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Essay, part of a Special Feature on Conservation of Boreal Birds

Conservation planning for boreal birds in a changing climate: a framework for action

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ABSTRACT. The boreal forests of North America support billions of birds of over 300 species. The region remains mostly intact but is expected to undergo major changes over the next century due to anthropogenic climate change. This warming, and resulting changes in moisture regimes, are altering vegetation and disturbance dynamics, and will likely result in expansion of grasslands and deciduous forests, strongly challenging bird species to keep pace. We present a vulnerability-adaptation framework to guide bird conservation based on species' individual vulnerability and exposure to climate change. For sensitive species with declining populations, conservation should focus on management of current threats and species recovery in situ to improve adaptive capacity and facilitate future shifts in distribution. Sensitive species with high exposure to climate change may warrant more extensive intervention, such as habitat manipulation or even translocation. For species with lower sensitivity and stable populations, but high climate change exposure, long-term investments in protecting refugia and "stepping stones" will be most effective. In general, across all species, land-based approaches that "conserve nature's stage" by promoting geophysical diversity and habitat connectivity, maintaining natural disturbance dynamics, and facilitating broad shifts in bird distribution may prove most effective in maintaining species diversity. Implementation of this framework will require large-scale, interagency coordination on recovery plans, as well as adaptive forest management, designation of critical habitat, and land protection. Challenges include data gaps, uncertainty about future conditions, coordination of conservation actions during the nonbreeding periods, and the region's vast scale. However, given the region's continental importance, successful implementation of this framework could benefit birds throughout the western hemisphere.

Planification de la conservation des oiseaux de la forêt boréale dans un climat en évolution : un cadre d'action

RÉSUMÉ. Les forêts boréales d'Amérique du Nord abritent des milliards d'oiseaux de plus de 300 espèces. La région reste en grande partie intacte mais devrait subir d'importants changements au cours du prochain siècle en raison du changement climatique anthropique. Ce réchauffement, et les changements de régimes d'humidité qui en résultent, modifient la dynamique de la végétation et des perturbations, ce qui entraînera probablement une expansion des prairies et des forêts de feuillus, ce qui compliquera fortement la donne pour les espèces d'oiseaux concernées. Nous présentons un cadre d'adaptation à la vulnérabilité pour guider la conservation des oiseaux en fonction de la vulnérabilité individuelle de chaque espèce et de son exposition aux changements climatiques. Pour les espèces sensibles dont les populations sont en déclin, la conservation devrait être axée sur la gestion des menaces actuelles et le rétablissement des espèces in situ afin d'améliorer la capacité d'adaptation et de faciliter les futurs changements de répartition. Les espèces sensibles fortement exposées aux changements climatiques peuvent nécessiter des interventions plus poussées, telle que la manipulation de l'habitat ou même la translocation. Pour les espèces moins sensibles et les populations stables, mais tout de même exposées aux changements climatiques, des investissements à long terme pour protéger les refuges et les « tremplins » seront plus efficaces. En général, pour toutes les espèces, les approches terrestres qui « préservent la nature en l'état » en favorisant la diversité géophysique et la connectivité de l'habitat, en maintenant la dynamique des perturbations naturelles et en facilitant de grands changements dans la répartition des oiseaux peuvent s'avérer plus efficaces pour maintenir la diversité des espèces. La mise en oeuvre de ce cadre nécessitera une coordination interinstitutionnelle à grande échelle sur des plans de rétablissement, ainsi que la gestion des forêts adaptative, la désignation d'habitats essentiels et la protection des terres. Les défis comprennent des lacunes dans les données, comme l'incertitude quant aux conditions futures, la coordination des mesures de conservation en dehors de la période de reproduction et la vaste étendue de la région. Cependant, étant donné l'importance de la région à l'échelle continentale, la réussite de la mise en oeuvre de ce cadre pourrait profiter aux oiseaux de tout l'hémisphère occidental.

Key Words: *boreal; climate change; climate exposure; conservation; refugia; vulnerability*

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INTRODUCTION

The approximately 600 million ha North American boreal region represents 25% of the intact forest landscapes remaining globally (Lee et al. 2006, Potapov et al. 2017). Referred to as North America's "bird nursery," the boreal region supports over 300 regularly breeding bird species, and is estimated to provide more than half of the overall breeding habitat for 96 North American bird species and over 80% of breeding habitat for 35 of these (Wells and Blancher 2011). Boreal wetlands provide migratory stopover or breeding habitat for approximately 7 million shorebirds, representing 19 species, and 26 million waterfowl, representing 35 species (Slattery et al. 2011, Wells and Blancher 2011). While development pressures are increasing, especially in the southern portion, the North American boreal biome remains relatively unfragmented compared to other major forests around the world (Lee et al. 2006, Potapov et al. 2017), with only approximately 5% of Canada's boreal region directly disturbed by human activity (Pasher et al. 2013) and an even smaller proportion in Alaska (United States).

The conservation and socioeconomic importance of boreal birds is well recognized. Many efforts exist to quantify existing threats to bird abundance and distribution, mostly relating to direct habitat disturbance and fragmentation (e.g., Schmiegelow et al. 1997, Drapeau et al. 2000, Hobson et al. 2013, Bayne et al. 2016). However, anthropogenic climate change presents new challenges for biologists and managers. In this paper, we summarize projected impacts of climate change in the boreal region of North America, with an overview of projected responses and potential vulnerabilities of boreal birds to climate change. We then present a conceptual framework for advancing boreal bird conservation based on each species' vulnerability to changing climate, summarize key strategies for climate-smart boreal bird conservation, and provide suggestions for addressing climate-change related conservation challenges.

THE CHANGING BOREAL CLIMATE

Boreal climates are characterized by long, cold winters and short, cool summers (Brandt et al. 2013). Although average annual precipitation is low, moisture is retained because of cold temperatures and minimal evapotranspiration, thereby maintaining large wetland complexes and coniferous forests. Climates within the current boreal biome are projected to undergo significant changes in the future, with an average warming of 2 °C expected from 2000 to 2050 (Price et al. 2013, Gauthier et al. 2015), and up to 4-5 °C by the end of the 21st century if global anthropogenic greenhouse gas emissions are not controlled (Price et al. 2013). This warming will translate into a longer growing season, with an expected increase of more than 400 growing degree days by the end of the 21st century in the western boreal plains (Pacific Climate Impacts Consortium, https://pacificclimate.org/analysis-tools/plan2adapt). Warmer temperatures will be accompanied by increases in annual precipitation (Meehl et al. 2007), but also decreases in available moisture (Hogg and Bernier 2005), with substantial differences between western and eastern regions (Boulanger et al. 2017). In western regions, increased precipitation will be offset by higher evapotranspiration rates. Longer and more severe droughts will likely result in serious tree-killing events that may ultimately transform closed boreal forests into open woodlands (Scheffer et al. 2012). In eastern forests, where moisture is less limiting, conversion to more productive temperate forests may occur as critical temperature isoclines shift northward (Price et al. 2013).

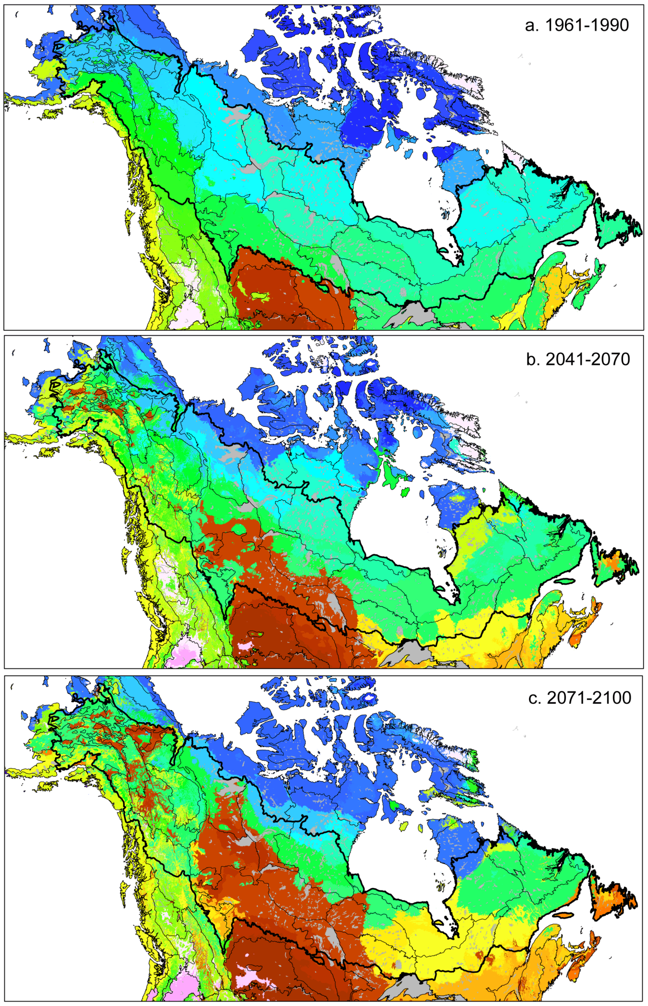
In upcoming decades, warmer temperatures and increased drought will likely result in more frequent disturbance events from large wildfires (Boulanger et al. 2014) and population outbreaks of bark beetles and defoliators (Price et al. 2013), although with significant uncertainty as to magnitude (Boulanger et al. 2016). Throughout the boreal region, a disturbance-mediated competitive shift from mid- to late-successional coniferous species, such as white spruce (*Picea glauca*) and balsam fir (*Abies balsamifera*), to deciduous species such as trembling aspen (*Populus tremuloides*), oak (*Quercus* spp.), and maple (*Acer* spp.) is expected (Boulanger et al. 2017). Thawing of permafrost may temporarily convert low-lying sections of boreal regions from forest-wetland mosaics to sparsely treed, permafrost-free wetlands (Baltzer et al. 2014). Declining water tables are likely to alter nonpermafrost wetland landscapes (Thompson et al. 2017), although negative feedbacks that retain moisture during dry periods may result in peatland systems persisting well beyond climatically suitable conditions (Waddington et al. 2015).

Ecosystem changes are likely to be rapid and dramatic in the boreal biome compared to other regions of the world. Climate velocity—the speed at which species and ecosystems must migrate to keep pace with climate change (Loarie et al. 2009)—is particularly high, because of a combination of relatively flat topography and higher rates of warming in the north (Hamann et al. 2014). Over the long term, assuming eventual equilibrium between climate and vegetation, the North American boreal biome is projected to both shift northward (Rowland et al. 2016) and to shrink in size by an estimated 14–42% by the end of the 21st century (Appendix 1, Fig. 1; see also Rehfeldt et al. 2012). In the short term, however, this rapid change means that the majority of the present boreal biome will be in a state of disequilibrium between climate and biota. These changes will occur in the presence of ongoing industrial development, including extensive forestry across the southern half of the boreal region, widespread oil and gas exploration in the western sedimentary basin, large-scale hydroelectric projects, and mineral extraction projects throughout the biome (Brandt et al. 2013). Thus, combined increases in human and climate-induced disturbance are likely to further reduce the extent and connectivity of boreal forest ecosystems.

BOREAL BIRD VULNERABILITY TO CLIMATE CHANGE

As with other species, boreal bird distributions are generally projected to shift northward and upslope with climate change (Rodenhouse et al. 2008, Ralston and Kirchman 2013, Marcot et al. 2015, Stralberg et al. 2015*a*). Although historical distributional shifts have not been documented for many boreal bird species in North America (but see McClure et al. 2012, DeLuca and King 2017), research from Fennoscandia indicates northward shifts in species richness (Virkkala and Lehikoinen 2014) and pronounced range contractions in long-distance migrants in particular (Virkkala et al. 2018). A warmer climate may enable the immigration of new species from southern grasslands and eastern deciduous forests into the current boreal region, ultimately resulting in a northward shift in species richness patterns (Berteaux et al. 2010, Langham et al. 2015, Nixon et al. 2016). However, most current boreal-breeding species will face substantial declines in suitable habitat by the end of the century because the northward expansion of forested habitats will not compensate for anticipated conversion of coniferous forest to deciduous woodland and grassland in the south (Stralberg et al. 2015*a*).

Fig. 1. Model-predicted (a) baseline (1961–1990), (b) midcentury (2041–2070), and (c) end-of-century (2071–2100) changes in boreal ecoregions for an ensemble of 15 global climate models under representative concentration pathway (RCP) 8.5. Boreal, hemi-boreal, and western forested regions are shown in green and blue-green shades; arctic ecoregions are in blue shades; prairie/parkland ecoregions are in brown shades; and temperate forest ecoregions are in yellow and orange shades. Boreal ecoregions are also outlined in black. See Appendix 1 for detailed methods and results for all North American ecoregions.



In light of these anticipated changes in habitat, all boreal bird species will be affected in some way by climate change. Understanding the degree of threat to individual species requires knowledge about their vulnerability to climate change, which is a function of intrinsic factors determined by species traits, as well as extrinsic factors determined by environmental conditions (Pacifici et al. 2015). Indeed, climate-change vulnerability has been defined as a combination of climate exposure, sensitivity, and adaptive capacity (Dawson et al. 2011). Climate exposure is typically considered in terms of the magnitude of change in long-term climate and climate variability experienced by a species (Beever et al. 2016, Foden and Young 2016). Sensitivity refers to the degree a species is affected by climate variability, and is a function of species' traits, including thermal tolerance, degree of ecological specialization, phenology, and vital rates (Foden and Young 2016). Adaptive capacity describes the ability of a species to adjust to climate change, and includes dispersal capacity, evolutionary capacity (genetic variability), and behavioral modifications (phenotypic plasticity; Dawson et al. 2011, Beever et al. 2016). The species that are most vulnerable to climate change are those that are exposed to large changes in climatically suitable habitat, have high sensitivity to climate change, and have low adaptive capacity (Beever et al. 2016, Foden and Young 2016). Boreal species occupy a diversity of niches, and exhibit a variety of life history characteristics, resulting in a range of exposure, sensitivity and adaptive capacity levels. Nevertheless, we provide some generalizations herein.

Climate exposure

Given the high expected rates of temperature increase in the north, boreal breeding species are likely to be among the most exposed to future changes in climate in a North American context (Rodenhouse et al. 2008). In particular, winter residents, which comprise ~20% of all boreal bird species (Erskine 1977), may experience the largest direct changes in climate (Rodenhouse et al. 2009), while many Neotropical migrant species, i.e., long-distance migrants, may be less climate-exposed because of their reduced dependence on ecosystems influenced by northern climates. It should be noted, however, that resident species are already adapted to a much broader range of annual temperatures and weather conditions than migrant species, for which small temperature increases may be more meaningful. Furthermore, climate exposure of migratory species is compounded by an additional set of changes on their wintering grounds and along migration routes (Small-Lorenz et al. 2013).

