The pace of past climate change vs. potential bird distributions and land use in the United States

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Abstract

Climate change may drastically alter patterns of species distributions and richness, but predicting future species patterns in occurrence is challenging. Significant shifts in distributions have already been observed, and understanding these recent changes can improve our understanding of potential future changes. We assessed how past climate change affected potential breeding distributions for landbird species in the conterminous United States. We quantified the bioclimatic velocity of potential breeding distributions, that is, the pace and direction of change for each species' suitable climate space over the past 60 years. We found that potential breeding distributions for landbirds have shifted substantially with an average velocity of 1.27 km yr^{-1}, about double the pace of prior distribution shift estimates across terrestrial systems globally (0.61 km yr^{-1}). The direction of shifts was not uniform. The majority of species' distributions shifted west, northwest, and north. Multidirectional shifts suggest that changes in climate conditions beyond mean temperature were influencing distributional changes. Indeed, precipitation variables that were proxies for extreme conditions were important variables across all models. There were winners and losers in terms of the area of distributions; many species experienced contractions along west and east distribution edges, and expansions along northern distribution edges. Changes were also reflected in the potential species richness, with some regions potentially gaining species (Midwest, East) and other areas potentially losing species (Southwest). However, the degree to which changes in potential breeding distributions are manifested in actual species richness depends on landcover. Areas that have become increasingly suitable for breeding birds due to changing climate are often those attractive to humans for agriculture and development. This suggests that many areas might have supported more breeding bird species had the landscape not been altered. Our study illustrates that climate change is not only a future threat, but something birds are already experiencing.

Keywords: anthropogenic land use, climate change, distribution shifts, Maxent, North American breeding landbirds, species distribution model, species richness

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Introduction

Rapid changes in climate in the past have resulted in distributional shifts of species (Huntley & Webb, 1989; Davis & Shaw, 2001; Huntley *et al.*, 2010) and as species respond individualistically to changes in climate (Ackerly *et al.*, 2010), understanding the species-specific response and exposure to shifts in climate is important (Serra-Diaz *et al.*, 2014). Indeed, climate change over the last century is already affecting many species, causing

distributional shifts and changes in phenology (Parmesan & Yohe, 2003; Parmesan, 2006; Chen *et al.*, 2011). The general trend is that species distributions are shifting poleward and upslope (Parmesan & Yohe, 2003; Root *et al.*, 2003) in response to changing climate, but shifts are far from uniform and some species have shifted downslope or nonpoleward (Crimmins *et al.*, 2011; Tingley *et al.*, 2012). One potential reason for the lack of directional uniformity in range shifts is that different climate factors have differing priority in shaping ranges. Climate influences species distribution dynamics and range limits in a number of ways, including through their interaction with species' physiology (e.g., Andrewartha

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& Birch, 1954; Chown *et al.*, 2010). Species' performance varies in response to many environmental factors including temperature, precipitation, and water availability (Crimmins *et al.*, 2011; Vanderwal *et al.*, 2013), and also pH, and humidity (Beever and Belant, 2011). Phenotypic and behavioral plasticity in response to climate variability, governed by genetic makeup of a population (Chown *et al.*, 2010), reflects sensitivity or tolerance to environmental change. In addition to direct effects on species, climate affects distributions through its modulation of interactions with other species, such as critical food plants (Schweiger *et al.*, 2008; Anderson *et al.*, 2009), prey species, predators, or competitors (Poloczanska *et al.*, 2008; Schweiger *et al.*, 2008). Thus, it is likely that recent shifts in species distributions are a result of changes in climate, mediated by both the direct physiological boundaries determined by climate factors and the indirect influences climate has on species' biological interactions (Thomas, 2010). Heterogeneity in species distributional shifts is also attributable to local variability in climate velocity (Loarie *et al.*, 2009; Burrows *et al.*, 2011; Pinsky *et al.*, 2013). Although the broadest regional and global trends are poleward shifts in distribution, there is a substantial subset of species that respond to local climates where velocity vectors do not follow regional or global trends (Pinsky *et al.*, 2013).

A final factor influencing distributional shifts of species is the location of suitable landcover, or habitat. Specificity in selection of different landcover, or habitat types, is, widespread among bird species, especially during the breeding season (i.e., different species affiliate predictably with grassland, shrubland, upland forest, or floodplain forest). Therefore, the coincidence of suitable climatic conditions with appropriate landcover strongly influences species' distributions. Both natural forces and anthropogenic activities that convert, degrade, or restore natural landcover all play an important role in shaping the patterns of species distribution in the past, present, and future (Jetz *et al.*, 2007). Interestingly, areas of high human density, and thus anthropogenic landcover types, are often associated with a high predicted carrying capacity for species indicating that humans select areas with environmental conditions that are also ideal for birds (Hansen *et al.*, 2011; Pidgeon *et al.*, 2014). With future rates of land-cover conversion predicted to increase (Ordonez *et al.*, 2014), it is important to assess how both climate and landcover affect species distribution shifts. Given this complexity, determining how recent climate change affected the area of suitable climate for each species will be important for ultimately predicting future responses to further changes in climate. In addition, because survival of species depends on their ability to track shifts of suitable climate in geographic space (Serra-Diaz *et al.*,

2014), predicting changes in species distributions is important for conservation planning.

Climate velocity, defined as the rate and direction of change in climate conditions at a given location over a period of time (Loarie *et al.*, 2009), is a metric for identifying regions where it is particularly challenging for species to track shifts in climate space. However, given that species respond to different aspects of the climate, and that local climate velocities may not reflect global trends, velocities need to be calculated for species, not just for climate variables (Vanderwal *et al.*, 2013; Serra-Diaz *et al.*, 2014). Species-specific velocity measures, or bioclimatic velocity, can help to identify how conditions for a given species in a given place have changed in the past and how they may change under future climatic conditions.

Our goal was to determine how change in climate over the last 60 years has affected areas climatically suitable for breeding landbird species in the conterminous United States and to assess species-specific bioclimatic velocities. Climate is a key driver in shaping distributions of North American bird species (Jiménez-Valverde *et al.*, 2011), suggesting that landbirds are an ideal taxa for such a study. We expected species' potential breeding distributions, as measured by species-specific suitable climate space during the breeding season within the conterminous United States, have changed over the last 60 years. We also expected the extent of such changes to be variable and sometimes unexpected, because both local variability in climate velocity and individual species or guild-climate relationships exert influence on distributional patterns. We hypothesized that potential breeding distributions of birds are related to climate factors beyond just mean temperature, as factors such as precipitation strongly influence food availability, either directly or indirectly affecting both survival and reproductive success in birds. In addition, we expected bioclimatic velocities and distribution shifts to vary among bird guilds and regional climate experienced at local scale, rather than be homogenous among species guilds or across the entire study area. Lastly, we hypothesized that areas where potential species richness has increased over the last 60 years would also be associated with the greatest landcover modification. Therefore, we asked:

1. How have the potential breeding distributions of species' suitable climate space changed in terms of bioclimatic velocity, extent, and location of distribution edges
2. What aspect of climate is most strongly related to the shifts, and why might this be so
3. Which species guilds have experienced the biggest shifts

4. Which regions had the largest change in species, reflected in potential species richness increase or decrease

5. Lastly, how does anthropogenic land use relate to climate-based projections of species potential breeding distributions, distributional change, and richness

Materials and methods

Bird data

We obtained breeding bird occurrence data (April–July) from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) for 298 landbird species recorded within the breeding season in the conterminous United States from 1950 to 2011. We removed records with no reported date, and those with spatial errors and those with fewer than 30 observations (see Table S1 for number of occurrences per species). We eliminated from consideration species whose breeding range is either exclusively or primarily north or south of the conterminous US border, and species nesting offshore. A total of 5 829 508 occurrence records across 285 breeding bird species remained that met our criteria. We assessed landbird species individually and grouped within three sets of functional guilds based on (a) migratory habit [long-distance ($n = 130$), short-distance ($n = 74$), and permanent resident ($n = 81$)]; (b) primary food category during the breeding season (carnivore ($n = 35$), herbivore ($n = 12$), invertivore ($n = 123$), and omnivore ($n = 115$)); and (c) foraging site [aerial ($n = 50$), bark ($n = 22$), floral hover ($n = 9$), ground ($n = 129$), lower canopy ($n = 49$), and upper canopy ($n = 26$)] (adapted from Albright *et al.*, 2010; De Graaf *et al.*, 1985; and Poole, 2005). See Table S1 for more details on species guilds.

