Projecting boreal bird responses to climate change: the signal exceeds the noise

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Abstract. For climate change projections to be useful, the magnitude of change must be understood relative to the magnitude of uncertainty in model predictions. We quantified the signal-to-noise ratio in projected distributional responses of boreal birds to climate change, and compared sources of uncertainty. Boosted regression tree models of abundance were generated for 80 boreal-breeding bird species using a comprehensive data set of standardized avian point counts (349 629 surveys at 122 202 unique locations) and 4-km climate, land use, and topographic data. For projected changes in abundance, we calculated signal-to-noise ratios and examined variance components related to choice of global climate model (GCM) and two sources of species distribution model (SDM) uncertainty: sampling error and variable selection. We also evaluated spatial, temporal, and interspecific variation in these sources of uncertainty. The mean signal-to-noise ratio across species increased over time to 2.87 by the end of the 21st century, with the signal greater than the noise for 88% of species. Across species, climate change represented the largest component (0.44) of variance in projected abundance change. Among sources of uncertainty evaluated, choice of GCM (mean variance component = 0.17) was most important for 66% of species, sampling error (mean = 0.12) for 29% of species, and variable selection (mean = 0.05) for 5% of species. Increasing the number of GCMs from four to 19 had minor effects on these results. The range of projected changes and uncertainty characteristics across species differed markedly, reinforcing the individuality of species' responses to climate change and the challenges of one-size-fits-all approaches to climate change adaptation. We discuss the usefulness of different conservation approaches depending on the strength of the climate change signal relative to the noise, as well as the dominant source of prediction uncertainty.

Key words: avian density; boosted regression trees; boreal birds; boreal forest; climate change; global climate models; signal-to-noise ratio; species distribution models; uncertainty; variance partitioning.

Introduction

Based on recent warming trends and global climate model (GCM) projections for the next century, the North American boreal forest is likely to experience particularly large changes in temperature and moisture availability (Balling et al. 1998, IPCC 2001). Climate change within the boreal region has already led to increased drought- and insect-induced tree mortality (Allen et al. 2010, Michaelian et al. 2010, Peng et al. 2011), wetland drying (Klein et al. 2005), and wildfire activity (Podur et al. 2002, Gillett et al. 2004, Soja et al. 2007). By virtue of its large size and relative intactness, the boreal forest is thought to provide a large proportion of North America's breeding bird habitat (Wells and Blancher 2011). Therefore, species presently restricted to boreal regions may experience range reductions if those biomes shift northward and decrease in area, as projected for North America (Rehfeldt et al. 2012). However, positive temperature affinities and broad climatic tolerances suggest that many other species could expand their breeding distributions within the boreal region (Cumming et al. 2014). Recent northward range expansions of breeding birds have already been documented and attributed to climate change in temperate North America (Hitch and Leberg 2007), as well as in Europe (Thomas and Lennon 1999, Devictor et al. 2008).

As evidence has mounted for anthropogenic climate change and its widespread effects on species' distributions, it has increasingly been incorporated in systematic

conservation planning efforts (e.g., Hannah et al. 2007, Carroll et al. 2009, Shaw et al. 2012). Accordingly, there is growing interest in forecasting the potential ecological impacts of climate change with an understanding of the associated uncertainties. Species distribution models (SDMs) have been widely used to project geographic changes in species' climatic habitat suitability (e.g., Peterson et al. 2002, Thuiller et al. 2005, Huntley et al. 2008). This correlative approach is based on the premise that the environmental niche of a species (sensu Grinnell 1917) may be quantified and used to develop spatial predictions of species' distributions under given environmental conditions, including future climates (Guisan and Zimmermann 2000, Peterson 2001). Paleo-ecological analysis of fossil pollen data suggests that, in the absence of climate conditions with no current analog, substitution of space for time is generally valid (Prentice et al. 1991, Huntley et al. 1993, Roberts and Hamann 2012), although differences in short-term predictability across taxa and ecological traits do exist (Kharouba et al. 2009, Dobrowski et al. 2011, Eskildsen et al. 2013). Passerine birds are not well represented in the fossil record, but molecular analyses are consistent with avian tracking of changes in climate and vegetation throughout Pleistocene glaciation cycles (Mengel 1964, Weir and Schluter 2004, Lovette 2005). Current climate has been found to be an important predictor of continental-scale avian distributions (Araújo et al. 2009, Jiménez-Valverde et al. 2011, Cumming et al. 2014), although not without skepticism (Bahn et al. 2006, Beale et al. 2008). Species' realized niches are also limited by biotic interactions (Hutchinson 1957), but empirical (Lovette and Hochachka 2006, Rubidge et al. 2011) and theoretical (Soberón 2007, Araújo and Rozenfeld 2014) evidence suggests that interactions that cannot be defined climatically are mostly local-scale processes that have minimal influence on broadscale distribution patterns (Rehfeldt et al. 2012).

Assuming that climatic niches of species are conserved over time (Wiens et al. 2010) and equilibrium with climate is maintained (Araújo and Pearson 2005), projecting species' long-term distributional responses to climate change will be problematic when uncertainty overpowers the prediction signal. Uncertainty surrounding future climate change trajectories (Murphy et al. 2004), combined with high variability among the SDMs themselves (Elith et al. 2006), has raised concerns about the utility and reliability of future projections. This has led to the development of ensemble forecasting approaches that use multiple models (Araújo and New 2007, Dormann et al. 2008b), as well as efforts to quantify and compare different aspects of prediction uncertainty. Although several studies have partitioned the variance in SDM-based future projections (Dormann et al. 2008a, Buisson et al. 2009, Diniz-Filho et al. 2009, Mbogga et al. 2010, Garcia et al. 2012), few have evaluated uncertainty with respect to the magnitude of predicted change (but see Thuiller 2004). High predic-

tion error may be outweighed by large directional changes in distribution and abundance. Thus, species-specific estimates of uncertainty ("noise") vs. change magnitude (the "signal") are needed over space and time.

A primary source of noise in future projections is the extrinsic variation among GCMs (hereafter "GCM uncertainty"). Although different GCMs are mostly based on the same physical principles (Jun et al. 2008, Masson and Knutti 2011, Pennell and Reichler 2011), the projections that they produce can be quite variable (Murphy et al. 2004, Kingston et al. 2009). Some GCMs are clearly better than others (Wang et al. 2007, Scherrer 2011), but metrics for model evaluation are not straightforward, and prediction patterns among GCMs can vary spatially as well as temporally (Tebaldi et al. 2005, Kang and Cressie 2013). Thus, the influence of GCM variability on SDM predictions depends not only on which model is considered, but also on the variables, seasons, and geographic areas that are important for a given species.

Considering the large variation among GCM projections, it is notable that intrinsic variation among SDM algorithms has often been found to be even larger (Dormann et al. 2008a, Buisson et al. 2009, Diniz-Filho et al. 2009, Garcia et al. 2012; but see Mbogga et al. 2010). However, high SDM variability may be driven by many factors, including the use of lower-performance algorithms (Elith et al. 2006, Hijmans and Graham 2006), sparse or inconsistent data (Araújo et al. 2005, Dormann et al. 2008a), poor or inconsistent model-building strategies (Meynard et al. 2013), extrapolation outside the range of data (Elith and Graham 2009), and improper handling of spatial dependence (Swanson et al. 2012). Some of these sources of error can be manipulated or controlled to reduce prediction uncertainty. In particular, by reducing model variability due to spatial dependence, inappropriate extrapolation, and model specification, one can focus on evaluating two fundamental sources of SDM-based (intrinsic) uncertainty: predictor variable selection and sampling error.