The level of an individual species' climate exposure will also depend strongly on its climatic niche. Despite relatively large and intact current ranges, forest-associated species are more threatened by loss of habitat corresponding to their climatic niches than are grassland or woodland-associated birds (Langham et al. 2015, Stralberg et al. 2018*a*). Furthermore, for boreal-breeding species, changes in breeding niches are projected to be more substantial on average than changes in wintering niches (Naujokaitis-Lewis 2014, Langham et al. 2015). Some species with the largest projected loss of climatic niche space include boreal forest specialists like Black-backed Woodpecker (*Picoides arcticus*; Tremblay et al. 2018), Gray-cheeked Thrush (*Catharus minimus*; Stralberg et al. 2015*a*), Bicknell's Thrush (*Catharus bicknelli*; Rodenhouse et al. 2008, Cadieux et al. 2019), Rusty Blackbird (*Euphagus carolinus*; Stralberg et al. 2015*a*), Blackpoll Warbler (*Setophaga striata*; Ralston and Kirchman 2013), and Palm Warbler (*Setophaga palmarum*; Langham et al. 2015, Stralberg et al. 2015*a*). In comparison, many boreal species that nest in deciduous stands also have ranges that extend south into eastern deciduous forests. These species may experience gains in habitat suitability in some portions of their current range, especially in parts of the eastern boreal region that could experience increased productivity (D'Orangeville et al. 2016, Boulanger et al. 2017) and an increase in temperate tree species (Fisichelli et al. 2014). However, in the western boreal plains, habitat suitability for deciduous forest-associated species will likely decline, assuming that drought conditions and disturbance eventually lead to projected grassland conversion and forest loss (Stralberg et al. 2018*b*). Thus, niche loss and by extension climate exposure will likely vary by region.

Climate sensitivity

Most boreal species are estimated to have large, relatively stable populations because of their large, intact breeding ranges (Rosenberg et al. 2016). In addition, boreal birds exhibit a relatively low level of niche partitioning and habitat specialization (Mahon et al. 2016), perhaps due in part to the highly dynamic nature of the boreal forest biome (Schmiegelow and Mönkkönen 2002). These factors may generally result in low climate sensitivity of boreal bird species. However, species associated with late seral-stage forests are likely more sensitive than early-seral associates because of lag times associated with vegetation growth and stand development (Stralberg et al. 2015*b*). For example, impacts of climate change are likely to be detrimental for Black-backed Woodpecker, an indicator species for deadwood and old-growth biodiversity in eastern boreal forests (Tremblay et al. 2009, 2010). Indeed, simulations of landscape change suggest up to a 92% decline in potential productivity for this species under all climate-change scenarios considered, primarily based on increased levels of natural and anthropogenic disturbance in the future (Tremblay et al. 2018).

In addition, species with declining populations have reduced ability to shift their distributions in response to climate change, as well as higher rates of extirpation along the trailing edges of their distributions (Ralston et al. 2017). Some boreal bird species may already be declining because of deteriorating habitat conditions on wintering grounds and along migratory routes, reductions in insect prey, or direct habitat loss. For example, Olive-sided Flycatcher (*Contopus cooperi*) declined by 2.6% per year (range 1.91% to 3.34%) between 1970 and 2015, and by ~79% from 1968 to 2006 (Environment and Climate Change Canada 2017), despite high availability of its suitable breeding habitat: forest edges and openings, especially recent burns. The high rate of decline combined with low breeding densities suggest a high sensitivity to climate change, especially to extreme weather events that may result in widespread nest failure or mortality (Anctil et al. 2017). Species with small population sizes are particularly sensitive to extreme weather events and other short-term fluctuations from which it may be difficult to recover (Sæther et al. 2016). For example, Bicknell's Thrush is among the few range-restricted boreal species in North America (see Text Box 1). The high variability in this species' reproductive success (Townsend et al. 2015) and its small population size suggest high sensitivity to change. Furthermore, given the high proportion of migratory species in the boreal region, most boreal-breeding species will face additional pressures from threats occurring over the nonbreeding portions of the annual cycle including changes on wintering grounds and during migration (Lemoine et al. 2007).

For waterfowl, the abundant bogs and fens of the boreal region provide important breeding grounds, especially during years of drought in the North American prairies (Johnson and Grier 1988, Bethke and Nudds 1993). With some exceptions, most boreal waterfowl species have stable long-term trends, although species that breed late in the season are considered more sensitive to climate change, consistent with the hypothesis that increased temperatures may result in trophic mismatches between breeding ducks and their insect prey (Drever et al. 2012). Many shorebirds species that nest in the boreal region are showing population declines, however, and those species that migrate the longest distances are thought to be most sensitive (Thomas et al. 2006).

Box 1. Bicknell's Thrush

Bicknell's Thrush is listed as Threatened in Canada (Environment and Climate Change Canada 2016) and vulnerable globally (BirdLife International 2018). The species inhabits dense (≥ 15,000 stems/ha) balsam fir forest stands at high elevations in the northeastern United States and eastern Canada (Connolly et al. 2002, Aubry et al. 2011, 2016, Townsend et al. 2015). Both habitat loss and the indirect effects of climate change, whereby increased temperatures are reducing available habitat via shifts in the balsam fir/spruce-mountain forest ecotone, are identified as threats to this species (COSEWIC 2009). Bicknell's Thrush has a highly restricted breeding range, and bioclimatic models project a loss of > 50% of its northeastern U.S. habitat over the next 30 years (Rodenhouse et al. 2008). In eastern Canada, forest landscape simulations also suggest dramatic declines in low-elevation habitat for Bicknell's Thrush by 2100, while higher elevation (> 900 m) areas would likely act as climate refugia for the species (Cadieux et al. 2019). Thus, among boreal bird species, the Bicknell's Thrush is one of the most vulnerable to climate change, as it demonstrates (1) high long-term climate exposure based on the projected decline of its habitat, (2) short-term demographic sensitivity based on its low population size and variability in its reproductive success (Townsend et al. 2015), and (3) low adaptive capacity as a result of its long-distance migration strategy.

Adaptive capacity

Adaptive capacity is characterized by dispersal ability, genetic diversity (leading to directional selection), or phenotypic plasticity (leading to behavioral change). For example, some winter resident species, including irruptive species such as Pine Siskin (*Spinus pinus*), may have high capacity to respond to changing climate because of their ability to track fluctuating resources, such as climate-driven seed masting events (Strong et al. 2015). Conversely, long-distance migrant species may be less flexible (Small-Lorenz et al. 2013). As warmer climates cause earlier insect emergence and plant green-up, there is concern about mismatches in the timing of migratory bird arrival, compared with prey availability (Both and Visser 2001). Research from Europe suggests long-distance migrants have particularly inflexible ("hard-wired") migration schedules, compared to short-distance migrants (Both et al. 2009), and that phenological mismatches between migratory birds and insect prey can lead to population declines (Both et al. 2006). The high proportion of Neotropical migrant species in the boreal region suggests overall low adaptive capacity with respect to arrival times, resulting in greater potential disjuncts under shifting climate conditions (Both et al. 2009), especially where flexibility of migratory patterns is low (Gilroy et al. 2016). Thus far, however, mismatches between the timing of green-up and bird arrival have been documented for temperate North American species, but not boreal species (Mayor et al. 2017). Boreal species could be less sensitive than temperate birds to such mismatches if food availability is not limiting throughout the breeding season.

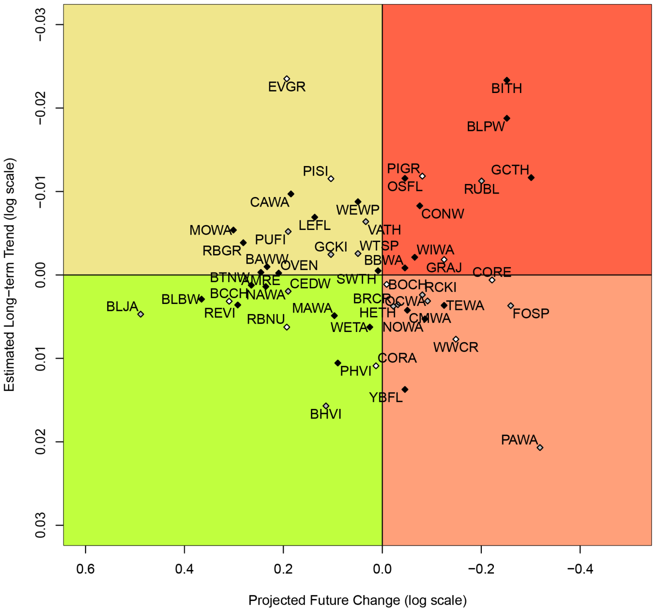
Although phenology and migration flexibility have received most research attention, the integration and characterization of adaptive capacity, particularly in relation to the role of genetic variability (Bay et al. 2018) and phenotypic plasticity, remains an emerging and active area of research (Beever et al. 2016, Wade et al. 2017).

Assessing vulnerability

According to the Partners in Flight (PIF) Watch List, only six of 86 species that are identified as species of conservation concern rely primarily on boreal habitats for breeding (Rosenberg et al. 2016). Climate change is identified as a major threat to persistence for only three of these species: Bicknell's Thrush (see Text Box 1), Rusty Blackbird, and Olive-sided Flycatcher. However, the combination of high future climate-change exposure in the north, loss of climates suitable for coniferous forests, and low adaptive capacity of long-distance migrants, means that boreal birds may become more vulnerable to extinction in the future.

There are multiple approaches and established frameworks for performing climate change vulnerability assessments (CCVA; Pacifici et al. 2015). Many of these involve assessing multiple species traits (e.g., Bagne et al. 2011, Young et al. 2016, Gardali et al. 2012). Some involve other indicators of climate sensitivity and adaptive capacity, such as population size and trend estimates (Gregory et al. 2009, U.S. Environmental Protection Agency 2009), while others use projections based on global climate models to estimate climate exposure (Gardali et al. 2012, Case and Lawler 2016, Aubin et al. 2018). Although a comprehensive analysis is outside the scope of this review, we present a first-order approximation of vulnerability of boreal forest birds for illustrative purposes. For a set of 54 forest-associated passerine species, we plotted long-term trend estimates (Environment and Climate Change Canada 2017), as a proxy for climate sensitivity (Ralston et al. 2017), against projections of midcentury climatic suitability according to Stralberg et al. (2015*a*) as a proxy for climate exposure (Fig. 2, Appendix 2). For Bicknell's Thrush, not covered by Stralberg et al. (2015*a*), we used an unpublished projection for Canada from Cadieux and Tremblay based on a model developed from U.S. data by Lambert and McFarland (2004). Migratory status was overlaid as an indicator of adaptive capacity. According to this classification, the PIF-identified climate-vulnerable species also fall into the high vulnerability category, as do species like Blackpoll Warbler and Gray-cheeked Thrush. Common Redpoll (*Acanthis flammea*) and Pine Grosbeak (*Pinicola enucleator*) may be considered to have high climate exposure and sensitivity, but also high adaptive capacity due to their resident status and nomadic habits. Other declining species such as Evening Grosbeak (*Coccothraustes vespertinus*) and Canada Warbler (*Cardellina canadensis*) have relatively low climate exposure, and may therefore be considered less climate-vulnerable; whereas other species with high climate exposure, such as Palm Warbler, may not be particularly climate-sensitive, at least according to recent trends. We acknowledge that Breeding Bird Survey trends are biased toward the southern boreal region and may not adequately represent trends in northern populations (Van Wilgenburg et al. 2018). Thus, we caution against overinterpretation and suggest that a more rigorous, in-depth CCVA be performed to adequately characterize vulnerability and situate risks.

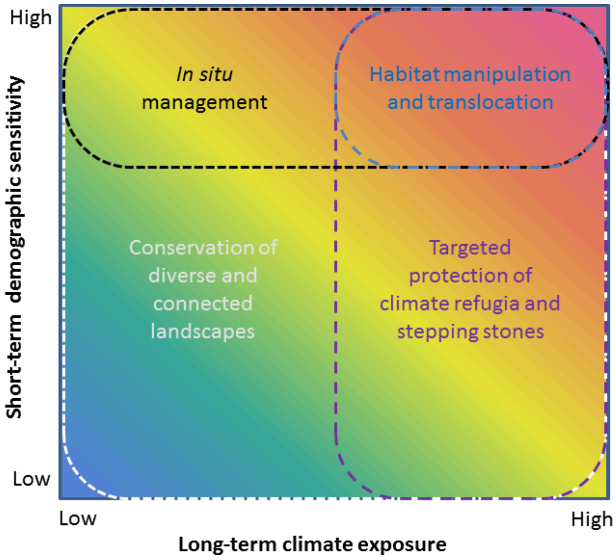
Fig. 2. Components of climate-change vulnerability plotted for 54 boreal-breeding passerine species (see Appendix 2 for species names and data values). Long-term trend values are based on Canada-wide BBS trend estimates (Environment and Climate Change Canada 2017), converted to proportional change and log-transformed. For all species but Bicknell's Thrush (BITH; *Catharus bicknelli*), projected future change values are based on midcentury (2041–2070) climate-based mean density estimates for the North American boreal region (Stralberg et al. 2015*a*), converted to proportional change and log-transformed. For BITH, the future projection is from Cadieux and Tremblay (*unpublished*) based on a model from Lambert and McFarland (2004). Symbols for each species are colored according to migratory status: black = long-distance migrant; gray = short-distance migrant; and white = resident or nomadic.



CONSERVATION STRATEGIES

In an era of rapid environmental change, it is paramount to consider future potential changes alongside current environmental conditions to conserve and manage populations (Araújo et al. 2004, Veloz et al. 2013). However, selecting effective conservation strategies is a nontrivial task that can vary by species and ecosystems and the associated climate change risks, amongst other factors. We present a conceptual framework for advancing effective conservation strategies for boreal birds in a changing climate based on species' vulnerability, adapted from the landscape-based framework proposed by Gillson et al. (2013). Importantly, we extend vulnerability assessments into the conservation decision space and link vulnerability rankings to four corresponding conservation strategies: in situ habitat management, habitat manipulation and translocation, targeted protection of climate refugia and stepping stones, and conservation of diverse and connected landscapes (Fig. 3). Species' climate change vulnerability can be plotted along the axes of long-term climate exposure, sensitivity, and adaptive capacity. For simplicity, we combined the axes of sensitivity and adaptive capacity, given that adaptive capacity is not easily estimated at the species level. This combined axis is termed short-term demographic sensitivity, and refers to intrinsic factors determined by species traits, as opposed to extrinsic factors determined by environmental change. Species location along the two axes in this framework suggests the nested suite of conservation strategies best suited to their circumstances. We elaborate each of the conservation strategies, and then consider the potential for integration via systematic conservation planning.

