Modeled distribution shifts of North American birds over four decades based on suitable climate alone do not predict observed shifts

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HIGHLIGHTS

- The distribution centroids of 250 bird are computed across the U.S. in 1969–2011.
- Great differences of direction and velocity exist between observed and modeled shifts.
- Migratory ability and adaptability predict higher velocity of the observed shifts.
- Climate change exposure affects observed velocities of neotropical and wetland birds.
- Only boreal forest birds show significantly faster climate-modeled shift velocity.

GRAPHICAL ABSTRACT
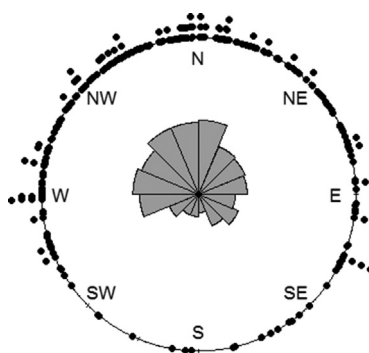
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ABSTRACT

As climate change alters the global environment, it is critical to understand the relationship between shifting climate suitability and species distributions. Key questions include whether observed changes in population abundance are aligned with the velocity and direction of shifts predicted by climate suitability models and if the responses are consistent among species with similar ecological traits. We examined the direction and velocity of the observed abundance-based distribution centroids compared with the model-predicted bioclimatic distribution centroids of 250 bird species across the United States from 1969 to 2011. We hypothesized that there is a significant positive correlation in both direction and velocity between the observed and the modeled shifts. We then tested five additional hypotheses that predicted differential shifting velocity based on ecological adaptability and climate change exposure. Contrary to our hypotheses, we found large differences between the observed and modeled shifts among all studied bird species and within specific ecological guilds. However, temperate migrants and habitat generalist species tended to have higher velocity of observed shifts than other species. Neotropical migratory and wetland birds also had significantly different observed velocities than their counterparts, which may be due to their climate change exposure. The velocity based on modeled bioclimatic suitability did not exhibit significant differences among most guilds. Boreal forest birds were the only guild with significantly faster modeled-shifts than the other groups, suggesting an elevated conservation risk for high latitude and altitude species. The highly idiosyncratic species responses to climate and the mismatch between

shifts in modeled and observed distribution centroids highlight the challenge of predicting species distribution change based solely on climate suitability and the importance of non-climatic factors traits in shaping species distributions.

1. Introduction

Climate change is causing shifts in the spatial distributions of many species as they track suitable environmental conditions (Pecl et al., 2017). Climate constrains species distributions through multiple processes, such as altering dispersal and colonization limits and modifying the distribution of habitat and resources (Walther et al., 2002; Parmesan and Yohe, 2003). Indeed, paleo-records indicate that range shifts were common in response to past changes in climate (Huntley and Webb, 1989; Davis and Shaw, 2001).

With climate change affecting the entire globe, a strong focus of recent conservation and ecological research has been to understand the consequences of climate change for species distributions and to develop management actions that help alleviate climate effects. Changes in climatic factors through time can alter the multidimensional niche space of species and thus create mechanisms to change biological responses (e.g., growth rate, mortality rate, and abundance) within a species' range (Maguire, 1973).While climate-based species distribution models are commonly used to project change in species distributions (Pearson and Dawson, 2003; Hijmans and Graham, 2006), the development of reasonable strategies for supporting climate change adaptation is complicated by idiosyncratic species' responses to climate change (Tingley et al., 2009; La Sorte and Jetz, 2012; Gibson-Reinemer and Rahel, 2015; Bai et al., 2018). While there is evidence to support temperature-driven poleward range shifts (Devictor et al., 2008; Hiddink et al., 2015), precipitation changes often serve as counter forces that result in patterns of distribution shifts that are not aligned with temperature or precipitation alone (Walther et al., 2007; La Sorte and Jetz, 2012; Tingley et al., 2012; VanDerWal et al., 2013). This raises the question of whether observed changes in population abundances are aligned with the velocity and direction of changing climate suitability captured by a large number of bioclimatic variables and if the relationship between the two is consistent within guilds and among species with similar ecological traits.

