RESEARCH ARTICLE

Predicted range shifts in North American boreal forest birds and the effect of climate change on genetic diversity in blackpoll warblers (*Setophaga striata*)

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Abstract As North American species' ranges shift northward in response to climate change, populations isolated in high-elevation habitat "islands" at the southern edge of distributions are predicted to decrease in size or be extirpated. Levels of genetic structure and gene flow and the number of private alleles held within these peripheral populations can be used as a measure of the potential loss of genetic diversity due to climate change. We use GIS-based climate niche models to project geographic distributions of 15 boreal forest bird species for the year 2080 under two carbon emissions scenarios to predict the extent to which ranges will shift, leading to the extirpation of isolated populations at the southern periphery of the boreal forest. Breeding distributions of nearly all boreal bird species are predicted to expand as they shift northward, but will dramatically decrease or be completely lost from mountain populations in New York, Vermont, and New Hampshire by 2080. To examine the effect of these shifts on gene pools of migratory bird species we genotyped 178 blackpoll warblers (*Setophaga striata*) at nine microsatellite loci, sampling four imperiled high-elevation populations and four northern populations. In *S. striata* 10.4 % of microsatellite alleles were confined to populations expected to be lost due to climate change. However, these accounted for a nonsignificant percent of the genetic structure, and loss of these alleles would not significantly erode species heterozygosity or allelic richness. Our results indicate that isolated southern populations of *S. striata*, and possibly other migratory species with high gene flow, do not represent genetically isolated, independently evolving units. Efforts to mitigate the effect of climate change on boreal forest birds should focus on species in which peripheral populations harbor significant genetic diversity.

Keywords Species distribution models · Climate change · *Setophaga striata* · Conservation genetics · Microsatellites · Boreal forest birds

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Introduction

As global climates warm, species in the northern hemisphere are predicted to shift their ranges poleward (Huntley et al. 2008; Zuckerburg et al. 2009) or up in elevation (Moritz et al. 2008) as they track suitable conditions (Tingley et al. 2009). Populations at the southern edge of species' ranges, especially those isolated at high elevations, are expected to be the first affected by climate change as warming decreases suitability of southern habitats (Hampe and Petit 2005; Hodkinson 2005; Waite and Strickland 2006). If these southern isolates represent independently evolving gene pools, global climate warming may threaten genetic diversity important for the long-term survival and adaptability of species (Lacy 1997). Loss of genetic diversity can increase the effects of inbreeding (Keller and Waller 2002) and decrease reproductive fitness (McAlpine 1993; Westemeier et al. 1998), both of which elevate extinction risk (Frankham and Ralls 1998; Saccheri et al.

1998; Frankham 2005). Because of this, maintenance of genetic diversity is a primary goal of many conservation programs (Frankham et al. 2010).

Geographic patterns of genetic variation and structure were shaped in part by past episodes of climate change (Avise 2004; Hewitt 2004) and we should expect modern, ongoing climate change to similarly affect genetic structure by shifting ranges and reshuffling gene pools. Isolated populations may be unable to track conditions because of barriers to dispersal, and local extirpations may become common as changing conditions outpace the adaptation and dispersal of plant and animal populations. Loss of populations could mean loss of alleles, decrease in intraspecific genetic variation, and increase in extinction risk (Frankham 2005). Many studies have documented the loss of genetic variation within species following human caused reductions in distribution or population sizes (Paxinos et al. 2002; Bellinger et al. 2003; Leonard et al. 2005; Taylor et al. 2007; Mitrovski et al. 2008; Larsson et al. 2008). Species with small, geographically isolated populations and poor dispersal abilities may be especially vulnerable, but Leonard et al. (2005) showed that even wide ranging, highly mobile species lose significant numbers of alleles when populations are extirpated. Therefore, as we enter this age of accelerated change in species distributions, it becomes increasingly important that biologists document levels and distributions of genetic variation and examine the ways that the current warming trend will affect genetic diversity in wild populations (Banks et al. 2010).

GIS-based niche models can be used to predict how climate change will affect species distributions (Hijmans and Graham 2006; Huntley et al. 2006; Loarie et al. 2008; Tolley et al. 2009). Species distribution models (SDMs) use climate variables found at sites of known occurrences to project distribution elsewhere, or onto predicted future conditions (Peterson 2001; Hijmans and Graham 2006). SDMs lend themselves well to integration with phylogeographic research (Richards et al. 2007; Pease et al. 2009; Kozak et al. 2008; Knowles 2009), but few studies have used SDMs in combination with genetic data to predict changes in gene pools under projected climate warming scenarios (Tolley et al. 2009; Habel et al. 2010). The present study is among the first to predict the affects of anticipated climate change and range shifts on genetic diversity within and among wild populations (see also Habel et al. 2010; Jay et al. 2012).

Our focus is on bird species with boreal–montane distributions in the contiguous boreal forest of Alaska and Canada and the archipelago of montane spruce-fir islands that occur above 1000 m elevation in northeastern North America (Able and Noon 1976). These species are expected to respond differently to climate change than species adapted to habitats at lower latitudes and altitudes

(Galbreath et al. 2009; Muster et al. 2009). Montane populations of boreal forest birds that breed in the White Mountains of New Hampshire, Green Mountains of Vermont, and the Adirondack and Catskill Mountains of New York include resident and migratory birds of special conservation concern to state wildlife management agencies due to their strict habitat requirements, small population sizes, and declining population trends (Rich et al. 2004; King et al. 2008). King et al. (2008) detected a significant negative population trend in at least three species of montane forest birds in the White Mountains over a 10 year period from 1993 to 2003. These populations may be especially vulnerable to climate warming as the ecology and habitat are altered by warming temperatures (Hodkinson 2005; King et al. 2008; Rodenhouse et al. 2009).

