).

3.3 Changes in biological community composition and species turnover

Arthropods influence Arctic plant and animal diversity and are a fundamental component of food webs (Hodkinson and Coulson 2004). Large variability in arthropod abundance and biodiversity trends are common in the Arctic, such as cyclical abundances of the autumnal moth observed from 1968-2020 in the Swedish Lapland (Nielsen et al. 2013, Andersson et al. 2022). Contrasting temporal trends in total abundance of multiple arthropod groups have been observed in Greenland, where decomposers increased in some habitats and key pollinator fly species decreased in others (Gillespie et al. 2020). As permafrost thaws and the soil active layer increases, we can expect impacts on belowground biodiversity, such as increased abundance of soil microbes and proliferation of extensive mycorrhizal networks (Callaghan et al. 2004). Depending on soil drainage following permafrost thaw, arbuscular mycorrhizal-dependent plant species such as marsh cinquefoil (*Potentilla palustris*) may promote mycorrhizal network formation and dominate in upland, drier sites, while the non-mycorrhizal tussock cottongrass will likely have an advantage in inundated soils (Schütte et al. 2019). Drier top soils following permafrost loss have led to drastic modifications in methanogenic and methanotrophic microbial communities (Keuschnig et al. 2022). While soil biodiversity and vegetation composition changes, the degree of change in soil temperature, soil moisture, and active layer depth will also be impacted by unknown factors, such as invasive species, extreme weather-events and the frequency and timing of freeze-thaw events (Nielsen and Wall 2013). For instance, extreme winter warming has shown to negatively impact microarthropods reliant on wet soils and water films, and declines are expected to be more severe in warmer and drier conditions (Bokhorst et al. 2012).

Large knowledge gaps exist regarding how Arctic biological community composition will evolve in the face of environmental change (**Table 1**). Arctic bird communities are impacted by a multitude of factors beyond climate change, such as predation, egg harvesting, industrial activity, and increased vegetation cover (Doyle et al. 2020). Denser and taller vegetation can have contrasting effects on Arctic birds, as some species like the ground-nesting passerines, may benefit, but most species decline when vegetation becomes too tall (Thompson et al. 2016). Many Arctic species are expected to experience changes in population connectivity (Niskanen et al. 2019), and in recently deglaciated areas (i.e. glacier forelands), glacier melt will expose more land, serving as potential colonization grounds for many Arctic species. What colonizers arrive first can also impact soil attributes, especially if vegetation shifts occur faster than soil development. If cryptogams are the first colonizers to arrive in a newly deglaciated area, for instance, the formation of slightly acidic soil may restrict some plants, soil microbes, and other species from establishing. These areas can serve as potential refugia for cold-adapted species as environmental change persists, but may also be difficult for thermophilic Arctic plants to establish due to colder microhabitats. Some deglaciated areas may support 'novel ecosystems,' where modified abiotic factors create incipient ecosystems with no previous or current analog under climate change (Reu et al. 2014, Parmesan et al. 2022).

Other unknowns concern how environmental change will influence changes in community composition, species turnover, and migration, especially across geopolitical boundaries: what will Arctic biotic community composition look like in the future? For instance, intergovernmental cooperation influencing species management and conservation policy can influence population connectivity and abundance, as gray wolf (*Canis lupus*) populations migrate frequently between Norway and Sweden (Kaspar et al. 2022). Changes in the range and abundance of Arctic species and ensuing shifts in biotic community composition are expected to impact biodiversity at both micro- and macro scale, and mismatches between peak prey availability and loss of pre-migration and staging (areas to refuel and rest) habitat (Smith et al. 2020) can influence Arctic bird abundance. Based on a dataset from 1980-2017 across circumarctic sites, waders, which comprise nearly half of Arctic terrestrial bird species, had the largest proportion of species abundance declines, while almost half of waterfowl species increased in abundance (Smith et al. 2020). Increases and decreases in soil microbial diversity and arthropod diversity may impact plant and animal diversity and abundance (Hodkinson and Coulson 2004, Schmidt et al. 2017b). Lack of arthropod monitoring and limited inclusion in long-term research suggests that arthropod species may disappear before being identified as environmental change progresses in the Arctic (Gillespie et al. 2020), highlighting the necessity to better catalog biodiversity of these communities and improve understanding of their influence on ecosystem functioning and trophic structure (Taylor et al. 2020). In many Arctic ecosystems, muscid flies have been identified as the most common (and efficient) pollinators, and declining muscid fly diversity and abundance, along with increasing flowering phenological mismatch, could threaten reproductive success of many Arctic plant species (Tiusanen et al. 2016). The frequency of Arctic plant sexual reproduction via animal pollination is predicted to decrease in some species and increase in others due to a shorter flowering window under climate change (Schmidt et al. 2016). Yet, earlier flowering can also lead to increased reproductive fitness as more flowers and fruits are produced due to longer development time (Collins et al. 2024). Extrapolating trends in animal pollination in the Arctic is uncertain because of high turnover of pollinator species (Cirtwill et al. 2018), as well as conflicting projections regarding range expansions and contractions of arthropods (Elberling and Olsen 1999, Gillespie et al. 2020).

How vegetation composition will change in the future, especially regarding species turnover and invasive species, is uncertain and can impact ecosystem function. While dynamic global vegetation models consistently project woody shrub and boreal forest expansion into tundra regions, disturbance factors, such as insect damage, wildfires, extreme weather events, dynamics of permafrost thaw/active layer depth, and nutrient availability are poorly simulated or unrepresented (Peng et al. 2021, Parmesan et al. 2022, Heffernan et al. 2024). Soil moisture dynamics can inform on plant community composition as thirty years of vegetation survey data showed that the strong spatial relationships between plant traits (such as height, specific leaf area, leaf nitrogen content) along temperature and soil moisture gradients were mostly explained by species turnover (Bjorkman et al. 2018). Plant community height increased across all sites as taller, thermophilous plant species increased, particularly in areas where soil moisture was high (Bjorkman et al. 2018). Disturbance events and soil nutrient content can also inform on Arctic vegetation shifts, as abrupt permafrost thaw (leading to thaw ponds) and low nutrient availability can promote graminoid dominance, and ultimately how carbon cycling may shift under vegetation change (Wein and Bliss 1974, van der Kolk et al. 2016, Parmesan et al. 2022). Other underrepresented plant and soil communities, such as cryptograms, rhizosphere microbes, and biocrusts (moss, lichen and cyanobacteria communities on the soil surface), will likely be impacted as shrubs and other vegetation types increase in abundance and expand their ranges northwards (Wullschleger et al. 2015, Bokhorst et al. 2023, Gu et al. 2023). Biocrust soils in the Arctic can fix and store significant amounts of carbon in the surface soil layer (Juottonen et al. 2020, Jung et al. 2018), and changes in biocrust extent and thickness need to be investigated to better understand impacts on carbon cycling (Williams et al. 2017, Colella et al. 2020). High grazing intensities have also been shown to drive plant communities towards graminoid and forb-dominated communities (Olofsson et al. 2001, van der Wal 2006, Kitti et al. 2009, Olofsson and Post 2018). Furthermore, herbivores can mitigate the climate-driven expansion of deciduous shrubs (Post and Pedersen 2008, Olofsson et al. 2009), whereas less palatable evergreen shrubs are not influenced by large herbivores to the same extent (Vowles et al. 2017a, b). Impacts of reindeer grazing on vegetation have also been shown to be habitat-specific (influenced by historic and current land use) and indirect, as reindeer primarily modify soil nutrient cycling (Stark et al. 2023). While biomass increases have been predicted for the Arctic tundra, there is growing evidence that tree expansion into tundra may not increase carbon storage as models predict (Canadell et al. 2021). In Abisko, for instance, total ecosystem carbon storage is greater in tundra heath (owing to greater soil carbon stocks) than in the mountain-birch forest, and high plant activity in the forest during the growing season stimulates the decomposition of older soil organic matter (Hartley et al. 2012). Mountain birches have been shown to facilitate birch seedling performance and survival at high-stress sites (Eränen and Kozlov 2008) and can also facilitate establishment of other species by improving soil fertility (Mikola et al. 2018). It is uncertain whether tundra plant community composition in the direct vicinity of birch individuals will become more similar to the composition found in the nearby birch forest (Sundqvist et al. 2008). Thus, with multiple factors driving vegetation change in the Arctic, it is uncertain if adding single factors will create additive effects on biotic community structure or generate new communities (Wang et al. 2021, Parmesan et al. 2022, Scharn et al. 2022).

