

Macrorefugia for North American trees and songbirds: Climatic limiting factors and multi-scale topographic influences

Diana Stralberg¹  | Carlos Carroll²  | John H. Pedlar³ | Chad B. Wilsey⁴ | Daniel W. McKenney³ | Scott E. Nielsen¹ 

¹Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

²Klamath Center for Conservation Research, Orleans, California

³Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste Marie, Ontario, Canada

⁴National Audubon Society, San Francisco, California

Correspondence

Diana Stralberg, Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, Alberta T6G 2H1, Canada.
Email: stralber@ualberta.ca

Funding information

Wilburforce Foundation; MacArthur Foundation

Editor: Marie-Josée Fortin

Abstract

Aim: To inform conservation planning in the face of climate change, our objectives were to map spatial patterns of tree and songbird macrorefugia; to identify climatic limiting factors by region and taxonomic group; and to quantify multi-scale topographic components of end-of-century biotic refugia.

Location: United States and Canada outside the far north.

Time period: End of the 21st century.

Major taxa studied: Trees and songbirds.

Methods: We used species distribution models for 324 trees and 268 songbirds to develop a macrorefugia index using species-specific climate velocity. Maps of multispecies refugia potential were developed for each taxonomic/functional group and quantile regression was used to identify climatic limiting factors and relationships with multi-scale topographic variables.

Results: End-of-century macrorefugia for both trees and songbirds were concentrated in western mountains and, to a lesser extent, in north-eastern coastal regions. For the highest-value refugia, precipitation was generally most limiting in the north, and warm temperatures and moisture availability were limiting in the south. Tree refugia were more limited by precipitation and moisture, while songbird refugia were more limited by temperature. Upper-percentile refugia, but not median values, were well explained by topographic conditions. Songbird refugia were strongly associated with elevation, while coastal proximity and landform composition (particularly headwaters) were important for both groups. There was a general lack of concordance between patterns of current species richness and future climate refugia.

Main conclusions: Macrorefugia patterns are partly explained by steep elevational or latitudinal temperature gradients and/or moderate climates, such as coastal regions. However, climatic limiting factors for these refugia suggest contrasts in the ecological processes governing warm-end range limits for different taxa in different regions. Our framework can be applied to other regions, taxa, and time periods to generate and explain biologically meaningful indices of macrorefugia for conservation planning.

KEYWORDS

biotic refugia, climate change, climate velocity, conservation planning, environmental limiting factors, macrorefugia, passerines, quantile regression, woody plants

1 | INTRODUCTION

Conservation in the face of climate change is inherently complex, as it involves the identification of priority areas to protect a wide range of species with disparate habitat characteristics, shifting geographically over time. Given these trade-offs, 'climate-smart' conservation planning will inevitably involve a combination of strategies and objectives to accommodate change, while efficiently conserving as many species and communities as possible (Groves et al., 2012). One such planning component involves the identification of climate refugia, that is, regions of relative stability for multiple species under climate change (Ashcroft, 2010; Keppel et al., 2012). Whether they persist long term or serve as stepping stones for population migration (Hannah et al., 2014), refugia represent areas of high conservation value in a changing climate (Morelli et al., 2016). Over the long term, they are thought to support high levels of endemism (Sandel et al., 2011) and serve as centers of genetic diversity (Hewitt, 1996; Petit et al., 2002). Although the concept of refugia is straightforward, there is no standard quantitative approach for locating biologically meaningful climate refugia at broad spatial scales.

Climate refugia may be defined as *in situ* or *ex situ* (Ashcroft, 2010). *In situ* refugia are characterized by relatively constant climate conditions that facilitate species persistence (Keppel et al., 2012) or, for individual species, overlap between current and future climatic niches (Stralberg et al., 2015). *Ex situ* refugia may vary in proximity to a species' current distribution, with consequent implications for their overall value. The concept of climate velocity (Loarie et al., 2009) – the speed at which an organism must migrate to keep pace with climate change – provides a tool for ranking *ex situ* refugia. Various velocity metrics can be used to identify species and ecosystems most vulnerable to climate change (Loarie et al., 2009; Serra-Diaz et al., 2014). The gradient approach, which calculates climate velocity as the ratio of temporal and spatial change gradients (Loarie et al., 2009), can be used to assess climate vulnerability of geographic locations in general (Garcia, Cabeza, Rahbek, & Araújo, 2014), or with respect to specific species, that is, biotic or bioclimatic velocity (Serra-Diaz et al., 2014). However, analog-based approaches (Hamann, Roberts, Barber, Carroll, & Nielsen, 2015; Ordoñez & Williams, 2013) are more directly suitable for identifying common destinations under climate change. With the nearest-analog method (Hamann et al., 2015), both forward and backward velocity can be calculated relative to distinct climate types (climatic velocity) or species' niches (biotic velocity), providing complementary information (Batllori, Parisien, Parks, Moritz, & Miller, 2017; Carroll, Lawler, Roberts, & Hamann, 2015). Forward velocity is calculated by measuring the distance from a given present-day location to the nearest future location with a similar climate or species niche. Conversely, backward velocity takes future climates or niches and calculates distances to the nearest current analogs. Therefore, backward velocity can be used to rank areas according to their refugia potential for a given time period (Carroll et al., 2017). Biotic velocity-based refugia represent areas of future climatic suitability for a species that are in close proximity to its current distribution. Recognizing the large potential for lagged ecosystem responses to climate change, these are places with an increased chance of rapid colonization (or persistence) in the presence of climate change.

One may also distinguish between macro- and microrefugia. The former are defined by sustained climatic suitability along broad spatial and temporal gradients, and the latter suggest a decoupling of local climate conditions from the surrounding landscape (Ashcroft, 2010; Dobrowski, 2011). Cold microrefugia may be driven by factors ranging in scale from north-facing slopes and cold-air drainages (Dobrowski, 2011) to local topographic concavity and canopy density (Lenoir, Hat-tab, & Pierre, 2017). The local climate phenomena that determine microrefugia are not captured by global climate model (GCM) projections (Keppel et al., 2012; Lenoir et al., 2017). In contrast, macrorefugia, the focus of this paper, are driven by broader-scale climate gradients that are generally captured by downscaled GCM projections.

To better anticipate climatically driven macrorefugia, it is useful to identify common limiting factors, that is, the climate variables that determine species' warm-end range limits – and thereby limit cold refugia – either directly, via physiological tolerance, or indirectly, via biotic interactions. For example, maximum summer temperatures above certain thresholds may cause direct heat-related mortality (Albright et al., 2017). Similarly, available moisture limits the growth and regeneration of many plant species; for example, the zero isocline of the climatic moisture index (precipitation minus potential evapotranspiration) appears to determine the southern and western limits of forests in North America (Hogg, 1997). Less directly, some winter-dormant plants require cold temperatures for normal budburst (Harrington & Gould, 2015). Alternatively, the climate variables that determine southern range limits may operate through the exclusion of competing species rather than direct physiological mechanisms (MacArthur, 1972; but see Cahill et al., 2014). Climatic limiting factors are likely to vary by region based on general climate regimes.

While the refugia potential of an area depends on the climatic niches of the species or ecosystems of interest, cold macrorefugia can be expected to exhibit some universal characteristics across species based on underlying topographic conditions. At the continental scale, polar amplification creates a higher rate of warming at northern latitudes, thereby increasing climate velocity (Carroll et al., 2015), whereas oceanic buffering of extreme temperatures reduces the rate of warming in coastal regions (Ackerly et al., 2010), resulting in lower climate velocity and higher refugia potential (Burrows et al., 2011). At a regional scale, mountain range orientation and geometry (Elsen & Tingley, 2015) influence the quantity and accessibility of future climate refugia. At landscape and local scales, refugia potential may be influenced by general terrain complexity, as well as the prevalence of specific landforms, such as high plateaus and gentle slopes (Lawler et al., 2015). Thus, certain topographic variables may serve as independent proxies for multispecies refugia. As such it is important to understand the extent to which topography predicts macrorefugia locations.

Here we developed a spatially explicit, species-level macrorefugia index derived from backward biotic velocity calculations, which we used to generate multispecies refugia indices for two functional/taxonomic groups: trees and passerine birds (hereafter 'songbirds'). Quantile regression analysis was then used to identify limiting factors and common topographic predictors of biotic macrorefugia across different regions of the United States and Canada. Specifically, our objectives

were to (a) identify spatial patterns of tree and songbird macrorefugia; (b) identify climatic limiting factors by region and taxonomic group; and (c) quantify multi-scale topographic components of end-of-century biotic refugia. More broadly, our approach can be used to map and explain refugia for any taxa, regions and time periods of interest.