To assess the risk of extirpation of these populations in the present century, we develop SDMs for 15 species of boreal forest birds with disjunct populations in the mountains of New York, Vermont, and New Hampshire in combination with 70-year projections of climate change based on alternative carbon emissions scenarios (published by the Intergovernmental Panel on Climate Change 2000). For one species, blackpoll warbler (*Setophaga striata*), we compare predicted climate-induced shifts in distribution to genetic data from nine microsatellite loci to estimate potential loss of genetic diversity at the regional scale. We document the presence of unique genotypes in populations predicted to be extirpated, and test the hypothesis that these disjunct, high-elevation populations are important reservoirs of genetic variation and therefore of high conservation concern. We discuss how climate change is predicted to affect diversity and structure within blackpoll warblers, and how this relates to the conservation of avian communities at the southern periphery of the boreal forest biome.

Methods

Species distribution modeling

We constructed SDMs for 15 migratory and resident bird species that are coniferous forest specialists with breeding ranges in the North American boreal forest belt and in the mountains of New York and New England. Because our focus is on montane populations at the southern periphery of their species' range, we excluded species with extensive distribution south of New York (e.g., winter wren, *Troglodytes hiemalis*). Additionally, we excluded nomadic species with irruptive population dynamics (e.g., white-winged crossbill, *Loxia leucoptera*) because specimen occurrence data for these species are difficult to translate into distribution models. SDMs for each species were constructed from occurrence data in the form of georeferenced museum specimens which we

obtained by searching ornithological specimen collections (see Acknowledgments) in ORNIS (http://olla.berkeley.edu/ornisnet/) and Global Biodiversity Information Facility (GBIF; http://www.gbif.org) in March 2011. Due to the small number of specimens of Bicknell's thrush (*Catharus bicknelli*) in online databases, occurrence data based on observations from GBIF were also included in the SDM for this species. Georeferenced occurrence records with coordinate uncertainties greater than 20 km were excluded from analyses. For records lacking uncertainty estimates, we examined verbal locality descriptions and culled all records that were not precise at least to the level of county or municipalities (e.g., records from "Manitoba", or "Yukon River"). All occurrence records were plotted and compared with published range maps (Poole 2005) to verify accuracy. A small number of records that fell outside of known breeding distributions, which may represent late spring migrants, were excluded. Coordinate uncertainty is of larger concern in mountainous regions where environmental conditions can vary on a smaller spatial scale, but very few of the records we obtained ($\ll 1$ %) for any species were from mountain regions. To increase samples from high elevation sites in the southern boreal, we also included occurrences of blackpoll warbler and Bicknell's thrush from our own field work in the Adirondack and Catskill mountains of New York; these occurrences have coordinate uncertainties less than 10 m.

Thirty-six GIS layers describing monthly temperature and precipitation at a 2.5 arc-minute grid were obtained for the present and 2080 from http://www.worldclim.org. Data layers for current climate were interpolated from weather station data observed around the globe between 1950 and 2000 (Hijmans et al. 2005). Future climate data layers are calculated for 2080 according to the Hadley Centre Coupled Model version 3 (HadCM3; Gordon et al. 2000) under carbon emissions scenarios A2 and B2 (IPCC Intergovernmental Panel on Climate Change 2000). Both emissions scenarios represent models of continuous global human population growth. The rate of growth, and thus change in climate, is faster in A2 than in B2 (IPCC Intergovernmental Panel on Climate Change 2000). The average global temperature is predicted to raise ~ 3 °C under A2 by 2080 and ~ 2 °C under B2 (IPCC Intergovernmental Panel on Climate Change 2001). In New York, Vermont, and New Hampshire, maximum July temperature is predicted to increase an average of 4.90 and 3.25 °C by 2080 under scenarios A2 and B2, respectively. Here, we use two scenarios to represent a range of possible futures, with A2 as a more severe scenario, and B2 a more conservative scenario. However, recent evidence suggests increasing CO_2 emissions have already outpaced conservative IPCC (Intergovernmental Panel on Climate Change 2000) scenarios (Raupach et al. 2007; Beaumont et al. 2008; La Sorte and Jetz 2010). Newer, less conservative scenarios of

climate change (IPCC Intergovernmental Panel on Climate Change 2007) were examined but ultimately not used in the present study because novel environments (falling outside of current conditions used to train models) are predicted to cover much of the study area under these scenarios. All data layers were converted and clipped in ArcMap (ESRI; Redlands, CA) to include only North America.

Climate variables were combined with occurrence data for each of the study species in MAXENT (Phillips et al. 2006) to project current distribution and predict 2080 distribution under the alternative emissions scenarios. To assess the accuracy of projected distributions 20 % of occurrences (selected at random) were withheld from model training and used to test model performance as measured as the area under the receiver operating characteristic curve (Phillips et al. 2006). Area under the curve (AUC) provides a single measure of performance independent of threshold, and can be interpreted as the probability of a presence and an absence each being correctly classified, such that AUC values close to 1.0 represent high performance (Phillips et al. 2006).

MAXENT outputs distributions as a single raster layer, the value of each cell across the study area representing the probability of occurrence. These were converted to shape files of dichotomous presence-absence distribution maps in ArcMap using the 10th percentile of training data as the probability threshold (Phillips et al. 2006). ArcMap was used to calculate the area and centroid (or geometric center) for current and future distributions under A2 and B2 scenarios in the HadCM3 model. The change in area, and distance and direction between current and future centroids were used to quantify the effects of climate change on bird species distributions. The fates of mountain populations by 2080 were quantified for each species by calculating the predicted change in area in New York, Vermont, and New Hampshire. Populations predicted to lose greater than 99 % of their area were classified as extirpated.

Genetic data and analyses

Tissue samples (blood, muscle, or feather) were obtained from 178 *S. striata* from eight populations in the southeastern part of their breeding range including Catskill Mountains, New York ($n = 20$); Adirondack Mountains, New York ($n = 21$); Green Mountains, Vermont ($n = 29$); White Mountains, New Hampshire ($n = 27$); Quebec ($n = 35$); New Brunswick ($n = 26$); Nova Scotia ($n = 11$); and Newfoundland ($n = 9$). Whole blood samples and feathers were collected in the field from birds that were captured, banded and released. Blood was stored in Queen's Lysis Buffer (Seutin et al. 1991) and feathers were sealed in paper envelopes; these samples were kept at ambient temperature until returned to the lab, and then stored at −20 °C.