Climate data

We obtained monthly total precipitation and temperature maxima and minima data for the conterminous United States for each month between 1947 and 2011 from the PRISM dataset (4-km resolution, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). We aggregated monthly climate data into eight BIOCLIM variables (using ANUCLIM, http://fennerschool.anu.edu.au/research/products/anuclim-vrsn-61), including mean annual temperature (°C), temperature seasonality (standard deviation *100), maximum temperature of the warmest period (°C), minimum temperature of the coldest period (°C), annual precipitation (mm), precipitation in the wettest quarter (mm), precipitation in the driest quarter (mm), and precipitation seasonality (coefficient of variation). We calculated climate variables for three time periods: 6, 12 and 36 months prior. For the 6-month period, we did not include precipitation in the wettest and driest quarters as these are generally calculated at 12-month or longer intervals. This gave us a total of 22 climate variables for use in our models. These time periods represent a range from short-term (6 months) to long-term climate variables (36 months).

Model estimation

We developed single breeding season species distribution models for each of the 285 bird species using Maxent (Phillips & Dudík, 2004; Phillips *et al.*, 2006) and a spatio-temporal occurrence approach (Reside *et al.*, 2010; Vanderwal *et al.*, 2013; B.L. Bateman, A.M. Pidgeon, V.C. Radeloff, C.H. Flather, J. VanDerWal, H.R. Akcakaya, W.E. Thogmartin, T.P. Albright, S.J. Vavrus, P.J. Heglund, in review) with a target-group background. The spatio-temporal occurrence approach allowed us to identify the climate conditions occurring in the period just prior to each individual bird's occurrence record. That is, for each occurrence record, we extracted the data for the 22 variables (six variables for prior 6 months and eight variables each for the prior 12 and 36 months). These occurrence data with correct temporally associated climate were used to parameterize a single model for each species during the breeding season. We used a target-group background, which uses the occurrence records of all birds as background data, to address temporal and spatial biases in the database (Phillips & Dudik, 2008; Reside *et al.*, 2010). We used Maxent for modeling species distribution because it consistently outperforms other species distribution modeling algorithms (Elith *et al.*, 2006; Hijmans & Graham, 2006; Elith & Graham, 2009).

To examine the magnitude and direction of shifts in potential breeding distributions, we mapped the output of each species' modeled suitable climate space for each month of the breeding season, from April 1950 through July 2011. We created monthly binary suitable distribution maps for each species, where areas above the equal-training sensitivity and specificity logistic threshold in Maxent (Phillips *et al.*, 2006) were considered suitable. This threshold is more conservative (higher omission rates, lower fractional predicted area) than other threshold options and we employed it to identify high-quality sites (higher probability of occurrence) within each species' distribution.

Model evaluation

We evaluated the performance of each potential breeding distribution model using area-under-the-curve (AUC) scores. To reduce bias in model performance estimates, we assessed models using tenfold cross-validation and testing AUC scores (Elith *et al.*, 2011; Bateman *et al.*, 2012). In addition, we analyzed an independent bird dataset not contained within the GBIF database, the North American Breeding Bird Survey (BBS; Sauer *et al.*, 2014), for our independent validation. We did this to compare modeling results resulting from unsystematically collected occurrence records (GBIF) with that of a standardized survey (BBS). To assess model predictive performance, calculate the AUC based on the independent BBS dataset, that is, the rate at which species occurrences recorded in the BBS were predicted correctly by our GBIF-based models as potential habitat. Sufficient BBS abundance data were available for 190 of the bird species that we had modeled. We resampled the BBS abundance data into presence and absence records calculated AUC scores for them.

Variables of importance

To examine which climate variables contributed the most to our models, we extracted permutation importance measures from Maxent outputs. We then summarized the top three variables across all species and for each guild. We also determined the most important variables defining breeding bird suitable distribution across all species, as well as categories representing (1) all three time periods (6, 12, or 36 months), (2) temperature vs. precipitation variables, and (3) BIOCLIM variables that were representative of extreme conditions (maximum temperature of the warmest period, minimum temperature of the coldest period, precipitation in the driest quarter, and precipitation in the wettest quarter; $N = 10$) with mean annual conditions (mean annual temperature, annual precipitation; $N = 6$) and seasonality of conditions (temperature and precipitation seasonality; $N = 6$) to identify which were most strongly associated with species occurrence. As these categories have unequal variable counts, we also provide weighted averages reflecting the number of variables which are in each of these categories.

Bioclimatic velocity and distribution shifts

To assess how changes in climate patterns over the past 60 years affected bird species potential breeding distributions in the conterminous United States, we calculated (a) the center of gravity (midpoint of suitable distribution, (b) distribution edges (the north, south, east, and west limits of latitude and longitude at the 10th percentile of the distribution), and (c) the area of projected suitable climate for each species (breeding season month; April through July, 244 monthly predictions spanning 1950–2011) using the R package SDMTools (Vanderwal et al., 2013). Here, we defined potential breeding distribution as the suitable climate space projected onto the landscape through time.

For each species, we calculated three linear regression models to estimate changes in distributional area during the breeding season, the center of gravity (latitude and longitude), and the distribution edges (latitude and longitude) as a function of time (Vanderwal et al., 2013). These regressions characterized change in total area of potential distributions and the rate and direction (bioclimatic velocity) of change in distributional shifts (center of gravity and distribution edges). We calculated bioclimatic velocity of distributional shift from the fitted values of latitude and longitude, with April 1950 and July 2011 as the temporal endpoints, using Vincenty's formula (Vincenty, 1975) to accommodate different cell widths at different latitudes caused by map projections (as per Loarie et al., 2009; Vanderwal et al., 2013). We also calculated velocity over this 61 year period for the individual breeding months of April, May, June, and July to determine the degree to which different start and end months influence results. We report the geometric means and standard deviations of velocity to account for skew in the ratio of temporal to spatial gradient (as per Loarie et al., 2009; Vanderwal et al., 2013). We then summarized velocities for each guild and for each ecoregion (we assigned species to ecoregions according

to where the center of gravity of their distribution fell). We characterized the 25% of species with the most strongly positive slopes in the area-with-time linear model as having experienced an expansion in potential breeding distribution ($N = 71$ species), and the 25% of species with the most strongly negative slopes as having experienced contraction in distribution ($N = 71$ species). We considered all other species as not having experienced credible change in the extent of suitable distribution. We estimated the change in area and derived the slope based on the proportion of change in area regardless of the magnitude of change (e.g., species with small ranges losing 10% of their potential breeding distribution area would have the same slope as larger-ranged species, even though a larger-ranged species would lose more total area). To assess changes in distribution edges, we assessed the proportion of species having positive or negative slopes for the linear model of distribution edges in each cardinal direction as a function of time. For each species, we derived the direction of distribution shifts from the species-specific bioclimatic velocity measure and assigned a bearing (north, northeast, east, southeast, south, southwest, west, or northwest). We then mapped bioclimatic velocity as the distance and direction of shifts in breeding distribution for each species across the contiguous United States and within ecoregions (Bailey's Ecoregions (Fig. 1), as modified by Albright et al., 2010), using the fitted values of the regression of the center of gravity with April 1950 as the start point and July 2011 as the endpoint.