Predictor variable or model selection (hereafter "variable uncertainty") may have a large influence on SDM predictions (Mbogga et al. 2010, Synes and Osborne 2011, Braunisch et al. 2013), especially when important correlated variables decouple in the future. For example, many species' distributions are limited by the extent of agricultural land use (e.g., Siriwardena et al. 2000) or by the distribution of wetlands (e.g., Calmé and Desrochers 2000) more than by climate. Agriculture is constrained by current climate, particularly in northern environments, and the effects of climate and land use on bird distributions can be hard to disentangle (Clavero et al. 2011). However, land use will not necessarily track climate in the future, such that present confounding of climate and land use could lead to errors in future projections. Northern wetland distribution is also correlated with climate at continental extents, due
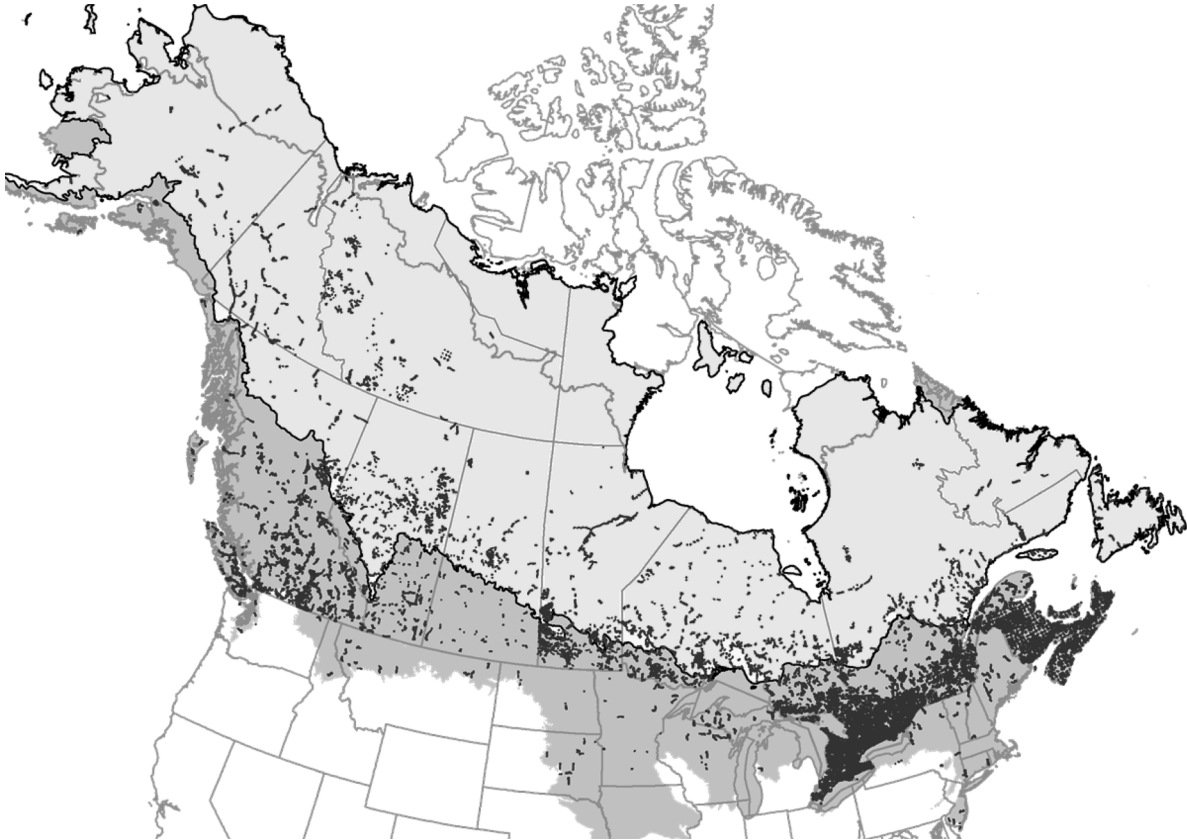
Fig. 1.   Boreal and southern arctic study area shown in light gray, with boreal/arctic boundary as a gray line. Additional ecoregions projected to move into the study area by 2100 are depicted in darker gray. Point-count locations sampled for modeling are shown in black.

to the propensity for excess moisture to persist in colder environments. Despite reports of rapid boreal wetland drying attributed to recent climate change (e.g., Klein et al. 2005), loss of wetlands may take longer, depending on size and local hydrology, providing another mecha-nism by which presently correlated variables could become decoupled.

Sampling error (hereafter "sampling uncertainty") results from various elements of epistemic uncertainty ("uncertainty associated with knowledge of the state of a system"; Regan et al. 2005), including measurement error, sampling bias, and inherent variability in the abundance of organisms across space and time (Elith et al. 2002). This type of uncertainty is often reflected in the differences among SDM algorithms that produce a wide range of individual model specifications. Multi-model predictions based on a diverse assortment of SDM techniques therefore can produce more robust predic-tions than single models (Thuiller et al. 2009). However, ensemble methods based on a single type of model (e.g., boosted regression trees) have similar strengths (Lawler et al. 2006), and bootstrapping methods may be used to estimate sampling error.

Here, we used an extensive boreal bird data set for North America (Cumming et al. 2010) to evaluate the

signal-to-noise ratio for projected changes in boreal bird abundance over the next century. We also compared different sources of uncertainty related to factors extrinsic (GCM uncertainty) and intrinsic (sampling and variable uncertainty) to SDMs. We evaluated spatial, temporal, and species-specific variation in each source of prediction uncertainty.

METHODS

Study area and avian survey data

We developed climate-change projections for boreal and southern arctic level II ecological regions as delineated by the Commission for Environmental Cooperation (CEC 1997). This included all subunits within the Taiga, Hudson Plain, and Northern Forests ecological regions, as well as the southern subunits of the Tundra ecological region (Alaska Tundra, Brooks Range Tundra, Southern Arctic), and boreal portion of the Northwestern Forested Mountains ecological region (Boreal Cordillera); see Fig. 1. We used data from avian point-count surveys (Ralph et al. 1995) that were conducted from 1992 to 2010 within the Nearctic boreal region (Brandt 2009), as compiled by the Boreal Avian Modelling (BAM) project (Cumming et al. 2010). This

included primarily off-road data from numerous inventory, monitoring, research, and impact assessment projects, including Provincial Breeding Bird Atlases and the Alaska Landbird Monitoring Survey, but also roadside point-count surveys conducted as part of the North American Breeding Bird Survey, BBS (Sauer et al. 2011). To account for anticipated shifts of southern climate conditions into currently boreal regions, we included point-count data from the same period collected in ecoregions within the continental United States and southern Canada that are south of the current boreal region, with climate conditions that are projected to shift northward into the study area within the next 100 years (Rehfeldt et al. 2012). This primarily consisted of BBS data, but also included off-road data from the western Great Lakes region (Hanowski and Niemi 1995).

Our initial compilation included data from 128 distinct projects with a total of 356 018 surveys at 125 547 unique locations (Fig. 1). To reduce the confounding influence of anthropogenic disturbance on modeled climate relationships, we removed surveys that had been conducted at agricultural, urban, or barren sites, according to the CEC's North American Land Change Monitoring System (NALCMS) land cover data set. We also removed surveys known to be conducted after recent timber harvest or other anthropogenic disturbance activities (not including fire), as mapped by Global Forest Watch Canada, the Alberta Biodiversity Monitoring Institute, and the United States LAND-FIRE program. For our analysis, 349 629 surveys at 122 202 unique locations remained.

Climate data

Interpolated climate data were generated based on the parameter–elevation regressions on independent slopes model (PRISM) for the 1961–1990 normal period (Daly et al. 2008) and bioclimatic variables were derived according to Wang et al. (2012) and Hamann et al. (2013). Climate variables were chosen based on several criteria, including relevance to vegetation distributions (Hogg and Bernier 2005), avoidance of extreme colinearity (Dormann et al. 2013), and a preference for seasonal over annual variables when they showed high correlations. The final set of variables included extreme minimum temperature (EMT), chilling degree-days (DD0), growing degree-days (DD5), seasonal temperature difference (TD), mean summer precipitation (MSP), climate moisture index (CMI), and summer climate moisture index (CMIJJA). For complete variable definitions, see Appendix A: Table A1.

