ORIGINAL ARTICLE

Stacked species distribution models and macroecological models provide congruent projections of avian species richness under climate change

Trisha Distler[1],*, Justin G. Schuetz[1], Jorge Velásquez-Tibatá[1] and Gary M. Langham[2]

[1]National Audubon Society, San Francisco, CA 94104, USA, [2]National Audubon Society, Washington, DC 20036, USA

ABSTRACT

Aim Using survey data for North American birds, we assess how well historical patterns of species richness are explained by stacked species distribution models and macroecological models. We then describe the degree to which projections of future species richness differ, employing both modelling approaches across multiple emissions scenarios.

Location USA and Canada.

Methods We use Audubon Christmas Bird Count and North American Breeding Bird Survey data to estimate current and future species richness of birds using two distinct approaches. In the first, we model richness by stacking predictions from individual species distribution models. In the second, we model richness directly, ignoring the contributions of specific taxa to richness estimates.

Results The two modelling approaches show similar accuracies when validated with historical observations, particularly winter observations, and result in similar patterns of richness when projected onto current and future climate spaces. Patterns of projected change in species richness differed markedly between winter and summer seasons regardless of modelling approach. Our models suggest that bird species richness in winter will increase or remain stable across much of North America. In contrast, species richness in summer is projected to decrease over much of North America, except part of northern Canada, suggesting that climate may constrain many breeding bird species and communities in the future.

Main conclusions Stacked species distribution models and macroecological models produce similar estimates of current and future species richness for each of two seasons despite being built on different concepts of community assembly. Our results suggest that, although the mechanisms that shape geographical variation in biodiversity remain uncertain, these limitations do not impede our ability to predict patterns of species richness at broad scales. Congruence of species richness projections across modelling approaches is encouraging for conservation planning efforts that focus on retaining biodiversity into the future.

Keywords
Biodiversity, birds, climate change, conservation, macroecology, North America, seasonality, species distribution models.

*Correspondence: Trisha Distler, National Audubon Society, 220 Montgomery Street, San Francisco, CA 94104, USA.
E-mail: climatescience@audubon.org

INTRODUCTION

Human-induced climate change is increasingly being recognized as a fundamental driver of biological processes and patterns, and as a threat to the persistence of many species (Thomas *et al.*, 2004). Recent climate change has already caused shifts in the geographical ranges of myriad species (Root & Schneider, 2002; Parmesan, 2006; Hitch & Leberg, 2007) and ongoing climate change is expected to result in even greater redistributions of taxa (Hannah *et al.*, 2005; Devictor *et al.*, 2008). Although species richness remains a standard index of biodiversity and currency for conservation efforts (Margules & Pressey, 2000; Brooks *et al.*, 2006), climate-change mitigation and adaptation strategies often rely on modelling and then combining the responses of individual species to changing conditions, rather than modelling richness *per se* (Lawler *et al.*, 2009; Stralberg *et al.*, 2009; Araújo *et al.*, 2011; Bellard *et al.*, 2012). It is unclear whether this difference in modelling perspectives – which reflects different assumptions about the processes that control community assembly – affects the accuracy of current richness estimates or projections of future changes in species richness.

In most cases, species richness is estimated by stacking individual species distribution models (Algar *et al.*, 2009; Mateo *et al.*, 2012). Individual species distribution models are constructed by relating occurrence data to environmental variables (e.g. temperature and rainfall data) and projecting the modelled relationships onto geographical space (Elith *et al.*, 2008; Huntley *et al.*, 2008; Barbet-Massin *et al.*, 2009; Lawler *et al.*, 2009; Stralberg *et al.*, 2009). Species distribution models often rely on the concept of niche conservatism (the tendency of species to retain ancestral ecological characteristics), and assume that environmental variables will play an important and consistent role in shaping species distributions (Wiens & Graham, 2005). If environmental variables change over time, species are expected to shift their geographical ranges in response to those changes rather than adapting *in situ*. The use of species distribution models to forecast future distributions has been criticized for making simplistic assumptions about dispersal potential and biotic interactions within current or emerging communities (Dormann, 2007). More elaborate models that explicitly incorporate dispersal processes and species interactions often provide similar estimates of current species distributions, but can produce divergent results when projected onto future climate spaces (Hijmans & Graham, 2006; Morin & Thuiller, 2009; Kearney *et al.*, 2010; Buckley *et al.*, 2011). Given the challenges of gathering empirical data on dispersal and biotic interactions, species distribution models remain the most widely used method for projecting the impacts of climate change on species distributions (Huntley *et al.*, 2008; Barbet-Massin *et al.*, 2009; Lawler *et al.*, 2009; Stralberg *et al.*, 2009). When applied across large extents, they remain useful for informing conservation planning at broad spatial scales (Pearson & Dawson, 2003; Wiens *et al.*, 2009; Araújo & Peterson, 2012).

Macroecological models offer an alternative framework for estimating species richness at broad spatial scales, one that emphasizes the realized properties of communities rather than the idiosyncrasies of component species (Ferrier & Guisan, 2006). In macroecological modelling, richness is estimated directly using variables thought to influence the number of coexisting species (Whittaker *et al.*, 2001; Gotelli *et al.*, 2009; Guisan & Rahbek, 2011; Calabrese *et al.*, 2014). Energy and water availability, environmental heterogeneity, disturbance, and regional history may each play a role in controlling species richness (Wright, 1983; Currie, 1991; Latham & Ricklefs, 1993; Whittaker *et al.*, 2001). In addition, numerous studies have shown that variation in species richness across continents is strongly correlated with contemporary climate (Wright, 1983; Hawkins *et al.*, 2003; Field *et al.*, 2009). Macroecological modelling can be implemented using a variety of modelling techniques, including curve-fitting, predictive simulation and correlative approaches (Hawkins *et al.*, 2003; Currie *et al.*, 2004; Rahbek *et al.*, 2007; Gotelli *et al.*, 2009). Few macroecological studies have explored the consequences of future climate change on biodiversity (but see Currie, 2001; Menéndez *et al.*, 2006; Algar *et al.*, 2009), despite decades of research and strong evidence for an association between climate variables and biodiversity (Dormann, 2007; Algar *et al.*, 2009).