Fig. 3. Vulnerability–adaptation framework, adapted from Gillson et al. (2013), depicting appropriate conservation actions suggested by individual species' short-term demographic sensitivity and long-term climate exposure. Short-term demographic sensitivity combines climate sensitivity and adaptive capacity, and high values indicate species with population dynamics strongly affected by climate or under strong risk of extinction. Climate exposure refers to the extent to which species rely on habitats or regions expected to undergo significant changes under warming climate. This figure should be interpreted similarly to a Punnett square, where species are assigned a value along these two axes, which then determines the conservation strategies best suited to their circumstances.



In situ management

For demographically sensitive species with declining populations, adaptation to climate change depends on management of current threats and species recovery in situ, to improve adaptive capacity and facilitate future shifts in distribution (Fig. 3, upper portion). Species that are highly climate-sensitive or currently at risk of extinction, but that have projected increases in future habitat suitability (low climate exposure), may eventually benefit from climate change once populations are stabilized, suggesting that major up-front conservation investments can prevent the need for future action. Given that species with declining populations often experience contracting range margins (Lawton 1993, Lenoir and Svenning 2015), sometimes in conjunction with decreasing local densities, potential distributional increases in response to climate change may not occur until current populations are stable or increasing. Consequently, investments in future suitable habitat may be premature or at least lower priority for these species. Instead, it will first be necessary to invest in measures aimed at increasing local populations and preventing further declines via critical habitat protection. For example, climate change may eventually benefit Canada Warbler, a species listed as Threatened under Canada's Species at Risk Act (SARA), given projected increases in deciduous vs. coniferous tree species. However, individuals of this species tend to be clustered spatially and local populations are often relatively isolated, which may be exacerbated by industrial development (Grinde and Niemi 2016, Hunt et al. 2017). Thus, increasing current habitat availability and connectivity will be more important than protecting areas of projected future occupancy for Canada Warbler and other similar species.

Habitat manipulation and translocation

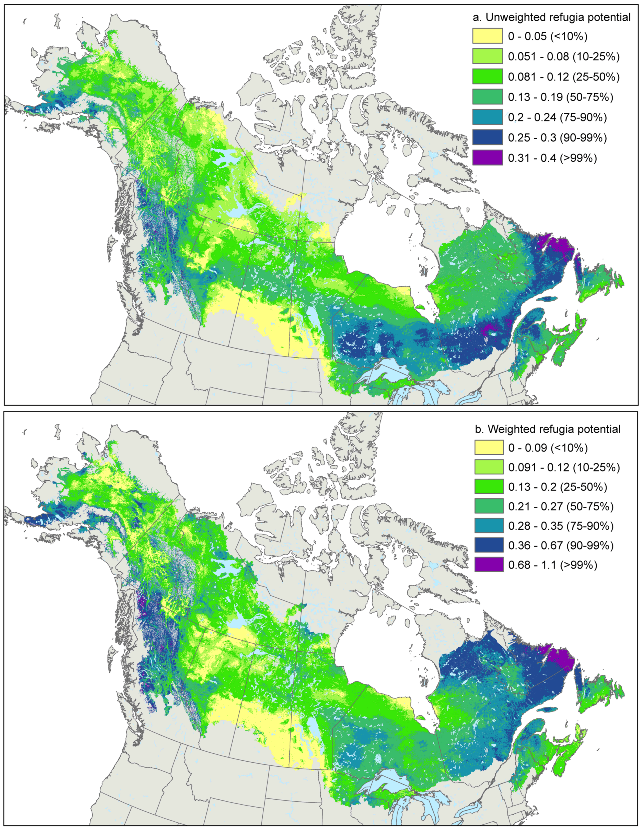
Species that are demographically sensitive and declining, and also subject to high climate exposure, may warrant more extreme intervention, such as habitat manipulation or even translocation (Griffith et al. 1989; Fig. 3, right). In the near term, large-scale reforestation conducted postharvest or postfire, especially based on climatically suitable genotypes (Millar et al. 2007, Gray and Hamann 2011), can help encourage the growth of tree species that might otherwise not have suitable conditions for establishment because of drought conditions (Gauthier et al. 2014). However, when the magnitude of change is great enough that species can no longer persist in their existing landscapes, species management must be viewed from a much broader scale perspective, and managed translocation (also known as assisted migration or assisted colonization) of individuals into newly suitable habitats outside of their current range may be considered (McLachlan et al. 2007, Hoegh-Guldberg et al. 2008). In managed forests, this effort may involve translocation of tree species or genotypes in conjunction with forestry operations (Gray et al. 2011, Williams and Dumroese 2013). Although translocation of birds has previously only been conducted in conjunction with captive breeding and for critically endangered species with very small populations (Griffith et al. 1989), more proactive programs could be established with wild populations. Given the potential for unintended consequences such as community disruption and disease spread (Ricciardi and Simberloff 2009), translocation should be approached with caution and considered for movements within, rather than between, biogeographic regions (Hoegh-Guldberg et al. 2008). For example, the current break in boreal forest habitat across the northwestern cordillera mountain ranges spanning Alaska and the Yukon could be bridged via translocation. Although climate projections suggest increased future connectivity across the cordillera (Stralberg et al. 2017), and some species have recently appeared on the Alaska side (Gibson and Withrow 2015), translocation could speed up the process, also facilitating future upslope migration.

Targeted protection of climate refugia and stepping stones

For boreal bird species with high climate exposure, but no present indication of population decline, conservation investments may be most efficiently directed toward identification and protection of climate refugia, areas of relative stability for one or more species under climate change (Ashcroft 2010, Keppel et al. 2012, Michalak et al. 2018), and stepping stones (Fig. 3, right-hand portion). More specifically, refugia may be defined as “areas relatively buffered from contemporary climate change over time that enable persistence of valued physical, ecological, and socio-cultural resources” (Morelli et al. 2016). Whether they persist indefinitely or represent short-term “hold-outs” (Hannah et al. 2014), refugia represent areas of high conservation value in a changing climate, and may support higher levels of endemism over the long term (Sandel et al. 2011). In the boreal region, given rapid rates of change over large areas, this effort will involve identifying macro-scale climate refugia, largely driven by proximity to cooler and wetter high elevation and coastal influences (Stralberg et al. 2015*b*).

Using a climate velocity-based approach to mapping individual species refugia (Stralberg et al. 2018*a*), areas of highest end-of-century refugia potential for forest-associated boreal birds were found primarily in western mountainous portions of Alaska, British Columbia, and the Yukon, and along the Québec and Labrador coasts in the east (Fig. 4, Appendix 3). Depending on species’ weightings, portions of Ontario and interior Québec also had high refugia potential. Generally speaking, these refugia can be characterized as areas of relatively moderate climates, e.g., marine and lacustrine coastal areas, and mountain areas projected to remain cool and wet in a rapidly warming climate. Individual species refugia were also found along the latitudinal and elevational ecotones that currently represent species’ northern range limits, e.g., the boreal-taiga transition zone. Importantly, however, refugia are not static and will contract over time in a period of rapid change. Thus, conservation efforts will need to consider multiple time periods and the resulting “temporal corridors” (Rose and Burton 2009) or “stepping stones” (Hannah et al. 2014) needed to bolster species’ existing populations and facilitate gradual distribution shifts. For example, a conservation prioritization exercise focused on boreal passerine refugia found significant overlap among solutions for different time periods, but also suggested that to conserve an area representing 10% of combined boreal species’ habitat throughout the 21st century, three times as much land would be needed compared to present-day conditions (Stralberg et al. 2015*b*). Efficiencies are gained by conserving more land; e.g., 30% of combined habitat value can be obtained with only twice the land area of present-day conditions.

Fig. 4. Multispecies end-of-century refugia index for 53 boreal forest-associated species. Using an approach based on locating nearest climatic analogs (Stralberg et al. 2018*a*), we calculated individual species refugia indices (0 = low, 1 = high) based on end-of-century climate projections (Stralberg et al. 2015*a*) and averaged them to obtain a multispecies index of refugia value. Areas of highest combined future refugia potential (dark blue) include western mountain regions and eastern coastal regions with a maritime influence. These areas represent the most efficient options for protecting current boreal forest species and communities. See Appendix 3 for detailed methods and midcentury results.



Climatic microrefugia, driven by local terrain effects such as aspect and cold air drainage, have also been advocated as important conservation priorities in regions of rugged terrain and steep climatic gradients (Ashcroft 2010, Dobrowski 2011). The generally flat terrain and corresponding climate gradients may mean limited opportunity exists for climatic microrefugia over much, but not all of the boreal region. However, other types of refugia, i.e., wetlands and riparian zones (Selwood et al. 2015, McLaughlin et al. 2017), and various types of fire refugia (Krawchuk et al. 2016, Nielsen et al. 2016), may play an important role yet to be fully understood in boreal regions. For example, moisture-conserving peatland systems may be able to persist longer than surrounding upland forests (Waddington et al. 2015, Schneider et al. 2016, Thompson et al. 2017), serving as climate refugia for some species.

Conservation of diverse and connected landscapes

In general, land-based approaches such as "conserving nature's stage" (Beier and Brost 2010) by promoting geophysical diversity (Anderson and Ferree 2010), maintaining natural disturbance dynamics (Noss 2001, Leroux et al. 2007), and maintaining habitat connectivity to facilitate broad-scale distributional shifts, e.g. along gradients (Halpin 1997, Noss 2001, Hodgson et al. 2009), may prove most effective in maintaining biodiversity without requiring certainty about specific long-term changes in climate (Fig. 3, entire square). Given the magnitude of change expected and the number of species affected by climate change, individual species management will become increasingly inefficient for conservation of bird diversity. In the large and relatively intact boreal region, some researchers simply call for large-scale protection to maintain natural disturbance processes and wide-ranging species (Badiou et al. 2013). More targeted approaches aim to optimize the selection of large, representative, and intact benchmarks for conservation, in conjunction with broad-scale adaptive management of remaining areas (Leroux et al. 2007, Schmiegelow et al. 2014). In a climate-change context, several species-neutral approaches have been suggested that de-emphasize the "actors" (species) and focus instead on the "stage" (environmental setting) that maintains diversity. Species-neutral strategies proposed for efficient use of conservation resources in a changing climate include the identification of (1) representative "land facets" or "enduring features" composed of different combinations of geomorphological features to preserve diversity in different forms (Anderson and Ferree 2010, Beier and Brost 2010, Theobald et al. 2015, Magness et al. 2018); (2) areas of low climate velocity and high diversity of microclimates to indicate high macro- and microrefugia potential (Ackerly et al. 2010, Lawler et al. 2015, Carroll et al. 2017); and (3) climate corridors (Carroll et al. 2018) and environmental gradients (Noss 2001) to facilitate distribution shifts.

Climate-smart systematic conservation planning

Although these conservation strategies may be applied on an individual species basis (or independent of species, in the case of species-neutral approaches), multispecies planning processes are likely more efficient. Systematic conservation planning (SCP) involves finding efficient solutions to representative reserve design according to explicit conservation objectives and constraints (Margules and Pressey 2000). In a rapidly changing world with increasing constraints, spatially explicit systematic conservation planning tools such as Zonation (Moilanen 2007) and Marxan (Ball et al. 2009) will be increasingly useful for navigating complex conservation objectives. Beyond the identification of recommended protected areas per se, SCP algorithms and tools are useful for identifying geographic areas of high diversity, abundance, and complementarity among species. These tools can be adapted to consider projected future species distributions and discount for future (and current) uncertainty (Carroll et al. 2010, Kujala et al. 2013, Loyola et al. 2013, Watson et al. 2013). Indeed, they have already been applied to boreal forest vegetation (Powers et al. 2017) and passerine birds (Stralberg et al. 2015*b*, 2018*c*) at a continental scale.

Boreal bird-focused Zonation analyses for the Canadian boreal region (Stralberg et al. 2018*c*) highlighted the large contrasts between conservation priorities based on current versus future projected distributions of birds. However, by considering both current and future (midcentury) projected distributions, conservation priorities changed more subtly, with key northern regions of increased importance under climate change easily identified by difference maps. In that exercise, discounting areas with high landscape disturbance and prediction uncertainty, as well as weighting species according to their population status, helped to constrain solutions and identify areas with consistently high conservation value under multiple different sets of assumptions. Nevertheless, results varied greatly not just according to the time periods considered, but also with respect to conservation objective (diversity or representation) and geographic focus (regional or boreal-wide). This variation reflects in part the broad, dispersed ranges of boreal passerines and lack of clear diversity hotspots for these species; but it also emphasizes the importance of a priori articulation of conservation objectives and constraints (Stralberg et al. 2018*c*).

Indeed, the central challenge with SCP is to identify conservation objectives in a world filled with trade-offs and value judgments, including whether to weight some species and ecosystems higher than others, and whether to focus on long-term refugia or areas of imminent threat. Conservation triage entails selecting species (McIntyre et al. 1992) or populations (McDonald-Madden et al. 2008) to be conserved based on their probability of survival given a certain level of investment. Meeting this objective may mean sacrificing some highly vulnerable species with low probability of survival. Fundamentally, however, triage simply implies a prioritization of actions to maximize conservation benefit (Bottrill et al. 2008).

Our vulnerability-conservation strategy framework for boreal birds can also be used to guide inputs to multispecies conservation planning exercises, and is not intended as a prescriptive one-size-fits-all approach. For example, the relative weighting of species' current vs. future distributions may be informed by species' sensitivity and estimated population trends. In addition, maintenance of climate refugia and protection and conservation of stepping stones may constitute appropriate planning objectives for species with high climate exposure. Nevertheless, given the inherent trade-offs among species, "climate-smart" conservation planning will need to involve a combination of objectives and strategies to accommodate change while efficiently conserving as many species and communities as possible (Hansen et al. 2010, Groves et al. 2012).

