# Climate-change refugia in boreal North America: what, where, and for how long?

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**The vast boreal biome plays an important role in the global carbon cycle but is experiencing particularly rapid climate warming, threatening the integrity of valued ecosystems and their component species. We developed a framework and taxonomy to identify climate-change refugia potential in the North American boreal region, summarizing current knowledge regarding mechanisms, geographic distribution, and landscape indicators. While "terrain-mediated" refugia will mostly be limited to coastal and mountain regions, the ecological inertia (resistance to external fluctuations) contained in some boreal ecosystems may provide more extensive buffering against climate change, resulting in "ecosystem-protected" refugia. A notable example is boreal peatlands, which can retain high surface soil moisture and water tables even in the face of drought. Refugia from wildfire are also especially important in the boreal region, which is characterized by active disturbance regimes. Our framework will help identify areas of high refugia potential, and inform ecosystem management and conservation planning in light of climate change.**

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High-latitude regions around the world are experiencing particularly rapid climate change. These regions include the 625 million ha North American boreal region, which contains 16% of the world's forests and plays a major role in the global carbon cycle (Brandt *et al.* 2013). Boreal ecosystems are particularly susceptible to rapid climate-driven vegetation change initiated by stand-replacing natural disturbances (notably fires), which have increased in number, extent, and frequency (Kasischke and Turetsky 2006; Hanes *et al.* 2018) and are expected to continue under future climate change (Boulanger *et al.* 2014). Such disturbances will increasingly complicate species persistence, and it will therefore be critical to identify locations of possible climate-change refugia (areas "relatively buffered from contemporary climate change") (Morelli *et al.* 2016). These "slow lanes" for biodiversity will be especially important for conservation and management of boreal species and ecosystems (Morelli *et al.* 2020).

## In a nutshell:

- Major climate-induced changes are anticipated for the ecosystems and biota of the large and diverse North American boreal region
- To guide conservation and management in boreal ecosystems, scientists and resource managers must identify areas that can serve as refugia from climate change
- Boreal mountain regions offer more opportunities to shelter species in microclimates within complex terrain as compared with flat, interior regions
- Some boreal forest elements, such as peat-forming wetlands, are naturally buffered from climate change by internal processes
- We developed a framework and taxonomy for identifying, characterizing, and mapping boreal refugia

Practically speaking, the refugia concept can translate into specific sites or regions that are expected to be more resistant to the influence of climate change than other areas ("in situ refugia"; Ashcroft 2010). Refugia may also encompass sites or regions to which species may more readily retreat as climate conditions change ("ex situ refugia"; Ashcroft 2010; Keppel *et al.* 2012), as well as temporary "stepping stones" (Hannah *et al.* 2014) linking current and future habitats. In addition to areas that are climatically buffered, fire refugia – "places that are disturbed less frequently or less severely by wildfire" (Krawchuk *et al.* 2016) – may also play key roles in promoting ecosystem persistence under changing conditions (Meddens *et al.* 2018).

Previous examinations of climate-change refugia have primarily emphasized external, terrain-mediated mechanisms. Factors such as topographic shading and temperature inver-

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sions can promote local microscale decoupling from regional climates, or microrefugia (Dobrowski 2011), whereas factors such as elevation and coastal proximity can result in regional-scale decoupling, leading to macrorefugia (Stralberg *et al.* 2018). Given the influence of climate warming on water availability, researchers have also identified terrain-mediated hydrologic refugia (McLaughlin *et al.* 2017; Cartwright *et al.* 2020), or wetlands fed by large groundwater flow systems that are buffered from climate-change influences (Winter 2000).

In comparison with terrain-mediated refugia, relatively little attention has been given to processes internal to an ecosystem that can also lead to decoupling from regional temperature and/or moisture regimes, conferring extended resistance to climatic change. When an ecosystem is maintained in a relatively stable condition by such internal processes, we suggest that it is "ecosystem-protected", a term introduced by Shur and Jorgenson (2007) to classify the controls that maintain permafrost (perennially frozen ground, overlain by a seasonally thawed active layer) in the landscape. Although most natural systems exhibit some level of ecological inertia (resistance to external fluctuations), the level of stability varies according to the strength of relevant ecological feedbacks, as well as the frequency and intensity of disturbance (Johnstone *et al.* 2016). For example, eco-hydrological feedbacks (Waddington *et al.* 2015), species interactions, and ecosystem engineering by plants and animals (Bulleri *et al.* 2018) can alter local hydrological dynamics independent of regional climatic conditions, such that ecosystems are maintained despite regional moisture limitations. Climatic buffering of this type may be sustained for long periods in the absence of major disturbance (eg Shur and Jorgenson 2007).

Both terrain-mediated and ecosystem-protected refugia can delay the effects of climate change for at least some plant and animal species, allowing them more time to disperse or adapt. The potential of a given area to serve as a refugium in the future can be estimated at broad spatial scales from projections of shifts in climate over space and time obtained from climate model simulations (Carroll *et al.* 2017; Michalak *et al.* 2020). However, climate models are spatially coarse, and downscaled projections typically assume that terrain-driven patterns remain constant through time. Assessment and mapping of refugia potential at finer spatial scales may therefore depend primarily on a combination of climatic proxy metrics (eg terrain characteristics) and expert opinion.