Potential species richness

To map the number of species in a given geographic area for which climate space was suitable in each decade, we first averaged the binary potential distributions (i.e., geographic areas with model suitability values above our selected threshold for defining species climate suitability) for each breeding month in a given year for each species. We then used these annual maps to summarize the average location of potential breeding distribution for each species per decade, starting with the 1950s (1950–1959) and ending with the 2000s (2000–2011). Next, we calculated the number of species within each grid cell for the periods 1950–1959 and 2000–2011 to generate two potential richness maps Monthly, annual and decadal potential distribution maps for two species, the Fox Sparrow (*Passerella iliaca*) and the Northern Cardinal (*Cardinalis cardinalis*), are shown in Fig. S1. We selected these species *post hoc* for contrast. Fox Sparrow is a short distance migrant that shows interannual variability in its breeding distribution and model outputs showed high testing AUC scores with independent BBS data; Northern Cardinal is a permanent resident with a fairly consistent breeding distribution and shows low testing AUC scores with independent BBS data. These maps, summarized for all species, represent *potential* richness as they are based solely on climate variables. We compared landbird potential richness for the 1950s and 2000s to determine whether the distribution of suitable climate conditions for landbird breeding species had changed over the past
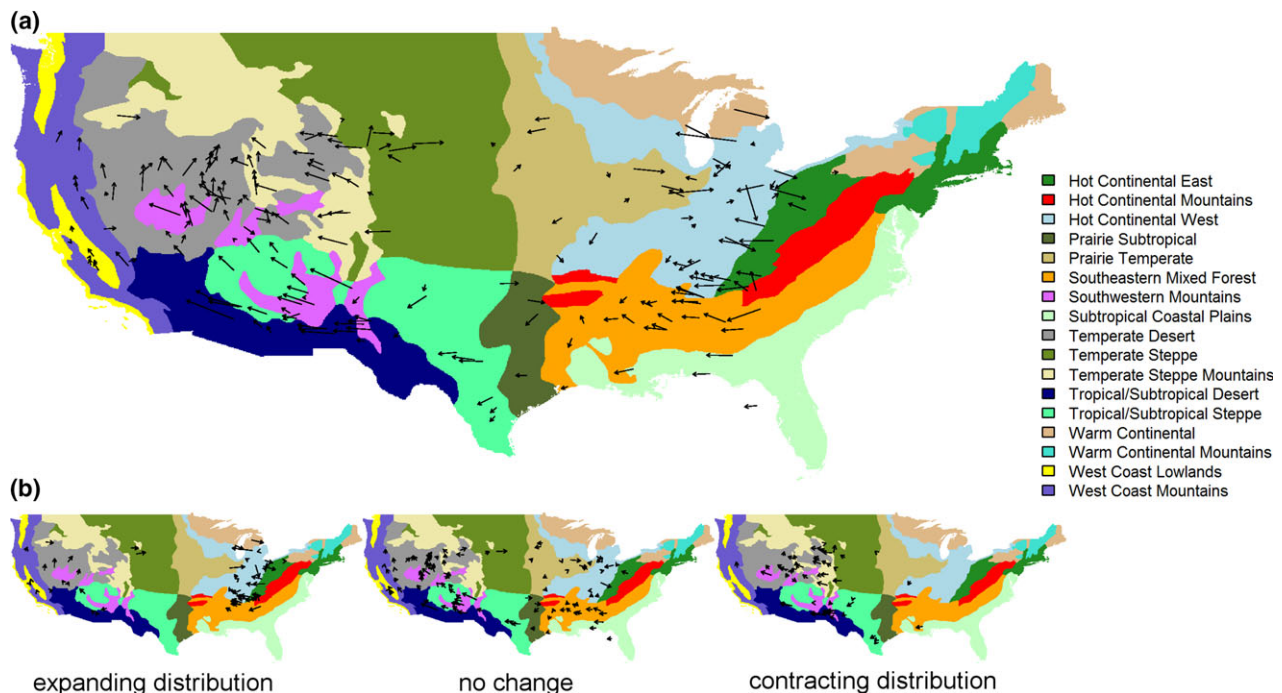
(a)

(b)

expanding distribution   no change   contracting distribution

Fig. 1 Change in potential breeding distributions for all (a) 285 US landbird species between 1950 and 2011. Arrows represent individual species change in magnitude and direction of the center of gravity of potential breeding distributions between 1950 and 2011. Changes in distribution are assessed on changes in area of suitable climate space between 1950 and 2011 (actual change in area is not represented graphically here), b) identified as landbird species with expanding, contracting or no change in potential breeding distribution. Legend is for Modified Baileys ecoregions, as per Albright *et al.* (2010), for the continental US.

60 years. To do this, we calculated the difference between the potential species richness of the 1950s and 2000s and mapped where potential species richness had increased or decreased.

To determine the extent to which potential species richness measures reflected realized species richness, we looked for consensus between the two. We estimated realized species richness measured from field observations, as characterized in North American Breeding Bird Survey data (BBS; Sauer *et al.*, 2014). We obtained BBS bird data for the entire time period for which they are available (1967–2012) and for all routes within the conterminous United States. We calculated realized species richness for the set of landbird species for which we had modeled potential breeding distributional area (285 species, see Results) on each BBS route, using the program COMDYN (Hines *et al.*, 1999) to estimate route-level species richness from raw BBS count data accounting for heterogeneity in species detection (as per Lepczyk *et al.*, 2008; Pidgeon *et al.*, 2007). We averaged the species richness estimator for the 2000s (2000–2011) to minimize the effects of annual variability in bird count data (Lepczyk *et al.*, 2008) and calculated the difference between the estimated realized richness with the potential richness. For our consensus map, we limited the spatial extent of the potential richness map to that of the BBS realized richness map, due to incomplete coverage of BBS routes across the conterminous United States. In addition, the BBS realized richness map had a coarser spatial resolution (50 km) than the potential richness (4 km). Thus, we analyzed the richness consensus map at the larger spatial scale

while reflecting the missing location coverage from the BBS data. This richness consensus map allowed us to visualize where potential species richness (based on climate models) overpredicts, underpredicts, or matches estimated species richness (as determined from field observations).

Land use

To assess the relation between land-use and potential species richness, we compared our consensus richness map with data from the 2006 National Land Cover Database (NLCD 2006) for the conterminous United States (Fry *et al.*, 2011). We selected land-cover classes representing anthropogenic land use, including developed land (developed – open space, low intensity, medium intensity, and high intensity) and agricultural land (pasture hay, cultivated crops), as indicators of a lack of natural habitat (Lepczyk *et al.*, 2008). All other land-cover classes were considered natural for the purpose of our study. We then made a comparison of the land-use map with our consensus richness map to determine the extent to which land use may have limited the full exploitation of areas with suitable climate during breeding. In addition, we stratified the average value across all grid cells of the consensus map by land-cover class to determine the average extent of over- or underpredictions of potential species richness (based on climate) vs. estimated species richness (based on BBS data).Finally, we compared our land-use map with our distributional change map to assess how land use affected gains in potential

species richness over the 60-year period. Here, we calculated the average change in potential species richness across all grid cells of the distributional change map for all land-cover classes, and the average change in potential species richness for species with expanding breeding distributions in geographic areas dominated by anthropogenic land-use classes vs. natural land-cover classes.