CHALLENGES AND APPROACHES TO CONSERVATION OF BOREAL BIRDS IN A CHANGING CLIMATE

In addition to the universal conservation challenges associated with climate change, such as scale and uncertainty (e.g., Root and Schneider 2006, Heller and Zavaleta 2009), we identify three main challenges to conservation of boreal birds in particular: (1) lack of baseline information to detect and attribute past and ongoing changes in boreal bird populations; (2) uncertainties as to the near-term ecological consequences of climate change, especially at the forest stand level; and (3) complexities associated with the large spatial scales at which changes in boreal bird communities will occur, as well as migratory life cycles that span much of the western hemisphere. We detail these three challenges and indicate some of the approaches, including organizational structures and tools, available to address them.

Data gaps in a changing climate call for proactive investments in monitoring

Boreal bird conservation is challenged by a lack of data and resources, especially with respect to migratory species for which knowledge of wintering ground conditions and associated vulnerabilities is scarce. Trend data are often biased and incomplete, and specific habitat requirements and distributional limits are still under study. Boreal bird population trends are uncertain, and reliability is classified as poor for 60% of species (Blancher et al. 2009), with available data not representative of boreal forest geography (Machtans et al. 2014, Desrochers and Drolet 2017) or disturbance levels (Van Wilgenburg et al. 2015). Indeed, the majority of Breeding Bird Survey data come from the southern portion of the biome and sampling efforts are inconsistent across the boreal forest region (Niemi et al. 1998, Schmiegelow and Mönkkönen 2002, Blancher et al. 2009, Machtans et al. 2014). Across all four boreal bird conservation regions (BCRs) in Canada, improving monitoring and filling knowledge gaps are key components of landbird conservation strategies (Environment and Climate Change Canada 2013). As well, the definition and identification of critical habitat for boreal species listed as at-risk under SARA is challenging because of incomplete knowledge of their large breeding range limits, variations in habitat requirements across those large ranges, and the likely role of wintering ground conditions in population declines (Wilson et al. 2018).

These data challenges will be exacerbated by climate change, which is occurring without adequate understanding of historic and current northern distributional limits, population sizes, and population-limiting factors. Detection and attribution of change is particularly challenging without extensive baseline knowledge and sampling effort. For example, some steeply declining species like Blackpoll Warbler and Rusty Blackbird are also among the most data poor. These particular species are projected to experience large contractions in the climatic suitability of their northern forested habitats, and are thus among the most vulnerable from a bioclimatic niche standpoint (Stralberg et al. 2015*a*). Historical declines for Rusty Blackbird coincide with climatic warming and multidecadal climate cycles (McClure et al. 2012), and also with loss and degradation of wintering ground habitat and historical blackbird control programs (Greenberg and Matsuoka 2010). Accordingly, disentangling causes of decline, especially for migratory species, will remain a formidable obstacle in the allocation of scarce conservation resources. A proactive investment in the monitoring of northern species and analysis of historical changes in abundance and distribution will be key to improving conservation outcomes under climate change. Within our framework (Fig. 3), improved information on population trend and status can refine the position of each species within the spectrum of short-term demographic sensitivity, thereby facilitating the decisions about whether species conservation should focus on landscape-level strategies or intensive approaches such as translocation and in situ management.

Uncertainties about future change scenarios can be evaluated with landscape simulation tools

Although detection and causal attribution of historical change are challenging, projections of future boreal climatic niches are fairly consistent, with the climate-change “signal” greater than the model “noise” for most passerine species (Stralberg et al. 2015*a*). Greater uncertainty lies with the rate of change in the boreal region, given the potential for lags in vegetation and other ecosystem responses to climate change, and with species’ ability to keep pace or adapt to changing climates, especially given other anthropogenic disturbances and climate-induced changes in natural disturbance regimes (Boulanger et al. 2017). Vegetation is a key habitat component for boreal birds, but plant species may respond slowly to new conditions as local climates improve or deteriorate. Consequently, although boreal birds are highly vagile and can theoretically track shifting climatic niches, many species will be held back because of delayed response of habitat components to climate change (Vissault 2016). Others may face new competition or predation pressures as southern-associated species advance northward. Such differential species’ responses to climate change are likely to result in altered biotic interactions, leading to unanticipated trajectories of community change (Blois et al. 2013). Boreal bird communities may thus build considerable immigration credit and extinction debt locally, because of time lags in species colonization and extinction (Jackson and Sax 2010). Transient surpluses and deficits in regional bird diversity have important ramifications for conservation. For example, protecting an area where both the current vegetation and local climate are suitable may benefit that species in the near term, but only until the new climate makes the area unsuitable. Particularly uncertain is how long wetland habitats can persist in a state of disequilibrium, given the negative feedbacks that maintain moisture in these systems, especially in larger peatland complexes (Waddington et al. 2015). Differential rates of change in upland and lowland habitats may result in novel landscapes and hydrologic systems, posing challenges for species and managers (Schneider et al. 2016). Therefore, improved ecological forecasts are needed to fully describe the extent of long-term climate exposure for boreal birds, and thus allow us to evaluate for which species and in which regions targeted protection of climate refugia is possible, or whether we will need to rely on broader approaches based on conservation of biophysical diversity.

It is increasingly possible to simulate realistic scenarios of landscape change that can inform focused, short-term management questions at landscape and regional scales. Dynamic simulation models are needed to address short-term, i.e., decadal scale, vegetation trajectories. Landscape simulation frameworks such as LANDIS-II (Scheller and Mladenoff 2004, Scheller et al. 2007) and ALFRESCO (Rupp et al. 2000) include modules to simulate stand-, e.g., forest succession or growth, and landscape-scale, e.g., natural and anthropogenic disturbances, processes at meaningful temporal and spatial scales, allowing for the characterization of wildlife habitats (Rupp et al. 2006). Furthermore, despite significant scale challenges (Cushman et al. 2007), landscape simulation models can be used to simulate the impact of climate change on various ecological processes (Scheller et al. 2007), and may be useful to predict the impacts of changing climate on bird habitats (Marcot et al. 2015, Tremblay et al. 2018, Cadieux et al. 2019). By incorporating spatial legacies of the landscape, future dynamics of forest disturbances, and trajectories of vegetation succession, landscape simulation models can provide more realistic projections of bird habitats than species distribution models alone (De Cáceres et al. 2013, Vissault 2016). Where data permit, species' demographic responses to climate and landscape change can be simulated with metapopulation dynamics models that incorporate species sensitivity and adaptive capacity through modeled vital rates (Keith et al. 2008, Naujokaitis-Lewis et al. 2013, Bonnot et al. 2018). Major developments are still needed to improve the spatial and temporal scope of these models, and address key uncertainties such as peatland and permafrost dynamics. Nonetheless, land-use planning processes will increasingly depend on such approaches to address the complexities of climate change.

Large-scale changes and migratory life cycles require continent-wide collaboration

Finally, given the large areas and high climate velocities found in the boreal region, changes in boreal bird communities will occur at large spatial extents that cross international and other jurisdictional boundaries (Naujokaitis-Lewis 2014, Stralberg et al. 2017). Southern portions of the eastern boreal region are likely to experience colonization by eastern deciduous forest-associated birds (Berteaux et al. 2010), while grassland-associated species will expand into southern parts of the western boreal region (Nixon et al. 2016), raising the issue of what should be considered invasive vs. natural (Boulanger et al. 2016). In the north, discontinuities between the United States (Alaska) and Canada in suitable habitat for a number of boreal species are projected to disappear under future climates, opening up new range expansion corridors through the Yukon and Alaska, with high potential for novel species communities to form (Stralberg et al. 2017). Furthermore, because of the migratory habits of most boreal species, breeding population abundances are linked to conditions on wintering grounds and along migration routes (Marra et al. 1998, Norris and Taylor 2005, Wilson et al. 2018). Annual life cycle analysis has been identified as a major deficit in avian research, and more studies of wintering ground effects and migratory connectivity between breeding and wintering grounds are needed (Faaborg et al. 2010, Marra et al. 2015).

Thus, in a changing climate, the combination of broad-scale range shifts and complex annual cycles will shift management responsibilities and generate new questions about where conservation efforts are most efficiently enacted. This situation increases the need for cross-jurisdictional and interagency collaboration in the management of migratory bird species, and suggests that international organizations such as Partners in Flight (PIF) and associated regional joint ventures will play an important role in the development of climate-smart conservation measures for boreal birds. The PIF Landbird Conservation Plan (Rosenberg et al. 2016) considers climate change and wintering ground factors in its vulnerability assessment, but more research and data are needed to adequately address climate-change threats. Also, given PIF's huge geographic and taxonomic scope, more focused and direct international partnerships, preferably based on migratory connectivity patterns, are needed to conserve migratory boreal birds in the face of climate change. Voluntary, collaborative partnerships such as the Northwest Boreal Landscape Conservation Cooperative in Alaska, British Columbia, and the Yukon and Northwest Territories (https://nwblcc.org/) currently provide among the only opportunities to incorporate the broad-scale challenges of climate change into avian conservation planning in ways that cut across jurisdictional boundaries.

CONCLUSION

The boreal region of North America is expected to experience rapid and dramatic changes in climate over upcoming decades. Resulting ecological changes will lead to a pronounced shift in the conservation landscape. Because of its vast size and the predominance of land undisturbed by industrial activity, the boreal region is particularly well suited to accommodation of change via a large landscape conservation approach, especially in northern reaches. However, prioritization of limited conservation resources will be needed if development continues to increase the human footprint on the landscape. Furthermore, some species may need active intervention to persist in the face of rapid change, especially given additional pressures during nonbreeding portions of the annual cycle. Our vulnerability-adaptation framework accommodates differential vulnerability and provides guidance on strategies to pursue for different species, recognizing that multiple strategies are often needed. Of course it is impossible to prescribe comprehensive, long-term conservation actions for such a wide range of species, and detailed scrutiny of individual species' life histories, habitat associations, and population demographics will be needed to inform specific conservation measures. Although our proposed framework can guide conservation action based on species' individual needs, its implementation will require large-scale, interagency coordination on recovery plans, as well as flexibility and forethought in the management of forests, the designation of critical habitat, and the establishment of protected areas.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1363

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Appendix 1. Climate-projected distributional shifts for North American ecoregions

Data available at: http://doi.org/10.5281/zenodo.1407176 and https://adaptwest.databasin.org/pages/ecoregion-displacement-and-refugia

Climate model projections suggest major North American biome shifts in response to anthropogenic climate change (Rehfeldt et al. 2012). Such shifts could have profound influences on native flora and fauna, many of which would have to move long distances to track their climatic niches. To evaluate potential ecosystem changes at a somewhat finer scale, we projected the change in climate space for level III ecoregions (Commission for Environmental Cooperation 1997) as surrogates for multiple associated species and ecological communities. First, we developed a random forest model (Breiman 2001) to predict ecoregion class from bioclimatic variables (Table A1.1), using 1-km interpolated climate data for the 1969-1990 normal period (Hamann et al. 2013), available at http://adaptwest.databasin.org/pages/adaptwest-climatena.

R Code for this portion follows:

```
library(randomForest)
library(raster)

#eco = project directory
setwd(eco)
datlcc <- read.csv("CECEcoregionSampleLCC.csv")
cececo <- read.csv("CECecoregions.csv")
LCC <- CRS("+proj=lcc +lat_1=49 +lat_2=77 +lat_0=0 +lon_0=-95 +x_0=0 +y_0=0 +
ellps=GRS80 +units=m +no_defs")

#cur = directory containing grids representing derived climate variables
setwd(cur)
clim <- list.files(cur, pattern =".asc$")
curclim<-stack(clim)
temp <- raster(clim[1])
ID <- as.data.frame(rasterToPoints(temp))
names(ID)[3] <- "ID4km"
ID$ID <- row.names(ID)
IDR <- raster(ncols=ncol(temp), nrows=nrow(temp), xmn=xmin(temp), xmx=xmax(te
mp), ymn=ymin(temp), ymx=ymax(temp))
IDRR <- rasterize(as.matrix(ID[,1:2]), IDR, as.numeric(ID[,4]))
curclim <- addLayer(curclim,IDRR)

setwd(eco)
sampleclim<-cbind(datlcc,extract(curclim,as.matrix(cbind(datlcc[,3],datlcc[,4
]))))
sc <- na.omit(sampleclim)
names(sc)[ncol(sc)] <- "IDgrid"
sc$NA_L3CODE <- as.factor(as.character(sc$NA_L3CODE))
lu <- as.data.frame(levels(sc$NA_L3CODE))
lu$level <- row.names(lu)
```

```
names(lu)[1] <- "NA_L3CODE"
write.csv(lu,file="ecoregionlu.csv",row.names=FALSE)

eco.rf <- randomForest(y=sc$NA_L3CODE, x=sc[,5:(ncol(sc)-1)],importance = TRU
E, proximity = TRUE, data=sc)
round(importance(eco.rf), 2)
varImpPlot(eco.rf)
ecocurr <- predict(curclim,eco.rf)
projection(ecocurr) <- LCC
writeRaster(ecocurr,filename="currentlcc.tif",datatype='INT4S',format="GTiff"
,overwrite=TRUE)
curfreq <- freq(ecocurr)
ecolu <- merge(lu,curfreq,by.x="level",by.y="value")
names(ecolu)[3] <- "curr"
```

Table A1.1: Bioclimatic variables used as inputs to random forest models (from Hamann et al. 2013)

MAT: mean annual temperature (°C)
MWMT: mean temperature of the warmest month (°C)
MCMT: mean temperature of the coldest month (°C)
TD: difference between MCMT and MWMT, as a measure of continentality (°C)
MAP: mean annual precipitation (mm)
MSP: mean summer (May to Sep) precipitation (mm)
AHM: annual heat moisture index, calculated as (MAT+10)/(MAP/1000)
SHM: summer heat moisture index, calculated as MWMT/(MSP/1000)
DD0: degree-days below 0°C (chilling degree days)
DD5: degree-days above 5°C (growing degree days)
DD18: degree-days below 18°C
DD18: degree-days above 18°C
NFFD: the number of frost-free days
bFFP: the julian date on which the frost-free period begins
eFFP: the julian date on which the frost-free period ends
FFP: frost-free period
PAS: precipitation as snow (mm)
EMT: extreme minimum temperature over 30 years
EXT: extreme maximum temperature over 30 years
Eref: Hargreave’s reference evaporation
CMD: Hargreave’s climatic moisture index
RH: mean annual relative humidity (%)
Tavewt: winter (Dec to Feb) mean temperature (°C)
Tavesm: summer (Jun to Aug) mean temperature (°C)
PPTwt: winter (Dec to Feb) precipitation (mm)
PPTsm: summer (Jun to Aug) precipitation (mm)

This model was then used to project ecoregions onto future mid-century (2041-2070) and end-of-century (2071-2100) climate conditions. Climate projections were based on 1-km downscaled climate anomalies (Wang et al. 2016) generated by an ensemble of 15 widely-used global climate models (GCM) from the Coupled Model Intercomparison Project, Phase 5 (CMIP5, Taylor et al. 2012), available at http://adaptwest.databasin.org. We used representative concentration pathway (RCP) 8.5, to represent the 21st century conditions that are to be expected without dramatic reductions in greenhouse gas emissions or technological fixes (Fuss et al. 2014). We also evaluated RCP 4.5 to represent a future in which significant emissions reductions are achieved.

