Borealization of tundra ecosystems with climate and land-use change

Mariana Verdonen[1], Isabel C Barrio[1], Laura Barbero-Palacios[2], Efrén López-Blanco[3,2], James D M Speed[4], Mathilde Defourneaux[1], Mariana García Criado[5,6], Mathilde Le Moullec[2], Jarad P Mellard[7], Alejandro Salazar[1], Kristine Bakke Westergaard[4], Jón Guðmundsson[1], Niels Martin Schmidt[3,8], Bjarni D Sigurdsson[1], Gunnar Austrheim[4], Anne D Bjorkman[9,10], Katrín Björnsdóttir[9], Jane Uhd Jepsen[11,7], Emmanuel P Pagneux[1], Beatrice M Trascau[4], David R Williamson[4], Ása L Aradóttir[1], Alexandra Barry[9], Tanguy Bernard[7], Elias Koivisto[12], Timo Kumpula[12], Miguel Villoslada[12,13], Isla Myers-Smith[14,5]

Correspondence: Mariana Verdonen, mariana@lbhi.is

[1] Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Reykjavík, Iceland

[2] Greenland Institute of Natural Resources, Nuuk, Greenland

[3] Department of Ecoscience, Aarhus University, Roskilde, Denmark

[4] Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway

[5] School of Geosciences, University of Edinburgh, Edinburgh, UK

[6] Centre for Ecological Research and Forestry Applications, Barcelona, Spain

[7] Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway

[8] Arctic Research Centre, Aarhus University, Aarhus, Denmark

[9] Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

[10] Gothenburg Global Biodiversity Centre, Gothenburg, Sweden

[11] Norwegian Institute for Nature Research, Fram Centre, Tromsø, Norway

[12] Department of Geographical and Historical studies, University of Eastern Finland, Joensuu, Finland

[13] Institute of Agriculture and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia

[14] Department of Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, Canada

Abstract

As the colder regions of the planet warm, species are moving northward and upward from the boreal forest to the tundra biome, a process that has been referred to as borealization. Here, we examine the diverse uses of the term borealization and propose the concept of tundra borealization for terrestrial environments to specifically describe shifts in species composition from boreal to tundra ecosystems. We summarise the evidence to date for borealization of plant and animal communities in tundra ecosystems and the different approaches that can be used to quantify borealization. We discuss how land-use change is interacting with climate change, leading to species and community reorganization in colder biomes, and the consequences of borealization for food webs, ecosystem functions and northern livelihoods. Our perspective brings together the different definitions and lines of evidence for borealization in terrestrial ecosystems to emphasize this important ecological process and rapidly evolving area of research.

Introduction

Climate and land-use changes are driving species redistributions globally [1]. These shifts in species distributions imply a reshuffling of biotic communities and the breakdown of biogeographic barriers [2]. With rapid warming at high latitudes and elevations [3], ecological transitions involving the redistribution of species are underway. The term 'borealization' has been used to describe some of these transitions, which are characterized by the expansion of boreal species into Arctic ecosystems [4,5]. While boreal species can move northward and upward, Arctic and alpine species have limited escape routes. Therefore, understanding the causes and consequences of these ecological transitions is fundamental for the conservation of Arctic ecosystems. The term borealization has been widely used in marine systems to describe the northward range expansion of fish and zooplankton species [4,6]. Similar species distribution shifts have been reported in terrestrial ecosystems [5] but in these cases the term borealization has not been consistently applied.

Here, we aim to call attention to the concept of borealization and its wide-ranging consequences. First, we review existing definitions of the term borealization across disciplines and establish a working definition to apply the concept to terrestrial ecosystems and the present-day latitudinal and elevational shifts of boreal species into tundra ecosystems, including Arctic, Oroarctic and alpine tundra [7]. Second, we summarise different approaches to quantify borealization in terrestrial communities and review the patterns, drivers and consequences of borealization. Finally, we identify future research priorities, aiming to bring researchers together to understand climate and land-use change impacts in the rapidly warming tundra biome.

Defining borealization

Although shifts in the distribution of boreal and Arctic species have been a naturally recurring phenomenon in marine and terrestrial environments in past periods of cooling and warming, like in the early Holocene [8], the term borealization has not been widely used in the scientific literature (**Figure 1**). A search on Web of Science and Scopus on 29th January 2025 for the term "borealization" OR "borealisation" retrieved 75 unique documents published until the end of 2024. The first results include a few isolated cases dating back to the mid-1990s, with an increase in the use of the term in the 2000s by different disciplines. To the best of our knowledge, the term borealization was first used in 1944 [9] to describe processes leading to the speciation of pear trees (*Pyrus*) in the colder environments of their northern range. In the 1990s, the term was used by the forest science community to describe the silvicultural practices favouring pine and spruce in central European forests, leading to an increased resemblance to northern taiga forests and the subsequent decline of species and features indicative of temperate deciduous forests [10]. Similarly, the term has been used to describe the replacement of temperate tree species by boreal species in southern Sweden [11] and in the New England Acadian Forest [12]. In these cases, borealization was interpreted as the movement of northern species to more southerly areas. Interestingly, this is the use of the term that has been adopted in the humanities, where the borealization of southern European literature reflects elements of northern influence [13].