Muscle samples ($n = 10$ of 178) were taken from whole birds prepared as museum voucher specimens. Whole birds were transported on ice and kept frozen until specimen preparation, after which time muscle samples were stored at -80 °C. Genomic DNA was extracted from all tissue samples using a DNeasy tissue extraction kit (Qiagen; Valencia, California) following manufactures protocol for animal tissues with the following modifications: final elution was done in two rounds of 75 μL, each followed by an incubation period of 5 min at room temperature.

Blackpoll Warblers were genotyped at 9 microsatellite loci previously developed for Yellow Warbler (*S. petechia*; Dpu15, Dpu16; Dawson et al. 1997), Kirtland's Warbler (*S. kirtlandii*; DkiB12, DkiB102, DkiD102, DkiD120; King et al. 2005), and Golden-winged Warbler (*Vermivora chrysoptera*; VeCr02, VeCr04, VeCr08; Stenzler et al. 2004). Multiple loci were amplified simultaneously in 10 μL multiplex PCRs containing 1.0 μL DNA template ($\sim$5.0 ng); 1.0 μL primer mix (3–4 primer pairs in H_2O, each primer at 2.0 μM); 5.0 μL Qiagen Multiplex PCR Master Mix (HotStar *Taq* polymerase, 6 mM $MgCl_2$, and a dNTP mix); and 3 μL of pure H_2O. Cycling protocol consisted of a 15 min initial activation at 95 °C; 25 cycles of denaturation (30 s at 94 °C), annealing (90 s at 58 °C), and extension (60 s at 72 °C); and a final extension of 30 min at 60 °C. PCR products were analyzed on an ABI 3130 Genetic Analyzer (Applied Biosystems; Carlsbad, California), and alleles were manually scored using the program GENE MAPPER (Applied Biosystems).

Exact tests for departure from Hardy–Weinberg equilibrium (HWE) were performed in GENEPOP version 4.0 (Raymond and Rousset 1995). Proportion of polymorphic loci (P), allelic diversity (A), allelic richness (A_R), observed and expected heterozygosity (H_o, H_e), and number of private alleles (alleles found in only one population) were calculated for each population in the computer programs GDA (Lewis and Zaykin 1999) and FSTAT (Goudet 1995), and used as measures of genetic diversity. Allelic diversity and richness are similar measures of variation, but differ in that allelic richness accounts for unequal sampling among populations and loci. We used pairwise F_{ST} values (between all possible pairs of the eight sampling sites, designated *a prior* as populations), and AMOVAs performed in ARLEQUIN version 3.0 (Excoffier et al. 2005) to estimate population genetic structure. Gene flow among populations was measured as the number of migrants per generation (N_m), and was estimated in GENEPOP using the average frequency of private alleles per population after correction for sample size (Slatkin 1985; Barton and Slatkin 1986). We conducted a principal components analysis (PCA) implemented in Eigensoft (Patterson et al. 2006) and STRUCTURE analyses (Pritchard et al. 2000) for three run iterations of $K = 1$ through $K = 8$ assuming an admixture ancestry model and

correlated allele frequencies. To predict the affects of a range shift by 2080 on genetic diversity we recalculated A_R, H_o and H_e excluding samples from disjunct populations predicted to go extinct, and assumed that alleles confined to these populations would be lost from the 2080 gene pool. We used Wilcoxon signed rank tests, performed in SPSS v.19 (IBM), to test for significant changes in mean number of alleles per locus, A_R, H_o and H_e.

Results

Species distribution models

A total of 15 species met the inclusion criteria (Table 1), including resident and migratory species from nine avian families, and ten genera. A total of 3879 unique occurrence points was used averaging 258.6 per species (range 52–633; Table 1). Model performances were high for all species (mean AUC = 0.976, minimum AUC = 0.963). Visual inspection of projected current distributions generally fit well to published modern distribution maps. The climatic variable which contributed most to each projection differed among species, but was most often maximum October temperature (7 out of 15 species; range of contribution 23.7–44.6 %; Table 1), and was a temperature variable, rather than a precipitation variable, in every case.

Changes in distribution due to climate change

Range-wide breeding distribution area is predicted to increase for most study species by 2080, with mean increases of 35.9 and 29.5 % under emissions scenarios A2 and B2, respectively (Table 1). Predicted change in breeding range area under the A2 scenario ranged across species from a 20.4 % decrease to a 107.4 % increase. Under the B2 scenario, change in area ranged from a 24.0 % decrease to a 99.6 % increase. Eleven species were predicted to expand their range under both scenarios, while three species were predicted to contract their range under both scenarios. One species, Bicknell's thrush, showed an increase under one scenario, and a decrease under the other.

Under both scenarios, the centroid of each species is predicted to shift northward, with most species shifting northwest (Fig. 1). The mean predicted shift between current and 2080 centroids is 934.0 km for A2 and 772.1 km for B2 (Table 1). This northward shift means that despite an increase in area over the entire range, local populations at the southern periphery of the current range are predicted to decrease drastically in size or disappear (Fig. 2). Under the A2 scenario, 12 of 15 study species are predicted to be extirpated (99–100 % decrease) from New York, Vermont and New Hampshire by 2080, and two more species ranges

Table 1 Predicted effects of climate warming on breeding distributions of fifteen species of boreal forest birds