Results

Of our original set of the 285 breeding landbird species that we modeled, 238 had AUC scores greater than 0.75, and 255 had AUC scores greater than 0.70 (see Table S1 for AUC results). As our goal was to assess the change in potential breeding distributions of species' suitable climate space, we included all 285 species in the distributional change analysis (average scores for training AUC 0.859, 0.10 SD and cross-validation AUC 0.855, 0.10 SD; Table S1). Model testing with the independent BBS data confirmed that the models were able to accurately predict bird species presence and absence (BBS validation AUC 0.89, 0.09 SD).

The mean bioclimatic velocity rate (or pace) at which potential breeding distributions moved, across all 285 species, was 1.27 km yr^{-1} (Table 1a). Mean bioclimatic velocity for individual months were 1.58 km yr^{-1} for April, 1.21 km yr^{-1} for May, 1.35 km yr^{-1} for June, and 1.45 km yr^{-1} for July, which were slightly different than the overall bioclimatic velocity over all breeding months. Certain guilds and ecoregions experienced mean bioclimatic velocity rates greater than 1.27 km yr^{-1}. These included migratory species (Table 1b), carnivores and invertivores (Table 1c), as well as species that forage in the lower canopy, aerially, or on bark (Table 1d). Among ecoregions, birds with potential breeding distributions centered within the Hot Continental East, Warm Continental, and Hot Continental Mountain ecoregions exhibited the highest pace of shifting distribution, with a mean of 2.14, 1.92, and 1.89 km yr^{-1} respectively, while species of the West Coast Lowlands exhibited the lowest pace of change, at 0.45 km yr^{-1} (Table 1e). Species within the Warm Continental ecoregion had the greatest variability, of potential breeding distribution movement, whereas species in the Hot Continental East and Prairie Subtropical ecoregions had the lowest variability. Species in the Hot Continental East ecoregion had the lowest variability, and those in the West Coast lowlands, West Coast Mountains, and Subtropical Coastal Plain ecoregions experienced the lowest (mean) pace in species potential breeding distributions (Table 1e). The spatial distribution of suitable climate, or the direction of bioclimatic velocity, shifted considerably from 1950 to 2011 for many species (Fig. 1a; Table S1). For the majority of spe-

cies, potential breeding distribution shifted West (27.4%), Northwest (22.8%), or North (14.0%), and shifts were accompanied by distribution expansions and contractions. For species for which the areal extent of suitable climate space did not change, shifts in distribution centers were toward the West (22.3%), Northwest (21.7%), or North (18.9%) (Fig. 1b; Table S1).

The majority of species for which the area of potential breeding distributions contracted since 1950 were centered in the Western United States (Fig. 1b) and there was a general shift westward of suitable climate space of all bird species in the United States (Fig. 1; 38.0% moving West and 23.9% Northwest; Table S1). Distribution contractions generally occurred in an east–west direction; 83.1% of species exhibiting contractions lost suitable area along their eastern distribution edge; and 64.8% of species lost suitable climate space along their western distribution edge (Table S1).

Species with expanding potential breeding distributions occurred primarily in the East and Midwest (Hot Continental West, Southeastern Mixed Forest, and Hot Continental East), but also included some species in the West (West Coast Mountains and Temperate Desert, Fig. 1b). In the case of species with an expanding potential breeding distribution, distribution centers shifted West (26.7%) or Northwest (23.9%) (Table S1). Expansions in potential breeding distributions occurred mainly along the northern edge (78.9% of species with expanding distributions; Table S1).

The three most important climate variables in our models, as determined by the percent contribution during model training, were mean temperature in the preceding 36 months (18.2% average permutation importance) and precipitation during the driest quarter in the preceding 36-months (14.4% average permutation importance) permutation importance. Temperature seasonality in the preceding 36 months was the third most important variable (8.5% average permutation importance). Overall, we found that climate variables incorporating the preceding 36 months had the greatest permutation importance (63.0% average permutation importance, 66.8% weighted average, $N = 8$), whereas variables for the preceding 12 months (17.4% average permutation importance, 18.5 weighted average, $N = 8$) and 6 months (19.6% average permutation importance, 15.6 weighted average, $N = 6$) were less important. However, short-term climate variability variables (6 and 12 preceding month variables combined) were still more important than longer term means (36 preceding month variables); the weighted average contribution to species models was 34% and 66%, respectively.

The top three variables varied among guilds with different migratory habits, food selection, and foraging microsite (Table 2). Mean temperature in the preceding

Table 1 Geometric mean bioclimatic velocity (km yr^{-1}, 1 SD) of potential breeding distributions between 1950 and 2011 for (a) all species and birds grouped by their, (b) migratory habit, (c) feeding guild, (d) location of foraging, and (e) the ecoregion in which their center of distribution occurs (Modified Baileys Ecoregions, as per Albright *et al.*, 2010). Presented are the geometric mean (geo.mean) rate, geometric standard deviation (geo.minus.sd, geo.plus.sd), number of bird species (*N*)

Category	geo.mean	geo.minus.sd	geo.plus.sd	*N*
(a) All Species				
Breeding Season	1.27	0.64	2.52	285
April	1.58	0.79	3.14	285
May	1.21	0.57	2.58	285
June	1.35	0.66	2.77	285
July	1.45	0.47	4.46	285
(b) Migratory Habit				
Long Distance	1.34	0.67	2.69	130
Short Distance	1.31	0.69	2.46	74
Permanent Resident	1.15	0.57	2.31	81
(c) Feeding Guild				
Carnivore	1.46	0.76	2.81	35
Invertivore	1.44	0.74	2.79	123
Omnivore	1.11	0.55	2.24	115
Herbivore	0.81	0.35	1.85	12
(d) Location of Foraging				
Lower Canopy	1.96	1.12	3.43	49
Aerial	1.95	0.92	4.09	50
Upper Canopy	1.92	0.87	4.23	26
Ground	1.37	0.70	2.67	129
Floral Hover	1.33	0.63	2.82	9
Bark	1.12	0.61	2.06	22
(e) Modified Baileys Ecoregion				
Hot Continental East	2.14	1.73	2.63	7
Warm Continental	1.92	0.67	5.51	5
Hot Continental Mountains	1.89	1.40	2.56	3
Prairie Temperate	1.54	0.68	3.49	28
Tropical/Subtropical Desert	1.53	0.87	2.71	12
Tropical/Subtropical Steppe	1.46	0.96	2.21	25
Temperate Steppe Mountains	1.43	0.78	2.63	17
Southwestern Mountains	1.23	0.60	2.54	23
Outliers	1.23	0.95	1.58	2
Southeastern Mixed Forest	1.22	0.76	1.97	19
Hot Continental West	1.22	0.55	2.70	43
Temperate Steppe	1.20	0.51	2.83	32
Temperate Desert	1.18	0.77	1.80	44
Prairie Subtropical	1.09	0.84	1.43	5
Subtropical Coastal Plain	1.03	0.47	2.25	4
West Coast Mountains	0.85	0.40	1.78	11
West Coast Lowlands	0.45	0.20	0.97	5

36 months, followed by precipitation of the driest quarter in the preceding 36 months, was the variables contributing most to models of species of all migratory habits (Table 2a) as well as for all feeding guilds (Table 2b), and for all foraging locations except for floral hoverers (Table 2c). For floral hoverers, precipitation of the driest quarter in the preceding 36 months had a stronger influence on potential breeding distributions. For long-distance migrants and bark foragers,

although mean temperature in the preceding 36 months had the highest permutation importance, precipitation of the driest preceding 36 months was a close second with near equal values (Table 2c). Temperature seasonality (6-, and 36-month time lags) and minimum temperature of the coldest month were also important variables for several guilds (Table 2).