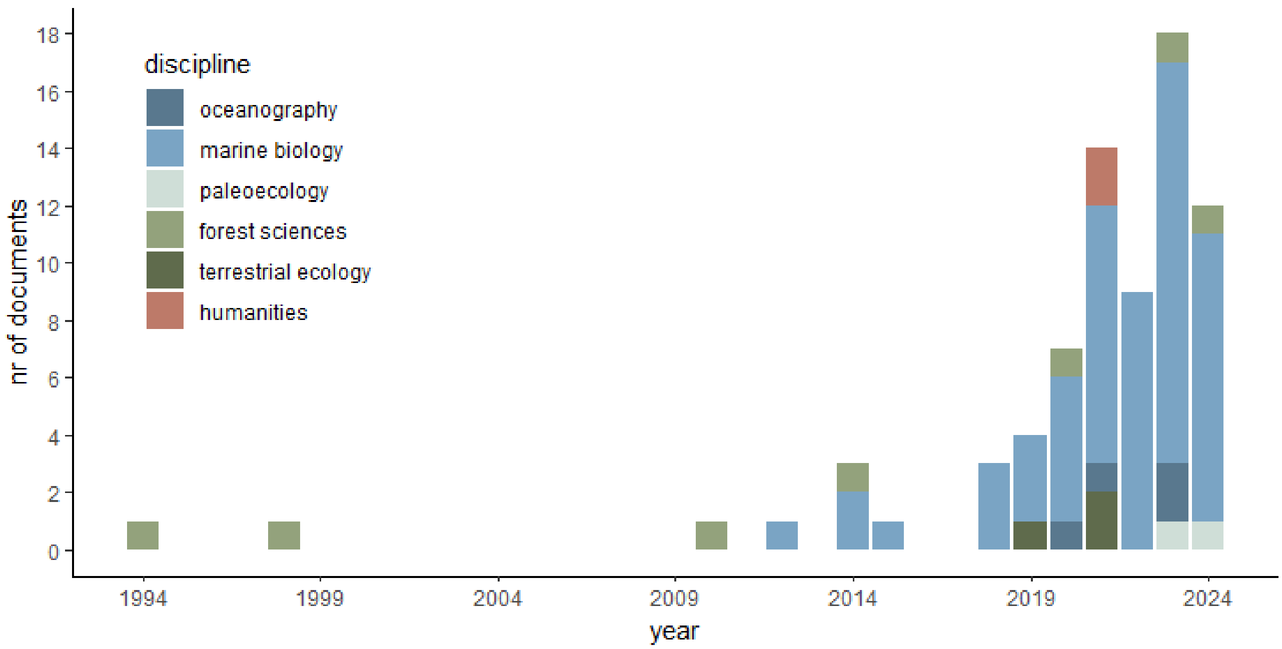

Figure 1. The use of the term borealization in the scientific literature became more frequent after 2010, especially in marine sciences. A search in Scopus and Web of Science on 29th January 2025 retrieved 75 articles published between 1994 and 2024. The number of scientific articles published each year is shown, coloured by scientific discipline.

More recently the term borealization has been adopted by the physical oceanography community, where it has been used to refer to the anomalous advection of water and biota from the Atlantic and Pacific Oceans into the Arctic Ocean [14]. Some authors, however, restrict the use of the term borealization to the biotic response associated with the physicochemical changes in the marine environment, which are in turn referred to as *atlantification* [15]. In this context, borealization implies the movement of species adapted to higher salinity and warmer waters, often associated with the retraction of Arctic specialist species, leading to changes in the ecology, distribution and phenology of local marine organisms [4,6]. In marine biology, a variety of terms have been coined to describe species redistributions and the associated changes in fish assemblages depending on the thermal affinity of the species in the community, including: *borealization* and *deborealization* (reflecting, respectively, increases and decreases in cold-affinity), as well as *tropicalization* and *detropicalization* (reflecting increases and decreases in warm-affinity) [16,17]. It is important to note that the use of the term borealization in physical oceanography and marine biology leads to opposite definitions, describing an increase in the representation of warm-adapted species in high latitudes (*sensu* Fossheim et al. [4] or of cold-adapted species in temperate waters (*sensu* McLean et al. [17], depending on the geographical position from which the term is being defined (red arrows in **Figure 2**).