Species, migratory tendency		n	Change in Area (%)		Centroid Shift (km)		AUC	Most contributing variable (%)
			A2	B2	A2	B2		
Falcipennis canadensis, spruce grouse	S	193	−11.3	−3.7	1075.0	902.8	0.971	Max. October Temp. (43.8)
Picoides dorsalis, three-toed woodpecker	S	113	46.8	29.6	909.8	532.0	0.971	Max. May Temp. (25.0)
Picoides arcticus, black-backed woodpecker	S	149	18.0	25.2	931.2	1160.0	0.989	Max. April Temp. (34.5)
Empidonax flaviventris, yellow-bellied flycatcher	M	180	28.4	32.8	709.2	492.7	0.969	Max. October Temp. (23.7)
Perisoreous canadensis, gray jay	S	391	−20.4	−24.0	1282.0	811.0	0.977	Max. May Temp. (36.7)
Poecile hudsonica, boreal chickadee	S	187	50.2	48.4	1013.0	1014.0	0.976	Max. October Temp. (44.6)
Regulus calendula, ruby-crowned kinglet	m	291	−4.2	−4.9	897.5	600.2	0.965	Max. October Temp. (41.0)
Catharus bicknelli, Bicknell's thrush	M	203	28.1	−7.3	193.9	179.8	1.000	Max. February Temp. (24.2)
Catharus ustulatus, Swainson's thrush	M	570	37.1	32.5	790.9	659.9	0.975	Max. April Temp. (45.3)
Oreothylpis peregrina, Tennesee warbler	M	159	23.3	18.9	829.8	840.9	0.977	Max. October Temp. (42.2)
Setophaga striata, blackpoll warbler	M	205	69.4	43.3	1377.0	1408.0	0.968	Min. September Temp. (20.8)
Setophaga castanea, bay-breasted warbler	M	138	107.5	99.6	803.5	811.0	0.992	Min. May Temp. (36.2)
Setophaga tigrina, Cape May warbler	M	52	93.3	77.6	976.5	720.7	0.984	Min. May Temp. (32.2)
Setophaga coronata, yellow-rumped warbler	m	633	10.1	23.2	1101.0	832.7	0.966	Max. October Temp. (36.4)
Zonotrichia albicollis, white-throated sparrow	m	415	62.6	51.7	707.8	615.3	0.963	Max. October Temp. (38.0)

Seasonal migratory tendency is coded as *S* sedentary, *M* long-distance migration (winters south of United States), and *m* short-distance migration, *n* number of occurrence points used in MAXENT modeling. Change in area and centroid shifts are calculated from the difference between each species' modeled current distribution and predicted distribution in 2080 under two emissions scenarios, A2 and B2. Model performance is reported as area under curve (AUC). Most contributing variables are those that contributed the most to each species model

Fig. 1 Polar plots of the predicted shift of geographic range centroids from projected current to predicted 2080 for 15 study species. Each *box* represents a species and its position relative to the origin represents the predicted direction and distance of the shifts in response to each emissions scenario. *Circles* represent the average shift over all species. *Scale* units are kilometers
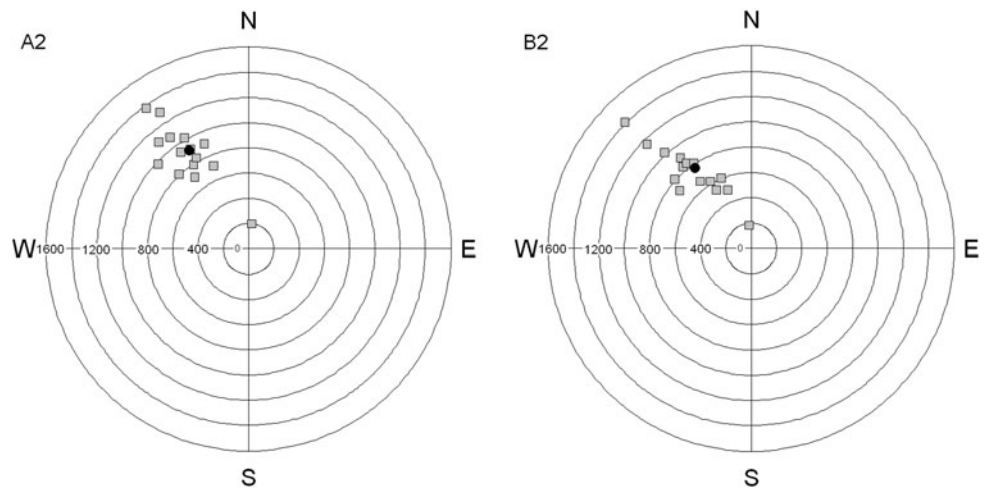
will decrease by at least 90 % in this region (Table 2). Under the B2 scenario, seven species are predicted to be extirpated and four will decrease by greater than 90 % of their current range in these states. Blackpoll warblers are predicted to be extirpated from New York, all of New England, and New Brunswick by 2080 under A2 conditions (Fig. 3). Under the B2 scenario, less than 3 % of mountain populations will remain in New York, Vermont, and New Hampshire, while larger populations in Quebec, New Brunswick, Nova Scotia and Newfoundland will persist (Fig. 3). These results are the basis for the prediction that

microsatellite alleles restricted to mountain populations will be lost by 2080, but that genetic variation present in Quebec, New Brunswick, Nova Scotia and Newfoundland will persist.

Loss of genetic diversity

From 178 blackpoll warbler samples, we obtained scorable allelic data from a mean of 168.4 individuals per locus. Genetic diversity within blackpoll warblers is high; every locus is polymorphic ranging in number of alleles from 6 to

Fig. 2 Diversity maps combining the projected presence of 15 study species and predicting the change in the diversity of boreal forest bird species in New York, Vermont, and New Hampshire by 2080 under A2 and B2 carbon emission scenarios
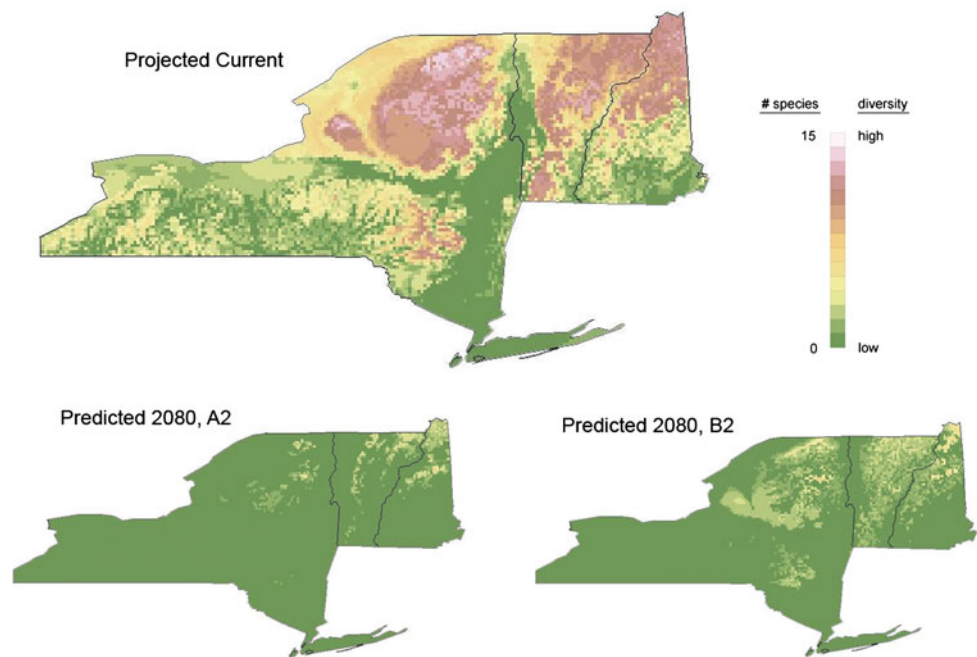