The following code generates projections for each representative and time period:

```
fut = directory containing grids representing derived future climate variable
s
rcp <- c("rcp45","rcp85")
time <- c("2050s","2080s")
for (j in rcp) {
    for (k in time) {
            w  <- paste(fut,"NA_ENSEMBLE_",j,"_",k,"_Bioclim_ASCII/",sep="")
            setwd(w)
            futclim <- list.files(w,pattern=".asc$")
            s <-stack(futclim)
            p <- predict(s,eco.rf)
            projection(p) <- LCC
            futfreq <- as.data.frame(freq(p))
        names(futfreq)[2] <- paste(i,j,sep="_")
        ecolu <- merge(ecolu,futfreq,by.x="level",by.y="value")
            writeRaster(p, filename=paste(eco,"pred",j,k,sep="_"),datatype='I
NT4S',format="GTiff", overwrite=TRUE)
            }
    }
```

Results for RCP 4.5 and RCP 8.5 are shown in Figures A1.1 and A1.2, respectively:

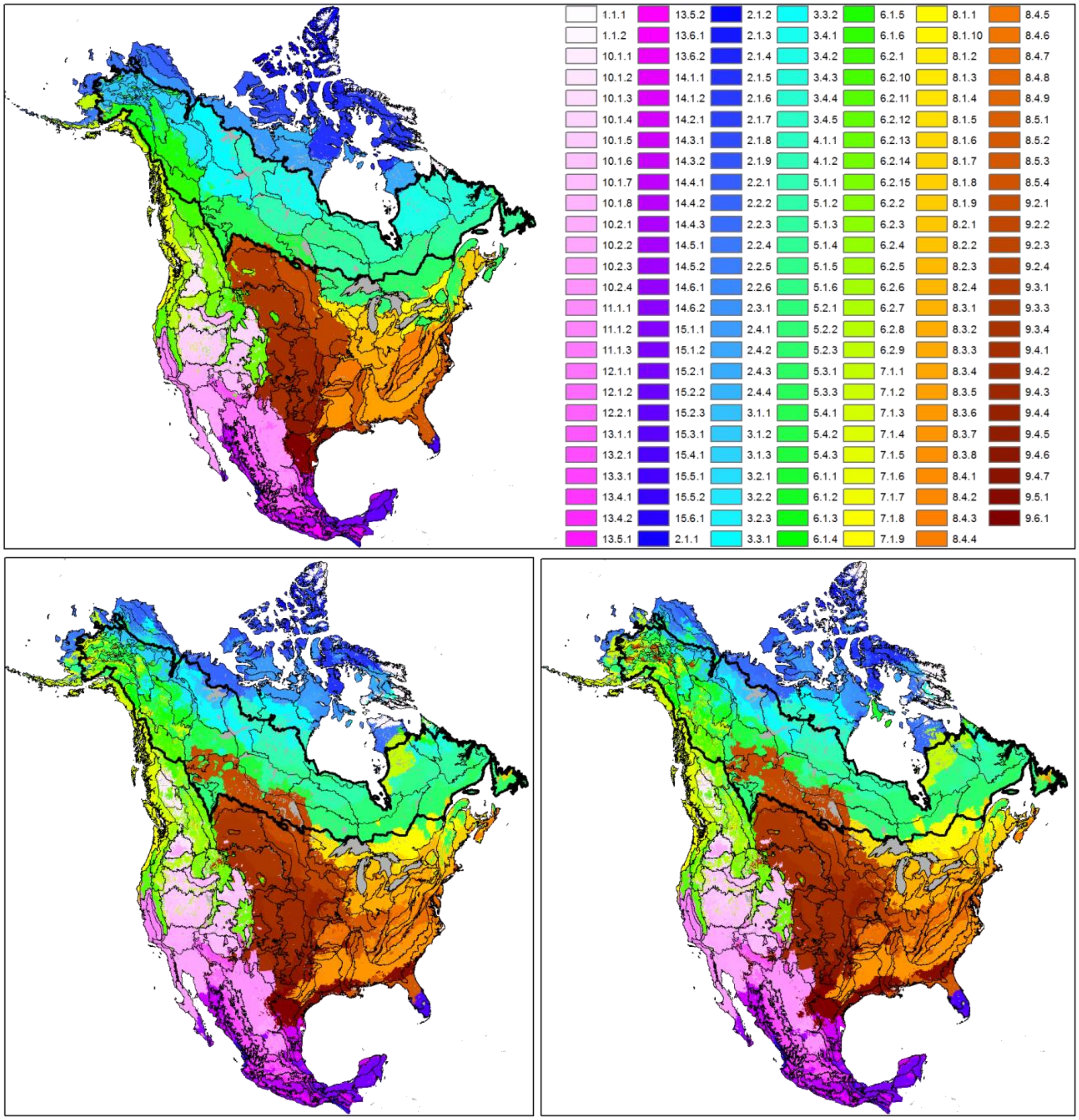

Figure A1.1. *Model-predicted (a) baseline, (b) mid-century, and (c) end-of-century changes in North American ecoregions for RCP 4.5. Boreal, hemi-boreal, and western forested regions are shown in green and blue-green shades; arctic ecoregions are in blue shades; prairie/parkland ecoregions are in brown shades; and temperate forest ecoregions are in yellow and orange shades (see Table A1.1 for full list of ecoregions). Boreal ecoregions are also outlined in black.*

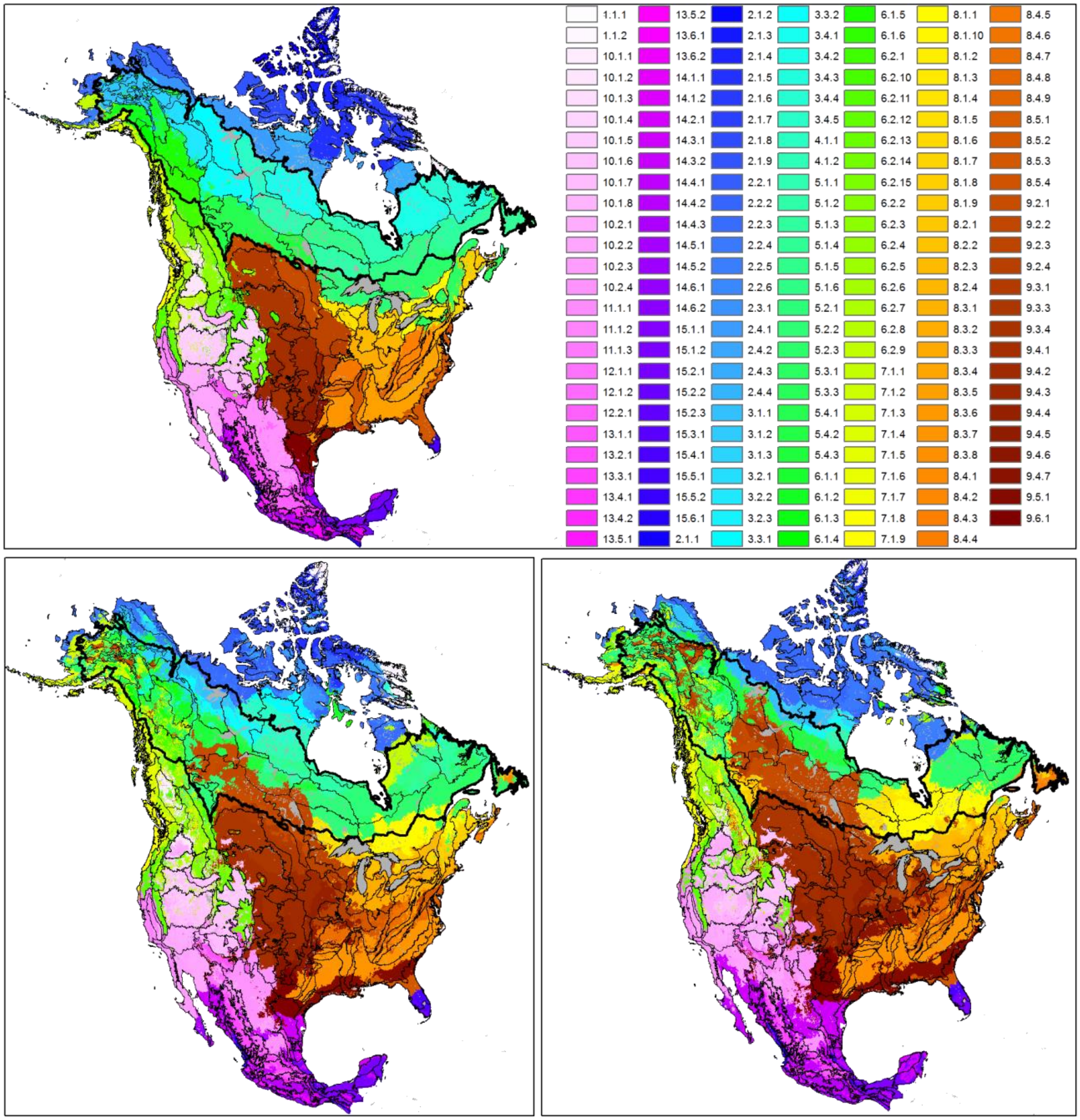

Figure A1.2. *Model-predicted (a) baseline, (b) mid-century, and (c) end-of-century changes in North American ecoregions for RCP 8.5. Boreal, hemi-boreal, and western forested regions are shown in green and blue-green shades; arctic ecoregions are in blue shades; prairie/parkland ecoregions are in brown shades; and temperate forest ecoregions are in yellow and orange shades (see Table A1.1 for full list of ecoregions). Boreal ecoregions are also outlined in black.*

Next, we used the following code to calculate the change in area (16 km2 pixels) for each Level III ecoregion (Table A1.2):

```
groups <- c("pred_rcp45_2050s","pred_rcp45_2080s","pred_rcp85_2050s","pred_rc
p85_2080s")
setwd(eco)
for (i in groups) {
    g <- list.files(eco,pattern=i)
    g1 <- grep(pattern=".tif$",g,value=TRUE)
    m <- raster(g1)
    futfreq <- as.data.frame(freq(m))
    names(futfreq)[2] <- i
    ecolu <- merge(ecolu,futfreq,by.x="level",by.y="value",all.x=TRUE)
    }
ecolu1 <- merge(unique(cececo[,c(2:4)]),ecolu[,2:7],by="NA_L3CODE")
write.csv(ecolu1,file="ecoregion_changesummary.csv",row.names=FALSE)
```

Table A1.2. Model-projected changes by ecoregion (sq km):

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
1.1.1	Ellesmere and Devon Islands Ice Caps	100,895	34,322	12,388	5,563	NA
1.1.2	Baffin and Torngat Mountains	147,147	256,752	278,424	235,507	106,740
10.1.1	Thompson-Okanogan Plateau	79,481	128,181	102,991	93,853	17,523
10.1.2	Columbia Plateau	87,319	128,349	130,511	133,438	92,006
10.1.3	Northern Basin and Range	163,503	52,087	28,000	26,510	2,500
10.1.4	Wyoming Basin	142,375	20,672	10,308	8,748	317
10.1.5	Central Basin and Range	248,329	178,117	161,763	171,074	44,943
10.1.6	Colorado Plateaus	148,135	410,063	445,829	458,570	479,993
10.1.7	Arizona/New Mexico Plateau	170,714	215,623	216,068	215,201	137,227
10.1.8	Snake River Plain	71,248	34,098	22,125	20,400	1,620
10.2.1	Mojave Basin and Range	145,279	178,168	214,764	239,676	559,531
10.2.2	Sonoran Desert	249,917	313,014	308,390	333,780	477,826
10.2.3	Baja Californian Desert	125,247	108,494	133,306	143,065	130,262
10.2.4	Chihuahuan Desert	560,769	634,266	615,488	614,688	512,968
11.1.1	California Coastal Sage, Chaparral, and Oak Woodlands	118,844	119,971	124,429	124,621	148,146
11.1.2	Central California Valley	59,912	55,961	47,599	41,428	920
11.1.3	Southern and Baja California Pine-Oak Mountains	40,794	52,147	49,068	48,033	34,558

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
12.1.1	Madrean Archipelago	119,798	120,764	113,420	110,430	109,247
12.1.2	Piedmonts and Plains with Grasslands, Xeric Shrub, and Oak and Conifer Forests	225,107	159,305	140,803	136,965	67,801
12.2.1	Hills and Interior Plains with Xeric Shrub and Mesquite Low Forest	117,722	115,409	104,551	100,841	60,874
13.1.1	Arizona/New Mexico Mountains	119,795	121,932	125,652	120,830	138,375
13.2.1	Sierra Madre Occidental with Conifer, Oak, and Mixed Forests	203,850	129,997	119,021	106,488	64,358
13.3.1	Sierra Madre Oriental with Conifer, Oak, and Mixed Forests	99,879	112,527	125,093	125,837	102,492
13.4.1	Interior Plains and Piedmonts with Grasslands and Xeric Shrub	30,155	13,136	9,148	8,526	1,347
13.4.2	Hills and Sierras with Conifer, Oak, and Mixed Forests	90,230	56,118	46,624	41,800	21,474
13.5.1	Sierras of Jalisco and Michoacan with Conifer, Oak, and Mixed Forests	45,189	29,437	30,622	27,347	19,195
13.5.2	Sierras of Guerrero and Oaxaca with Conifer, Oak, and Mixed Forests	93,219	56,589	51,279	46,021	21,458
13.6.1	Central American Sierra Madre with Conifer, Oak, and Mixed Forests	24,543	10,157	8,224	8,785	2,653
13.6.2	Chiapas Highlands with Conifer, Oak, and Mixed Forest	47,734	30,717	26,910	25,142	11,528
14.1.1	Coastal Plain with Low Tropical Deciduous Forest	45,021	67,157	58,930	52,306	26,294
14.1.2	Hills and Sierra with Low Tropical Deciduous Forest and Oak Forest	32,934	27,023	22,562	21,273	9,515
14.2.1	Northwestern Yucatan Plain with Low Tropical Deciduous Forest	21,348	31,181	43,435	42,619	120,368
14.3.1	Sinaloa Coastal Plain with Low Thorn Tropical Forest and Wetlands	55,351	184,089	253,772	303,349	693,883
14.3.2	Sinaloa and Sonora Hills and Canyons with Xeric	116,252	161,186	188,683	190,719	386,533

