Modeling avifaunal responses to climate change across Alberta's Natural Regions

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INTRODUCTION

The composition of much of North America's avifauna can be attributed to ~2.5 million years of dramatic climate change (Johnson and Cicero 2004, Weir and Schluter 2004, Lovette 2005). During the repeated glacial and interglacial periods of the Pleistocene epoch, Nearctic bird species are presumed to have expanded and retracted their ranges from glacial refugia, resulting in isolation and subsequent divergence of sister taxa (Mengel 1964). Trees such as spruces (*Picea* spp.) spread during the rapid warming and glacial retreat of the early Holocene epoch (~9,000–14,000 years before present), and northern ecosystems achieved their current form during a relatively stable climate over the last 8,000 years (Dyke 2005). Songbirds have presumably tracked these changes in climate and vegetation to recolonize previously glaciated regions within Canada. This is supported by the strong associations between current patterns in climate and current patterns in avian distribution (Jiménez-Valverde et al. 2011, Cumming et al. in press) and diversity (Hawkins and Porter 2003), as well as phylogenetic reconstructions (Ruegg et al. 2006, Waltari et al. 2007). Thus, these species should be well-adapted to respond to future changes in climate by shifting their distribution and abundance as suitable climates and vegetation become available in new areas.

In this study we used bioclimatic niche models to project shifts in songbird distribution and abundance within Alberta in response to projected changes in climate for three future time periods: 2011–2040, 2041–2070, and 2071–2100. We evaluated potential responses for 84 species of songbirds using data from avian point-count surveys conducted across Alaska and Canada from 1992–2010, and recently compiled by the Boreal Avian Modelling Project (BAM; Cumming et al. 2010). We used these data to develop models of current breeding density for each species at a 4-km x 4-km resolution (hereafter 4-km grid cell) using 7 baseline (1961–1990) bioclimatic variables as predictors. The resulting modeled relationships were used to project the spatial distribution and abundance of each species in each of the four time periods, given projected climate conditions. For each species, we then examined the differences in abundance between time periods in each 4-km grid cell to identify areas of Alberta that are projected to have large increases in abundance, large decreases in abundance, or stable abundances through time.

Our bioclimatic niche models assume (1) climate strictly limits the distribution of individual bird species either directly through its effects on avian physiology, migration, or life history, or indirectly through its effects on vegetation; and (2) an equilibrium relationship between avian distribution and abundance and climate conditions exists and will hold into the future, which implies that shifts in vegetation will keep pace with changes in climate. We recognize that these assumptions are not likely to hold because avian site fidelity, avian competition, and rates of vegetation migration and succession may slow the rate that birds can shift their ranges in response to rapid climate change. If birds cannot shift their ranges quickly in response to climate change, then areas within species' current ranges that retain favorable climate conditions into the future will be particularly important in allowing species to adapt to climate change. Therefore, as second step toward understanding avian responses to future climate change we used our bioclimatic envelope models to identify current and future areas of high climatic suitability for each species and calculated the area of overlap for each future time period. We interpreted these areas of overlap as potential climate refugia because they are likely to continue to provide suitable habitat even as the climate changes.

METHODS

Study area and avian survey data

We developed scenario-based projections of the effects of climate change on songbirds across Alberta's Natural Regions, as defined and delineated by the Natural Regions Committee (2006; http://tpr.alberta.ca/parks/heritageinfocentre/naturalregions/). We used data from avian point-count surveys across Canada and northern U.S. states that were conducted from 1992–2010 and compiled by BAM (Cumming et al. 2010). This included data from point-count surveys conducted as part of the North American Breeding Bird Survey (BBS; Sauer et al. 2011), the Alaska Landbird Monitoring Survey (Handel and Cady 2004), and Provincial Breeding Bird Atlases (www.bsc-

eoc.org/volunteer/atlas/index.jsp), as well as a wide variety of individual inventory, monitoring, research, and impact assessment projects (Cumming et al. 2010). The BAM database includes nearly all of the point-count surveys conducted across the Nearctic boreal as defined by Brandt (2009), as well as other

portions of Canada. We also used point-count data from the continental U.S. whose climate space is likely to shift northward in the future. This primarily consisted of BBS data, but also included recent contributions to the BAM dataset from the western Great Lakes region (Hanowski and Niemi 1995). This resulted in data from 128 distinct projects that collectively surveyed 125,547 unique point-count locations with a total of 356,018 surveys (Figure 1). To reduce the confounding influence of anthropogenic disturbance on modeled climate relationships, we removed surveys that were conducted at agricultural, urban, or barren sites, according to the CEC's North American Land Change Monitoring System (NALCMS; http://www.cec.org/Page.asp?PageID=924&ContentID=2819) landcover dataset. We also removed surveys known to be conducted after recent timber harvest or other anthropogenic disturbance activities, as mapped by Global Forest Watch Canada (http://www.globalforestwatch.ca/) and the United States LANDFIRE program (http://www.landfire.gov/disturbance.php). This resulted in 122,202 point-count locations and 349,639 surveys.

Density estimation

In order to estimate avian density from the point-count surveys compiled by BAM, we had to account for two quantities: (1) the proportion of the survey area that was effectively sampled during the surveys (effective area sampled), and (2) the proportion of birds present in the effective area sampled that were detected during the survey (detection probability). These two proportions allowed us to transform the raw survey counts into estimates of density (males per ha) (Nichols et al. 2009, Farnsworth et al. 2005). The effective area sampled and the detection probability for a point-count survey often vary among species, with environmental conditions during surveys, and with the survey protocol employed. These factors should therefore be accounted for when estimating avian density. For example, the effective area sampled by a point-count survey is largely determined by distance that birds can be seen and heard. The effectively area sampled therefore tends to decrease (1) with increases in the sound frequency of bird songs, (2) with increases in the amount of forest canopy closure at survey points, (3) from roadside to off-road surveys, and (4) with increases in the point-count radius (Matsuoka et al. 2012, Sólymos et al. in press). Conversely, the detection probability for songbirds is largely determined by the rate that birds

sing. The detection probability therefore generally (1) increases with increases in species-specific singing rates, (2) decreases with the time since sunrise and date since spring arrival, and (3) increases with the length of time observers spend counting birds at a point (count duration) (Barker and Sauer 1995, Farnsworth et al. 2002).

For each species we used a combination of distance sampling (Buckland et al. 2001) and removal models (Barker and Sauer 1995, Farnsworth et al. 2002) to estimate the effective area sampled and the detection probability, respectively. Distance sampling models the decay in avian detections with increases in the distance between birds and observers, while removal models estimate the rate that birds give detectable cues and are therefore removed from the population of undetected birds present at a sampling site during a survey (Farnsworth et al. 2005). We also evaluated how the effective areas sampled and the detection probability varied with differences in survey protocol (count radius, roadside sampling, count duration) and survey conditions (time of day, day of year, and vegetation cover) (Sólymos et al. in press). We calculated the product of the effective area sampled and the detection probability as a correction factor for each combination of species, point-count location, and point-count visit. We then used the log of the correction factor as an offset in our species distribution models, which assume a Poisson error distribution. This is analogous to how offsets are commonly used in linear generalized linear models to account for differences in survey effort among sampling units (Sólymos et al. in press, Jones et al. 2002).

The 84 species we examined in this report each had a total ≥75 detections during surveys conducted with multiple time and/or distance intervals—general requirements for fitting distance sampling (Buckland et al. 2001) and removal models (Sólymos et al. in press). Three of these species are listed as threatened or of special concern under Canada's Species-at-Risk Act: Olive-sided Flycatcher *Contopus cooperi* (COSEWIC 2007), Canada Warbler *Cardellina canadensis* (COSEWIC 2008), and Rusty Blackbird *Euphagus carolinus* (COSEWIC 2006). Rusty Blackbird is also listed as vulnerable and Olive-sided Flycatcher as near-threatened according to the IUCN Red List.

Climate data

We used a set of 7 derived bioclimatic variables (Table 1) as predictors in our species distribution models. These variables were chosen from a larger set of bioclimatic variables that have previously been used to summarize climate conditions in the western boreal forest (Mbogga et al. 2010, Schneider et al. 2009) and represent variables of hypothesized relevance to songbird distributions, either directly or via vegetation patterns. Although climate variables are intrinsically highly correlated, we avoided extremely correlated (r < 0.85 at point-count locations) pairs of variables and preferentially selected variables that represent seasonal conditions (e.g., mean summer precipitation) over correlated annual indices (e.g., annual precipitation).

We calculated the baseline values of each of the bioclimatic variables at a 4-km resolution using monthly climate normals of temperature and precipitation averaged over 1961–1990. These monthly climate normals came from instrument-measured climate data that were interpolated by PRISM (Daly et al. 2002) and WorldClim (Hijmans et al. 2005). The western North American portion of these data are described by Wang et al. (2011). We also calculated the future projected values of each of the 7 bioclimatic variables for each 4-km grid cell in each of three consecutive future 30-year periods: 2011–2040, 2041–2070, and 2071–2100. We did so by first downscaling projected climate anomalies in monthly temperature and precipitation between the baseline period of 1961–1990 and each future period, and then applying the climate anomalies to the interpolated climate normals for each 4-km grid cell in each future period of the for each 4-km grid cell in each future period of 1961–1990 and each future period, and then applying the climate anomalies to the interpolated climate normals for each 4-km grid cell in each future period. We then used the resulting projections of temperature and precipitation to calculate derived bioclimatic variables for each future time period.