Previous studies that have compared stacked species distribution models and macroecological models have suggested that both are suitable for estimating richness, but are accompanied by different strengths and weaknesses. Stacked species distribution models retain information on the constituent species within an area, but can overpredict richness in species-rich areas (Algar *et al.*, 2009; Dubuis *et al.*, 2011; Guisan & Rahbek, 2011). Macroecological models tend to outperform stacked species distribution models in terms of the accuracy and precision of richness estimates and force us to seek general rules driving the assemblage of species, but they cannot provide any information on species composition (Algar *et al.*, 2009; Dubuis *et al.*, 2011; Guisan & Rahbek, 2011). To date, no study has compared the performance of stacked species distribution models and macroecological models at different times of the year or explored which climatic variables inform estimates of seasonal species richness.

In this study we use Audubon Christmas Bird Count (CBC) and North American Breeding Bird Survey (BBS) data to describe current patterns of species richness for birds in North America, using two alternative approaches. In the first approach, we model species richness within an area by stacking individual species distribution models built with occurrence data and bioclimatic predictors. In the second, we use macroecological models to characterize species richness directly using the number of co-occurring species as the response variable and bioclimatic variables as predictors. We then assess the predictive performance of the two approaches using historical data, make projections into the future (2070–2099), and compare the resulting patterns of richness between the two approaches. In doing so, we (1) provide

novel projections of future species richness for North American birds across two seasons, and (2) assess congruence in future projections of species richness built on differing concepts of community assemblage.

MATERIALS AND METHODS

Bird data

Bird distribution data were obtained from two sources: the Audubon Christmas Bird Count (CBC) (National Audubon Society, New York; available at: http://birds.audubon.org/about-christmas-bird-count) and the North American Breeding Bird Survey (BBS) (USGS Patuxent Wildlife Research Center, Laurel, MD, USA; available at: https://www.pwrc.usgs.gov/bbs/about/). These surveys are remarkable in that they have been conducted in a similar fashion over a long period of time and large spatial extent. CBC surveys are conducted by citizen scientists within circles of 15–mile (24.1 km) diameter for one 24-h period during a 4-week interval centred on December 25. For this study, all circles that fell within the boundaries of Canada, the contiguous United States and Alaska were included in the analyses (see Fig. S1 in Appendix S1 of the Supporting Information). We elected not to include data from other areas due to their relatively incomplete geographical sampling and relatively poor spatio-temporal resolution of climate data. For every circle and count year, we distilled raw count data into presence/absence information for each species.

The Breeding Bird Survey was initiated in 1966 to monitor bird populations in the summer months. Most BBS routes in the United States and Canada are surveyed in June but some are run between May and mid-July. Survey routes are 24.5 miles long with stops at 0.5-mile intervals. At each stop, participants conduct a 3-minute point count and record birds seen or heard (Sauer *et al.*, 2011). For our analyses, we used data for the first 30 stops (*c.* 24 km) in an effort to balance the geographical scales at which CBC and BBS sample the landscape and to maintain a reasonable match to the resolution of our climate data (10 km × 10 km). We only used data for the United States and Canada and we distilled raw count data for every route and year into presence/absence information for each species.

Climate data

We obtained contemporary climate data from the Canadian Forest Service (CFS) (McKenney *et al.*, 2011) and extracted climate data to the midpoint of each CBC circle and to the start-point of each BBS route, using the CFS website (https://glfc.cfsnet.nfis.org/mapserver/cl_p/climatepoints.php). We matched bird data and climate data on an annual basis, assuming that climate variables from the year leading up to each survey would best inform our understanding of occurrence data (i.e. for CBC count year x and BBS survey year x, we used climate data from year $x - 1$). For instance, climate

data for the year *prior* to a CBC survey event would include monthly climate data from that winter's survey, because each CBC survey date is considered the 1st of January following the December counts: survey data labelled '2000' thus spans December 1999 and January 2000. This is important because our climate parameters include indices of minimum and maximum monthly temperatures and precipitation, as well as mean variables. Similarly, climate data from the prior year matched to BBS survey events would encompass the winter climate preceding the summer (breeding) season.

To characterize future climates and establish a spatial context for predictions, we added future climate anomaly grids to baseline climate data obtained from CFS covering the United States and Canada. Generating future climate anomaly grids required several processing steps. First, we obtained spatially downscaled WorldClim climate grids (5′ resolution) for 2070–2099 (available from the International Center for Tropical Agriculture, CIAT: http://www.ccafs-climate.org/statistical_downscaling_delta/) for 13 combinations of emissions scenarios and general circulation models (GCMs; see Table S1 in Appendix S1). CIAT produced the grids by adding statistically downscaled IPCC Fourth Assessment (IPCC, 2007) future climate grids to contemporary WorldClim climate data (Ramirez-Villegas & Jarvis, 2010). We then subtracted contemporary WorldClim grids for monthly minimum temperature, maximum temperature and precipitation from the CIAT future grids to isolate predicted changes in climate from WorldClim baseline values. Finally, we added these monthly anomaly grids to CFS mean climate grids for the baseline period (1971–2000). This ensured that we matched our contemporary climate grids with IPCC AR4 anomaly grids to produce high-resolution future climate grids for our study region.

After creating our future climate grids, we transformed raw temperature and precipitation data into a series of 17 bioclimatic variables (Nix, 1986; Hijmans *et al.*, 2005) using DIVA 7.5 (available at: http://www.diva-gis.org/) and the RASTER package 1.9 (Hijmans & Etten, 2011) in the statistical software R 2.13 (R Development Core Team, 2011). Bioclimatic variables are thought to represent biologically meaningful combinations of the original monthly climate variables, because they aggregate climate information in ways that are known to drive biological processes (Nix, 1986; Phillips *et al.*, 2006).