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
	Shrub and Low Tropical Deciduous Forest					
14.4.1	Balsas Depression with Low Tropical Deciduous Forest and Xerophytic Shrub	94,443	142,241	155,449	167,393	217,971
14.4.2	Chiapas Depression with Low Deciduous and Medium Semi-Deciduous Tropical Forest	27,227	13,295	11,191	10,296	9,580
14.4.3	Valleys and Depressions with Xeric Shrub and Low Tropical Deciduous Forest	27,146	38,202	36,891	37,294	35,815
14.5.1	Tehuantepec Canyon and Plain with Low Tropical Deciduous Forest and Low Thorn Tropical Forest	19,737	41,575	43,559	41,086	52,429
14.5.2	South Pacific Hills and Piedmonts with Low Tropical Deciduous Forest	66,703	85,395	99,426	102,297	119,513
14.6.1	Los Cabos Plains and Hills with Low Tropical Deciduous Forest and Xeric Shrub	16,353	42,909	43,769	41,573	23,672
14.6.2	La Laguna Mountains with Oak and Conifer Forest	2,570	1,344	1,185	1,126	501
15.1.1	Gulf of Mexico Coastal Plain with Wetlands and High Tropical Rain Forest	92,436	160,749	153,390	154,527	136,595
15.1.2	Hills with Medium and High Evergreen Tropical Forest	106,764	75,092	81,041	90,784	119,204
15.2.1	Plain with Low and Medium Deciduous Tropical Forest	63,136	123,240	125,750	130,375	93,831
15.2.2	Plain with Medium and High Semi-Evergreen Tropical Forest	46,630	34,045	29,748	22,123	2,786
15.2.3	Hills with High and Medium Semi-Evergreen Tropical Forest	78,883	5,709	6,137	5,979	6,417
15.3.1	Los Tuxtlas Sierra with High Evergreen Tropical Forest	10,762	2,087	1,633	1,416	13,724
15.4.1	Southern Florida Coastal Plain	38,967	74,884	83,614	78,635	40,314

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
15.5.1	Nayarit and Sinaloa Plain with Low Thorn Tropical Forest	9,738	2,650	1,532	1,425	1,651
15.5.2	Jalisco and Nayarit Hills and Plains with Medium Semi-Evergreen Tropical Forest	20,266	42,203	49,771	52,308	75,866
15.6.1	Coastal Plain and Hills with High and Medium-High Evergreen Tropical Forest and Wetlands	20,201	25,035	18,554	17,797	7,691
2.1.1	Sverdrup Islands Lowland	62,199	75	NA	NA	NA
2.1.2	Ellesmere Mountains and Eureka Hills	152,595	20,260	8,298	4,690	NA
2.1.3	Parry Islands Plateau	84,303	6,226	581	303	NA
2.1.4	Lancaster and Borden Peninsula Plateaus	153,401	100,458	57,518	52,380	2
2.1.5	Foxe Uplands	359,792	172,936	212,147	159,876	76,162
2.1.6	Baffin Uplands	148,664	39,067	32,090	28,237	22,447
2.1.7	Gulf of Boothia and Foxe Basin Plains	147,691	94,997	44,196	30,062	4,356
2.1.8	Victoria Island Lowlands	173,942	17,900	1,278	105	NA
2.1.9	Banks Island and Amundsen Gulf Lowlands	160,336	239,188	224,215	194,489	15,065
2.2.1	Arctic Coastal Plain	58,756	95	2,266	5,255	22,959
2.2.2	Arctic Foothills	123,434	235,933	305,118	459,436	119,091
2.2.3	Subarctic Coastal Plains	100,808	229,447	323,128	388,110	1,281,925
2.2.4	Seward Peninsula	59,337	156,920	256,979	281,469	286,106
2.2.5	Bristol Bay-Nushagak Lowlands	63,649	106,118	103,595	106,972	389,553
2.2.6	Aleution Islands	12,993	4,767	2,467	2,058	1,132
2.3.1	Brooks Range/Richardson Mountains	140,490	131,925	94,546	71,108	NA
2.4.1	Amundsen Plains	285,721	491,512	345,481	217,998	44,812
2.4.2	Aberdeen Plains	280,025	34,118	100	NA	NA
2.4.3	Central Ungava Peninsula and Ottawa and Belcher Islands	168,795	136,014	90,049	83,728	57,559
2.4.4	Queen Maud Gulf and Chantrey Inlet Lowlands	112,616	NA	NA	NA	NA
3.1.1	Interior Forested Lowlands and Uplands	154,744	214,494	244,642	302,972	397,504
3.1.2	Interior Bottomlands	147,095	104,970	89,188	60,760	24,020
3.1.3	Yukon Flats	43,564	57,030	38,887	47,545	20,218
3.2.1	Ogilvie Mountains	78,032	84,458	80,561	67,101	40,699
3.2.2	Mackenzie and Selwyn	149,527	32,955	14,823	6,602	NA

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
	Mountains					
3.2.3	Peel River and Nahanni Plateaus	101,694	26,898	15,237	8,576	NA
3.3.1	Great Bear Plains	294,795	199,901	184,944	169,822	NA
3.3.2	Hay and Slave River Lowlands	273,770	329,298	260,311	228,498	88,246
3.4.1	Kazan River and Selwyn Lake Uplands	344,325	49,210	26,918	6,432	NA
3.4.2	La Grande Hills and New Quebec Central Plateau	367,682	55,553	3,009	482	NA
3.4.3	Smallwood Uplands	260,456	72,043	45,379	31,847	8,018
3.4.4	Ungava Bay Basin and George Plateau	124,658	16,561	15,184	14,273	175
3.4.5	Coppermine River and Tazin Lake Uplands	247,484	278,724	261,461	289,089	3,376
4.1.1	Coastal Hudson Bay Lowland	79,752	39,794	39,597	27,964	NA
4.1.2	Hudson Bay and James Bay Lowlands	277,767	56,692	24,743	18,601	4,711
5.1.1	Athabasca Plain and Churchill River Upland	261,634	180,539	172,825	169,140	61,254
5.1.2	Lake Nipigon and Lac Seul Upland	217,842	383,191	334,585	292,786	77,691
5.1.3	Central Laurentians and Mecatina Plateau	302,052	319,010	262,655	245,088	61,726
5.1.4	Newfoundland Island	125,291	159,633	150,097	145,165	141,949
5.1.5	Hayes River Upland and Big Trout Lake	264,910	99,563	68,160	60,244	1,195
5.1.6	Abitibi Plains and Riviere Rupert Plateau	287,990	145,527	142,434	111,390	15,384
5.2.1	Northern Lakes and Forests	297,661	550,438	693,642	770,212	567,791
5.2.2	Northern Minnesota Wetlands	39,487	NA	NA	NA	NA
5.2.3	Algonquin/Southern Laurentians	350,698	443,628	423,668	436,081	460,129
5.3.1	Northern Appalachian and Atlantic Maritime Highlands	213,235	297,005	324,996	338,882	484,216
5.3.3	North Central Appalachians	40,906	5,581	6,484	7,114	15,510
5.4.1	Mid-Boreal Uplands and Peace-Wabaska Lowlands	384,861	384,235	311,499	240,506	112,622
5.4.2	Clear Hills and Western Alberta Upland	147,911	76,236	63,250	52,958	8,624
5.4.3	Mid-Boreal Lowland and Interlake Plain	137,275	232,935	277,233	324,472	401,337

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
6.1.1	Interior Highlands and Klondike Plateau	125,183	86,212	115,739	128,553	19,129
6.1.2	Alaska Range	101,281	86,438	91,774	95,471	35,952
6.1.3	Copper Plateau	25,317	7,840	1,044	376	21
6.1.4	Wrangell and St. Elias Mountains	58,813	35,893	27,452	23,311	14,394
6.1.5	Watson Highlands	215,821	109,456	57,769	43,653	6,952
6.1.6	Yukon-Stikine Highlands/Boreal Mountains and Plateaus	162,769	50,965	43,275	34,939	23,134
6.2.1	Skeena-Omineca-Central Canadian Rocky Mountains	146,470	160,853	135,239	120,210	50,879
6.2.10	Middle Rockies	161,078	55,926	45,646	40,694	18,262
6.2.11	Klamath Mountains	59,290	100,615	113,637	116,533	190,016
6.2.12	Sierra Nevada	56,436	44,004	41,467	40,535	22,943
6.2.13	Wasatch and Uinta Mountains	95,639	85,060	84,545	82,247	40,683
6.2.14	Southern Rockies	146,075	79,895	64,838	51,395	25,539
6.2.15	Idaho Batholith	74,737	76,608	70,690	73,617	53,969
6.2.2	Chilcotin Ranges and Fraser Plateau	113,621	7,374	2,090	1,782	122
6.2.3	Columbia Mountains/Northern Rockies	161,058	252,240	264,915	271,050	274,785
6.2.4	Canadian Rockies	106,010	53,214	33,347	23,701	3,133
6.2.5	North Cascades	41,160	35,151	31,590	30,225	19,980
6.2.6	Cypress Upland	22,463	925	2,326	3,179	3,527
6.2.7	Cascades	48,106	30,917	32,153	30,980	24,273
6.2.8	Eastern Cascades Slopes and Foothills	76,924	50,858	39,265	37,516	10,082
6.2.9	Blue Mountains	81,264	122,265	114,078	110,356	113,839
7.1.1	Ahklun and Kilbuck Mountains	62,628	210,151	224,034	200,959	32,945
7.1.2	Alaska Peninsula Mountains	54,947	28,924	27,208	26,629	22,337
7.1.3	Cook Inlet	31,714	258,308	325,196	360,731	204,427
7.1.4	Pacific Coastal Mountains	109,324	110,053	113,038	112,518	87,051
7.1.5	Coastal Western Hemlock-Sitka Spruce Forests	96,025	167,783	176,032	178,428	163,666
7.1.6	Pacific and Nass Ranges	99,230	133,991	150,169	153,362	154,938
7.1.7	Strait of Georgia/Puget Lowland	48,048	37,542	41,816	44,456	80,267
7.1.8	Coast Range	57,502	111,722	124,460	125,210	146,726

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
7.1.9	Willamette Valley	19,425	4,945	3,615	3,925	12,446
8.1.1	Eastern Great Lakes Lowlands	185,396	399,806	511,228	563,219	801,293
8.1.10	Erie Drift Plain	54,959	3,115	593	373	182
8.1.2	Lake Erie Lowland	71,512	71,944	50,905	53,404	21,297
8.1.3	Northern Allegheny Plateau	56,906	1,487	534	560	23,971
8.1.4	North Central Hardwood Forests	107,373	103,169	108,931	101,597	237,007
8.1.5	Driftless Area	56,904	27,122	6,541	9,722	56,230
8.1.6	Southern Michigan/Northern Indiana Drift Plains	81,430	23,829	17,145	13,253	417
8.1.7	Northeastern Coastal Zone	61,604	230,818	254,436	245,976	200,520
8.1.8	Acadian Plains and Hills	111,308	40,773	46,764	37,862	28,274
8.1.9	Maritime Lowlands	46,701	13,691	12,593	8,969	8,838
8.2.1	Southeastern Wisconsin Till Plains	41,043	42,756	43,861	32,257	90,658
8.2.2	Huron/Erie Lake Plains	54,469	85,966	67,329	61,276	28,067
8.2.3	Central Corn Belt Plains	92,678	73,997	100,504	140,394	250,957
8.2.4	Eastern Corn Belt Plains	87,010	39,615	33,682	36,241	8,857
8.3.1	Northern Piedmont	42,573	170,005	167,343	153,662	53,715
8.3.2	Interior River Valleys and Hills	131,437	373,661	383,500	408,178	433,738
8.3.3	Interior Plateau	145,391	60,581	57,552	55,578	50,507
8.3.4	Piedmont	199,405	24,230	20,990	15,243	2,166
8.3.5	Southeastern Plains	304,687	9,091	6,755	7,501	3,549
8.3.6	Mississippi Valley Loess Plains	85,927	13,701	11,629	9,952	22,612
8.3.7	South Central Plains	178,978	701,415	692,767	704,770	611,455
8.3.8	East Central Texas Plains	62,055	166,974	215,681	249,240	433,078
8.4.1	Ridge and Valley	85,618	29,098	16,038	10,560	2,334
8.4.2	Central Appalachians	89,927	51,069	40,889	44,792	66,604
8.4.3	Western Allegheny Plateau	83,575	8,479	4,804	3,360	15
8.4.4	Blue Ridge	51,004	33,856	35,301	35,072	66,437
8.4.5	Ozark Highlands	109,761	76,718	42,713	26,546	1,981
8.4.6	Boston Mountains	24,203	60,902	63,537	39,483	5,440
8.4.7	Arkansas Valley	38,145	140,421	168,122	184,531	89,087
8.4.8	Ouachita Mountains	30,471	87,982	86,472	65,818	32,104
8.4.9	Southwestern Appalachians	61,141	14,531	10,304	8,422	5,821
8.5.1	Middle Atlantic Coastal	114,545	16,124	25,858	17,272	22,159

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
	Plain					
8.5.2	Mississippi Alluvial Plain	149,150	337,261	334,998	319,597	370,833
8.5.3	Southern Coastal Plain	186,085	95,570	86,825	80,677	60,148
8.5.4	Atlantic Coastal Pine Barrens	20,263	22,794	35,426	36,084	99,628
9.2.1	Aspen Parkland/Northern Glaciated Plains	318,674	466,186	519,631	546,675	837,779
9.2.2	Lake Manitoba and Lake Agassiz Plain	106,437	403,991	440,897	460,192	452,954
9.2.3	Western Corn Belt Plains	218,212	262,681	224,934	223,667	209,025
9.2.4	Central Irregular Plains	134,204	204,341	223,959	238,121	321,836
9.3.1	Northwestern Glaciated Plains	366,518	251,564	231,664	245,870	563,860
9.3.3	Northwestern Great Plains	368,298	448,245	460,729	457,994	390,148
9.3.4	Nebraska Sand Hills	82,506	46	27	60	4,846
9.4.1	High Plains	292,621	434,924	488,715	495,241	467,915
9.4.2	Central Great Plains	272,514	356,382	397,340	404,906	632,890
9.4.3	Southwestern Tablelands	239,595	364,196	362,126	335,141	293,115
9.4.4	Flint Hills	48,028	113,851	146,532	151,212	154,204
9.4.5	Cross Timbers	108,973	104,547	117,198	141,406	379,103
9.4.6	Edwards Plateau	111,195	113,999	97,552	80,404	27,236
9.4.7	Texas Blackland Prairies	65,484	90,892	78,487	87,808	204,468
9.5.1	Western Gulf Coastal Plain	115,252	270,442	323,841	345,851	502,966
9.6.1	Southern Texas Plains/Interior Plains and Hills with Xerophytic Shrub and Oak Forest	192,562	253,019	291,794	296,432	391,367