2 | METHODS

2.1 | Study area

Our study area consisted of the continental United States and most of Canada (Supporting Information Figure S1), where fairly extensive and consistent species occurrence data were available, leaving out portions of North America in the far north (Canadian high Arctic) and south (Mexico, Central America and the Caribbean islands). We did include the southern Arctic region, which was represented in the avian dataset, albeit less extensively than other regions. Although new species may move into the study area in a warmer future, bioclimatic modeling suggests that future biome types already exist within the study area (Rehfeldt, Crookston, Sáenz-Romero, & Campbell, 2012).

2.2 | Species distribution models

We used existing songbird (Distler, Schuetz, Velásquez-Tibatá, & Langham, 2015; Schuetz et al., 2015) and newly updated tree (McKenney, Pedlar, Rood, & Price, 2011) species distribution models (SDMs) developed for Canada and the United States, both of which were based on a common 10-km baseline climate interpolation for the 1971–2000 normal period (McKenney, Hutchinson et al., 2011). Climate projections for the 30-year period representing end-of-century conditions (2071–2100) were based on 10-km downscaled climate anomalies (McKenney, Hutchinson et al., 2011) generated by four widely used GCMs from the Coupled Model Intercomparison Project, Phase 5 (CMIP5, Taylor, Stouffer, & Meehl, 2012): CanESM2, CESM1-CAM5, HadGEM2-ES and MIROC-ESM. These particular GCMs were selected for downscaling by the Canadian Forest Service based on availability of key variables such as solar radiation, wind speed and humidity, as well as temperature and precipitation, to support various forest modeling efforts (McKenney et al., 2013). We compared representative concentration pathways (RCP) 4.5 and 8.5 to bracket a range of future emissions levels; however, the latter best matches the 21st century conditions that are to be expected without dramatic reductions in greenhouse gas emissions or technological fixes (Fuss et al., 2014).

Tree data sources included the U.S. Forest Service Forest Resource Inventory dataset (Gray et al. 2012), forest inventory data from provincial agencies and ecologists in Canada, various arboretum and herbarium collections, and citizen scientists. Due to uneven sampling effort across the study area, tree occurrence locations were filtered such that a maximum of one occurrence record was associated with each 10-km pixel. To achieve a consistent and unbiased group of species to evaluate, we started with the U.S. Geological Survey's list of U.S. trees with mapped distributions (Little, 1971, 1976, 1977, 1978), which also includes all Canadian tree species, and excluded species for which

fewer than 30 records were available. This resulted in 324 species and recognized subspecies (Supporting Information Table S1). Models were updated with new data obtained since the last published version (McKenney, Pedlar et al., 2011), with particular focus on newly compiled data from species-rich California (Thornhill et al., 2017).

Songbird data were obtained from the North American Breeding Bird Survey (Sauer et al. 2012), an annual roadside survey extending across most of the United States and Canada. Surveys are point counts separated by 0.8-km intervals. The first 30 points were used to determine presence or absence of a species within a pixel, approximately corresponding with the resolution of the 10-km interpolated climate data. Although data and models for non-passerine species were also available, we restricted our analysis to 268 terrestrial passerine species (Supporting Information Table S2), the group for which point-count protocols are best suited. This was done to improve consistency among species' detectability, but also to eliminate arbitrary influences of species with distributions linked to major water bodies or shorelines.

Predictions of songbird probability of occurrence were based on boosted regression tree (Friedman, Hastie, & Tibshirani, 2000) models built from presence and absence locations (see Distler et al., 2015 for details), while predictions of tree distribution were based on MAXENT (Phillips, Anderson, & Schapire, 2006) models using presence-only locations (see McKenzie, Pedlar et al., 2011 for details). Given the 10-km resolution of the climate data, these predictions are appropriate for the identification of macrorefugia, as determined by factors ranging from broad-scale continental circulation patterns to local terrain variability. Topographically based microrefugia locations are not discernable at this resolution.

For both tree and songbird models, we applied a probability of occurrence threshold based on mean probability of occurrence within the study area as an index of prevalence (Manel, Williams, & Ormerod, 2001; Supporting Information Tables S1 and S2). Visual inspection confirmed that these thresholds resulted in presence maps aligned with published range maps.

2.3 | Biotic velocity and refugia indices

Presence predictions from tree and songbird SDMs were used to calculate backward biotic velocity (Carroll et al., 2015) for each species, based on four binary representations of climatically suitable niche space (one per GCM). Within each RCP, for each species-GCM combination i , we calculated the distance (d_{ij}) in km from each future (2071–2100) distribution pixel j to the nearest current distribution pixel. Our assumption was that longer distances (larger backward velocity values) represented lower refugia potential, and our primary objective was to rank refugia potential by distance. For the purposes of generating an index, however, we needed to identify a nonlinear distance decay function that would strongly down-weight larger distances, given the low probability of natural dispersal and colonization success. In order to ground this function in biological data and established dispersal theory, we assumed a fat-tailed dispersal kernel, which accommodates rare long-distance dispersal events, and has been invoked to explain the rapid post-glacial recolonization of trees across northern North America

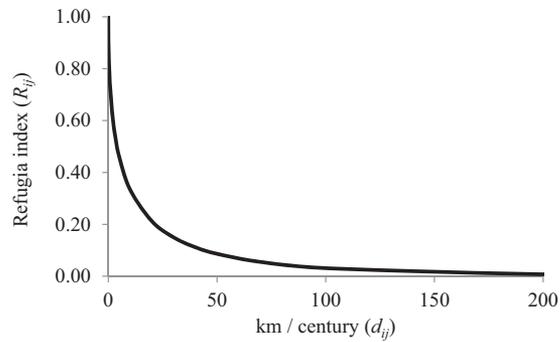


FIGURE 1 Negative exponential distance decay function used to calculate the refugia index, $R_{ij} = \exp\left(-\frac{d_{ij}^c}{\alpha}\right)$, where $c = 0.5$ and $\alpha = 8.333$ (the value resulting in a mean dispersal distance of 50 km per century, based on the first moment of the dispersal kernel)

at the end of the Late Pleistocene age (Clark et al., 1998). We defined our standardized index of refugia potential, R_{ij} , as the negative exponential portion of a fat-tailed dispersal kernel (Clark et al., 1998):

$$R_{ij} = \exp\left(-\frac{d_{ij}^c}{\alpha}\right) \quad (1)$$

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 .09 at

50 km, and then slowly converges toward 0 (Figure 1). Although birds can disperse much farther and faster due to their ability to fly, we assumed a similar dispersal potential of that of trees based on the vegetation requirements that help define suitable habitat for birds.

For each RCP, standardized refugia index values were averaged across the four GCMs to yield an ensemble index for each species (see Figure 2 for schematic representation of index calculations). Pixels with no suitable niche space for a given GCM were converted to zero to down-weight their importance in subsequent ensemble calculations. To down-weight species with increased climatic suitability under climate change, the ensemble refugia index was then divided by the mean proportional change in total potential distribution area across GCMs (future/present area; Supporting Information Tables S1 and S2) and averaged across all study species to weight by overall species change. 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 a given species, 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. We also derived separate indices for four different vegetation-based groupings of songbirds (allaboutbirds.org): forest (99 species), open woodland (64 species), shrub (49 species) and grassland (29 species) (Supporting Information

