

# Multidirectional abundance shifts among North American birds and the relative influence of multifaceted climate factors

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## Abstract

Shifts in species distributions are major fingerprint of climate change. Examining changes in species abundance structures at a continental scale enables robust evaluation of climate change influences, but few studies have conducted these evaluations due to limited data and methodological constraints. In this study, we estimate temporal changes in abundance from North American Breeding Bird Survey data at the scale of physiographic strata to examine the relative influence of different components of climatic factors and evaluate the hypothesis that shifting species distributions are multidirectional in resident bird species in North America. We quantify the direction and velocity of the abundance shifts of 57 permanent resident birds over 44 years using a centroid analysis. For species with significant abundance shifts in the centroid analysis, we conduct a more intensive correlative analysis to identify climate components most strongly associated with composite change of abundance within strata. Our analysis focus on two contrasts: the relative importance of climate extremes vs. averages, and of temperature vs. precipitation in strength of association with abundance change. Our study shows that 36 species had significant abundance shifts over the study period. The average velocity of the centroid is  $5.89 \text{ km}\cdot\text{yr}^{-1}$ . The shifted distance on average covers 259 km, 9% of range extent. Our results strongly suggest that the climate change fingerprint in studied avian distributions is multidirectional. Among 6 directions with significant abundance shifts, the northwestward shift was observed in the largest number of species ( $n = 13$ ). The temperature/average climate model consistently has greater predictive ability than the precipitation/extreme climate model in explaining strata-level abundance change. Our study shows heterogeneous avian responses to recent environmental changes. It highlights needs for more species-specific approaches to examine contributing factors to recent distributional changes and for comprehensive conservation planning for climate change adaptation.

## KEYWORDS

abundance shift, bird, breeding bird survey, climate change fingerprint, climate change metrics, climate change velocity, density shift, multidirectional distribution shift

## 1 | INTRODUCTION

### 1.1 | Continental scale abundance shifts

Shift in species distributions is considered one of the major fingerprints of species response to climate change, and observations of distribution changes are of great interest to ecologists and conservation practitioners (Parmesan & Yohe, 2003). Global climate change poses a serious threat to biodiversity because of the rapid rate of change and the inability of species to relocate or adapt (Loarie et al., 2009; Parmesan & Yohe, 2003; Walther et al., 2002). Recent meta-analyses have concluded that a wide range of animal and plant species are exhibiting shifts in their distributions (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Cristine & Kerr, 2015; Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2002). Most prior studies, however, have focused on shifts of species' range edges based primarily on presence-absence information. Range edges represent areas where frequent local colonization and/or extinction occur, and changes in range edges likely do not provide a comprehensive summary of large scale distribution dynamics (Currie & Venne, 2016; Huang, Sauer, Swatantran, & Dubayah, 2016; Taheri, Naimi, & Araújo, 2016). Additionally, shifts in species abundance structure (also referred to as density shifts [Virkkala & Lehikoinen, 2014]) can occur without significant change of range edges (Illán et al., 2014; Massimino, Johnston, & Pearce-Higgins, 2015; Rapacciuolo et al., 2014; Virkkala & Lehikoinen, 2014). Specifically, widespread species with spatial ranges limited by geographical features (e.g., coast lines) are normally excluded in range shift analyses as they have no space to shift their range edge. But abundance shift analysis is applicable to such cases, and thus the change in abundance structure as a metric of change greatly expands the pool of species for which species distribution shifts can be considered and analyzed. Furthermore, analyses of change in abundance within ranges has great statistical power for detecting large scale changes of species distribution due to the rich population dynamic imbedded in abundance counts and great spatial coverage of population data included (Illán et al., 2014; Stephens et al., 2016; Stralberg et al., 2015). However, such studies at the continental scale are lacking.

### 1.2 | Directionality of distribution shifts

So far, studies have mostly focused on the latitudinally poleward and elevationally upward shifts of species distributions to trace changes in suitable temperature (Hickling, Roy, Hill, Fox, & Thomas, 2006; Hitch & Leberg, 2007; Parmesan et al., 1999; Thomas & Lennon, 1999). This is expected, in part, because latitude and elevation gradients are broadly correlated with changes in surface temperature. Biological responses to temperature are relatively well understood and predictable for most species (Root et al., 2003). However, species' distribution shifts can be multidirectional due to a variety of environmental factors that limit or promote redistribution of population (Barbet-Massin & Jetz, 2014; Gillings, Balmer, & Fuller, 2015; VanDerWal et al., 2013). Specifically, precipitation and the

combination of temperature and precipitation are among the key factors hypothesized to cause multidimensional distribution shifts (Tingley, Monahan, Beissinger, & Moritz, 2009; VanDerWal et al., 2013). Evidence to support the multidirectionality hypothesis, however, has been mostly based on model projections or regional studies (Gillings et al., 2015; Tingley et al., 2009; VanDerWal et al., 2013). A systematic analysis that examines the directionality of the recent climate change fingerprint at the continental scale is needed.

### 1.3 | Relative influence of climatic components on distribution shifts

Evaluating the environmental drivers of distribution shifts is a critical aspect of improving predictive distribution studies and developing reasonable plans for climate change mitigation (Barbet-Massin & Jetz, 2014; Goetz, Sun, Zolkos, Hansen, & Dubayah, 2014). With a long list of climatic metrics that measure multiple aspects of climate change condition and are derived from different databases, it is often challenging in macroecological studies to identify specific climatic variables that are relevant to large number of species involved. Climate variables are often grouped to describe unique aspects of climatic condition (e.g., temperature, precipitation), or to represent methodologically different ways of collecting and quantifying climate data (e.g., metrics derived from monthly climate records vs. metrics based on daily records, or station-based extrapolated data vs. remotely sensed data) (Baker, Hartley, Butchart, & Willis, 2016; Deblauwe et al., 2016; Tingley et al., 2009; VanDerWal et al., 2013). Therefore, a central question remains regarding the relative influence of different subsets of climate variables on distribution shifts.