More specifically, we first obtained general circulation model (GCM) projections of monthly temperature (mean, minimum, maximum) and precipitation from the Intergovernmental Panel on Climate Change 4th Assessment Report (IPCC 2007) as part of the World Climate Research Programme's Coupled Model Intercomparison Project phase 3 multi-model dataset (http://www-

pcmdi.llnl.gov/ipcc/info_for_analysts.php; (Meehl et al. 2007). Historical projections were taken from the 20th century simulation, which were generally initiated between 1850 and 1880 and run through 1999 or 2000. Projections for each future period were taken from the SRESA2 (high) emission scenario (IPCC

2000), run from 2000 or 2001 through at least 2099 or 2100. Projections of monthly temperature and total precipitation were averaged across multiple GCM runs (if available) for each thirty-year period. We used all 19 GCMs available for the SRESA2 emission scenario, with grid cell resolutions ranging from 1.125° to 5° (Table 2).

For each future time period, we calculated climate anomalies as the absolute change in temperature and the percent change in precipitation between the projected values for each future period and the projected climate normals for the baseline period. Projected precipitation anomalies were capped at 500% of the projected normal to prevent unrealistic values stemming from chance differences at the low end of the precipitation spectrum. We clipped the projected climate anomalies to North America, downscaled them to a 0.5° resolution using a thin-plate spline interpolation, and then added the downscaled anomalies to the 4-km interpolated climate normals (described above). We did not have future projections for minimum and maximum temperature for 13 of the 19 GCMs. We therefore used the average temperature anomalies in place of minimum and maximum temperature anomalies to calculate future projected minimum and maximum temperature averaged across GCMs. Mean monthly projections of monthly temperature and precipitation were used to calculate the derived bioclimatic variables (Table 1) for each 4-km gird cell in each future time period. We averaged each bioclimatic variable across the GCM projections to create an ensemble mean, which we then used in our future climate scenarios. We performed all climate data manipulations using the program R, version 2.12.1 (R Development Core Team 2010).

Land-use and topography data

For a second set of models, we also included key land-use/landcover variables that may constrain or enhance bird abundance. Using the 250-m NALCMS landcover dataset, we calculated the current proportions of agriculture, urban development, water, and wetlands within each 4-km grid cell. A topographic wetness index (Gessler et al. 1995) derived from a 4-km digital elevation model was used as an additional surrogate for wetland areas.

Species distribution models

We used boosted regression trees (BRT; De'ath 2007, Elith et al. 2008) to model avian densities at the level of the individual point-count station. Boosting (Freund and Schapire 1996) is a powerful machine-learning approach that improves prediction accuracy of tree-based models (Breiman et al. 1984) by building a sequential ensemble of decision trees, with each tree fit in an iterative manner to the residuals of the previously fit model in the ensemble. BRT thereby finds and averages several "rough rules of thumb" rather than seeking a single highly accurate prediction rule (Elith et al. 2008). We used the 'dismo' (Hijmans et al. 2011), 'gbm' (Ridgeway 2010), and 'raster' (Hijmans and van Etten 2012) packages for R (R Core Team 2012) to build BRT models for each species and generate spatial predictions. We used the raw survey count at a point-count location as the response variable and include the log-transformed correction factor as an offset (see **Density estimation**) to obtain estimates of avian density (males per ha). For these count data we deemed the Poisson distribution appropriate and specified a Poisson generalized boosted model (GBM) in the BRT estimation. The Poisson GBM uses an exponential function of the linear predictor in the gradient boosting algorithm (Friedman 2001, 2002) used to fit the models. This is analogous to standard GLM settings, justifying the use of log-transformed correction factors as offsets (see **Density estimation**).

For each species, we estimated density in each 4-km grid cell as the average from 11 BRT models, each fit to a separate bootstrap replicate of 18,299 sampling units. We defined sampling units as the combination of the site (route, plot, or other local grouping of point counts) and 4-km grid cell (n = 39,186 total sampling units) and randomly selected for analysis a single point-count survey from each selected sampling unit in each bootstrap iteration. This was to minimize spatial autocorrelation in surveys among points at the same site and temporal autocorrelation in surveys of points that were survey multiple times within or among years. We accounted for additional spatial autocorrelation among nearby sampling units by weighting the selection probabilities of each sampling unit by the inverse of the total number of surveys within the 20-km x 20-km area surrounding the sampling unit. We minimized the influence of poorly sampled areas in each bootstrap replicate by randomly selecting only 1/3 of the sampling units with ≤ 10 surveys. In each model run, we used a tree complexity of 3, learning rate of 0.001, bag fraction

of 0.5, and a Poisson distribution. The tree complexity specified the number of variables that can be included in an interaction terms (interaction depth), the learning rate weighted the contribution of each model to the prediction, and the bag fraction specified the proportion of data used to build the models (Elith et al. 2008). According to recommendations by Elith et al. (2008) we increased the learning rate to 0.005 if the limit of 10,000 trees was achieved (no further increases were necessary). We reduced it to 0.0001 if fewer than 1,000 trees were obtained, thereby ensuring optimality of the final number of trees.

Model summaries

For each of the 84 species modeled (Table 3), we applied the fitted BRT models to current and future climate conditions to predict avian density in each 4-km grid cell in each time period across the study region. For each species, we applied the fitted BRT models to current and future climate conditions to predict avian density in each 4-km grid cell in each time period across the study region. Predictions were averaged across the 19 GCMs and 11 bootstrap runs and then clipped to the province of Alberta. To calculate projected changes in potential abundance, we first summed the estimates of avian abundance (males/ha * 1600 ha) across grid cells to estimate abundance for each time period. We then calculated the projected percent change in abundance from current to each future time period within each of five natural regions of Alberta: Boreal/Shield, Parkland, Grassland, Foothills, and Mountains. Bootstrap variance was included in these estimates.

To indicate the spatial uncertainty in these projections we provided examples of differences across four GCMs (using a single bootstrap replicate) representing the range of alternative futures projected: the Canadian CCCMA CGCM3.1 (warmer and wetter), the United States GFDL CM2.1 (warmer and much drier), the German MPI ECHAM5 (warmer and drier, near-average across GCMs), and the United Kingdom Met Office HadGEM1 (much warmer and drier) (see Appendix 1, GCM Recommendations for Alberta). This was done for a few species for illustration purposes, but maps for any GCM and species combination are available upon request. Bootstrap CV maps were also presented for the same species but are available for other species upon request, as are GCM CV maps.

Second, we identified areas of projected stability as climate-change "refugia". This was done to address the fact that limitation in avian dispersal or lags in vegetation response may prevent some bird species from shifting their distributions and adjusting their abundances in tandem with the projected changes in climate, thereby limiting the potential for our projected changes to be fully realized. We defined refugia as areas predicted to have a higher than average density for a species in the current baseline period, as well as a particular future time period. To do this, we calculated the mean density for that species within Alberta for the current period, and then defined "core" habitat within each time period as the 4-km grid cells with greater than average density. For each combination of species, we then calculated the proportion of 4-km grid cells identified as core habitat in the baseline period that were also identified as core habitats in each future period. We compared these results with calculations based on probability of occurrence (derived from density) and found little difference for most species so we used the more straightforward density criteria to be consistent with our modeling unit.

RESULTS

Model validation

Prediction success of boosted regression tree models, assed via cross-validation, ranged from poor (0.003 deviance explained, 0.060 correlation for Common Raven *Corvus corax*) to excellent (0.530 deviance explained, 0.497 correlation for Clay-colored Sparrow *Spizella pallida*) (Table 3). On average across species, the inclusion of land-use and topography variables (in addition to climate) did not improve cross-validation correlation or deviance explained. However, for 33 (out of 84) individual species, models were significantly improved in terms of one or both of these diagnostics based on a paired t-test across bootstrap runs (n = 11). For 14 other species, climate-only models were significantly better. For the remaining 40 species there was no significant difference in model performance between climate-only and climate + land-use + topography models.

Projected changes in potential abundance

Of the 84 species currently breeding in Alberta, 42 were projected on average (across bootstrap runs) to decline in potential abundance across the province by 2040; 48 species by 2070; and 50 species

by 2100 (Table 4). Of these, the projected direction of change was uncertain (i.e., bootstrapped 95% confidence intervals contained 0) for 9 species by 2040, 4 by 2070, and 0 by 2100. The species with largest percent projected mean decreases within Alberta by mid-century (2070) were Tennessee Warbler *Oreothlypis peregrina* (-83%), Lincoln's Sparrow *Melospiza lincolnii* (-68%), and Gray Jay *Perisoreus canadensis* (-68%) (Table 4). By 2100, the list of species with the largest projected decreases became Tennessee Warbler (-97%), Connecticut Warbler *Oporornis agilis* (89%), and Bay-breasted Warbler *Dendroica castanea* (-86%). Also among the species with large projected century-long declines were Canada Warbler (-45%), Rusty Blackbird (-43%), and Olive-sided Flycatcher (-47%), three species at risk that have experienced steep declines in recent decades.