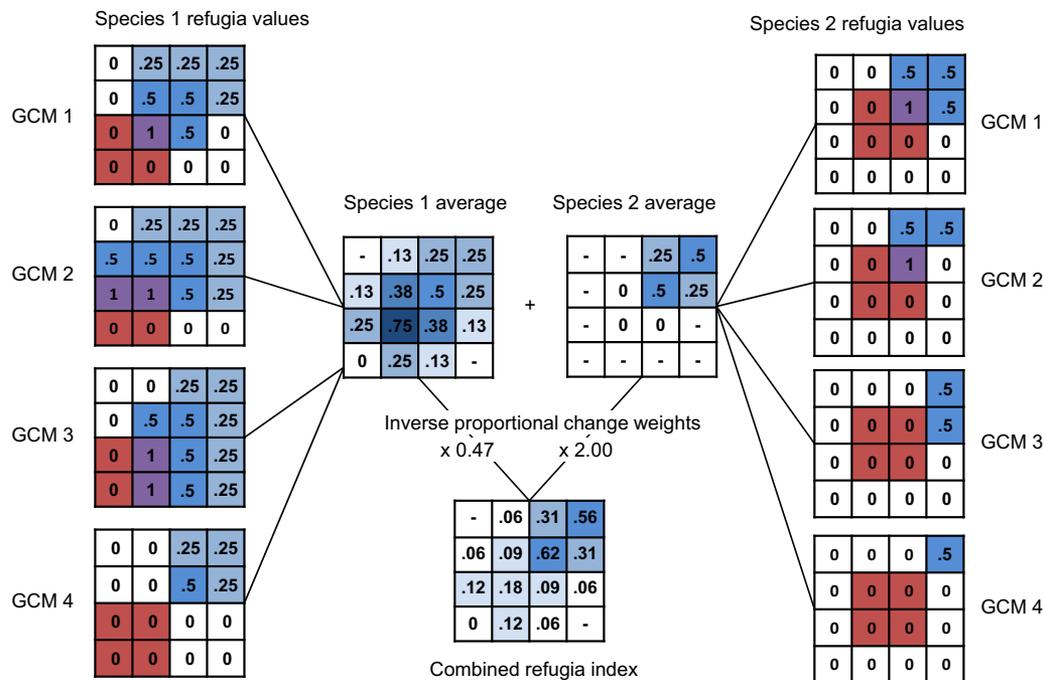


FIGURE 2 Schematic example of refugia index calculation for two hypothetical species and four global climate models (GCMs). Current distributions are shown in red; future distributions in blue; and overlap in purple. Hypothetical species-specific refugia index values are shown for each GCM on the periphery, and averaged across GCMs in the top center. Combined refugia index values represent the mean of the individual species averages, weighted by the inverse proportional change in overall climatic suitability for the species (current prevalence/future prevalence), truncated above values of 2.0 (i.e., change values below 0.5). For species 1, current prevalence is 0.25 (4 cells out of 16) and future prevalence is 0.53 (8.48 cells on average), resulting in an inverse proportional change of $0.25/0.53 = 0.47$; for species 2, $(0.25/0.11) = 2.27$, truncated to 2.0. Dashes represent areas of baseline species' absence, which are excluded from calculations

TABLE 1 Environmental covariates used in quantile regression analysis of North American tree and songbird refugia

Category	Variable name	Definition
Continental position	Lat	Degrees north latitude
	CoastDist	Distance to nearest maritime coast
Regional topography	TPI9	Topographic position index ^a based on 9 × 9 window
	TPI25	Topographic position index ^a based on 25 × 25 window
	TPI81	Topographic position index ^a based on 81 × 81 window
	NSCorr	North-south corridor potential (derived from flow direction based on mean elevation across 5 × 5 window)
Landscape topography	Rough	Roughness index based on 3 × 3 window
	TPI	Topographic position index based on 3 × 3 window
	Elev	Mean elevation of 10-km pixel
	ElevDiv	Land-facet diversity within 10-km pixel (Gini-Simpson index)
	Valley	Proportion of valley landforms within 10-km pixel
	Hilltop	Proportion of hilltop in valley landforms within 10-km pixel
	Headwater Ridge	Proportion of headwater landforms within 10-km pixel Proportion of ridge and peak landforms within 10-km pixel
Climate	TempAnn	Mean annual temperature (BIO1)
	TempWarm	Mean temperature of warmest quarter (BIO10)
	TempCold	Mean temperature of coldest quarter (BIO11)
	PrecipAnn	Annual precipitation (BIO12)
	PrecipWarm	Precipitation of warmest quarter (BIO18)
	CMI	Climatic moisture index (mm precipitation – mm potential evapotranspiration), modified Penman-Monteith method

^aTopographic position index for window size w (TPI w) was calculated as $\text{Elev}/(\text{ElevMean} + 0.5)$, where Elev = mean elevation of 10-km pixel and Elev-Mean = mean 10-km pixel elevation across the surrounding $w \times w$ window.

Table S2). Species with other primary habitat affiliations (marsh, town, shoreline, mountain or lake/pond) were included only within the combined index.

To evaluate potential discrepancies among GCMs, we also calculated individual songbird refugia indices for each GCM under RCP 8.5 and calculated Pearson correlation coefficients for each pair ($n = 175,920$ pixels).

We calculated a species richness index for each species group by averaging current binary presence/absence predictions across species. We reclassified current species richness and refugia values into three groups defined by percentiles (<.50, .50-.75, >.75), and identified areas of overlap between high current species richness and future refugia value. Finally, we compared tree and songbird refugia by converting ensemble index values to ranks and calculating pixel-level differences.

2.4 | Climatic limiting factors

We used linear quantile regression (Koenker & Jose, 1999) to identify which projected future climatic variables best represent limiting factors for tree and songbird cold refugia. Quantile regression provides a more complete picture by modeling all quantiles of a distribution, rather than assuming relationships between mean values (Cade & Noon, 2003). Using the 'quantreg' package (Koenker 2018) for R (R Core Team 2017), we developed models relating the distributions of combined refugia index values and each of six end-of-century (2071–2100) bioclimatic variables (Table 1). The climate variables were selected *a priori* to represent potential warm-end range-limiting factors: summer, winter

and annual temperatures (Nix, 1986); annual and summer precipitation (Nix, 1986); and a climatic moisture index (CMI; Hogg, 1997).

Model inputs were based on a regular sample of 17,550 10-km pixels (c. 10% of the study area). Although limiting factors may be defined as 'thresholds that determine the maximum or minimum biological response for a given suite of environmental conditions' (Greenberg, Santos, Dobrowski, Vanderbilt, & Ustin, 2015), we focused on the near-maximum (99.9th percentile), as well as several key upper percentile thresholds (50-75-90-99) consistent with those used for mapping. Following the methods of Greenberg et al. (2015), we used the resulting beta coefficients to predict refugia values for a given percentile across the study area based on six different univariate models. The limiting factor at each pixel location was defined as the climatic variable that resulted in the lowest predicted refugia value. We repeated this 100 times with bootstrap samples taken from the regular sample of the study area, and identified the most frequently selected variable, as well as its frequency of selection as a measure of variability.

2.5 | Environmental predictors

Because our refugia indices were derived from species distribution models based on climate variables, it was clear that climate variables would be more explanatory than topographic variables. Accordingly, our goal was not so much to compare the predictive abilities of these two variable sets, but to quantify the hierarchical contributions of multi-scale topographic factors in determining climatic refugia potential. Topographic variables were grouped according to scale (Table 1). Continental position variables were latitude and distance to nearest major coastline. At the

regional scale, we calculated a north–south corridor potential (NSCorr) to quantify the geographic orientation of the major topographic gradient, hypothesizing that north–south-oriented mountain ranges would provide less resistance for climate-induced range shifts. We used the ‘terrain’ function in the ‘raster’ package (Hijmans and van Etten 2012) to calculate flow direction (eight neighbors) based on an aggregated 2,500-km² elevation raster, and then multiplied this value by the slope based on the same elevation layer. The other regional variables consisted of different scales of a topographic position index (TPI) measuring the elevational position of a 10-km pixel in relation to its surrounding neighborhood in dimensions of 9², 25² and 81² pixels (pixel elevation divided by mean surrounding neighborhood elevation). At the landscape scale we calculated terrain roughness and topographic position within a 3² pixel area using the ‘terrain’ function in the ‘raster’ package for R. To capture local terrain diversity (Bailey, Boyd, Hjort, Lavers, & Field, 2017; Carroll et al., 2017), we also calculated terrain characteristics within each 10-km pixel, including land-facet diversity (Gini-Simpson index) and proportional coverage of different landform types, based on North American land facets (adaptwest.databasin.org). Pairwise Pearson correlation coefficients did not exceed .75. Importantly, these topographic covariates were not used as predictors in the underlying species distribution models, which were strictly climate-based. At the 10-km resolution of our models, we did not expect direct effects of topography per se; only indirect influences via climate parameters (e.g., elevation and latitude as proxies for temperature). Rather, we considered topographic variables in terms of their influence on the *configuration* of suitable habitat, and thus the rate of change measured by the biotic velocity metric.

Using the same regular sample, we developed a nested set of linear quantile regression models to identify the relative contributions of multi-scale topographic and climatic factors (Table 1) to different quantiles of tree and songbird macrorefugia. Again we focused on key upper percentile thresholds (50-75-90-99-99.9). We first developed separate models for each set of variables: continental, regional, landscape and local topography; and climate. We then constructed a set of nested models, evaluating the relative added contributions of each set of variables at each stage using a pseudo-R² metric specific to quantile regression (Koenker & Jose, 1999). Starting with a model containing only continental-scale variables, we compared the increase in fit gained by adding successively finer-scale static topographic variables (regional, landscape and local). We then evaluated the additional contribution of future climatic variables (linear terms only). Our rationale for this sequence was based on a spatially hierarchical view of topographic controls on species’ distributions.