In this study, we first seek to compare the effect of average climatic conditions (summarized from monthly climate records) with the effect of extreme climate conditions (from daily climate data) on stratum-specific abundance change rates across ranges of avian species. Previously, average climate metrics have dominated climate change studies. One of the most frequent sources of climatic data among ecologists is Bioclim variables (Nix, 1986). The Bioclim metrics are a series of climate indices derived from monthly temperature and precipitation records, and they summarize annual and seasonal average, extreme, and variation of temperature and precipitation aggregated at relatively coarse temporal scales. These metrics have been widely used in species distribution models and as measures of climate change conditions (Brown & Yoder, 2015; Franklin et al., 2013; Kumar & Stohlgren, 2009; Rödder, Schmidtlein, Veith, & Lötters, 2009; Songer, Delion, Biggs, & Huang, 2012; Synes & Osborne, 2011; Webber et al., 2011). Recently, however, there are an increasing number of studies that have shown that the frequency and intensity of extreme climate events could have great impacts on species range and abundance structure (Cavanaugh et al., 2014; Crozier, 2003; Easterling et al., 2000; Karl, Nicholls, & Ghazi, 1999; Parmesan, Root, & Willig, 2000). Datasets such as the Expert Team on Climate Change Detection and Indices (ETCCDI) based on daily measurements of temperature and precipitation (Sillmann & Roeckner, 2007), can capture the intensity and frequency of climate extremes. The

ETCCDI dataset provides an alternative source of climate change metrics for species distribution studies. Climate extreme events described from daily weather data thus constitute contrasting metrics to associate with distributional changes.

Furthermore, the majority of the climate change and distribution shift literature focuses on the effect of temperature, which has long been considered the most important climatic metrics limiting species distributions (Jeffree & Jeffree, 1994; Root, 1988; Thomas & Lennon, 1999; Williamson, 1975). Influence of changing precipitation was either omitted, or often considered to have an effect similar to that of temperature change (VanDerWal et al., 2013). However, focusing only on the effect of temperature change can lead to an underestimation of the climate change fingerprint resulting from precipitation related climate events (Illán et al., 2014; Tingley et al., 2009; VanDerWal et al., 2013). Thus, we also seek to compare the strength of relationships of avian abundance change to a suite of temperature variables and to a suite of precipitation variables.

The overall goals of this study are, first, to understand the directionality and velocity of shifts in avian abundance distribution in North America for permanent resident species over the past four decades. Second, for species changing in distribution, we compare the relative strength of association of climate and bird abundance change based on two contrasting pairs of climate variables: average-extreme and temperature-precipitation. To achieve the first goal, we use distribution centroids to test the multidirectionality of the abundance shifts among 57 North American permanent resident birds as shown by North American Breeding Bird Survey (BBS) data (Sauer et al., 2013). We quantify the cardinal and intercardinal directional shifts and velocity of the shifts for species with significant abundance shift. For the second goal, we model the change in abundance across physiographic strata to examine the relative influence of the two pairs of contrasting climate metric sets.

Specifically, we utilize 44 years of BBS data and characterize the direction and velocity of the abundance shifts using centroids of yearly species distributions (Huang et al., 2016). To compare the influence of two pairs of climate change components, we use four alternative climate models: the average climate, extreme climate, temperature, and precipitation models. The models are established to explain the changes of population abundance across physiographic strata.

## 2 | MATERIALS AND METHODS

### 2.1 | Bird data

We used the BBS data to estimate avian abundance shifts. The BBS is an annual road side survey with more than 5000 routes covering most of North America. Since the beginning of the survey in 1966, competent volunteers survey routes on a yearly basis during breeding season. Three minute point counts are conducted at 50 sample points along a 39.43 km long route. Birds heard or seen within 0.4 km radius of the counting locations are recorded during the point counts (Robbins, Bystrak, & Geissler, 1986; Sauer et al., 2014).

We included 44 years (1969–2012) of BBS data in the contiguous United States and southern Canada for our analysis, because the spatial and temporal coverage of the data are more consistent for these regions and periods. We focused our study on permanent resident bird species, so that a wide range of climate metrics generated from different times of the year could be directly related to the bird survey records. A bird species was selected for our analysis if it is listed as permanent resident species in the State of North America's Birds report (North American Bird Conservation Initiative, 2014) and its range intersects with at least 10 BBS strata (the details of BBS strata definition is described in the Abundance Centroid section below). The minimum strata number was set so that the species would have sufficient abundance variability over its range for the centroid analysis. The screening process resulted in the inclusion of 57 permanent resident species for our analysis (Tables S1 and S2).

### 2.2 | Direction and velocity of distribution shifts

We used a hierarchical Bayesian model to provide stratum-specific annual estimate of species abundance. These stratum-level abundance indices were then used to construct annual distribution centroids which were further used to document the direction and velocity of distribution changes.

#### 2.2.1 | Abundance centroid

We adapted the method outlined in Huang et al. (2016) to calculate annual centroid coordinates. Centroids were derived statistics based on stratum-specific annual abundance indices. We first divided each bird species range into a list of physiographic strata (referred to as BBS strata in this study). BBS strata were defined as the intersection of U.S. states, Canadian provinces, and Bird Conservation Regions (BCRs) boundaries. The BCRs were developed by the North American Bird Conservation Initiative to represent regions with relative homogeneity of bird communities, habitats, and resource management issues. The BCR/state-province strata design has been widely used as basic spatial structure for regional population summaries (Sauer et al., 2013). Across North America the density of survey routes varies greatly, with lower route densities in the western United States and in northern Canada. Because avian assemblages and abundance patterns tend to be different among physiographic regions, the strata scheme helped to partition the sample routes into relatively homogeneous regions/units with consistent geographic characteristics and route concentrations. (Link & Sauer, 2002; Sauer, Fallon, & Johnson, 2003; Sauer & Link, 2011). For our analysis, we included 158 strata, 131 of which are in the United States (Ranging between 3,000 to 247,000 km<sup>2</sup>) with an average size of about 59,000 km<sup>2</sup>, and 27 of which are in Canada (ranging between 15,000 to 503,000 km<sup>2</sup>) with an average size of 198,000 km<sup>2</sup> (Figure 2). We only used strata with more than 4 survey routes on which the species was encountered to ensure adequate samples in each stratum, excluding a few small strata in the analysis (Figure 2) (Huang et al., 2016). A hierarchical Bayesian model was used to calculate

the stratum-specific annual abundance index  $N_{it}$  (Huang et al., 2016; Link & Sauer, 2002; Sauer & Link, 2002) (see Text S1 for more details of Bayesian model structure and parameterization). The model accounts for year ( $t$ ), stratum ( $i$ ), and observer effect, and specifies prior distributions for parameters and hyperparameters (Huang et al., 2016; Link & Sauer, 2002; Sauer & Link, 2002). To calculate the location of an annual centroid, the coordinates ( $X_t$  and  $Y_t$ ) of centroids were calculated as a yearly mean of strata centroids locations ( $x_i$  and  $y_i$ ) weighted by  $N_{it}$  (Equation 1). Note that stratum-specific annual abundance indices ( $N_{it}$ ) were also used to calculate abundance change rates at the strata level when evaluating the influence of different climatic factors (described in Abundance Change Modeling section below).