To represent potential future climates for three consecutive 30-year periods (2011–2040, 2041–2070, and 2071–2100), we used projections from the CMIP3 multi-model data set, corresponding to the fourth IPCC assessment report (Meehl et al. 2007). To limit computation time, we selected a subset of four complementary GCMs that spanned a range of project-ed growing-season temperatures and precipitation levels within our study area: the German MPI ECHAM5, the Canadian CCCMA CGCM3.1, the United States GFDL CM2.1, and the United Kingdom Met Office HadGEM1 (Appendix A: Table A2, Fig. A1). Model projections were added as anomalies to the 4-km resolution 1961–1990 baseline data using the delta method and bilinear interpolation according to Wang et al. (2012). The data used in this study are part of a more comprehensive data set for North America, described in Appendix A and the Supplement. For this analysis, we adopted a scenario of high and monotonically increasing emissions (SRES A2; IPCC 2001), reflecting actual emissions during the decade elapsed since the scenario was defined (Raupach et al. 2007). Nineteen GCMs had runs available under the A2 emissions scenario.

The most highly correlated climate variables within our model-building data set (averaged across bootstrap samples, as described in the next section) were EMT and DD01 ($r = -0.88$), followed by MSP and CMIJJA ($r = -0.80$) (Appendix B: Table B1). Within the boreal and subarctic study area, the most highly correlated variables were CMI and CMIJJA ($r = 0.91$) and CMI and MSP ($r = 0.87$). Averaging across all 19 GCMs available for scenario A2, we found limited future decoupling (decrease in correlation over time) within the set of climate variables used, although there were differences between the model-building data set and prediction data sets (Appendix B: Fig. B1). EMT, DD0, and TD were the variables among which study area-wide correlations changed the most over time and were the most different from correlations within the model-building data set.

Land use and topography data

For a second set of models, we included a set of key land use/land cover variables that may influence bird abundance. We used the 250-m NALCMS land cover data set to calculate the current proportions of agriculture (AGRICULT), urban development (URBAN), open water (WATER), and wetlands (WETLAND) within each 4-km grid cell. We also derived a compound topographic index, CTI (Gessler et al. 1995)—or wetness index—from a 4-km digital elevation model and used it as a surrogate for wetland areas. The CTI was intended to differentiate lowland vs. upland vegetation types, in order to constrain future projections accordingly. These variables were not highly correlated with the seven climate indices or with each other (Appendix B: Table B1), and only minor future decoupling was observed.

We did not include proportions of natural upland land cover types, given the strong climatic basis for vegetation distribution at this resolution (Hamann and Wang 2006, McKenney et al. 2007). Limitation of data quality and coverage prevented adequate modeling and prediction of these remotely sensed land cover types relative to climate at such a broad scale.

Density models

We made use of the abundance information contained in point-count data by using survey- and species-specific correction factors, as described in Sólymos et al. (2013), to standardize density estimates across diverse protocols and environmental conditions. We examined 80 boreal-breeding passerine species with mapped breeding ranges (Ridgely et al. 2005) covering at least 10% of the boreal region (P. Blancher, *unpublished data*), as defined by Partners in Flight bird conservation regions 4, 6, 7, and 8 (Rich et al. 2004), which coincide with the boreal portion of our study area (Fig. 1). Each species also had surveys conducted with multiple time and/or distance intervals, general requirements for fitting the distance sampling (Buckland et al. 2001) and removal models (Sólymos et al. 2013) used to generate the correction factors.

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. We used the 'dismo' (Hijmans et al. 2011), 'gbm' (Ridgeway 2012) and 'raster' (Hijmans and van Etten 2012) packages for R (R Development Core Team 2012) to build BRT models for each species and then generate spatial predictions. We used the raw survey count at a point-count location as the response variable and included the log-transformed correction factors derived by Sólymos et al. (2013) as offsets to model avian density (number of males per hectare). For these count data, we specified a Poisson generalized boosted model (GBM) in the BRT estimation. The Poisson GBM uses an exponential function of the linear predictor within a gradient boosting algorithm (Friedman 2001, Ridgeway 2012).

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); from each sampling unit with >10 surveys, we randomly selected a single point-count survey in each bootstrap iteration. This was to minimize spatial autocorrelation in surveys among points at the same site and temporal autocorrelation among surveys at the same point. 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 20×20 km area surrounding the sampling unit. We minimized the influence of single data points by randomly selecting only one-third of the sampling units with ≤ 10 surveys in each bootstrap replicate. This procedure resulted in a total of 18 299 sampling units for each bootstrap replicate.

For each BRT model, we used a stepwise procedure and 10-fold cross-validation to identify the optimal number of trees needed to maximize the mean deviance explained. In each model run, we used a tree complexity of 3, learning rate of 0.001, and a bag fraction of 0.5. To ensure that the optimal number of trees could be found (Elith et al. 2008), we increased the learning rate to 0.005 if the limit of 10 000 trees was achieved, and reduced it to 0.0001 if fewer than 1000 trees were obtained. Using the optimal number of trees, we calculated 10-fold cross-validation statistics (proportion of deviance explained and Pearson's correlation coefficient) to assess prediction accuracy. For each species, we compared these statistics between the two variable sets (climate-only and climate + land use + topography) using paired t tests ($n = 11$ bootstrap replicates). Significance values were adjusted for multiple comparisons using a Holm (1979) correction. The importance of each model covariate was assessed by averaging the proportion of total deviance explained by a particular variable over all 11 bootstrap replicates.

Abundance projections

For each of the 80 boreal-breeding bird species, we applied the fitted BRT models to current and future climate conditions to predict avian density in each 4-km grid cell in the boreal/southern arctic study area. We multiplied the predicted density estimates for each grid cell (males/ha as an estimate of breeding pair density) by the grid cell area (1600 ha), and summed these values across grid cells to estimate total potential abundance.

We evaluated two sets of covariates: climate-only and climate + land use + topography. We generated models for 11 bootstrap samples, which were identical across species and covariate sets. We evaluated fitted BRTs under projected climates of alternate GCMs for three future time periods (2011–2040, 2041–2070, and 2071–2100).

For each species, we produced a total of 22 models from 11 bootstrap replicates and two variable sets for the 1961–1990 baseline period. We then produced a balanced set of future projections (264 total) for each species. This included predictions for all combinations of 11 bootstrap replicates, two variable sets, four GCMs, and three future time periods, for a total of 286 predictions for each species. To better assess the full range of variability across GCMs, we also generated an additional set of projections across the remaining 15 GCMs using just one bootstrap replicate, two variable sets, and three future time periods. This resulted in an additional 90 predictions, for a grand total of 376, including projections for the 1961–1990 baseline period.

Quantifying prediction uncertainty

To evaluate the overall signal-to-noise ratio for the projected change in overall abundance, we calculated Cohen's d (defined as the difference between means divided by the pooled standard deviation; Cohen 1992) for each species and each future time period compared to the baseline period, with variances pooled across the two time periods of interest for each calculation. For each time period, d was calculated for the full-factorial combination of 11 bootstrap replicates, two variable sets, and four GCMs ($n = 88$).

Next, to compare the climate change effect size to the variance components attributable to each source of uncertainty, we conducted two analyses of variance (ANOVA) for each species. Using projected change in overall abundance as the dependent variable, we first conducted four-factor ANOVAs with balanced data using just the four complementary GCMs ($n = 264$; 11 bootstrap replicates $\times$ 2 variable sets $\times$ 4 GCMs $\times$ 3 future time periods). We partitioned the sums of squares among the effects of time period (climate change effect), sampling uncertainty, variable uncertainty, and GCM uncertainty, as well as the interactions between GCM and time, and variable and time. Variance components for each of these factors were calculated as the partial sum of squares divided by the total sum of squares (η^2). To evaluate the additional uncertainty introduced by considering the full suite of available GCMs (an additional 15 models), we also conducted an unbalanced ANOVA using type II sums of squares (Langsrud 2003) ($n = 354$; 264 original $+$ 90 additional) with the 'car' (Fox and Weisberg 2011) package for R. For comparison across species, proportional abundance change was plotted against total uncertainty (sum of variance components for all uncertainty sources, including residuals).