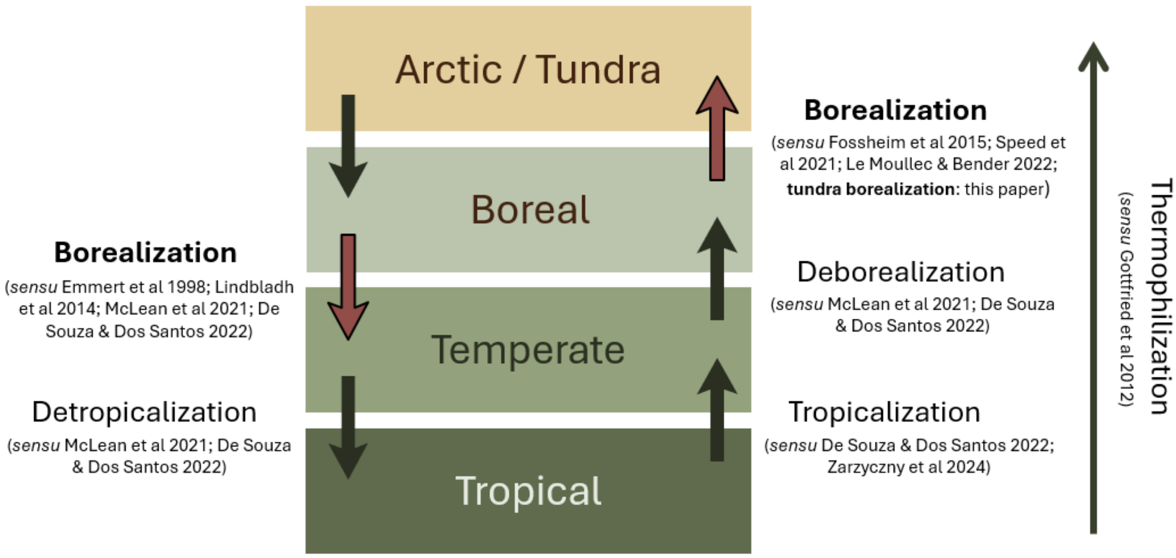

Figure 2. Terms used to describe species redistributions across biome boundaries in marine and terrestrial environments as a response to climate change, including *borealization* and *deborealization* (as an increase and decrease of cold-affinity), *tropicalization* and *detropicalization* (as an increase and decrease of warm-affinity), and *thermophilization* (increase in warm-adapted species with increasing temperatures). So far, there is no term describing the transition of Arctic species into the boreal biome. Importantly, borealization (red arrows) can represent opposite processes according to different sources. Here we define tundra borealization as the range expansion of boreal species into terrestrial tundra ecosystems, possibly accompanied by a loss of tundra specialist species.

The term borealization has been used to a much lesser extent in the terrestrial realm [5,18]. Instead, other terms describe processes analogous to those described in marine environments. For instance, the idea of temperature-driven changes in species distributions is directly related to the concept of *thermophilization* used to describe the increase of warm-adapted and the decline of cold-adapted species in terrestrial plant and animal communities as a response to warming [19,20]; **Figure 2**). In turn, northward range shifts of cold-adapted Arctic species have been referred to as *Arctic squeeze*, as their ranges shrink with no possibility to expand further north [21]. There has also been extensive literature reporting changes in the taiga-tundra boundary [22], particularly describing shifts in the boreal treeline [23] and increases in primary productivity in tundra regions, the so-called *Arctic greening* [24]. However, these changes have rarely been explicitly referred to as borealization. Similarly, the term borealization does not appear in the freshwater ecosystem literature despite analogous changes in Arctic freshwater fish communities. Instead, the increase in boreal species in these communities is typically linked to the concept of invasive species [25]. Finally, the boreal biome only occurs in the Northern Hemisphere [26], therefore the term borealization in terrestrial ecosystems has not been used in the Southern Hemisphere, although similar processes are occurring in southern tundra regions [27].

