Research

Biogeography of boreal passerine range dynamics in western North America: past, present, and future

Diana Stralberg, Steven M. Matsuoka, Colleen M. Handel, Fiona K. A. Schmiegelow, Andreas Hamann and Erin M. Bayne

D. Stralberg (diana.stralberg@ualberta.ca) and E. M. Bayne, Dept of Biological Sciences, Univ. of Alberta, Edmonton, AB, Canada. – S. M. Matsuoka and C. M. Handel, US Geological Survey, Alaska Science Center, Anchorage, AK, USA. – F. K. A. Schmiegelow, A. Hamann and DS, Dept of Renewable Resources, Univ. of Alberta, Edmonton AB, Canada.

Many of the Neotropical migrant bird species that breed throughout the Canadian boreal region are not found in the Alaskan boreal region, separated by the northwestern cordilleran mountains, despite the presence of climatically suitable habitat. We asked whether biological or climatic factors constrain certain species from crossing this geographic barrier. Analyzing a comprehensive dataset for 80 boreal passerine species, we used phylogenetic logistic regression to evaluate the relative importance of physical, migratory and competition metrics versus current and paleoclimatic suitability factors. Controlling for current climatic suitability within boreal Alaska, we found that species with the greatest climatic suitability across the northwestern cordillera, presently and also during the mid-Holocene period, were most likely to be regular breeders in the Alaskan boreal region. Migratory strategy also played a role, but could not be disentangled from its strong phylogenetic basis. Our analysis suggests that the perceived barrier of the northwestern cordillera may be easily weakened as climate change improves conditions there for many forest species. The weakening of this barrier may lead to relatively rapid range expansions and the reshuffling of species communities. Species' realized distributional shifts will be a function of the interplay between a changing climate and static topographic features.

Physiographic barriers to recolonization post glaciation are reflected in current species' distributions and diversity patterns at high latitudes, especially in Europe (Svenning and Skov 2004, Fløjgaard et al. 2011, Hortal et al. 2011). North American distributions are generally less constrained, in that major mountain ranges have a north-south rather than east-west orientation, thus facilitating northward expansion of species. However, portions of the western cordilleran mountain ranges that stretch across western North America may have served as barriers to longitudinal expansion for some species. During glacial periods of the Pleistocene epoch, widespread North American temperate and boreal bird species are presumed to have retracted their ranges into geographically isolated refugia, leading to the divergence of sister taxa and ultimately to speciation (Mengel 1964, Johnson and Cicero 2004, Weir and Schluter 2004, Lovette 2005). During alternating interglacial periods, the western cordillera has served to further isolate many species' populations, contributing to the formation of distinct eastern and western subspecies (Milot et al. 2000).

The current North American boreal biome is geographically extensive, spanning from Alaska to Newfoundland, but it is disrupted by the northern portion of the western cordillera, hereafter referred to as the 'northwestern cordillera' (Fig. 1). Although most boreal tree species (with the exception of *Abies balsamea*) and many bird species occur on both sides of the cordilleran mountain ranges, passerine diversity is higher on the Canadian side of the cordillera than in the Alaskan boreal region (Distler et al. 2015). Many of the Neotropical migrant species that breed throughout the Canadian boreal region are not found in Alaska, despite the presence of climatically suitable habitat, e.g. Tennessee warbler *Oreothlypis peregrina*, palm warbler *Setophaga palmarum*, Cape May warbler *S. tigrina*, and bay-breasted warbler *S. castanaea* (Stralberg et al. 2015b). Predicted suitable Alaskan habitats for these and other species are largely discontiguous with current Canadian boreal breeding ranges (Fig. 2). Presumably, geographic barriers to movement or competition from closely related taxa have prevented some species of eastern origins from crossing the northwestern cordillera into the Alaskan boreal region (Fig. 3).

At the last glacial maximum (LGM) ~ 20 000 yr before present (YBP), boreal forest tree species (e.g. *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Abies balsamea*, *Populus tremuloides*, *Betula papyrifera*) were displaced to a contiguous boreal forest refugium in the southeastern United States, according to vegetation reconstructions based on pollen data from sediment cores (Overpeck et al. 1992, Jackson et al. 2000, Dyke 2005). Trees that recolonized the North American boreal region during the late Pleistocene and early

Figure 1. North American ecoregions. CEC (1997) level II ecoregions used in analysis: 3.1 Alaska Boreal Interior (study area); 3.2 Taiga Cordillera; 3.3 Taiga Plain; 5.4 Boreal Plain; 6.1 Boreal Cordillera. Additional ecoregions evaluated for last glacial maximum projections (portions above 30°N latitude): 6.2, 7.1, 10.1–2, 11.1 (western); 8.1–5, 9.2–4 (eastern). Northwestern cordilleran ecoregions (3.2 and 6.1) are shown with stippled pattern. Boreal ecoregions are shown in gray. Map projection is Lambert azimuthal equal-area.

Holocene epochs are generally assumed to have originated from this single refugium. Thus, if boreal birds require those tree species as habitat, it is plausible that most birds colonized the boreal forest from this eastern refugium post glaciation. That many migratory birds seem to follow an eastern migration route supports this hypothesis. However, genetic evidence suggests that small pockets of white spruce *Picea glauca* and other boreal tree species may have persisted as cryptic refugia in Beringia (Anderson et al. 2006). Furthermore, many boreal bird species have wide-ranging distributions and are capable of using a wide variety of boreal and non-boreal tree species as habitat. Thus, today's boreal bird species may have had multiple geographically isolated refugia across North America during the Pleistocene epoch. Genetic evidence from a few species like Swainson's thrush *Catharus ustulatus*, Wilson's warbler *Cardellina pusilla*, and yellow warbler *Setophaga petechia* support a multiple refugia hypothesis (Milot et al. 2000, Clegg et al. 2003, Ruegg et al. 2006, 2014b).

Also of interest is the relatively warm Holocene climatic optimum (mid-Holocene) ~ 6000 YBP, which may have

allowed some species to cross the northwestern cordillera via short-term connections of climatically suitable habitat. The mid-Holocene warm period may have been similar to future projected conditions under increased CO_2 levels (Strong and Hills 2003). Therefore, species with projected mid-Holocene climatic suitability across the northwestern cordillera should have been more likely to successfully colonize the Alaskan boreal region than species with no such historical opportunities, assuming that species' northern limits are primarily climate-limited (MacArthur 1972, Root 1988).

To the extent that avian distributions, or parts thereof, are climate-driven (Jiménez-Valverde et al. 2011, Cumming et al. 2014), paleoclimate reconstructions can be used in a niche-modelling framework to hindcast species' distributions (Kerr and Dobrowski 2013). LGM hindcasts identify locations of probable glacial refugia for extant species (Huntley et al. 2013, Levinsky et al. 2013). These can then be used to generate hypotheses about migratory route origins (Ruegg et al. 2006) or about the current population structure of individual species (Ralston and Kirchman 2012).
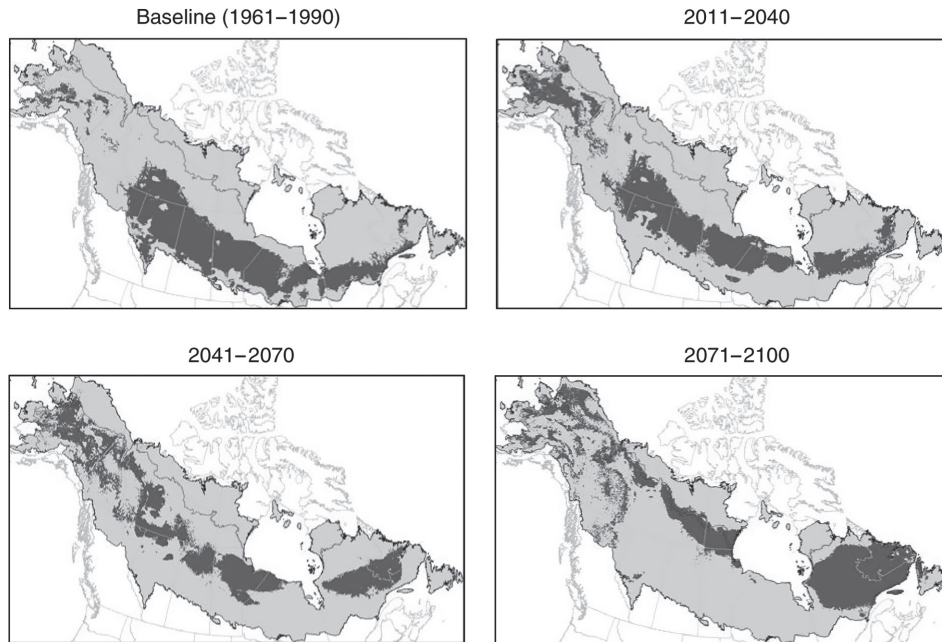
Figure 2. Climatically suitable core habitat for an example species in current and future time periods. Climatically suitable habitat (gray) for Tennessee warbler *Oreothlypis peregrina*. Data are from Stralberg et al. (2015b). Discontinuous patches of suitable habitat with the Alaska Boreal Interior are currently unoccupied by regularly breeding birds although territorial singing males have recently been documented there (Gibson 2011).