Finally, to evaluate the relative magnitudes of each uncertainty source with respect to abundance projections, we calculated several versions of the coefficient of variation (CV); i.e., the standard deviation divided by the mean. For each species and time period, we calculated the CV in overall abundance for each source of uncertainty: sampling, variable, and GCM (future time periods only). Calculations were based on the full-factorial set of predictions (four complementary GCMs), and CV values for each uncertainty source were calculated with predictions for the other sources of uncertainty held constant at their average values. To evaluate spatial patterns of uncertainty for each species, using the same method, we also calculated the CV in density (males/ha) at the 4-km grid cell level for each source of uncertainty in each time period.

<center>RESULTS</center>

<center>*Model evaluation*</center>

All confidence ranges represent 5th and 95th percentiles except when otherwise noted. Across 80 species, prediction success of climate-only BRT models, assessed via cross-validation, averaged 0.222 (0.069, 0.462) in the deviance explained, and 0.225 (0.071, 0.474) in the Pearson correlation coefficient (Appendix C: Table C1). On average across species, the addition of land use and topographic variables to the climate-only models did not markedly improve cross-validation correlation (difference $= 0.003 \pm 0.014$ SD) or deviance explained (difference $= 0.002 \pm 0.011$ SD). However, for 18 of 80 species, the climate-only models were significantly improved by adding the land use and topography variables, in terms of one or both diagnostics after

multiple comparison correction. The climate-only model was significantly better for only one species.

Across species, temperature variables, on average, explained 0.145 (0.038, 0.330) of total deviance, and moisture variables explained 0.074 (0.017, 0.156) in climate-only models (Appendix C: Table C2). With models that also included land use and topographic variables, 0.051 (0.004, 0.167) of the deviance explained was accounted for by these additional variables, primarily agricultural land use proportion and compound topographic index (Appendix C: Table C3). Based on visual inspection of variable response curves from all 11 bootstrap runs, a total of 32 species exhibited clear monotonic decreases in abundance in response to agricultural land use proportion across bootstrap iterations; seven species had a clear negative response to urban land use proportion.

<center>*Projected changes in potential abundance*</center>

Of the 80 species modeled, 30 were projected to decline in potential abundance across the boreal and southern arctic regions by 2040; 34 species by 2070; and 37 species by 2100 (Appendix D: Table D1). Considering all sources of prediction uncertainty, projected declines were unequivocal (i.e., confidence intervals around projected change values did not contain zero) for 15 species by 2040, 18 by 2070, and 30 by 2100. Projected increases were unequivocal for 35 out of 50 species by 2040, 37 out of 46 by 2070, and 35 out of 43 by 2100. The distribution of projected species' responses shifted negatively and became increasingly dispersed over time, reflecting larger magnitudes of increase and decrease in abundance (Table 1).

Most species exhibited a northward (toward higher elevations) distributional shift in response to climate change (Appendix D: Fig. D1). Species' range centroids shifted an average of 18 m upward in elevation, 3 degrees north in latitude, and 3 degrees west in longitude by the end of the century (Table 2). Although areas of high richness of boreal species were projected to shift northward in distribution, total potential abundance across all species was projected to decline within the study area. Decreases in boreal species richness and density over time were most apparent in the interior west (Fig. 2). Projected current and future density layers (mean and CV across all sources of uncertainty) are *available online*.[8]

<center>*Prediction uncertainty relative to change*</center>

On average across 80 species, the signal-to-noise ratio, as measured by Cohen's d, was greater than 1 (i.e., signal $>$ noise) for all three future time periods (Fig. 3). For the 2011–2040 time period, mean d was 1.42 (0.11, 3.49), and was greater than 1 for 46 species (Appendix D: Table D2). For the 2041–2070 time period, mean d

[8] http://borealbirds.databasin.org/

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TABLE 1. Frequency of projected percentage change in abundance across 80 boreal-breeding bird species.

Time period	Number of species showing the specified change in abundance					
	>50% decrease	25–50% decrease	25% decrease to 25% increase	25–50% increase	50–100% increase	>100% increase
2011–2040	0	7	50	18	4	1
2041–2070	2	10	33	7	16	10
2071–2100	10	16	17	6	10	21

Notes: Mean change values for each species are based on 11 bootstrap iterations, two variable sets, and four global climate models (GCMs). For individual species' projections, see Appendix D: Table D1.

increased to 2.38 (0.31, 5.32), and was greater than 1 for 59 species. By 2071–2100, mean *d* was 2.87 (0.73, 5.33), and was greater than 1 for 70 species.

Results from the balanced ANOVA indicated that the greatest source of variability in abundance predictions across species was attributed to the effect of climate change over time, with mean variance component = 0.442 (0.134, 0.760) (Table 3). When 19 GCMs were considered in an unbalanced ANOVA, the mean variance component of climate change decreased slightly to 0.397 (0.098, 0.725) (Table 3). For 21 species, sampling error represented the largest source of uncertainty (mean variance component = 0.118 across all 80 species) (Table 3; Appendix D: Table D3). For 13 of these species, sampling uncertainty was greater than the climate change effect. For 53 species, GCM represented the largest source of uncertainty (mean variance component = 0.174). However, it was only greater than the climate change effect for 10 species. When all 19 GCMs were considered, the mean variance component of GCM uncertainty increased to 0.228, compensating for a decrease in time- and sampling-related components. Variable selection resulted in a large variance component (up to 0.745) for a few species, but it was the greatest source of uncertainty for only four species (mean variance component = 0.047).

By definition, prediction uncertainty (calculated as the sum of all variance components except climate change from the balanced ANOVA) was negatively related to the magnitude of projected change in total abundance (Fig. 4), but a wide range of response magnitudes was seen along the range of prediction uncertainty. Prediction uncertainty was generally low relative to the projected magnitude of change for species with large projected increases. Species with the highest overall prediction uncertainty were evenly split between those with high sampling uncertainty and those with high GCM uncertainty.

Spatial and temporal uncertainty

The magnitude and relative importance of the three components of prediction uncertainty changed over time (Table 4). Averaging across all 80 species, sampling error was the greatest source of uncertainty in current predictions of potential population size (as measured by CV), but uncertainty decreased over time, from an average of 0.129 (0.036, 0.390) in the current period to 0.099 (0.032, 0.228) by the end of the century. Variable-related uncertainty exhibited the opposite trend, increasing in importance over time from 0.058 (0.009, 0.163) to 0.115 (0.007, 0.347), as did uncertainty across the four GCMs, which more than doubled in magnitude from 0.092 (0.028, 0.161) in the 2011–2040 period to 0.216 (0.054, 0.505) in the 2071–2100 period (Table 4). When 19 GCMs were considered, the CV attributed to this component further increased to 0.266 (0.086, 0.630) by the end of the century.

Spatial patterns of uncertainty in the density predictions varied widely across species (Appendix D: Fig. D2), but for the current period it was concentrated in northern portions of the study area, where data are sparser (Fig. 5). Over time, areas of high sampling uncertainty were greatly reduced, as northern areas were projected to warm and thus more closely resemble the current climates of well-sampled boreal regions (Fig. 5a). By the end of the century, the small remaining areas of high variable uncertainty were concentrated in the western interior boreal region (Fig. 5b). Uncertainty based on four complementary GCMs increased over time, eventually overshadowing the other two sources of

TABLE 2. Projected changes over time in indices of spatial distribution (with 5th and 95th percentiles in parentheses) across 80 boreal-breeding bird species.