Due to all these inconsistencies and the multiple terms used to refer to similar processes, unifying terminology is important. We therefore define **tundra borealization** (hereafter 'borealization') as all biogeographic processes in tundra ecosystems or in the boreal-tundra transition zone characterized by the range expansion or increased abundance of boreal species, possibly accompanied by the simultaneous range retraction or decline in abundance of tundra specialist species, that lead to tundra ecosystems becoming more boreal-like in their community composition and functioning. This definition includes Arctic, Oroarctic (i.e., subarctic mountains) and alpine tundra, as ecological changes in these systems should be comparable. By the boreal-tundra transition zone we refer to the broad geographic band at the cold edge of the boreal forest, where forest structure changes across a temperature gradient (both latitudinally and altitudinally), from forested to tundra landscapes [28]. Borealization may involve gradual movements over time, or sporadic long-distance dispersal events that lead to the establishment of stable populations within the tundra. Although transient movements of species may not be considered borealization if populations do not establish, they may be indicative of future borealization. Our definition of tundra borealization also includes the establishment of species of boreal origin that are introduced in the tundra by human activity.

Quantifying borealization

The definition of tundra borealization as the increased representation of boreal species in tundra requires first defining what makes a species or its traits boreal, and by opposition, what makes a species a tundra species. Species may be classified as boreal, tundra or tundra-boreal based on the predominant biome in their current distribution ranges, as defined by occurrence data (e.g., GBIF data [29]; **Figure 3**) or range maps (e.g., IUCN range maps [5]). For some taxa, such categorizations have been developed based on expert knowledge, as for vascular plants [30], songbirds [31] or multiple taxa [32]. Similarly, species traits can be used to quantify borealization based on the relative abundance of boreal traits in the community. In marine biology, traits like body size, diet and habitat preference [33] or trophic position [34] have been used to characterize boreal and Arctic species. In terrestrial systems, traits like the thermal niche, specific leaf area or plant height (**Figure 3**) could be used, but a better characterization of boreal and tundra traits is currently missing.