Factors other than climate may also explain the exclusion of bird species from the Alaskan boreal region. Despite the tremendous mobility of migratory birds, their ties to southern wintering grounds and fidelity to migratory routes may reinforce geographic separation. Long-distance migrants have been shown to exhibit less longitudinal variation in their ranges than resident species, despite greater mobility (Böhning-Gaese et al. 1998). Strong genetic programming of migration timing (Both et al. 2006, Stanley et al. 2012) also suggests greater dispersal constraints on long-distance migrants, and the added energetic costs of longer migration routes may limit resources required for the exploration of new suitable habitat.

Indeed, among passerines, almost all resident species in the North American boreal region have broad distributions and occur on both the Alaskan and Canadian sides of the cordillera – e.g. boreal chickadee *Poecile hudsonicus* and gray jay *Perisoreus canadensis*. They also tend to occupy high-elevation habitats, among others, providing range contiguity across the northwestern cordillera. Many cold-adapted winter residents such as chickadees (Paridae) and nuthatches (Sittidae) have pan-boreal (i.e. Eurasian) origins and a long evolutionary history in cold climates (Mayr 1946). Conversely, many migratory species of the Canadian boreal forest do not occur west of the cordillera in boreal Alaska. Most of these belong to the New World warblers (Parulidae), a group that has experienced fairly recent (Pliocene) diversification from its Neotropical origins, especially within the *Setophaga* (formerly *Dendroica*) genus (Lovette and Bermingham 1999).

Passerine species that breed predominantly in Nearctic boreal regions tend to migrate to wintering grounds in Central or South America. Those that breed regularly in boreal Alaska, e.g. blackpoll warbler *Setophaga striata*, alder flycatcher *Empidonax alnorum*, and gray-cheeked thrush *Catharus minimus*, all have boreal distributions across the northwestern cordillera, and are thought to migrate along eastern migratory corridors (Lowther 1999, Lowther et al. 2001, DeLuca et al. 2013), suggesting eastern distributional origins. Alaskan boreal populations of widespread migratory species such as Swainson's thrush and yellow warbler are also thought to follow eastern migratory routes to Central and South American wintering sites, even though coastal Alaska populations use shorter western migratory routes (Ruegg et al. 2006). Other migratory species in boreal Alaska generally have shorter migration routes, wintering in the United States and/or northern Mexico – e.g. Townsend's warbler *Setophaga townsendi*, ruby-crowned kinglet *Regulus calendula*, and yellow-rumped warbler *Setophaga coronata*. Thus the passerine avifauna of boreal Alaska appears to lack western long-distance migrants.

Passage across the northwestern cordillera between Alaska and Canada involves environmentally harsh landscapes at high elevations and/or northern latitudes. Although the likelihood that individuals breed at or near their place of origin (natal philopatry) is thought to be lower in migratory species than in resident species, isolated populations are thought to exhibit higher rates of natal philopatry (Weatherhead and Forbes 1994, Hobson et al. 2004). This suggests that species may fill spatially contiguous suitable habitats first and may be less likely to colonize areas that are spatially disjunct at a broad spatial extent. Likewise, small, disjunct populations are more likely to become extinct (MacArthur and Wilson 1963). The relatively young age of the boreal forest also translates into fewer opportunities for chance colonization events of habitat west of the cordillera.
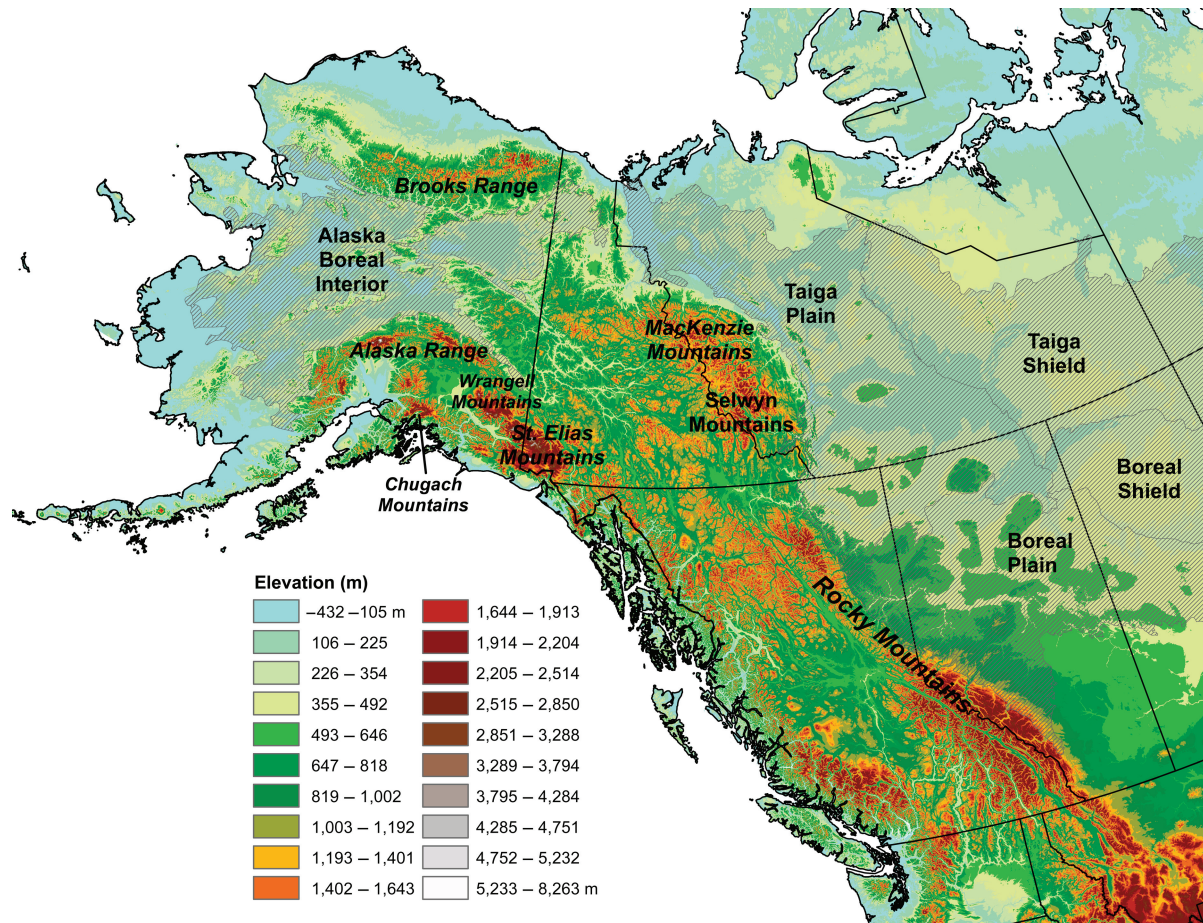
Figure 3. Northwestern cordilleran mountain ranges that present potential barriers between non-mountain boreal ecoregions in Canada and Alaska. Non-mountain boreal ecoregions, as mapped by the CEC (1997), are indicated by cross-hatching: Alaska Boreal Interior, Taiga Plain, Taiga Shield, Boreal Plain, and Boreal Shield. Only the northernmost portion of the Rocky Mountains was considered in our analysis (Fig. 1). Map projection is Yukon Albers equal-area conic.

For many species with refugia in the eastern U.S. at the end of the LGM, environmentally suitable connections across the cordillera may not yet have developed, or enough time may not yet have elapsed for birds to disperse across them.

The reason for exclusion of some species from the Alaskan boreal region has implications for expected outcomes of projected climate change. Almost all Canadian boreal species that are not currently found in the Alaskan boreal region are projected to experience increased climatic suitability in Alaska within the next 30–90 yr (Stralberg et al. 2015b). How likely are these projected distributional shifts for different species? Will the northwestern cordillera provide an effective barrier to range shifts? Or will increased connectivity of suitable climates facilitate northwestern migration of Canadian boreal species into Alaska? We proposed that for each boreal species not currently found in the Alaskan boreal region there are two potential explanations for their exclusion, with contrasting implications for future climate change outcomes: 1) the northwestern cordillera constitutes a long-term barrier to birds as a function of life-history characteristics, including a) migratory strategy or distance; b) physical traits; or c) competition from recently diverged congeneric species. That is, suitable habitat in Alaska is not occupied due to evolutionary constraints that

may or may not respond to changing selection pressures in the future. 2) The northwestern cordillera constitutes a temporary barrier to birds as a function of climate and glaciation history. That is, suitable habitat in Alaska is not occupied by many migratory species due to climate factors during and after the last glacial maximum, including a) a current lack of suitable habitat connectivity across the northwestern cordillera connecting Canada and Alaska; b) a lack of mid-Holocene habitat suitability within boreal Alaska or across the northwestern cordillera; and/or c) distance from LGM glacial refugia (i.e. eastern vs western U.S. or Beringia).