Time period	Mean latitude (°N)	Mean longitude (°W)	Mean elevation (m)
Current	56.2 (49.9, 63.3)	−98.7 (−115.7, −86.4)	473.2 (371.6, 686.8)
2011–2040	57.2 (50.3, 63.2)	−99.9 (−116.0, −88.0)	477.7 (375.1, 698.1)
2041–2070	58.0 (50.9, 64.1)	−100.8 (−116.3, −88.4)	481.4 (378.8, 674.5)
2071–2100	59.2 (52.4, 64.9)	−101.7 (−114.2, −89.3)	490.9 (387.5, 642.5)

Note: Species-level values are based on 11 bootstrap iterations, two variable sets, and four GCMs.

a) Species richness　　　　　　　b) Total density

Projection years

1961–1990

2011–2040

2041–2070

2071–2100

0 2 4 6 8 10 12 14

Estimated no.
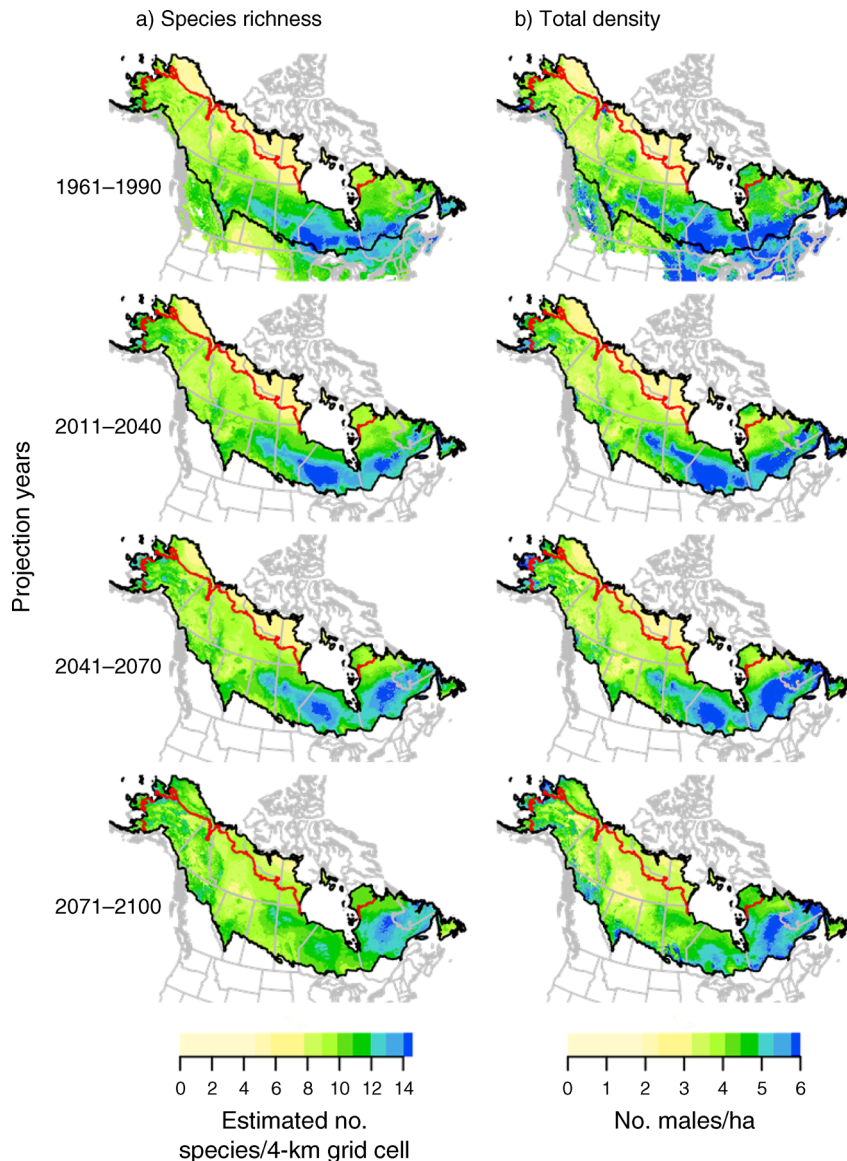species/4-km grid cell

0 1 2 3 4 5 6

No. males/ha

FIG. 2. Projected change over time in (a) boreal-breeding bird species richness and (b) total density of boreal-breeding birds. Species richness within each 4-km grid cell was calculated by converting density to probability of occurrence and summing probabilities across 80 species. The boreal/arctic boundary is shown in red.

uncertainty in most of the study area (Fig. 5c), with pockets of high GCM uncertainty concentrated in the northwest.

DISCUSSION

Signal vs. noise in projections of abundance

For projections of species' responses to future climate change to be useful, the magnitude of a species' projected response needs to be understood relative to the magnitude of uncertainty (Thuiller 2004). We found that for 58% of 80 boreal songbird species over the next 30 years—increasing to 88% of species by the end of the century—the climate change "signal" in

projections of abundance was greater than the "noise" generated by uncertainty due to a combination of sampling error, variable selection, and choice of global climate model (GCM). Despite the future increase in GCM uncertainty over time, this variability was swamped by the increasing magnitude of the projected directional change (positive or negative) in species abundance. This suggests that the predicted trajectories of avian responses to future climates are relatively robust for informing conservation planning and resource management decisions under climate change. Although the strength of a projected warming signal compared to GCM "noise" has been demonstrated (Kang and Cressie 2013), we found that the additional
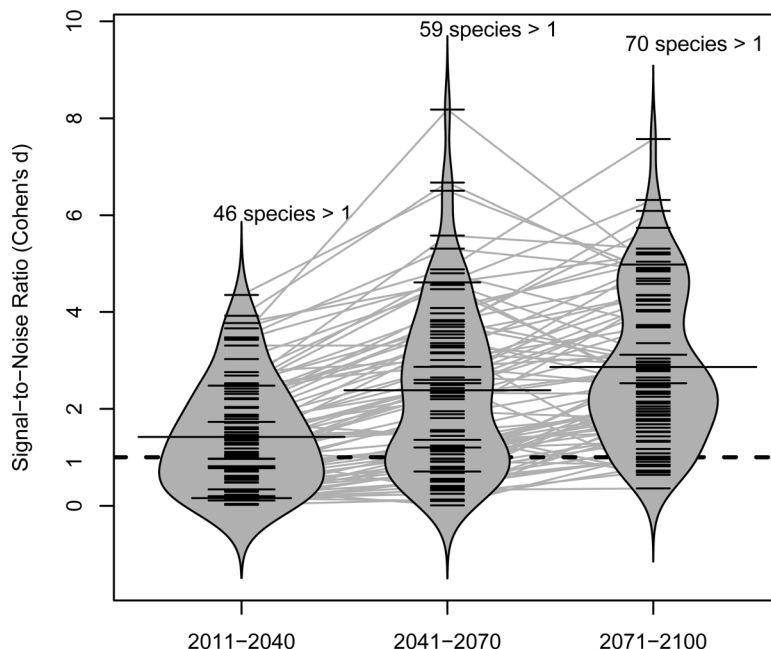
Fig. 3. Change in the distribution of signal-to-noise ratios (Cohen's d) over time for 80 boreal bird species' abundance projections. The violin plots show the shapes of the distribution for each time period, with wider regions representing more common d values. Violin plots were generated using the beanplot package for R (Kampstra 2008) with a density bandwidth of 0.5 and Gaussian kernel estimation, where bandwidth is the standard deviation of the kernel. Gray lines link each species through the different time periods. The dashed line represents $d = 1$; above this line, the climate change signal is greater than the noise due to the sources of uncertainty examined. Narrow black lines represent the 80 species; longer lines black lines extending beyond the violins represent mean d values for each time period.

uncertainties introduced by the species modeling process (specifically, sampling error and variable selection) generally did not overwhelm the climate change signal. This result appears consistent with Thuiller (2004), who found a majority (56%) consensus among different combinations of GCMs and SDMs for

mid-century species turnover projections in European plant communities.