Mean temperature in the preceding 36 months and precipitation of the driest quarter in the preceding

Table 2 Top three variables (determined by the percent contribution during model training in Maxent) for (a) migratory habitat guild, (b) feeding guild, (c) location of foraging guild, and (d) change in distribution area. Values in parenthesis represent mean and standard deviation of model permutation importance of that variable per guild. Precip, precipitation; Temp, temperature; Min, minimum; Qtr, quarter; Mo, month, 6 m, 12 m, 36 m= Time Lag in months (m)

	Long Distance	Permanent Resident	Short Distance			
(a) Migratory Habit Guild						
1	Mean Temp 36 m (12.89, 15.49)	Mean Temp 36 m (25.19, 23.92)	Mean Temp 36 m (19.89,18.34)			
2	Precip Driest Qtr 36 m (12.73, 13.28)	Precip Driest Qtr 36 m (19.97, 20.24)	Precip Driest Qtr 36 m (10.48, 11.15)			
3	Temp Seasonality 6 m (9.55, 7.59)	Min Temp Coldest Mo 36 m (8.82, 9.96)	Temp Seasonality 36 m (9.53, 10.67)			
	Carnivore	**Herbivore**	**Invertivore**	**Omnivore**		
(b) Feeding Guild						
1	Mean Temp 36 m (18.64, 17.66)	Mean Temp 36 m (30.13, 26.90)	Mean Temp 36 m (16.15, 15.88)	Mean Temp 36 m (19.03, 20.81)		
2	Precip Driest Qtr 36 m (10.21, 11.36)	Precip Driest Qtr 36 m (18.94, 16.98)	Precip Driest Qtr 36 m (13.55, 16.09)	Precip Driest Qtr 36 m (15.62, 17.90)		
3	Min Temp Coldest Mo 36 m (9.19, 8.65)	Min Temp Coldest Mo 36 m (8.71, 11.75)	Temp Seasonality 36 m (8.52, 8.99)	Temp Seasonality 36 m (9.47, 10.02)		
	Aerial	**Bark**	**Floral Hover**	**Ground**	**Lower Canopy**	**Upper Canopy**
(c) Foraging Microsite Guild						
1	Mean Temp 36 m (17.40, 16.74)	Mean Temp 36 m (19.83, 18.48)	Precip Driest Qtr 36 m (28.79, 24.98)	Mean Temp 36 m (17.93, 18.61)	Mean Temp 36 m (17.90, 18.18)	Mean Temp 36 m (21.19, 25.39)
2	Precip Driest Qtr 36 m (11.99, 13.31)	Precip Driest Qtr 36 m (19.06, 24.04)	Mean Temp 36 m (15.62, 20.68)	Precip Driest Qtr 36 m (14.13, 15.20)	Precip Driest Qtr 36 m (14.79, 16.80)	Temp Seasonality 6 m (10.71, 8.86)
3	Temp Seasonality 6 m (8.96, 8.45)	Temp Seasonality 36 m (8.79, 9.00)	Min Temp Coldest Mo 36 m (12.11, 9.40)	Min Temp Coldest Mo 36 m (9.04, 9.80)	Mean Temp 6 m (8.32, 9.59)	Mean Temp 6 m (9.19, 7.43)
	Expanding	**Contracting**	**No Change**			
(d) Change in Distribution Area						
1	Mean Temp 36 m (14.79, 12.63)	Mean Temp 36 m (22.10, 23.95)	Mean Temp 36 m (17.96, 18.23)			
2	Precip Driest Qtr 36 m (14.25, 18.66)	Precip Driest Qtr 36 m (14.26, 14.58)	Precip Driest Qtr 36 m (14.15, 16.21)			
3	Min Temp Coldest Mo 36 m (9.39, 8.47)	Annual Precip 36 m (10.20, 13.90)	Temp Seasonality 36 m (9.03, 8.10)			

36 months were the most important variables across all species (Table 2d). However, minimum temperature of the coldest period was more important for species with expanding distributions, whereas annual precipitation was more important for species with contracting distributions (Table 2d). Across all species, temperature variables were more important than precipitation variables (temperature variables contributed on average 67.8%, 71.6% weighted average (N = 12) to species models vs. 32.2%, 28.4% weighted average (N = 10) across precipitation variables). BIOCLIM variables that were representative of extreme conditions were more important (40.2% average permutation importance, 52.8% weighted average) than those that were representative of mean annual conditions (37.0% average per-

mutation importance 29.2% weighted average) or seasonality of conditions (22.8% average permutation importance 18.0 weighted average).

Maps of landbird potential species richness (285 species) for the 2000s showed high potential species richness in the Midwest and Northeast, as well as in parts of the Southwest and California (Fig. S2a). Potential species richness changed considerably between the 1950s and the 2000s (Fig. 2a). Potential species richness declined in particular in the West, northern Texas, western Oklahoma, western Kansas, eastern New Mexico, parts of eastern Washington, western Montana and northern Idaho, and along the California–Arizona border. Declines in richness were also seen in Missouri and southern Illinois, and in Mississippi. However,

there were also large gains in potential species richness, especially in the Midwest (Minnesota, Iowa, North and South Dakota) and the Central Appalachians (West Virginia, Virginia). Gains in richness were also seen in southern Louisiana, Florida, and western California and Oregon.

Estimated species richness (from BBS data) showed generally similar patterns as potential richness), although estimated richness was much lower than potential richness (Fig. S2b). However, our climate-based models overpredicted richness at a high magnitude in the Midwest, parts of the Northeast, and the Southwest with the only underpredicted richness occurring in the Northwest (Fig. 3a). As expected, our potential richness maps contained much greater over- (up to 110 species) than underprediction (up to 19 species) and indicated more widespread suitable climate space for many species than was realized.

Areas where we overpredicted species richness matched closely with areas of anthropogenic land use, particularly in the Midwest and Northeast (Fig. 2b, 3b). Across all land-cover classes, the potential richness maps overpredicted an average of 57.2, 20.9 SD species However, in areas with natural landcover, overprediction was less (54.7, 21.0 SD species) than in areas with anthropogenic land use (62.6, 19.0 SD overall, 58.6, 21.2 SD for developed, and 63.8, 18.1 SD species for agriculture). That is, areas where greater predicted potential species richness was not realized overlapped spatially with anthropogenic land use, particularly agriculture. Underpredictions were rare (0.40% of the consensus map) and occurred mainly in shrub/scrub or evergreen forests.