We also specifically summarized changes for boreal ecoregions (4.1, 5.4, 5.1, 3.4, 3.3, 3.2, 3.1, and 6.1) (Table A1.3):

Table A1.3. Model-projected changes by boreal ecoregion (sq km):

NA_L3CODE	NA_L3NAME	curr	rcp45_2050s	rcp45_2080s	rcp85_2050s	rcp85_2080s
3.1.1	Interior Forested Lowlands and Uplands	154,744	214,494	244,642	302,972	397,504
3.1.2	Interior Bottomlands	147,095	104,970	89,188	60,760	24,020
3.1.3	Yukon Flats	43,564	57,030	38,887	47,545	20,218
3.2.1	Ogilvie Mountains	78,032	84,458	80,561	67,101	40,699
3.2.2	Mackenzie and Selwyn Mountains	149,527	32,955	14,823	6,602	NA
3.2.3	Peel River and Nahanni	101,694	26,898	15,237	8,576	NA

	Plateaus				
3.3.1	Great Bear Plains	294,795	199,901	184,944	169,822	NA
3.3.2	Hay and Slave River Lowlands	273,770	329,298	260,311	228,498	88,246
3.4.1	Kazan River and Selwyn Lake Uplands	344,325	49,210	26,918	6,432	NA
3.4.2	La Grande Hills and New Quebec Central Plateau	367,682	55,553	3,009	482	NA
3.4.3	Smallwood Uplands	260,456	72,043	45,379	31,847	8,018
3.4.4	Ungava Bay Basin and George Plateau	124,658	16,561	15,184	14,273	175
3.4.5	Coppermine River and Tazin Lake Uplands	247,484	278,724	261,461	289,089	3,376
4.1.1	Coastal Hudson Bay Lowland	79,752	39,794	39,597	27,964	NA
4.1.2	Hudson Bay and James Bay Lowlands	277,767	56,692	24,743	18,601	4,711
5.1.1	Athabasca Plain and Churchill River Upland	261,634	180,539	172,825	169,140	61,254
5.1.2	Lake Nipigon and Lac Seul Upland	217,842	383,191	334,585	292,786	77,691
5.1.3	Central Laurentians and Mecatina Plateau	302,052	319,010	262,655	245,088	61,726
5.1.4	Newfoundland Island	125,291	159,633	150,097	145,165	141,949
5.1.5	Hayes River Upland and Big Trout Lake	264,910	99,563	68,160	60,244	1,195
5.1.6	Abitibi Plains and Riviere Rupert Plateau	287,990	145,527	142,434	111,390	15,384
5.4.1	Mid-Boreal Uplands and Peace-Wabaska Lowlands	384,861	384,235	311,499	240,506	112,622
5.4.2	Clear Hills and Western Alberta Upland	147,911	76,236	63,250	52,958	8,624
5.4.3	Mid-Boreal Lowland and Interlake Plain	137,275	232,935	277,233	324,472	401,337
6.1.1	Interior Highlands and Klondike Plateau	125,183	86,212	115,739	128,553	19,129
6.1.2	Alaska Range	101,281	86,438	91,774	95,471	35,952
6.1.3	Copper Plateau	25,317	7,840	1,044	376	21
6.1.4	Wrangell and St. Elias Mountains	58,813	35,893	27,452	23,311	14,394
6.1.5	Watson Highlands	215,821	109,456	57,769	43,653	6,952
6.1.6	Yukon-Stikine Highlands/Boreal Mountains and Plateaus	162,769	50,965	43,275	34,939	23,134

This translates into 14% and 42% losses of boreal climate space by 2041-2070 and 2071-2100, respectively, based on RCP 8.5; or 9% and 13% losses based on RCP 4.5

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Appendix 2. Components of climate-change vulnerability for 54 boreal-breeding passerine species. Long-term trend values are based on Canada-wide BBS % change for 2002-2015 (Environment and Climate Change Canada 2017). For all species but Bicknell's Thrush (BITH), projected future change values are based on mid-century (2041-2070) mean potential density estimates for the North American boreal region based on the A2 emission scenario and four global climate models (GCM) (Stralberg et al. 2015b). For BITH, the future projection is based on a model from Lambert and McFarland (2004) applied to RCP 4.5 GCM projections by Cadieux and Tremblay (unpublished).

Species Code	Common Name	Genus	Species	Migratory Status	Trend	Future Change
AMRE	American Redstart	*Setophaga*	*ruticilla*	Neotropical migrant	-0.071	0.76
BAWW	Black-and-white Warbler	*Mniotilta*	*varia*	Neotropical migrant	-0.226	0.71
BBWA	Bay-breasted Warbler	*Dendroica*	*castanea*	Neotropical migrant	-0.193	-0.1
BCCH	Black-capped Chickadee	*Poecile*	*atricapillus*	Resident	0.729	1.04
BHVI	Blue-headed Vireo	*Vireo*	*solitarius*	Short distance migrant	3.68	0.3
BITH	Bicknell's Thrush	*Catharus*	*bicknelli*	Neotropical migrant	-5.23	-0.44
BLBW	Blackburnian Warbler	*Dendroica*	*fusca*	Neotropical migrant	0.671	1.32
BLJA	Blue Jay	*Cyanocitta*	*cristata*	Short distance migrant	1.09	2.08
BLPW	Blackpoll Warbler	*Dendroica*	*striata*	Neotropical migrant	-4.23	-0.44
BOCH	Boreal Chickadee	*Poecile*	*hudsonicus*	Resident	0.261	-0.02
BRCR	Brown Creeper	*Certhia*	*americana*	Short distance migrant	0.867	-0.05
BTNW	Black-throated Green Warbler	*Dendroica*	*virens*	Neotropical migrant	0.284	0.84
CAWA	Canada Warbler	*Wilsonia*	*canadensis*	Neotropical migrant	-2.21	0.53
CEDW	Cedar Waxwing	*Bombycilla*	*cedrorum*	Short distance migrant	0.452	0.55
CMWA	Cape May Warbler	*Dendroica*	*tigrina*	Neotropical migrant	0.979	-0.11
CONW	Connecticut Warbler	*Oporornis*	*agilis*	Neotropical migrant	-1.89	-0.16
CORA	Common Raven	*Corvus*	*corax*	Resident	2.54	0.03
CORE	Common Redpoll	*Carduelis*	*flammea*	Nomadic	0.141	-0.4
EVGR	Evening Grosbeak	*Coccothraustes*	*vespertinus*	Nomadic	-5.27	0.56
FOSP	Fox Sparrow	*Passerella*	*iliaca*	Short distance migrant	0.852	-0.45
GCKI	Golden-crowned Kinglet	*Regulus*	*satrapa*	Short distance migrant	-0.563	0.27

Species Code	Common Name	Genus	Species	Migratory Status	Trend	Future Change
GCTH	Gray-cheeked Thrush	*Catharus*	*minimus*	Neotropical migrant	-2.65	-0.5
GRAJ	Gray Jay	*Perisoreus*	*canadensis*	Resident	-0.422	-0.25
HETH	Hermit Thrush	*Catharus*	*guttatus*	Short distance migrant	0.823	-0.07
LEFL	Least Flycatcher	*Empidonax*	*minimus*	Neotropical migrant	-1.58	0.37
MAWA	Magnolia Warbler	*Dendroica*	*magnolia*	Neotropical migrant	1.13	0.25
MOWA	Mourning Warbler	*Oporornis*	*philadelphia*	Neotropical migrant	-1.23	1
NAWA	Nashville Warbler	*Vermivora*	*ruficapilla*	Neotropical migrant	0.322	0.72
NOWA	Northern Waterthrush	*Seiurus*	*noveboracensis*	Neotropical migrant	1.22	-0.18
OCWA	Orange-crowned Warbler	*Vermivora*	*celata*	Short distance migrant	0.722	-0.19
OSFL	Olive-sided Flycatcher	*Contopus*	*cooperi*	Neotropical migrant	-2.63	-0.1
OVEN	Ovenbird	*Seiurus*	*aurocapillus*	Neotropical migrant	-0.052	0.62
PAWA	Palm Warbler	*Dendroica*	*palmarum*	Short distance migrant	4.88	-0.52
PHVI	Philadelphia Vireo	*Vireo*	*philadelphicus*	Neotropical migrant	2.46	0.23
PIGR	Pine Grosbeak	*Pinicola*	*enucleator*	Nomadic	-2.69	-0.17
PISI	Pine Siskin	*Carduelis*	*pinus*	Nomadic	-2.62	0.27
PUFI	Purple Finch	*Carpodacus*	*purpureus*	Short distance migrant	-1.19	0.55
RBGR	Rose-breasted Grosbeak	*Pheucticus*	*ludovicianus*	Neotropical migrant	-0.885	0.91
RBNU	Red-breasted Nuthatch	*Sitta*	*canadensis*	Resident	1.45	0.56
RCKI	Ruby-crowned Kinglet	*Regulus*	*calendula*	Short distance migrant	0.551	-0.17
REVI	Red-eyed Vireo	*Vireo*	*olivaceus*	Neotropical migrant	0.832	0.96
RUBL	Rusty Blackbird	*Euphagus*	*carolinus*	Short distance migrant	-2.56	-0.37
SWTH	Swainson's Thrush	*Catharus*	*ustulatus*	Neotropical migrant	-0.114	0.02
TEWA	Tennessee Warbler	*Vermivora*	*peregrina*	Neotropical migrant	0.844	-0.25
VATH	Varied Thrush	*Ixoreus*	*naevius*	Short distance migrant	-1.46	0.08
WETA	Western Tanager	*Piranga*	*ludoviciana*	Neotropical migrant	1.45	0.06
WEWP	Western Wood-Pewee	*Contopus*	*sordidulus*	Neotropical migrant	-2	0.12
WIWA	Wilson's Warbler	*Wilsonia*	*pusilla*	Neotropical migrant	-0.486	-0.14
WTSP	White-throated Sparrow	*Zonotrichia*	*albicollis*	Short distance migrant	-0.589	0.12

Species Code	Common Name	Genus	Species	Migratory Status	Trend	Future Change
WWCR	White-winged Crossbill	*Loxia*	*leucoptera*	Nomadic	1.79	-0.29
YBFL	Yellow-bellied Flycatcher	*Empidonax*	*flaviventris*	Neotropical migrant	3.21	-0.1

Appendix 3. Velocity-based macrorefugia for boreal passerine birds

Data available at: http://doi.org/10.5281/zenodo.1299880

Climate refugia—areas of species persistence under climate change—may vary in proximity to a species' current distribution, with major implications for their conservation value. Thus, the concept of climate velocity (Loarie et al. 2009)—the speed at which an organisms must migrate to keep pace with climate change— is useful to compare and evaluate refugia. Climate velocity metrics have been used to identify species and ecosystems that are most vulnerable to future climate change, as indicated by high climate velocity (Loarie et al. 2009, Burrows et al. 2011, Serra-Diaz et al. 2014). Using new methods, both forward and backward velocity can be calculated, providing complementary information about patio-temporal responses to climate change (Hamann et al. 2014, Carroll et al. 2015). In particular, backward velocity calculations—and the corresponding distance traveled to reach a given future suitable climate—can be used to identify areas of high potential refugium value for a given time period and species (Stralberg et al. 2018). Velocity-based refugia for a given species represent areas of future climatic suitability that are in close geographic proximity to currently occupied areas, i.e., where chances of rapid colonization (or persistence) in response to climate change is high.

Refugia layers were calculated for 53 forest-associated species (Table A3.1) based on spatial density models for baseline and projected future climates (Stralberg et al. 2015a, Stralberg et al. 2015b). Mean density estimates within 4-km grid cells were converted to binary estimates of suitable core habitat, defined as the grid cells where the model-predicted density exceeded the mean baseline (1961-1990) predicted density for that species within the study area (Stralberg et al. 2015a), defined here as Brandt's (2009) boreal region of North America. Core habitat predictions were then used to calculate backward biotic velocity (Carroll et al. 2015) for each species, based on four different CMIP3 (Meehl et al. 2007) global climate models (MPI ECHAM5, CCCMA CGCM3.1, GFDL CM2.1, and HadGEM1), two different time periods (2041-2070 and 2071-2100), and a high-end, business-as-usual emissions scenario (SRES A2, IPCC 2001)[1]. For each species / climate model / time period combination *i*, we calculated the distance (d_{ij}) in km from each future distribution pixel *j* to the nearest current distribution pixel. The assumption was that longer distances (larger backward velocity values) represented lower refugia potential, and the primary objective was to rank refugia potential by distance.

From these distance / time (velocity) layers, we applied the refugia metric described in Stralberg et al. (2018), which uses a non-linear distance decay function to down-weight larger distances, given the low probability of natural dispersal and colonization success. The decay function is based on a fat-tailed dispersal kernel, which accommodates rare long-distance tree dispersal events, and has been invoked to explain the rapid post-glacial recolonization of trees across

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[1] CMIP3 model projections have not been shown to differ substantially in magnitude or spatial pattern from those of newer CMIP5 models (Knutti and Sedláček 2012).

northern North America at the end of the Late Pleistocene age (Clark et al. 1998). Although birds can disperse much farther and faster due to their ability to fly, we assumed that bird dispersal would be limited by tree dispersal.

The standardized index of refugium potential, R_{ij}, is defined as the negative exponential portion of a fat-tailed dispersal kernel (Clark et al. 1998):

$$\mathrm{R_{ij}} = \exp\left(-\left|\frac{\mathrm{d_{ij}}}{\alpha}\right|^{c}\right),$$

where $c = 0.5$ (Clark et al. 1998) and $\alpha = 8.333$ (the value resulting in a mean dispersal distance of 50 km per century, based on the first moment of the dispersal kernel). The index has a value of 1 when $d_{ij} = 0$ (i.e., for *in situ* refugia), rapidly declines to a value of 0.09 at 50 km, and then slowly converges toward 0.