Uncertainty due to GCM projections

By the end of the century, the largest source of prediction uncertainty across species was the choice of

TABLE 3. Variance components for four sources of variability (and interactions) in projected abundance change summarized across 80 boreal- and arctic-breeding species (a) for four complementary GCMs and (b) for all 19 GCMs available for the A2 emissions scenario (IPCC AR4).

Statistic	Time	Sampling	Variable	GCM	GCM × time	Variable × time	Remaining
a) Four GCMs							
Mean	0.442	0.118	0.047	0.174	0.107	0.017	0.095
2 SD	0.404	0.298	0.190	0.224	0.154	0.050	0.172
5th percentile	0.134	0.005	0.028	0.000	0.018	0.000	0.014
95th percentile	0.760	0.424	0.388	0.146	0.260	0.066	0.246
No. spp., largest	N/A	21	4	53	1	0	1
No. spp., >Time	N/A	13	3	10	6	0	9
b) All 19 GCMs							
Mean	0.397	0.090	0.045	0.228	0.134	0.016	0.090
2 SD	0.417	0.261	0.187	0.250	0.172	0.047	0.188
5th percentile	0.098	0.004	0.076	0.000	0.039	0.000	0.011
95th percentile	0.725	0.327	0.457	0.146	0.327	0.061	0.216
No. spp., largest	N/A	10	4	58	8	0	0
No. spp., >Time	N/A	13	3	21	14	0	11

Notes: Variance components are based on an ANOVA with three future time periods (climate change effect), two variable sets, and 11 bootstrap sampling iterations. No. spp., largest is the number of species for which that source of uncertainty was greatest; No. spp., >Time is the number of species for which that source of uncertainty was greater than the time effect. N/A means not applicable. The last column includes all other sources of variability, including unspecified interactions. For species-specific results, see Appendix D: Table D2.
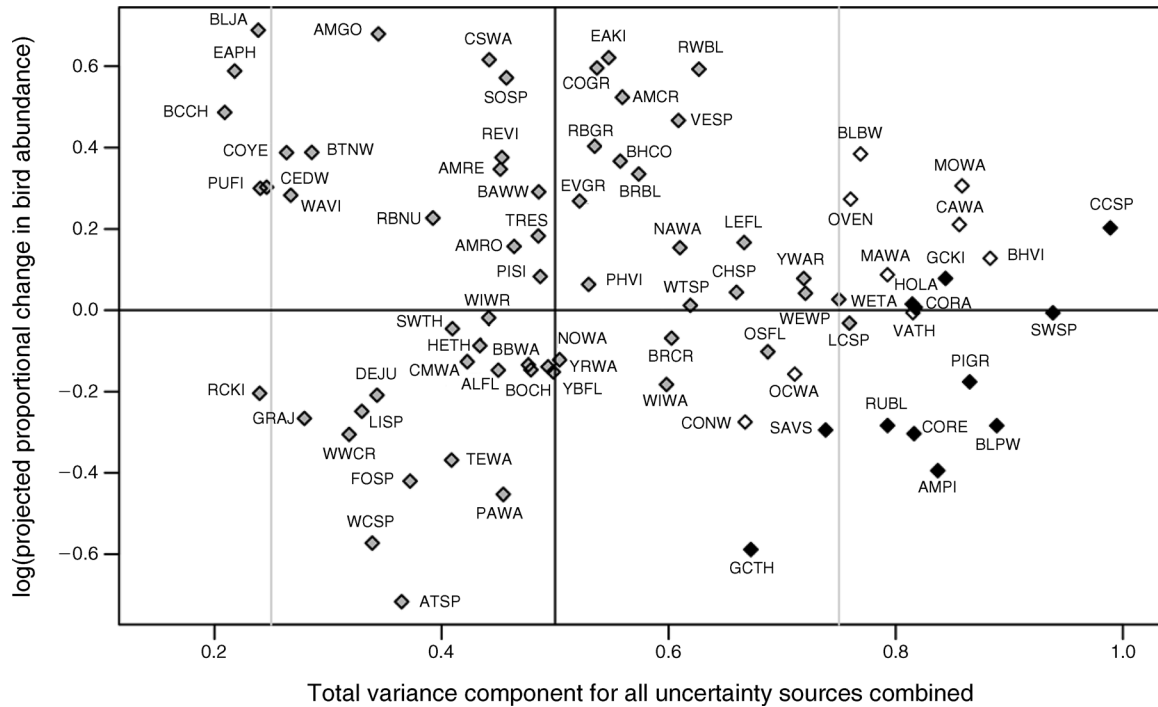
Fig. 4. The magnitude of projected proportional change in abundance (*y*-axis) plotted against the magnitude of uncertainty (*x*-axis) by the end of the century (2071–2100) for 80 boreal bird species based on four complementary global climate models (GCMs). For species code identifications, see Appendix C: Table C1. Symbol fills indicate the greatest source of variability: climate change effect for species in gray; GCM for species in white; sampling or variable selection (CCSP only) for species in black. The *x*-axis represents the sum of all variance components except the climate change effect. The *y*-axis represents the log-transformed projected proportional change + 1 ($y = 0$ indicates no change).

GCM, indicating that multiple complementary GCMs should be used to capture the range of alternative futures. Direct comparison with other variance partitioning studies (Dormann et al. 2008*a*, Buisson et al. 2009, Diniz-Filho et al. 2009, Mbogga et al. 2010, Garcia et al. 2012) is complicated by differences in taxa, geographic regions, data resolution, and specific GCMs and time periods. However, our high-end estimate of 23% of variation due to GCM was comparable to the other study in this group (Garcia et al. 2012) that considered a full suite of available GCMs (17 vs. 19 in our study). The relatively small (6%) increase in variance from 4 to 19 GCMs reflects the high redundancy among these models (Masson and Knutti 2011) and suggests that a well-selected subset can appropriately reflect

climate model uncertainty. Furthermore, GCMs are not of equal accuracy (Scherrer 2011), so the use of poorly performing GCMs may be counterproductive (Räisänen 2007). Despite the large amount of uncertainty contributed by choice of GCM, we identified only 10 species for which the GCM-related uncertainty was consistently greater than the overall climate change effect (up to 21 when all 19 GCMs were considered). For these species primarily associated with deciduous forest (e.g., Mourning Warbler *Geothlypis philadelphia* and Canada Warbler *Cardellina canadensis*), future abundance trajectories were often nonlinear and diverged substantially over time, with larger projected decreases associated with the drier GCMs (Appendix D: Fig. D3). Areas of high GCM uncertainty were primarily located in the western interior

TABLE 4.   Sources of prediction uncertainty (coefficient of variation) over time averaged across 80 boreal- and arctic-breeding bird species; confidence intervals in parentheses represent 5th and 95th percentiles.

Time period	Sampling	Variable	GCM-4	GCM-19
1961–1990	0.129 (0.036, 0.390)	0.058 (0.009, 0.163)	N/A	N/A
2011–2040	0.110 (0.028, 0.305)	0.051 (0.010, 0.136)	0.092 (0.028, 0.161)	0.131 (0.034, 0.276)
2041–2070	0.097 (0.027, 0.247)	0.072 (0.002, 0.230)	0.146 (0.041, 0.344)	0.184 (0.065, 0.385)
2071–2100	0.099 (0.032, 0.228)	0.115 (0.007, 0.347)	0.216 (0.054, 0.505)	0.266 (0.086, 0.630)

Notes: Sampling uncertainty is due to variation across 11 bootstrap samples; model uncertainty is due to variation between climate-only and climate + land use + topography models. Global climate model uncertainty is due to variation across four complementary models (GCM-4) and all 19 models (GCM-19) available for the A2 emissions scenario (IPCC AR4). N/A means not applicable.

boreal region, where available moisture is generally low, and small fluctuations in moisture may lead to major vegetation differences such as grassland vs. forest, or conifer vs. deciduous tree species (Hogg 1994, Schneider et al. 2009, Mbogga et al. 2010).