Similarly, areas showing gains in potential species richness between the 1950s and 2000s were mostly in regions with anthropogenic land use (Fig. 3b). Species
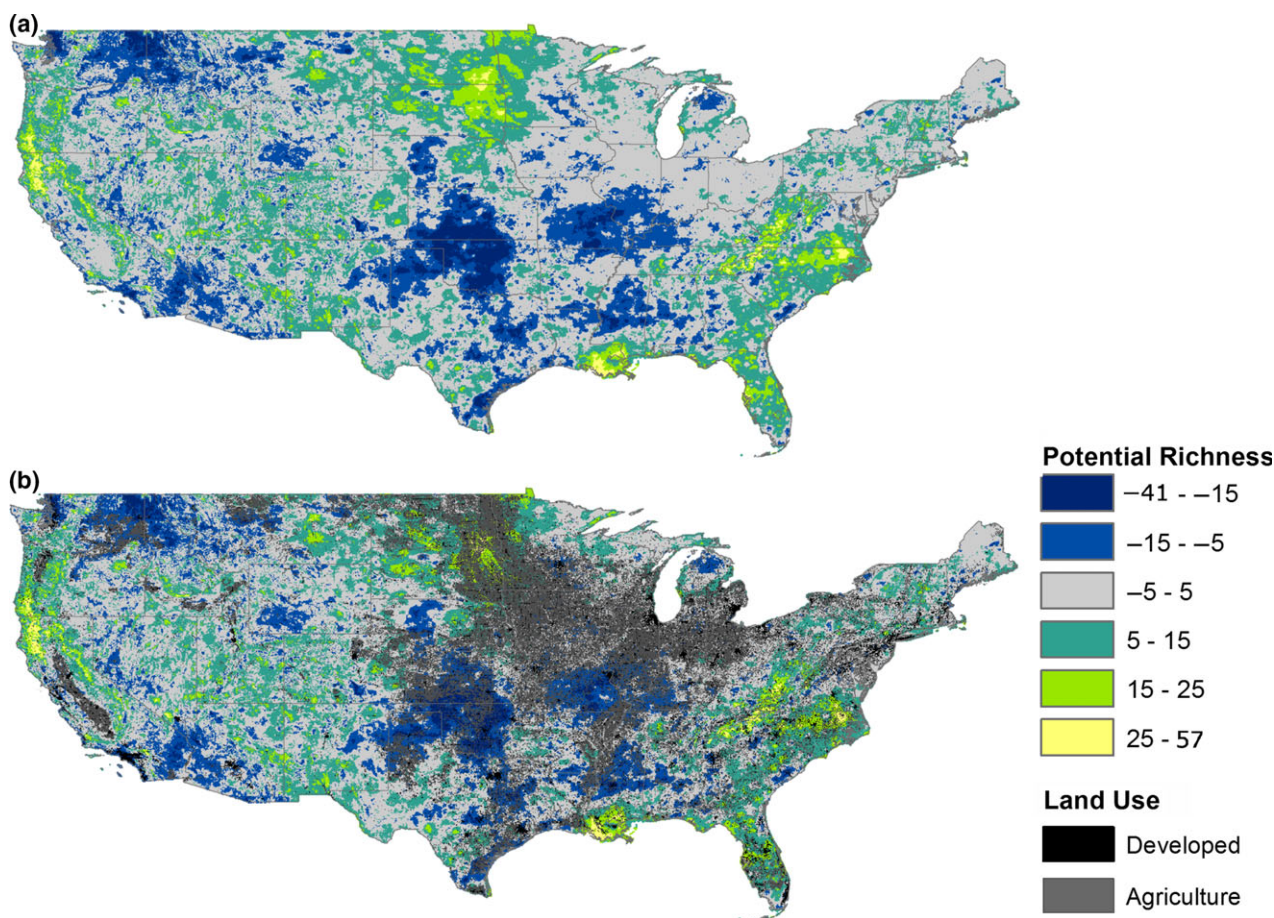

Fig. 2 Distributional change map between the 1950s and the 2000s for 285 US landbird species showing (a) change in potential species richness and (b) the distributional change map overlaid with anthropogenic land-use (developed lands and agriculture) land-cover classes.
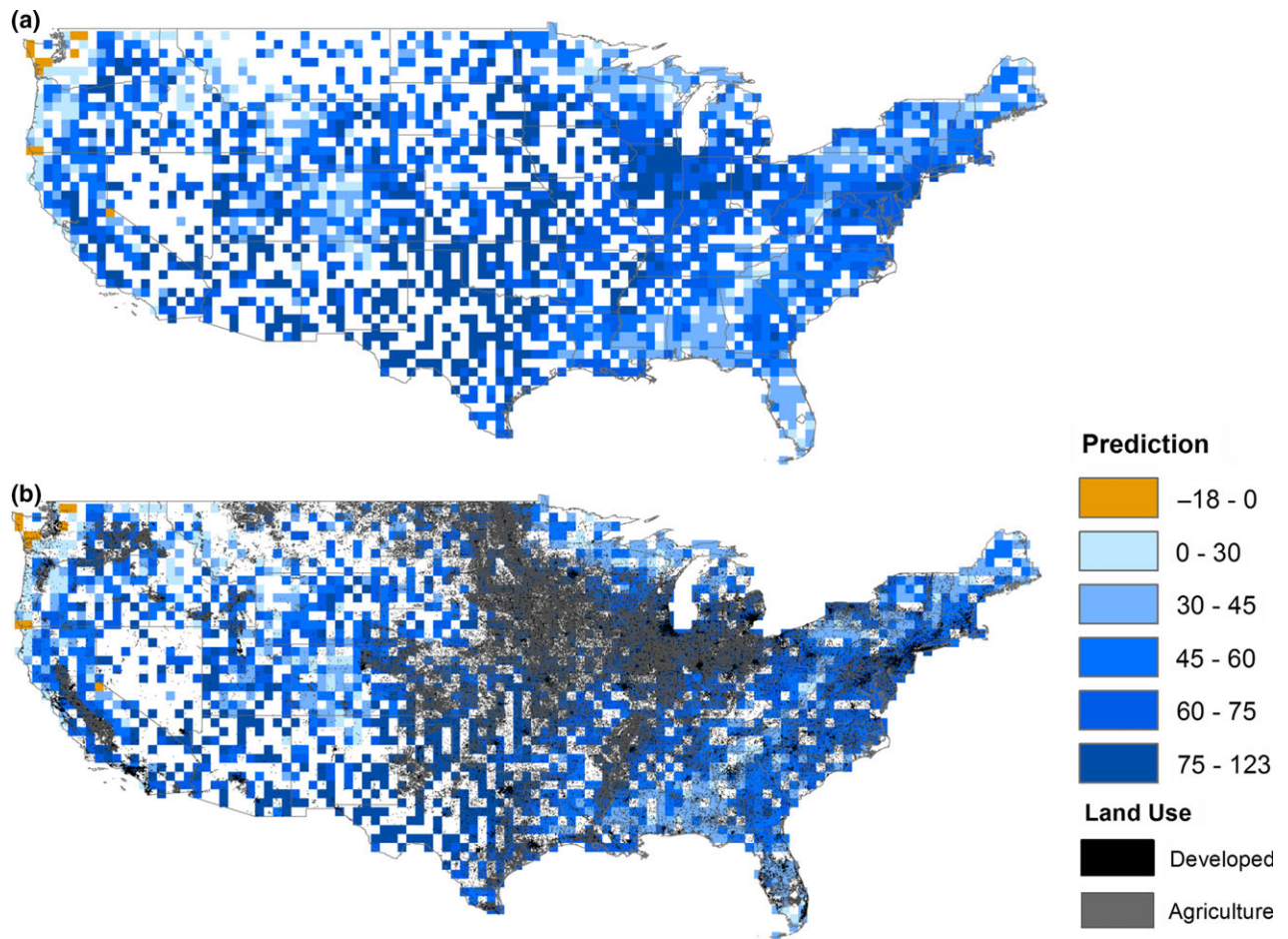
Fig. 3 Richness consensus map visualizing (a) where potential species richness overpredicts, underpredicts, or has similar values to estimated species richness for the 2000s, and (b) the consensus map overlaid with anthropogenic land-use land-cover classes. Areas in white are where BBS route coverage is missing and the consensus map could not be calculated.

that saw expansions in their potential breeding distributions were expanding into areas where anthropogenic land use was likely to occur, meaning that the natural habitats of these areas were altered. The average net change in potential species richness across the conterminous United States for all species was 1.83, 8.51 SD species, with an average increase of 6.85, 5.92 for areas that gained or showed no change in species richness and an average loss of −6.24, 5.18 in areas that lost species richness When looking at species with expanding potential breeding distributions, the average net change in potential species richness across the conterminous United States within all land-cover classes was 2.75, 3.83 SD species. However, the potential species richness increase for species with expanding potential breeding distributions in areas of natural landcover was 2.18, 3.53 SD species, whereas areas with anthropogenic land use gained 4.05, 4.17 SD species (3.35, 3.52 SD species for developed and 4.22, 4.28 SD species for agriculture).