Future outlook of the ecosystem-climate-human nexus

The extent that ocean acidification, surface water and surface air temperature rise will influence the northward range expansions of Arctic species, the reorganization of polar systems, and deterioration of the cold barrier between the Subarctic forest and Arctic tundra is uncertain (**Table 1**; Constable et al. 2022). Reductions of seasonal sea ice, loss of multi-year ice, and altered wind patterns are expected to facilitate interactions between coastal communities, tourism, shipping, and commercial fishing industries. While Coupled Model Intercomparison

Project Phase 6 (CMIP6) climate projections perform better than earlier models at predicting sea ice loss for a given amount of carbon dioxide emissions, they are unable to project the future extent of Arctic sea-ice cover with confidence (Notz and SIMIP Community 2020). Therefore, the degree to which the health, security, and subsistence resource availability of Indigenous Peoples could be impacted by dwindling sea-ice area is largely unknown (Constable et al. 2022). While decreased abundance of caribou and reindeer are affected by multiple climate factors, caribou population declines have been partly attributed to reduced lichen consumption (observations by Inuit hunters; Knotsch and Lamouche 2010). The degree to which lichen cover and diversity will be lost as tundra plant communities shift under climate change (Elmendorf et al. 2012), and how this will further impact reindeer populations are unknown. Several components of terrestrial biodiversity are severely understudied in the Arctic (e.g. Taylor et al. 2020). We currently lack a sufficient overview of the Arctic diversity for several organism groups such as arthropods, bryophytes, and lichens, and the absence of these groups in climate change models hampers the ability to assess how biodiversity and ecosystem functioning will be impacted. The extent to which economic development and natural resource extraction will increase in the Arctic is also uncertain and has the potential to dramatically impact Arctic local human communities and species due to increased ship traffic, noise (and other) pollution, increased carbon emissions, damage to Arctic summering and breeding grounds, and interruption of subsistence practices (Kaspar et al. 2022). Additionally, as permafrost thaw and glaciers melt, sequestered pollutants, microparasites, and hazardous waste in Arctic environments will likely remobilize and increase risk exposure to ecosystems and humans (Wang et al. 2019, Colella et al. 2020), potentially leading to wide-scale negative impacts on biodiversity, ecosystem function, and health. Integrative frameworks to examine how human and natural systems are coupled (socio-environmental interactions) and how drivers in other regions affect the Arctic (and vice-versa) are needed to increase resilience of Arctic species and systems under climate change (Kapsar et al. 2022).

Warming in the Arctic has occurred at nearly four times the global average since 1979 (Rantanen et al. 2022), prompting environmental and ecosystem changes such as shifts in phenology, subsistence resources, biodiversity, species distributions, snow regimes, sea ice, permafrost extent, and carbon and nutrient cycling. Arctic tipping elements, such as loss of Arctic sea ice, AMOC collapse, and boreal forest dieback may be triggered by anthropogenic-caused climate change by 2100, potentially leading to a cascade of impacts that could drastically alter Arctic ecosystems and the global climate system (Armstrong McKay et al. 2022). Wide-ranging impacts on humans in the Arctic have only been superficially explored at present, especially in relation to changes in climate, ecosystem function, and biodiversity response.

Pairing robust scientific models that utilize long-term monitoring, spatial genomics, and baseline and resampled datasets with integrative assessments are needed to better predict ecological response as well as capture complex causal chains in coupled human and natural systems. To capture these complex dynamics, human responses to environmental change must be included in models, such as integrated climate assessments (Maxwell et al. 2015, Beckage et al. 2022). Strategies to increase the resilience of species and humans to environmental change are imperative, and urgently needed to protect Arctic ecological and social systems. These strategies should include pathways to facilitate swift response to unprecedented change, such as decentralized governance and management policy to promote inclusivity, (especially in regards to gender, social justice, and equity), incorporation of Indigenous Peoples and knowledge in co-management of Arctic research and resources, creating local, publicly-available tools for regional weather, climate, and ecosystem response, and international collaboration and governance for adaptation and carbon mitigation policy (Andersson 2021, Constable et al. 2022).

As it pertains to science, few current approaches to inter- and trans-disciplinary science policy interfaces integrate Indigenous knowledge and local knowledge, which can be used to better understand how environmental change in the Arctic impacts species distributions at the ecosystem level (Ksenofontov et al. 2019, Knopp et al. 2022). The inclusion of Indigenous- and local knowledge leverages the use of diverse knowledge types to inform biodiversity assessments (Pascual et al. 2021). Thus, peoples' perspectives and participation matter when it comes to designing conservation policies, because any effective policy needs to be implemented and respected by people in the end (Barry et al. 2015, Neuteleers et al. 2021). In consideration of the continued influence of colonialism and rare inclusion of Indigenous knowledge in science policy and governance, achieving climate justice for Indigenous populations is still a distant reality (Whyte et al. 2019, Chakraborty and Sherpa 2021, IPBES 2022).

Due to colonial legacies, Indigenous Arctic populations have not been included in the decision-making processes pertaining to their land. This is one of several factors contributing to the heightened impacts of climate change they are now experiencing (Whyte et al. 2019). While not being historically responsible for anthropogenic climate change, they are the ones bearing the consequences. Indigenous knowledge, grounded on an ontology that understands people and the Earth as one, has been consistently overlooked and neglected by settler states, increasing the vulnerability of these populations and perpetrating historical injustices and inequities (Whyte et al. 2019, Snook et al. 2020, Ford et al. 2021). Settler states, such as Canada, are moving to rectify this situation by encouraging inclusive governance and Indigenous leadership, (e.g. the development of local community-based monitoring systems for hunters and fishers) to document changes in the environment (Danielsen et al. 2014, AMAP 2017). Yet, Indigenous knowledge remains largely tokenized (at best) in governmental frameworks (Whyte et al. 2019). For instance, the incorporation of biodiversity and nature value into national-level policy is very limited, and ≤ 5% of valuation studies have reported integration into policy (IPBES 2022).

To date, research has focused on the influence of environmental change in the North American Arctic, rather than climate change impacts in the Arctic at a global level, leading to a biased view of the impacts on humans and natural systems (Metcalfe et al. 2018, Kaspar et al. 2022). Additionally, when considering climate change impacts on the environment, Arctic residents often cite factors such as tourism, international trade, and natural resource development, in contrast to researchers that typically consider climate change to be the sole external influence (Moerlein and Carothers 2012). These gaps in the academic approach highlight the necessity of incorporating both social and environmental change into Arctic climate change research and assessments. The migration of species across geopolitical boundaries as environmental change progresses will have a dramatic impact on local Arctic communities and future management of fauna and flora of the region. The identification and protection of refugial populations and habitat corridors, to uphold and potentially increase population connectivity and migration, can promote species and overall ecosystem resilience in the Arctic. Indigenous Peoples and culture should be explicitly integrated in research and resource management (Johnson et al. 2015, Brattland and Mustonen 2018). Increased intergovernmental collaboration at a circumarctic and global scale needs to be prioritized to create comprehensive and effective policies and a nexus approach will foster deeper knowledge of the region and inclusive conservation and management. By reviewing current understanding and outlining knowledge gaps, we call for mobilization towards more adaptable governance systems to promote resilience of humans and natural systems in a changing Arctic.

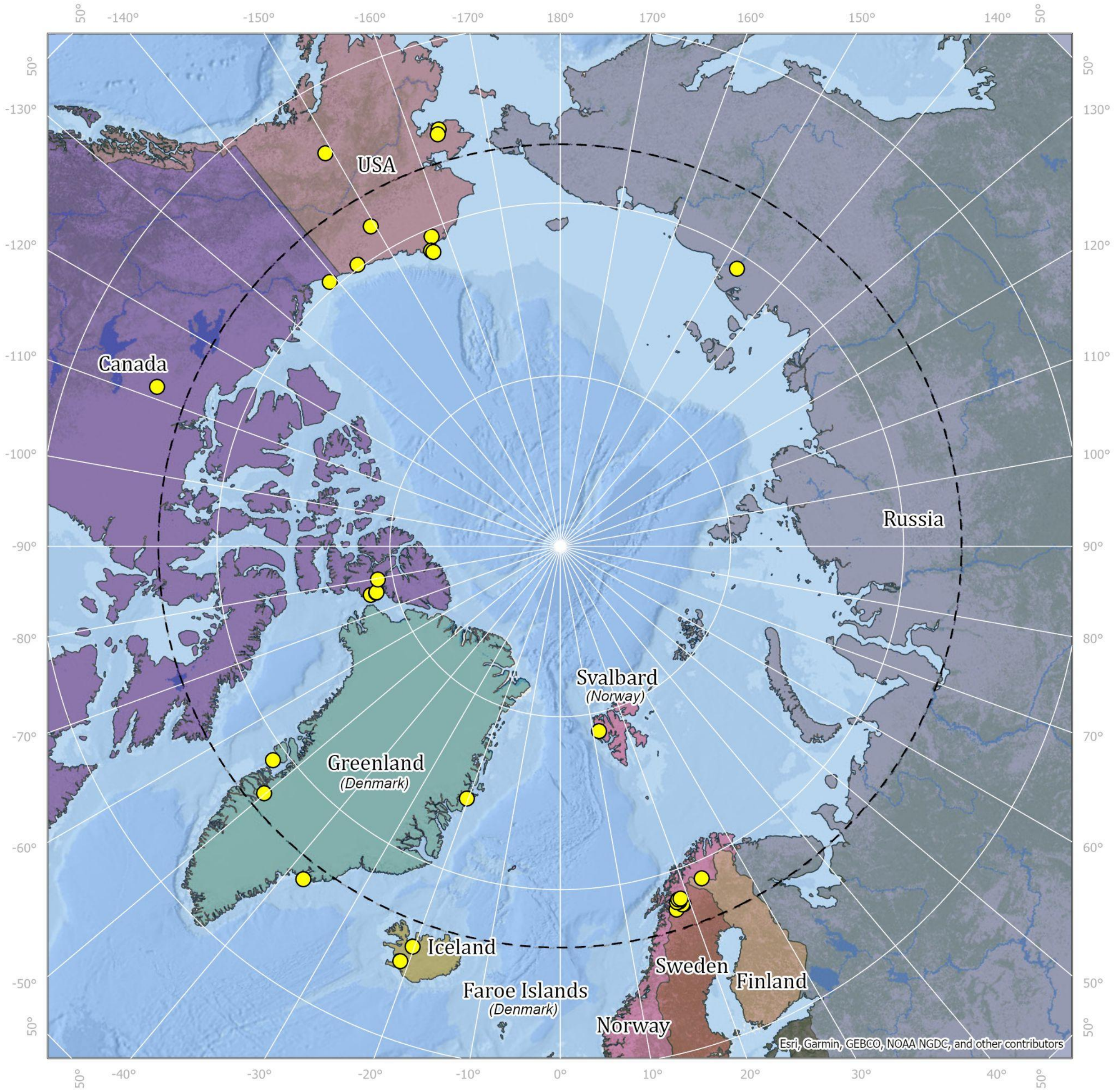
Tables

Table 1. Some outstanding questions regarding future conditions within the ecosystem-climate-human nexus across a range of future greenhouse gas emission pathways.