For each time period, standardized refugia index values were averaged across the four GCMs to yield an ensemble index for each species. Pixels with no suitable niche space for a given GCM were converted to zero to down-weight their importance in subsequent ensemble calculations.

Two version of a multi-species index were generated: (1) an unweighted simple average across all 53 species, and (2) a version weighted by species' projected distributional responses to climate change, following methods in Stralberg et al. (2018). For the weighted multi-species refugia index, each species' ensemble refugia index was divided by the mean proportional change in total potential distribution area (future/present area) for that species (see Stralberg et al. 2015b) and then averaged across all species. For species with projected future decreases in suitable niche space, proportional change values were truncated at 0.5, yielding a maximum weighted refugia value of 2. For any given species, in both the weighted and unweighted versions, pixels with no suitable niche space during the baseline period or in the future under any of the four GCMs were omitted in the species averaging process so as to prevent the index from being driven primarily by species richness; zero values were assigned where suitable baseline niche space was not projected to be occupied in the future. R code is available on GitHub at https://github.com/dstralberg/Refugia/blob/master/StralbergEtAlGEB2018Macorefugia.Rmd.

The weighted refugia index for 53 boreal songbird species under for the 2041-2070 time period ranged from 0.032 (1st percentile) to 0.779 (99th percentile), with a median of 0.200 and an even distribution (Table A3.2). The highest weighted refugia values (99th percentile) were located in the mountains of British Columbia and along the Labrador coast; values in the 90th percentile were found throughout western mountains and in northern and eastern Quebec, and Newfoundland and Labrador (Figure A3.1a). In general, the lowest weighted refugia values (10th percentile) were found in western interior boreal regions. Weighted refugia values were lower for the 2071-2100 time period, ranging from 0.002 to 0.675 (Table A3.2) but followed similar spatial patterns (Figure A3.1b). Unweighted refugia index values ranged from 0.006 and 0.001 (1st percentile) to 0.421 and 0.297 (99th percentile) for the 2041-2070 and 2071-2100 time periods, respectively (Table A3.2, Figure A3.2). The highest unweighted refugia values were found in central Ontario and Québec, and northern Newfoundland for the 2041-2070 period, but were concentrated mostly along the Labrador coast by the 2071-2100 period.

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Table A3.1. 53 forest-associated species included in refugia index

Code	Species common name (*scientific name*)
AMRE	American Redstart (*Setophaga ruticilla*)
BAWW	Black-and-white Warbler (*Mniotilta varia*)
BBWA	Bay-breasted Warbler (*Setophaga castanea*)
BCCH	Black-capped Chickadee (*Poecile atricapillus*)
BHVI	Blue-headed Vireo (*Vireo solitarius*)
BLWA	Blackburnian Warbler (*Setophaga fusca*)
BLJA	Blue Jay (*Cyanocitta cristata*)
BLPW	Blackpoll Warbler (*Setophaga striata*)
BOCH	Boreal Chickadee (*Poecile hudsonicus*)
BRCR	Brown Creeper (*Certhia americana*)
BTNW	Black-throated Green Warbler (*Setophaga virens*)
CAWA	Canada Warbler (*Cardellina canadensis*)
CEDW	Cedar Waxwing (*Bombycilla cedrorum*)
CMWA	Cape May Warbler (*Setophaga tigrina*)
CONW	Connecticut Warbler (*Oporornis agilis*)
CORA	Common Raven (*Corvus corax*)
CORE	Common Redpoll (*Acanthis flammea)*
DEJU	Dark-eyed Junco (*Junco hyemalis*)
EVGR	Evening Grosbeak (*Coccothraustes vespertinus*)
FOSP	Fox Sparrow (*Passerella iliaca*)
GCKI	Golden-crowned Kinglet (*Regulus satrapa*)
GCTH	Gray-cheeked Thrush (*Catharus minimus*)
GRAJ	Gray Jay (*Perisoreus canadensis*)
HETH	Hermit Thrush (*Catharus guttatus*)
LEFL	Least Flycatcher (*Empidonax minimus*)
MAWA	Magnolia Warbler (*Setophaga magnolia*)
MOWA	Mourning Warbler (*Geothlypis philadelphia*)
NAWA	Nashville Warbler (*Oreothlypis ruficapilla*)
NOWA	Northern Waterthrush (*Parkesia noveboracensis*)
OCWA	Orange-crowned Warbler (*Oreothlypis celata*)
OSFL	Olive-sided Flycatcher (*Contopus cooperi*)
OVEN	Ovenbird (*Seiurus aurocapilla*)
PAWA	Palm Warbler (*Setophaga palmarum*)
PHVI	Philadelphia Vireo (*Vireo philadelphicus*)
PIGR	Pine Grosbeak (*Pinicola enucleator*)
PISI	Pine Siskin (*Spinus pinus*)
PUFI	Purple Finch (*Carpodacus purpureus*)
RBGR	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)

Code	Species common name (*scientific name*)
RBNU	Red-breasted Nuthatch (*Sitta canadensis*)
RCKI	Ruby-crowned Kinglet (*Regulus calendula*)
REVI	Red-eyed Vireo (*Vireo olivaceus*)
RUBL	Rusty Blackbird (*Euphagus carolinus*)
SWTH	Swainson's Thrush (*Catharus ustulatus*)
TEWA	Tennessee Warbler (*Oreothlypis peregrina*)
VATH	Varied Thrush (*Ixoreus naevius*)
WETA	Western Tanager (*Piranga ludoviciana*)
WEWP	Western Wood-Pewee (*Contopus sordidulus*)
WIWA	Wilson's Warbler (*Cardellina pusilla*)
WIWR	Winter Wren (*Troglodytes hiemalis*)
WTSP	White-throated Sparrow (*Zonotrichia albicollis*)
WWCR	White-winged Crossbill (*Loxia leucoptera*)
YBFL	Yellow-bellied Flycatcher (*Empidonax flaviventris*)
YRWA	Yellow-rumped Warbler (*Setophaga coronata*)

Table A3.2. Percentile values of velocity-based multi-species refugia indices for 53 boreal-breeding songbird species.

	1%	10%	25%	50%	75%	90%	99%
2050s, weighted	0.032	0.243	0.317	0.399	0.484	0.589	0.779
2080s, weighted	0.002	0.090	0.137	0.200	0.281	0.386	0.675
2050s, unweighted	0.006	0.108	0.159	0.218	0.292	0.358	0.421
2080s, unweighted	0.001	0.055	0.083	0.123	0.185	0.241	0.297

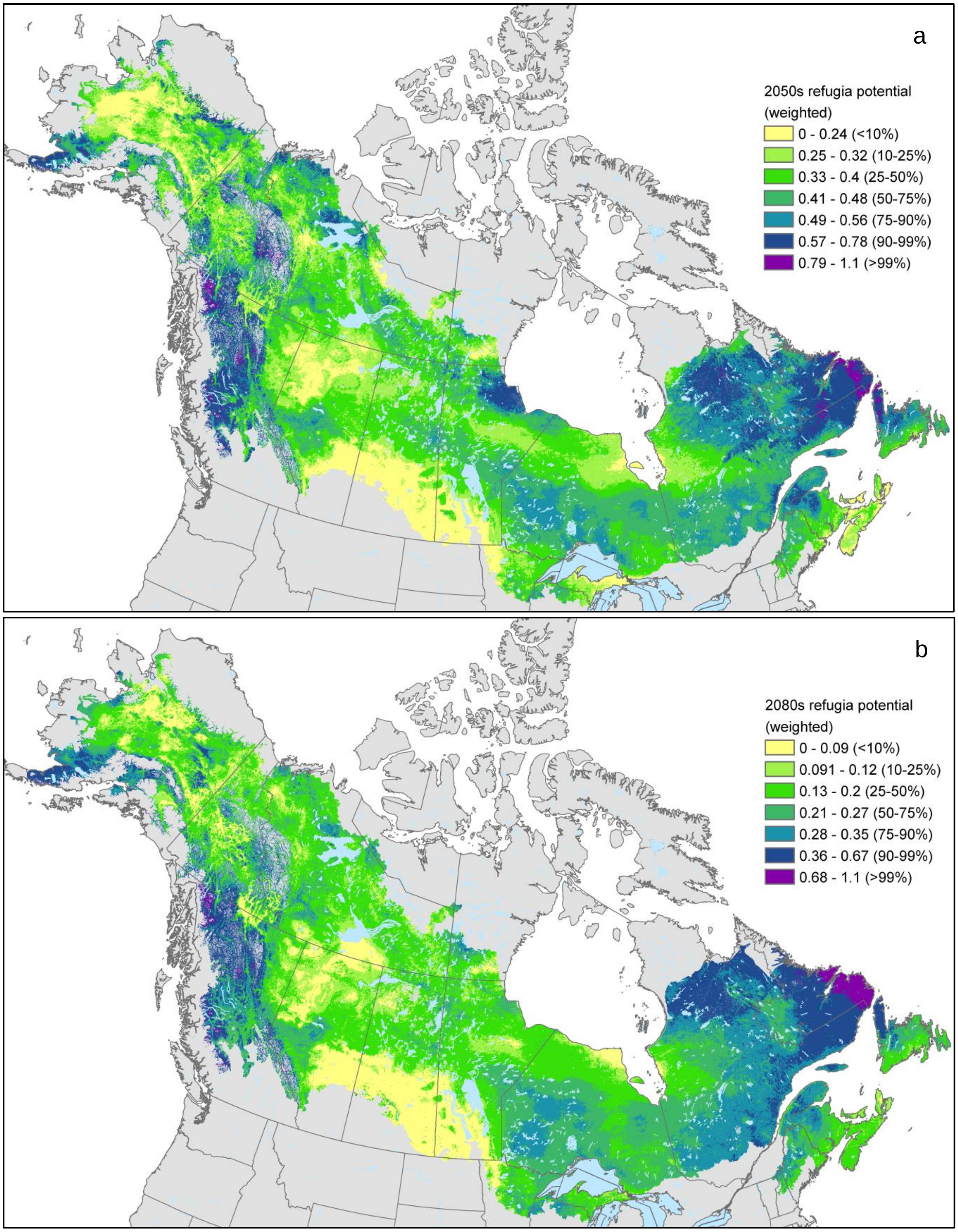

Figure A3.1. Multi-species refugia indices for (a) 2041-2070 and (b) 2071-2100, averaged across 53 forest-associated boreal-breeding species, weighted by species' projected distributional responses to climate change and mapped by percentiles. Areas covered in rock or snow/ice according to 30-m 2010 North American landcover data have been masked out.

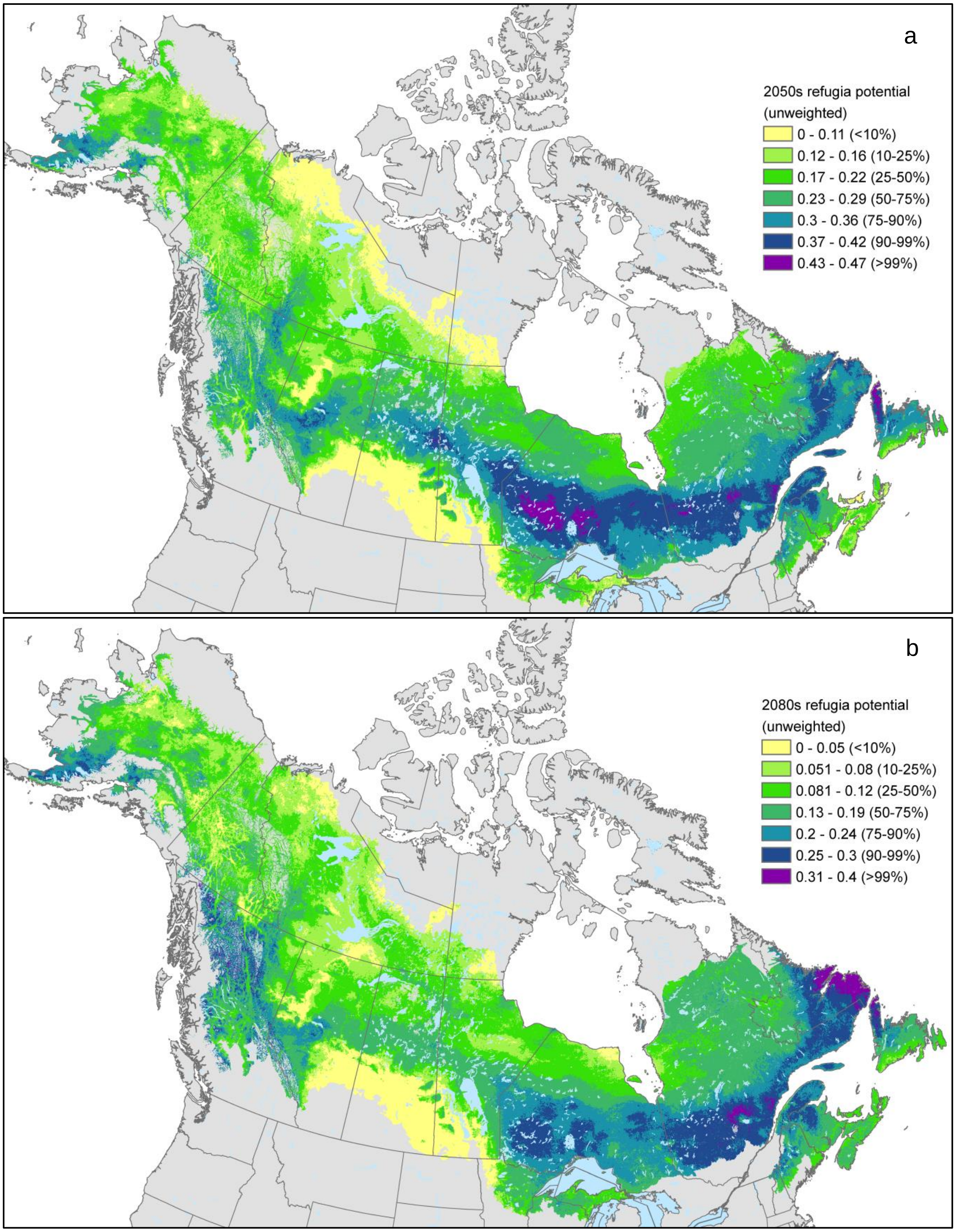

Figure A3.2. Multi-species refugia indices for (a) 2041-2070 and (b) 2071-2100, averaged across 53 forest-associated boreal-breeding species mapped by percentiles. Areas covered in rock or snow/ice according to 30-m 2010 North American landcover data have been masked out.