Within the boreal natural region, 44 Alberta-breeding species were projected to decline in abundance by mid-century (2041-2070), the largest percent declines being projected for Tennessee Warbler (-83%), Fox Sparrow *Passerella iliaca* (-76%), and Lincoln's Sparrow (-72%) (Table 5). Within the parkland region, 39 species were projected to decline by 2070, of which the top three were Tennessee Warbler (-92%), Gray Jay (-79%), and Lincoln's Sparrow (-78%). Sixty-two species were project to decline in abundance within the grassland region (greatest declines projected, from largest to smallest, for Clay-colored Sparrow, Swainson's Thrush *Catharus ustulatus*, and Ruby-crowned Kinglet *Regulus calendula*), 58 species within the foothills region (greatest declines for Connecticut Warbler, Tennessee Warbler, and Ruby-crowned Kinglet), and 25 species within the mountain region (greatest declines for White-crowned Sparrow *Zonotrichia leucophrys*, Tennessee Warbler, and Gray Jay).

The largest projected increases in potential abundance across the province by mid-century were for American Goldfinch *Spinus tristis* (328%), Gray Catbird *Dumetella carolinensis* (308%), and Redwinged Blackbird *Agelaius phoeniceus* (306%) (Table 4). For the boreal natural region, the same three species ranked highest in terms of increases (all > 500%) (Table 5). The largest projected increases in the parkland region were for Chestnut-sided Warbler *Dendroica pensylvanica*, Blackburnian Warbler *Dendroica fusca*, and Blue Jay *Cyanocitta cristata* (all > 500%). In the grassland region, Brown Thrasher *Toxostoma rufum*, Common Grackle *Quiscalus quiscula* and Eastern Kingbird *Tyrannus tyrannus* ranked

highest. In the foothill region it was Eastern Kingbird, Horned Lark *Eremophila alpestris*, and Brown Thrasher; in the mountain region it was House Wren *Troglodytes aedon*, American Redstart *Setophaga ruticilla*, and American Crow *Corvus brachyrhynchos*.

For the majority of species, future projections did not differ substantially between climate-only and climate + land use + topography models (Figure 2). However, for several species the inclusion of these additional variables resulted in significant differences in end-of-the century abundance projections (differences were generally not apparent earlier). Most of the species for which the inclusion of land-use and topography variables resulted in different future projections also demonstrated improvements in model predictive ability with the inclusion of those variables (Table 3), for example agriculture-associated species such as American Crow and American Goldfinch. However, differences in abundance projections were also observed for species with better performing climate-only models—e.g., Clay-colored Sparrow and House Wren, as well as some with no significant difference between model performance, e.g., Blackand-white Warbler and Yellow Warbler.

Spatial changes in projected density

The distributions of most species were projected to shift northward and upslope toward the end of the century, with many species projected to first increase within the province as suitable climate space expands, and then decrease by the end of the century, as much of that climate space is projected to shift outside of the province (Figures 3-5). Coniferous boreal forest species such as Bay-breasted and Tennessee Warbler were projected to shift almost entirely out of the province, while deciduous-associated species such as Ovenbird and Canada Warbler were generally projected to contract their distributions in the central part of the province and move up-slope into the highland regions. Mountain species such as Varied Thrush and Townsend's Warbler were generally projected to move up-slope, experiencing a range contraction, while grassland-associated species generally experienced large projected expansions into the current boreal region.

Climate change refugia

The projected climate-change refugia for most species decreased in area over time as species' distributions diverged from current conditions (Figure 6, Table 6). The primary exception was for southern species, which were projected to expand northward while their current distributions were largely retained as suitable climates (due to suitable climate space south and east of Alberta). Averaged across 84 Alberta species, the percent of core area remaining in refugia was $79 \pm 2\%$ (SE) for 2011–2040, $59 \pm 4\%$ for 2041–2070, and $42 \pm 4\%$ for 2071–2100. The species with the smallest projected percent of core area remaining as refugia for the 2011–2040 period were White-winged Crossbill (35%), Western Tanager (37%), and Lincoln's Sparrow (40%) (Table 6). By 2071–2100, twenty-one species had projected refugia less than 10% of their current core area; for nine species refugia constituted less than 1% of the current core area: Bay-breasted Warbler, Cape May Warbler, Connecticut Warbler, Tennessee Warbler, Rusty Blackbird, White-winged Crossbill, Lincoln's Sparrow, Philadelphia Vireo, and Gray Jay.

DISCUSSION

Our bioclimatic niche models revealed the potential for dramatic northward shifts in suitable climates for Alberta-breeding songbirds based on projections of climate change over the next century. If these changes in climate are accompanied by rapid northward shifts in vegetation, and barring substantial *in situ* adaptation to climate change, then our models imply large long-term shifts in avian distribution and abundance from the parkland and boreal regions northward out of Alberta, with large potential declines in abundance identified for many forest species. Population declines may be exacerbated by increases in the cost of migration due to lengthening migration distances as well as hypothesized phenological mismatches in insect availability and breeding arrival times (Both et al. 2010).

A likely alternative, however, is that changes in vegetation will lag behind the rapid northward shift in suitable climates, as mature forest stands persist in areas that become climatically unsuitable for regeneration. If this scenario prevails then projected declines along the "trailing" (southern or lowelevation) edge of species' distributions may not be observed within the model-projected timeframe. Likewise, "leading" (northward or high-elevation) edge expansions may be slowed by plant dispersal limitations and edaphic constraints. To the extent that modeled avian climate responses are directly

related to climate conditions—e.g., via physiological tolerance or food web processes that operate on shorter time scales—this lag time may be reduced, especially in areas that do not experience wholesale shifts in vegetation. Given these uncertainties in the rates of response to climate change, climate-change "refugia"—core areas of a species' distribution that are projected to remain suitable over time—should be particularly important for birds, and may represent areas of stable or increasing populations. The proportion of a species' core range maintained as refugia is likely to influence its ability to maintain its population size through time. Large losses of core area without compensatory northward shifts may result in population declines unless the losses are mitigated by increases in breeding density within the current range—a possibility if current populations are below carrying capacity, i.e., if habitat is not currently limiting avian densities.

For three species of concern—Olive-sided Flycatcher, Blackpoll Warbler *Setophaga striata*, and Rusty Blackbird—our models projected that suitable climatic conditions for breeding in Alberta will be highly reduced in the future. Models for a fourth species of concern—Canada Warbler—contained greater uncertainty, although the projected trend in abundance was also negative for this species. This has the potential to exacerbate the already steep population declines of these species (Sauer and Link 2011). For Rusty Blackbird, recent declines have already been attributed to climate change (McClure et al. 2012), as well as potential associations with wetland drying (Matsuoka et al. 2010) and forest management of climate-triggered insect epidemics (Powell et al. 2010).

Our analysis also identified several species likely to increase within Alberta, including the brood parasite Brown-headed Cowbird *Molothrus ater*. Increases in cowbirds may have negative consequences for other boreal-breeding species, particularly open-cup nesters that have not evolved mechanisms to resist cowbird parasitism. In addition, two corvids—American Crow and Blue Jay—are projected to increase within Alberta, potentially increasing nest predation for many species. Cowbirds and crows are often tied to agricultural land use, however, and our models incorporating land use suggest that a shift in agriculture would need to accompany climate change for large increases to occur.

This was also the case for several non-pest grassland species, some of which exhibited dramatically different responses to climate change depending on whether land use was accounted for in the model. For one range-restricted species, Clay-colored Sparrow, future projections were completely reversed, such that large increases became large declines in the absence of a shift in agriculture. Likewise, for a few species exhibiting negative landscape-scale associations with agriculture, models incorporating land use suggested that projected declines based on climate-only models may be reduced (e.g., Ovenbird *Seiurus aurocapillus*) or reversed (e.g., Blackburnian Warbler) if the distribution of agricultural land use does not track climate change.

Finally, although patterns of change were generally similar among GCMs representing warmer and drier conditions (in terms of available moisture, not necessarily precipitation), we found significant variability in the magnitude (i.e., timing) of change, generally swamping the model uncertainty reflected by the bootstrap variance. Under the scenario of a warmer and wetter future, as represented by the Canadian climate model, patterns of change were significantly different for many species (fewer declines, more increases). Although this model is in the minority, and would appear to contradict recent trends toward drier conditions in the province, it cannot be excluded from the realm of possibility. However, in light of the strong agreement among most GCMs for a drier future, it appears prudent to plan for the outcomes represented by the ensemble mean predictions, which reflect the drier projections. In this case, high uncertainty about the magnitude of change remains, but projections are situated along the same trajectory, suggesting that the timing of change is the biggest outstanding question for avian conservation planning and management. Coupled with uncertainties about the timing of vegetation responses to climate, this emphasizes the importance of long-term monitoring to detect early indications of change.

Conservation and management implications

Our analysis represents a first step toward understanding the potential for boreal bird populations and communities to respond to future changes in climate. If our projections of population changes are a reflection of the future to come, avian conservationists will be faced with severe declines in listed and near-listed species (Olive-sided Flycatcher, Rusty Blackbird), increases in perceived pests (Brown-headed

Cowbird, American Crow), and a possible reshuffling of the Alberta avifauna. However, our models are not mechanistic and do not explicitly incorporate the vegetation changes that we assume will be necessary for these changes in bird communities to take place. Predicting how quickly vegetation will respond to climate change is complicated by plant dispersal rates, forest successional and disturbance dynamics, edaphic constraints, and other limitations to vegetation change. Furthermore, our model-predicted densities represent potential niches, unconstrained by current range limits. Thus, current populations may be overestimated due to unoccupied but "suitable" climate space.