Nexus Component	Future Outlook Questions
Ecosystems	● How will “overshooting” (temporarily or not) 1.5°C warming affect Arctic species and ecosystems? ● What ecosystem changes are possible due to (individually and in combination): i. loss of surface soil because of permafrost thaw and collapse, ii. shrubification of the landscape; iii. movement and biotic community change of the forest-tundra ecotone, iv. winter warming events that could potentially cause massive vegetation/foraging source loss, v. change in growing season length, vi. large-scale losses through wildfires and other disturbances? ● To what extent could the rate of genetic mutation change (mutational meltdown/extinction vortex) in Arctic species under climate change?
Humans	● How much of the Arctic will be converted to cropland, pasture and/or otherwise modified due to natural resource extraction, tourism, and other development projects as climate change progresses? ● Will silviculture expand into the Arctic, and if so, to what extent and how will permafrost thaw, ecosystem processes, and biodiversity be impacted?

	● How will cultural heritage, subsistence harvesting, society, and language of Sámi, Inuit, and other Indigenous Peoples be impacted? ● How will forest-ecotone advancement facilitate disease transmission to humans by increasing habitat for animal and insect vectors? ● How will the release of sequestered pollutants and disease from permafrost thaw impact biological and human communities?
Climate	● What greenhouse gas emission scenario will most likely follow at the end of the 21st century? ● What happens when climate change in the Arctic triggers global tipping points? ● How will terrestrial ecosystem and vegetation changes influence the surface energy balance, aerosols and clouds? ● How often will extreme events occur and what kinds of regional and global impacts will they have? ● How strong will the climate feedback from thawing permafrost and wetland methane emissions be?

Figures



Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Figure 1. Map showing the territory of the eight Arctic States (Canada, The Kingdom of Denmark, Finland, Iceland, Norway, The Russian Federation, Sweden, and The United States of America (USA)) and plot-based vegetation research studies examining abundance and phenological change at 32 ITEX sites in the Arctic (above 63°N) from Bjorkman et al., 2020. Yellow circles indicate site location. The Arctic States and their associated territories are as follows: Canada, The Kingdom of Denmark, Finland, Iceland, Norway, The Russian Federation, Sweden, and The United States of America. The Arctic Circle is represented with a black dashed line.

Literature cited

Abass, K., Emelyanova, A., & Rautio, A. (2018). Temporal trends of contaminants in Arctic human populations. *Environmental Science and Pollution Research*, *25*, 28834-28850.

Abbott, R. J., & Brochmann, C. (2003). History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Molecular Ecology*, *12*(2), 299-313.

ACIA, 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. ACIA Overview report. Cambridge University Press, 140 pp.

Alsos, I. G., Engelskjøn, T., & Brochmann, C. (2002). Conservation genetics and population history of *Betula nana*, *Vaccinium uliginosum*, and *Campanula rotundifolia* in the arctic archipelago of Svalbard. *Arctic, Antarctic, and Alpine Research*, *34*(4), 408-418.

Alsos, I. G., Engelskjøn, T., Gielly, L., Taberlet, P., & Brochmann, C. (2005). Impact of ice ages on circumpolar molecular diversity: insights from an ecological key species. *Molecular Ecology*, *14*(9), 2739-2753.

Alsos, I. G., Ehrich, D., Thuiller, W., Eidesen, P. B., Tribsch, A., Schönswetter, P., et al. (2012). Genetic consequences of climate change for northern plants. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1735), 2042-2051.

Alsos, I. G., Sjögren, P., Brown, A. G., Gielly, L., Merkel, M. K. F., Paus, A., et al. (2020). Last Glacial Maximum environmental conditions at Andøya, northern Norway; evidence for a northern ice-edge ecological “hotspot”. *Quaternary Science Reviews*, *239*, 106364

Alsos, I. G., Sjögren, P., Edwards, M. E., Landvik, J. Y., Gielly, L., Forwick, M., et al. (2016). Sedimentary ancient DNA from Lake Skartjørna, Svalbard: Assessing the resilience of arctic flora to Holocene climate change. *The Holocene*, *26*(4), 627-642.

AMAP, 2017. Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. xiv + 269 pp.

Andersson, C. (2021). BioDiv-Support: scenario-based decision support tool for policy planning and adaptation to future challenges in biodiversity and ecosystem services. In *EGU General Assembly Conference Abstracts* (pp. EGU21-14412).

Andersson, G., von Proschwitz, T., Fägerström, C., Green, M., Smith, H. G., & Lindström, Å. (2022). Arthropod populations in a sub-arctic environment facing climate change over a half-century: variability but no general trend. *Insect Conservation and Diversity*, *15*(5), 534-542.

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., et al. (2022). Exceeding 1.5 C global warming could trigger multiple climate tipping points. *Science*, *377*(6611), eabn7950.

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., & Óskarsson, G. J. (2012). Climate-related variations in the occurrence and distribution of mackerel (Scomber scombrus) in Icelandic waters. *ICES Journal of Marine Science*, *69*(7), 1289-1297.

Barry, T., & Price, C. (2015). Arctic biodiversity: From science to policy. *Journal of Environmental Studies and Sciences*, *5*, 283-287.

Basu, N., Abass, K., Dietz, R., Krümmel, E., Rautio, A., & Weihe, P. (2022). The impact of mercury contamination on human health in the Arctic: A state of the science review. *Science of the Total Environment*, *831*, 154793.

Beamish, A., Raynolds, M. K., Epsteine, H., Frost, G. V., Macanderd, M. J., Bergstedt, H., Bartsch, A., Kruse, S., Miles, V., Tanis, C. M., Heim, B., Fuchs, M., Chabrillat, 'S., Shevtsova, J., Verdonen, M., Wagner, J. Recent trends and remaining challenges for optical remote sensing of Arctic tundra vegetation: A review and outlook. *Remote Sensing of the Environment* 246, 111872

Beckage, B., Moore, F. C., & Lacasse, K. (2022). Incorporating human behaviour into Earth system modelling. *Nature Human Behaviour*, *6*(11), 1493-1502.

Bennike, O., & Böcher, J. (1990). Forest-tundra neighbouring the North Pole: plant and insect remains from the Plio-Pleistocene Kap København formation, North Greenland. *Arctic*, 331-338.

Berner, J., Brubaker, M., Revitch, B., Kreummel, E., Tcheripanoff, M., & Bell, J. (2016). Adaptation in Arctic circumpolar communities: food and water security in a changing climate. *International Journal of Circumpolar Health*, *75*(1), 33820.

Berner, L. T., Jantz, P., Tape, K. D., & Goetz, S. J. (2018). Tundra plant above-ground biomass and shrub dominance mapped across the North Slope of Alaska. *Environmental Research Letters*, *13*(3), 035002.

Berner, L. T., Orndahl, K. M., Rose, M., Tamstorf, M., Arndal, M. F., Alexander, H. D., et al. (2024). The Arctic plant aboveground biomass synthesis dataset. *Scientific data*, *11*(1), 305.

Birkeland, S., Skjetne, I. E. B., Brysting, A. K., Elven, R., & Alsos, I. G. (2017). Living on the edge: conservation genetics of seven thermophilous plant species in a high Arctic archipelago. *AoB Plants*, *9*(1), plx001.

Birks, H. H. (1991). Holocene vegetational history and climatic change in west Spitsbergen-plant macrofossils from Skardtjørna, an Arctic lake. *The Holocene*, *1*(3), 209-218.

Biskaborn, B. K., Smith, S. L., Noetzli, J., Matthes, H., Vieira, G., Streletskiy, D. A., et al. (2019). Permafrost is warming at a global scale. *Nature Communications*, *10*(1), 264.

Bjorkman, A. D., García Criado, M., Myers-Smith, I. H., Ravolainen, V., Jónsdóttir, I. S., Westergaard, K. B., et al. (2020). Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. *Ambio*, *49*, 678-692.

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., et al. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57-62.

Bliss, L. C. (1958). Seed germination in arctic and alpine species. *Arctic*, *11*(3), 180-188.

Bokhorst, S., Bjerke, J. W., Street, L. E., Callaghan, T. V., & Phoenix, G. K. (2011). Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO_2 flux responses. *climat Biology*, *17*(9), 2817-2830.

Bokhorst, S., Bjerke, J. W., Phoenix, G. K., Jaakola, L., Mæhre, H. K., Tømmervik, H. (2023) Sub-arctic mosses and lichens show idiosyncratic responses to combinations of winter heatwaves, freezing and nitrogen deposition. *Physiologia Plantarum*. 175:e13882.