3 | RESULTS

3.1 | Refugia indices

Proportionately more songbirds were projected to increase their climatically suitable niche space in the future compared to trees (Supporting Information Tables S1 and S2). The weighted refugia index for 324 tree species under RCP 8.5 ranged from 0.000 (1st percentile) to 0.360 (99th percentile), with a median of 0.123 and an even distribution

(Supporting Information Table S3). The highest values (99th percentile) of tree refugia were located in western mountains; values in the 90th percentile were also located in eastern forest regions (Figure 3a). In general, the lowest refugia values (10th percentile) were found in interior portions of the continent. Refugia index values were much higher under RCP 4.5 (Supporting Information Table S3) but followed similar spatial patterns (Supporting Information Figure S2a).

The weighted refugia index for 268 songbird species under RCP 8.5 ranged from 0.078 (1st percentile) to 0.612 (99th percentile), with a median value of 0.211 (Supporting Information Table S3). Compared with trees, values of songbird refugia were higher overall, with a more left-skewed distribution. The 99th percentile values of songbird refugia were also located in western mountains, while 90th percentile values were located in northern and southern interior regions (Figure 3b). Similar to trees, the lowest refugia values (10th percentile) were mainly found in interior portions of the continent, but generally more dispersed. Refugia values for songbirds under RCP 4.5 were also larger in magnitude (Supporting Information Table S3) but followed similar spatial patterns as trees, with the exception of the far north, which had higher relative importance under RCP 4.5 compared to RCP 8.5 (Supporting Information Figure S2b). Pearson correlations among refugia values based on different individual GCMs were remarkably high (Supporting Information Figure S3), ranging from .89 (MIROC-ESM and CanESM2) to .99 (MIROC-ESM and HadGEM2-ES). Thus, we focused on the GCM ensemble. Areas of highest variability among GCMs were primarily in northern regions (Supporting Information Figure S4).

Under both RCPs evaluated, the highest values (99th percentile) of combined tree and songbird refugia were located mostly in western mountains (Figure 3c, Supporting Information Figure S2c). Other major concentrations of high refugia values (90th percentile) were found in eastern and north-eastern forests. For regions with generally low refugia value, predictions can be rescaled by ecoregion to indicate relative refugia potential (Supporting Information Figure S5).

Based on percentile ranks, the areas of the continent in which songbird refugia were much higher than tree refugia were primarily in the north and south-west (Figure 3d, Supporting Information Figure S2d). Areas of the continent in which refugia values were much greater for trees than for songbirds were northern forests and portions of south-eastern coastal regions.

The area of overlap between relatively high (75th percentile) tree species richness and relatively high tree refugia potential was located mostly within south-eastern regions, while smaller areas of overlap were found in the south-west (Figure 4a). Most of the high-value refugia were found in the west and did not overlap with areas of high current species richness in the east. For birds, most of the overlapping high refugia/high richness areas were in the west (Figure 4b). Large areas of high species richness in the east did not overlap with areas of high-value refugia, mostly in the east and north.

Partitioning index values by habitat association, forest bird refugia generally followed the overall pattern for songbirds, but with higher values in the south-east, as with trees (Supporting Information Figure S6a). In comparison, open woodland bird refugia were more evenly distributed throughout the continent, with higher values in

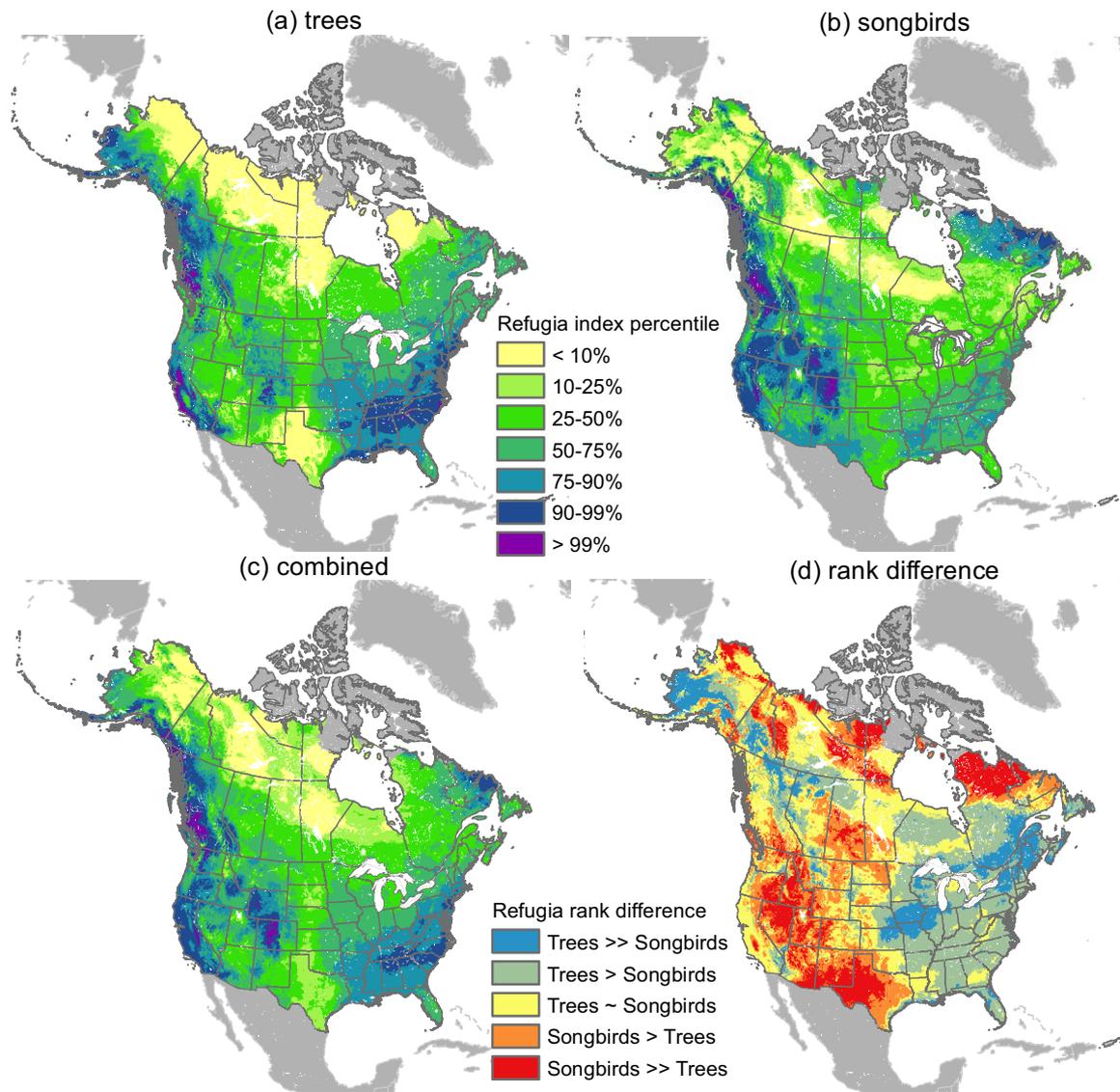


FIGURE 3 Multispecies end-of-century (2071–2100) refugia indices averaged across (a) 324 tree species, (b) 268 songbird species and (c) all species combined, weighted by projected climate-change response. Legend breaks are defined by percentile values. (d) Difference between refugia percentile ranks for trees and songbirds. Radiative forcing values: Representative Concentration Pathway 8.5. Map projection: Lambert Azimuthal Equal Area

eastern and southern boreal forests (Supporting Information Figure S6b). Shrub bird refugia were mostly concentrated in the north (Supporting Information Figure S6c). Grassland species had lower values of refugia overall, with the highest values occurring primarily in northern interior regions (Supporting Information Figure S6d).

3.2 | Climatic limiting factors

Climatic variables limiting cold refugia for trees were similar across lower percentile thresholds, with different patterns emerging at the highest percentile (Figure 5a, Supporting Information Figure S7a), along with greater variation among bootstrap replicates (Supporting Information Figure S8). For the 99.9th percentile, mean summer temperature was negatively limiting (i.e., lower mean summer temperatures were required to achieve higher refugia values) in the south-eastern portion of the continent and in

the Pacific Northwest, while CMI was positively limiting (i.e., higher CMI needed for higher refugia values) in south-western regions (Figure 5a, Supporting Information Figure S7a). Annual precipitation was positively limiting over much of the north and interior west, while summer precipitation was negatively limiting in eastern and western coastal regions. For the 50th percentile, temperature was positively limiting in the north, while precipitation was positively limiting in the south-western portion of the continent and CMI was positively limiting in the south-east (Figure 5a, Supporting Information Figure S7a). Limiting factors for 75th and 90th percentile thresholds were similar to the 50th percentile, while 99th percentile limiting factors were intermediate to these results.