Species distribution models

Species distribution models are formulated by using a modelling algorithm to describe the relationships between geographically coincident environmental variables and bird occurrence data. Species were modelled using boosted regression trees (Appendix S1). We built separate distribution models for winter and summer seasons, using CBC and BBS data, respectively. For CBC analyses, we included the number of survey hours invested in each CBC circle as a predictor variable in addition to the 17 bioclimatic variables in order

to account for uneven observer effort across circles. The number of participating individuals and the duration of counts vary among CBC circles and through time, thus the number of party-hours is often used as a covariate to account for this variation in analyses based on CBC data (Link *et al.*, 2008). We used 19,272 records collected at 2278 circles from the years 2000 to 2009 to train our models (matched to the corresponding climate on a yearly basis) and 30,630 independent historical records collected from 1980 to 1999 (matched to the corresponding climate on a yearly basis) to assess the predictive ability of our models. This approach allowed us to take advantage of increased geographical sampling in recent years to build models, as well as using the availability of abundant historical data to assess the predictive ability of our models outside the current time-period and climate space. We constructed models for 543 species that occur in the United States and Canada during the winter.

Our analysis of BBS data was similar in approach, with small adjustments to account for differences in data sets and survey protocols. Instead of survey effort, which varied in the CBC, but was constant in the BBS, we used Julian date to account for variation in timing of surveys across the summer season. We felt this was important, because species occurrences and detection probabilities may have been associated with the timing of BBS surveys. For example, surveys that take place later in the summer may miss bird species that have completed their breeding season and become less conspicuous or departed for their wintering grounds. We used 25,081 records collected along 3718 routes for the years 2000–2009 to train our models (matched to the corresponding climate on a yearly basis) and 41,959 independent historical records collected for the years 1980–1999 (matched to the corresponding climate on a yearly basis) to test the predictive performance of our models. We constructed models for 508 species that occur in the United States and Canada during the summer.

Projecting distributions and estimating species richness

To describe the current distributions, we projected species distribution models for all winter species (n = 543 species) and summer species (n = 508 species) into a mean climate space for the current time period (1999–2008; '2000s') accompanied by mean survey effort and Julian date grids for winter and summer seasons, respectively. We also projected models into 13 future climate spaces that reflect different combinations of possible emissions scenarios and GCMs (Table S1), all describing climate projections for the period 2070–2099 (hereafter, 'the 2080s'). We then used consensus forecasting to average predictions across general circulation models within each combination of emissions scenario and GCM (Araújo & New, 2007). Consensus forecasting is a form of ensemble modelling that uses the central tendency (e.g. mean or median value) from a set of possible models (Araújo *et al.*, 2005). The ratio-

nale behind consensus forecasting is that the 'signal' of interest emerges from the 'noise' associated with individual model errors and uncertainties (Araújo *et al.*, 2005; Araújo & New, 2007). This process resulted in three future prediction grids for each species in each season, one for each emissions scenario (B2, A1B and A2). All projections were performed using the RASTER (Hijmans & Etten, 2011) and DISMO packages (Hijmans *et al.*, 2011) in R.

To obtain maps of estimated species richness for the current winter and summer seasons, we stacked climatic suitability values for individual species distribution models within each season. To generate maps of estimated species richness for the future winter and summer seasons, we averaged suitability values for each species within each future emissions scenario and season, and then stacked them across all species. Given the debate surrounding the choice of thresholds for SDMs (e.g. Liu *et al.*, 2005; Freeman & Moisen, 2008; Nenzén & Araújo, 2011) and the potential for problems with overprediction (e.g. Dubuis *et al.*, 2011), we restricted our methods to stacked continuous models.

Macroecological modelling

To estimate species richness using observation records, we added the number of species in each CBC circle and along the first 30 stops of each BBS route for the winter and summer seasons, respectively, for each year in the current period (2000–2009). We then generated our macroecological models using boosted regression tree models in R, with species richness as our response variable and the aforementioned 17 bioclimatic variables as predictors. We also included predictors for observer effort (CBC) and Julian date (BBS). We matched bird data (2000–2009) with climate data (1999–2008) on a yearly basis to match the methods used in building our species distribution models. We built boosted regression tree models for the winter and summer seasons separately and modelled the response variable using a Poisson link function. We then projected our macroecological models for each season using the same 13 future-climate spaces and consensus forecasting techniques described above for the 2080s (Table S1). This process resulted in three future prediction grids for each modelling approach, one for each emissions scenario (B2, A1B and A2). (See Appendices S1 & S2 for details on modelling methods, the evaluation of model performance when applied to additional time-periods, and the prediction of distributional responses to future climates.)

RESULTS

Model performance and important predictors

Species distribution models were found to be effective in predicting the distributions of individual taxa, when validated with historical observations from 1980 to 1999 (winter models: median AUC score = 0.96, interquartile

range = 0.92–0.98; summer models: median AUC score = 0.95, interquartile range = 0.90–0.98; Table 1; see Appendix S2 for details of historical analyses). To assess how well these same species distribution models combined to predict species richness, we summed historical projections across all species for every survey performed from 1980 to 1999 and compared the resulting richness values to the observed species-richness data from the same surveys (Fig. 1). During the winter, stacked species distribution models predicted historical richness observations very accurately (linear regression: slope = 1.02 ± 0.00, intercept = −1.78 ± 0.19; Fig. 1) with high precision (Pearson's r = 0.925). Predictions of historical summer richness derived from stacked models were less accurate (linear regression: slope = 0.89 ± 0.01, intercept = 5.68 ± 0.26) and less precise (Pearson's r = 0.606). Stacked species distribution models and macroecological models predicted historical richness more accurately than current richness, particularly during the summer season (see Table S2 in Appendix S1).

Macroecological models were able to estimate historical species richness (1980–1999) slightly better than stacked species distribution models. In the winter, the macroecological model showed essentially no bias in estimating historical species richness (linear regression: slope = 1.00 ± 0.00, intercept = −1.23 ± 0.19) and precision equivalent to stacked-model predictions (Pearson's r = 0.924; Fig. 1). During the

Table 1 Predictive performance of species distribution models (SDM) and macroecological models (MEM) for North American birds. Cross-validation measures of deviance explained and correlation indicate the mean (SD) value across taxa. Measures of AUC (area under the curve of a receiver operating characteristic plot) indicate the median (interquartile range) value across taxa using training data (2000–2009) and independent historical test data (1980–1999) as indicated; AUC measures are not appropriate for the evaluation of macroecological models.