If migratory strategy, interspecific competition, or physical factors constrain species from crossing the cordillera, this could result in major range constrictions among boreal specialists in the future, as southern range boundaries shift northward without compensation in the north. If it is simply a matter of climatic habitat connectivity, however, distributional shifts could occur in the future as soon as contiguous suitable climates become available. In some cases, this may involve a time lag due to the time required for forest growth and succession to catch up with the altered climate (Stralberg et al. 2015a). The relative importance of these various constraints is likely to vary by species and phylogenetic origin.

In this study, we conducted a phylogenetic regression analysis to assess the relative importance of life-history characteristics versus post-glaciation climatic factors on the current distributions of North American boreal-breeding species west of the northwestern cordillera in the Alaskan boreal region. We tested the following hypotheses: 1) that lack of connected, climatically suitable habitat prevented some species of eastern origins from crossing the northwestern cordillera into the Alaskan boreal region; 2) that species with very distant eastern LGM refugia were less likely to successfully colonize the Alaskan boreal region than those with western refugia; 3) that species with possible Beringian LGM refugia are more likely to presently occur in boreal Alaska than those without; and 4) that certain life-history traits or competition from closely related taxa have inhibited some species from occupying the Alaskan boreal region. We then used the results of the most supported models of current distribution to predict which species are most likely to shift their distributions from Canada into boreal Alaska in the future based on projected climatic suitability in the northwestern cordillera. To our knowledge, this is the first phylogenetic consideration of the potential interplay between a changing climate and static topographic features in determining future species' distributions.

Methods

Study area and species

We evaluated potential drivers of breeding population occurrence within the Alaskan boreal region for 80 boreal forest songbird species for which species distribution models were available (Stralberg et al. 2015b). All of these species were predicted to have suitable climates for breeding within the approximately 400 000 km² Alaskan boreal region (Table 1). We defined the Alaskan boreal region as the Alaska Boreal Interior (3.1) level II ecoregion, an ecological region that is separated from the Western Taiga Plain (3.3) and Boreal Plain (5.4) by the northwestern cordillera, defined as adjacent Taiga Cordillera (3.2) and Boreal Cordillera (6.1) ecoregions (CEC 1997) (Fig. 1). We used recently compiled information on breeding distribution of birds in Alaska (Gibson 2011, Gibson and Withrow 2015) to determine which of the 80 species are currently considered regular breeders in the Alaska Boreal Interior region (Table 1). To quantify climatically suitable areas for each species, we used density-based boosted regression tree (BRT) models previously developed using a standardized avian survey dataset from across northern North America (Cumming et al. 2010). The model extent included boreal, hemi-boreal and other sub-boreal regions containing climates projected to move northward into the current boreal region within the next century (Stralberg et al. 2015b). Log-transformed survey- and species-specific correction factors derived by Sólymos et al. (2013) were used as offsets in a Poisson generalized boosted model (GBM) to model avian density (males per ha). Density offsets were previously generated by fitting distance sampling (Buckland et al. 2001) and removal models (Sólymos et al. 2013) across multiple distance and time intervals to account for differences in survey methods

and environmental conditions. Model-predicted density estimates were used to project the amount of suitable habitat anticipated within the Alaska Boreal Interior ecoregion (see below).

Paleo-hindcasting

To represent paleoclimate conditions, we obtained temperature and precipitation anomalies for 6000 (mid-Holocene, MH) and 21 000 YBP (last glacial maximum, LGM) based on millennial equilibrium projections from two U.S. global climate models (GCM) that were part of the Paleoclimate Modelling Intercomparison Project, Phase II: 1) the community climate model ver. 1 (CCM1) developed by the National Center for Atmospheric Research (Kutzbach et al. 1998) and 2) the Geophysical Fluid Dynamics Laboratory (GFDL) model, from the National Oceanic and Atmospheric Administration. Monthly temperature and precipitation anomalies were combined with 4-km 1961–1990 baseline interpolated climate data < http://esapubs.org/archive/appl/A025/005/suppl-1.php > (Stralberg et al. 2015b) to develop millennial-scale hindcasts for average monthly climate conditions (Roberts and Hamann 2015). We converted these monthly variables to bioclimatic indices (Table 2) and used them as inputs to existing BRT models of avian density developed from current climate data (Stralberg et al. 2015b). Eleven bootstrap replicates (constrained by computation time) were averaged to create a single mean density map for each period. For cross-species comparisons, we converted density estimates within 4 km × 4 km grid cells for each species to binary estimates of its suitable core habitat, defined as areas where the species' predicted density exceeded its mean baseline predicted density within the boreal and sub-boreal model-building area (Stralberg et al. 2015a). Although somewhat arbitrary, the mean density threshold that we used to define core habitat is analogous to prevalence-based thresholds for probability of occurrence models, which yield high predictive performance compared to other threshold criteria (Freeman and Moisen 2008). Visual map inspection confirmed that these thresholds resulted in maps that were well aligned with published range maps outside of Alaska. Maps of current predictions and hindcasts for each species and GCM are provided in Supplementary material Appendix 1 (CCM1) and Appendix 2 (GFDL).

Climate suitability variables

To compare modern connectivity of suitable climates across the northwestern cordillera to that of the mid-Holocene period, we calculated the total model-predicted core area for current and mid-Holocene periods within the Taiga Cordillera (3.2) and Boreal Cordillera (6.1) ecoregions combined (Fig. 1; Supplementary material Appendix 3). We deemed traditional landscape connectivity metrics (sensu McGarigal and Marks 1995) inappropriate to address the broad temporal and spatial scales of interest and used a simple metric for climatic connectivity. We assessed climatic connectivity with a one-sided paired t-test to determine whether the mean total amount (log-transformed) of

Table 1. Range characteristics of 80 boreal study species. Species currently occurring as regular breeders in the Alaska Boreal Interior (AKBreed) according to Gibson (2011) or Gibson and Withrow (2015) are indicated by '1'. Breeding ranges are characterized as boreal/arctic (BA), boreal + western (BW), boreal + eastern (BE), or WR (wide-ranging), and migratory strategy is characterized as R (winter resident), LD (long-distance migrant), or SD (short-distance migrant).

Code	Common name (Scientific name)	AKBreed	Breed range	Mig. strat.
Tyrannidae				
OSFL	Olive-sided flycatcher *Contopus cooperi*	1	WR	LD
WEWP	Western wood-pewee *Contopus sordidulus*	1	BW	SD
YBFL	Yellow-bellied flycatcher *Empidonax flaviventris*	0	BE	LD
ALFL	Alder flycatcher *Empidonax alnorum*	1	BE	LD
LEFL	Least flycatcher *Empidonax minimus*	0	WR	LD
EAPH	Eastern phoebe *Sayornis phoebe*	0	BE	SD
EAKI	Eastern kingbird *Tyrannus tyrannus*	0	BE	LD
Vireonidae				
BHVI	Blue-headed vireo *Vireo solitarius*	0	BE	SD
PHVI	Philadelphia vireo *Vireo philadelphicus*	0	BE	LD
WAVI	Warbling vireo *Vireo gilvus*	0	WR	LD
REVI	Red-eyed vireo *Vireo olivaceus*	0	BE	LD
Corvidae				
GRAJ	Gray jay *Perisoreus canadensis*	1	BW	R
BLJA	Blue jay *Cyanocitta cristata*	0	BE	R
AMCR	American crow *Corvus brachyrhynchos*	0	WR	SD
CORA	Common raven *Corvus corax*	1	WR	R
Alaudidae				
HOLA	Horned lark *Eremophila alpestris*	1	WR	SD
Hirundinidae				
TRES	Tree swallow *Tachycineta bicolor*	1	WR	LD
Paridae				
BCCH	Black-capped chickadee *Poecile atricapillus*	1	WR	R
BOCH	Boreal chickadee *Poecile hudsonicus*	1	BA	R
Sittidae				
RBNU	Red-breasted nuthatch *Sitta canadensis*	1	WR	R
Certhiidae				
BRCR	Brown creeper *Certhia americana*	1	WR	R
Troglodytidae				
WIWR	Winter wren *Troglodytes hiemalis*	0	WR	SD
Regulidae				
GCKI	Golden-crowned kinglet *Regulus satrapa*	1	WR	SD
RCKI	Ruby-crowned kinglet *Regulus calendula*	1	WR	SD
Turdidae				
GCTH	Gray-cheeked thrush *Catharus minimus*	1	BA	LD
SWTH	Swainson's thrush *Catharus ustulatus*	1	WR	LD
HETH	Hermit thrush *Catharus guttatus*	1	WR	SD
AMRO	American robin *Turdus migratorius*	1	WR	SD
VATH	Varied thrush *Ixoreus naevius*	1	BW	SD
Bombycillidae				
CEDW	Cedar waxwing *Bombycilla cedrorum*	0	WR	SD
Motacillidae				
AMPI	American pipit *Anthus rubescens*	1	BW	SD
Fringillidae				
PIGR	Pine grosbeak *Pinicola enucleator*	1	BW	R
PUFI	Purple finch *Haemorhous purpureus*	0	WR	SD
WWCR	White-winged crossbill *Loxia leucoptera*	1	BW	R
CORE	Common redpoll *Acanthis flammea*	1	BA	R
PISI	Pine siskin *Spinus pinus*	1	BW	SD
AMGO	American goldfinch *Spinus tristis*	0	WR	SD
EVGR	Evening grosbeak *Coccothraustes vespertinus*	0	BW	R
Parulidae				
OVEN	Ovenbird *Seiurus aurocapilla*	0	BE	LD
NOWA	Northern waterthrush *Parkesia noveboracensis*	1	WR	LD
BAWW	Black-and-white warbler *Mniotilta varia*	0	BE	LD
TEWA	Tennessee warbler *Oreothlypis peregrina*	0	BE	LD
OCWA	Orange-crowned warbler *Oreothlypis celata*	1	WR	SD
NAWA	Nashville warbler *Oreothlypis ruficapilla*	0	WR	LD
CONW	Connecticut warbler *Oporornis agilis*	0	BE	LD
MOWA	Mourning warbler *Geothlypis philadelphia*	0	BE	LD
COYE	Common yellowthroat *Geothlypis trichas*	0	WR	SD