Bokhorst, S., Phoenix, G. K., Bjerke, J. W., Callaghan, T. V., Huyer-Brugman, F., & Berg, M. P. (2012). Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology*, *18*(3), 1152-1162.

Brattland, C., & Mustonen, T. (2018). How traditional knowledge comes to matter in Atlantic salmon governance in Norway and Finland. *Arctic*, *71*(4), 375-392.

Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Johnstone, J. F., Wagner, J. L., Chavez, A. S., et al. (2001). Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology*, *82*(1), 18-32.

Bring, A., Fedorova, I., Dibike, Y., Hinzman, L., Mård, J., Mernild, S. H., et al. (2016). Arctic terrestrial hydrology: A synthesis of processes, regional effects, and research challenges. *Journal of Geophysical Research: Biogeosciences*, *121*(3), 621-649.

Brochmann, C., Brysting, A. K., Alsos, I. G., Borgen, L., Grundt, H. H., Scheen, A. C., & Elven, R. (2004). Polyploidy in arctic plants. *Biological Journal of the Linnean Society*, *82*(4), 521-536.

Cai, Z., You, Q., Wu, F., Chen, H. W., Chen, D., & Cohen, J. (2021). Arctic warming revealed by multiple CMIP6 models: evaluation of historical simulations and quantification of future projection uncertainties. *Journal of Climate*, *34*(12), 4871-4892.

Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., et al. (2004). Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *AMBIO: A Journal of the Human Environment*, *33*(7), 404-417.

Callaghan, T. V., & Jonasson, S. (1995). Arctic terrestrial ecosystems and environmental change. *Philosophical Transactions of the Royal Society of London. Series A: Physical and Engineering Sciences*, *352*(1699), 259-276.

Canadell, J.G., P.M.S. Monteiro, M.H. Costa, L. Cotrim da Cunha, P.M. Cox, A.V. Eliseev, S. Henson, M. Ishii, S. Jaccard, C. Koven, A. Lohila, P.K. Patra, S. Piao, J. Rogelj, S. Syampungani, S. Zaehle, and K. Zickfeld, 2021: Global Carbon and other Biogeochemical Cycles and Feedbacks. In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 673–816.

Canosa, I. V., Ford, J. D., McDowell, G., Jones, J., & Pearce, T. (2020). Progress in climate change adaptation in the Arctic. *Environmental Research Letters*, *15*(9), 093009.

Chadburn, S. E., Burke, E. J., Cox, P. M., Friedlingstein, P., Hugelius, G., & Westermann, S. (2017). An observation-based constraint on permafrost loss as a function of global warming. *Nature Climate Change*, *7*(5), 340-344.

Chakraborty, R., & Sherpa, P. Y. (2021). From climate adaptation to climate justice: Critical reflections on the IPCC and Himalayan climate knowledges. *Climatic Change*, *167*(3-4), 49.

Chapin, F. S., and Shaver, G. R. (1985). Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, *66*(2), 564-576.

Chen, Y., Romps, D. M., Seeley, J. T., Veraverbeke, S., Riley, W. J., Mekonnen, Z. A., & Randerson, J. T. (2021a). Future increases in Arctic lightning and fire risk for permafrost carbon. *Nature Climate Change*, *11*(5), 404-410.

Chen, Y., Hu, F. S., & Lara, M. J. (2021b). Divergent shrub-cover responses driven by climate, wildfire, and permafrost interactions in Arctic tundra ecosystems. *Global Change Biology*, *27*(3), 652-663.

Cirtwill, A. R., Kaartinen, R., Rasmussen, C., Redr, D., Wirta, H., Olesen, J. M., et al. (2023). Stable pollination service in a generalist high Arctic community despite the warming climate. *Ecological Monographs*, *93*(1), e1551.

Cirtwill, A. R., Roslin, T., Rasmussen, C., Olesen, J. M., & Stouffer, D. B. (2018). Between-year changes in community composition shape species' roles in an Arctic plant–pollinator network. *Oikos*, *127*(8), 1163-1176.

Clarke, C. L., Alsos, I. G., Edwards, M. E., Paus, A., Gielly, L., Haflidason, H., et al. (2020). A 24,000-year ancient DNA and pollen record from the Polar Urals reveals temporal dynamics of arctic and boreal plant communities. *Quaternary Science Reviews*, *247*, 106564.

Cline, T. J., Ohlberger, J., & Schindler, D. E. (2019). Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution*, *3*(6), 935-942.

Cockerill, C. A., Hasselgren, M., Dussex, N., Dalén, L., von Seth, J., Angerbjörn, A., et al. (2022). Genomic consequences of fragmentation in the endangered fennoscandian arctic fox (Vulpes lagopus). *Genes*, *13*(11), 2124.

Colella, J. P., Talbot, S. L., Brochmann, C., Taylor, E. B., Hoberg, E. P., & Cook, J. A. (2020). Conservation genomics in a changing Arctic. *Trends in Ecology & Evolution*, *35*(2), 149-162.

Collins, C. G., Elmendorf, S. C., Hollister, R. D., Henry, G. H., Clark, K., Bjorkman, A. D., et al. (2021). Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nature Communications*, *12*(1), 3442.

Collins, C. G., Angert, A. L., Clark, K., Elmendorf, S. C., Elphinstone, C., & Henry, G. H. (2024). Flowering time responses to warming drive reproductive fitness in a changing Arctic. *Annals of Botany*, mcae007.

Constable, A.J., S. Harper, J. Dawson, K. Holsman, T. Mustonen, D. Piepenburg, and B. Rost, 2022: Cross-Chapter Paper 6: Polar Regions. In: *Climate Change 2022: Impacts, Adaptation and Vulnerability.* Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 2319–2368.

Cunsolo Willox, A., Stephenson, E., Allen, J., Bourque, F., Drossos, A., Elgarøy, S., et al. (2015). Examining relationships between climate change and mental health in the Circumpolar North. *Regional Environmental Change*, *15*, 169-182.

Curasi, S. R., Fetcher, N., Hewitt, R. E., Lafleur, P. M., Loranty, M. M., Mack, M. C., et al. (2022). Range shifts in a foundation sedge potentially induce large Arctic ecosystem carbon losses and gains. *Environmental Research Letters*, *17*(4), 045024.

Dalen, L., & Hofgaard, A. (2005). Differential regional treeline dynamics in the Scandes Mountains. *Arctic, Antarctic, and Alpine Research*, *37*(3), 284-296.

Danby, R. K., & Hik, D. S. (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, *95*(2), 352-363.

Danielsen, F., Topp-Jørgensen, E., Levermann, N., Løvstrøm, P., Schiøtz, M., Enghoff, M., & Jakobsen, P. (2014). Counting what counts: using local knowledge to improve Arctic resource management. *Polar Geography*, *37*(1), 69-91.

Davey, C. M., Devictor, V., Jonzén, N., Lindström, Å., & Smith, H. G. (2013). Impact of climate change on communities: revealing species' contribution. *Journal of Animal Ecology*, *82*(3), 551-561.

Dawson, J., Pizzolato, L., Howell, S. E., Copland, L., & Johnston, M. E. (2018). Temporal and spatial patterns of ship traffic in the Canadian Arctic from 1990 to 2015. *Arctic*, *71*(1), 15-26.

Deslippe, J. R., & Simard, S. W. (2011). Below-ground carbon transfer among *Betula nana* may increase with warming in Arctic tundra. *New Phytologist*, *192*(3), 689-698.

Dial, R. J., Maher, C. T., Hewitt, R. E., & Sullivan, P. F. (2022). Sufficient conditions for rapid range expansion of a boreal conifer. *Nature*, *608*(7923), 546-551.

Ditlevsen, P., & Ditlevsen, S. (2023). Warning of a forthcoming collapse of the Atlantic meridional overturning circulation. *Nature Communications*, *14*(1), 1-12.

Dobbert, S., Pape, R., and Löffler, J. (2021). Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. *Ecosphere* 12.

Donaldson, S. G., Van Oostdam, J., Tikhonov, C., Feeley, M., Armstrong, B., Ayotte, P., et al. (2010). Environmental contaminants and human health in the Canadian Arctic. *Science of the Total Environment*, *408*(22), 5165-5234.

Doyle, S., Gray, A., & McMahon, B. J. (2020). Anthropogenic impacts on the demographics of Arctic-breeding birds. *Polar Biology*, *43*(12), 1903-1945.

Drewniak, M., Dalaklis, D., Kitada, M., Ölçer, A., & Ballini, F. (2018). Geopolitics of Arctic shipping: the state of icebreakers and future needs. *Polar Geography*, *41*(2), 107-125.

Eidesen, P. B., Ehrich, D., Bakkestuen, V., Alsos, I. G., Gilg, O., Taberlet, P., et al. (2013). Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. *New Phytologist*, 200, 898–910.

Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., et al. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, *15*(2), 164-175.

Elmhagen, B., Berteaux, D., Burgess, R. M., Ehrich, D., Gallant, D., Henttonen, H., et al. (2017). Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research*, *36*(sup1), 3.

Elphinstone, C., Hernández, F., Todesco, M., Légaré, J. S., Cheung, W., Sokoloff, P. C., et al. (2024). Multiple Pleistocene refugia for Arctic Bell-Heather revealed with genomic analyses of modern and historic plants. *Journal of Biogeography*.

Elven, R., Murray, D. F., Razzhivin, V. Y., & Yurtsev, B. A. (2011). Annotated checklist of the Panarctic Flora (PAF).