For songbirds, limiting factors were somewhat similar to those for trees at lower percentile thresholds, especially in interior northern and western portions of the continent (Figure 5b). At the 50th percentile threshold there was greater divergence in coastal regions, where CMI

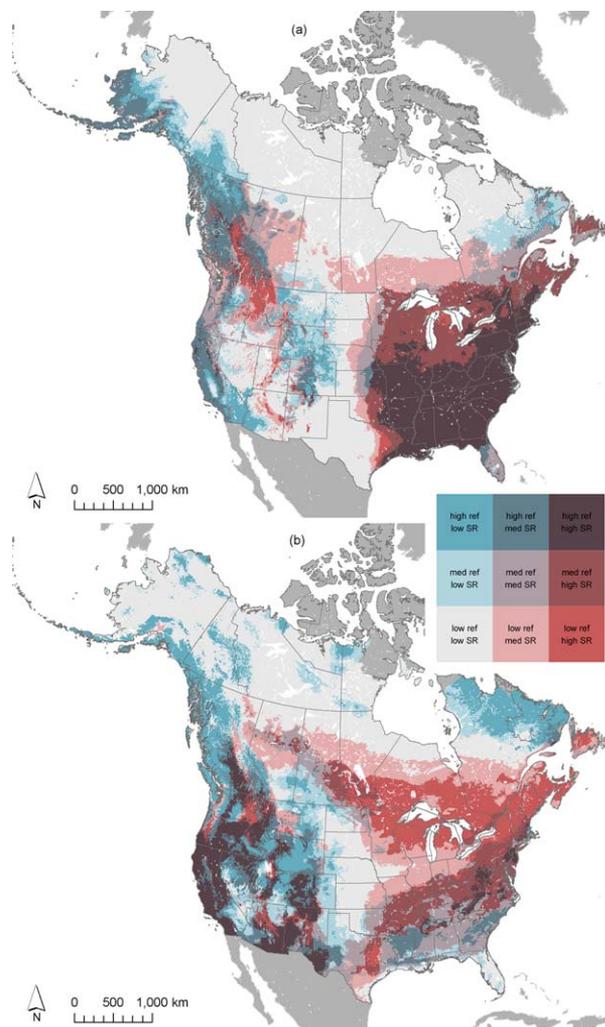


FIGURE 4 End-of-century weighted refugia index (ref) versus current species richness index (SR) for (a) trees and (b) songbirds. Low/medium and medium/high percentage thresholds are .25 and .75, respectively. Radiative forcing values: Representative Concentration Pathway 8.5. Map projection: Lambert Azimuthal Equal Area

was negatively limiting, and in the south-eastern portion of the continent, where summer precipitation was negatively limiting (Figure 5b, Supporting Information Figure S7b). At higher percentile thresholds there was more divergence with trees, with greater negative temperature limitations throughout much of the continent (Figure 5b, Supporting Information Figure S7b). Limiting factor frequencies generated by bootstrap resampling results were high except near the boundaries of limiting factor influences (Supporting Information Figure S8).

3.3 | Environmental predictors

In terms of explanatory power, model fit generally increased with percentile threshold, although less so for trees (Figure 6a) than for songbirds (Figure 6b). Quantile regression models based on topographic variables explained up to .49 (pseudo- R^2) of the variation in tree refugia and .69 of the variation in songbird refugia at the 99.9th percentile threshold, increasing to .74 and .93, respectively,

when linear climate variables were added (Table 2). When variable sets were added sequentially, the largest increase in fit generally came with the addition of climate variables for trees (Figure 6a), and regional or landscape topography variables for songbirds (Figure 6b).

Based on combined models for tree refugia, both latitude and distance to coast had strong negative effects, with the former most important at the 50th percentile, and the latter more important at the 99.9th percentile threshold (Figure 7a). In terms of topographic predictors, headwater and valley landforms were most important, with the same general pattern of reversed importance across percentile thresholds. Elevation was negative for all but the 99th and 99.9th percentiles. Patterns for birds differed primarily in that latitude and elevation both had increasingly positive effects at higher percentile thresholds (Figure 7b).

4 | DISCUSSION

Using a multispecies macrorefugia index based on biotic velocity, our results indicated that future cold refugia potential in North America is highest in western mountains and, to a lesser extent, eastern coastal and mountain regions. For the highest-value refugia locations, future climatic limiting factors were consistent over large regions, with precipitation generally most limiting in northern and western regions, and warm temperatures limiting in the south. In the south-west, the CMI was more limiting than pure temperature metrics. Generally speaking, these results are intuitive and consistent with continental temperature and precipitation patterns, but they are also in contrast with presumed species richness drivers – temperature in the north and precipitation in the south (Hawkins et al., 2003). Accordingly, we found a general lack of agreement between patterns of current species richness and future climate refugia.

We also found substantially different refugia patterns between trees and songbirds. Songbird refugia values were generally higher overall than tree refugia values, and were relatively prevalent in northern and intermountain-western regions, while tree refugia potential was greater in boreal and eastern temperate forest regions. This largely reflects the wider array, and generally broader width and larger geographic size of songbird niches, compared with trees. Clearly, songbird niches and refugia will be constrained by underlying vegetation patterns, and tree refugia will affect songbirds; but the broad environmental niches of most songbird species generally encompass those of several tree species, as well as treeless areas, allowing for greater flexibility and potential for range expansion. Because our refugia index was weighted by species' proportional change in climatic niche over time, areas of future importance for these climate-increasing species contributed minimally to refugia potential.

Furthermore, North American vascular plant species display much higher rates of endemism than birds (Kier et al., 2009), driven in part by stronger influences of dispersal limitation and interspecific competition. More localized tree distributions with narrower latitudinal ranges than songbirds led to lower refugia values, but also more complex regional refugia patterns, which more closely resembled refugia based on velocity of more narrowly defined climate types (Carroll et al., 2017).

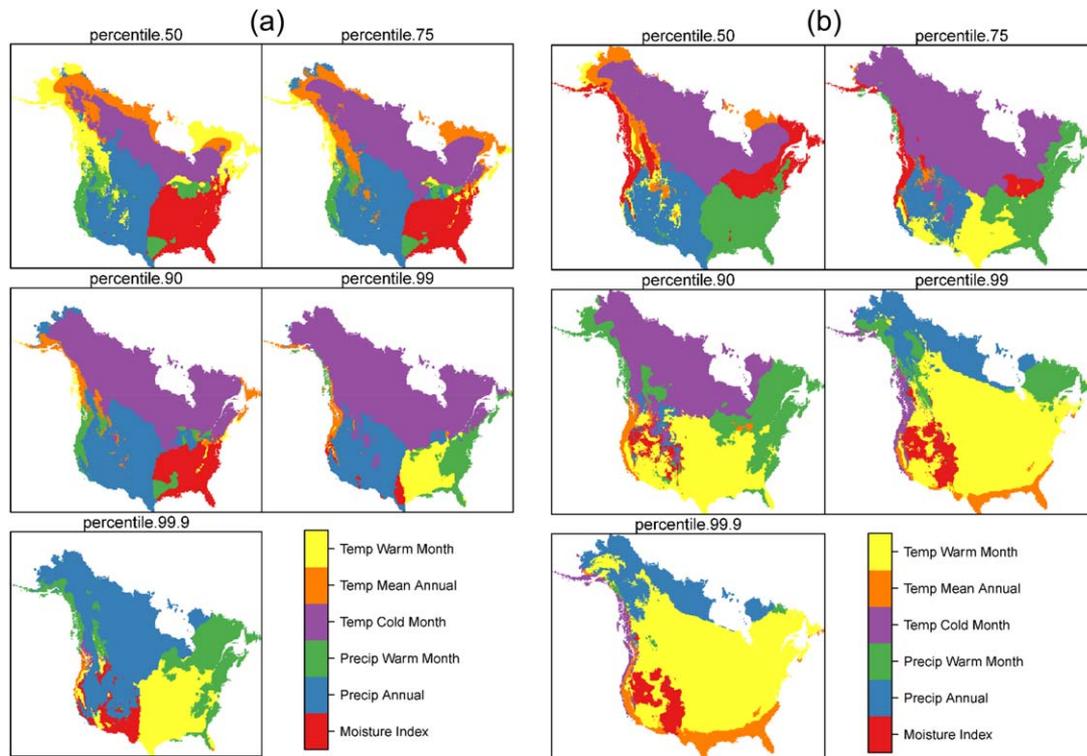


FIGURE 5 Most frequently selected climatic limiting factors for end-of-century (a) tree and (b) songbird refugia based on bootstrapped quantile regression coefficients for 50th, 75th, 90th, 99th and 99.9th percentile refugia thresholds. Radiative forcing values: Representative Concentration Pathway 8.5. Map projection: Lambert Azimuthal Equal Area

Interestingly, combined tree and songbird refugia were more similar to areas of predicted low future vascular plant turnover (Zhang et al., 2017) than tree refugia alone.