To identify climate-change refugia in boreal North America, we must first understand key processes and features that determine ecosystem persistence. We start by distinguishing unique characteristics of the boreal biome, and identifying differences among its major regions. We then develop a framework and taxonomy to describe boreal refugia characteristics, reviewing the state of knowledge regarding processes, spatial scales, geographic distributions, and potential indicators of refugia.

## North American boreal biome

The North American boreal biome is vast and geomorphically diverse, extending from interior Alaska in the west to Newfoundland and Labrador in the east, and from north of the Arctic Circle in the northwest to the Laurentian Great Lakes in the southeast (Figure 1; Brandt *et al.* 2013). Although development pressures are increasing, this remote biome remains relatively pristine compared to tropical and temperate biomes. Climatically, the region is characterized by long, cold winters and short, cool summers, resulting in continuous to isolated occurrence of permafrost across three-quarters of its land area (Gauthier *et al.* 2015), and by the predominance of cold-tolerant species (Brandt *et al.* 2013). Average annual precipitation is relatively low, but cold temperatures limit evapotranspiration, usually resulting in surplus moisture, and consequently the region supports extensive forest cover and large peat-forming wetland complexes (hereafter "peatlands").

Although precipitation may increase with climate change in boreal regions, amounts are unlikely to meet the temperature-inflated evaporative demand, thereby leading to future reductions in moisture availability (WebTable 1; Hogg and Hurdle 1995; Price *et al.* 2013). In drier western regions, longer and more severe droughts and increased wildfire frequency and severity may ultimately transform conifer-dominated boreal forests into deciduous forests, shrublands, or grasslands (Johnstone *et al.* 2010; Scheffer *et al.* 2012; Rupp *et al.* 2016); substantial changes in this direction have already been detected (Wang *et al.* 2020). Higher temperatures and more frequent drought conditions are also leading to the drying and shrinking of wetlands and lakes in parts of boreal Alaska (Klein *et al.* 2005), whereas in the interior boreal plain, peatland responses to climate change may lag behind those of adjacent upland forests (Schneider *et al.* 2016). In wetter eastern forests, conversion to more productive temperate mixed deciduous and conifer forests may occur in the south (Evans and Brown 2017), while boreal conditions are more likely to persist in the north (D'Orangeville *et al.* 2016). Along the southern limit of permafrost distribution, increasing temperatures have caused widespread thaw (Helbig *et al.* 2016; Olefeldt *et al.* 2016). Associated ground subsidence (thermokarst), accelerated by wildfire (Gibson *et al.* 2018), is driving a variety of ecosystem changes, including conversion of forest to open wetlands (Baltzer *et al.* 2014; Lara *et al.* 2016), drought stress (Walker and Johnstone 2014; Sniderhan and Baltzer 2016), and lake level declines (Roach *et al.* 2013).

The boreal biome is characterized by active natural disturbance regimes – primarily wildfire and outbreaks of defoliating insects – operating across large areas. Frequent mixed-severity fires help maintain a dynamic and heterogeneous landscape (Burton *et al.* 2008; Whitman *et al.* 2018), and ecological adaptations make many boreal forest species inherently resilient to, and even dependent upon, recurrent natural disturbance events (eg Héon *et al.* 2014). However, under warmer and drier climate conditions, coupled with increased levels of disturbance, these ecosystems are becoming more susceptible to rapid and large-scale change (Erni *et al.* 2017; Seidl *et al.* 2017). Natural and anthropogenic disturbances, especially when severe or compounded, may initiate changes in successional pathways and lead to rapid and widespread ecosystem transitions (eg Johnstone *et al.* 2010). The extent to which mature forest stands can escape or withstand fire and other disturbances will therefore be a key factor in determining their near-term climate-change resilience (Krawchuk *et al.* 2020).

In the absence of or following some low-severity disturbance events, the ecological inertia inherent in some mature, healthy, boreal forest stands may be sufficient to delay climate-driven vegetation transitions. As compared to most organisms, trees have long life cycles, and mature conifers can persist in areas where seedling establishment is greatly constrained by thick forest floor layers (Brown *et al.* 2015). Furthermore, mature forests generate their own microclimates that may buffer temperature and moisture conditions in the forest understory (De Frenne *et al.* 2013), providing refugia for plants and animals (Turlure *et al.* 2010; Betts *et al.* 2018). The extent to which mature forests will be able to withstand drought and other climatic stressors depends in part on tree density and the degree of crown closure (De Frenne *et al.* 2013). The processes and landscape features that maintain refugia from climate change – either directly by buffering temperature or moisture extremes, or indirectly by avoiding disturbance – may vary greatly across the boreal biome, given its extent and diversity (Figures 1 and 2).