Given these uncertainties in using climate niche models to project future avian distributions and the difficulties in developing continental mechanistic predictions of ecosystem change (e.g., Gilman et al. 2010), the refugia approach we used may be a practical alternative to help direct avian conservation in the face of climate change. The refugia can be used to identify the areas that have the greatest potential to retain core populations of boreal bird species as climate changes rapidly over the next century. These climate refugia might therefore be used to help prioritize lands for future conservation or to evaluate the effectiveness of existing and proposed protected areas networks (Araújo et al. 2004, Hannah et al. 2005). Although coarse in scale, the spatial resolution of our models is on par with the scales necessary to incorporate disturbance dynamics into regional boreal conservation planning (Leroux et al. 2007). Nevertheless, we also recognize the value of identifying finer-scale "microrefugia" (Ashcroft 2010, Rull 2009). These are likely to be concentrated in areas of high topographic and climatic diversity (Ackerly et al. 2010, Dobrowski 2010) and may be particularly useful for focusing conservation efforts at local and regional scales.

Next steps

In the short term, we will be refining the models presented in the report and plan to complete two manuscripts that synthesize the findings herein in terms of boreal songbird vulnerability, sources of prediction uncertainty, and spatial conservation priorities relative to current projections of climate change in northern North America. As an extension of this modeling effort, we are also evaluating the importance of historical biogeographic factors in determining current distributional patterns, as well as potential

future implications of projected range expansion and fragmentation. In the coming year, we will be working at finer spatial scales to incorporate vegetation succession, disturbance dynamics, land use, and climate change into more dynamic and mechanistic models that will allow us to evaluate the relative and cumulative effects of these different drivers of landscape change on boreal birds. We plan to use a combination of vegetation data from forest resource inventories (forest type x age), models of climatic influences on natural disturbance regimes (fire and insect outbreaks) and plant succession, simulations of industrial land use (timber harvest and energy sector development), and more refined models of birdhabitat relationships.

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Table 1. Derived bioclimatic variables used as predictors in species distribution models for boreal songbirds.

msp	Mean summer (May-Sep) precipitation (mm)
dd51	Degree days above 5 °C
dd01	Degree days below 0 °C
emt	Extreme minimum temperature (°C)
td	Difference between mean warm month and cold month temperatures (°C)
cmi	Climate moisture index (precipitation – potential evapotranspiration) (mm)
cmijja	Summer climate moisture index (Jun/Jul/Aug) (mm)_

Modeling Avifaunal Responses to Climate Change

Final report

Table 2. General circulation models (GCM) and country of origin, their spatial resolution, and their associated number of runs for each century and climate variable. The projected climate variables include monthly precipitation (precip) and monthly average (tavg), minimum (tmin), and maximum (tmax) temperature.

	Spatial resolution			20th ce	entury		21st century			
GCM, Country	x (°)	y (°)	precip	tavg	tmax	tmin	precip	tavg	tmax	tmin
BCCR-BCM2.0, Norway	2.81250	2.81250	1	1	1	1	1	1	1	1
CCSM3, USA	1.40625	1.40625	8	8	7	7	5	5	2	2
CGCM3.1(T47), Canada	3.75000	3.75000	5	5	0	0	5	5	0	0
CNRM-CM3, France	2.81250	2.81250	1	1	0	0	1	1	0	0
CSIRO-Mk3.0, Australia	1.87500	1.87500	3	3	3	3	1	1	1	1
CSIRO-Mk3.5, Australia	1.87500	1.87500	3	3	3	3	1	1	1	1
ECHAM5/MPI-OM, Germany	1.87500	1.87500	4	4	0	0	3	3	0	0
ECHO-G, Germany/Korea	3.75000	3.75000	3	3	0	0	3	3	0	0
GFDL-CM2.0, USA	2.50000	2.00000	3	3	0	0	1	1	0	0
GFDL-CM2.1, USA	2.50000	2.00000	3	3	0	0	1	1	0	0
GISS-ER, USA	5.00000	3.91305	9	9	0	0	1	1	0	0
INGV-ECHAM4, Italy	1.12500	1.12500	1	1	0	0	1	1	0	0
INM-CM3.0, Russia	5.00000	4.00000	1	1	1	1	1	1	1	1
IPSL-CM4, France	3.75000	2.50000	2	2	0	0	1	1	0	0
MIROC3.2(medres), Japan	2.81250	2.81250	3	3	3	3	3	3	3	3
MRI-CGCM2.3.2, Japan	2.81250	2.81250	5	5	0	0	5	5	0	0
PCM, USA	2.81250	2.81250	4	4	2	2	3	4	0	0
UKMO-HadCM3, UK	3.75000	2.46575	2	2	0	0	1	1	0	0
UKMO-HadGEM1, UK	1.87500	1.24138	2	1	0	0	1	1	0	0

Table 3. Mean cross-validation statistics for climate-only vs. climate + land use + topography models across 11 bootstrap iterations containing 10 cross-validation runs each. Significantly greater cross-validation statistics (n=11) based on pairwise t-tests are indicated in bold (* p < 0.05, ** p < 0.005).

		Climate-only		Climate + La	nd Use + Topo
Species		Deviance	Correlation	Deviance	Correlation
Code	Common Name (Scientific Name)	Explained	Coefficient	Explained	Coefficient
ALFL	Alder Flycatcher (Empidonax alnorum)	0.123	0.230	0.115	0.233
AMCR	American Crow (Corvus brachyrhynchos)	0.108	0.196	0.158**	0.246**
AMGO	American Goldfinch (Spinus tristis)	0.253	0.333	0.267**	0.339*
AMRE	American Redstart (Setophaga ruticilla)	0.164*	0.329*	0.153	0.314
AMRO	American Robin (Turdus migratorius)	0.085	0.250	0.105**	0.275**
BAOR	Baltimore Oriole (Icterus galbula)	0.310	0.302	0.305	0.302
BAWW	Black-and-white Warbler (Mniotilta varia)	0.152	0.216	0.143	0.217
BBWA	Bay-breasted Warbler (Setophaga castanea)	0.218	0.229	0.221	0.229
BCCH	Black-capped Chickadee (Poecile atricapillus)	0.120	0.200	0.119	0.202
BHCO	Brown-headed Cowbird (Molothrus ater)	0.303	0.324	0.324**	0.326
BHVI	Blue-headed Vireo (Vireo solitarius)	0.176	0.252	0.173	0.251
BLBW	Blackburnian Warbler (Setophaga fusca)	0.217	0.276	0.222	0.271
BLJA	Blue Jay (Cyanocitta cristata)	0.202**	0.240	0.197	0.238
BLPW	Blackpoll Warbler (Setophaga striata)	0.198	0.250	0.193	0.236
BOCH	Boreal Chickadee (Poecile hudsonicus)	0.140	0.157	0.130	0.151
BRBL	Brewer's Blackbird (Euphagus cyanocephalus)	0.294	0.203	0.292	0.207
BRCR	Brown Creeper (Certhia americana)	0.040	0.104	0.043	0.108
BRTH	Brown Thrasher (Toxostoma rufum)	0.170	0.171	0.174	0.166
BTNW	Black-throated Green Warbler (Setophaga virens)	0.223	0.292	0.219	0.293
CAWA	Canada Warbler (Cardellina canadensis)	0.126	0.206*	0.122	0.200
CCSP	Clay-colored Sparrow (Spizella pallida)	0.530	0.497*	0.532	0.484
CEDW	Cedar Waxwing (Bombycilla cedrorum)	0.069	0.110	0.067	0.110
CHSP	Chipping Sparrow (Spizella passerina)	0.082	0.185	0.085**	0.187
CMWA	Cape May Warbler (Setophaga tigrina)	0.196*	0.195	0.183	0.189
COGR	Common Grackle (Quiscalus quiscula)	0.338	0.322	0.352**	0.335*
CONW	Connecticut Warbler (Oporornis agilis)	0.244	0.180	0.239	0.177