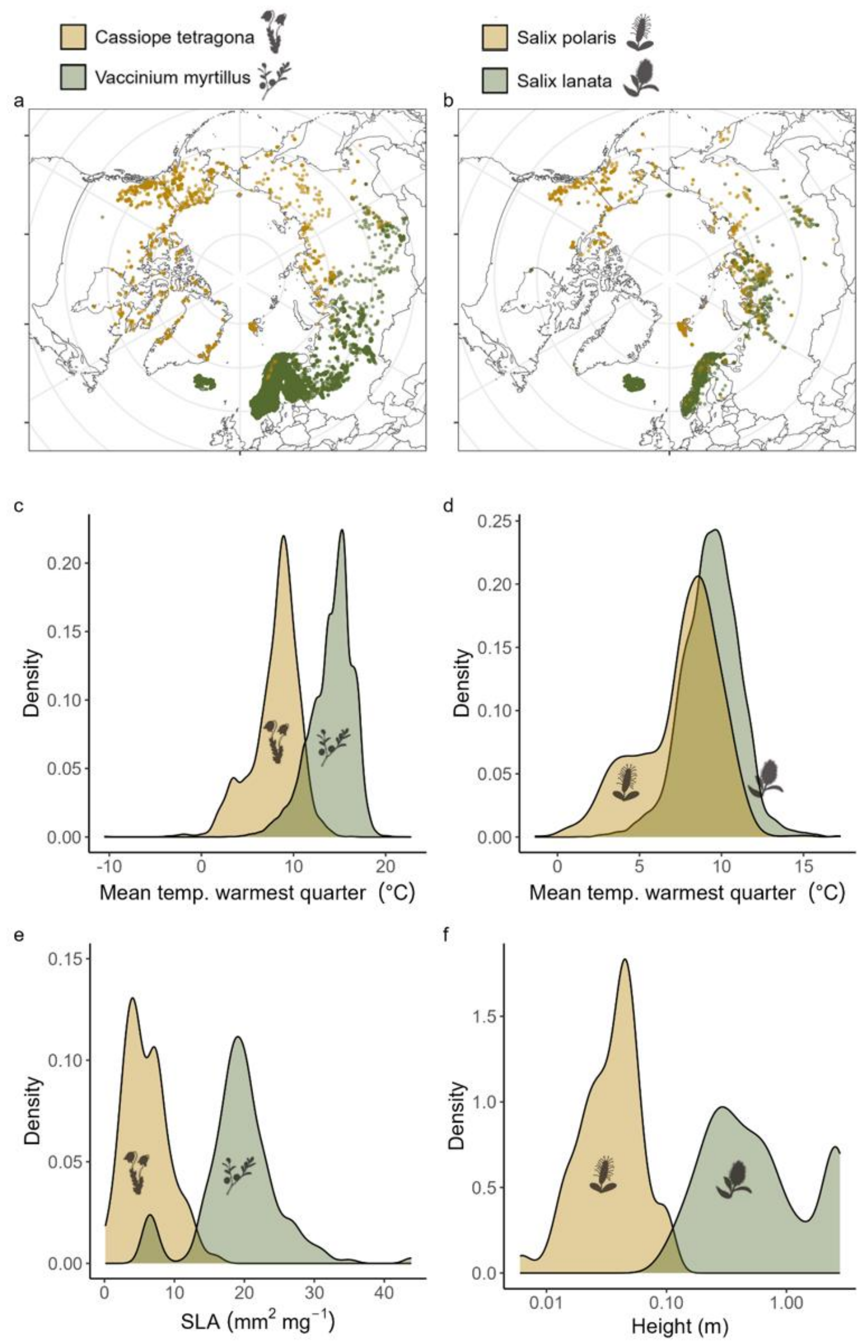

Figure 3. Based on their geographical distribution, species can be classified as typically tundra (brown) or boreal (green). Here, pairs of key tundra and boreal plant species filling similar ecological niches (left: *Cassiope tetragona* and *Vaccinium myrtillus*; right: *Salix polaris* and *Salix lanata*) show different geographic extents (**a, b**) within Arctic tundra and boreal biomes [35]. Their thermal niches (mean temperature of the warmest quarter; **c, d**) and traits like specific leaf area (SLA, **e**) and plant height (**f**) may or may not overlap. Data for species occurrence come from GBIF [29], climate data to calculate thermal niches come from Fick and Hijmans [36] and traits from Kattge et al. [37].

Similar to species' traits being characterized as 'boreal' or 'tundra', gene variants can be qualified as 'warm' or 'cold' adapted. Thus, borealization can be quantified at the genetic level with the occurrence and frequency of 'warm adapted' alleles introgressed into tundra (sub-)species from hybridization with their boreal sister species [38]. For instance, populations of snowshoe hares (*Lepus americanus*) in regions with shorter snow-covered seasons increasingly show a brown winter coat instead of their characteristic white coat, following the introgression and increase in frequency of an allele from black-tailed jackrabbit [39]. Another example is the Atlantic puffin (*Fratercula arctica*), in which hybridization has been described between large-bodied High Arctic and temperate subspecies [40]. Still, evidence for recent hybridization events in the Arctic remains scarce.

At the community level, borealization can be seen as an increase in the presence or the relative abundance of boreal species or their traits in tundra communities, as well as the concomitant range retractions of tundra specialist species. Indices like the Community Thermophilization Index (CTI) have been widely applied to measure borealization of marine [17] and freshwater fish [41], and terrestrial plant communities [19]. CTI measures the mean thermal affinity of a community and has been used to characterize responses to climate change [16]. An alternative approach could involve directly measuring colonization or increasing abundance of boreal species [42], to capture the transition of tundra ecosystems toward more boreal-like conditions.

Finally, at the ecosystem level the rates and patterns of some ecosystem processes can abruptly change across the biome boundary. For example, background invertebrate herbivory on woody plants is eight times higher in the boreal forest than in the tundra [43]. Changes in the rates of such processes could be interpreted as indicators of borealization. Similarly, declines in mean carbon residence times in tundra and amplification of seasonal changes in CO_2 concentration have been interpreted as a transition toward a boreal carbon cycle regime [44]. Characterizing which ecosystem processes reflect borealization is not straightforward, but such approaches could help in assessing the pervasiveness of borealization of tundra ecosystems and better understand its consequences.

New technologies can further improve our monitoring of borealization, from genomics to novel Earth observation products. For example, genomic differentiation between Arctic species and their boreal sister (sub-)species can be used to identify the introgression of adaptive alleles and target their functions [40]. On the other end of the gradient, hyperspectral imaging in combination with computer vision and machine learning, enables more accurate tracking of land use and land cover changes [45], mapping ranges of individual species [46] and measuring vegetation traits [47]. Increasingly common low-cost hyperspectral sensors on Unoccupied Aerial Vehicles [48] and small satellites now within the budget of academic groups [49] make it possible to target regions of interest most relevant to questions on borealization.

Patterns of borealization

The borealization of tundra ecosystems can manifest in different ways. Clear examples of tundra borealization include treeline advance, range expansions and increases in abundance of boreal mammals and invertebrate herbivores, along with the associated range contractions of tundra specialist species. Early estimates of treeline advance based on dynamic vegetation models predicted that more than 40% of Arctic tundra could be lost by 2100 [50]. Site-specific studies have shown an elevational treeline advance of three meters per decade in alpine areas in Maine, USA (Tourville et al. 2023), and a latitudinal advance of 340 meters per year of birch treelines in northern Norway [51]. However, treeline advance is far from universal and most observations do not match these rapid rates [23,52]. Yet, other changes at treeline, such as increased productivity, survival or recruitment might be early indicators that these transitions are already underway [53].