$$X_t = \frac{\sum_i N_{i,t} * x_i}{\sum_i N_{i,t}}, \quad Y_t = \frac{\sum_i N_{i,t} * y_i}{\sum_i N_{i,t}}. \quad (1)$$

Inferences for both directly estimated and derived parameters (e.g., centroid coordinates and population abundance indices) in the analysis are based on posterior distributions, computed using the Markov Chain Monte Carlo (MCMC) method (Link & Sauer, 2002). In this study, we computed three independent Markov chains of length 40,000, and discarded the first 20,000 as burn-in samples. After the first 20,000 iterations, posterior samples were computed every 20 iterations (thinning rate of 20) so that estimates of posterior distribution were based on 3,000 (3 chains  $\times$  20,000 iterations/20 thinning rate) samples. Based on prior testing and procedures in Huang et al. (2016), these samples are sufficient for quantifying changes in avian distributions. The same number of posterior samples was thus available for each  $N_{it}$  and yearly centroid coordinates. The variability of posterior samples represents the uncertainty of  $N_{it}$  estimation and also of the derived parameters based on  $N_{it}$  (e.g., total abundance index over all strata, abundance change rate). The samples from the posterior distributions were used to compute statistical attributes such as median value and confidence interval (CI) of parameters. Note that the sum of population abundance indices over all strata was also calculated as an index of annual total population. For each posterior iteration, the annual total population index over time was fitted with a linear model. A species population status was classified as increasing, decreasing, or stable, when the distribution of linear slope estimated from composite (summed) indices over all strata for a species is significantly larger than zero, smaller than zero, or not significantly different from zero, as judged using 95% CIs.

## 2.2.2 | Direction and velocity of shifts

For each species, we regressed annual centroids' latitudinal and longitudinal coordinates separately against year, fitting the data with linear regression models during the MCMC analysis, computing the posterior distribution of the slope parameter. The species was identified as having a significant shift of abundance structure in one of the four cardinal directions (north, east, south, and west) if the regression slopes was significantly larger or lower than 0. A 95% CI

was computed to determine the level of significance. A significantly positive slope in latitudinal direction thus indicates a significant northward abundance shift. A significant shift toward an intercardinal direction (northeast, northwest, southeast, and southwest) was identified when a species had significant abundance shifts in both latitudinal and longitudinal directions.

The velocity of the abundance shift at the latitudinal direction or the longitudinal direction was estimated as the change of distance per year (slope). It is a measure of speed ( $\text{km}\cdot\text{yr}^{-1}$ ) that centroid shifted over the study period. The combined velocity was calculated with Equation (2). Note that when the species exhibited no significant abundance shift in either latitudinal or longitudinal direction, the velocity of shift at that direction was considered zero.

$$\sqrt{\text{velocity}_{\text{lat.}}^2 + \text{velocity}_{\text{lon.}}^2}, \quad (2)$$

where  $\text{velocity}_{\text{lat.}}$  and  $\text{velocity}_{\text{lon.}}$  were the velocity in the latitudinal and longitudinal direction respectively. Because widespread species with more distant physiographic strata tend to have larger potential variability in centroid locations (Huang et al., 2016), to account for the differences in range sizes, we calculated a standardized velocity index to account for the size of ranges. The index is a ratio of shifted distance ( $\text{velocity} \times 44$  year) to the east-west or north-south extent of the range when there is a significant shift to a cardinal direction. When there is a significant intercardinal direction shift, the index is calculated as the ratio of shifted distance to the hypotenuse of east-west and north-south extent. For instance, a velocity ratio of 0.1 to the east direction indicates that the abundance centroid has shifted 10% of the east-west extent of the range.

## 2.3 | Abundance change modeling

For species with significant distribution shifts, we evaluate the relative influence of different suites of climate change conditions by constructing alternative climatic models to predict the abundance change rate across strata. Four explanatory models (average climate, extreme climate, temperature, and predication model) were constructed using metrics from two climatic datasets. The predictive ability of each climate model was evaluated using the correlation between modeled and observed abundance change rates. The relative influence of average vs. extreme climate factors and temperature vs. precipitation climate factors were compared using the results from the correlation analysis. Because consistent climate data were only available for the contiguous United States, we only modeled the change of avian abundance for strata in the contiguous United States to be consistent with coverage of these climatic data.

The stratum-specific abundance change rates  $r_i$ , was defined as the natural logarithm of the ratio of the average abundance indices in 2003–2012 to the average abundance indices in 1969–1978 (Equation 3). The 10 year mean was used to average out the short term variability of population and climatic fluctuations.

$$r_i = \ln \left( \frac{N_{i2003-2012}}{N_{i1969-1978}} \right) \quad (3)$$

A positive  $r$  indicates an increasing population, whereas a negative  $r$ , a declining population. Posterior distributions of population change rates were calculated for each stratum based on 3000 MCMC samples. We used four suites of climate metrics (the average climate, extreme climate, temperature, and precipitation metrics) to predict the abundance change rate across strata which is described in detail below.

### 2.3.1 | Average and extreme climate data

Average climate conditions were characterized by using 19 Bioclim indices derived from monthly temperature and precipitation records (Nix, 1986). We used the station-based monthly data from the United States Historical Climatology Network (USHCN) version 2.5 serial (Menne, Williams, & Vose, 2009; Williams, Menne, Vose, & Easterling, 2006). We used the “DISMO” package (Hijmans, Phillips, Elith, & Leatherwick, 2015) in the R software environment (R Development Core Team, 2011) to calculate 19 Bioclim variables using monthly data at the station level (Table S1). Out of 19 Bioclim variables, 11 were temperature indices and seven were precipitation indices (Table S1). Stations were selected if they had consistent climate records over the periods of 1969–1978 and 2003–2012. We analyzed 1218 stations (Fig. S1) over the continental United States for our analysis.

We used the indices defined by the Expert Team on Climate Change Detection and Indices (ETCCDI) to capture change of climate extremes (Sillmann & Roeckner, 2007). The ETCCDI indices were derived from daily temperature and precipitation data that support more detailed measurement of extreme climate events such as the annual frequency of days with temperatures below 0°C and the maximum number of dry spell days. We used 15 of the ETCCDI extreme climate indices that quantify annual or seasonal extreme conditions (Table S1) (Sillmann, Kharin, Zhang, Zwiers, & Bronaugh, 2013). Among the 15 ETCCDI indices, seven of the indices measure temperature related events, and 8 measure precipitation related events (Table S1). As with Bioclim variables, station data in the United States were selected if they had full coverage of the specific ETCCDI index values over the periods of 1969–1978 and 2003–2012. We included data from 1130 ETCCDI stations across United States for our analysis (Fig. S1).