			te-only	Climate + Land Use + Topo		
Species		Deviance	Correlation	Deviance	Correlation	
Code	Common Name (Scientific Name)	Explained	Coefficient	Explained	Coefficient	
CORA	Common Raven (Corvus corax)	0.003*	0.060*	-0.003	0.050	
COYE	Common Yellowthroat (Geothlypis trichas)	0.136	0.246	0.142**	0.254**	
CSWA	Chestnut-sided Warbler (Setophaga pensylvanica)	0.267	0.333	0.273*	0.341*	
DEJU	Dark-eyed Junco (Junco hyemalis)	0.197	0.297	0.204**	0.298	
EAKI	Eastern Kingbird (Tyrannus tyrannus)	0.216	0.222	0.225*	0.224	
EAPH	Eastern Phoebe (Sayornis phoebe)	0.162	0.172*	0.149	0.166	
EVGR	Evening Grosbeak (Coccothraustes vespertinus)	0.069	0.115	0.078	0.117	
FOSP	Fox Sparrow (Passerella iliaca)	0.419**	0.434*	0.406	0.421	
GCKI	Golden-crowned Kinglet (Regulus satrapa)	0.114	0.171	0.127**	0.181**	
GRAJ	Gray Catbird (Dumetella carolinensis)	0.155	0.212	0.167*	0.219	
GRCA	Gray Jay (Perisoreus canadensis)	0.237**	0.295*	0.211	0.286	
HAFL	Hammond's Flycatcher (Empidonax hammondii)	0.321	0.261	0.317	0.261	
HETH	Hermit Thrush (Catharus guttatus)	0.112	0.241	0.119**	0.250**	
HOLA	Horned Lark (Eremophila alpestris)	0.467	0.413	0.482*	0.409	
HOWR	House Wren (Troglodytes aedon)	0.277**	0.263**	0.249	0.232	
LCSP	Le Conte's Sparrow (Ammodramus leconteii)	0.207	0.184*	0.178	0.157	
LEFL	Least Flycatcher (Empidonax minimus)	0.092*	0.162**	0.080	0.150	
LISP	Lincoln's Sparrow (Melospiza lincolnii)	0.186	0.254	0.189	0.253	
MAWA	Magnolia Warbler (Setophaga magnolia)	0.298	0.412	0.300	0.416*	
MOWA	Mourning Warbler (Geothlypis philadelphia)	0.166	0.226	0.167	0.230	
NOWA	Northern Waterthrush (Parkesia noveboracensis)	0.140	0.201	0.137	0.195	
OCWA	Orange-crowned Warbler (Oreothlypis celata)	0.273	0.298	0.271	0.297	
OSFL	Olive-sided Flycatcher (Contopus cooperi)	0.078	0.126	0.077	0.131*	
OVEN	Ovenbird (Seiurus aurocapilla)	0.301	0.453	0.309**	0.461**	
PAWA	Palm Warbler (Setophaga palmarum)	0.226*	0.251	0.210	0.239	
PHVI	Philadelphia Vireo (Vireo philadelphicus)	0.255	0.271	0.252	0.268	
PIGR	Pine Grosbeak (Pinicola enucleator)	0.052	0.084	0.052	0.088	
PISI	Pine Siskin (Spinus pinus)	0.168	0.181	0.185*	0.195*	
PUFI	Purple Finch (Carpodacus purpureus)	0.095*	0.129*	0.071	0.114	
RBGR	Rose-breasted Grosbeak (Pheucticus ludovicianus)	0.159	0.210	0.169*	0.220*	

		Climate-only		Climate + Lar	nd Use + Topo
Species		Deviance	Correlation	Deviance	Correlation
Code	Common Name (Scientific Name)	Explained	Coefficient	Explained	Coefficient
RBNU	Red-breasted Nuthatch (Sitta canadensis)	0.097	0.178	0.107**	0.187*
RCKI	Ruby-crowned Kinglet (Regulus calendula)	0.276	0.419	0.285**	0.426**
REVI	Red-eyed Vireo (Vireo olivaceus)	0.286	0.437	0.287	0.442**
RUBL	Red-winged Blackbird (Agelaius phoeniceus)	0.156	0.166	0.157	0.171
RWBL	Rusty Blackbird (Euphagus carolinus)	0.307	0.370	0.332**	0.374
SAVS	Savannah Sparrow (Passerculus sandwichensis)	0.195	0.320	0.252**	0.341*
SEWR	Sedge Wren (Cistothorus platensis)	0.239	0.167	0.210*	0.157
SOSP	Song Sparrow (Melospiza melodia)	0.227	0.372	0.263**	0.408**
SWSP	Swamp Sparrow (Melospiza georgiana)	0.156	0.194	0.149	0.181
SWTH	Swainson's Thrush (Catharus ustulatus)	0.227	0.423	0.245	0.429**
TEWA	Tennessee Warbler (Oreothlypis peregrina)	0.429	0.535	0.442*	0.543
TOWA	Townsend's Warbler (Setophaga townsendi)	0.396	0.342	0.395	0.333
TRES	Tree Swallow (Tachycineta bicolor)	0.070	0.115	0.098**	0.139*
VATH	Varied Thrush (Ixoreus naevius)	0.373	0.376	0.378	0.375
VEER	Veery (Catharus fuscescens)	0.235	0.303	0.240**	0.310**
VESP	Vesper Sparrow (Pooecetes gramineus)	0.462	0.457	0.474**	0.459
WAVI	Warbling Vireo (Vireo gilvus)	0.274	0.340	0.267	0.342
WBNU	White-breasted Nuthatch (Sitta carolinensis)	0.134	0.123	0.135	0.122
WCSP	White-crowned Sparrow (Zonotrichia leucophrys)	0.558	0.527	0.556	0.528
WETA	Western Tanager (Piranga ludoviciana)	0.333	0.336	0.331	0.339
WEWP	Western Wood-Pewee (Contopus sordidulus)	0.278	0.295	0.272	0.295
WIWA	Wilson's Warbler (Cardellina pusilla)	0.291	0.357	0.288	0.354
WIWR	Winter Wren (Troglodytes hiemalis)	0.244	0.340	0.254**	0.350**
WTSP	White-throated Sparrow (Zonotrichia albicollis)	0.279	0.434	0.276	0.434
WWCR	White-winged Crossbill (Loxia leucoptera)	0.106	0.118	0.102	0.116
YBFL	Yellow-bellied Flycatcher (Empidonax flaviventris)	0.243	0.303	0.252**	0.310*
YRWA	Yellow-rumped Warbler (Setophaga coronata)	0.155	0.304	0.178**	0.318**
YWAR	Yellow Warbler (Setophaga petechia)	0.143	0.271	0.144	0.260

Table 4. Projected changes in potential abundance (± 2 SE) for 84 species across three future time periods averaged across 4 GCMs. Standard errors are based on 2 models (climate-only and climate + land-use + topography), 11 bootstrap runs, and 4 GCMs (CCCMA CGCM3, MPI ECHAM5, GFDL CM2.1, UKMO HadGEM1). Species common and scientific names are given in Table 3.

	Estimated Potential C	Current	t Future Projected Change						
Species	Abundance (million	pairs)	2011-2040	2041-2070	2071-2100				
ALFL	$3.94 \pm$	0.39	$-17\%~\pm~14\%$	$-34\% \pm 27\%$	$-55\% \pm 27\%$				
AMCR	$1.12 \pm$	0.46	$53\%~\pm~63\%$	$63\%~\pm~80\%$	$51\%~\pm~102\%$				
AMGO	2.26 ±	1.38	$81\% \pm 101\%$	$241\% \pm 237\%$	$408\%~\pm~288\%$				
AMRE	$5.58 \pm$	0.64	$36\% \pm 44\%$	$34\% \pm 66\%$	$-20\% \pm 62\%$				
AMRO	$8.92 \pm$	0.91	$19\%~\pm~19\%$	$40\% \pm 23\%$	$78\% \pm 52\%$				
BAOR	0.29 ±	0.22	$25\% \pm 103\%$	91% ±238%	$220\%~\pm~452\%$				
BAWW	$1.43 \pm$	0.36	$32\% \pm 47\%$	$46\%~\pm~70\%$	$34\%~\pm~128\%$				
BBWA	2.90 \pm	0.79	$-22\% \pm 44\%$	$-55\% \pm 39\%$	$-81\% \pm 19\%$				
BCCH	$3.15 \pm$	0.36	$49\%~\pm~50\%$	$93\% \pm 52\%$	129% ± 86%				
BHCO	6.15 \pm	1.54	$26\%~\pm~41\%$	98% ±156%	$258\% \pm 307\%$				
BHVI	1.49 \pm	0.43	$0\% \pm 35\%$	$-19\% \pm 46\%$	$-43\% \pm 38\%$				
BLBW	0.83 \pm	0.29	106% ±122%	$149\% \pm 164\%$	$92\%~\pm~190\%$				
BLJA	0.25 \pm	0.04	$66\%~\pm~76\%$	166% ±156%	$256\% \pm 478\%$				
BLPW	2.06 \pm	0.43	$-27\%~\pm~20\%$	$-37\% \pm 27\%$	$-45\% \pm 35\%$				
BOCH	3.97 \pm	1.32	$-22\% \pm 22\%$	$-44\% \pm 24\%$	$-62\% \pm 18\%$				
BRBL	1.82 ±	1.08	$7\% \pm 65\%$	$30\% \pm 117\%$	$75\% \pm 177\%$				
BRCR	$1.13 \pm$	0.22	$-2\% \pm 23\%$	$-12\% \pm 30\%$	-27% ± 34%				
BRTH	0.03 \pm	0.03	$72\% \pm 168\%$	298% ± 624%	$746\% \pm 779\%$				
BTNW	1.16 ±	0.23	$19\% \pm 45\%$	$19\% \pm 67\%$	-7% ± 93%				
CAWA	0.76 \pm	0.44	$4\%~\pm~56\%$	$-4\% \pm 64\%$	$-26\% \pm 82\%$				
CCSP	$5.43 \pm$	1.13	$-9\% \pm 60\%$	$-24\% \pm 84\%$	$-48\% \pm 70\%$				
CEDW	4.47 \pm	0.66	$38\%~\pm~37\%$	$66\% \pm 39\%$	$82\% \pm 59\%$				
CHSP	13.11 ±	1.08	$-10\% \pm 11\%$	$-16\% \pm 12\%$	-22% ± 21%				
CMWA	2.56 \pm	0.67	$-22\% \pm 43\%$	$-51\% \pm 39\%$	-79% ± 13%				
COGR	1.89 \pm	0.66	$59\% \pm 80\%$	245% ± 425%	916% ±1361%				
CONW	0.46 \pm	0.17	$-25\% \pm 69\%$	$-61\% \pm 45\%$	$-84\% \pm 29\%$				
CORA	$1.02 \pm$	0.16	$3\% \pm 19\%$	$-2\% \pm 22\%$	$-20\% \pm 30\%$				
COYE	2.01 \pm	0.43	$43\%~\pm~49\%$	$96\% \pm 74\%$	134% ± 149%				
CSWA	0.62 ±	0.17	127% ±165%	222% ± 273%	199% ± 473%				
DEJU	6.21 ±	0.95	$-28\%~\pm~16\%$	$-49\% \pm 22\%$	-66% ± 17%				
EAKI	0.62 ±	0.32	$79\% \pm 107\%$	260% ± 390%	597% ± 651%				
EAPH	0.15 \pm	0.07	$28\%~\pm~65\%$	112% ±173%	$248\% \pm 280\%$				
EVGR	0.68 \pm	0.28	$37\%~\pm~53\%$	$46\% \pm 62\%$	$32\% \pm 70\%$				
FOSP	0.88 \pm	0.21	$-34\% \pm 21\%$	$-47\% \pm 25\%$	-55% ± 34%				
GCKI	$4.84~\pm$	0.53	$4\%~\pm~23\%$	-11% ± 39%	$-38\% \pm 34\%$				
GRAJ	$6.35 \pm$	1.16	$-42\% \pm 23\%$	$\textbf{-68\%}~\pm~18\%$	$-84\% \pm 6\%$				
GRCA	0.42 ±	0.21	$71\%~\pm~96\%$	242% ± 310%	484% ± 332%				