## Boreal mountains

The Rocky Mountain and Pacific Coast ranges (Western, Boreal, and Taiga Cordillera ecoregions) (Figure 1) contain varied terrain and steep elevation gradients that should, when slopes are stable, facilitate the movement of boreal species upslope to locations with suitable climatic conditions in the future (Figure 2a). Multiple spatial metrics based on climate and terrain characteristics suggest

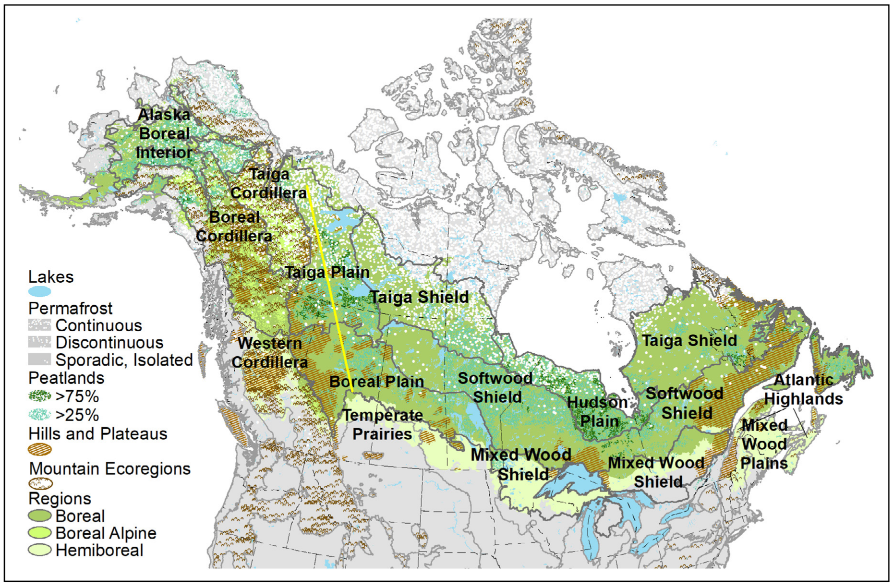



**Figure 1.** Boreal region (green) following Brandt *et al.* (2013) with Commission for Environmental Cooperation Level II ecoregions superimposed. Refugia processes outlined in Figure 2 correspond with key map features: mountain ecoregions, boreal plateaus and peatlands, major lakes, and oceanic coastlines. Approximate placement of the peatland–permafrost transect described in Figure 4 is depicted as a solid yellow line. See Panel 1 and WebPanel 1 for peatland and permafrost map sources, respectively.

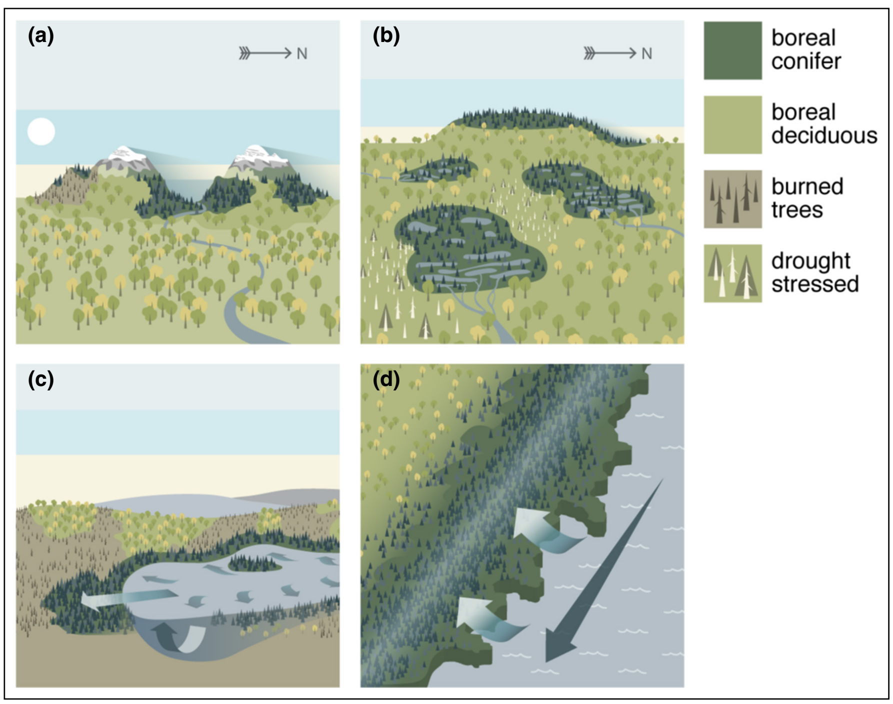



**Figure 2.** Key features supporting refugia in the boreal biome (Figure 1): (a) mountains, (b) boreal interior plateaus and peatlands, (c) major lakes, and (d) oceanic coastlines. Areas where boreal forest conditions are more likely to persist relative to the surrounding landscape are shown with dark green shading. All terrain renditions are exaggerated, as is the size of individual trees relative to landscape elements. Arrows in panel (c) represent lake upwelling and onshore breezes; arrows in panel (d) represent cold ocean currents and onshore breezes producing coastal fog.

relatively high macro- and microrefugia potential in these regions (Michalak *et al.* 2020).