Borealization of plant communities can also be detected at macroecological scales [53]. Richness of typically boreal plant species has increased across sites in the Russian Arctic [54], and the previously herbaceous-dominated communities in interior Alaska, USA, have transformed into shrub-dominated boreal communities with poorly drained and acidic soils [18]. Similarly, poleward range contractions have been reported for Arctic plants, such as Beringian endemic species [55]. However, reports to date come from site-specific studies, and biome-wide assessments are largely lacking (but see García Criado et al. [42]. In general, the species most likely to expand into the tundra are boreal species that already have established outlier populations in the Arctic [32]. Similar patterns have been found in marine ecosystems, where migration contributed less than resident species in community reassembly [16].

Animal communities in the Arctic also show evidence of borealization [5,56]. For example, moose (*Alces alces* [57]), beaver (*Castor canadensis* [58]), snowshoe hares (*Lepus americanus* [59]), red fox (*Vulpes vulpes* [56,60]), boreal bird species [31] and forest geometrid moths [61] have expanded into the tundra. In turn, range contractions and northward shifts in the distribution ranges of Arctic birds and mammals have also been reported [30], including range retractions of Arctic specialist lemmings [62] and freshwater crustaceans [63]. Invertebrate herbivores also appear to track climate effects, with population outbreaks expanding northward to tundra habitats [64].

Some of the observed species distribution changes may not directly represent borealization but can foster ecosystem or biome shifts. For example, one of the most conspicuous processes of vegetation change in low Arctic and alpine regions is the increase in height, width, dominance and expansion of shrubs, a process known as shrubification [65]. In some cases, shrubification can represent borealization, for instance when dwarf shrubs are replaced by tall boreal shrubs or when the more thermophilic (southern) species increase in abundance more than the northern, cold-adapted shrub species. Shrubification usually comes at the expense of other non-shrub functional groups, such as bryophytes, lichens and forbs [66,67], but it can also promote borealization through enhancing the establishment of trees on peatlands [68], and increasing habitat availability for boreal species in the tundra [31,69]. As shrubification progresses we expect a transformation of ecological communities, with greater prevalence of species that have warmer ranges that extend further into the boreal forest [5,70], and wildlife such as moose and beaver [57,58].

Drivers of borealization

Many of the species distribution shifts and changes in abundance described above have been related to climate change, as species follow the poleward and upslope shift of isotherms to track their climate niches [71]. Paleoecological studies have shown that the position of Arctic and alpine treelines has shifted synchronously with climate in the past [72] and similar distribution shifts have been reported for animal communities in both terrestrial and marine environments from subfossil bone remains [8]. Indeed, in Arctic ecosystems the transition between the tundra and forested systems is assumed to be controlled primarily by climate and its associated changes in permafrost [73], so ongoing and projected climate change in the Arctic is expected to affect this biome boundary.

In addition to climate, other factors such as direct human management can contribute to the expansion of boreal species into tundra. For example, the northward spread of red foxes into the Canadian Arctic has been facilitated by human presence and anthropogenic food subsidies [60]. Studies in Fennoscandia show that changes in reindeer management that increase the availability of carcasses over winter can favour red fox colonization and survival in the tundra [74]. As well, human activities and infrastructure can promote the establishment and spread of non-native vascular plants in Arctic and alpine areas [75,76]. Humans can also actively contribute to borealization by planting boreal tree species onto treeless areas [77], or by facilitating natural regeneration where boreal species had been suppressed by land use and forest harvest [78]. Similarly, land-use changes, such as the abandonment of slash-and-burn cultivation or grazing by sheep and cattle in northern Europe, can lead to natural forest regeneration and borealization [11], especially in areas where grazing management has driven the expansion of semi-natural treeless areas [79].

Many observations of species distribution shifts however do not match increases in temperature. Only about half (52%) of the circumpolar treelines are advancing while the rest remain stable or recede [52]. Further, the northward advance of treelines is much slower than would be expected if vegetation remained in equilibrium with climate [52], except in some notable cases where favourable conditions allow for rapid expansion [80]. The heterogeneous responses of the tundra-forest boundary to climate change depend on local variations in biotic and abiotic conditions [81]. For example, herbivory can mitigate treeline advance [82] as animals select more palatable and nutritious species which are in turn the ones responding more strongly to warming [83]. Other disturbances, like water-logging and ground subsidence induced by permafrost thaw [84] or altered fire regimes [85], could counteract trends of increasing plant productivity and shrubification associated with early indications of borealization of tundra ecosystems. Finally, landscape modification by humans can be an important barrier to climate-induced species distribution shifts [71]. Further research to disentangle the effects of climate and land-use change on species distribution changes in boreal and tundra ecosystems is needed [56].