Eränen, J. K., & Kozlov, M. V. (2008). Increasing intraspecific facilitation in exposed environments: consistent results from mountain birch populations in two subarctic stress gradients. *Oikos*, *117*(10), 1569-1577.

Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J., Steltzer, H., & Wallenstein, M. D. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*, *20*(10), 3256-3269.

Fall, J. A. (2016). Regional patterns of fish and wildlife harvests in contemporary Alaska. *Arctic*, 47-64.

Fawcett, D., Pearce, T., Notaina, R., Ford, J. D., & Collings, P. (2018). Inuit adaptability to changing environmental conditions over an 11-year period in Ulukhaktok, Northwest Territories. *Polar Record*, *54*(2), 119-132.

Fedewa, E. J., Jackson, T. M., Richar, J. I., Gardner, J. L., & Litzow, M. A. (2020). Recent shifts in northern Bering Sea snow crab (*Chionoecetes opilio*) size structure and the potential role of climate-mediated range contraction. *Deep Sea Research Part II: Topical Studies in Oceanography*, *181*, 104878.

Fenger-Nielsen, R., Elberling, B., Kroon, A., Westergaard-Nielsen, A., Matthiesen, H., Harmsen, H., et al. (2020). Arctic archaeological sites threatened by climate change: A regional multi-threat assessment of sites in south-west Greenland. *Archaeometry*, *62*(6), 1280-1297.

Feodoroff, P. (2021). Indigenous Female Bodies as Indicators of Change. In: 2021 Compendium of Indigenous Knowledge and Local Knowledge: Towards Inclusion of Indigenous Knowledge and Local Knowledge in Global Reports on Climate Change [Mustonen, T., S. L. Harper, M. Rivera Ferre, J. Postigo, A. Ayanlade, T. Benjaminsen, R. Morgan and A. Okem (eds.)]. SnowChange Cooperative, Kontiolahti, Finland, pp. 1.

Forbes, B. C., Kumpula, T., Meschtyb, N., Laptander, R., Macias-Fauria, M., Zetterberg, P., et al. (2016). Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. *Biology Letters*, *12*(11), 20160466.

Ford, J. D., Pearce, T., Canosa, I. V., & Harper, S. (2021). The rapidly changing Arctic and its societal implications. *Wiley Interdisciplinary Reviews: Climate Change*, *12*(6), e735.

Frei, E. R., & Henry, G. H. (2021). Long-term effects of snowmelt timing and climate warming on phenology, growth, and reproductive effort of Arctic tundra plant species. *Arctic Science*, *8*(3), 700-721.

Gibson, J., Adlard, B., Olafsdottir, K., Sandanger, T. M., & Odland, J. Ø. (2016). Levels and trends of contaminants in humans of the Arctic. *International Journal of Circumpolar Health*, *75*(1), 33804.

Gilg, O., Kovacs, K. M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., et al. (2012). Climate change and the ecology and evolution of Arctic vertebrates. *Annals of the New York Academy of Sciences*, *1249*(1), 166-190.

Gillespie, M. A. K., Alfredsson, M., Barrio, I. C., Bowden, J. J., Convey, P., Culler, L. E., et al. (2020). Status and trends of terrestrial arthropod abundance and diversity in the North Atlantic region of the Arctic. *Ambio*, *49*, 718-731.

Grigorieva, E. A. (2024). Climate Change and Human Health in the Arctic: A Review. *Climate*, *12*(7), 89.

Gu, Q., Yu, Q., Grogan, P. (2023) Cryptogam plant community stability: Warming weakens influences of species richness but enhances effects of evenness. *Ecology* 2023;104:e3842.

Gunn, A. (2016). *Rangifer tarandus*: The IUCN Red List of Threatened Species 2016. e.T29742A22167140. Gland: International Union for Conservation of Nature.

Gustafson, A., Miller, P. A., Björk, R. G., Olin, S., & Smith, B. (2021). Nitrogen restricts future sub-arctic treeline advance in an individual-based dynamic vegetation model. *Biogeosciences*, *18*(23), 6329-6347.

Hamrick, J. L., & Godt, M. W. (1996). Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*(1345), 1291-1298.

Hanaček, K., Kröger, M., Scheidel, A., Rojas, F., & Martinez-Alier, J. (2022). On thin ice–The Arctic commodity extraction frontier and environmental conflicts. *Ecological Economics*, *191*, 107247.

Harper, S. L., C. Wright, S. Masina and S. Coggins, 2020: Climate change, water, and human health research in the Arctic. *Water Security*, *10*, 100062.

Hartley, I. P., Garnett, M. H., Sommerkorn, M., Hopkins, D. W., Fletcher, B. J., Sloan, V. L., et al. (2012). A potential loss of carbon associated with greater plant growth in the European Arctic. *Nature Climate Change*, *2*(12), 875-879.

Heffernan, E., Epstein, H. E., McQuinn, T. D., Lutz, D., Rogers, B. M., Virkkala, A. M., & Armstrong, A. H. (2024). Comparing assumptions and applications of dynamic vegetation models used in the Arctic-Boreal Zone of Alaska and Canada. *Environmental Research Letters*.

Hegedűs, D., Ballinger, A. P., & Hegerl, G. C. (2024). Observed links between heatwaves and wildfires across Northern High Latitudes. *Environmental Research Letters*.

Hodkinson, I. D., and Coulson, S. J. (2004). Are High Arctic terrestrial food chains really that simple?–The Bear Island food web revisited. *Oikos, 106(2), 427-431.*

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world’s marine ecosystems. *Science*, *328*(5985), 1523-1528.

Hoegh-Guldberg, O., D. Jacob, M. Taylor, M. Bindi, S. Brown, I. Camilloni, A. Diedhiou, R. Djalante, K.L. Ebi, F. Engelbrecht, J. Guiot, Y. Hijioka, S. Mehrotra, A. Payne, S.I. Seneviratne, A. Thomas, R. Warren, and G. Zhou, (2018). Impacts of 1.5ºC Global Warming on Natural and Human Systems. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)] (pp. 175-311). IPCC Secretariat.

Hofgaard, A., Dalen, L., & Hytteborn, H. (2009). Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science*, *20*(6), 1133-1144.

Holtmeier, F. K., & Broll, G. (2017). Treelines—Approaches at different scales. *Sustainability*, *9*(5), 808.

Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A., Ping, C. L., et al. (2014). Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences*, *11*(23), 6573-6593.

Huntington, H. P., Danielson, S. L., Wiese, F. K., Baker, M., Boveng, P., Citta, J. J., et al. (2020). Evidence suggests potential transformation of the Pacific Arctic ecosystem is underway. *Nature Climate Change*, *10*(4), 342-348.

IPBES (2022). Summary for Policymakers of the Methodological Assessment Report on the Diverse Values and Valuation of Nature of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Pascual, U., Balvanera, P., Christie, M., Baptiste, B., González-Jiménez, D., Anderson, C. B., Athayde, S., Chaplin-Kramer, R., Jacobs, S., Kelemen, E., Kumar, R., Lazos, E., Martin, A., Mwampamba, T. H., Nakangu, B., O'Farrell, P., Raymond, C. M., Subramanian, S. M., Termansen, M., Van Noordwijk, M., and Vatn, A. (eds.). IPBES secretariat, Bonn, Germany.

IPBES (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (pp. XIV-LXI). Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Roy Chowdhury, R., Shin, Y. J., Visseren-Hamakers, I. J., Willis, K. J., and Zayas C.N. (eds.). IPBES secretariat, Bonn, Germany.

IPCC (2019). IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. Cambridge, UK and New York, NY.

IPCC (2022). Summary for Policymakers [P.R. Shukla, J. Skea, A. Reisinger, R. Slade, R. Fradera, M. Pathak, A. Al Khourdajie, M. Belkacemi, R. van Diemen, A. Hasija, G. Lisboa, S. Luz, J. Malley, D. McCollum, S. Some, P. Vyas, (eds.)]. In *Climate Change 2*. Cambridge, UK and New York, NY.

Jackson, L. C., & Wood, R. A. (2018). Hysteresis and resilience of the AMOC in an eddy-permitting GCM. *Geophysical Research Letters*, *45*(16), 8547-8556.

Järvinen, O., Kouki, J., & Häyrinen, U. (1987). Reversed latitudinal gradients in total density and species richness of birds breeding on Finnish mires. *Ornis Fennica*, *64*(2), 67-73.

Jenkins, L. K., Barry, T., Bosse, K. R., Currie, W. S., Christensen, T., Longan, S., et al. (2020). Satellite-based decadal change assessments of pan-Arctic environments. *Ambio* 49, 820–832.

Jensen, A. M. (2020). Critical information for the study of ecodynamics and socio-natural systems: Rescuing endangered heritage and data from Arctic Alaskan Coastal sites. *Quaternary International*, *549*, 227-238.

Jørgensen, L. L., Primicerio, R., Ingvaldsen, R. B., Fossheim, M., Strelkova, N., Thangstad, T. H., et al. (2019). Impact of multiple stressors on sea bed fauna in a warming Arctic. *Marine Ecology Progress Series*, *608*, 1-12.

Johnson, N., Alessa, L., Behe, C., Danielsen, F., Gearheard, S., Gofman-Wallingford, V., et al. (2015). The contributions of community-based monitoring and traditional knowledge to Arctic observing networks: reflections on the state of the field. *Arctic*, 28-40.