Given that air temperatures decrease predictably with increasing elevation, cooler and wetter conditions supporting boreal ecosystems will necessarily persist longer at high elevations, and may also provide opportunities for establishing ex situ refugia through treeline advance, depending on suitable substrate and moisture availability. Furthermore, rugged terrain results in a wide diversity of microclimate types (Ackerly *et al.* 2010) and facilitates microclimate protection through a range of mechanisms (Dobrowski 2011). For example, incised valleys are prone to temperature inversions, as cold air flows down from higher elevations and collects in valley bottoms, buffering them from rising regional temperatures (Dobrowski 2011). Steep canyons are also relatively shaded from incoming solar radiation, and can accumulate water from surrounding slopes. Likewise, north-facing slopes are particularly sheltered from solar radiation and heat accumulation. Mean annual air temperature differences of 6°C between north- and south-facing slopes can occur in steep mountainous terrain (Gruber *et al.* 2004). However, changes in these ecosystems may not be readily apparent until critical temperature or moisture thresholds are crossed. For instance, montane grassland systems generally occur on south- but not north-facing slopes within the arid Boreal Cordillera. Permafrost distribution is also limited to north-facing slopes within much of the discontinuous permafrost zone.

Despite their limited extent, groundwater-fed wetlands within lowland portions of mountain landscapes are relatively buffered from drought (Winter 2000). Glacially fed streams also provide additional cooling effects and suitable conditions for arctic and alpine mosses and vascular plants (Hogg 1993). Although species composition may change in the future, the persistence of cooler conditions locally may create refugia for boreal species in a warmer climate. Mountain regions also have relatively high potential for fire refugia, due to many of the same topographic factors that provide climatic buffering. Shelter from wind and shade from solar radiation influence microclimate and forest structure, as well as fire ignition and spread potential (Krawchuk *et al.* 2016). In the Canadian Rockies, persistent fire refugia are associated with sheltered

**Panel 1. Peatland dynamics**

Boreal peatlands store a substantial fraction of global carbon and are estimated to cover 22% of Canada's boreal and subarctic regions (Tarnocai *et al.* 2011). In Canada, peatlands are defined as wetlands with organic deposits at least 40 cm deep (NWWG 1997), and include bog, fen, and some swamp wetland types. Globally important peatlands are concentrated in the Hudson Plain and Taiga Plain ecoregions of Canada, as well as in the Alaska Boreal Interior ecoregion (Figure 1), where local drainage is suppressed by low relief.

Boreal peatlands, often dominated by *Sphagnum* spp, create robust ecosystems through the accumulation of organic matter that largely excludes all but slow-growing trees (van Breemen 1995), most notably black spruce (*Picea mariana*). Peatland persistence depends on a combination of groundwater and precipitation inputs, and placement above impermeable substrates such as clay or rock in low-relief landscapes to maintain a water surplus that is central to ecosystem function (Hokanson *et al.* 2018). Hydrologically isolated bogs in cool, continental climates may therefore have high refugia potential due to their physical placement and high peat density (Kettridge *et al.* 2016), which promote soil-water conditions that optimize moss growth (Figure 3). However, peatlands with external water sources, such as fens underlain by coarse-textured soils and connected to regional non-saline groundwater, are able to exist in drier and warmer conditions compared to bogs that rely solely on precipitation and internal water conservation mechanisms (Halsey *et al.* 1995).

Forested peatlands are also relatively resilient to disturbance (Thompson and Waddington 2013) and burn less severely (Whitman *et al.* 2018), especially when connected to groundwater supplies (Hokanson *et al.* 2016). Loss of peat through decomposition tends to be slow due to cool anaerobic conditions that are in part maintained by numerous water-conserving feedback mechanisms, such as the generally lower hydraulic conductivity of deeper and more decayed peat horizons (Waddington *et al.* 2015). Yet if water tables are lowered through human disturbance and/or climatic drying, extensive peat loss can occur through faster aerobic decomposition and burning, resulting in altered vegetation trajectories (Turetsky *et al.* 2015). Understanding controls of peatland persistence at multiple scales under climate change and direct anthropogenic disturbance is critical to predicting the potential of peatlands to exist as ecological refugia in a changing climate.