Table 2 Predicted percent change in area in NY, VT, and NH by 2080 for 15 study species under alternative climate change scenarios A2 and B2

Species	Percent change in area	
	A2	B2
Falcipennis canadensis	−100.0	−99.9
Picoides dorsalis	−99.8	−100.0
Picoides arcticus	−100.0	−100.0
Empidonax flaviventris	−95.7	−67.9
Perisoreus canadensis	−100.0	−100.0
Poecile hudsonica	−100.0	−99.9
Regulus calendula	−100.0	−100.0
Catharus bicknelli	−92.0	−81.8
Catharus ustulatus	−99.5	−98.5
Oreothlypis peregrina	−100.0	−80.5
Setophaga striata	−100.0	−97.4
Setophaga castanea	−82.8	−50.2
Setophaga tigrina	−99.4	−94.3
Setophaga coronata	−99.8	−98.7
Zonotrichia albicollis	−99.9	−99.3

28 (Table 3). All populations have high allelic diversity (mean number of alleles, $A = 8.49$) and moderate observed and expected heterozygosity (mean $H_o = 0.583$; mean $H_e = 0.694$) (Table 4). One locus pair, DkiB102 and VeCr04, showed marginally significant linkage disequilibrium ($P = 0.045$). Exact tests for departure from HWE were significant for 24 of 72 locus–population combinations and

for a global test across all loci and populations. After Bonferroni corrections, no locus pairs were significant for linkage disequilibrium and 7 of 72 locus–population combinations remained significant for departure from HWE. Because no locus consistently departed from HWE in all populations, all loci were included in analyses of geographic genetic structure.

Pairwise F_{ST} values were significant for 9 of the 28 (32.1 %) possible population pairs, and highest between Nova Scotia and all other populations (−0.034 to 0.050), but no F_{ST} values were greater than 0.050, indicating a lack of genetic structure at this geographic scale. Pairwise F_{ST} values among mountain populations were all lower than 0.020 (one out of six population pairs significant, 16.7 %). AMOVA likewise showed that a small, non-significant portion of variation within blackpoll warblers is due to differences among populations (0.52 %, $P = 0.127$). Gene flow is high, with $N_m = 5.44$ migrants per generation calculated for the entire sample after correction for sample size. One migrant per generation is generally considered sufficient to counter population divergence due to genetic drift (Slatkin 1985, 1987). No pairwise population estimates of N_m were suggestive of low gene flow ($N_m < 1.0$). No geographic structure was detected in either the PCA or STRUCTURE analyses. PCA detected two significant principle components which described only 6.31 % of the variation, but a plot of these axes (not shown) revealed no distinct geographic clusters. STRUCTURE identified $K = 1$ as the most likely value (largest mean value of Ln P(D)), though Ln P(D) values for $K = 1$ and $K = 2$ were not significantly different ($t = 2.47$, $P = 0.069$). For all

Fig. 3 MAXENT projections for *Setophaga striata* in northeastern North America. **a** Projected current distribution. *Black circles* indicate populations sampled for microsatellite analysis. *AD* Adirondacks Mountains, New York; *CA* Catskill Mountains, New York; *VT* Green Mountains, Vermont; *NH* White Mountains, New Hampshire; *NB* Christmas Mountains, New Brunswick; *QU* Gaspé peninsula, Quebec; *NS* Cape Breton, Nova Scotia; *NL* Newfoundland. **b** Predicted 2080 distribution under carbon emissions scenario A2. **c** Predicted 2080 distribution under carbon emissions scenario B2
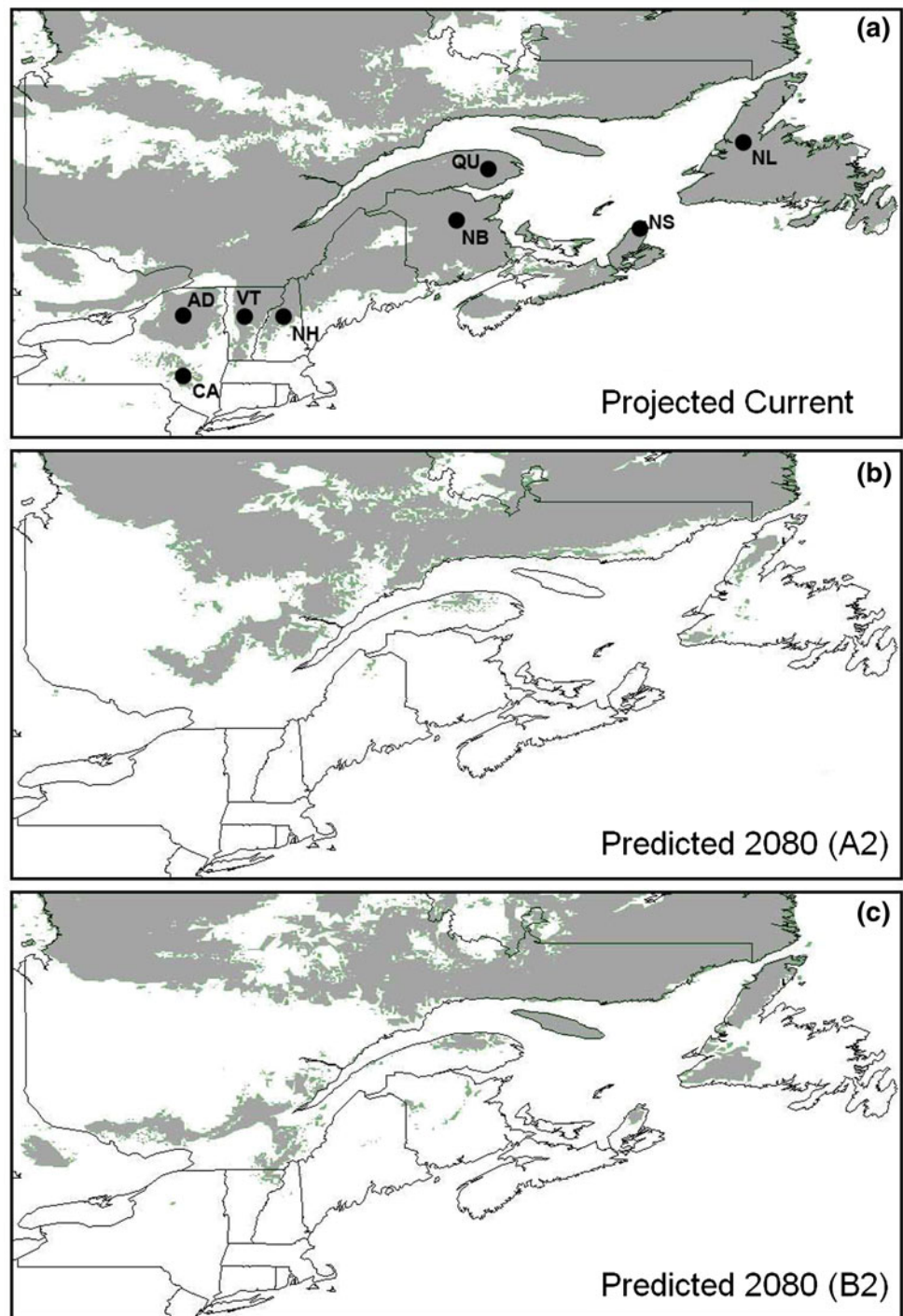
values of *K*, the assignment probability (*Q*) of each individual was roughly equal for all populations (i.e. the probability of belonging to any of *K* populations = 1/*K*).