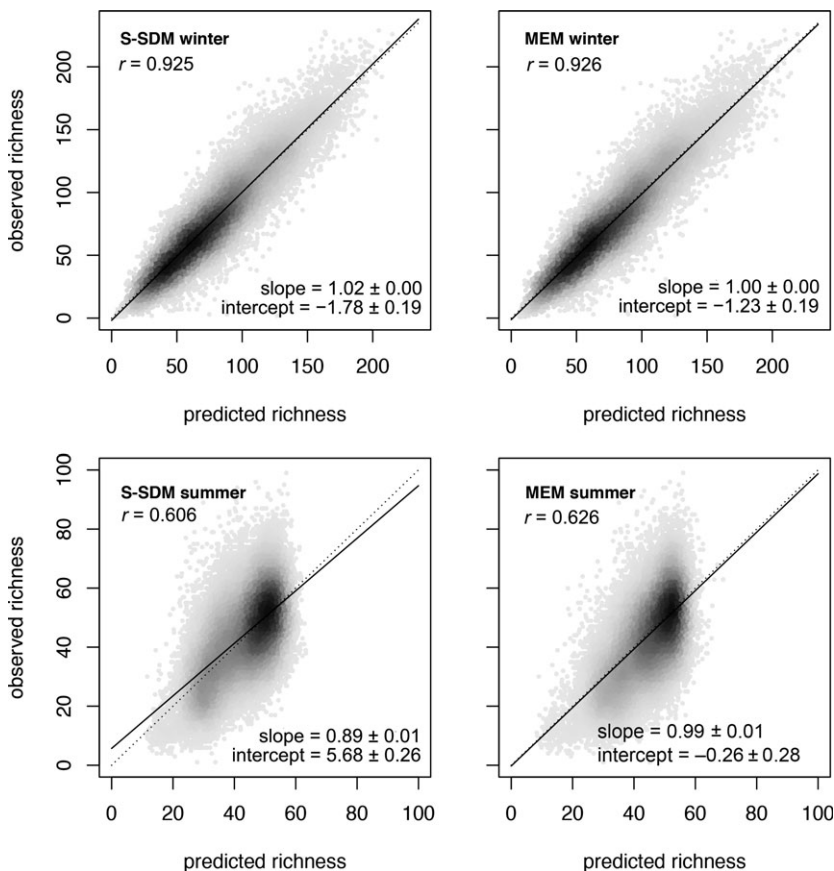|	Winter models		Summer models	
	SDM average	MEM	SDM average	MEM
Deviance explained (cross-validation)	0.72 (0.15)	0.87	0.64 (0.17)	0.51
Correlation (cross-validation)	0.64 (0.19)	0.93	0.50 (0.20)	0.71
AUC (training data 2000–2009)	0.98 (0.97–0.99)	–	0.97 (0.96–0.99)	–
AUC (test data 1980–1999)	0.96 (0.92–0.98)	–	0.95 (0.90–0.98)	–

Figure 1 Correlations between predicted and observed species richness of North American birds for winter and summer seasons for stacked species distribution models (S-SDM) and macroecological models (MEM). Species distribution models were built for each species and then summed to estimate species richness. Species distribution models and macroecological models were built using bird and climate data for the survey years 2000–2009, then projected to historical climate surfaces for the years 1979–1998 and tested with observed data from these historical time periods (winter: n = 30,632; summer: n = 41,959). The dashed line indicates the line $y = x$; the solid line has the intercept and slope described by the regression parameters in each plot.

summer season, historical projections of species richness derived from the macroecological model appeared to be much less biased (linear regression: slope = 0.99 ± 0.01, intercept = −0.26 ± 0.28) than those derived from stacked species distribution models, although precision improved only slightly (Pearson's r = 0.626; Fig. 1). These results suggest that predictions of species richness are more reliable for the winter than the summer, and that macroecological models may provide more accurate estimates of summer richness than stacked species distribution models.

When averaging across individual species distribution models for all winter species, the annual mean temperature, mean temperature of the coldest quarter, precipitation of the warmest quarter and isothermality were the bioclimatic variables that made the greatest relative contributions to model fits (Table 2, and see Fig. S2 in Appendix S1). In the winter macroecological model, the mean temperature of the coldest quarter contributed most to the model fit, followed by minimum temperature of the coldest month, annual mean temperature and annual temperature range (Table 2). Partial dependence plots for these variables in the macroecological model indicated a positive relationship between temperature and species richness during the winter, suggesting that cold temperatures play a dominant role in shaping patterns of species richness during the winter (see Fig. S3a in Appendix S1).

During the summer season, the annual mean temperature, isothermality, mean temperature of the warmest quarter, maximum temperature of the warmest month and annual precipitation contributed most to the fit of single-species distribution models (Table 2). The variables with the highest relative contributions to the macroecological model for the summer season were annual precipitation, mean temperature of the warmest quarter, mean diurnal range, annual mean temperature and isothermality (Table 2). Partial dependence plots for the macroecological model indicated a positive relationship of richness with precipitation up to 120 mm, a hump-backed relationship with temperature, and a generally negative relationship with diurnal temperature fluctuations (Fig. S3b).

Current and future patterns of species richness

Stacked species distribution models and macroecological models provided similar estimates of current species richness within seasons (winter: Pearson's r = 0.99; summer: Pearson's r = 0.92). Patterns of richness differed markedly between seasons, however, regardless of modelling approach (Fig. 2). For both stacked species distribution models and the macroecological model, the estimated winter richness peaked along the Pacific, Atlantic and Gulf coasts of North America and in the Central Valley of California. Higher latitudes and areas with higher elevation supported fewer species (Fig. 2). In the summer season, estimated richness was highest in a large swathe extending from the eastern and north-eastern United States into southern Canada. Northern Canada and the desert south-western USA supported fewer species (Fig. 2). Differences between models were evident in the

Table 2 Summary of variable contributions to model fits for species distribution models (SDM) and macroecological models (MEM) for North American birds. Contributions for individual species distribution models were averaged across all species. The most important variables are marked in bold.