Consequences of borealization

Borealization will have wide-ranging consequences, from feedbacks to local and regional climate, to altered trophic interactions, changes in biodiversity and impacts to local livelihoods (**Figure 4**). Vegetation shifts from tundra to boreal forest have profound bioclimatic implications for land-surface processes and climate feedbacks [50]. The tundra-boreal forest boundary represents a marked shift in plant structure and stature, resulting in stark contrasts in surface characteristics and ground thermal regimes, which are especially pronounced during snow-covered season [73,86]. While tall-statured canopy has a cooling effect on the ground temperature in summer, snow trapping by trees and tall shrubs insulates the ground and has a strong warming effect during the cold season [86]. Further, the transition zone between tundra and forest has lower summer and winter albedo compared to shrub tundra [73]. These differences in snow cover and albedo enhance net radiation in forests relative to tundra with broad implications for local and regional climate [73,86]. At the same time, land-use change [87] or warming [88] can increase nitrogen fixation in tundra soils, enhancing fertility and driving plant community shifts towards woody dominance. Woody plant encroachment can in turn alter soil community composition and functioning through root structure, rhizodeposition, and litter quality and quantity [89], further promoting borealization of the tundra. In addition, the expansion of boreal species into tundra can compound or counteract the effects of climate change. For example, the range expansion of beavers in the Arctic has been associated with increased permafrost thaw due to pond formation [58] and increased methane emissions [90] that further accelerate warming. In contrast, the expansion of outbreaking boreal insect pests [61] can reduce plant productivity and shrubification associated with climate change.

Range shifts of boreal species into the tundra restructure Arctic communities and alter trophic interactions [91]. Northward expanding boreal predators like the red fox (*Vulpes vulpes*) are often opportunistic generalists. Unlike tundra predators, which tend to be specialists relying on small mammals as prey, and reproduce only during peak prey abundance [92], generalists can maintain relatively stable populations during low rodent cycles by exploiting alternative food sources, such as ground-nesting birds [56,92]. This alternative prey mechanism can also lead to apparent competition among prey species [93], which arises when two organisms share the same predator. Apparent competition has been considered a main driver of population declines in North American caribou (*Rangifer tarandus*), especially at its southern distribution range where caribou overlaps with the northward expansion of boreal herbivores like moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). These forest ungulates are followed by their main predator, the grey wolf (*Canis lupus*) resulting in an indirect increased predation pressure on caribou [94].

The influx of boreal species leads to increases in biodiversity, but these might only be a transitory phase followed by declines driven by losses and redistribution of Arctic species, as described in marine environments [15]. Further, boreal species are likely to be less tolerant to Arctic conditions, such as the occurrence of extreme climatic events, preventing the long-term establishment of their populations [95]. In marine systems, the reorganization of community structure associated with borealization has been related to loss of resilience of the new communities [96]. Similarly, a species' genetic diversity may first increase from hybridization between boreal and tundra species, yet, the resilience of hybrids to extreme events is often lower than the specialized native species [40]. Positive selection that favors these hybrid genotypes remains rarely documented in the Arctic. While positive selection of some alleles favorable to the warmer conditions may fix them in Arctic populations [39,40], the long-term outcome may be an overall reduction in genetic diversity [40]. Ultimately, if tundra species decline, hybridization could rescue some Arctic genes from going extinct [38]. The consequences of borealization-associated biodiversity changes for tundra community composition and ecosystem functions remain to be addressed.

Finally, borealization will have socio-ecological and socio-economic consequences. For example, projections of future biomass production under climate change suggest the potential expansion of economic activities like sheep farming in Southwest Greenland [97]. In turn, increases in the abundance of tall shrubs in tundra and changes in snow properties can alter migratory routes and food resources of reindeer and caribou affecting the livelihoods that depend on them [98]. Incoming boreal species, particularly predators like wolves and bears, raise safety concerns for local communities and negatively impact regional economies by attacking semi-domestic reindeer or entering fishing grounds [99]. Conversely, declines in tundra species threaten food security of Arctic communities that use native flora and fauna for subsistence [100]. With ongoing changes in climate and patterns of human use, the susceptibility of Arctic and alpine environments to invasive species is likely to increase [30], posing additional threats to biodiversity and people's overall quality of life.