(Continued)

Table 1. (Continued)

Code	Common name (Scientific name)	AKBreed	Breed range	Mig. strat.
AMRE	American redstart *Setophaga ruticilla*	0	WR	LD
CMWA	Cape May warbler *Setophaga tigrina*	0	BE	LD
MAWA	Magnolia warbler *Setophaga magnolia*	0	BE	LD
BBWA	Bay-breasted warbler *Setophaga castanea*	0	BA	LD
BLBW	Blackburnian warbler *Setophaga fusca*	0	BE	LD
YWAR	Yellow warbler *Setophaga petechia*	1	WR	LD
CSWA	Chestnut-sided warbler *Setophaga pensylvanica*	0	BE	LD
BLPW	Blackpoll warbler *Setophaga striata*	1	BA	LD
PAWA	Palm warbler *Setophaga palmarum*	0	BE	LD
YRWA	Yellow-rumped warbler *Setophaga coronata*	1	WR	SD
BTNW	Black-throated green warbler *Setophaga virens*	0	BE	LD
CAWA	Canada warbler *Cardellina canadensis*	0	BE	LD
WIWA	Wilson's warbler *Cardellina pusilla*	1	WR	LD
Emberizidae				
ATSP	American tree sparrow *Spizelloides arborea*	1	BA	SD
CHSP	Chipping sparrow *Spizella passerina*	1	WR	SD
CCSP	Clay-colored sparrow *Spizella pallida*	0	BE	LD
VESP	Vesper sparrow *Pooecetes gramineus*	0	WR	SD
SAVS	Savannah sparrow *Passerculus sandwichensis*	1	WR	SD
LCSP	Le Conte's sparrow *Ammodramus leconteii*	0	BE	SD
FOSP	Fox sparrow *Passerella iliaca*	1	BW	SD
SOSP	Song sparrow *Melospiza melodia*	0	WR	SD
LISP	Lincoln's sparrow *Melospiza lincolnii*	1	WR	SD
SWSP	Swamp sparrow *Melospiza georgiana*	0	BE	SD
WTSP	White-throated sparrow *Zonotrichia albicollis*	0	BE	SD
WCSP	White-crowned sparrow *Zonotrichia leucophrys*	1	WR	SD
DEJU	Dark-eyed junco *Junco hyemalis*	1	WR	SD
Cardinalidae				
WETA	Western tanager *Piranga ludoviciana*	0	BW	LD
RBGR	Rose-breasted grosbeak *Pheucticus ludovicianus*	0	BE	LD
Icteridae				
RWBL	Red-winged blackbird *Agelaius phoeniceus*	1	WR	SD
RUBL	Rusty blackbird *Euphagus carolinus*	1	BA	SD
BRBL	Brewer's blackbird *Euphagus cyanocephalus*	0	WR	SD
COGR	Common grackle *Quiscalus quiscula*	0	BE	SD
BHCO	Brown-headed cowbird *Molothrus ater*	0	WR	SD

suitable core habitat available for 80 species of boreal passerines within the cordillera during the mid-Holocene was significantly greater than that currently available, and found that it was not (p > 0.05 for both CCM1 and GFDL). However, the amount of mid-Holocene suitable core habitat was greater than current suitable core habitat for some species and GCMs (Supplementary material Appendix 3). Thus we retained these variables for modelling purposes.

To test the potential effects of the location of LGM refugia on the likelihood of a species currently occurring in the Alaskan boreal region, we first used BRT model projections to estimate for each species the area of LGM suitable core habitat available as glacial refugia in eastern U.S. ecoregions: Eastern Temperate Forests (ecoregion numbers 8.2–8.5) and Great Plains (9.2–9.4), vs western U.S. ecoregions: Western Cordillera (6.2), Marine West Coast Forest (7.1), Cold Deserts (10.1), and Mediterranean California (11.1) (Fig. 1; Supplementary material Appendix 3). We then calculated a log-transformed ratio of the area in eastern versus western refugia, which ranged from –0.84 (strongly

Table 2. Mean bioclimatic variable values by time period, boreal ecoregion, and GCM. Northwestern Cordillera = Taiga Cordillera + Boreal Cordillera. MH = Mid-Holocene. GFDL and CCM1 are global climate models (GCM).

	Northwestern Cordillera			Alaska Boreal Interior		
Variable	Current	MHGFDL	MHCCM1	Current	MHGFDL	MHCCM1
Mean cold month temperature (°C)	–20.5	–21.1	–15.6	–21.7	–22.3	–14.6
Mean warm month temperature (°C)	11.5	13.1	12.7	14.8	16.0	15.8
Chilling degree days ($<0°C$)	2945	2986	2628	3164	3188	2716
Growing degree days ($>5°C$)	630	682	743	967	995	1102
Extreme minimum temperature (°C)	–50.0	–47.1	–49.8	–51.8	–48.7	–54.0
Annual temperature difference (°C)	32.1	34.1	28.3	36.5	38.3	30.4
Annual climatic moisture index (mm)	41.5	41.5	48.6	14.0	16.9	12.8
Summer climatic moisture index (mm)	5.2	4.8	5.5	–2.3	1.6	–2.1
Mean summer precipitation (mm)	358	364	406	257	309	277

western LGM distribution) to 4.24 (strongly eastern). We also calculated the (log-transformed) area of LGM suitable core habitat contained in the ice-free Alaska Boreal Interior (Beringian refugia) (Anderson et al. 2006). See Table 3 for a list of all climate suitability variables.

Life-history variables

For each species, we used Birds of North America species accounts (Poole 2005) to summarize a suite of life history characteristics, selected a priori, that were related to migratory strategy, physical traits, and feeding and habitat guilds (Table 3). To address congeneric exclusion, we calculated an index of competition from related taxa currently occupying the Alaska Boreal Interior ecoregion. For our 80 study species and closely related taxa, we downloaded a random subset of 500 equally likely phylogenetic trees, compiled in a Bayesian framework (<birdtree.org>, Jetz et al. 2012) based on full trees from the Hackett et al. (2008) backbone (see example tree in Fig. 4). Using the 'ape' package (Paradis et al. 2004) for R ver. 3.1.2 (R Core Team), we calculated

correlations among species pairs based on the lengths of shared branches (Garland and Ives 2000), and then averaged those resulting phylogenetic correlation matrices (Martins and Hansen 1997). For each of our 80 study species, the maximum pairwise correlation between that species and other species defined as regular breeders in the Alaskan boreal region (Gibson 2011, Gibson and Withrow 2015) was used as an index of competition pressure (Supplementary material Appendix 4). We did this rather than restricting our focus to sister species because we found no true boreal sister species that do not already co-occur in the Canadian boreal region. The closest geographically separated pair, black-throated green and Townsend's warbler *Setophaga virens* and *S. townsendi*, are no longer considered sister taxa based on molecular data (Johnson and Cicero 2004).