| Predictor	Variable contribution (%)			
	Winter models		Summer models	
	SDM average	MEM	SDM average	MEM
Annual mean temperature	**13.4**	**11.7**	**12.2**	**7.0**
Mean diurnal range in temperature	6.5	1.6	6.2	**10.8**
Isothermality (diurnal range/annual range)	**7.4**	1.1	**9.5**	**5.9**
Maximum temperature of the warmest month	4.3	0.6	**7.0**	5.5
Minimum temperature of the coldest month	6.0	**17.0**	4.1	2.1
Annual temperature range	6.0	**2.4**	4.2	4.7
Mean temperature of the wettest quarter	4.2	0.5	4.4	2.4
Mean temperature of the driest quarter	3.1	1.4	4.1	2.8
Mean temperature of the warmest quarter	6.2	1.0	**8.6**	**11.7**
Mean temperature of the coldest quarter	**8.6**	38.5	4.6	2.4
Annual precipitation	5.2	0.7	**6.8**	**26.2**
Precipitation of the wettest month	2.3	0.4	2.8	1.7
Precipitation of the driest month	1.0	0.2	1.5	0.8
Precipitation of the wettest quarter	2.4	0.3	3.0	2.4
Precipitation of the driest quarter	3.0	0.2	4.7	3.1
Precipitation of the warmest quarter	**7.8**	0.8	6.6	3.1
Precipitation of the coldest quarter	4.1	0.4	5.7	4.5
Number of survey hours	**8.6**	**21.2**	–	–
Julian date	–	–	3.7	2.9
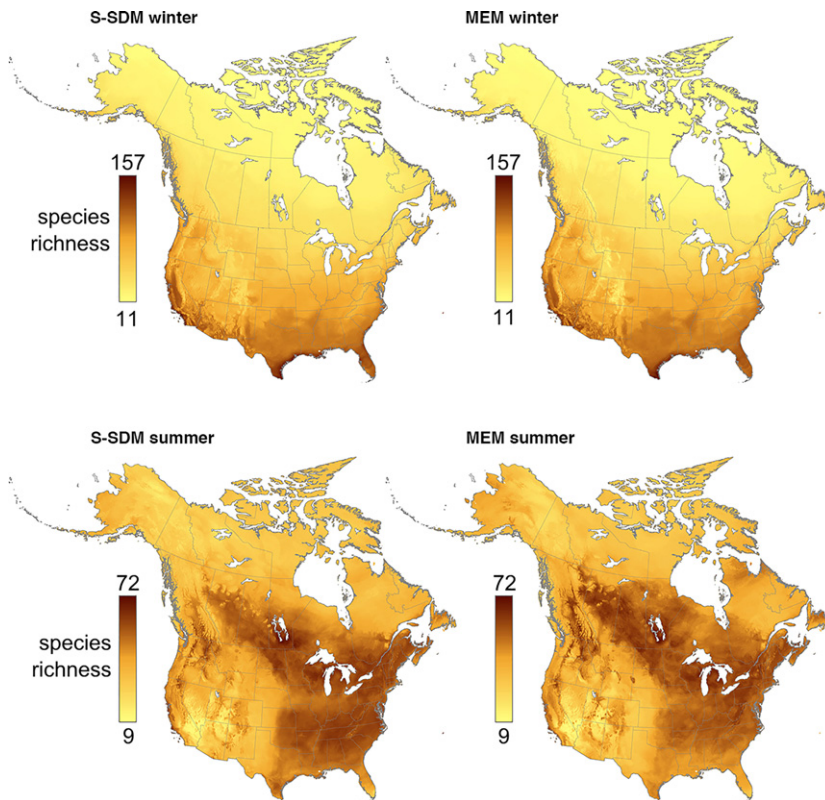
Figure 2 Estimates of current winter and summer species richness (2000–2009) of North American birds derived from stacked species distribution models (S-SDM) and macroecological models (MEM).

summer, with the macroecological model estimating lower richness than the stacked models across sections of the south-eastern United States, and higher richness in parts of the Pacific Northwest and areas bordering Hudson Bay.

The stacked species distribution models and macroecological models also yielded broadly similar projections of change in species richness from the 2000s to 2080s (Figs 3 & 4). With small differences across modelling approaches and emissions scenarios, winter species richness is projected to increase across most of the central and northern portions of the contiguous United States (particularly around the Great Lakes), in western Alaska, and in southern sections of Canadian provinces (Manitoba, Ontario and Quebec; Fig. 3). In contrast, summer species richness is expected to decline over much of the area where species richness is currently estimated to be highest (Fig. 4). Summer species richness is expected to increase in the northern Canadian provinces (Yukon, Northwest Territories, Alberta, Saskatchewan, Manitoba, Ontario and Quebec), central Alaska and a belt in the south-western United States that includes south-eastern California, Arizona, New Mexico and western Texas. Notably, declines in species richness are expected in central Florida, south-eastern Texas and California's Central Valley, regardless of season, future emissions scenarios or the modelling method employed.

Analyses of variance components corroborated the mapping results. The most complex model we generated to characterize differences between current and future species richness received all of the support in a variance components analysis (see Table S3 in Appendix S1). Random effects for regional geography (i.e. Bird Conservation Regions), season, emissions scenario and model type all played a role in explaining the variation in species richness changes between the 2000s and the 2080s (Table S3). Differences across regional geography and seasonal effects accounted for 24.8% and 17.6% of the total variance, respectively (Table 3). Relatively little of the total variance in change values could be attributed to differences between emissions scenarios (1.5%) and almost none of it could be attributed to differences in the two modelling approaches (0.4%), suggesting that they produce nearly identical richness predictions. Approximately 55.7% of the variance could not be attributed to regional geography, seasons, scenarios or models.