Uncertainty due to sampling error

Sampling error in the data used to build the model explained ~10% of the variance, on average, but much more for approximately a dozen species. The species with highest sampling error were generally less well represented in our data set, mostly due to their high-latitude affinities but also probably due to low densities; e.g., Rusty Blackbird *Euphagus carolinus* and American Pipit *Anthus rubescens*. This reflects the obvious fact that SDM accuracy may be reduced when limited occurrence data are available (Stockwell and Peterson 2002), especially when using more complex methods such as boosted regression trees (Wisz et al. 2008). For this small subset of species with sparse data, current models probably could be improved by targeted surveys, especially in climatically underrepresented northern regions. However, despite large error bounds, most of these species were projected to decrease in abundance over time, with high signal-to-noise ratios. As such, their models are still informative, especially from the standpoint of identifying species most vulnerable to climate change. For almost all species examined, the sampling uncertainty decreased over time, as poorly sampled climates to the north were replaced by better-sampled climates to the south, i.e., eastern deciduous forest and interior grassland biomes. The relative lack of projected novel climate emergence (Williams et al. 2007) within our large study area (Rehfeldt et al. 2012) makes sampling uncertainty a much smaller problem than might otherwise be the case (e.g., Stralberg et al. 2009, Zurell et al. 2012). However, the regions with highest future sampling-related prediction uncertainty (mostly in Alaska) did tend to correspond with projected non-analog climates according to Rehfeldt et al. (2012), suggesting that signal-to-noise ratios may be much lower in regions that experience major novel climate development. These high-uncertainty regions may also be related to the partial decoupling of minimum annual temperature from temperature seasonality and growing-season heat sums (Appendix B).

Uncertainty due to predictor variables

Variable uncertainty was a minor component of the variability in future projections for all but a handful of the species that we evaluated. This probably reflected the low overall correlation between climate and land use variables in our data set, as well as the relatively strong predictive power of climate, compared to land use and topography, at a 4-km resolution. However, this source of uncertainty was important for a few species, primarily those with strong agricultural land use relationships such as Clay-colored Sparrow *Spizella pallida* (positive)

and Blue-headed *Vireo solitarius* (negative). This suggests that, when variable relationships are strong, minimal broadscale decoupling is sufficient for local variations in projections to arise. When climate and land use are confounded, the effects of climate on species' distributions may be overestimated, thereby misleading both the climate change projections (Clavero et al. 2011) and the conservation decisions based upon them. Consequently, there is a need for observational data sets that span a range of land use and climate conditions. This requirement is not always satisfied by roadside data from the North American Breeding Bird Survey (BBS; McKenney et al. 2001, Sauer et al. 2011), which comprise the primary distributional data available for climate change projection purposes in North America (e.g., Matthews et al. 2011; National Audubon Society 2014). In the boreal region in particular, roads and therefore BBS routes are simultaneously biased toward southern climates and agriculturally dominated landscapes (NABCI Canada 2012; Machtans et al. 2014). Our extensive data set, which included data from more remote parts of the boreal region, markedly reduced this bias.

Although the inclusion of land use and topography variables did not strongly influence range-wide predictions for most species, it was sometimes quite important locally. By the end of the century, variable uncertainty was concentrated in the southern portions of the boreal region, where the potential to support agricultural land uses in the future is greatest due to projected transition to prairie ecosystems (Frelich and Reich 2009). Unfortunately, boreal-wide spatially explicit projections of agricultural expansion generally do not exist, except for coarse (0.5° grid cell resolution) global projections that do not indicate any noticeable projected land-use conversion for the region (Strengers et al. 2004, Jetz et al. 2007, Hof et al. 2011). Other modeling efforts have focused on climatic suitability and plant hardiness zones (McKenney et al. 2001), which can be considered equivalent to our climate-only model and used to infer change (i.e., agricultural land uses shift with climate). However, projections that include socioeconomic and other policy drivers (e.g., Bierwagen et al. 2010, Radeloff et al. 2011) would be necessary to adequately project local responses to the combined effects of climate and land-use change.

Other potential sources of uncertainty

It is rarely possible to evaluate and quantify all potential sources of uncertainty, some of which stem from vagueness of terms (Regan et al. 2005). For example, our models were intended to predict potential breeding-bird abundance based on climatic suitability. Actual bird numbers will depend on multiple demographic factors (e.g., overwinter survival and dispersal) that are not easily incorporated into a distribution modeling approach (but see Keith et al. 2008, Zurell et al. 2009, Fordham et al. 2013). Even within the more
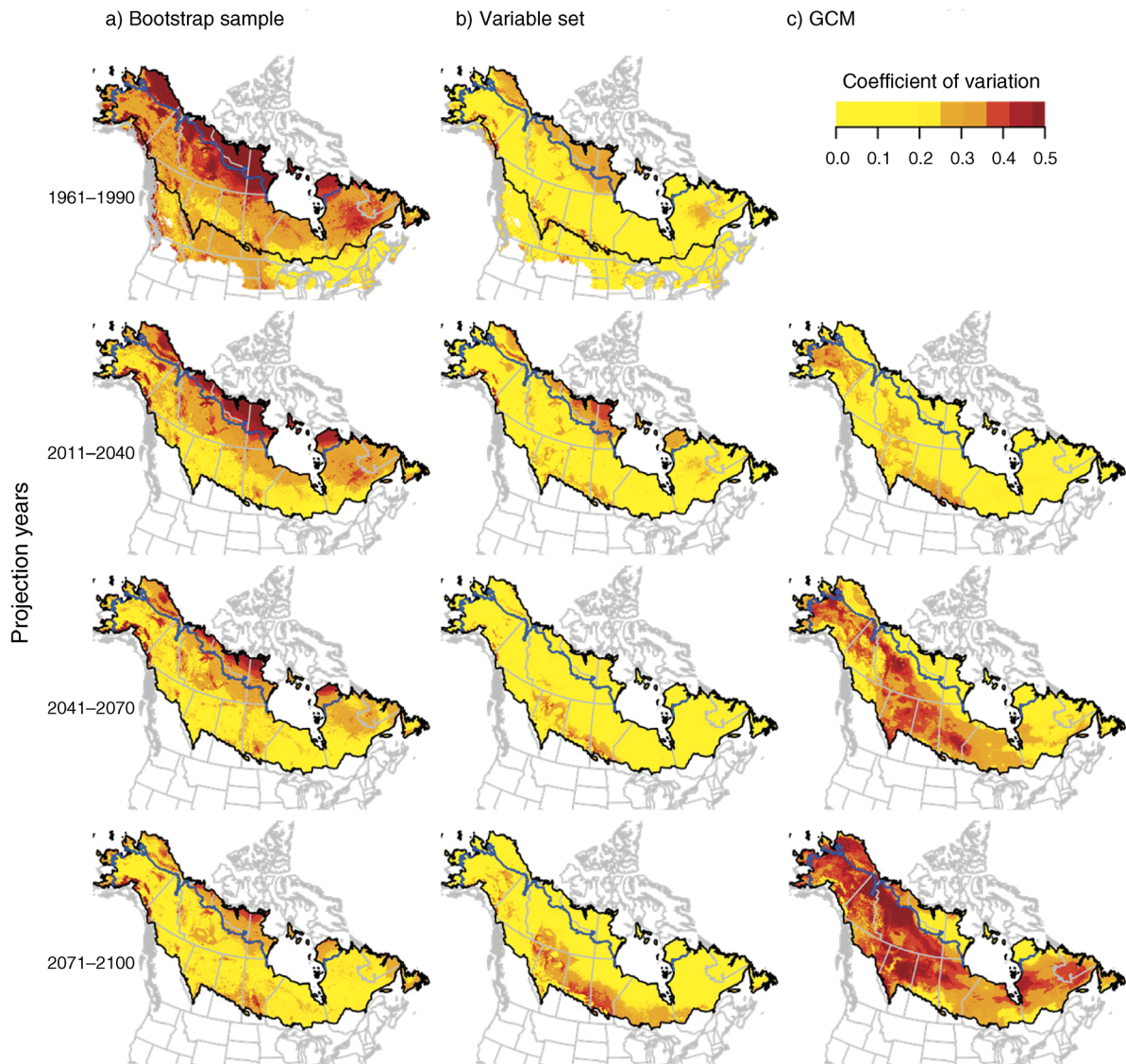
FIG. 5. Spatial and temporal representations of the coefficient of variation in projected abundance at the 4-km grid cell level across multiple sources of uncertainty, averaged over 80 boreal-breeding bird species. (a) Sampling uncertainty due to variation across 11 bootstrap samples; (b) variable uncertainty due to variation between climate-only and climate + land use + topography models; and (c) GCM uncertainty due to variation across four complementary GCMs.