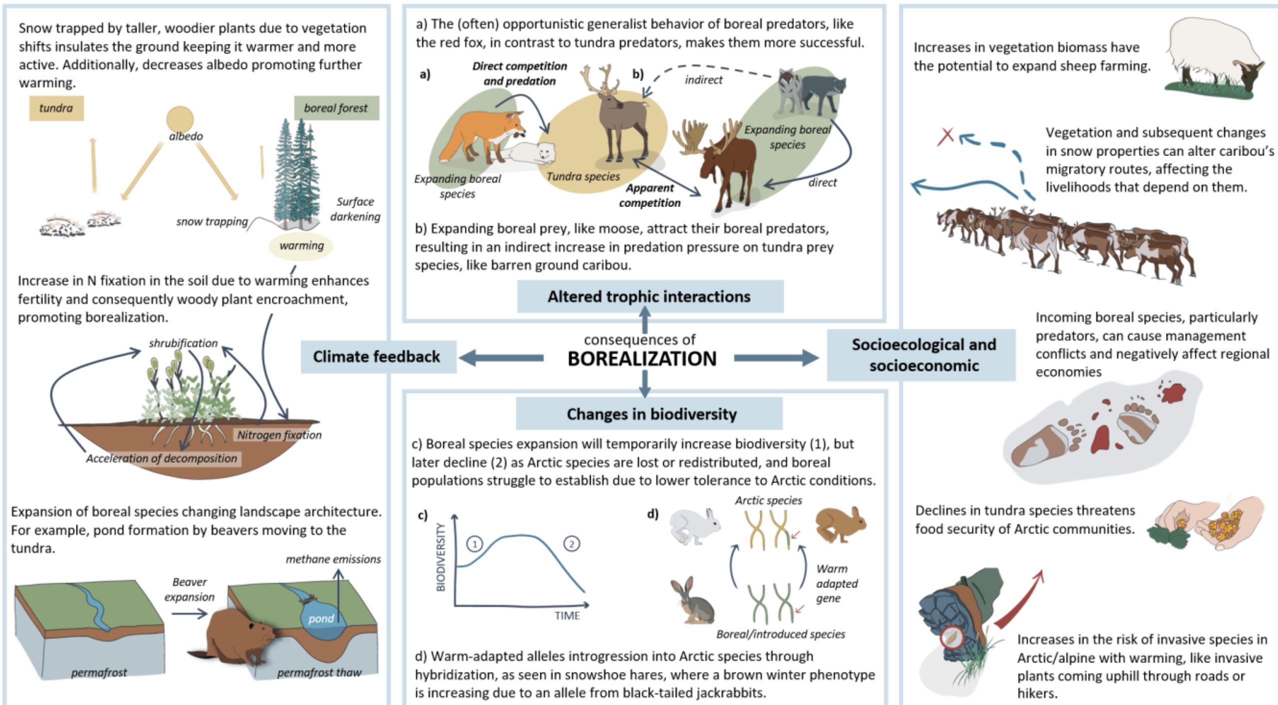

Figure 4. Borealization of tundra ecosystems will have wide-ranging consequences, from feedbacks to regional and global climate, to altered trophic interactions, changes in biodiversity and socioecological and socioeconomic impacts.

Conclusions and future research

As the climate continues to warm, species reorganize across biome boundaries, with northward and upward movement from the boreal biome into tundra, leading to restructured food webs, altered ecosystem functions, and significant impacts to northern livelihoods. Here, we define the process of tundra borealization as the range expansion or increased abundance of boreal species, possibly accompanied with the range retraction or decline in abundance of tundra specialist species. With the loss of tundra ecosystems, we also lose the values, ecosystem services, and biodiversity unique to these environments. Key areas of research to better understand and predict the ecological impacts of borealization on tundra ecosystems include examining trait distributions of boreal and tundra species and documenting hybridization in tundra species, as well as comprehensive syntheses and biome-wide assessments of borealization across tundra plant and animal communities. Despite growing interest in borealization, little is known about the responses of non-vascular plants, fungi, and microbial communities, or the consequences of borealization to phenological synchrony between interacting organisms. Additionally, research is needed on the functional pathways driving borealization and its effects on ecosystem processes and species interactions. A critical knowledge gap remains regarding the consequences of biodiversity shifts driven by borealization, particularly their impacts on community composition and ecosystem functioning. Further efforts are also needed to disentangle the effects of climate and land-use changes, examine anthropogenic influences, and evaluate socio-ecological and economic consequences of tundra borealization. However, to make progress in this field we need consensus on terminology, methods and research scope. Only with this consensus perspective can we move forward to uncover the borealization that is transforming tundra ecosystems with accelerating climate change.

Author contribution statement

MVe and ICB led the manuscript preparation; IMS conceptualised the paper; LBP produced the figures with contributions from MVe, ICB, ELB, JDMS, MLM, MD, BMT; all authors contributed to content development and approved the final version.

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