### 2.3.2 | Temperature and precipitation data

Because 11 of the Bioclim variables and seven of the ETCCDI indices describe various temperature conditions (Table S1), the temperature metric set was defined to encompass these 18 metrics. Likewise, the precipitation metric set included the rest of the metrics from both datasets (seven from the average climate and eight from the extreme climate dataset).

### 2.3.3 | Predictive model and climate influence evaluation

To evaluate the explanatory ability of the different climate components in predicting composite abundance change rate at strata level, we first summarized climate change variables within strata using four sets of aforementioned station-based climate metrics. We then used these four sets of variables separately to predict species abundance change rates across strata. The model performances were measured by the strength of association between predicted and observed abundance change rate.

For each weather station, the mean and standard deviation of every climatic metrics were calculated for each of the two periods (1969–1978 and 2003–2012), and the change over two periods were summarized, producing two variables for each climate metric. We quantified the change of standard deviation of the index values because species distributions were documented to not only respond to change of climate trend (e.g., mean temperature) but also to change of temporal variability of climate variables (e.g., extent of deviation of temperature) (Chan et al., 2016; Vasseur et al., 2014).

For each stratum and each variable generated, we summarized the maximum, minimum, median value among all available weather stations, producing six variables ( $2 \times 3$ ) for each climate metric. This process generated 108 ( $18 \times 2 \times 3$ ) average climate variables, 90 ( $15 \times 2 \times 3$ ) extreme climatic variables, 108 ( $18 \times 2 \times 3$ ) temperature variables, and 90 ( $15 \times 2 \times 3$ ) precipitation variables. We then created four predictive climatic models that used these four groups of predictive variables correspondingly.

We used the random forests (RF) algorithm (Breiman, 2001) to predict the population change rate over the study period. The RF model is known to perform well with small number of observations and large number of predictive variables without overfitting (Breiman, 2001). Random forest model draws a large number of bootstrap samples from the original data, each sample is used to construct an unpruned regression tree. At each node, a sample of size  $p/3$  predictors are randomly selected to determine the best split, where  $p$  is the total number of predictors available. The results are computed by aggregating predictions of all trees (Liaw & Wiener, 2002). For each tree, about 37% of data are randomly drawn as the out-of-bag (OOB) observations and excluded in the model construction. The OOB error estimation provides a cross-validation mechanism, thus conventionally test sets or additional cross-validation is not necessary. Overall, the RF model is well suited for our study because the model is robust even with significant covariance between predictive variables (Biau, 2012; Breiman, 2001), as commonly exists between climatic and habitat metrics (Huang, Swatantran, Dubayah, & Goetz, 2014).

We used the `RANDOMFOREST` R package (Liaw & Wiener, 2002) to build RF models. For each species and each type of climate model, we built 3,000 iterative RF models with the posterior samples from the MCMC process. We set the number of trees to be 4,000 for all RF models to allow convergence of mean residual error so the model performance remained stable regardless of the random seed used.

We evaluated the explanatory ability of the different climate models using Spearman's rank correlation coefficient (Spearman's  $\rho$ ) between predicted and observed abundance change rate. Spearman's rank correlation coefficient was chosen because it is straightforward way to evaluate the strength of positive association between different group of climatic variables and observed abundance change rate. It provides consistency of analyses between species even when the heterogeneous spatial distribution of some species' abundance count across region results in deviation from normality (Illán et al., 2014). For each species every climate model would produce 3000 Spearman's  $\rho$  for evaluation.

We compared the relative influence of different groups of climatic factors by conducting the 2 pair-wise comparisons of models' explanatory ability (Spearman's  $\rho$ ) based on a range of CIs computed from the posterior distributions of the 3,000 replicates. The average climate model was compared with extreme climate model, and temperature model with precipitation model. We used 6 CIs based on percentiles ranging from 90% to 70% with 5% interval to account for the high variability of the abundance growth rate.

### 3 | RESULTS

We first report the summary of the species with significant abundance shifts, and show the direction and velocity of these shifts. Secondly, for species with significant abundance shifts, we compare the predictive power of two pairs of climatic models (the temperature model with the precipitation model, and the extreme climate model with the average climate model) in explaining the variability of abundance change rate across strata.

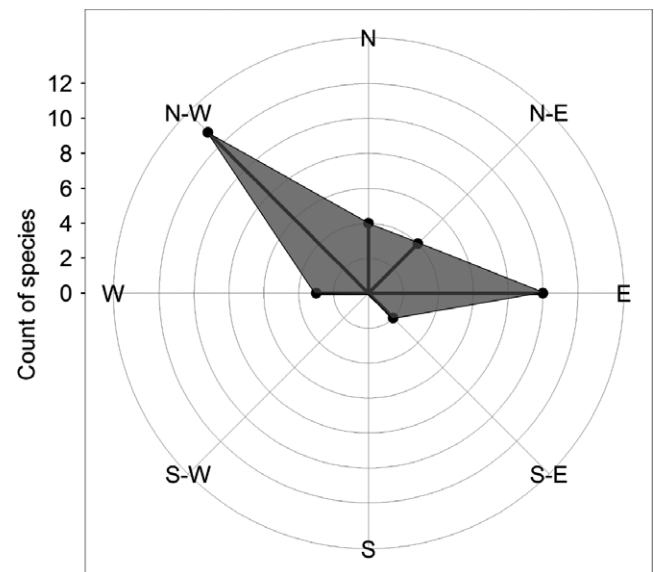
#### 3.1 | Multidirectionality

Among the 57 permanent resident species analyzed, 63% (36) showed significant centroid shifts in at least one direction (Figure 1, Table 1). The northwestward abundance shift was exhibited among the largest number of species (13, 22.8%), followed by eastward (10, 17.5%), northward (4, 7%), northeastward (4, 7%), westward (3, 5.3%), and southeastward shift (2, 3.5%). Note that no species shifted its abundance distribution significantly in the southward and southwestward direction (Figure 1, Table 1).

Species with a significant increase in total population accounted for the greatest number (44%; 16 species) of the significant abundance shifts, followed by species with a significant decline of total population (31%; 11 species), and the ones with stable population (25%; nine species) (Table 2).