tangible sources of "epistemic" (known) uncertainty (Regan et al. 2005), we could not evaluate every potential contributor. Given the strong climatic basis for vegetation distribution at this resolution (Hamann and Wang 2006, McKenney et al. 2007), we assumed that avian responses to climate change would be driven by climate's direct effects on vegetation, and we did not attempt to disentangle these effects. Thus the accuracy of short-term projections may be compromised when vegetation is in disequilibrium with climate (Svenning and Sandel 2013). However, because our intent was to evaluate trajectories of potential change rather than projected conditions for specific time periods, the

specific years were less important than the climate conditions that they represent.

Furthermore, our evaluation of variable uncertainty was limited to a subset of climate and land-use variables among which future decoupling was limited and localized. There may be other correlated, but unmeasured, climate variables, such as interannual variability (Cumming et al. 2014), that also decouple in the future, leading to additional prediction uncertainty. However, we were limited to existing GCM projections that do not yet adequately model changes to interannual climate variability (Mehta et al. 2010). More dramatically, inadequate representation of major positive feedbacks such as changes in albedo due to snow/ice (Screen and

Simmonds 2010) and cloud cover (Fasullo and Tren-berth 2012) may also mean a substantial underestima-tion of climate sensitivity among current GCMs (Hansen et al. 2013). Consideration of more extreme scenarios could overwhelm the signal with noise, but we have focused here on generally accepted projections based on the so-called "fast feedbacks" (Rohling et al. 2012) for which short-term responses are better under-stood. Our results must be interpreted within these boundaries.

Conservation and management implications

A striking aspect of our results is the wide range of projected changes and uncertainty characteristics exhib-ited across species. Without quantitative analysis, we found some consistent and anticipated patterns among the species modeled. Species with the most northerly distributions often had high sampling uncertainty, due to sparse data, but also had large projected declines, leading to high signal-to-noise ratios that increased over time. Southern grassland-associated species were all projected to increase, but a combination of high variable uncertainty (due to positive associations with agricul-ture) and high GCM uncertainty led to low signal-to-noise ratios among this group. Deciduous forest-associated species tended to have high GCM uncertain-ty, given the potential for rapid broadscale conversion of deciduous and mixed forest to grassland, depending on "tipping points" in available moisture (Price et al. 2013). Although less common species generally had high sampling uncertainty, the signal-to-noise ratio for these species could easily be much higher than for common, high-abundance species with little projected response to climate change. Variability among species responses to climate change may be attributed to a variety of traits, the importance of which is not well understood (Kharouba et al. 2013). For birds, larger ranges are generally associated with lower model accuracy (Stock-well and Peterson 2002, McPherson et al. 2004, Segurado and Araújo 2004, McPherson and Jetz 2007). Other factors such as migratory behavior, trophic level/feeding guild, habitat specialization, and habitat association (especially wetland affinity) have been found to be important, but not consistently across regions and taxonomic subsets (Brotons et al. 2004, Huntley et al. 2004, Hernandez et al. 2006, McPherson and Jetz 2007). Further analysis is needed to better explain interspecific variation in climate change response, uncertainty, and signal-to-noise ratio.

However, this reinforces the individuality of species' responses to climate change (Williams and Jackson 2007, Stralberg et al. 2009), and highlights the challenges of adopting one-size-fits-all approaches to climate change adaptation. Where feasible, land-based ap-proaches that maintain natural disturbance dynamics (Noss 2001, Leroux et al. 2007) and facilitate broadscale distributional shifts, e.g., along gradients (Halpin 1997, Noss 2001, Hodgson et al. 2009), may prove most effective in maintaining species diversity without requir-ing certainty about long-term outcomes. Such approach-es are particularly viable in northern regions that are still relatively intact, such as the North American boreal forest.

However, individual species management is warranted for species of high conservation concern. Several studies have demonstrated the long-term inadequacy of relying solely on current environmental conditions to conserve and manage future species populations (Araújo et al. 2004, Veloz et al. 2013). Nevertheless, different conser-vation approaches may be justified depending on the strength of the climate change signal relative to the noise. When prediction uncertainty is high, there is greater risk associated with focusing on areas of predicted future climatic suitability (Fuller et al. 2008, Carroll et al. 2009, Carvalho et al. 2011). In these cases, a greater emphasis on areas of predicted overlap between current and future climatic distributions, i.e., macrorefugia (Keppel et al. 2012), may be appropriate. Conversely, justification is greater for an emphasis on future climate space when prediction uncertainty is low compared to the magnitude of change (Hamann and Aitken 2012, Oliver et al. 2012). The range of uncertainty exhibited across species also suggests a need for differential and quantitative weighting in assess-ments of climate change vulnerability (e.g., Gardali et al. 2012).

The dominant source of prediction uncertainty is also an important consideration in evaluating conservation and research strategies. For some species, especially those that are sensitive to changes in moisture balance, different GCMs result in distinctly different future trajectories. These species may be most effectively managed in an adaptive framework that considers the likelihood of alternative climate futures, updated as new information becomes available about GCM accuracy and reliability. Long-term monitoring at stationary locations will be a critical component of adaptive management efforts (Nielsen et al. 2009). For species with high sampling or variable uncertainty, the choice of GCM is less important within the already large range of future trajectories. In such cases, short-term efforts may be well spent by improving models through additional targeted sampling, e.g., in our case, in underrepresented northern regions, and in agricultural landscapes within marginal climates, respectively. It will also be important to study potential climate change effects on agricultural land uses (David and Marshall 2008), so that they may be factored into conservation decisions.

Finally, of immediate conservation concern within the boreal region is the rapid rate of industrial development, including forestry, energy, and other resource extrac-tion, which could dramatically alter forest habitat over coming decades (Schneider et al. 2003, Hauer et al. 2010). Landscape-level effects of anthropogenic distur-bance on avian communities (Schmiegelow et al. 1997, Drapeau et al. 2000, Hobson and Bayne 2000), and

avian vegetation type/age class relationships (Hobson and Schieck 1999, Schieck and Song 2006) have been identified regionally, and could be quantified across larger spatial extents with the development of comprehensive, standardized vegetation (e.g., Beaudoin et al. 2014; Cumming et al. *in press*) and anthropogenic disturbance (e.g., Pasher et al. 2013) data sets. With a better understanding of future development and vegetation trajectories, more temporally and spatially refined avian projections can also be generated. In the meantime, we suggest that bioclimatic models, when constructed carefully with accompanying uncertainty estimates, can provide useful projections for a majority of passerine species and should be interpreted in the context of associated uncertainties to inform conservation and management decisions.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D and the Supplement are available online: http://dx.doi.org/10.1890/13-2289.1.sm