	Estimated Potential C	Current	Futur		
Species	Abundance (million	pairs)	2011-2040	2041-2070	2071-2100
HAFL	$1.66 \pm$	0.29	$1\% \pm 36\%$	$-10\% \pm 53\%$	-12% ± 53%
HETH	2.98 \pm	0.43	$-15\% \pm 19\%$	$-33\% \pm 31\%$	$-56\% \pm 30\%$
HOLA	8.29 ±	2.70	$-2\% \pm 63\%$	$14\% \pm 97\%$	$63\%~\pm~146\%$
HOWR	$3.52 \pm$	0.99	$6\% \pm 77\%$	$31\% \pm 143\%$	$65\%~\pm~171\%$
LCSP	0.28 \pm	0.21	$-7\%~\pm~78\%$	$-12\% \pm 87\%$	$-47\% \pm 61\%$
LEFL	$5.51 \pm$	1.09	$-4\% \pm 23\%$	$-13\% \pm 27\%$	$-39\% \pm 42\%$
LISP	3.24 ±	0.43	$-40\%~\pm~18\%$	$-67\%~\pm~19\%$	$-82\% \pm 7\%$
MAWA	4.00 \pm	1.14	$0\% \pm 36\%$	$-15\% \pm 45\%$	$-40\% \pm 38\%$
MOWA	1.20 \pm	0.25	$23\%~\pm~67\%$	$4\% \pm 88\%$	$-31\% \pm 111\%$
NOWA	1.20 \pm	0.19	$-16\%~\pm~11\%$	$-34\% \pm 25\%$	$-51\% \pm 15\%$
OCWA	$3.02 \pm$	0.51	$-31\% \pm 20\%$	$-47\%~\pm~16\%$	$-54\% \pm 18\%$
OSFL	0.28 \pm	0.07	$-19\% ~\pm~ 20\%$	$-33\% \pm 20\%$	$-45\%~\pm~~15\%$
OVEN	4.62 ±	0.79	$15\% \pm 34\%$	$-3\% \pm 66\%$	$-32\% \pm 100\%$
PAWA	1.19 ±	0.40	$-40\% \pm 35\%$	$-62\% \pm 22\%$	$-74\% \pm 16\%$
PHVI	0.82 ±	0.21	$-7.4\% \pm 31\%$	$-34\% \pm 39\%$	$-64\% \pm 25\%$
PIGR	0.39 ±	0.21	$-12\% \pm 51\%$	$-21\% \pm 54\%$	$-29\% \pm 57\%$
PISI	$12.51 \pm$	3.28	$-23\% \pm 41\%$	$-49\% \pm 32\%$	-66% ± 24%
PUFI	0.73 \pm	0.28	$17\%~\pm~43\%$	$27\% \pm 46\%$	$34\% \pm 55\%$
RBGR	0.78 \pm	0.25	$8\% \pm 42\%$	$23\% \pm 79\%$	$11\% \pm 161\%$
RBNU	$3.64 \pm$	0.60	$7\% \pm 16\%$	$-3\% \pm 32\%$	-21% ± 49%
RCKI	7.68 \pm	0.65	$-26\%~\pm~18\%$	$-55\% \pm 30\%$	-80% ± 13%
REVI	5.29 \pm	0.73	$33\% \pm 48\%$	$34\% \pm 72\%$	$5\%~\pm~128\%$
RUBL	0.36 \pm	0.21	$-32\% \pm 39\%$	$-43\% \pm 33\%$	-46% ± 31%
RWBL	3.35 \pm	1.56	$58\% \pm 74\%$	$180\% \pm 262\%$	338% ± 362%
SAVS	5.90 \pm	1.78	$21\%~\pm~47\%$	$35\% \pm 79\%$	$37\%~\pm~100\%$
SEWR	0.05 \pm	0.05	$23\%~\pm~99\%$	$91\% \pm 146\%$	$132\%~\pm~259\%$
SOSP	$2.22 \pm$	0.83	$55\% \pm 58\%$	$129\%~\pm~87\%$	$191\%~\pm~161\%$
SWSP	$1.03 \pm$	0.39	$10\% \pm 42\%$	$15\% \pm 45\%$	$14\% \pm 55\%$
SWTH	10.48 \pm	0.85	$-19\%~\pm~15\%$	$-46\% \pm 37\%$	$-74\% \pm 22\%$
TEWA	19.04 \pm	2.26	$-57\% ~\pm~ 36\%$	$-82\% \pm 20\%$	$-96\% \pm 5\%$
TOWA	0.89 \pm	0.31	$-6\%~\pm~51\%$	$-22\%~\pm~61\%$	$-30\% \pm 64\%$
TRES	2.77 \pm	1.11	$16\% \pm 34\%$	$50\% \pm 70\%$	$132\%~\pm~152\%$
VATH	1.20 \pm	0.26	$-19\% ~\pm~ 29\%$	$-36\% \pm 34\%$	-51% ± 35%
VEER	0.44 ±	0.06	$102\% \pm 114\%$	$189\% \pm 121\%$	$204\%~\pm~203\%$
VESP	4.41 \pm	1.18	$0\% \pm 43\%$	$10\% \pm 70\%$	$25\%~\pm~~86\%$
WAVI	$3.00 \pm$	0.55	$4\%~\pm~17\%$	$1\% \pm 28\%$	$1\% \pm 28\%$
WBNU	0.18 \pm	0.04	$31\% \pm 40\%$	$117\% \pm 198\%$	$315\% \pm 316\%$
WCSP	0.62 ±	0.04	$-33\%~\pm~16\%$	$-45\%~\pm~16\%$	$-54\% \pm 11\%$
WETA	1.42 \pm	0.48	$-32\% \pm 31\%$	$-46\% \pm 26\%$	$-57\% \pm 26\%$
WEWP	0.57 \pm	0.35	$-14\% ~\pm~ 33\%$	$-20\% \pm 34\%$	$-18\% \pm 49\%$
WIWA	2.70 \pm	0.38	$-24\% \pm 19\%$	$-43\% \pm 25\%$	$-59\% \pm 19\%$
WIWR	0.70 \pm	0.15	$-2\% \pm 37\%$	$-19\%~\pm~45\%$	$-36\% \pm 53\%$

	Estimated Potential C	urrent	Future Projected Change						
Species	Abundance (million	pairs)	2011-2040	2041-2070	2071-2100				
WTSP	7.58 \pm	0.48	$-13\% \pm 23\%$	$-38\% \pm 38\%$	$-60\% \pm 45\%$				
WWCR	5.47 \pm	1.60	$-39\% ~\pm~ 27\%$	$-64\% \pm 20\%$	-77% ± 15%				
YBFL	0.79 \pm	0.17	$-6\% \pm 36\%$	$-26\% \pm 38\%$	-46% ± 33%				
YRWA	17.76 \pm	1.96	$-33\% \pm 27\%$	$-56\% \pm 25\%$	-76% ± 16%				
YWAR	5.81 \pm	1.11	$-6\% \pm 33\%$	$3\% \pm 49\%$	$29\%~\pm~101\%$				