#### 3.2 | Velocity of abundance shifts

The velocity of centroid shift over the study period ranged from 0.52 km·yr<sup>-1</sup> (Carolina Chickadee) to 21.25 km·yr<sup>-1</sup> (Great Horned Owl) (Table 1). On average the velocity of the species with significant abundance shifts was 5.89 km·yr<sup>-1</sup> (Table 1). As we



**FIGURE 1** The number of species that experienced significant shifts in different directions. A total of 36 studied species exhibited significant centroid movement in at least one direction. Note that no species has shown significant abundance shift southward or southwestward

mentioned, the potential range of raw centroid velocity is dependent on range size, and therefore all the velocity comparisons were based on velocity ratio which accounted for range extent in different directions. The species with significant southeastward movements showed the fastest mean velocity ratio (0.13), followed by the species that shifted westward (0.10), eastward (0.10), and northwestward (0.08) (Figures 2 and 3). The northeastward and northward abundance shifts were the slowest (mean velocity ratios are both 0.08 [Figure 3]). Inca Dove, Common Ground Dove, and Black-capped Chickadee (velocity ratios: 0.23, 0.20, and 0.17 correspondingly) had the fastest abundance shifts (Figure 2, Table 1). Across all directions the average velocity ratio was 0.09.

#### 3.3 | Influence of different climatic factors on shifting abundances

Among the 36 species with significant abundance shifts, the abundance change rate of 18 species can be explained by at least one climatic model with significant positive correlation coefficients (Table S3). The average climate model had significantly positive rank correlation coefficients between observed and predicted abundance change rate for 16 species (mean  $\rho = 0.39$ ), whereas the extreme climate model had significantly positive rank correlation coefficient for 10 species (mean  $\rho = 0.39$ ). In comparison, 17 species showed significantly positive rank correlation coefficients between observed and predicted abundance change rates with the temperature model (mean  $\rho = 0.40$ ). Thirteen (13) species had significantly positive rank correlation coefficients with the precipitation model (mean  $\rho = 0.37$ ) (Table S3).

**TABLE 1** Attributes of species with significant abundance shifts

ID	Common name	Scientific name	Velocity ratio	Shifted distance (km)	Velocity (km yr <sup>-1</sup> )	Shift direction	Population status
1	Northern Bobwhite	<i>Colinus virginianus</i>	0.1166	382	8.68	Northwest	Decrease
2	Scaled Quail	<i>Callipepla squamata</i>	0.0385	49	1.11	West	Decrease
3	California Quail	<i>Callipepla californica</i>	0.0769	66	1.50	East	Increase
4	Sharp-tailed Grouse	<i>Tympanuchus phasianellus</i>	0.1448	243	5.52	East	Stable
5	Wild Turkey	<i>Meleagris gallopavo</i>	0.1557	743	16.89	Northeast	Increase
6	Common Ground-Dove	<i>Columbina passerina</i>	0.1968	598	13.59	West	Stable
7	Inca Dove	<i>Columbina inca</i>	0.2376	463	10.52	East	Increase
8	Black Vulture	<i>Coragyps atratus</i>	0.0972	339	7.70	Northwest	Increase
9	Great Horned Owl	<i>Bubo virginianus</i>	0.1276	935	21.25	Southeast	Decrease
10	Greater Roadrunner	<i>Geococcyx californianus</i>	0.1007	229	5.20	East	Stable
11	Hairy Woodpecker	<i>Picoides villosus</i>	0.0408	198	4.50	East	Increase
12	Downy Woodpecker	<i>Picoides pubescens</i>	0.0228	113	2.57	East	Increase
13	Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.0513	286	6.5	Northeast	Increase
14	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	0.0447	137	3.11	Northwest	Increase
15	Steller's Jay	<i>Cyanocitta stelleri</i>	0.0357	97	2.20	Northwest	Stable
16	Western Scrub-Jay	<i>Aphelocoma californica</i>	0.0604	168	3.82	Northwest	Stable
17	Common Raven	<i>Corvus corax</i>	0.0645	308	7	West	Increase
18	Fish Crow	<i>Corvus ossifragus</i>	0.0753	199	4.52	Northwest	Increase
19	Great-tailed Grackle	<i>Quiscalus mexicanus</i>	0.1057	294	6.68	Northwest	Increase
20	Lesser Goldfinch	<i>Spinus psaltria</i>	0.0870	269	6.11	Northwest	Stable
21	Rufous-crowned Sparrow	<i>Aimophila ruficeps</i>	0.1243	286	6.50	Northwest	Decrease
22	Northern Cardinal	<i>Cardinalis cardinalis</i>	0.0141	65	1.48	Northwest	Increase
23	Pyrrhuloxia	<i>Cardinalis sinuatus</i>	0.1416	230	5.23	Northwest	Decrease
24	Northern Mockingbird	<i>Mimus polyglottos</i>	0.0206	51	1.16	North	Decrease
25	Curve-billed Thrasher	<i>Toxostoma curvirostre</i>	0.1540	199	4.52	North	Decrease
26	Carolina Wren	<i>Thryothorus ludovicianus</i>	0.0318	94	2.14	Northwest	Increase
27	White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.0803	369	8.39	East	Increase
28	Brown-headed Nuthatch	<i>Sitta pusilla</i>	0.0603	122	2.78	Northeast	Stable
29	Pygmy Nuthatch	<i>Sitta pygmaea</i>	0.1167	237	5.39	North	Stable
30	Tufted Titmouse	<i>Baeolophus bicolor</i>	0.0313	99	2.25	Northeast	Increase
31	Black-capped Chickadee	<i>Poecile atricapillus</i>	0.1736	813	18.48	East	Increase
32	Carolina Chickadee	<i>Poecile carolinensis</i>	0.0147	23	0.52	North	Decrease
33	Mountain Chickadee	<i>Poecile gambeli</i>	0.0602	177	4.02	Northwest	Decrease
34	Chestnut-backed Chickadee	<i>Poecile rufescens</i>	0.0264	27	0.61	East	Decrease
35	Bushtit	<i>Psaltriparus minimus</i>	0.0800	145	3.30	East	Stable
36	Verdin	<i>Auriparus flaviceps</i>	0.1358	258	5.83	Southeast	Decrease

Species' abundance change rate for the majority of species with significantly positive association could be explained by multiple climate models (Table S3). Eight species showed significantly positive rank correlation coefficient by all four models, followed by three and three species whose abundance change rate can be explained by three and two climate models respectively. The abundance change rate of four species can be explained significantly by one climate model (Table S3). The results also showed that half (18) of species abundance change could not be explained by any climate model.

