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).

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-
sions can promote local microscale decoupling from regional climates, or microrefugia (Dobrowski 2011), whereas factors such as elevation and coastal proximity can result in regionalscale 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 (Buller 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

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**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...
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.

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).
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 disjoint 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 disjoint 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.

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 (e.g., 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
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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