Phylogenetic logistic regression analysis

We used phylogenetic logistic regression analysis (Ives and Garland 2010) to evaluate the relative influence of each climate-suitability and life-history variable on current

Table 3. Climate and life-history variables included in phylogenetic logistic regression analysis. See Fig. 1 for ecoregion definitions. GCM = global climate model: CCM1 = NCAR community climate model, ver. 1 GFDL = Geophysical Fluid Dynamics laboratory model. Model ID relates variables to candidate models in Table 4.

| Category	Sub-category	Variable abbreviation	Model ID	Variable description
Climatic suitability	Current	CurrCordillera	A	Log-transformed area of current suitable habitat contained in the Boreal and Taiga Cordillera ecoregions
	Mid-Holocene (MH, 6000 YBP)	MHCordilleraCCM1 MHCordilleraGFDL	B C	Log-transformed area of GCM-predicted MH suitable habitat contained in the Boreal and Taiga Cordillera ecoregions
		MHCordDiffCCM1 MHCordDiffGFDL	N/A	Log-transformed difference between area of current suitable habitat and GCM-predicted MH suitable habitat (used only in combined model with CurrCordillera)
	Last Glacial Maximum (LGM, 21000 YBP)	LGMEastCCM1 LGMEastGFDL	D E	Ratio of log-transformed area of GCM-predicted LGM suitable habitat (glacial refugia) contained in eastern U.S. ecoregions to area of LGM suitable habitat contained in western U.S. ecoregions
		LGMAlaskaCCM1 LGMAlaskaGFDL	F G	Log-transformed area of LGM suitable habitat contained in the Alaska Boreal Interior ecoregion
Life history	Migratory strategy	Resident SDMigrant	H	Migratory status (LDMigrant as contrast)
		LatMean LatMax LonMean	H	Mean and maximum latitude, and mean longitude of species' wintering range (courtesy of S. Crawford and T. Rich)
		SAWinter	H	Approximate proportion of wintering grounds in South America (0/0.5/1) (Poole 2005)
	Physical traits and habitat	Mass	I	Log-transformed mean body size (g) (Poole 2005)
		ClutchSize	I	Mean clutch size (Poole 2005)
		Insectivore Frugivore	I	Primary feeding guild (omnivore as contrast) (Poole 2005)
		Forest Woodland Shrub Wetland	I	Primary habitat association (grassland as contrast) (Poole 2005)
	Competition	Compet	J	Maximum phylogenetic correlation coefficient with species currently in Alaska Boreal Interior
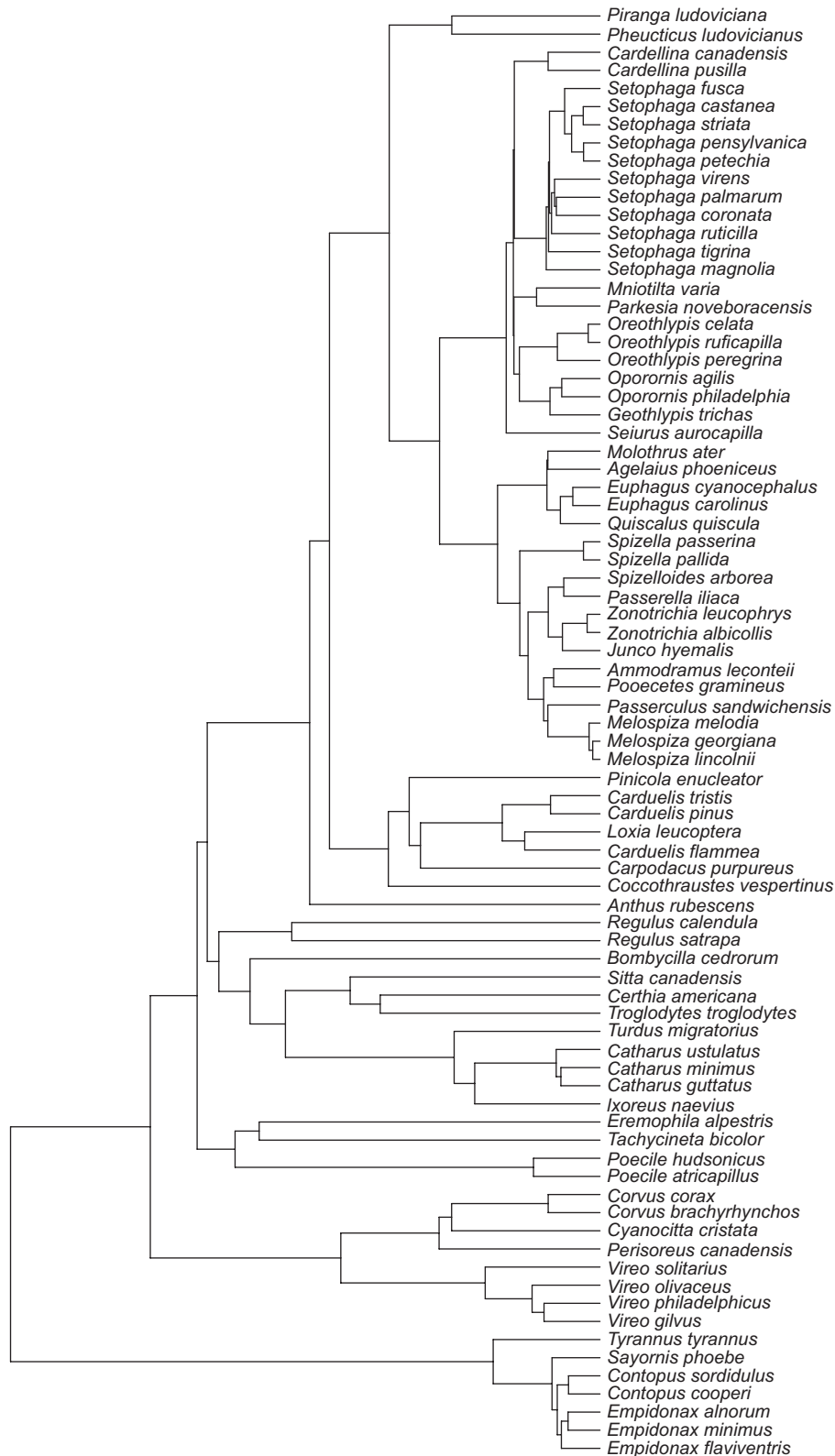
Figure 4. Sample phylogeny for the 80 boreal-breeding species analyzed. One of 500 phylogenies (each considered equally likely) obtained from <www.birdtree.org> (Jetz et al. 2012).

presence/absence of species as regular breeders in the Alaska Boreal Interior while accounting for trait covariance among related species. We included log-transformed area of current suitable core habitat within the Alaska Boreal Interior as an offset in the models to account for current climatic suitability for each species. Correlation matrices for 500 phylogenetic trees, as described above, were used to conduct a series of phylogenetic logistic regression analyses using the 'phylolm'

package (Tung Ho and Ané 2014) for R, which uses an iterative penalized quasi-likelihood approach to estimate the phylogenetic parameter or transition rate, α, and covariate coefficients, β. Results from the 500 models were averaged for interpretation.

We used a stepped approach for testing models. We first developed a phylogenetic logistic regression model for each a priori subcategory of life-history and climate covariates (Table 3) to assess the relative explanatory power of each, including log-transformed current predicted Alaska Boreal Interior core area for each species as an offset. Continuous independent variables were standardized to a mean of zero and standard deviation of 1 to allow for comparison of resulting model coefficients. We then combined variables from top individual climatic and life-history models based on Akaike's information criterion corrected for small sample sizes (AICc scores), dropped non-explanatory variables, and evaluated support for alternative combined models compared with the offset-only null model (based on AICc and Pseudo-R²). We also evaluated the importance of individual coefficients and α values, and calculated the area under the curve (AUC) of the receiver operating characteristics (ROC) plot for the average model using the 'AUC' package for R (Ballings and Van den Poel 2013).

Finally, to evaluate the influence of phylogenetic correlation, we compared coefficients from phylogenetic logistic regression models with those from standard logistic regression models containing the same terms.

Evaluating future habitat potential

We used AICc differences (Δ_i) to identify the top-ranking combined models for current species occurrence and assign weights to each model (Burnham and Anderson 2002). To predict future occupancy, we replaced current estimated cordilleran habitat suitability values with mean future climate-change projected values, where applicable, for three future time periods: 2011–2040 (2020s), 2041–2070 (2050s), and 2071–2100 (2080s), based on projections from Stralberg et al. (2015b). Projections from each model were multiplied by AICc weights ($\exp(-0.5^*\Delta_i)$) and then summed together to obtain an AICc-weighted model-averaged projection. We used current mean prevalence (in our case, 38/80 species currently in Alaska, or $p > 0.475$) as the presence/absence threshold, as recommended by Freeman and Moisen (2008).

Results

Model fit and variable importance

Among phylogenetic logistic regression models that used a single set of climatic factors or life-history traits to explain the current occurrence of species regularly breeding in the Alaskan boreal region, we found greatest support for the model based on current northwestern cordilleran climate suitability (mean AICc difference (Δ_i) = 0; Table 4). The second-ranked model, based on mid-Holocene cordilleran climate suitability (according to the GFDL projection), had much lower support ($\Delta_i = 7.9$). The next three models, which also included past climatic condition variables (mid-Holocene cordilleran climate (CCM1), LGM eastern refugia (CCM1), and LGM Alaska refugia (GFDL)), had about equal but less support than the top two models ($\Delta_i = 16.6$–18.8) (Table 4). Other models that performed better than the null model were (in order): LGM Alaska refugia (CCM1), migratory strategy, and LGM eastern refugia (GFDL). The models based on competition and physical trait variables did not perform better than the null model.