Pair comparisons of extreme-average and temperature-precipitation models showed variable model performances among different climatic models and within 3000 posterior iterations for each model. For average-extreme comparison, with the CIs ranging from 90% to 70%, the average climate model had significantly higher rank correlation coefficients than the extreme climate model in explaining the abundance change rate of three to seven species. For the temperature-precipitation comparison, the temperature model had significantly higher rank correlation coefficient than the precipitation

**TABLE 2** The directions of the abundance shifts and the population status for the 36 species that exhibited significant shifts

Direction	Declined population	Increased population	Stable population
East	1	6	3
North	3	0	1
Northeast	0	3	1
Northwest	4	6	3
Southeast	2	0	0
West	1	1	1
Sum	11 (31%)	16 (44%)	9 (25%)

model in explaining the abundance change of five to six species (Figure 4, Table S4). The precipitation model consistently outperformed the temperature model in explaining the abundance change of Inca Dove at any given CI width (Figure 4, Table S4). Note that extreme climate model did not have significantly stronger predictive ability than the average climate model to explain any species population change rate at any CI. As one would expect, varying CIs showed similar patterns with varying levels of significance: 60% of the species whose abundance change rate could be explained with significant margin by one model over the other did not change with different CIs, thus we plotted the results with 90% CI (Figure 4) and listed the rest of the result in Table S4.

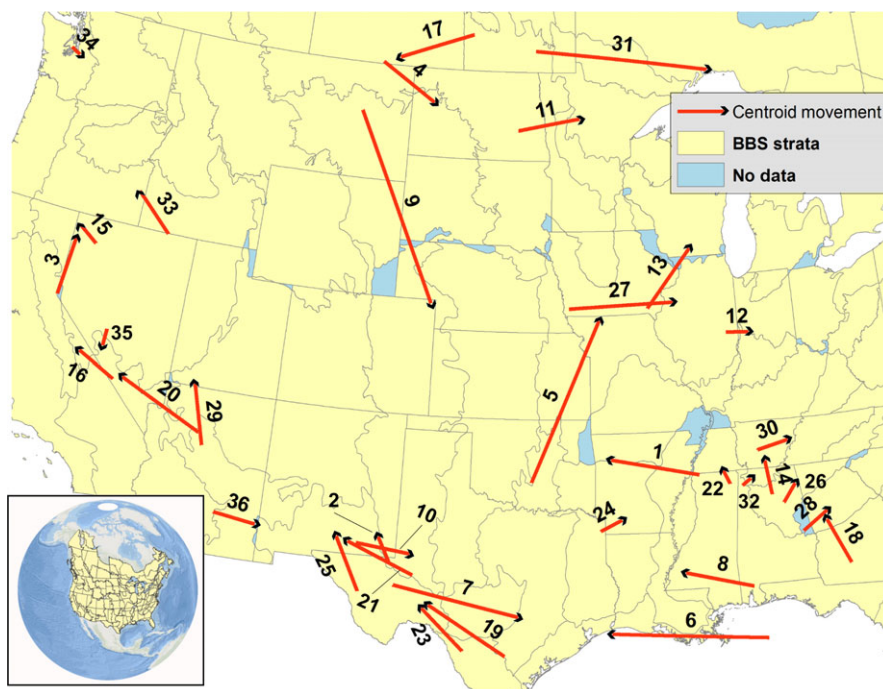
For the 8 species that had been singled out in pair-model comparison with 90% CI (Figure 4), seven of them had increased total populations; Curved-billed thrasher was an exception with declining population (Table 1). For these species, the average climate model showed the highest predictive ability with Carolina Wren with the median rank correlation coefficient  $\rho = 0.54$  (Figure 4, Fig. S2, Table S3).

The temperature model had the strongest rank correlation coefficient with Curve-billed Thrasher with a median  $\rho = 0.62$  (Figure 4, Fig. S2, Table S3). Inca Dove had the highest rank correlation coefficient by the precipitation model at a median  $\rho = 0.81$  (Figure 4, Fig. S2, Table S3).

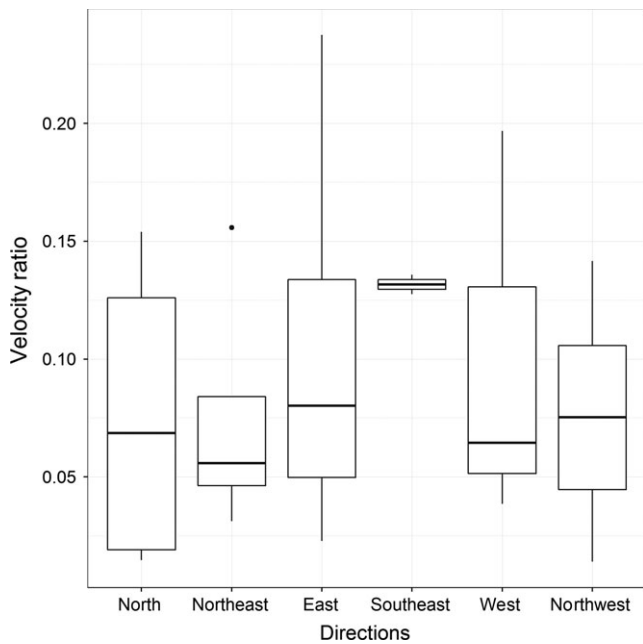
## 4 | DISCUSSION

Avian species are highly mobile, and could potentially respond quickly to changes in environmental conditions (Tingley et al., 2009). Previous studies on changing avian distributions have primarily been focused on shifting range edges based on presence and absence data (Currie & Venne, 2016; Hitch & Leberg, 2007; La Sorte & Thompson, 2007; Thomas & Lennon, 1999). Our study provides the first evidence to support multidirectional abundance shifts utilizing centroid of distribution that reflect changes in avian abundance data at the continental scale.