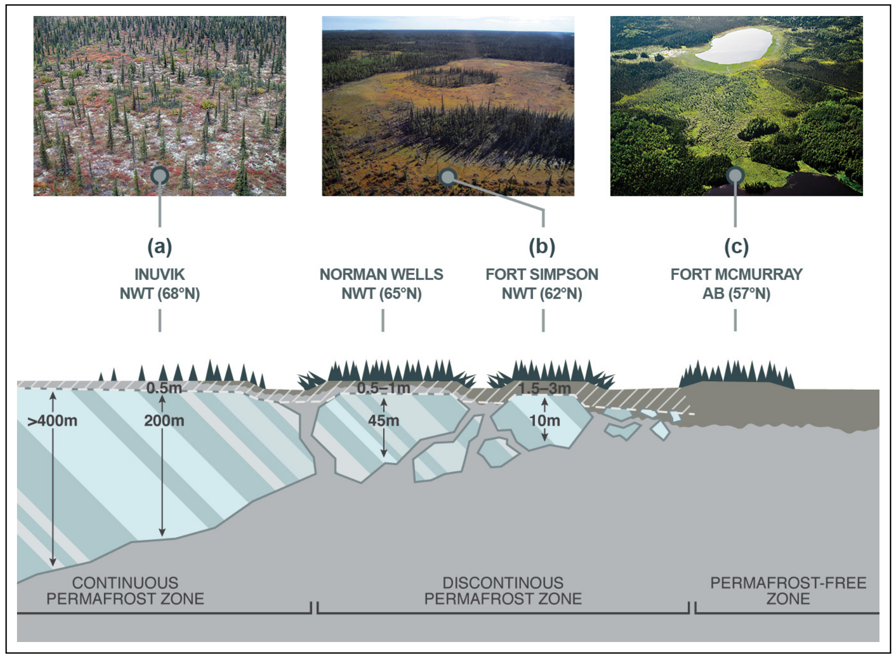
A Hillman

**Figure 3.** Bog peatland near Utikuma Lake, in Alberta, Canada. This site is in the permafrost-free zone (see Figure 4). The impermeable mineral substrate limits drainage, thus promoting peatland water storage, and supporting *Sphagnum* moss productivity. Note the presence of a sparse black spruce (*Picea mariana*) canopy and ample black spruce regeneration.

slopes and high-elevation areas of discontinuous vegetation cover, which often correspond with local headwaters (Rogeau *et al.* 2018).

## Interior plains and plateaus

In contrast to boreal mountain systems, the dominant interior ecosystems within the Boreal, Taiga, and Hudson Plain ecoregions, as well as the Boreal and Taiga Shield ecoregions (Figure 1), are relatively flat and likely to be exposed to high climate-change velocities (Stralberg *et al.* 2018). As a result, organisms will need to move long distances to track changing conditions (Figure 2b). Across these boreal interior landscapes, terrain diversity is limited to minor plateaus and hill systems with several hundred meters of elevation gain. Although topographic relief is relatively low, even small gains in elevation – such as the tops of certain plateaus – may promote the growth of subarctic vegetation. Similar hill systems within the warmer and drier prairie ecoregions contain island forests dominated by boreal tree species, providing possible contemporary analogs for future, high-elevation refugia in the boreal forest.



(c) M Rapinski

**Figure 4.** Hypothetical transect across peatland portions of the western Taiga Plain and Boreal Plain ecoregions (see Figure 1 for location), indicating the north–south transition from continuous to discontinuous permafrost and then to permafrost-free landscapes. (a) At northern latitudes, where permafrost is thick and continuous, the seasonally thawed ("active") layer (white hatching) is thin and comprises both organic soil (dark gray) and mineral soil (light gray); tree density is low and permafrost is relatively stable. (b) In the discontinuous permafrost zone, the organic soil layer deepens and extends below the active layer; trees occur primarily on permafrost peat plateaus where permafrost is warmer, thinner, and – under a changing climate – increasingly vulnerable to thaw and ground surface subsidence, leading to waterlogging and forest loss. (c) In the permafrost-free zone, the organic soil layer is thick and supports trees on raised peat domes within extensive bog and fen peatland complexes that retain moisture through internal eco-hydrological feedbacks (see Panel 1). Diagram is not to scale; approximate tree height is 5–10 m. NWT = Northwest Territories; AB = Alberta.

Interior lowlands and plateaus are characterized by the predominance of extensive peatlands (Figures 2b and 3; Panel 1), which retain high surface soil moisture and water tables, even in the sub-humid western boreal forest (Waddington *et al.* 2015). In permafrost-free regions with deep and extensive organic soils, peatlands may be protected from drying due to water retained through eco-hydrological inertia (Schneider *et al.* 2016). Furthermore, depending on local hydrology and geology, peatland processes may also promote resilience of surrounding upland forests to drought and reduce their exposure to fire (Hokanson *et al.* 2018). Beavers (*Castor canadensis*) can also act as ecosystem engineers, creating and maintaining wetlands as well as buffering forest landscapes from drought over multiple decades (Hood and Bayley 2008).

The influence of permafrost is prominent in the Taiga Plain and western Taiga Shield ecoregions, where it helps maintain low soil temperatures for the boreal ecosystems that overlay it (WebPanel 1). In northernmost parts of these ecoregions, permafrost is thick, cold, and continuous, suggesting it will be relatively stable at least until 2100 (Zhang *et al.* 2008); this thermal inertia is likely to maintain boreal forest conditions. Farther south, in the southern Taiga Plain and northern Boreal Plain ecoregions, where permafrost is thinner, warmer, and discontinuous, it is protected from increasing temperatures by ground vegetation and a thick organic soil layer on peat plateaus (Shur and Jorgenson 2007). However, permafrost thaw and forest loss are becoming increasingly widespread at these southern limits of permafrost (Baltzer *et al.* 2014; Helbig *et al.* 2016). Consequently, the latitudinal gradient in the rate of permafrost thaw, combined with eco-hydrologic feedbacks in southern permafrost-free zones, means that the greatest vulnerability of forested peatlands to climate change occurs at central latitudes, within the southern region of the discontinuous permafrost zone (Figure 4).