Jorgenson, M. T. (2013). 8.20 Thermokarst Terrains. *Treatise on Geomorphology*, 313-324.

Jung, P., Briegel-Williams, L. Simon, A., Thyssen, A., Büdel, B. (2018) Uncovering biological soil crusts: carbon content and structure of intact Arctic, Antarctic and alpine biological soil crusts. *Biogeosciences*, 15, 1149–1160.

Juottonen, H., Männistö, M., Tiirola, M., Kytoviita, M. M. (2020) Cryptogams signify key transitions of bacteria and fungi in Arctic sand dune succession. *New Phytologist* 226: 1836–1849.

Kapsar, K., Frans, V. F., Brigham, L. W., & Liu, J. (2022). The metacoupled Arctic: Human–nature interactions across local to global scales as drivers of sustainability. *Ambio*, *51*(10), 2061-2078.

Kasten, E., Krupnik, I., & Fondahl, G. (Eds.). (2024). *A Fractured North: Facing Dilemmas* (Vol. 1). BoD–Books on Demand.

Keuschnig, C., Larose, C., Rudner, M., Pesqueda, A., Doleac, S., Elberling, B., et al. (2022). Reduced methane emissions in former permafrost soils driven by vegetation and microbial changes following drainage. *Global Change Biology*, *28*(10), 3411-3425.

Killengreen, S. T., Ims, R. A., Yoccoz, N. G., Bråthen, K. A., Henden, J. A., and Schott, T. (2007). Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. *Biological Conservation*, *135*(4), 459-472.

Kim, Y. H., Min, S. K., Gillett, N. P., Notz, D., & Malinina, E. (2023). Observationally-constrained projections of an ice-free Arctic even under a low emission scenario. *Nature Communications*, *14*(1), 3139.

Knopp, J. A., Levenstein, B., Watson, A., Ivanova, I., & Lento, J. (2022). Systematic review of documented Indigenous Knowledge of freshwater biodiversity in the circumpolar Arctic. *Freshwater Biology*, *67*(1), 194-209.

Knotsch, C., & Lamouche, J. (2010). Arctic biodiversity and Inuit health.

Kohler, J., & Aanes, R. (2004). Effect of winter snow and ground-icing on a Svalbard reindeer population: results of a simple snowpack model. *Arctic, Antarctic, and Alpine Research*, *36*(3), 333-341.

Kokelj, S. V., & Jorgenson, M. T. (2013). Advances in thermokarst research. *Permafrost and Periglacial Processes*, *24*(2), 108-119.

Kowalczewski, E. and J. Klein, 2018: Sámi youth health, the role of climate change, and unique health-seeking behaviour. *International Journal of Circumpolar Health*, *77*(1), 1454785.

Ksenofontov, S., Backhaus, N., & Schaepman-Strub, G. (2019). 'There are new species': indigenous knowledge of biodiversity change in Arctic Yakutia. *Polar Geography*, *42*(1), 34-57.

Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, *90*(1), 68-77.

Kumpula, T., Pajunen, A., Kaarlejärvi, E., Forbes, B. C., & Stammler, F. (2011). Land use and land cover change in Arctic Russia: Ecological and social implications of industrial development. *Global Environmental Change*, *21*(2), 550-562.

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., et al. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, *29*(3), 724-737.

Lee, J.-Y., Marotzke, J., Bala, G., Cao, L., Corti, S., Dunne, J.P., Engelbrecht, F., Fischer, E., Fyfe, J.C., Jones, C., Maycock, A., Mutemi, J., Ndiaye, O., Panickal, S., & Zhou, T. (2021). Future Global Climate: Scenario-Based Projections and Near Term Information. In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 553–672.

Leffler, A. J., Klein, E. S., Oberbauer, S. F., & Welker, J. M. (2016). Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. *Oecologia*, *181*, 287-297.

Lehikoinen, A., Green, M., Husby, M., Kålås, J. A., & Lindström, Å. (2014). Common montane birds are declining in northern Europe. *Journal of Avian Biology*, *45*(1), 3-14.

Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., & Schellnhuber, H. J. (2008). Tipping elements in the Earth's climate system. *Proceedings of the National Academy of Sciences*, *105*(6), 1786-1793.

Lescop-Sinclair, K., & Payette, S. (1995). Recent advance of the arctic treeline along the eastern coast of Hudson Bay. *Journal of Ecology*, 929-936.

Li, B., Heijmans, M. M. P. D., Berendse, F., Blok, D., Maximov, T., and Sass-Klaassen, U. (2016). The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub *Betula nana* in northeast Siberian tundra. *Polar Biology*, *39*, 1245-1255.

Liu, J., Hull, V., Godfray, H. C. J., Tilman, D., Gleick, P., Hoff, H., et al. (2018). Nexus approaches to global sustainable development. *Nature Sustainability*, *1*(9), 466-476.

López-Blanco, E., Topp-Jørgensen, E., Christensen, T. R., Rasch, M., Skov, H., Arndal, M. F., et al. (2024). Towards an increasingly biased view on Arctic change. *Nature Climate Change*, 1-4.

MacDonald, G. M., Velichko, A. A., Kremenetski, C. V., Borisova, O. K., Goleva, A. A., Andreev, A. A., et al. (2000). Holocene treeline history and climate change across northern Eurasia. *Quaternary Research*, *53*(3), 302-311.

Maes, S. L., Dietrich, J., Midolo, G., Schwieger, S., Kummu, M., Vandvik, V., et al. (2024). Environmental drivers of increased ecosystem respiration in a warming tundra. *Nature*, 1-9.

Martín, J. M. R. (2018). Policies and Strategies for the Arctic: A Review of the Approaches to Human Security in the Arctic. *Human and Societal Security in the Circumpolar Arctic*, 19-49.

Mata, J. K., Martin, S. L., & Smith, T. W. (2023). Global biodiversity data suggest allopolyploid plants do not occupy larger ranges or harsher conditions compared with their progenitors. *Ecology and Evolution*, *13*(8), e10231.

Matthews Jr, J. V., & Ovenden, L. E. (1990). Late Tertiary plant macrofossils from localities in Arctic/Subarctic North America: A Review of the Data. *Arctic*, 364-392.

Mathisen, I. E., Mikheeva, A., Tutubalina, O. V., Aune, S., & Hofgaard, A. (2014). Fifty years of tree line change in the Khibiny Mountains, Russia: advantages of combined remote sensing and dendroecological approaches. *Applied Vegetation Science*, *17*(1), 6-16.

Maxwell, S. L., Venter, O., Jones, K. R., & Watson, J. E. (2015). Integrating human responses to climate change into conservation vulnerability assessments and adaptation planning. *Annals of the New York Academy of Sciences*, *1355*(1), 98-116.

McCarty, J. L., Aalto, J., Paunu, V. V., Arnold, S. R., Eckhardt, S., Klimont, Z., et al. (2021). Reviews & syntheses: arctic fire regimes and emissions in the 21st century. *Biogeosciences Discussions*, *2021*, 1-59.

McCarty, J. L., Smith, T. E. L., and Turetsky, M. R. (2020). Arctic fires re-emerging. *Nature Geoscience*, *13*(10), 658-660.

Mcgraw, J. B. (1995). Patterns and causes of genetic diversity in arctic plant. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 33–43.

Meimberg, H., Rice, K. J., Milan, N. F., Njoku, C. C., & McKay, J. K. (2009). Multiple origins promote the ecological amplitude of allopolyploid *Aegilops* (Poaceae). *American Journal of Botany*, *96*(7), 1262-1273.

Meltofte, H., Huntington, H. P., and Barry, T. (2013). Arctic Biodiversity Assessment: Status and trends in Arctic biodiversity. Akureyri.

Meredith, M. et al., 2019: Polar Regions. In *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* [Pörtner, H.-O., D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama and N. M. Weyer (eds.)], pp. 118.

Metcalfe, D. B., Hermans, T. D., Ahlstrand, J., Becker, M., Berggren, M., Björk, R. G., ... & Abdi, A. M. (2018). Patchy field sampling biases understanding of climate change impacts across the Arctic. *Nature Ecology & Evolution*, *2*(9), 1443-1448.

Mikola, J., Silfver, T., & Rousi, M. (2018). Mountain birch facilitates Scots pine in the northern tree line–does improved soil fertility have a role?. *Plant and Soil*, *423*, 205-213.

Moerlein, K. J., & Carothers, C. (2012). Total environment of change: impacts of climate change and social transitions on subsistence fisheries in northwest Alaska. *Ecology and Society*, *17*(1).

Mohite, P., Pandhare, R., Mukerjee, N., Sharma, R., Dey, A., Mohapatra, R. K., ... & Sah, R. (2023). Zombie virus revitalized from permafrost: Facts and fiction. *New Microbes and New Infections*, *53*.

Murray, D. F. (1995). Causes of arctic plant diversity: origin and evolution. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 21-32.

Mustonen, T., Mustonen, K., Kirillov, J., Paul, A., Koleshnikova, A., Kurzeneva, I., et al. (2021). Community-based monitoring in the Ponoy River, Kola Peninsula (Russia): Reflections on Atlantic salmon, pink salmon, Northern pike and weather/climate change. *Polar Biology*, *44*(1), 173-194.

Mustonen, T. and V. Shadrin, 2021: The River Alazeya: Shifting Socio-Ecological Systems Connected to a Northeastern Siberian River. *Arctic*, *74*(1).