Classical ecological theories hypothesize that along a key environmental gradient, species appear to be physically constrained in one direction and biologically constrained in the other (Brown, Stevens, & Kaufman, 1996; Coristine & Kerr, 2015; Guisan & Thuiller, 2005). Regardless of the type of forces at play, the predominant northward shifts (including northeastward and northwestward shifts) and rare southward shifts (including southeastward and southwestward shifts) observed in our study seem to show that the factors constraining population along the latitudinal direction have been disproportionately affected or operating differently. The environmental stressors limiting species' northern populations seem to have weakened due to the greater magnitude of climate change in high latitude regions (Roots, 1989; Serreze et al., 2000), while the stressors in the

**FIGURE 2** The directions and magnitudes of the centroid movement between 1969 and 2012 for the 36 species with significant abundance shifts. The arrows point from the 1969 centroids to the 2012 centroids. The labeled numbers correspond to the species ID listed in Table 1. The map also shows the delineation of BBS strata which defined as intersection of the U.S. states, Canadian provinces, and Bird Conservation Region boundaries





**FIGURE 3** The velocity of the abundance shifts in six directions. We measure the velocity of avian distribution shift by calculating velocity ratio, a standardized index to account for the size differences of ranges. The index is defined as a ratio of shifted distance to range extent. Across all direction the average velocity ratio for the species with significant abundance shifts is 0.09, indicating a shift of centroid covering 9% of the range extent over the studies period. The lower and upper box in this plot hinges denote the 25th and 75th quantiles. The upper/lower whisker extends from the hinge to the highest/lowest values within  $1.5 \times$  IQR of the hinge (IQR is the distance between the first and third quartiles)

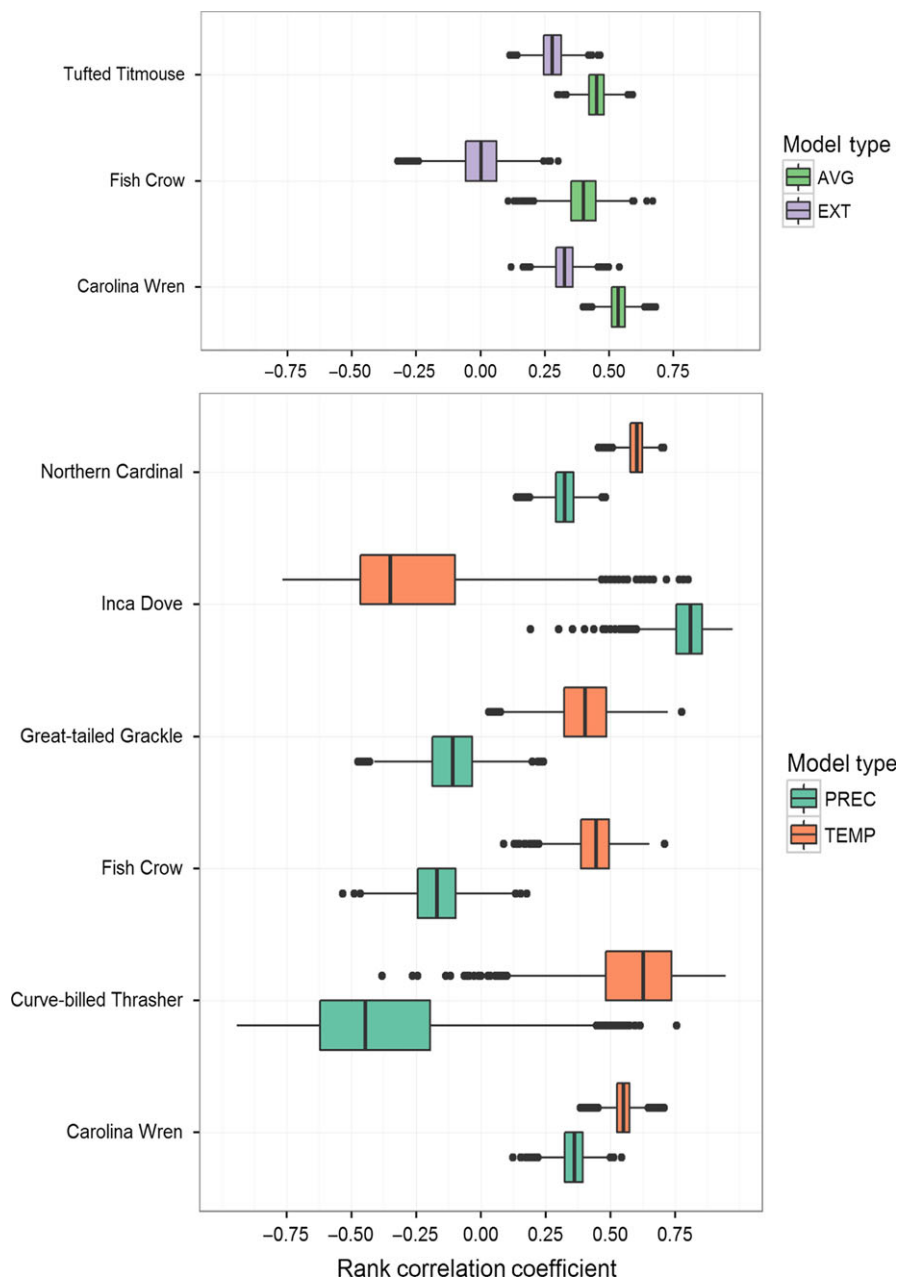
southern ranges remained relatively unchanged, if not strengthened. Therefore, the changes allowed for relatively more species to experience population growth across northern ranges, and more population decline across southern ranges which led to northward abundance shifts. This appears to agree with conventional theories that wintering birds northern distributions are limited primarily by ambient temperature in winter (Root, 1988), which can be weakened by warming climate (Jeffrey & Jeffrey, 1994). On the other hand, the southern distribution are believed to be limited mostly by other climatic factors and/or biotic interaction. Their connection with climate change is less straightforward but might remain strong as recent climate change proceeds (Gaston, 2003; Sagarin, Gaines, & Gaylord, 2006). Species abundances were observed to shift eastward and westward as rapidly as northward shifts which might suggest highly heterogeneous and drastic environmental change along longitudinal gradients. Our results show that the environmental forces that limit species distributions in east-west directions might be highly susceptible to changing climatic conditions.

Geographical restrictions are important limiting factors to species range, due to physical challenges in crossing geographical barriers such as mountain ranges. Our results indicate a high ratio of species experiencing longitudinal distribution shifts (Figure 1), and thus

provide little evidence to support the hypothesis that abundance changes within ranges are hindered by the North American mountain systems which are predominantly oriented in north-south direction. Such a pattern might be attributed to the fact that, unlike the shifting of range edges, the change of abundance distribution rely less on physical movement of populations. Redistribution of abundance could be the result of a population growth or a decline within existing species range and thus be less affected by geographical barriers. Landscape composition and configuration, particularly topographic variability, has the potential to significantly mediate species response to climate change (Gaüzère, Príncipe, & Devictor, 2016). Variable topography provides several mechanisms to mediate spatial responses to climate change including reducing the distance between isotherms and creating local climate refugia (Gaüzère et al., 2016; Lenoir et al., 2013; Loarie et al., 2009). The centroid analysis provides a new approach for future studies to evaluate the velocity of climate change responses.