	Potential Current Abundance x 10 ⁶ (1961-1990)							Mid-Century Projections (2041-2070)				
Species	Boreal	Parkland	Grassland	Foothills	Mountains	Total	Boreal	Parkland	Grassland	Foothills	Mountains	Total
ALFL	2.60	0.62	0.18	0.27	0.20	3.86	-35%	-17%	-27%	-43%	5 26%	-30%
AMCR	0.31	0.06	0.23	0.42	0.02	1.05	412%	286%	-65%	-8%	5 122%	125%
AMGO	0.70	0.11	0.60	0.35	0.09	1.85	545%	385%	104%	332%	51%	328%
AMRE	3.38	0.64	0.27	0.52	0.29	5.11	61%	83%	-47%	-60%	5 137%	50%
AMRO	4.33	1.12	1.47	0.90	0.82	8.65	24%	67%	47%	48%	45%	38%
BAOR	0.12	0.01	0.06	0.04	0.01	0.24	120%	58%	-21%	5 75%	5 15%	71%
BAWW	1.00	0.13	0.12	0.19	0.05	1.48	45%	242%	-7%	-27%	5 44%	49%
BBWA	2.57	0.08	0.04	0.07	0.03	2.79	-60%	-15%	-28%	-70%	5 19%	-58%
BCCH	1.61	0.38	0.58	0.42	0.19	3.19	94%	218%	23%	6 41%	88%	88%
BHCO	1.60	0.16	3.14	0.62	0.13	5.65	120%	24%	41%	264%	5 24%	87%
BHVI	1.09	0.22	0.08	0.14	0.04	1.57	-37%	66%	-31%	-66%	61%	-22%
BLBW	0.50	0.07	0.08	0.17	0.03	0.85	192%	544%	5 11%	-32%	58%	153%
BLJA	0.13	0.02	0.04	0.04	0.01	0.24	247%	518%	-58%	5 73%	5 47%	182%
BLPW	1.14	0.37	0.11	0.08	0.37	2.06	-60%	-69%	-1%	-11%	58%	-36%
BOCH	2.73	0.52	0.22	0.23	0.36	4.05	-49%	-51%	-26%	-53%	-9%	-45%
BRBL	0.28	0.02	1.38	0.16	0.02	1.87	197%	41%	-44%	273%	59%	22%
BRCR	0.79	0.09	0.10	0.08	0.07	1.12	-10%	-6%	-3%	-19%	5 -4%	-10%
BRTH	0.01	0.00	0.01	0.00	0.00	0.03	51%	13%	474%	567%	5 <u>3</u> %	186%
BTNW	0.72	0.26	0.03	0.13	0.05	1.19	12%	48%	-25%	-57%	5 93%	14%
CAWA	0.61	0.05	0.05	0.07	0.02	0.81	-15%	22%	-23%	-54%	39%	-16%
CCSP	2.02	0.04	1.22	2.12	0.02	5.42	203%	305%	-86%	-56%	55%	37%
CEDW	2.29	0.48	0.69	0.51	0.27	4.23	91%	163%	18%	5 22%	53%	77%
CHSP	8.86	1.68	1.07	1.01	0.79	13.41	-24%	0%	-8%	-22%	-12%	-19%
CMWA	2.34	0.07	0.05	0.05	0.05	2.56	-48%	-29%	-19%	-42%	-11%	-46%
COGR	0.84	0.15	0.40	0.16	0.14	1.69	68%	112%	395%	5 214%	5 23%	161%
CONW	0.41	0.01	0.00	0.03	0.00	0.46	-52%	-57%	-66%	-94%	-21%	-55%
CORA	0.60	0.11	0.15	0.09	0.08	1.03	9%	b 11%	-42%	-12%	6 0%	-1%
COYE	1.05	0.25	0.28	0.24	0.11	1.92	161%	121%	23%	5 106%	53%	123%

Table 5. Mean projected mid-century changes in potential avian abundance for 84 species by natural region based on climate-only models, averaged across 11 bootstrap model runs and 19 GCMs. Species common and scientific names are given in Table 3.

Potential Current Abundance x 10 ⁶ (1961-1990)							Mid-Century Projections (2041-2070)					
Species	Boreal	Parkland	Grassland	Foothills	Mountains	Total	Boreal	Parkland	Grassland	Foothills	Mountains	Total
CSWA	0.37	0.05	0.05	0.10	0.03	0.60	338%	565%	28%	-21%	28%	254%
DEJU	3.50	1.36	0.28	0.26	0.80	6.21	-61%	-60%	-49%	-59%	13%	-51%
EAKI	0.13	0.02	0.37	0.05	0.02	0.58	147%	34%	198%	888%	23%	232%
EAPH	0.07	0.01	0.03	0.02	0.01	0.13	173%	5 108%	0%	5 140%	13%	115%
EVGR	0.41	0.07	0.11	0.09	0.05	0.73	47%	5 121%	-35%	-26%	66%	33%
FOSP	0.46	0.11	0.02	0.02	0.23	0.84	-76%	-74%	-2%	-13%	10%	-49%
GCKI	2.18	1.41	0.35	0.29	0.68	4.91	-15%	-28%	-54%	-50%	20%	-18%
GRAJ	4.92	0.66	0.14	0.18	0.40	6.30	-70%	-79%	-33%	-63%	-33%	-68%
GRCA	0.13	0.02	0.16	0.05	0.02	0.36	527%	5 125%	167%	366%	36%	308%
HAFL	0.32	0.29	0.25	0.13	0.71	1.70	-5%	6%	-55%	-39%	-8%	-14%
HETH	1.93	0.38	0.11	0.16	0.43	3.01	-39%	-14%	-44%	-48%	-21%	-34%
HOLA	0.29	0.05	7.04	0.10	0.04	7.51	21%	5 2%	-23%	577%	22%	-13%
HOWR	0.97	0.07	0.54	1.73	0.03	3.34	356%	5 404%	44%	-5%	141%	118%
LCSP	0.26	0.01	0.01	0.04	0.00	0.32	53%	5 18%	-57%	-79%	-15%	31%
LEFL	3.96	0.47	0.33	0.97	0.13	5.86	17%	-21%	-50%	-67%	13%	-4%
LISP	2.09	0.68	0.10	0.15	0.25	3.27	-72%	-78%	-47%	-74%	-14%	-68%
MAWA	2.74	0.49	0.16	0.22	0.17	3.78	-36%	43%	-33%	-56%	117%	-20%
MOWA	0.87	0.16	0.04	0.14	0.03	1.24	10%	5 2%	-32%	-67%	40%	-1%
NAWA	0.70	0.13	0.20	0.16	0.06	1.24	134%	5 118%	-56%	4%	77%	83%
NOWA	0.70	0.21	0.07	0.07	0.14	1.19	-46%	-50%	-20%	-37%	45%	-34%
OCWA	1.96	0.32	0.22	0.15	0.40	3.05	-61%	-62%	-8%	-34%	-23%	-51%
OSFL	0.16	0.04	0.02	0.02	0.04	0.28	-40%	-47%	-19%	-30%	-17%	-35%
OVEN	4.16	0.29	0.07	0.31	0.03	4.86	-14%	5 118%	-27%	-58%	113%	-8%
PAWA	1.03	0.05	0.03	0.02	0.02	1.15	-68%	-15%	-7%	-21%	-1%	-62%
PHVI	0.61	0.07	0.04	0.08	0.01	0.82	-25%	-49%	-43%	-75%	8%	-33%
PIGR	0.20	0.05	0.04	0.03	0.08	0.40	-23%	-46%	-1%	-5%	-6%	-20%
PISI	4.54	4.60	0.55	0.66	2.75	13.10	-63%	-70%	-48%	-74%	-7%	-53%
PUFI	0.33	0.12	0.10	0.06	0.06	0.68	20%	5 44%	-8%	15%	46%	22%
RBGR	0.61	0.05	0.03	0.15	0.01	0.85	40%	5 157%	-23%	-51%	47%	28%
RBNU	2.21	0.68	0.31	0.38	0.29	3.88	-14%	-12%	-55%	-48%	32%	-17%

	Potential Current Abundance x 10 ⁶ (1961-1990)							Mid-Century Projections (2041-2070)					
Species	Boreal	Parkland	Grassland	Foothills	Mountains	Total	Bore	al	Parkland	Grassland	Foothills	Mountains	Total
RCKI	4.91	1.72	0.18	0.25	0.64	7.71	-(65%	-62%	-68%	-81%	5%	-59%
REVI	4.08	0.35	0.21	0.79	0.07	5.50		51%	5 212%	-15%	-43%	121%	6 46%
RUBL	0.28	0.02	0.03	0.02	0.02	0.37	-:	51%	-12%	-6%	<i>б</i> -6%	-10%	-39%
RWBL	0.93	0.09	0.97	0.75	0.06	2.80	5	80%	5 135%	105%	6 268%	53%	306%
SAVS	1.59	0.29	1.99	1.13	0.19	5.19	2	39%	6 46%	-40%	88%	7%	80%
SEWR	0.03	0.00	0.00	0.00	0.00	0.04	2	09%	5 71%	13%	6 163%	16%	5 174%
SOSP	0.85	0.14	0.41	0.37	0.10	1.87	3	32%	302%	21%	6 82%	61%	5 198%
SWSP	0.59	0.12	0.09	0.07	0.06	0.93		19%	5 15%	5%	6 18%	22%	5 17%
SWTH	7.25	1.48	0.36	0.45	1.01	10.55	-1	61%	-43%	-74%	-80%	9%	-53%
TEWA	17.88	1.31	0.06	0.20	0.19	19.64	-1	83%	-92%	-45%	<i>-</i> 87%	-33%	-83%
TOWA	0.13	0.10	0.04	0.03	0.59	0.89		-3%	-30%	-27%	б -14%	-22%	-20%
TRES	1.31	0.25	0.47	0.35	0.16	2.55		25%	6 46%	192%	б 1 7 %	26%	57%
VATH	0.22	0.26	0.04	0.04	0.65	1.21	-:	33%	-76%	-14%	-33%	-23%	-36%
VEER	0.19	0.04	0.12	0.07	0.02	0.45	3.	54%	5 415%	-9%	65%	68%	5 198%
VESP	0.34	0.02	2.89	0.89	0.03	4.17	4	83%	84%	-51%	43%	83%	5 15%
WAVI	0.90	0.64	0.55	0.39	0.67	3.16		31%	-17%	-45%	-26%	20%	-1%
WBNU	0.09	0.02	0.05	0.02	0.01	0.18		56%	5 28%	114%	6 204%	7%	5 79%
WCSP	0.32	0.05	0.03	0.02	0.19	0.62	-:	54%	-47%	5%	6 3%	-45%	-45%
WETA	1.12	0.07	0.14	0.11	0.08	1.53	-(60%	-28%	-50%	-50%	23%	-52%
WEWP	0.29	0.05	0.11	0.05	0.05	0.55	-	27%	-14%	-19%	-28%	-2%	-22%
WIWA	0.87	0.47	0.10	0.08	1.13	2.65	-:	50%	-77%	-7%	-22%	-27%	-42%
WIWR	0.49	0.10	0.03	0.05	0.02	0.70		30%	-13%	-24%	-46%	63%	-25%
WTSP	5.50	1.27	0.16	0.64	0.18	7.74		34%	-32%	-30%	<i>б</i> -74%	63%	-35%
WWCR	3.80	0.85	0.19	0.23	0.37	5.43	-(67%	-76%	-26%	-60%	-24%	-64%
YBFL	0.47	0.15	0.04	0.04	0.06	0.75		44%	-1%	-33%	-55%	89%	-25%
YRWA	11.44	4.15	0.43	0.58	1.30	17.91	-1	65%	-58%	-54%	-67%	-8%	-59%
YWAR	3.63	0.53	0.43	1.22	0.26	6.07		47%	5 10%	65%	6 -47%	45%	5 26%