A total of 22 alleles from 8 microsatellite loci were confined to single populations; these private alleles exist in all populations except Catskills and Green Mountains. Eight of the private alleles exist in mountain populations predicted to be extirpated by 2080 (Adirondacks [*n* = 3] and White

Mountains [*n* = 5]). An additional 6 alleles were found only in mountain populations (i.e., not found in Quebec, New Brunswick, Nova Scotia or Newfoundland). Together, these 14 "mountain" alleles represent 10.4 % of all alleles found within sampled blackpoll warblers. The loss of these alleles would result in a significant decrease in the mean number of alleles per locus (*P* = 0.028). However, all private alleles were low in frequency within populations and were found in

Table 3 Variation in blackpoll warblers at nine microsatellite loci

Locus	Recovery rate		# alleles	H_e	H_o	References
	n	$\%$				
DkiB12	177	99.4	11	0.274	0.276	King et al. (2005)
DkiB102	174	97.8	6	0.474	0.351	King et al. (2005)
DkiD102	159	89.3	28	0.915	0.748	King et al. (2005)
DkiD120	162	91.0	17	0.875	0.828	King et al. (2005)
Dpu15	172	96.6	19	0.825	0.576	Dawson et al. (1997)
Dpu16	176	98.9	13	0.799	0.727	Dawson et al. (1997)
VeCr02	169	94.9	9	0.582	0.615	Stenzler et al. (2004)
VeCr04	160	89.9	8	0.671	0.475	Stenzler et al. (2004)
VeCr08	167	93.8	24	0.902	0.731	Stenzler et al. (2004)
Mean	168.4	94.6	15	0.702	0.592	

Recovery rate is the number of individuals out of 178 that yielded scoreable allelic data. H_e expected heterozygosity, H_o observed heterozygosity

Table 4 Genetic variation among eight geographic populations of blackpoll warblers

Population	n	P	A	A_R	H_e	H_o	Private alleles
Catskill Mtns., NY	20	1.0	7.44	3.83	0.673	0.593	0
Adirondack Mtns., NY	21	1.0	9.11	4.20	0.714	0.659	3*
Green Mtns., VT	29	1.0	8.44	3.86	0.63	0.532	0
White Mtns., NH	27	1.0	9.78	4.36	0.702	0.593	5*
Quebec	35	1.0	11.22	4.26	0.703	0.591	6
New Brunswick	26	1.0	10.33	4.42	0.736	0.612	5
Nova Scotia	11	1.0	6.44	4.09	0.696	0.592	2
Newfoundland	9	1.0	5.11	4.17	0.7	0.495	1
Overall	178	1.0	8.49	4.15	0.694	0.583	22

n number of individuals from each population, P proportion of polymorphic loci, A Allelic diversity; mean number of alleles per locus, A_R allelic richness; mean number of alleles per locus with correction for unequal sample sizes, H_e expected heterozygosity, H_o observed heterozygosity. Private alleles are those found only in one population

Asterisk (*) denotes alleles predicted to be lost by the year 2080 based on MAXENT modeling

only one or a few sampled individuals. Removing "mountain" alleles from the gene pool would result in no significant change in allelic richness ($P = 0.678$), observed heterozygosity ($P = 0.767$), or expected heterozygosity ($P = 0.161$). Using an AMOVA, we found that the genetic differences between groups of populations predicted to persist and those predicted to be extinct by 2080 accounts for less than 1 % of the genetic structure within blackpoll warblers ($F_{CT} = 0.69$ %; $P = 0.069$). Put another way, more than 99 % of the genetic structure in blackpoll warblers will survive the predicted extirpations at the southern edge of its range. Thus, despite the predicted loss of many unique genotypes (representing over 10 % of microsatellite allelic diversity) climate change-induced range shifts will not likely affect the genetic structure, allelic richness, or heterozygosity of blackpoll warbler populations.