The selection of appropriate predictive climatic variables is critical for establishing accurate and transferable species distribution models (Barbet-Massin & Jetz, 2014). Here, we examine the relative influence of different groups of climatic predictors on long-term avian abundance changes. Most prior studies have attributed the poleward shifts of avian distributions to the increase in average temperature (Hitch & Leberg, 2007; La Sorte & Thompson, 2007; Maclean et al., 2008; Thomas & Lennon, 1999; Williamson, 1975). Our results show that temperature metrics explain the avian abundance change rate more than precipitation models. For some birds (e.g., Inca dove), however, the changing precipitation pattern is uniquely important in terms of predicting long-term abundance changes. It is worth noting that by focusing on comparing strength of association between different groups of climate variables and the observed population change rate, we inevitably emphasized less on some of the other related and meaningful questions such as: what are the species whose abundance change rate can be explained by specific climate model(s) with high predictability; what are the biological and physiological connection between driving climate variables and changing avian abundance? For the species whose abundance change rates show significant association with specific type of climatic factors (Figure 4), future research is needed to determine the link between the climate change processes and species-specific ecological responses.

Extreme climate conditions have been documented to directly or indirectly affect species distribution, community structure, abundance, and life history traits such as morphology, and reproduction (Cavanaugh et al., 2015; Parmesan et al., 2000; Rittenhouse et al., 2010). The influence of extreme climate events on species distribution can also be multidirectional, because one extreme climate event can often have opposite effects among different species or even among subspecies in the same habitat (Parmesan et al., 2000). Although frequent, large magnitude extreme climate events would eventually affect average climate metrics (they are thus correlated to some extent), species that are directly affected by extreme climate associate more closely with metrics and models



**FIGURE 4** The relative influence of climatic factors. The plot shows bird species whose abundance change rate could be explained with significant margin by one model over the other with 90% CI. The rank correlation coefficient between predicted abundance change rate and the actual rate is used as a measure of predictive ability of different climate models. Above: three species that had significantly higher rank correlation coefficient with average climate model than with the extreme climate model. Below: six species that had higher rank correlation coefficient with either the temperature model or precipitation model. The lower and upper box hinges represent the 25th and 75th quantiles. The upper/lower whisker extends from the hinge to the highest/lowest values within  $1.5 \times \text{IQR}$  of the hinge (IQR is the distance between the first and third quartiles)

based on frequencies and severity of weather events (Cavanaugh et al., 2014), and will be better modeled by using extreme climate metrics and models. Our results, however, did not show that the extreme climate model significantly improved the predictive ability to model long-term bird abundance changes across strata compared with average climate model. Although this comparison is informative at the temporal and spatial scales at which we defined extreme variables, we note that extreme climate can be extremely influential over very short time periods and at very local scales; these effects of extreme climate may not be adequately described by our analysis.

Change in land cover, human population and housing density are closely related to resources and disturbances presented to wildlife (Midgley, Hughes, Thuiller, & Rebelo, 2006; Rittenhouse et al., 2012; Thuiller et al., 2006), and thus are possible alternative factors that

can lead to systematic shifts of species distributions. In tests of alternative hypotheses, we also examined the explanatory power of a nonclimatic model utilizing changes of land cover types coverage (urban, forest, grassland, barren, agriculture, and wetland) and changes of rural and urban human population and housing density between two different periods (1988–1997 and 2003–2012) (See Text S2 for a detailed description of the methodology used). The results showed that during the studied period nonclimatic factors did not explain the changing abundance significantly better than climatic factors, except for one species (White-breasted Nuthatch) (Tables S4 and S5, Text S2). For such period, the trend still holds that the temperature/average climate models had consistently greater predictive ability than the precipitation/extreme climate models in terms of explaining more species strata-level abundance change at any given CI (Table S5, Text S2).

There is likely no single climatic factor that can explain the broad scale shifts of species abundance completely. A combination of different climatic and nonclimatic factors tend to be involved at such scale. Although our results showed the four climatic models had considerable predictive ability to explain the change of abundance for 10–17 species, none of the models could significantly explain the abundance change of more than half of the studied species that exhibited abundance shifts. Even for the species where the climate models showed strong predictive power, the models appeared to have limited ability to predict both population increase and decrease (e.g., Fig. S2). This suggests that multiple ecological processes are at play for many of the abundance shifts we are observing. For instance, warming winter conditions could lead to the expansion of northern range of a species, while other factors such as biotic interaction, or habitat conversion simultaneously reducing the abundance of the population in other parts of the range. To comprehensively account for such multifaceted abundance redistribution process, future research needs to incorporate climatic, nonclimatic, and locational information (e.g., spatial dependency) (Araújo & Luoto, 2007; Guisan & Thuiller, 2005; Thuiller et al., 2004; Václavík, Kupfer, & Meentemeyer, 2012).

Almost all the birds included in our study are wide-spread species, and although some are experiencing long-term population declines, none are in danger of extinction. The high ratio of multidirectional abundance shifts suggests a high level of environmental changes are occurring that redistribute populations across broad geographical scale. If the trend is consistent across taxonomic groups, it would pose even greater threat to rare and endangered species that have limited distribution and fragmented habitat (Songer et al., 2012; Walther et al., 2002). In general, rare species are more likely to be specialists, highly dependent on specialized habitat and climate niches, and with limited dispersal ability. The combination of these factors makes them less likely to benefit from emerging suitable habitat and/or increasing carrying capacity. Rare species are also likely more vulnerable to unfavorable environmental changes. The conservation planning for these species will require more comprehensive climate change adaptation and mitigation policies that focus on practices such as establishing new reserves and habitat corridors along not only the latitudinal but also longitudinal directions.

As anthropogenic climate change and other environmental changes continue to alter the earth ecosystem at unprecedented rates (Vitousek, Mooney, Lubchenco, & Melillo, 1997), it is increasingly critical to understand how species distributions respond to drastic changes at broad geographical scales (Gaston, 2003). Our study provides insight into the direction and velocity of the shifting avian abundance distributions, and shows how multifaceted climatic factors are associated with such shifts. Our results demonstrate the complex challenges faced when developing predictive models for biodiversity conservation, and calls attention to species-specific conservation planning and practices that must establish resilient wildlife habitat and reserve systems to prepare and adapt for such multidirectional and rapid changes of species abundance structure.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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