We also observed differences in climatic limiting factors for tree versus songbird refugia. Top percentile songbird refugia were generally limited more by temperature, while tree refugia were limited more by precipitation and CMI. These findings are consistent

with ecological differences between the two organismal groups. Many tree species and forest types are sensitive to seasonal water deficits (Littell, Peterson, & Tjoelker, 2008; Stephenson, 1990), whereas birds and other vertebrates can exploit a much broader range of niche characteristics, with relatively small physiological demands for water. However, songbirds may be more limited by high temperatures than trees, whether directly via physiological

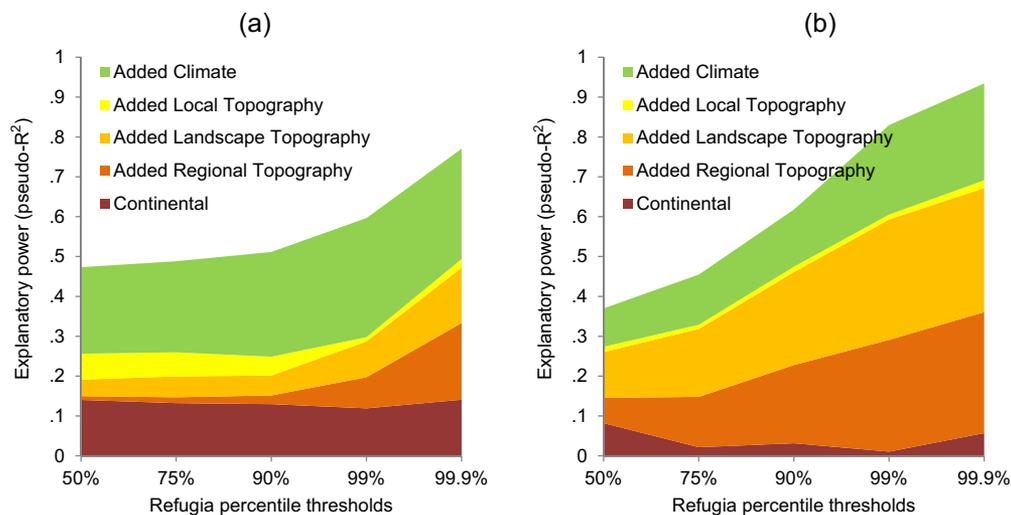


FIGURE 6 Added contributions of each variable set to pseudo- R^2 values for nested quantile regression models for North American (a) tree and (b) songbird end-of-century refugia indices (Representative Concentration Pathway 8.5) at 50th, 75th, 90th, 99th and 99.9th percentile thresholds

TABLE 2 Environmental predictors of tree and songbird end-of-century climate refugia, based on pseudo- R^2 values for quantile regression models.

Quantile	Separate					Sequential (cumulative)				
	.50	.75	.90	.99	.999	.50	.75	.90	.99	.999
Trees										
Continental position	.14	.13	.13	.12	.14	.14	.13	.13	.12	.14
Regional topography	.01	.01	.01	.06	.16	.15	.15	.15	.20	.33
Landscape topography	.02	.04	.05	.11	.18	.19	.20	.20	.29	.47
Local topography	.04	.04	.03	.10	.20	.26	.26	.25	.30	.49
Climate	.38	.37	.35	.39	.46	.47	.39	.39	.52	.74
Songbirds										
Continental position	.08	.02	.03	.01	.06	.08	.02	.03	.01	.14
Regional topography	.06	.10	.17	.24	.28	.15	.15	.23	.29	.36
Landscape topography	.15	.22	.33	.37	.40	.26	.32	.46	.59	.67
Local topography	.08	.17	.27	.32	.31	.27	.33	.47	.61	.69
Climate	.27	.34	.45	.58	.60	.37	.45	.62	.83	.93

Note. Variable groups were evaluated separately, as well as combined sequentially in the order shown ($n = 17,550$). Values for the latter represent incremental contributions to pseudo- R^2 .

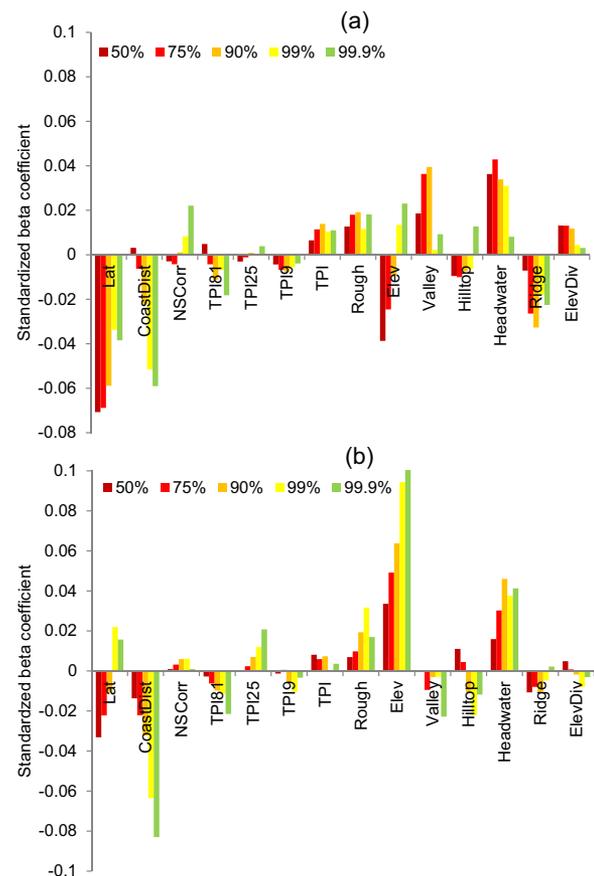
constraints (Albright et al., 2017), or indirectly via competition from cold-sensitive southern species (MacArthur, 1972).

Importantly, limiting factors for the 99.9th percentile refugia differed greatly from those for the median and other lower percentile values, for which precipitation was generally more limiting in the south, and cold temperatures were more limiting in the north. This indicates the value of modeling the entire distribution using quantile regression, rather than focusing on the mean or median. Higher percentile model parameters were also much more explanatory than median or other lower percentile parameters, especially with respect to topographic predictors, which explained approximately half and two-thirds of variation for trees and songbirds, respectively. For lower percentile values, topographic factors were much less important. Thus, while certain mountain and northern coastal areas may be considered fixed or universal refugia defined by topographic characteristics, lower-value transient or shifting refugia defined by climate conditions – that is, ‘stepping stones’ (Hannah et al., 2014) – are also important to identify, especially in relatively flat, interior regions.

With respect to the topographic correlates of macrorefugia, we found elevation to be of high direct importance for songbirds, likely due to its tight negative relationship with temperature as a function of adiabatic cooling. This was not the case for trees, except at the highest percentile threshold. Instead, we found relatively strong effects of landform composition: positive associations with headwaters (for both trees and songbirds) and valleys (trees only). Headwaters are associated with elevation and topographic position, and may provide a more locally relevant metric for refugia potential, compared to continuous metrics. The same applies to valleys, which reflect terrain variability and connectivity in a relative context. Thus, categorical representations of certain topographic landforms appear to provide useful first approximations of refugia potential across scales and regions, while also helping to delineate ecological units (land facets) to meet representation targets for conservation planning (Beier & Brost, 2010).

In terms of continental position, both tree and songbird refugia were found closer to coasts, due to climate-moderating maritime

influences. However, tree refugia were negatively associated with latitude while songbirds were positively associated, indicating the differential influences of greater rates of warming versus overall cooler temperatures towards the poles. This is likely explained by

**FIGURE 7** Effect sizes for continental position and topography variables in quantile regression models for North American (a) tree and (b) songbird end-of-century refugia indices (Representative Concentration Pathway 8.5) at 50th, 75th, 90th, 99th and 99.9th percentile thresholds. See Table 1 for variable definitions

the broader niches of songbirds, including several arctic species, resulting in lower biotic velocities and thus higher refugia values for cooler northern climates.