Discussion

How rapidly have the potential breeding distributions of species' suitable climate space changed in terms of bioclimatic velocity, extent, and location of distribution edges?

For breeding bird species in the contiguous United States, change in potential breeding distributions had an average bioclimatic velocity of 1.27 km yr^{-1} to the west, northwest, or north over the past 60 years. For some species, velocity has been even higher, up to 2.14 km yr^{-1} for species centered in the Hot Continental East Ecoregion, or 1.96 km yr^{-1} for the lower-canopy forager guild as a whole, with some individual's potential breeding distributions shifting at rates up to 5.51 km yr^{-1}. In almost all instances, the bioclimatic velocity in bird potential breeding distributions was higher than previous estimates of actual range shifts for terrestrial species of 0.61 km yr^{-1}

(Parmesan & Yohe, 2003). Our results are on par with findings in Australia, where the average bioclimatic velocity for over 450 bird species over the past 60 years was 1.27 km yr^{-1} (Vanderwal *et al.*, 2013). However, bioclimatic velocity for other taxa is lower globally; for 350 marine taxa in North America, the average bioclimatic velocity was around 0.8 km yr^{-1} over the last 40 years (Pinsky *et al.*, 2013), and for eight endemic tree species in California, bioclimatic velocity was estimated at 0.21 km yr^{-1} under future climate change scenarios (Serra-Diaz *et al.*, 2014). This highlights that climate influenced bioclimatic shifts are important at the global scale, but bird species may be either particularly sensitive to climate or may be particularly flexible, as a group, in their ability to respond to shifting climate.

The bioclimatic velocities of potential breeding distributions for the majority of species were also substantially higher than the velocities of the underlying climate variables themselves (e.g., 0.51 km yr^{-1} for temperature and ~0.2 km yr^{-1} for water balance variables (actual evapotranspiration and deficit) from 1976 to 2005 in the United States; (Dobrowski *et al.*, 2013). The reason why bioclimatic velocity of potential breeding distributions of birds exceeded that of temperature or precipitation alone is that bioclimatic velocities for breeding birds are a product of the velocities of multiple climate variables acting in combination (e .g. eight, as identified by Vanderwal *et al.*, 2013). Keeping pace with climatic isoclines requires relatively rapid distributional shifts (Loarie *et al.*, 2009; Ackerly *et al.*, 2010). With future estimated rates of change in the global velocity of temperature (0.42 km yr^{-1}) and precipitation (0.22 km yr^{-1}) predicted to remain relatively constant for the period of 2000–2100 (Loarie *et al.*, 2009), it will become increasingly important to understand sensitivities species have to climate combinations, conditions, and velocities beyond assessing temperature or precipitation alone (Tingley *et al.*, 2012; Vanderwal *et al.*, 2013).

What aspect of climate is most strongly related to the shifts, and why might this be so?

Northward shifts of birds have been documented in response to climate change within the United States in both breeding distributions (Hitch & Leberg, 2007) and winter distributions (La Sorte & Thompson, 2007). Here, we also found that the potential distribution edges of the majority of bird species expanded northward along species northern range edge, and many species' distribution centers shifted north and northwest-ward (36.8% of species) as well. However, many species do not exhibit poleward range shifts (Parmesan & Yohe, 2003; Crimmins *et al.*, 2011; Tingley *et al.*,

2012), and our results also showed considerable complexity in the movement of potential breeding distributions. The complexity in both the pace and direction of bioclimatic velocity observed in our study has also been noted among other regions and taxa (Pinsky *et al.*, 2013; Vanderwal *et al.*, 2013; Serra-Diaz *et al.*, 2014; Gillings *et al.*, 2015). A large proportion of the potential breeding distributions of species that we analyzed shifted westward (27.4% of species), and contraction of distributional area was largely on western and eastern distribution edges, not in the south. The distribution of most marine species, across various taxa, shifted north, however, a substantial proportion of species had shifts to the south, opposite to the expected poleward pattern (Pinsky *et al.*, 2013). One reason for these 'nonintuitive' shifts (Pinsky *et al.*, 2013) could be that species differ in terms of the climate aspects that most strongly limit their distributions, and different climate variables are exhibiting shifts in different directions.

Average temperature values alone may not be a good indicator of bioclimatic velocity, and species may be shifting in relation to the more complex local velocity (Pinsky *et al.*, 2013). This is supported by our results highlighting that, across all species, although long-term climate data and temperature were more influential, short-term climate data, precipitation conditions, as well as extreme conditions strongly influenced many species. In the United States between 1976 and 2005, temperature suitability generally shifted northward, but water balance (a measure of water and energy availability based on actual evapotranspiration and climatic water deficit) suitability shifted predominantly south or westward, and varied regionally (Dobrowski *et al.*, 2013). The Midwestern United States, which had the greatest increase in potential species richness in our study, has experienced increasingly wetter summer breeding seasons over the last 40 years (Kunkel *et al.*, 2013a). The Southwestern United States, where the most distribution contractions occurred, has seen highly variable precipitation, with drier conditions occurring over the last decade particularly in spring (Kunkel *et al.*, 2013b). The westward shifts of bird species potential breeding distributions and increased potential richness in the Midwest, in conjunction with contractions and loss of potential richness in the Southwest, suggest that precipitation plays a large role in shaping bird species distributions, which is supported by our finding that precipitation of the driest quarter was a key variable across all models. We note that it is not clear though whether bird distributions shifts are keeping pace with climate shifts, and that bird distributions may be becoming increasingly out of synchrony with their climate (Devictor *et al.*, 2012). To the extent that this is the case, it could have affected our

analysis, because our approach assumed that the relationship between bird distributions and climate variable did not change throughout our analysis period (Guisan & Zimmermann, 2000). However, both GBIF and BBS data have far more observations in recent decades, compared to earlier ones, and that precluded the analysis of shifts in the relationships of bird and climate variables over time.

In addition to mean annual temperature, precipitation of the driest quarter, annual precipitation and minimum temperature of the coldest month were among top variable in the models of breeding bird species with both contracting and expanding distributions, indicating the importance of extremes and precipitation in structuring potential species richness. Indeed, our results highlight that proxies for extreme conditions were in general more important than mean annual or seasonality of variables. Species with contracting distributions were influenced strongly by precipitation in addition to mean temperatures. In the southwestern United States, where many bird distributions contracted, both mean temperatures and frequency of heat waves have increased over the last 100 years, and particularly in the last two decades (Kunkel *et al.*, 2013b). The combination of dry and variable precipitation and increased temperatures and heat waves experience in the Southwest appears to negatively altered climate conditions for bird species in this region. These findings are in line with those of Albright *et al.* (2010), who found that hotter and drier conditions in the Southwest were associated with abundance declines in bird species. Additionally, birds in the southwestern United States are likely to remain vulnerable to future climate change (Jetz *et al.*, 2007), as predictions indicate a trend toward increased summer temperature and decreased precipitation, exacerbating and increasing drought in the region (Christensen *et al.*, 2007; Gutzler & Robbins, 2011).