In addition, the abundance of large, deepwater lakes throughout the interior boreal region may have moderating influences on local and regional climates, due to the high heat capacity of water, as well as cooling and moist onshore breezes, which may both reduce fire occurrence and buffer local climates (Parisien and Sirois 2003; Meunier *et al.* 2007). Onshore breezes may strengthen in magnitude and frequency as the difference between land and water surface temperatures increases (Figure 2c; WebPanel 2). Water can also act as a natural fuel break, and therefore islands and peninsulas can serve as fire refugia, allowing some forest stands to persist longer than the regional average (Nielsen *et al.* 2016).

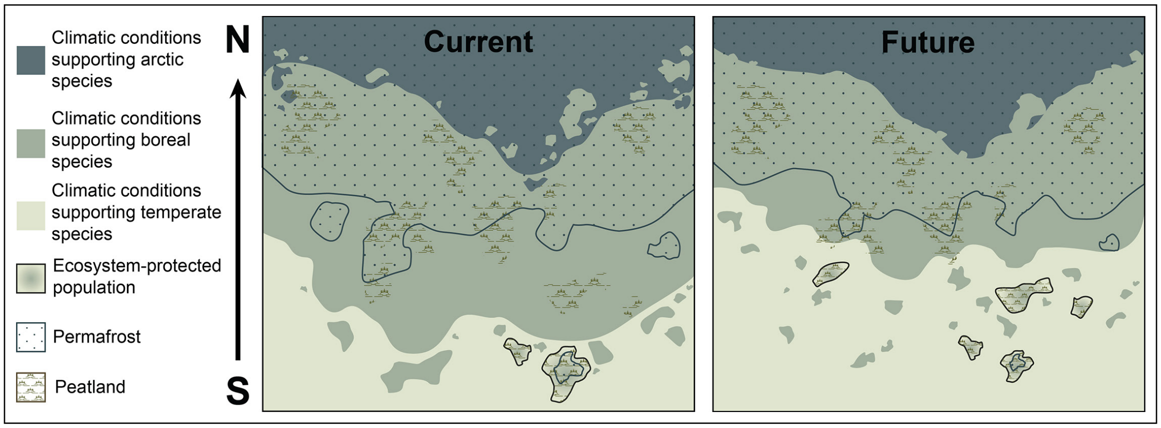



**Figure 5.** Range-based schematic of current and future boreal refugia potential for a hypothetical boreal species, including current disjunct populations south of the contiguous boreal region. Although the rate of warming is greater in northernmost boreal regions, there is less risk of wholesale biome transition, and macrorefugia potential is high. Southern regions are inherently more vulnerable to climate warming, but refugia may persist in areas of sheltered terrain or strong ecosystem protection. Current boreal remnants may provide contemporary analogs for future boreal refugia appearing at higher latitudes or elevations.

### Eastern and western coastal regions

The northeastern portion of the Boreal Shield and Taiga Shield ecoregions (parts of Québec, Labrador, and Newfoundland) (Figure 1) receives on average more than twice as much precipitation as the central and western boreal regions. As such, it may be considered an important boreal macrorefugium, given that it is much more likely to withstand increased evaporative stress and retain boreal climate conditions (Gauthier *et al.* 2015; D'Orangeville *et al.* 2016), although drought-driven decreases in productivity are expected under extreme warming scenarios (eg Girardin *et al.* 2016). These wetter conditions are a function of global circulation patterns that deliver moisture along multiple converging storm tracks. Eastern shield regions lack widespread permafrost and extensive wetland complexes that can protect ecosystems from climate warming. However, an important west-to-east gradient of increasing annual precipitation results in decreasing fire activity (Boulanger *et al.* 2014), favoring the development of fire refugia that may provide greater protection to ecosystems against disturbance-driven vegetation shifts (Gennaretti *et al.* 2014). Eastern coastal temperatures are also moderated by the Labrador Current, which cools the region and generates coastal fog where it meets the Gulf Stream (Figure 2d). These phenomena can likely maintain refugia across large areas, as coastal climates appear to remain relatively buffered by oceanic influences. On the west coast, forests within the Alaska Boreal Interior ecoregion are strongly influenced by the Pacific Ocean, and are therefore generally cooler and much wetter than nearby interior forests, resulting in greatly reduced rates of fire (Rupp *et al.* 2016).