Table 6. The total area within Alberta that is predicted to have a greater than average density during the baseline period of 1961–1990 based on climate-only models for each of 84 species. We refer to these as core areas. We also include the percentage of the core area that is projected to maintain a higher than average density in each of three future periods. We refer to these areas as refugia (Figure 6).

	Current	% core area remaining as refugia						
Species	core area (km ²)	2011-2040	2041-2071	2071-2100				
ALFL	309,360	54%	27%	9%				
AMCR	152,592	84%	70%	56%				
AMGO	173,472	100%	100%	100%				
AMRE	268,992	88%	68%	25%				
AMRO	251,968	100%	100%	100%				
BAOR	202,256	94%	74%	46%				
BAWW	301,088	86%	62%	34%				
BBWA	166,656	59%	5%	0%				
BCCH	296,480	100%	99%	93%				
BHCO	130,912	100%	100%	100%				
BHVI	247,776	79%	40%	7%				
BLBW	182,160	96%	87%	40%				
BLJA	220,864	81%	60%	36%				
BLPW	174,736	49%	23%	12%				
BOCH	294,208	53%	15%	3%				
BRBL	111,920	100%	98%	98%				
BRCR	197,152	78%	41%	3%				
BRTH	67,664	100%	100%	100%				
BTNW	242,112	95%	80%	42%				
CAWA	229,696	70%	38%	2%				
CCSP	174,928	83%	68%	16%				
CEDW	296,960	100%	100%	100%				
CHSP	299,312	78%	53%	28%				
CMWA	150,064	79%	23%	0%				
COGR	178,928	100%	100%	100%				
CONW	222,384	47%	10%	0%				
CORA	272,688	90%	82%	42%				
COYE	268,160	97%	98%	93%				
CSWA	188,368	95%	88%	77%				
DEJU	247,920	48%	26%	10%				
EAKI	102,912	100%	100%	100%				
EAPH	195,232	100%	100%	82%				
EVGR	277,392	92%	66%	17%				
FOSP	146,624	53%	25%	16%				
GCKI	188,768	89%	63%	34%				
GRAJ	290,048	43%	10%	1%				
GRCA	119,056	100%	100%	100%				

	Current	% core area remaining as refugia		
Species	core area (km ²)	2011-2040	2041-2071	2071-2100
HAFL	92,640	96%	91%	80%
HETH	275,936	72%	38%	17%
HOLA	78,400	100%	88%	89%
HOWR	132,256	93%	92%	99%
LCSP	285,904	90%	71%	51%
LEFL	251,760	89%	58%	22%
LISP	317,328	40%	10%	0%
MAWA	314,112	83%	39%	5%
MOWA	219,056	87%	65%	20%
NOWA	208,624	60%	24%	9%
OCWA	200,528	51%	23%	9%
OSFL	235,232	51%	25%	12%
OVEN	278,624	78%	56%	21%
PAWA	189,760	66%	22%	1%
PHVI	258,976	74%	30%	1%
PIGR	122,896	59%	32%	19%
PISI	139,040	70%	46%	23%
PUFI	263,440	96%	84%	72%
RBGR	198,512	96%	79%	52%
RBNU	313,888	83%	48%	13%
RCKI	293,888	56%	22%	4%
REVI	292,640	87%	72%	41%
RUBL	123,952	54%	12%	0%
RWBL	182,768	100%	100%	100%
SAVS	175,408	84%	72%	62%
SEWR	301,344	94%	98%	99%
SOSP	230,848	100%	100%	100%
SWSP	328,352	93%	89%	76%
SWTH	336,432	60%	28%	10%
TEWA	244,192	45%	5%	0%
TOWA	75,728	86%	72%	59%
TRES	184,576	99%	100%	100%
VATH	81,296	77%	50%	30%
VEER	221,472	100%	100%	100%
VESP	132,976	100%	100%	87%
WAVI	146,128	75%	71%	65%
WBNU	132,800	100%	100%	71%
WCSP	92,544	51%	27%	12%
WETA	248,928	37%	7%	4%
WEWP	225,616	62%	43%	32%
WIWA	120,416	61%	34%	19%
WIWR	243,648	87%	55%	15%
	Current	% core area remaining as refugia		
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Species	core area (km ²)	2011-2040	2041-2071	2071-2100
WTSP	298,112	78%	51%	6%
WWCR	306,080	35%	7%	0%
YBFL	280,224	66%	31%	10%
YRWA	253,136	45%	17%	2%
YWAR	191,328	88%	75%	92%

Figure 1. Boreal and southern arctic study area shown in yellow with boreal/arctic boundary in red. Additional ecoregions (<u>http://www.cec.org/Page.asp?PageID=122&ContentID=1329</u>) projected to move into study area by 2100 are depicted in green. Point-count locations sampled for modeling are shown in blue.



Figure 2. Projected changes in potential abundance for 84 species of boreal songbirds currently breeding in Alberta for three future time periods, averaged over 19 GCMs. Boxplots represent variability across bootstrap runs (n = 11); points outside whiskers are greater than 1.5 times the interquartile range. Two sets of models are compared: climate-only and climate + land use + wetlands. Table 3 includes the common and scientific names associated with the 4-letter species codes in the lower left of each graph.







BAOR







BBWA





BLBW





BRBL







BTNW

42





CMWA











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HETH

1961-1990

2011-2040

year

2041-2070

2071-2100



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HOLA

1961-1990

2011-2040

year

2041-2070

2071-2100





NOWA















PUFI

RBGR

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REVI

1961-1990

2011-2040

year

2041-2070

2071-2100

1

2071-2100



0.

RUBL

1961-1990

2011-2040

year

2041-2070



SEWR

SOSP



TEWA















WETA









YRWA

YWAR

Figure 3. Spatial predictions and projection of breeding density (males/ha) for 84 species based on climate-only models. Deviance explained was not improved by the inclusion of land-use or topographic variables. Spatial predictions are for the current period (A); spatial projections are for three future periods: (B, C, D). Table 3 includes the common and scientific names associated with the 4-letter species codes in the lower left of each map.























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Figure 4. Spatial predictions and projection of breeding density (males/ha) for 17 species based on two sets of models: climate-only (left) and climate + land use + topography (right) models. For these species, deviance explained was improved by the inclusion of land-use and topographic variables *and/or* ensemble mean future predictions were dramatically different spatially or numerically. Models with significantly higher deviance explained are marked with an asterisk. (A) Current period (1961-1990) (B-D) future projections for GCM ensemble means, 2011-2040, 2041-2070, 2071-2100. Table 3 includes the common and scientific names associated with the 4-letter species codes in the lower left of each map.












Figure 5. Uncertainty maps for 5 species examples based on 4 different GCMs and bootstrap variation. (A) Current period (1961-1990), (B-D) future projections, 2011-2040, 2041-2070, 2071-2100. CCCMA CGCM3.1 = warmer and wetter, MPI ECHAM5 = warmer and drier, near-average across GCMs, GFDL CM2.1 = warmer and much drier, UKMO HadGEM1 = much warmer and drier.



BBWA, bootstrap CV, GCM ensemble mean

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CAWA, bootstrap CV, GCM ensemble mean

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TEWA, bootstrap CV, GCM ensemble mean

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BLJA, bootstrap CV, GCM ensemble mean

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BLBW, bootstrap CV, GCM ensemble mean

Figure 6. Projected climate-change refugia for 84 species of boreal songbirds currently breeding in Alberta, based on means across bootstrap model replicates and GCMs. Refugia (dark green) are areas of overlap in the core distribution between the baseline period of 1961-1990 and each future time period (A, B, C); areas in gold represent baseline distribution lost; areas in light green represent future distribution gained; areas in gray represent the study area considered. Table 3 includes the common and scientific names associated with the 4-letter species codes in the lower left of each map (panel A).





