Phylogenetic correlation was highest (i.e. α was lowest) for the model based on mid-Holocene cordilleran climate suitability (GFDL), followed by models based on current and mid-Holocene (CCM1) cordilleran climate suitability, respectively. Other models had α values greater than 5, indicating that no meaningful phylogenetic correlation remained after accounting for migratory strategy, physical traits, competition, LGM refugia, or current climatic suitability of the Alaskan boreal region (null model). In other words, the current and mid-Holocene (GFDL and CCM1) cordilleran climate suitability models were the only models that were not confounded with phylogeny. Other models represent alternative explanations for patterns that could also be driven by phylogeny.

Among the candidate models that combined both climatic and life-history variables, the model that best ($\Delta_i = 0$) predicted occupancy of the Alaskan boreal region included current cordilleran climate suitability (with a positive association, +), the ratio of mid-Holocene (GFDL)

Table 4. AICc scores for candidate phylogenetic logistic regression models. Phylogenetic regression models for species core area within the Alaska Boreal Interior ecoregion were developed for 500 trees; AIC scores and α values (lower value = higher phylogenetic correlation) were averaged across 500 models. Variables included in each model are identified by model ID in Table 3.

Rank	ID	Model	AICc mean	AICc SD	α mean	α SD
1	A	Current northwestern cordilleran climate	59.47	0.113	1.307	1.941
2	C	Mid-Holocene cordilleran climate (GFDL)	67.39	1.767	0.508	1.524
3	B	Mid-Holocene cordilleran climate (CCM1)	76.08	3.741	1.536	2.440
4	D	Last glacial maximum eastern refugia (CCM1)	77.69	0.057	5.025	0.955
5	G	Last glacial maximum Alaska refugia (GFDL)	78.23	0.000	5.279	0.801
6	F	Last glacial maximum Alaska refugia (CCM1)	102.72	0.001	5.643	0.600
7	H	Migratory strategy	108.48	0.001	5.637	0.513
8	E	Last Glacial Maximum eastern refugia (GFDL)	109.47	0.002	5.697	0.580
9		Null model (offset only)	114.70	0.002	5.802	0.494
10	J	Competition	115.50	0.002	5.772	0.519
11	I	Physical traits (+ habitat)	119.41	0.002	5.742	0.543

to current cordilleran climate suitability (+), winter resident status (+), and use of South American wintering grounds (+) (Table 5). Current cordilleran climate suitability had the largest effect size by threefold. Thus, controlling for current climatic suitability within boreal Alaska, species with the greatest climatic suitability across the northwestern cordillera, now and during the mid-Holocene period, were most likely to currently occupy the Alaskan boreal region. Winter resident species were the most likely to occupy the Alaska Boreal Interior, followed by long-distance migrants with South American wintering grounds. That is, among long-distance migrants, those that winter in South America have been the most successful at colonizing the Alaska Boreal Interior.

The second-ranked model ($\Delta_i = 4.5$) included similar coefficients for the variables in the top model, but included the ratio of CCM1-predicted instead of GFDL-predicted MH climate suitability to current climate suitability (+), and also included a positive association with short-distance migrant status (Table 5). Other models contained different combinations of these variables with similar coefficient values. Higher-AICc models also included the CCM1-predicted eastern LGM refugia variable (−). The magnitude of proportion of variance explained (Pseudo-R²) and area-under-the-curve (AUC) values generally coincided with rankings based on AICc. That is, the top-ranked AICc model also had the largest Pseudo-R² (0.64) and largest AUC (0.97).

Compared with standard logistic regression models, the phylogenetic models had smaller coefficients for variables related to migratory strategy, highlighting the strong phylogenetic component to these variables (Table 5). The climatic suitability effects were smaller in the top two phylogenetic models, compared with the non-phylogenetic versions, but larger in some of the other models with negligible phylogenetic correlation.

Model predictions for current and future climate

Among the 42 boreal species not yet breeding regularly in the Alaskan boreal region, we identified six species that should breed there regularly now, according to our model predictions and using the current mean prevalence (0.475) as a threshold (Table 6, Table 7; Supplementary material Appendix 5). Breeding has, however, recently been documented for two of these six species within boreal-adjacent south-central Alaska (Gibson 2011). Among the 38 species that currently breed regularly in the Alaskan boreal region, there were only three species for which the averaged models predicted probabilities below the threshold: American pipit *Anthus rubescens*, horned lark *Eremophila alpestris*, red-winged blackbird *Agelaius phoeniceus*, all of which were either tundra- or wetland-associated (Table 6; Supplementary material Appendix 5).

Model-averaged projections for future periods suggested that up to 31 new species could occur as regular breeders in the Alaska Boreal Interior by the 2020s, up to 38 by the 2050s, and up to 40 by the 2080s (Table 6, Table 7; Supplementary material Appendix 5). Among these, the yellow-bellied flycatcher *Empidonax flaviventris* has just recently been recorded breeding within the Alaska boreal

Table 5. Mean logistic regression model coefficients and model diagnostics. Model coefficients and diagnostics for 7 candidate phylogenetic (P) and standard (non-phylogenetic, NP) logistic regression models of occurrence as a regular breeder in the Alaska Boreal Interior (Fig. 1) for 80 boreal-breeding species (Table 1). AICc scores, pseudo-R² values, and standardized regression coefficients for phylogenetic models were averaged across 100 models, each based on a different phylogenetic tree. Area-under-the-curve (AUC) was derived from mean model predictions.

Rank	/model	Model	AICc mean	AICc SD	Pseudo-R² mean	AUC
1	P	−0.87 + 5.04 × CurrCordillera + 1.70 × MHCordDiffGFDL + 0.66 × Resident + 0.29 × SAWinter	50.79	0.000	0.64	0.97
	NP	−1.01 + 5.35 × CurrCordillera + 1.95 × MHCordDiffGFDL + 0.99 × Resident + 0.34 × SAWinter	51.39		0.52	
2	P	−0.76 + 4.37 × CurrCordillera + 1.37 × MHCordDiffCCM1 + 0.97 × Resident + 0.71 × SDMigrant + 0.78 × SAWinter	55.32	0.002	0.63	0.96
	NP	−0.87 + 4.66 × CurrCordillera + 1.59 × MHCordDiffCCM1 + 1.44 × Resident + 1.00 × SDMigrant + 1.03 × SAWinter	52.79		0.53	
3	P	−0.86 + 3.45 × CurrCordillera + 0.96 × Resident + 0.66 × SDMigrant + 1.09 × SAWinter	58.88	0.001	0.58	0.94
	NP	−0.97 + 3.44 × CurrCordillera + 1.39 × Resident + 0.87 × SDMigrant + 1.34 × SAWinter	56.78		0.46	
4	P	−0.36 + 1.53 × MHCordilleraCMM1 − 1.20 × LGMEastCCM1 + 0.74 × Resident + 0.97 × SDMigrant + 0.76 × SAWinter	68.31	0.531	0.52	0.94
	NP	−0.52 + 1.37 × MHCordilleraCCM1 − 1.44 × LGMEastCCM1 + 1.03 × Resident + 1.11 × SDMigrant + 1.06 × SAWinter	60.00		0.45	
5	P	−0.30 + 1.01 × MHCordilleraGFDL + 1.01 × Resident + 0.98 × SDMig + 0.58 × SAWinter	69.77	0.009	0.48	0.91
	NP	−0.39 + 1.69 × MHCordilleraGFDL + 1.31 × Resident + 1.13 × SDMigrant + 0.72 × SAWinter	63.12		0.39	
6	P	−0.30 + 1.80 × MHCordilleraCCM1 + 0.99 × Resident + 1.17 × SDMig + 0.57 × SAWinter	76.11	0.002	0.43	0.91
	NP	−0.30 + 1.45 × MHCordilleraCCM1 + 1.26 × Resident + 1.27 × SDMig + 0.75 × SAWinter	66.78		0.35	
7	P	−0.40 − 1.49 × LGMEastCCM1 + 0.72 × Resident + 0.53 × SDMigrant + 0.56 × SAWinter	91.08	0.002	0.29	0.84
	NP	−0.42 − 1.25 × LGMEastCCM1 + 1.02 × Resident + 0.72 × SDMigrant + 0.77 × SAWinter	72.90		0.27	

Table 6. Actual numbers of species currently breeding regularly in boreal North America (including those currently in Alaskan boreal and those not yet breeding there); and numbers of those species that are projected to breed regularly in the Alaskan boreal region currently and during future 30-yr periods, based on a mean predicted prevalence threshold (p > 0.475) for AICc–weighted model-averaged predictions (Table 5).