4.1 | Conservation and research applications

On a relative basis, the continuous multispecies index developed here was relatively robust to the choice of GCM and RCP, implying that the metric can be used to inform regional conservation planning despite the uncertainty associated with the magnitude of future climate change. However, the index varied greatly depending on the species included and ecoregions considered. We found that macrorefugia locations for birds with specific habitat associations were best informed by habitat-specific indices, especially for non-forest species, which have lower overall refugia values. This highlights the importance of specifying target species (or ecosystems) and geographies for refugia analyses. However, we do not suggest that macrorefugia should be the sole focus of conservation prioritization exercises. Rather, they constitute one index of long-term sustainability potential within a larger conservation framework. Other indices may better represent fine-scale diversity and refugia potential (Carroll et al., 2017).

The general lack of concordance between current species richness and future climate refugia patterns suggests the need for 'bet-hedging' (Schloss et al., 2011; Schuetz et al., 2015) and strategic large-scale, long-term conservation designs. However, the limited overlap areas do suggest some immediate conservation opportunities. Given that large portions of the highest-value refugia are currently composed of barren rock or semi-permanent snow and ice, it is worth identifying those areas that are more likely to provide habitat for a range of species, as well as high-velocity areas for potential translocation of species with limited refugia (McLachlan, Hellmann, & Schwartz, 2007).

Although we have focused here on future climate change and conservation applications, our index may also be applied to paleo-hindcasting of species distributions at the Last Glacial Maximum c. 20 kya (e.g., Stralberg et al., 2017). Genetic studies from Europe in particular have found greater levels of genetic diversity in southern populations that are overlapping with or in closer proximity to ice-age refugia locations (Petit et al., 2003), suggesting long-term consequences of low-velocity refugia. Although this diversity 'hotspot' pattern may not apply to North America, where post-glacial expansion was less constrained by physiographic barriers (Lumibao, Hoban, & McLachlan, 2017), hindcast refugia indices could be used to evaluate relationships between glacial refugia and current genetic diversity patterns.

4.2 | Limitations

Although more biologically relevant to individual species than climatic indices, biotic indices have a greater potential to exhibit idiosyncratic behavior, given the influences of taxonomic representation, data quality and spatial domain. We tried to alleviate this by including as many species as possible, but the quality of the outputs still depends on the inputs. In this case, we have lower confidence in results for the northernmost portion of the study area, where data are most sparse.

Furthermore, results are limited by the coarse 10-km resolution at which climate inputs were downscaled. To assess individual species' refugia and limiting factors, or regional conservation planning concerns, finer-scale, regional density models may be more informative.

In addition, our results are limited by the assumptions of niche models: that correlations are meaningful, that species are currently in equilibrium with climate, that there are no dispersal limitations, and that biotic interactions are adequately captured by climate (Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). Where these assumptions are not met, we often find suitable but unoccupied niche space. For example, the Alaskan boreal interior region is climatically suitable for many boreal bird species that have not yet made it there due to lack of habitat connections across the western Cordillera (Stralberg et al., 2017). For trees, a few of the herbarium records used for modeling may be from outside a species' native distribution, also resulting in predictions more closely approximating species' fundamental (versus realized) niches. In such cases, refugia potential for actual species may be overestimated. Nevertheless, the environmental potential is there for other species and ecosystems that occupy similar niches. We also assume that assisted migration (McLachlan et al., 2007) can aid regeneration and establishment, thereby minimizing the importance of discrepancies. Indeed, experimental translocations of plant seedlings to environmentally suitable but not-yet-colonized regions have been successful (McLane & Aitken, 2011), suggesting that a species' fundamental niche is indeed a reasonable conservation target.

Finally, our index does not capture the implications of differential rates of migration among species (Iverson, Schwartz, & Prasad, 2004), climatic resistance across landscapes (Dobrowski & Parks, 2016) or land-use impediments (McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). This is particularly important for trees, many of which have demonstrated lower-than-expected migration rates in response to recent anthropogenic climate change (Zhu, Woodall, & Clark, 2012). For particularly dispersal-limited and rapidly declining species, assisted migration (McLachlan et al., 2007) may be needed to complement the conservation of likely refugia. Refined species-specific indices could also account for life history traits (Garcia, Araújo et al., 2014; Aubin et al., 2018), biotic interactions, successional trajectories and habitat associations (Stralberg et al., 2015).

5 | CONCLUSIONS

In the face of rapid climate change, biotic velocity can be used to quantify the refugia potential for a given species in a given location. Conservation planning efforts can be strengthened by incorporating macrorefugia indices for individual tree and songbird species such as developed here. Additionally, such analyses can increase our understanding of the climatic factors that limit macrorefugia, and how controls on species' warm-end range limits differ by geography and species group. This work provides a conceptual framework that may be easily applied to other regions, taxa and spatial scales to inform conservation planning.

ACKNOWLEDGMENTS

The Wilburforce Foundation provided support for DS, CC, and SN as part of the AdaptWest Climate Adaptation Planning Project (adaptwest.databasin.org; see site for data associated with this paper). We are grateful for the technical assistance of Kevin Lawrence and Pia Papadopol at the Canadian Forest Service (with financial support from the Forest Change Program); and Lotem Taylor at the National Audubon Society. We also thank David Ackerly, Andrew Thornhill, Brent Mishler and Bruce Baldwin at UC Berkeley for new tree data contributions. DS received additional support from the Boreal Avian Modelling Project (borealbirds.ca). CW was supported by a grant to Audubon by the MacArthur Foundation.

ORCID

Diana Stralberg  <http://orcid.org/0000-0003-4900-024X>

Carlos Carroll  <http://orcid.org/0000-0002-7697-8721>

Scott E. Nielsen  <http://orcid.org/0000-0002-9754-0630>

REFERENCES

- Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change: Implications for conservation biogeography. *Diversity and Distributions*, 16, 476–487.
- Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., ... Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences USA*, 114, 2283–2288.
- Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, 37, 1407–1413.
- Aubin, I., Boisvert-Marsh, L., Kebli, H., McKenney, D., Pedlar, J., Lawrence, K., ... Ste-Marie, C. (2018). Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity. *Ecosphere* 9:e02108
- Bailey, J. J., Boyd, D. S., Hjort, J., Lavers, C. P., & Field, R. (2017). Modelling native and alien vascular plant species richness: At which scales is geodiversity most relevant? *Global Ecology and Biogeography*, 26, 763–776.
- Battlori, E., Parisien, M.-A., Parks, S. A., Moritz, M. A., & Miller, C. (2017). Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network. *Global Change Biology*, 23, 3219–3230.
- Beier, P., & Brost, B. (2010). Use of land facets to plan for climate change: Conserving the arenas, not the actors. *Conservation Biology*, 24, 701–710.
- Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., ... Richardson, A. J. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334, 652–655.
- Cade, B. S., & Noon, B. R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, 1, 412–420.
- Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., ... Wiens, J. J. (2014). Causes of warm-edge range limits: Systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, 41, 429–442.
- Carroll, C., Lawler, J. J., Roberts, D. R., & Hamann, A. (2015). Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. *PLoS One*, 10, e0140486.
- Carroll, C., Roberts, D. R., Michalak, J. L., Lawler, J. J., Nielsen, S. E., Stralberg, D., ... Wang, T. (2017). Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. *Global Change Biology*, 23, 4508–4520.
- Clark, J. S., Fastie, C., Hurtt, G., Jackson, S. T., Johnson, C., King, G. A., ... Wyckoff, P. (1998). Reid's paradox of rapid plant migration: Dispersal theory and interpretation of paleoecological records. *BioScience*, 48, 13–24.
- Distler, T., Schuetz, J. G., Velásquez-Tibatá, J., & Langham, G. M. (2015). Stacked species distribution models and macroecological models provide congruent projections of avian species richness under climate change. *Journal of Biogeography*, 42, 976–988.
- Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, 17(2), 1022–1035.
- Dobrowski, S. Z., & Parks, S. A. (2016). Climate change velocity underestimates climate change exposure in mountainous regions. *Nature Communications*, 7, 12349.
- Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5, 772–776.
- Friedman, J. H., Hastie, T., & Tibshirani, R. (2000). Additive logistic regression: A statistical view of boosting. *Annals of Statistics*, 28, 337–407.
- Fuss, S., Canadell, J. G., Peters, G. P., Tavoni, M., Andrew, R. M., Ciais, P., ... Yamagata, Y. (2014). Betting on negative emissions. *Nature Climate Change*, 4, 850–853.
- García, R. A., Araújo, M. B., Burgess, N. D., Foden, W. B., Gutsche, A., Rahbek, C., ... Guilhaumon, F. (2014). Matching species traits to projected threats and opportunities from climate change. *Journal of Biogeography*, 41, 724–735.
- García, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344, 1247579.
- Gray, A. N., Brandeis, T. J., Shaw, J. D., McWilliams, W. H., & Miles, P. D. (2012). Forest inventory and analysis database of the United States of America (FIA). In J. Dengler, J. Oldeland, F. Jansen, M. Chytrý, J. Ewald, M. Finckh, ... J. H. J. Schaminee (Eds.), *Vegetation databases for the 21st century*. Biodiversity and Ecology (Vol. 4, pp. 225–231). Hamburg, Germany: University of Hamburg.
- Greenberg, J. A., Santos, M. J., Dobrowski, S. Z., Vanderbilt, V. C., & Ustin, S. L. (2015). Quantifying environmental limiting factors on tree cover using geospatial data. *PLoS One*, 10, e0114648.
- Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdeña, Z., ... Shafer, S. L. (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, 21, 1651–1671.
- Hamann, A., Roberts, D., Barber, Q., Carroll, C., & Nielsen, S. (2015). Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, 21, 997–1004.
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology and Evolution*, 29, 390–397.
- Harrington, C. A., & Gould, P. J. (2015). Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. *Frontiers in Plant Science*, 6, 120.
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., ... Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.
- Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58(3), 247–276.