Discussion

Our results are consistent with other climate-based distribution modeling studies that have predicted poleward range shifts and population declines or extirpations in high-altitude populations of birds (Huntley et al. 2006, 2008; Rodenhouse et al. 2008; Virkkala et al. 2008). Rodenhouse et al. (2008) modeled Bicknell's thrush distribution under scenarios of increasing temperature and found that a 1 °C increase in growing season temperature was enough to reduce potential Bicknell's thrush habitat by half, and a 3 °C increase nearly eliminated all suitable habitat from the northeast. Similarly, our modeled 2080 distribution for B2 scenario (comparable to a 3 °C increase in temperature) showed an 81.9 % decrease in area in New York, Vermont, and New Hampshire for Bicknell's thrush, and an average decrease in this region of 91.2 % for all species. Together these results make alarming predictions for the demise of populations at the southern periphery of species' ranges, but we find that for the majority of our study species expansion at the northern limit will outstrip loss at the trailing edge. Unlike in Eurasia, where the Arctic Ocean is a barrier to northward expansion (Virkkala et al. 2008), large tracts of land exist in North America north of present boreal bird distributions and may become suitable as climates warm. As a result, our study predicts that many species of North American boreal birds would have a net increase in distributional area by 2080.

It is important to note that all SDM projections represent *potential* future distributions made up of sites that are predicted to fall within suitable climatic conditions. Variables other than climate will surely affect *realized* distributions (Araujo and Luoto Araújo and Luoto 2007; Beale et al. 2008). It is generally agreed upon that at continental scales, climate variables alone are suitable for modeling species

distributions (Beerling et al. 1995; Pearson and Dawson 2003; Thuiller et al. 2004). Though Beale et al. (2008) argue against climate as a sole determinant of macroscale distribution in most European birds, they demonstrate that the association between climate and distribution is especially strong for species with northern distributions. At smaller spatial scales, biological interactions likely become increasingly important in limiting species ranges. The accuracy of predicted range changes in boreal birds will depend on how spruce-fir forest communities replace tundra communities at the northern limit of the boreal forest, and how quickly it is replaced by deciduous forest at the southern limit. The shift of forest ecotones may lag up to decades or centuries behind changes in climate (Parmesan 2006). If distributions of tree species are slower to shift, or shift according to different climatic variables, realized bird distributions in 2080 may be quite different than projected. However, changes in forest structure have already begun in montane habitats in northeastern North America (Beckage et al. 2008) and at the forest-tundra ecotone (Saurez et al. 1999; Dial et al. 2007).

Some long-term data sets on bird distributions suggest that boreal forest bird distributions have already begun to shift north. For example, comparisons of the first edition (Anderle and Carroll 1988) and second edition (McGowan and Corwin 2008) of the New York State Breeding Bird Atlas show that boreal forest species with a southern range limit in New York shifted the southern periphery of their ranges a mean of 11.4 km northward over the past 20 years (Zuckerburg et al. 2009). Of the 15 species used in the present study, nine were analyzed in Zuckerburg et al. (2009), and 5 showed a northern shift in latitudinal centroid whereas four showed a southern shift. This discrepancy between survey data over the last two decades and future changes inferred from SDMs is likely due to the differences in temporal and geographic scales of the analyses, or may reflect the accelerated pace of warming that is expected in the coming decades.

Five of our study species have been suggested as indicator species for overall ecosystem health and quality of montane spruce-fir forest (US Forest Service 2006; King et al. 2008), including blackpoll warbler, Bicknell's thrush, yellow-bellied flycatcher (*Empidonax flaviventris*), boreal chickadee (*Poecile hudsonica*), and spruce grouse (*Falcipennis canadensis*). The best indicator species are thought to be highly habitat specific and sensitive to environmental change (Landres et al. 1988; Carignan and Villard 2002), however, in our distribution modeling these species show very different responses. Spruce grouse and boreal chickadee, for example, are both predicted to lose area range-wide and become extirpated in mountain habitats under both emissions scenarios, whereas yellow-bellied flycatcher is predicted to expand its range on a continental

scale and lose relatively less area in mountain populations. This variation in responses among all 15 study species may be related to variation in the breadth of each species' niche, or to differences in the size of each species' breeding range. SDMs may provide an avenue for assessing which species are appropriate as indicators of habitat disturbance due specifically to climate change in the present century.

We employ a single method in modeling the distribution of boreal species under climate change, namely correlative distribution modeling using MAXENT. Others have demonstrated that predictions of distributions are variable among modeling methods (Thuiller 2004; Pearson et al. 2006), especially in the context of climate change and range-shifting species (Elith et al. 2010). The largest differences among model types may result from the treatment of absences, and the use of background points as absences should be carefully considered (Pearson et al. 2006; Elith et al. 2010). *S. striata* is thought to have quickly colonized its current distribution following the retreat of glaciers around 12 thousand years ago (Ralston and Kirchman 2012), and there is no evidence of range shift for this species at the temporal scale (several decades) of the observed occurrence and climate data (Eaton 1914; McGowan and Corwin 2008). In contrast to several bird species with breeding ranges predominantly in the southeastern United States which have been expanding their ranges northward in recent decades, nearly all of the 15 boreal species whose distributions we modeled have had stable ranges over this same time scale (McGowan and Corwin 2008). It is therefore appropriate to treat 'absences' in the modeled distributions as the result of unsuitable climates rather than as historic losses or range shifts. Furthermore, key trends of predictions from correlative models have been shown to be consistent with those from mechanistic approaches when finer details are ignored (Elith et al. 2010), though major differences in the distance and direction of predicted shifts can occur (Pearson et al. 2006). Important to the present study is the geographic scale at which populations are genetically structured, and the range shifts that may occur at this scale. The agreement of general trends between our predictions and previously published models for birds of northeastern North America (Rodenhouse et al. 2008) supports our conclusions of northward shifts at the regional scale.

Similarly, the choice of climate scenarios and of probability thresholds may also significantly affect modeling predictions. We use carbon emissions scenarios A2 and B2 according to IPCC (Intergovernmental Panel on Climate Change 2000), both of which may underestimate actual climate change according to more recent models (IPCC Intergovernmental Panel on Climate Change 2007). Newer scenarios (IPCC Intergovernmental Panel on Climate Change 2007), however, predict novel environments across

much of our study area in 2080, limiting the predictive ability of correlative methods such as MAXENT. We use the most restrictive threshold (10th percentile of training presences; Phillips et al. 2006) when converting probability distributions to presence–absence as it provides a projected current distribution that most closely matches known distribution of *S. striata* in northeastern North America. Given our results that all northeastern populations of *S. striata* are genetically similar, it is unlikely that variability among climate change scenarios or probability thresholds would qualitatively affect our conclusion that little genetic diversity is at risk from climate induced range shifts in this species.