For species with expanding distributions, minimum temperature of the coldest month was important, suggesting that temperature early in the breeding season mattered. The Midwest, into which many species distributions expanded, has seen warmer winters and springs but relatively cool summers in recent years suggesting less seasonality in temperature in this region (Kunkel *et al.*, 2013a). This underscores our finding that factors beyond increasing mean annual temperature affected recent shifts in potential breeding distributions. In addition, our results reaffirm the need to incorporate precipitation and other climate variables into future projected distributions, rather than solely focusing on poleward shifts and rising global temperatures (Pinsky *et al.*, 2013; Vanderwal *et al.*, 2013).

Which species guilds have experienced the biggest shifts?

Species within aerial, lower-, and upper-canopy foraging guilds experienced higher than average bioclimatic velocity rates, as did those within carnivore and invertivore feeding guilds. It is hard to anticipate the consequences of rapid change in potential breeding distribution of these guilds. As a highly mobile group, birds are likely to be able to keep up with the pace of change. However, stressors related to interspecies competition and availability of suitable habitat may have negative influences. Since the late 1960s, aerial insectivores (part of our invertivore guild) have declined in particular in the Northeast, which may be partly a result of climatic factors (Nebel *et al.*, 2010). As insect population dynamics are regulated by weather and climate (Kingsolver, 1989; Boggs & Inouye, 2012), shifting climate conditions over the last 60 years may have limited insect food availability during the critical breeding months (Whitehouse *et al.*, 2013; Wiebe & Gow, 2013; Winkler *et al.*, 2013). It is important to note, however, that given the variability among species and the number of species on which guild estimates are based, our estimates are only a snapshot of the overall picture of how recent climate change has affected breeding birds with similar functional characteristics.

Which regions had the largest change in species, reflected in potential species richness increase or decrease?

The magnitude of the changes in potential breeding distributions since 1950 was both large enough and consistent enough to cause notable changes in potential species richness in many locations. In the Midwest and Eastern United States, large gains in potential richness were noted. This was reflected in the large number of species shifting and expanding distributions in this region. Ecoregions in which the potential breeding distributions of high numbers of species expanded were also areas with the greatest rates of change in bioclimatic velocity (Hot Continental East, Warm Continental, and Hot Continental Mountains) or areas with high variability in bioclimatic velocity (Warm Continental). This suggests that within these ecoregions, climate has shifted more rapidly than in other ecoregions. Perhaps counterintuitively, despite the large number of species with westward shifting distributions, the most pronounced loss of species richness was in the Western United States, and we attribute this to the large number of species experiencing a contraction in distribution there. The elevational heterogeneity of the Western mountain ranges is at least partly responsible for these contractions, because the associated heterogeneity in

climate isoclines along elevational gradients creates a hard climate boundary limiting the area into which suitable climate space can expand (Körner, 2000, 2007). In this sense, species with continuing westward distributional shifts may run out of climate space (Ohlemüller, 2011) as distributional edges abut mountains. The suitable climate of species with centers of distributions in the Great Plains will become increasingly compressed, potentially causing a biological attrition effect similar to that predicted for tropical lowlands (Colwell *et al.*, 2008).

We stress, however, that we modeled changes in potential richness derived from species distribution models, which may or may not reflect actual changes in species richness. Our consensus richness maps revealed that our potential richness maps overpredicted species richness substantially (up to +123 species), especially in the Midwest, Northeast, and Southwest regions of the United States. Overpredictions are to be expected, as distribution models were built solely using climate variables and estimate something closer to the potential distribution rather than the actual distribution (Jimenez-Valverde *et al.*, 2008). Many factors in addition to climate contribute to a species' actual distribution, such as biotic interactions (Araújo & Luoto, 2007; Bateman *et al.*, 2012), meta-population dynamics (Brook *et al.*, 2009; Franklin, 2010), dispersal limitations (Bateman *et al.*, 2013), and disturbance regimes (Franklin, 2010) such as land use, to name a few. Therefore, climate-based distribution models reflect the fact that a species' suitable climate space is generally larger than the portion of that space actually occupied. Underpredictions were less intuitive, but were rare and infrequent (lowest value −19 species). Several factors could contribute to underprediction, including insufficient sampling of the entire range of suitable climate conditions (Pearson, 2010), sites that are higher in productivity than would be suggested by climate conditions (e.g., modified habitats such as irrigated agriculture), as well as local biotic interactions, or model algorithm choice (Sinclair *et al.*, 2010). As climate-only projections of species distributions are commonplace (see Pearson & Dawson, 2003; Franklin, 2010; Sinclair *et al.*, 2010), overpredictions in species distributions and richness are likely.

Lastly, how does anthropogenic land use relate to climate-based projections of species potential breeding distributions, distributional change, and richness?

We found that anthropogenic land use, particularly agriculture, was widespread in areas where high species richness was predicted, where species potential breeding distributions were expanding into, as well as where overpredictions occurred. This result suggests that many areas in the Midwest and Northeast might have supported more breeding bird species had the landscape not been altered. Landbird species richness and abundance in the United States is generally negatively associated with anthropogenic land use (Pidgeon *et al.*, 2007; Lepczyk *et al.*, 2008; Rittenhouse *et al.*, 2012). This negative association is especially apparent in habitat specialist species (Devictor *et al.*, 2008; Wood *et al.*, 2014). In addition to limiting species richness, land use may have negated potential expansions in distribution for some species. This may be the case for species with poor dispersal abilities (e.g., Galliformes) that are not able to keep pace with shifting climate, especially through altered habitats (Lu *et al.*, 2012). Indeed, areas with anthropogenic land use had the highest gains in potential species richness, suggesting that areas that have become increasingly suitable for birds due to changes in climate, are often those that are highly suitable for agriculture and development (Hansen *et al.*, 2011). Because habitats in these areas have been highly altered from their natural state it is not likely that birds with shifts to these areas will find much suitable habitat, and thus, the potential distribution shifts are unlikely to be realized. Our results may be a harbinger of a specific conservation issue under future climate change. Within the Eastern United States where potential breeding distributions of many of the species we studied expanded over the last 60 years, bird species are predicted to be vulnerable to land-use change (Jetz *et al.*, 2007) and land use is likely to intensify (Radeloff *et al.*, 2012; Lawler *et al.*, 2014), curtailing possible benefits to species of expanded distributions from changes in suitable climate space.

The results of our study suggest that species are already under pressure from recent climate change and factors such as land use and hard climate boundaries can exacerbate their problems. Furthermore, increasing temperature is certainly not the only issue and may not even be the most important factor influencing potential breeding distributions. Precipitation, climate variability, and extreme weather events also play an important role in shaping species distributions. Additionally, suitable climate space shifts in many different ways, not only poleward. Important insights can be gleaned from the association of past changes with altered species distributions. Future land-use scenarios provide an indication which species are potential winners or losers as climate changes, and indications how species may respond to future change, thus improving estimates of future projections in species distributions. These insights are necessary for mitigating the threat to biodiversity that climate change presents.

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Supporting Information

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

Figure S1. Maps representing each month within the year of 2011 and the 2011 annual average for (a) Fox Sparrow and (b) Northern Cardinal and annual averages for the years 1981, 1991, 2001, and 2011 and decade based summary map for 2000–2011 for (c) Fox Sparrow and (d) Northern Cardinal.

Figure S2. Species richness maps for 285 breeding US land-bird species for the period of 2000 to 2011 representing (a) estimated Species Richness (COMDYN richness) from BBS routes 2000–2012 and b) potential species richness from model outputs. Potential species richness is defined as the number of species that have suitable climate within a given grid cell.

Table S1. Detailed data for each species for which models converged, listing each species' AOU numeric code, scientific name, common name, the number of occurrences used in model training, migratory habit, feeding guild, and location of foraging.