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S., Wilmking, M., Hallinger, M., Blok, D., et al. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, *5*(9), 887-891.

Neuteleers, S., & Hugé, J. (2021). Value pluralism in ecosystem services assessments: Closing the gap between academia and conservation practitioners. *Ecosystem Services*, *49*, 101293.

Nicu, I. C., & Fatorić, S. (2023). Climate change impacts on immovable cultural heritage in polar regions: A systematic bibliometric review. *Wiley Interdisciplinary Reviews: Climate Change*, e822.

Nielsen, U. N., and Wall, D. H. (2013). The future of soil invertebrate communities in polar regions: Different climate change responses in the Arctic and Antarctic? *Ecology Letters*, *16*, 409–419.

Niskanen, A. K. J., Niittynen, P., Aalto, J., Väre, H., & Luoto, M. (2019). Lost at high latitudes: Arctic and endemic plants under threat as climate warms. *Diversity and Distributions*, *25*(5), 809-821.

Notz, D., & Community, S.I.M.I.P. (2020). Arctic sea ice in CMIP6. *Geophysical Research Letters*, *47*(10), e2019GL086749.

Oh, Y., Zhuang, Q., Liu, L., Welp, L. R., Lau, M. C., Onstott, T. C., et al. (2020). Reduced net methane emissions due to microbial methane oxidation in a warmer Arctic. *Nature Climate Change*, *10*(4), 317-321.

Parmesan, C., M.D. Morecroft, Y. Trisurat, R. Adrian, G.Z. Anshari, A. Arneth, Q. Gao, P. Gonzalez, R. Harris, J. Price, N. Stevens, and G.H. Talukdarr, 2022: Terrestrial and Freshwater Ecosystems and Their Services. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 197–377

Pascual, U., Adams, W. M., Díaz, S., Lele, S., Mace, G. M., & Turnhout, E. (2021). Biodiversity and the challenge of pluralism. *Nature Sustainability*, *4*(7), 567-572.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... & Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214.

Peng, X., Yu, M., & Chen, H. (2021). Projected changes in terrestrial vegetation and carbon fluxes under 1.5 C and 2.0 C global warming. *Atmosphere*, *13*(1), 42.

Peñuelas, J., Rutishauser, T., & Filella, I. (2009). Phenology feedbacks on climate change. *Science*, *324*(5929), 887-888.

Peterson, K. J., Powell, A. J., Tezaur, I. K., Roesler, E. L., Nichol, J., Peterson, M. G., et al. (2020). Arctic Tipping Points Triggering Global Change (LDRD Final Report) (No. SAND-2020-9932). Albuquerque, NM and Livermore, CA.

Phoenix, G. K., Bjerke, J. W., Björk, R. G., Blok, D., Bryn, A., Callaghan, T. V., et al. (in review) Browning events in Arctic ecosystems: diverse causes with common consequences. PLOS Climate

Post, E., Alley, R. B., Christensen, T. R., Macias-Fauria, M., Forbes, B. C., Gooseff, M. N., et al. (2019). The polar regions in a 2°C warmer world. *Science advances*, *5*(12), eaaw9883.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., et al. (2009). Ecological dynamics across the Arctic associated with recent climate change. *Science*, *325*(5946), 1355-1358.

Prevéy, J. S., Rixen, C., Rüger, N., Høye, T. T., Bjorkman, A. D., Myers-Smith, I. H., et al. (2019). Warming shortens flowering seasons of tundra plant communities. *Nature Ecology & Evolution*, *3*(1), 45-52.

Prevéy, J., Vellend, M., Rüger, N., Hollister, R. D., Bjorkman, A. D., Myers-Smith, I. H., et al. (2017). Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. *Global Change Biology*, *23*, 2660–2671.

Putkonen, J., Grenfell, T. C., Rennert, K., Bitz, C., Jacobson, P., & Russell, D. (2009). Rain on snow: little understood killer in the north. *Eos, Transactions American Geophysical Union*, *90*(26), 221-222.

Qiu, C., Ciais, P., Zhu, D., Guenet, B., Chang, J., Chaudhary, N., et al. (2022). A strong mitigation scenario maintains climate neutrality of northern peatlands. *One Earth*, *5*(1), 86-97.

Raheem, D. (2018). Food and nutrition security as a measure of resilience in the Barents region. *Urban Science*, *2*(3), 72.

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., et al. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168.

Rees, W. G., Hofgaard, A., Boudreau, S., Cairns, D. M., Harper, K., Mamet, S., et al. (2020). Is subarctic forest advance able to keep pace with climate change?. *Global Change Biology*, *26*(7), 3965-3977.

Repenning, C. A., & Brouwers, E. M. (1992). *Late Pliocene-early Pleistocene ecologic changes in the Arctic Ocean borderland*. Washington, DC: US Government Printing Office.

Reu, B., Zaehle, S., Bohn, K., Pavlick, R., Schmidtlein, S., Williams, J. W., & Kleidon, A. (2014). Future no-analogue vegetation produced by no-analogue combinations of temperature and insolation. *Global Ecology and Biogeography*, *23*(2), 156-167.

Rogelj, J., D. Shindell, K. Jiang, S. Fifita, P. Forster, V. Ginzburg, C. Handa, H. Kheshgi, S. Kobayashi, E. Kriegler, L. Mundaca, R. Séférian, and M.V. Vilariño, 2018: Mitigation Pathways Compatible with 1.5°C in the Context of Sustainable Development. In: *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 93-174.

Ruscio, B. A., Brubaker, M., Glasser, J., Hueston, W., & Hennessy, T. W. (2015). One Health–a strategy for resilience in a changing arctic. *International Journal of Circumpolar Health*, *74*(1), 27913.

Sauve, D., Divoky, G., & Friesen, V. L. (2019). Phenotypic plasticity or evolutionary change? An examination of the phenological response of an arctic seabird to climate change. *Functional Ecology*, *33*(11), 2180-2190.

Schaefer, K., Elshorbany, Y., Jafarov, E., Schuster, P. F., Striegl, R. G., Wickland, K. P., & Sunderland, E. M. (2020). Potential impacts of mercury released from thawing permafrost. *Nature communications*, *11*(1), 4650

Scharn, R., Brachmann, C. G., Patchett, A., Reese, H., Bjorkman, A. D., Alatalo, J. M., Björk, R. G., Jägerbrand, A. K. et al. (2021). Vegetation responses to 26 years of warming at Latnjajaure Field Station, northern Sweden. *Arctic Science*, *8*(3), 858-877.

Scharn, R., Negri, I. S., Sundqvist, M. K., Løkken, J. O., Bacon, C. D., Antonelli, A., et al. (2022). Limited decadal growth of mountain birch saplings has minor impact on surrounding tundra vegetation. *Ecology and Evolution*, *12*(6), e9028.

Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E. H., & Chapin III, F. S. (2012). Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences*, *109*(52), 21384-21389.

Schmidt, N. M., Christensen, T. R., & Roslin, T. (2017a). A high arctic experience of uniting research and monitoring. *Earth's Future*, *5*(7), 650-654.

Schmidt, N. M., Hardwick, B., Gilg, O., Høye, T. T., Krogh, P. H., Meltofte, H., et al. (2017b). Interaction webs in arctic ecosystems: Determinants of arctic change?. *Ambio*, *46*, 12-25.

Schmidt, N. M., Mosbacher, J. B., Nielsen, P. S., Rasmussen, C., Høye, T. T., & Roslin, T. (2016). An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography*, *39*(12), 1250-1252.

Schütte, U. M., Henning, J. A., Ye, Y., Bowling, A., Ford, J., Genet, H., et al. (2019). Effect of permafrost thaw on plant and soil fungal community in a boreal forest: does fungal community change mediate plant productivity response?. *Journal of Ecology*, *107*(4), 1737-1752.

Schuur, E. A., Abbott, B. W., Commane, R., Ernakovich, J., Euskirchen, E., Hugelius, G., et al. (2022). Permafrost and climate change: Carbon cycle feedbacks from the warming Arctic. *Annual Review of Environment and Resources*, *47*, 343-371.

Shadrin, V., 2021: Siberian Indigenous Observations of Climate Change. In: *2021 Compendium of Indigenous Knowledge and Local Knowledge: Towards Inclusion of Indigenous Knowledge and Local Knowledge in Global Reports on Climate Change* [Mustonen, T., S.L. Harper, M. Rivera Ferre, J. Postigo, A. Ayanlade, T. Benjaminsen, R. Morgan and A. Okem (eds.)]. SnowChange Cooperative, Kontiolahti, Finland, pp. 1.

Sigmond, M., Fyfe, J. C., Saenko, O. A., & Swart, N. C. (2020). Ongoing AMOC and related sea-level and temperature changes after achieving the Paris targets. *Nature Climate Change*, *10*(7), 672-677.

Slatyer, R. A., Umbers, K. D., & Arnold, P. A. (2022). Ecological responses to variation in seasonal snow cover. *Conservation Biology*, *36*(1), e13727.

Smith, P. A., McKinnon, L., Meltofte, H., Lanctot, R. B., Fox, A. D., Leafloor, J. O., et al. (2020). Status and trends of tundra birds across the circumpolar Arctic. *Ambio*, *49*, 732-748.

Snook, J., Cunsolo, A., Borish, D., Furgal, C., Ford, J. D., Shiwak, I., et al. (2020). “We’re made criminals just to eat off the land”: colonial wildlife management and repercussions on Inuit well-being. *Sustainability*, *12*(19), 8177.