DISCUSSION

Stacked individual species distribution models and macroecological models produced strikingly similar estimates of both current and future species richness, despite being built on very different concepts of community assembly. Patterns of projected change in species richness differed markedly between seasons under both modelling approaches. Our results suggest that bird species richness may increase from the 2000s to 2080s across much of North America during the winter. This pattern is consistent with documented responses to recent climate change (Parmesan, 2006; Hitch & Leberg, 2007), but contrasts starkly with projected changes in summer species richness. We anticipate that species richness
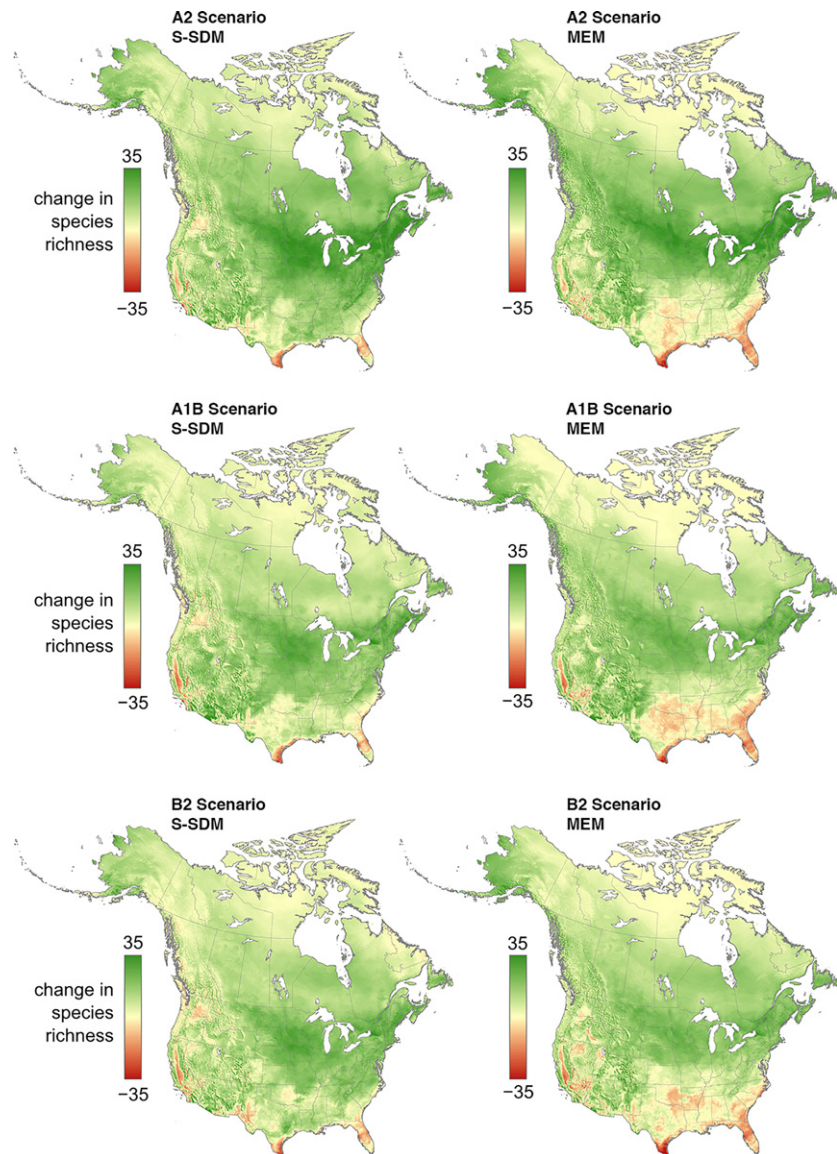
Figure 3 Projected changes in winter species richness of North American birds from the 2000s to 2080s derived from stacked species distribution models (S-SDM) and macroecological models (MEM). Projections are made for three future emissions scenarios: low emissions (B2), moderate emissions (A1B) and high emissions (A2).

will decrease over much of North America during the summer as a result of climate-induced constraints on individual bird species and/or communities. We note, however, that future summer richness may be higher than our analyses suggest, because of range expansion by Latin American species that were not modelled in this study. These general patterns for winter and summer bird communities were supported, with minor exceptions, across emissions scenarios (B2, A1B and A2) and modelling approaches.

Exploration of the contributions of variables in macroecological models, in particular, suggests why responses of bird communities to climate change across seasons are likely to be different. For the winter model, minimum-temperature variables played a dominant role in explaining species richness; for the summer model, the most important predictor variables were related to warmer temperatures and precipitation. Both of these results are consistent with predictions from the contemporary climate hypothesis, which suggest

that energy – often measured through temperature or productivity variables – places constraints on richness in areas with cold winter temperatures, or during periods of low plant productivity, whereas water availability becomes more important in areas with warm temperatures and thus higher plant productivity (Currie, 1991; Jetz & Rahbek, 2002; Hawkins *et al.*, 2003). The contributions of variables averaged across individual species distribution models suggest a similar set of mechanisms, but much less conspicuously.