Genetic diversity and conservation implications

Conservation priority is placed on 'evolutionarily significant units' (ESUs; Ryder 1986; Waples 1991; Moritz 1994; Green 2005), which are defined by Waples (1991) as populations that "are substantially reproductively isolated from other conspecific population units" and "represent an important component in the evolutionary legacy of the species." The degree to which geographically isolated populations comprise ESUs can be determined with the analysis of polymorphic genetic markers (Avise 1989; Moritz 1994). Our microsatellite results suggest that isolated mountain populations of blackpoll warblers are not high priority conservation targets. Low pairwise F_{ST} and high N_m estimates suggest gene flow among populations is high, and it is likely that all geographic populations examined here represent one large interbreeding population. By combining SDMs with these genetic data, we find that genetic diversity (in the form of rare private alleles) will be lost, but more than 99 % of genetic structure is predicted to survive past 2080. Based on these results, we conclude that climate induced range shifts in blackpoll warblers will likely not have negative genetic consequences.

At the same time, we recognize that standing genetic variation is important for future adaptation to changing environments and low frequency alleles may be targets of selection (Barret and Schluter 2007). However, the predicted loss in blackpoll warblers of 10 % of microsatellite diversity is lower than has been observed in other species with documented population bottlenecks due to habitat loss and direct human exploitation (Paxinos et al. 2002; Larson et al. 2002; Bellinger et al. 2003; Leonard et al. 2005; Larsson et al. 2008). These studies have used museum specimens or archeological samples to compare levels of contemporary and historic genetic variation. Greater prairie chicken (*Tympanuchus cupido*) populations in Wisconsin lost nearly 30 % of alleles from 1950 to present due to loss of habitat (Bellinger et al. 2003), and populations of sea otters (*Enhydra lutris*) exploited by fur traders lost 50 % of microsatellite alleles (Larson et al. 2002). Both of these species showed significant reduction in number of alleles

per locus and observed heterozygosity. In contrast, blackpoll warbler heterozygosity and genetic structure are not predicted to change significantly. Furthermore, the losses reported in the above cited studies were found throughout the species' ranges, and were associated with decreases in population size and distribution. Predicted losses in blackpoll warblers are only at the regional scale, and population sizes are expected to grow in proportion to predicted expansion of range wide breeding distribution. In the only other study to our knowledge that uses climate models and genetic data to predict future changes in gene pools as a result of climate warming, Habel et al. (2010) predict increased fragmentation of populations and loss of private alleles in the boreal–montane butterfly species *Lycaena helle* as warming reduces suitability at isolated high elevation habitats in central Europe. These populations, however, show higher numbers of private alleles and evidence of greater genetic differentiation ($R_{st} = 0.2643$, $P < 0.001$; Habel et al. 2010) than is present in blackpoll warblers. The potential for loss of diversity, and therefore conservation concern, is much higher in *L. helle*.

Our approach to predicting the genetic consequences of climate warming assumes that once climatic conditions are no longer favorable in a geographic region, populations will go extinct and alleles present in these populations will be lost. This "worst case scenario" may be abated if populations adapt to new conditions and persist, or if individuals disperse to newly suitable areas. Because of the timescale, adaptation to changing conditions seems unlikely (but see Baker et al. 2004; Parmesan 2006) and is unpredictable (Grant and Grant 2002; La Sorte and Jetz 2010). Dispersal to new locations is more likely, especially in migratory bird species. However, range shifts likely represent expansion from a leading edge. Whether trailing edge populations will disperse north into already populated regions in response to climate change is unknown (Hampe and Petit 2005). We have inferred high gene flow among sampled populations of blackpoll warblers and suspect that, despite its archipelago distribution in northeastern North America, barriers to dispersal for this species are minimal. If individuals at the southern periphery disperse in response to climate change, some alleles predicted to go extinct would not, and our predicted level of genetic loss would be an overestimation. This is no consolation for naturalists in New York, Vermont, and New Hampshire, but should dampen our alarm and discourage special conservation action for this species.

It is likely that populations of other bird species inhabiting these same habitat islands do represent ESUs and will require conservation action, and indeed much work is already underway to preserve populations of spruce grouse and Bicknell's thrush (Kerchner et al. 2009; Ross and Johnson 2011; Studds et al. 2012). The genetic consequences of climate change will vary among species

according to dispersal ability, migratory strategy, ecology, climate sensitivity and history of isolation. Comparing results across species can illuminate patterns of common histories, and will provide a more complete picture of the risks that the boreal bird community faces as a whole. Little is known regarding genetic substructure in other species whose distributions we modeled, with the exceptions of yellow-rumped warbler (*S. coronata*), which shows differences among eastern and western subspecies in nuclear DNA but not mitochondrial DNA (Milá et al. 2007; Brelsford et al. 2012), and gray jay (*Perisoreus canadensis*), which has extensive mitochondrial DNA differences among western populations but no genetic structure across the northern population stretching from Newfoundland to Alaska (van Els et al. 2012). Future research should focus on multilocus genotyping of birds from peripheral populations of other species, especially those predicted to decrease range-wide under both emissions scenarios such as gray jay, and ruby-crowned kinglet (*Regulus calendula*).

We acknowledge Green's (2005) warning that type I errors in conservation (rejecting a hypothesis of endangerment, when a population is truly endangered) are dire and irreversible. To account for this, Green advocates the inclusion of extinction risk in assessing conservation priority, and the methods outlined above may prove useful in such assessments. We are also aware of the limited nature of conservation resources, and caution that wrongly warning of endangerment could lead to the inappropriate allocation of these resources, perhaps at the detriment of truly endangered populations. We believe the methods outlined in the present study will allow conservation biologists to simultaneously assess population risk and evolutionary importance, and will lead to the more appropriate use of limited conservation resources.

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