- Hijmans, R. J., and J. van Etten. 2012. Package 'raster'. Retrieved from <http://cran.r-project.org/web/packages/raster/index.html>.
- Hogg, E. H. (1997). Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology*, 84(1–2), 115–122.
- Iverson, L. R., Schwartz, M. W., & Prasad, A. M. (2004). How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography*, 13, 209–219.
- Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., ... Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, 21, 393–404.
- Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibsch, P. L., Nowicki, C., ... Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences USA*, 106, 9322–9327.
- Koenker, R., & Jose, A. F. M. (1999). Goodness of fit and related inference processes for quantile regression. *Journal of the American Statistical Association*, 94, 1296–1310.
- Koenker, R. 2018. Package 'quantreg'. Retrieved from <http://cran.r-project.org/web/packages/quantreg>.
- Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., ... Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology*, 29, 618–629.
- Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, 40(2), 253–266.
- Littell, J. S., Peterson, D. L., & Tjoelker, M. (2008). Douglas-fir growth in mountain ecosystems: Water limits tree growth from stand to region. *Ecological Monographs*, 78, 349–368.
- Little, E. L. Jr. (1971). *Atlas of United States trees, volume 1, conifers and important hardwoods: Miscellaneous Publication 1146* (p. 9, 200 maps). Washington, DC: U.S. Department of Agriculture.
- Little, E. L. Jr. (1976). *Atlas of United States trees, volume 3, minor Western hardwoods: Miscellaneous Publication 1314* (p. 13, 290 maps). Washington, DC: U.S. Department of Agriculture.
- Little, E. L. Jr. (1977). *Atlas of United States trees, volume 4, minor Eastern hardwoods: Miscellaneous Publication 1342* (p. 17, 230 maps). Washington, DC: U.S. Department of Agriculture.
- Little, E. L. Jr. (1978). *Atlas of United States trees, volume 5, Florida: Miscellaneous Publication 1361* (262 maps). Washington, DC: U.S. Department of Agriculture.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462, 1052–1055.
- Lumibao, C. Y., Hoban, S. M., & McLachlan, J. (2017). Ice ages leave genetic diversity 'hotspots' in Europe but not in Eastern North America. *Ecology Letters*, 20, 1459–1468.
- MacArthur, R. H. (1972). *Geographical ecology*. New York, NY: Harper & Row.
- Manel, S., Williams, H. C., & Ormerod, S. J. (2001). Evaluating presence-absence models in ecology: The need to account for prevalence. *Journal of Applied Ecology*, 38, 921–931.
- McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences USA*, 113, 7195–7200.
- McKenney, D. W., Hutchinson, M. F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., ... Owen, T. (2011). Customized spatial climate models for North America. *Bulletin of the American Meteorological Society*, 92, 1611–1622.
- McKenney, D., Pedlar, J., Hutchinson, M., Papadopol, P., Lawrence, K., Campbell, K., ... Price, D. (2013). Spatial climate models for Canada's forestry community. *The Forestry Chronicle*, 89, 659–663.
- McKenney, D. W., Pedlar, J. H., Rood, R. B., & Price, D. (2011). Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Global Change Biology*, 17, 2720–2730.
- McLachlan, J. S., Hellmann, J. J., & Schwartz, M. W. (2007). A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, 21, 297–302.
- McLane, S. C., & Aitken, S. N. (2011). Whitebark pine (*Pinus albicaulis*) assisted migration potential: Testing establishment north of the species range. *Ecological Applications*, 22, 142–153.
- Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., ... Beissinger, S. R. (2016). Managing climate change refugia for climate adaptation. *PLoS One*, 11, e0159909.
- Ordóñez, A., & Williams, J. W. (2013). Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters*, 16, 773–781.
- Petit, R. J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., ... Vendramin, G. G. (2003). Glacial refugia: Hotspots but not melting pots of genetic diversity. *Science*, 300, 1563–1565.
- Petit, R. J., Brewer, S., Bordács, S., Burg, K., Cheddadi, R., Coart, E., ... Kremer, A. (2002). Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest Ecology and Management*, 156, 49–74.
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>.
- Rehfeldt, G. E., Crookston, N. L., Sáenz-Romero, C., & Campbell, E. M. (2012). North American vegetation model for land-use planning in a changing climate: A solution to large classification problems. *Ecological Applications*, 22, 119–141.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J., & Svenning, J.-C. (2011). The influence of late Quaternary climate-change velocity on species endemism. *Science*, 334, 660–664.
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J., & Link, W. A. (2012). *The North American breeding bird survey, results and analysis 1966–2009*. (Version 3.23). Laurel, MD: USGS Patuxent Wildlife Research Center.
- Schloss, C. A., Lawler, J. J., Larson, E. R., Papendick, H. L., Case, M. J., Evans, D. M., ... McRae, B. H. (2011). Systematic conservation planning in the face of climate change: Bet-hedging on the Columbia Plateau. *PLoS One*, 6(12), e28788.
- Schuetz, J. G., Langham, G. M., Soykan, C. U., Wilsey, C. B., Auer, T., & Sanchez, C. C. (2015). Making spatial prioritizations robust to climate change uncertainties: A case study with North American birds. *Ecological Applications*, 25(7), 1819–1831.
- Serra-Diaz, J. M., Franklin, J., Ninyerola, M., Davis, F. W., Syphard, A. D., Regan, H. M., & Ikegami, M. (2014). Bioclimatic velocity: The pace of species exposure to climate change. *Diversity and Distributions*, 20, 169–180.
- Stephenson, N. L. (1990). Climatic control of vegetation distribution: The role of the water balance. *The American Naturalist*, 135(5), 649–670.
- Stralberg, D., Bayne, E. M., Cumming, S. G., Sólymos, P., Song, S. J., & Schmiegelow, F. K. A. (2015). Conservation of future boreal forest bird

communities considering lags in vegetation response to climate change: A modified refugia approach. *Diversity and Distributions*, 21(9), 1112–1128.

Stralberg, D., Matsuoka, S. M., Handel, C. M., Schmiegelow, F. K. A., Hamann, A., & Bayne, E. M. (2017). Biogeography of boreal passerine range dynamics: Past, present, and future. *Ecography*, 40, 1050–1066.

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, 93, 485–498.

Thornhill, A. H., Baldwin, B. G., Freyman, W. A., Nosratinia, S., Kling, M. M., Morueta-Holme, N., ... Mishler, B. D. (2017). Spatial phylogenetics of the native California flora. *BMC Biology*, 15, 96.

Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences USA*, 106(Supplement_2), 19729–19736.

Zhang, J., Nielsen, S. E., Chen, Y., Georges, D., Qin, Y., Wang, S.-S., ... Thuiller, W. (2017). Extinction risk of North American seed plants elevated by climate and land-use change. *Journal of Applied Ecology*, 54, 303–312.

Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biology*, 18, 1042–1052.

BIOSKETCH

DIANA STRALBERG is a macroecologist and conservation biologist interested in understanding the climatic, physical and biogeographic drivers of species and ecosystem distributions, with an emphasis on climate-change projection and conservation planning priorities.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

DATA ACCESSIBILITY

Data inputs and derived metrics can be accessed at adaptwest.databasin.org.

How to cite this article: Stralberg D, Carroll C, Pedlar JH, Wilsey CB, McKenney DW, Nielsen SE. Macrorefugia for North American trees and songbirds: Climatic limiting factors and multi-scale topographic influences. *Global Ecol Biogeogr*. 2018;27:690–703. <https://doi.org/10.1111/geb.12731>