### Boreal remnants as analogs

Due to the overarching influence of latitude on global temperatures, southern boreal regions are inherently more vulnerable to climate warming (Figure 5). The influence of glacial retreat and gradual warming during the Late Pleistocene is evident in the current forest–grassland transition zone of western Canada, where white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) trees persist at the tops of plateaus surrounded by prairies (eg in the Cypress Hills of southern Alberta and Saskatchewan), as well as in sheltered sites along north-facing slopes of incised river valleys. Likewise, boreal vegetation persists at high elevations in the Appalachian Mountains of the northeastern US. In the Great Lakes region, strong upwelling dynamics on the west shore of Lake Michigan maintain boreal forest in a landscape otherwise naturally dominated by temperate deciduous species (Fisichelli *et al.* 2012). Other boreal remnants include terrain-mediated tamarack (*Larix laricina*) forests in northeast-facing depressions where cold air collects, and balsam fir (*Abies balsamea*) on talus slopes in limestone karst landscapes cooled by ice caves. Some disjunct boreal remnants are maintained not just by local topography but also by the presence of relict peat soils that formed thousands of years ago under cooler conditions, and associated eco-hydrological processes (Nagy and Warner 1999). Further study of these disjunct boreal remnants and their relict populations – including paleoecological history, topographic setting, and local climatic conditions – can help identify where analogous conditions and potential future refugia may exist within the wider boreal biome.

## A refugia framework and taxonomy

Adapting the definition given by Morelli *et al.* (2016), we define boreal refugia as *areas relatively buffered from contemporary climate change over time that enable persistence of boreal ecosystems*. Furthermore, we recognize a continuum ranging from high-to-low refugia potential, or inversely, from low-to-high climate-change vulnerability. Fundamentally, we consider a boreal refugium to be any area that maintains *predominantly boreal* species and ecological function, while recognizing that some ecological novelty in future climate-disrupted systems may be inevitable. Accordingly, we suggest that refugia potential varies in terms of *persistence over space and time*, as well as *ecological integrity* and *species composition*. For example, a northern boreal landscape that experiences permafrost thaw and associated landscape change could still remain fundamentally boreal even though local ecosystem processes and species composition may shift over time; thus, in a boreal-wide context it would be considered part of a dynamic, macroscale *boreal refugium*. However, forested ecosystems and underlying permafrost are more likely to persist in less fragmented landscapes with thick and extensive peat layers, resulting in spatially varying *boreal forest refugia* potential.

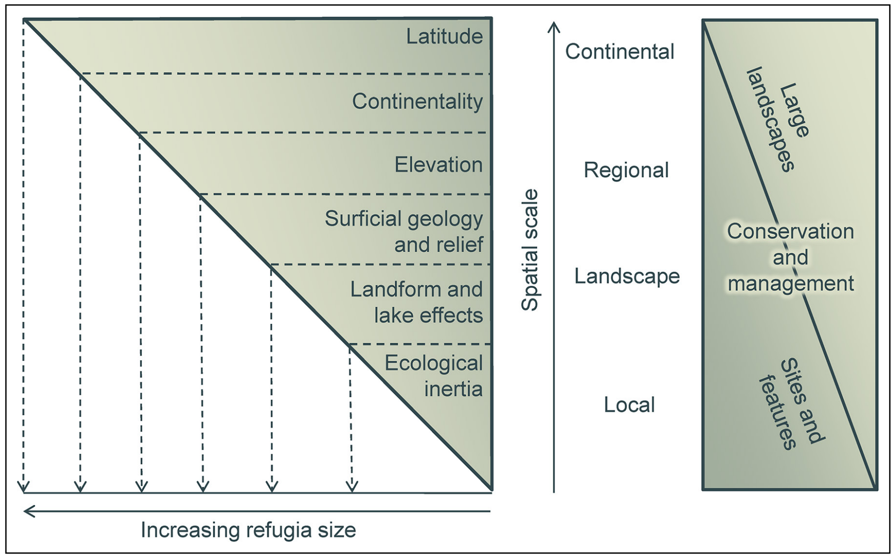



**Figure 6.** Processes governing refugia in the boreal region as hierarchical filters applied to the landscape. Continental-scale processes result in large and extensive macrorefugia, mostly at northern latitudes or in coastal regions. Outside of these macrorefugia, successively finer-scale processes are required to yield refugia, with ecological inertia providing the only potential for microrefugia in locations where physical landscape characteristics do not provide sufficient climatic buffering. This scale hierarchy also influences management strategies; large-scale landscape conservation planning is important for maintaining macrorefugia, while a focus on features and places is more appropriate for microrefugia.

## Refugia vary by spatial scale

Refugia processes operate at multiple spatial scales and can be described hierarchically (Figure 6). At a continental scale, latitudinal differences in sunlight and atmospheric circulation patterns limit warmer temperatures and hence maintain higher soil moisture content in high-latitude and coastal regions. Regionally, high-elevation areas have lower maximum temperatures due to adiabatic cooling (temperature decreasing with atmospheric pressure due to volume changes); as a consequence, evapotranspiration from substrates and vegetation is reduced. At the landscape level, terrain relief and surficial geology influence hydrology and water retention. Areas surrounding large lakes are climatically buffered by cold-water influences. More locally, terrain factors such as aspect (the direction that a slope faces) and landform types (topographic features such as valleys and ridgetops), as well as edaphic (soil-related) conditions and ecological processes, protect against temperature extremes and retain moisture. These local factors represent a last opportunity for boreal conditions to persist wherever regional tipping points (eg moisture thresholds) are crossed.