Current regular breeding distribution	Actual current	Projected to breed in Alaskan boreal			
		Current	2011–2040	2041–2070	2071–2100
Entire boreal	80	41	67	74	71
In Alaskan boreal	38	35	36	36	31
Not yet in Alaskan boreal	42	6	31	38	40

region and seven other species have recently been documented either exhibiting territorial behavior in the boreal interior or breeding in south-central Alaska (Gibson, 2011, Gibson and Withrow 2015). The models also predict, however, that among the 38 species that now regularly breed in the Alaskan boreal region, northwest cordilleran climate will remain suitable for as few as 31 of these by 2071–2100 (Table 6; Supplementary material Appendix 5).

Discussion

Despite the demonstrated influence of western cordilleran mountain ranges as barriers leading to vicariance of several wide-ranging North American passerine species (Milot et al. 2000, Kimura et al. 2002, Clegg et al. 2003), our analysis of boreal-breeding passerines suggested that the northern portion of this prominent geographic feature has not generally

Table 7. Species most likely to move into the Alaska Boreal Interior currently and during future 30-yr periods. Classifications are according to AICc-weighted model-averaged predictions using a threshold of p > 0.475 (Table 5). Species shown in bold have had recently documented breeding or territorial behavior in the Alaskan interior or in adjacent south-central Alaska (Gibson 2011, Gibson and Withrow 2015). See Supplementary material Appendix 5 for scientific names and probabilities across species and models.

Rank	Baseline (1961–1990)	2011–2040	2041–2070	2071–2100
1	Common grackle	Common grackle	**Tennessee warbler**	Red-eyed vireo
2	**Brown-headed cowbird**	**Tennessee warbler**	Cedar waxwing	Blue jay
3	Evening grosbeak	Evening grosbeak	Evening grosbeak	Cedar waxwing
4	Warbling vireo	American redstart	American redstart	Blackburnian warbler
5	American redstart	Cedar waxwing	Red-eyed vireo	Mourning warbler
6	**Song sparrow**	**Brown-headed cowbird**	White-throated sparrow	**Common yellowthroat**
7		Warbling vireo	**Common yellowthroat**	Evening grosbeak
8		White-throated sparrow	Common grackle	American redstart
9		**Song sparrow**	Mourning warbler	White-throated sparrow
10		**Purple finch**	**Least flycatcher**	Chestnut-sided warbler
11		**Common yellowthroat**	Blackburnian warbler	Black-and-white warbler
12		Western tanager	Warbling vireo	Ovenbird
13		**Least flycatcher**	**Song sparrow**	Common grackle
14		Red-eyed vireo	Blue jay	Canada warbler
15		Black-throated green warbler	Canada warbler	American goldfinch
16		Palm warbler	**Brown-headed cowbird**	**Least flycatcher**
17		American goldfinch	Black-throated green warbler	**Tennessee warbler**
18		Philadelphia vireo	**Purple finch**	Black-throated green warbler
19		American crow	Ovenbird	Red-breasted grosbeak
20		Vesper sparrow	Black-and-white warbler	Blue-headed vireo
21		**Cape May warbler**	American goldfinch	**Song sparrow**
22		Winter wren	Western tanager	**Purple finch**
23		Ovenbird	**Cape May warbler**	Magnolia warbler
24		Mourning warbler	Chestnut-sided warbler	Warbling vireo
25		Magnolia warbler	Magnolia warbler	Eastern phoebe
26		Swamp sparrow	Bay-breasted warbler	Bay-breasted warbler
27		Brewer's blackbird	Blue-headed vireo	American crow
28		Black-and-white warbler	Philadelphia vireo	Winter wren
29		Blue-headed vireo	Winter wren	Nashville warbler
30		Clay-colored sparrow	American crow	**Cape May warbler**
31		**Yellow-bellied flycatcher**	Red-breasted grosbeak	**Brown-headed cowbird**
32			Nashville warbler	Philadelphia vireo
33			**Yellow-bellied flycatcher**	Connecticut warbler
34			Vesper sparrow	Western tanager
35			Connecticut warbler	**Yellow-bellied flycatcher**
36			Palm warbler	Vesper sparrow
37			Brewer's blackbird	Eastern kingbird
38			Clay-colored sparrow	Swamp sparrow
39				Brewer's blackbird
40				Clay-colored sparrow

been a barrier for boreal species. Although many boreal species do not yet occupy climatically suitable habitat within the Alaskan boreal region, these species appear to be primarily those without climatically suitable habitat connections across the northwestern cordilleran region that bridges Canadian and Alaskan portions of the boreal forest biome. Furthermore, our analysis suggested that species that had more suitable habitat connections during the warmer mid-Holocene period are even more likely to breed in the Alaskan boreal region. These species may have had improved chances for colonization approximately 6000 YBP, supporting the hypothesis that Alaskan boreal occupancy may be a matter of both connectivity and time.

We also found a relatively weak relationship between Alaskan boreal occupancy and predicted LGM refugia south of the ice sheet. Paleoclimate hindcast projections for ~ 21 000 YBP indicated that species with mostly eastern refugia were less likely to have colonized the Alaskan boreal region than those with mostly western refugia, suggesting that the relatively longer distance from eastern refugia may have deterred or delayed some species, and that the Alaskan boreal region may have been colonized from both western and eastern LGM refugia. In general, however, species that are strictly boreal in their current distribution had largely eastern projected LGM refugia, whereas western refugia were associated with wide-ranging species that occur outside the boreal region (Fig. 5). Thus, it is also possible that all species colonized the Alaskan boreal region from eastern refugia, and that western forested refugia were sources of coastal or non-boreal interior populations in Alaska. Species with western refugia could have been more successful at colonizing the Alaskan boreal region due to greater mobility or other factors not directly related to LGM refugia per se.

We found some support for a relationship between potential climatic refugia in Alaska (Beringia) and current occupancy of the Alaskan boreal region, but only for one of the GCMs that we evaluated (GFDL). Resident boreal species that were able to persist in Alaska during the Pleistocene
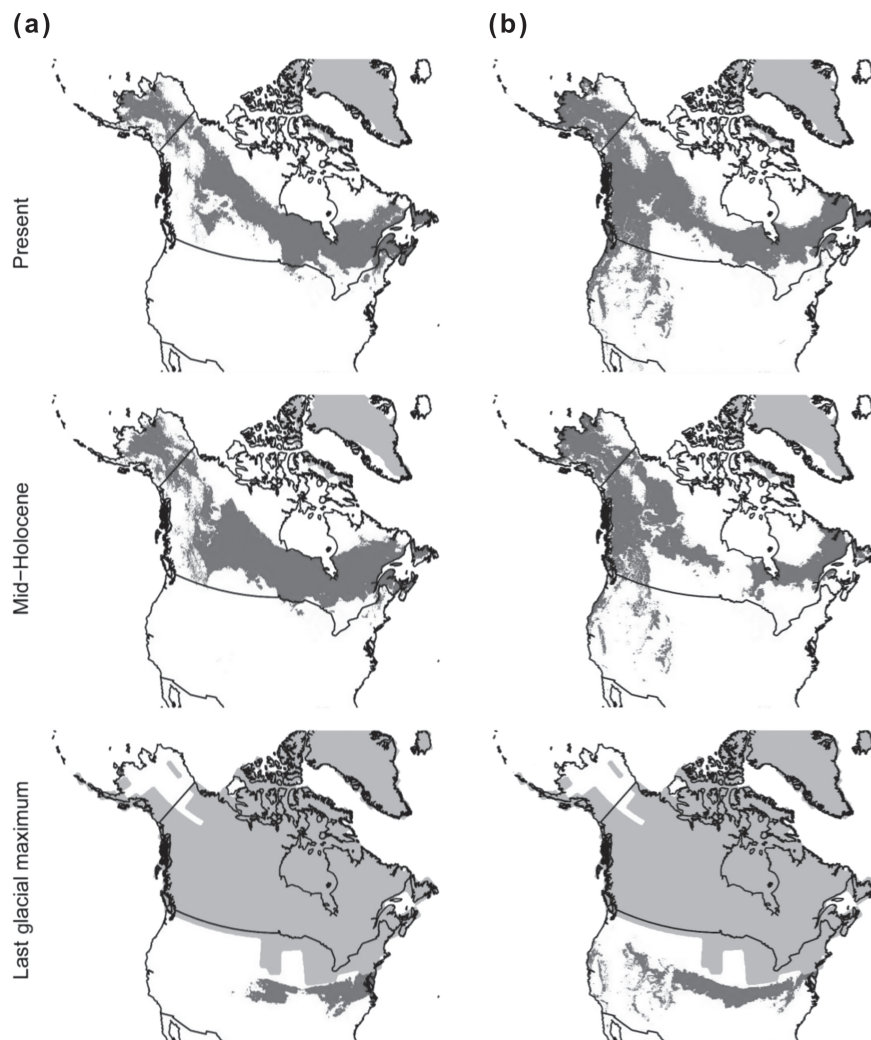

Figure 5. Climatically suitable core habitat in current, mid-Holocene, and LGM periods for two example species. Climatically suitable habitat (dark gray) for (a) alder flycatcher *Empidonax alnorum*, a largely boreal species, and (b) Swainson's thrush *Catharus ustulatus*, a wide-ranging species. Both are regular breeders in the Alaska boreal region with substantial climatically suitable habitat within the northwestern cordillera. Hindcasts are based on the CCM1 global climate model. Ice sheet extent shown in light gray. See Supplementary material Appendix 1 and Appendix 2 for remaining species.

period should still occur there today. However, due to the under-representation of arctic sites in our model-building dataset (Stralberg et al. 2015b), as well as the non-analog conditions that occurred in Beringia at the LGM (Roberts and Hamann 2012), our confidence in model projections for this time period and region is relatively low. It is also unknown whether migratory species crossed major ice sheets. Thus predicted Beringian refugia may only be realistic for a handful of cold-tolerant resident species – primarily those associated with tundra habitats, but potentially also a few forest-dependent species that were able to survive in small boreal refugia (Anderson et al. 2006).