We have greater confidence in projections of species richness during winter than in summer based on the validation of richness estimates using historical data. When we compared predictions of species richness from our models with historical records, correlations for the winter season (stacked species distribution models: Pearson's $r = 0.925$; macroecological models: $r = 0.924$) were stronger than those for the summer season (stacked species distribution models: $r = 0.606$; macroecological models: $r = 0.626$). The difference in preci-
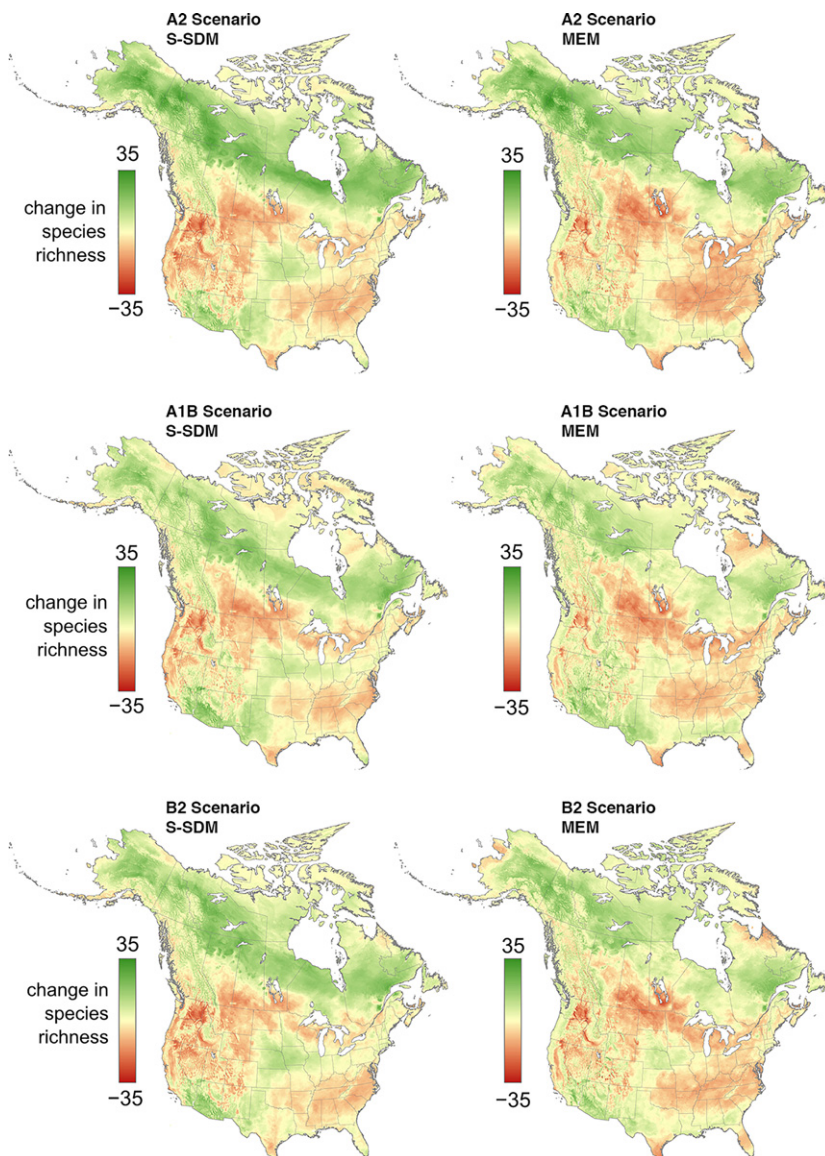
Figure 4 Projected changes in summer species richness of North American birds from the 2000s to 2080s derived from stacked species distribution models (S-SDM) and macroecological models (MEM). Projections are made for three future emissions scenarios: low emissions (B2), moderate emissions (A1B) and high emissions (A2).

Table 3 Variance component estimates of factors contributing to change in species richness values for North American birds between the 2000s and 2080s. Regional geographies were characterized using Bird Conservation Regions.

Grouping variable	Variance	Standard error	Proportion of total variance
Regional geography	28.09	5.30	0.25
Season	20.02	4.48	0.18
Scenario	1.70	1.30	0.02
Model type	0.51	0.71	0.00
Residual	63.20	7.95	0.56

sion of winter and summer predictions may reflect methodological differences in how data were collected for the CBC and BBS, with the CBC survey design better revealing relationships between bird occurrence data and climate variables. It is also possible that summer species distributions and richness are shaped by variables that we did not include in the analysis (e.g. normalized difference vegetation index, potential evapotranspiration or land cover; Hawkins, 2004) or alternatively that the difference between seasons may reflect real differences in the degree to which birds track climate in winter and summer seasons. Biotic interactions, rather than climate, may be the dominant force shaping species distributions in summer (MacArthur, 1972). At present, other studies do not help us to distinguish among these possibilities. On the one hand, Evans *et al.* (2006), using a standardized survey data set, found that species richness was correlated with climate and productivity variables for both winter and summer seasons and that the relationship was stronger for the winter season, a result that mirrors our own. On the other hand, Hurlbert & Haskell (2003), using a limited amount of CBC and BBS data, found the relationship between richness and available energy in North America to be similar across seasons despite enormous changes in the geographical pattern of productivity.

The congruence in our study of projections using species distribution models and those using macroecological models is generally consistent with findings from other studies (Algar *et al.*, 2009; Dubuis *et al.*, 2011), and suggests that an understanding of species-specific niche processes may not be necessary in order to model patterns of avian richness for the United States and Canada. Macroecological models may provide less biased and more precise estimates of species richness than those derived from stacking individual species distribution models, particularly during the summer. Although the causes of the climate–richness relationships may be poorly understood, this might not impede our ability to predict broad-scale patterns of diversity for conservation planning across large landscapes. Macroecological modelling may be especially valuable for the many geographical areas (and taxa) where comprehensive long-term datasets with large sample sizes are unavailable for individual species, or taxonomies have not been fully characterized.

Changes in patterns of species richness have important implications for systematic conservation planning (Brooks *et al.*, 2006). Biodiversity – as measured by species richness – is an important currency with which to establish conservation goals and assess the success or failure of conservation efforts (e.g. Margules & Pressey, 2000), although individual species may provide a focal point for management (e.g. Fleishman *et al.*, 2006). In the past, conservation planning has proceeded without regard to the changes in biodiversity that may result from climate change. It is now imperative that climate-change effects be included in planning efforts, given the rate at which climate is changing and the rate at which methods are being developed to model potential future distributions (Heller & Zavaleta, 2009; Kujala *et al.*, 2013). Forecasting the effects of climate change on biodiversity within an integrated framework of species distribution modelling and macroecological modelling could greatly improve our estimates of future biodiversity (Guisan & Rahbek, 2011).

CONCLUSIONS

Previous studies examining the impacts of climate change on bird distributions in the United States and Canada have tended to focus on a single season and have either used a subset of available species (Peterson, 2003; Hitch & Leberg, 2007; Stralberg *et al.*, 2009; Matthews *et al.*, 2011) or coarse occurrence data based on range maps (Jetz *et al.*, 2007; Lawler *et al.*, 2009). This is the first study to predict the potential impacts of climate change on avian species in the United States and Canada across seasons, at a relatively fine spatial scale, and for all species for which standardized survey data are available. We show that two different modelling approaches and conceptualizations of community assembly yield similar estimates of species richness under past, present and future climates. Based on our models, species richness in winter is expected to increase over much of the United States and Canada, but summer richness is expected to decline, and these patterns are largely congruent across future emissions scenarios. Projected declines in species richness in the southern portion of the United States could be misleading if species that occur in the Caribbean, Mexico, Central America and South America shift their distributions northwards. Future studies on climate change predictions for the United States and Canada would benefit greatly from including additional survey data that cover these geographical regions. The marked differences in forecasted responses of winter and summer communities to climate change have broad implications for conservation strategy in the United States and Canada and suggest that adaptation strategies will need to account for seasonal effects on individual species and groups of species.