## Refugia vary in strength over time

Given the current rapid rate of climate warming, many refugia may not be ecologically stable over the long term. Consequently, it is useful to characterize refugia features in terms of their persistence over time (McLaughlin *et al.* 2017). We consider the *strength* of refugia to be a combination of temporal persistence and the shape of the anticipated response to climate change and disturbance (Figure 7). Many terrain-mediated refugia processes – such as the decrease in air temperatures with elevation, or topographic shading from solar radiation – represent consistent but relatively weak decoupling from surrounding climate conditions, with gradual responses to warming. Other types of refugia depend on stronger feedback mechanisms that maintain relatively persistent cooler or wetter conditions as long as these processes continue, with non-linear or threshold responses to climate change when a tipping point is exceeded. For example, the thermal inertia of permafrost can maintain vegetation in a state of disequilibrium with the regional climate at millennial time scales (Herzschuh *et al.* 2016). However, when permafrost does thaw, often initiated by disturbance, rapid and dramatic land-cover changes may follow.

Ecological inertia may maintain forest composition in the absence of major disturbance for decades to centuries. Ecohydrological manipulation of water tables and soil moisture conditions by peatland plants can enable particularly strong resistance to natural disturbance as well as directional long-term change. The strength of these ecosystem-protected refugia will vary depending on differences in surficial geology, natural disturbance regime, and climate regime (Hokanson *et al.* 2018). In addition, other ecological factors, such as species traits and interactions (WebPanel 3), can also confer resistance at the species and community levels. Depending on the strength of the ecological feedbacks, ecosystem-protected refugia may persist longer than terrain-mediated refugia, which will eventually be overcome by the magnitude of warming. Consequently, ecological processes could become increasingly important as terrain-mediated refugia disappear.

Attempting to capture these concepts, we developed a framework and taxonomy of physical refugia *features* (eg

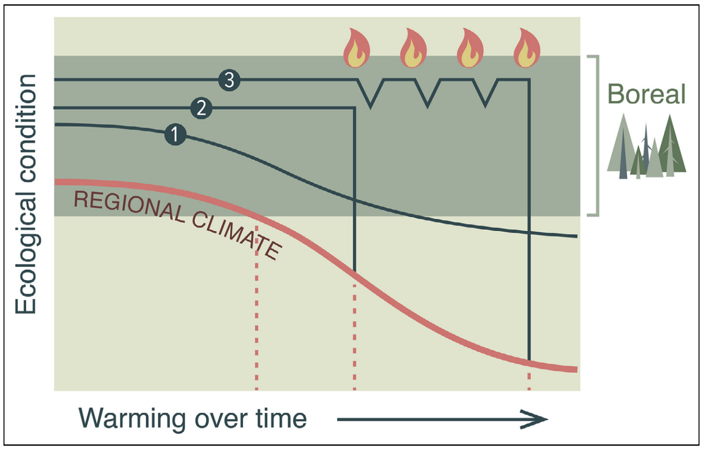



**Figure 7.** Conceptual illustration of refugia strength. As the regional climate (solid red line) warms, ecologically relevant climate conditions (abstracted as "ecological condition") diverge from the historical range of boreal conditions (dark green area). A *terrain-mediated* refugium (eg a north-facing slope) (1) may remain consistently cooler than the regional climate but will eventually become too warm to protect a boreal ecosystem. A mature forest stand (2) creates a cooler and moister *ecosystem-protected* refugium, which may resist change until a stand-replacing disturbance (fire icon) reverts it back to regional climate conditions. A forested peatland (3) may persist even longer as an *ecosystem-protected* refugium due to eco-hydrological feedbacks that make the system resilient to most wildfire (fire icons) and resistant to change for a longer period. The strength of a particular refugium is characterized both by the shape of the response curve (solid blue-gray line) and by the time at which it leaves the range of boreal conditions (intersection with dashed red line).

lakeshores or north-facing slopes), classified by *type* (terrain-mediated or ecosystem-protected) and *mechanism* (climatic buffering or disturbance avoidance) (WebTable 2). For each combination of refugia feature, type, and mechanism, we summarized information about spatial scale, potential indicator metrics, and regions of importance, as well as strengths, weaknesses, opportunities, and threats for management.

## Conservation implications and future outlook

Confronted with rapid climate change and pessimistic climatic projections, forest and land managers, as well as conservation practitioners, face the challenge of integrating climate-change refugia into already complex decision-making processes. Identifying and prioritizing relatively stable areas that are more likely to resist climate-change impacts will be important to better ensure positive conservation outcomes despite limited funds and resources, and will provide an additional lens through which to compare and contrast management options across a broad spectrum of land-use planning processes. The conservation and informed management of these areas of high refugia potential may help species and ecosystems to persist through the 21st century and beyond, providing safe havens for migration across the landscape, as well as facilitating adaptation to new conditions via heritable changes in populations connected within the landscape. Strategic protection of boreal refugia may also offer an opportunity for proactive management during a time when many practitioners are struggling to keep up with the accelerating consequences of climate change.

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