Importance of migratory strategy

Although past and present cordilleran climatic suitability were the strongest predictors of Alaskan boreal occupancy, we also found that migratory strategy, which has a strong phylogenetic component (Helbig 2003), was an important factor in determining which species have successfully colonized the Alaskan boreal region post glaciation. Most northern resident species are already found there, some of which may have persisted in Beringian refugia. Our results suggested that resident species with more southerly climate associations, such as blue jay *Cyanocitta cristata*, are likely to occur in the Alaskan boreal region by mid-century; the recent urbanization-driven westward expansion of this species (Smith 1978) suggests that further expansion is possible. Short-distance migrants were also more likely to occupy boreal Alaska and thus more likely to colonize in the near future than long-distance migrants, with exception of migrants with South American wintering grounds. The latter is consistent with leapfrog migration, documented within a number of northern species (Boland 1990, Bell 1997, Kelly et al. 2002), whereby individuals with more southerly wintering grounds often breed farther north and have longer migration routes, either to optimize resource utilization (Greenberg 1980, Pienkowski et al. 1985) or reduce competition (Lundberg and Alerstam 1986). This, combined with the lack of importance of any of the migration distance metrics we evaluated, suggests that migration distance per se is not a limiting factor for breeding range expansion, although strong genetic control of migration routes may limit the capacity of a species to alter its migration route, timing, and destination in the face of rapid climate change (Both et al. 2010, Ruegg et al. 2014a). Furthermore, wintering ground habitat quality and prey availability may frequently limit breeding populations (Sherry and Holmes 1996), perhaps sufficiently to prevent distributional expansion. Such factors would be difficult to incorporate into analyses such as this one, however.

We did not find any evidence that competitive exclusion or physical traits such as body size or clutch size affect a species' ability to colonize boreal Alaska. With respect to body size, it may be that migration counters the trend toward larger-bodied individuals and species in colder climates predicted by Bergmann's rule. Both body size and clutch size may also vary substantially across the range of a species (Hussell 1972, Dunn et al. 2000, Ashton 2002), reducing the reliability of general literature-derived values

for wide-ranging species, particularly given the paucity of northern data. With respect to competition, it is possible that we did not adequately quantify competition pressure. However, the generally low diversity of this region and relatively short time since glaciation suggest that lack of niche saturation is a more likely explanation for the small effect of competitive exclusion.

We did not evaluate the role of predation or other potentially influential species interactions. Red squirrels *Tamiasciurus hudsonicus* are important nest predators in boreal Alaska (Matsuoka et al. 2001, Matsuoka and Handel 2007), where spruce cones provide the primary food source for squirrels. However, squirrels appear to be the dominant predators of passerine nests throughout the North American boreal region (Darveau et al. 1997, Song and Hannon 1999, Ball 2013), suggesting that large numerical discrepancies in squirrels would be needed to effectively exclude species from the Alaska Boreal Interior. Some evidence suggests that nest predation rates are relatively low (~ 30%) in boreal forests relative to temperate forests (Darveau et al. 1997), and predation pressure has been shown to decrease with latitude in other taxa (shorebirds, McKinnon et al. 2010). Thus we considered it unlikely that predation pressure would limit population expansion into boreal Alaska, despite the strong role that predation plays in population dynamics of temperate forest birds (Sherry et al. 2015).

Perceived barrier weak

Our results generally suggest that the northwestern cordillera can be considered a 'weak' barrier, with a capacity for many additional species to disperse into Alaska if climatic connectivity is achieved in the future. Indeed, in recent years, the first breeding record has been documented for yellow-bellied flycatcher (Martin et al. 2006). Of the eight species we considered that were classified by Gibson (2011) or Gibson and Withrow (2015) as most likely to be added to the region's breeding avifauna, all were predicted by our model to be present under 2011–2040 climate conditions. These climate conditions are now being experienced in Alaska, as warming has occurred faster there than elsewhere in North America (ACIA 2005, Wendler and Shulksi 2009). Thus, it is possible that we are already seeing a change in cordilleran habitat suitability in response to recent anthropogenic climate change, and that some migratory species are in the process of adjusting their distributions to track climate (Fig. 2). Four of the species for which our model predicts current Alaskan boreal occupancy have not been detected there, which is not surprising given the plethora of factors that may contribute to successful range expansion and detection, and the large stochastic component (Pielou 1991). For example, the absence of American redstart *Setophaga ruticilla* and warbling vireo *Vireo gilvus* may be explained by their strong association with deciduous habitats, particularly along riparian corridors (Sherry and Holmes 1997, Gardali and Ballard 2000), which are largely discontinuous across the northwestern cordillera into boreal Alaska – but do connect with southeastern Alaska, where these species are found. Indeed, several other species – e.g. song sparrow *Melospiza melodia* and brown-headed cowbird

Molothrus ater – are known to breed in southern Alaska but not in boreal (interior) Alaska, suggesting that the east-west running Alaska Range, which contains Mount Denali, the highest peak in North America, may be as important a barrier as the north-south running MacKenzie, Selwyn, and northern Rocky Mountain ranges (Fig. 3). For a few individual species with sufficient published demographic information, potential routes for population expansion could be modeled dynamically by simulating reproduction, colonization and extinction events across changing future climate conditions.

Novel communities may emerge

The ecological implications of relatively rapid range expansions and consequent community reshuffling are difficult to anticipate (Stralberg et al. 2009). On the one hand, the lower passerine species diversity in boreal Alaska compared with boreal Canada, and its relatively long distance from presumed LGM boreal refugia, suggest that niches may not yet be saturated, such that new species could 'invade' without major known ecological ramifications. In general, northern range limits are thought to be more constrained by climate than by competition and other species interactions, compared with southern range limits (MacArthur 1972, Root 1988). This may explain the relative rapidity of documented range expansions, compared with range contractions (Parmesan et al. 1999). On the other hand, novel species communities may bring ecological surprises (Schneider and Root 1996, Williams and Jackson 2007), and warmer conditions may increase predation, nest parasitism, and competition pressures. Among the passerine species we examined that are not yet breeding in the Alaskan boreal, the two corvids – American crow *Corvus brachyrhynchos* and blue jay – are documented nest predators (Yahner and Scott 1988, Vander Haegen and Degraaf 1996) and could increase predation pressure for northern forest birds, altering population demographics. The brown-headed cowbird, which is among the species recently recorded in boreal Alaska, is a brood parasite whose range has expanded rapidly in western North America (Rothstein et al. 1980); its establishment in boreal Alaska could cause declines in nesting success among other passerine species, especially those that have no history with cowbirds. Although we did not find evidence of competitive exclusion currently keeping species out of Alaska, it is possible that expanding species may have detrimental competitive effects on closely related species, for example black-throated green warbler in Canada and Townsend's warbler in Alaska. With the exception of this example, however, closely related species pairs already co-occur elsewhere. A few unique species combinations may arise where Old World species such as Arctic warbler *Phylloscopus borealis* (Lowther and Sharbaugh 2014) and bluethroat *Luscinia svecica* (Guzy and McCaffery 2002) occupy boreal niches that could also be occupied by New World species. Although bluethroat currently occupies only tundra regions of Alaska, the species breeds in scrubby willow–alder–birch thickets over large areas of Europe and Asia (Guzy and McCaffery 2002), suggesting greater niche breadth than is realized in Alaska.

Conclusion

Our analysis of life-history traits and paleoclimate suitability found that species with the greatest climatic suitability across the northwestern cordillera, presently and also during the mid-Holocene period, were most likely to be regular breeders in the Alaskan boreal region. Migratory strategy also played a role, but could not be disentangled from its strong phylogenetic basis. This suggests that the perceived barrier of the northwestern cordillera may be easily weakened as climate change improves conditions for many forest species across this region, and demonstrates yet another way in which the anticipated climate-change impacts of the upcoming century and beyond may cause major changes in systems that are traditionally perceived as constant. Conservationists and land managers may need to to reconsider conservation policies and strategies in light of evolving ecological communities.

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Supplementary material (Appendix ECOG-02393 at <www.ecography.org/appendix/ecog-02393>). Appendix 1–5.