ACKNOWLEDGEMENTS

REFERENCES

Algar, A.C., Kharouba, H.M., Young, E.R. & Kerr, J.T. (2009) Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography*, **32**, 22–33.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, **22**, 42–47.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.

Araújo, M.B., Whittaker, R.J., Ladle, R.J. & Erhard, M. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, **14**, 529–538.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.

Barbet-Massin, M., Walther, B.A., Thuiller, W., Rahbek, C. & Jiguet, F. (2009) Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. *Biology Letters*, **5**, 248–251.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Science*, **313**, 58–61.

Buckley, L.B., Waaser, S.A., MacLean, H.J. & Fox, R. (2011) Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology*, **92**, 2214–2221.

Calabrese, J.M., Certain, G., Kraan, C. & Dormann, C.F. (2014) Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, **23**, 99–112.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, **137**, 27–49.

Currie, D.J. (2001) Projected effects of climate change on patterns of vertebrate and tree species richness in the conterminous United States. *Ecosystems*, **4**, 216–225.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2743–2748.

Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, **8**, 387–397.

Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P. & Guisan, A. (2011) Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. *Diversity and Distributions*, **17**, 1122–1131.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.

Evans, K.L., James, N.A. & Gaston, K.J. (2006) Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography*, **15**, 372–385.

Ferrier, S. & Guisan, A. (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, **43**, 393–404.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Fleishman, E., Noss, R.F. & Noon, B.R. (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators*, **6**, 543–553.

Freeman, E.A. & Moisen, G.G. (2008) A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling*, **217**, 48–58.

Gotelli, N.J., Anderson, M.J., Arita, H.T. *et al.* (2009) Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters*, **12**, 873–886.

Guisan, A. & Rahbek, C. (2011) SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, **38**, 1433–1444.

Hannah, L., Midgley, G.F., Lovejoy, T., Bond, W.J., Bush, M., Lovett, J.C., Scott, D. & Woodward, F.I. (2005) Conservation of biodiversity in a changing climate. *Conservation Biology*, **16**, 264–268.

Hawkins, B.A. (2004) Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. *Global Ecology and Biogeography*, **13**, 321–325.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, R.G. (2003) Energy, water, and broad-scale geographic patterns of richness. *Ecology*, **84**, 3105–3117.

Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.

Hijmans, R.J. & van Etten, J. (2011) *raster: geographic analysis and modeling with raster data*. R package version 1.9-46. Available at: http://cran.r-project.org/package=raster.

Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2011) *dismo: species distribution modeling*. R package version 0.7-11. Available at: http://cran.r-project.org/package=dismo.

Hitch, A.T. & Leberg, P.L. (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, **21**, 534–539.

Huntley, B., Collingham, Y.C., Willis, S.G. & Green, R.E. (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE*, **3**, e1439.

Hurlbert, A.H. & Haskell, J.P. (2003) The effect of energy and seasonality on avian species richness and community composition. *The American Naturalist*, **161**, 83–97.

IPCC (2007) *Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, e157.

Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203–213.

Kujala, H., Moilanen, A., Araújo, M.B. & Cabeza, M. (2013) Conservation planning with uncertain climate change projections. *PLoS ONE*, **8**, e53315.

Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90**, 588–597.

Link, W.A., Sauer, J.R. & Niven, D.K. (2008) Combining Breeding Bird Survey and Christmas Bird Count data to evaluate seasonal components of population change in northern bobwhite. *Journal of Wildlife Management*, **72**, 44–51.

Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York, USA.

Margules, C.R. & Pressey, L.P. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Mateo, R.G., Felicísimo, Á.M., Pottier, J., Guisan, A. & Muñoz, J. (2012) Do stacked species distribution models reflect altitudinal diversity patterns? *PLoS ONE*, **7**, e32586.

Matthews, S.N., Iverson, L.R., Prasad, A.M. & Peters, M.P. (2011) Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. *Ecography*, **34**, 933–945.

McKenney, D.W., Hutchinson, M.F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., Milewska, E., Hopkinson, R.F., Price, D. & Owen, T. (2011) Customized spatial climate models for North America. *Bulletin of the American Meteorological Society*, **92**, 1611–1622.

Menéndez, R., Megias, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1465–1470.

Morin, X.T. & Thuiller, W. (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90**, 1301–1313.

Nenzén, H.K. & Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling*, **222**, 3346–3354.

Nix, H.A. (1986) A biogeographic analysis of Australian elapid snakes. *Atlas of elapid snakes of Australia* (ed. by R. Longmore), pp 4–15. Australian Government Publishing Services, Canberra, Australia.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Peterson, A.T. (2003) Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. *Global Change Biology*, **9**, 647–655.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/.

Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 165–174.

Ramirez-Villegas, J. & Jarvis, A. (2010) *Downscaling global circulation model outputs: the delta method decision and policy analysis working paper No. 1*. International Center for Tropical Agriculture, Cali, Colombia.

Root, T.L. & Schneider, S.H. (2002) Climate change: overview and implications for wildlife. *Wildlife responses to climate change: North American case studies* (ed. by S.H. Schneider and T.L. Root), pp. 1–56. Island Press, Washington, DC.

Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J., Jr & Link, W.A. (2011) *The North American Breeding Bird Survey, results and analysis 1966–2009*. Version 3.23. 2011. US Geological Survey Patuxent Wildlife Research Center, Laurel, MD.

Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., Alexander, J.D., Wiens, J.A. & Root, T.L. (2009) Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS ONE*, **4**, e6825.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

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

Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496–506.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary methods, figures and tables.
Appendix S2 Summary of model performance for winter and summer species.

BIOSKETCH

The National Audubon Society Science Division provides analytical support for bird conservation efforts within our network (Audubon Chapters, Centers, Sanctuaries, State Offices, and Regional Offices) and in conjunction with partners. We use a variety of approaches to describe the patterns of bird distribution and abundance throughout the annual cycle and the processes that shape those patterns. The results of our work are used to identify conservation targets and prioritize conservation efforts from biological and sociological perspectives.

Editor: Richard Ladle