Stark, S., Horstkotte, T., Kumpula, J., Olofsson, J., Tømmervik, H., & Turunen, M. (2023). The ecosystem effects of reindeer (*Rangifer tarandus*) in northern Fennoscandia: Past, present and future. *Perspectives in Plant Ecology, Evolution and Systematics*, *58*, 125716.

Stenström, A., Olle Jonsson, B., Jónsdóttir, I. S., Fagerström, T., and Augner, M. (2001). Genetic variation and clonal diversity in four clonal sedges (*Carex*) along the Arctic coast of Eurasia. *Molecular Ecology*, *10*, 497–513.

Stephen, K. (2018). Societal impacts of a rapidly changing Arctic. *Current Climate Change Reports*, *4*(3), 223-237.

Stojak, J., and Jędrzejewska, B. (2022). Extinction and replacement events shaped the historical biogeography of Arctic mammals in Europe: new models of species response. *Mammal Review*, *52*, 507–518. doi:10.1111/mam.12298.

Stunz, E., Fetcher, N., Lavretsky, P., Mohl, J. E., Tang, J., Moody, M. L., et al. (2022). Landscape genomics provides evidence of ecotypic adaptation and a barrier to gene flow at treeline for the Arctic foundation species *Eriophorum vaginatum*. *Frontiers in Plant Science*, *13*, 1–18.

Sturm, M., Racine, C., & Tape, K. (2001). Increasing shrub abundance in the Arctic. *Nature*, *411*(6837), 546-547.

Sundqvist, M. K., Björk, R. G., & Molau, U. (2008). Establishment of boreal forest species in alpine dwarf-shrub heath in subarctic Sweden. *Plant Ecology & Diversity*, *1*(1), 67-75.

Taberlet, P., Zimmermann, N. E., Englisch, T., Tribsch, A., Holderegger, R., Alvarez, N., et al. (2012). Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. *Ecology Letters*, *15*, 1439–1448.

Tang, J., Zhou, P., Miller, P. A., Schurgers, G., Gustafson, A., Makkonen, R., et al. (2023). High-latitude vegetation changes will determine future plant volatile impacts on atmospheric organic aerosols. *npj Climate and Atmospheric Science*, *6*(1), 147.

Tape, K. E. N., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global change biology*, *12*(4), 686-702.

Tavera, E. A., Lank, D. B., Douglas, D. C., Sandercock, B. K., Lanctot, R. B., Schmidt, N. M., et al. (2024). Why do avian responses to change in Arctic green-up vary?. *Global change biology*, *30*(5), e17335

Taylor, J. J., Lawler, J. P., Aronsson, M., Barry, T., Bjorkman, A. D., Christensen, T., et al. (2020). Arctic terrestrial biodiversity status and trends: A synopsis of science supporting the CBMP State of Arctic Terrestrial Biodiversity Report. *Ambio 49*, 833–847.

Thoman, R. L., Moon, T. A., & Druckenmiller, M. L. (2023). NOAA Arctic Report Card 2023: Executive Summary.

Thomas, T. K., Ritter, T., Bruden, D., Bruce, M., Byrd, K., Goldberger, R., et al. (2016). Impact of providing in-home water service on the rates of infectious diseases: results from four communities in Western Alaska. *Journal of Water and Health*, *14*(1), 132-141.

Thompson, S. J., Handel, C. M., Richardson, R. M., & McNew, L. B. (2016). When winners become losers: predicted nonlinear responses of arctic birds to increasing woody vegetation. *PLoS One*, *11*(11), e0164755.

Tiusanen, M., Hebert, P. D., Schmidt, N. M., & Roslin, T. (2016). One fly to rule them all—muscid flies are the key pollinators in the Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1839), 20161271

Treharne, R., Bjerke, J. W., Tømmervik, H., Phoenix, G. K. (2020) Development of new metrics to assess and quantify climatic drivers of extreme event driven Arctic browning. *Remote Sensing of Environment*, 243, 111749.

Unc, A., Altdorff, D., Abakumov, E., Adl, S., Baldursson, S., Bechtold, M., et al. (2021). Expansion of agriculture in northern cold-climate regions: a cross-sectoral perspective on opportunities and challenges. *Frontiers in Sustainable Food Systems*, *5*, 663448.

van Beest, F. M., Beumer, L. T., Andersen, A. S., Hansson, S. V., & Schmidt, N. M. (2021). Rapid shifts in Arctic tundra species' distributions and inter-specific range overlap under future climate change. *Diversity and Distributions*, *27*(9), 1706-1718.

van der Kolk, H. J., Heijmans, M. M., Van Huissteden, J., Pullens, J. W., & Berendse, F. (2016). Potential Arctic tundra vegetation shifts in response to changing temperature, precipitation and permafrost thaw. *Biogeosciences*, *13*(22), 6229-6245.

van Westen, R. M., Kliphuis, M., & Dijkstra, H. A. (2024). Physics-based early warning signal shows that AMOC is on tipping course. *Science advances*, *10*(6), eadk1189.

Veraverbeke, S., Rogers, B. M., Goulden, M. L., Jandt, R. R., Miller, C. E., Wiggins, E. B., & Randerson, J. T. (2017). Lightning as a major driver of recent large fire years in North American boreal forests. *Nature Climate Change*, *7*(7), 529-534.

Virtanen, R., Oksanen, L., Oksanen, T., Cohen, J., Forbes, B. C., Johansen, et al. (2016). Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome. *Ecology and Evolution*, *6*(1), 143-158.

Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global change biology*, *15*(11), 2626-2633.

Vowles, T., Lovehav, C., Molau, U., & Björk, R. G. (2017a) Contrasting impacts of reindeer grazing in two tundra grasslands. *Environmental Research Letters*, 12(3): 034018.

Vowles, T., Molau, U., Gunnarsson, B., Hickler, T., Klemedtsson, L., & Björk, R. G. (2017b) Expansion of deciduous shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range. *Journal of Ecology*, 105(6): 1547-1561.

Vowles, T., & Björk, R. G. (2019). Implications of evergreen shrub expansion in the Arctic. *Journal of Ecology*, *107*(2), 650-655.

Waits, A., Emelyanova, A., Oksanen, A., Abass, K., & Rautio, A. (2018). Human infectious diseases and the changing climate in the Arctic. *Environment International*, *121*, 703-713.

Wang, Y., Pedersen, M. W., Alsos, I. G., De Sanctis, B., Racimo, F., Prohaska, A., et al. (2021). Late Quaternary dynamics of Arctic biota from ancient environmental genomics. *Nature*, *600*(7887), 86-92.

Wang, X., Wang, C., Zhu, T., Gong, P., Fu, J., & Cong, Z. (2019). Persistent organic pollutants in the polar regions and the Tibetan Plateau: A review of current knowledge and future prospects. *Environmental Pollution*, *248*, 191-208.

Wasowicz, P., Sennikov, A. N., Westergaard, K. B., Spellman, K., Carlson, M., Gillespie, L. J., et al. (2020). Non-native vascular flora of the Arctic: Taxonomic richness, distribution and pathways. *Ambio*, *49*, 693–703.

Wein, R. W., & Bliss, L. C. (1974). Primary production in arctic cottongrass tussock tundra communities. *Arctic and Alpine Research*, *6*(3), 261-274.

Wheeler, H. C., Høye, T. T., Schmidt, N. M., Svenning, J. C., & Forchhammer, M. C. (2015). Phenological mismatch with abiotic conditions—implications for flowering in Arctic plants. *Ecology*, *96*(3), 775-787.

Whyte, K., L Talley, J., & D. Gibson, J. (2019). Indigenous mobility traditions, colonialism, and the anthropocene. *Mobilities*, *14*(3), 319-335.

Williams, L., Borchhardt, N., Colesie, C., Baum, C., Komsic-Buchmann, K., Rippin, M., Becker, B., Karsten, U., Büdel, B. (2017) Biological soil crusts of Arctic Svalbard and of Livingston Island, Antarctica Polar Biol 40:399–411.

Witze, A. (2020). The Arctic is burning like never before - and that’s bad news for climate change. *Nature*, *585*, 336–337.

Wrona, F. J., Johansson, M., Culp, J. M., Jenkins, A., Mård, J., Myers-Smith, I. H., et al. (2016). Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. *Journal of Geophysical Research: Biogeosciences*, *121*(3), 650-674.

Wullschleger, S. D., Breen, A. L., Iversen, C. M., Olson, M. S., Näsholm, T., Ganeteg, U., et al. (2015). Genomics in a changing arctic: critical questions await the molecular ecologist. *Molecular Ecology*, *24*(10), 2301-2309.

Yang, Q., Dixon, T. H., Myers, P. G., Bonin, J., Chambers, D., Van Den Broeke, M. R., et al. (2016). Recent increases in Arctic freshwater flux affects Labrador Sea convection and Atlantic overturning circulation. *Nature communications*, *7*(1), 10525.

Zhang, J., Li, X. Q., Peng, H. W., Hai, L., Erst, A. S., Jabbour, F., et al. (2023). Evolutionary history of the Arctic flora. *Nature Communications*, *14*, 4021.

Zhang, W., Miller, P. A., Smith, B., Wania, R., Koenigk, T., & Döscher, R. (2013). Tundra shrubification and tree-line advance amplify arctic climate warming: results from an individual-based dynamic vegetation model. *Environmental Research Letters*, *8*(3), 034023.