Mechanisms that may cause differences in species response to climate change and may result in differential velocity (the rate of changes per unit time) in distribution shifts can be grouped into two categories: adaptive capacity and climate change exposure (Triviño et al., 2013; Garcia et al., 2014; Estrada et al., 2016). The adaptive capacity is a species' ecological adaptability and includes the ability to physiologically tolerate large variations in environmental conditions (e.g., temperature, precipitation), to disperse or relocate when in an adverse environment, and to utilize a broad spectrum of resources. Higher adaptability means that species can move faster due to migratory or dispersal ability (Peterson et al., 2002; Crick, 2004). The term sensitivity is sometimes used to indicate the lack of adaptability to measure climate change vulnerability (Ofori et al., 2017). Sensitivity is higher for species with ecological traits such as habitat specialization, narrow physiological tolerances, rarity, and other factors that limit population growth and potentially restrict distribution shifts (Foden et al., 2013). For instance, bird species with highly specialized habitat or dietary requirements are predicted to respond slower to changing climate and thus have a lower velocity of distribution shifts than generalist species (Crick, 2004; Mattila et al., 2011; Davey et al., 2012).

The second group of mechanism centers on climate change exposure and reflect the extent and magnitude of climate-driven environmental changes within the species' range. For example, smaller climate change exposure occurs in mountainous regions, where steep spatial gradients of physical conditions across elevation ensure that temperature and precipitation conditions within a short distance are within the suitability requirements of a given species as climate changes (Loarie et al., 2009). In contrast, higher climate change exposure is expected in flat areas where travel distances to pursue suitable temperature and precipitation are large (Peterson, 2003;

Loarie et al., 2009). Similarly, because climate change is predicted to be particularly rapid at high latitudes (Soja et al., 2007; Huang et al., 2017b), boreal and arctic wildlife species are likely to shift their distributions more rapidly than temperate or tropical species. Furthermore, large extents of the boreal region are flat, which may further increase distributional velocity. Accordingly, long-distance migrants, such as neotropical migratory birds in North America, maybe less affected by climate change than short-distance or resident species because their wintering ground is less exposed to frequent and severe extreme winter weather (Walther et al., 2002).

The effects of climate change on species' ranges and distributions have primarily been characterized via either the analysis of observed range shifts or modeled projections of shifts in suitability. Observed distribution change can be measured along range edges or centroids (Parmesan et al., 1999; La Sorte and Jetz, 2012; Huang et al., 2016). The velocity and direction of the distribution shift is the length and direction of the vector pointing from the earlier range edge or centroid to the more recent one. Here, we chose to use centroids to characterize the distribution because it accounts for comprehensive information derived from species' full range and are readily derivable for both observed and projected distributions.

Measuring change in species abundance centroids (density distribution) captures the shift in distribution by accounting for the fluctuation of species abundance estimates at the center of various sub-regions (Virkkala and Lehikoinen, 2014; Huang et al., 2016, 2017a). It is thus a way to characterize the observed distribution shifts. Conversely, modeled predictions of shifts in species distributions are based primarily on species' bioclimatic suitability, which defines suitable climatic space. The bioclimatic suitability is derived from species distribution models built using detailed climate data and a large number of species occurrence data for each time period (Pearson and Dawson, 2003; Hijmans and Graham, 2006; Heikkinen et al., 2006; Bateman et al., 2016a). Bioclimatic centroids characterize the shift in species' climatic niche conditions and thus can be used to represent the model-predicted distribution shifts. Empirical evidence also showed that species abundance declines with distance from the centroid of species' bioclimatic suitability (environmental space), suggesting that bioclimatic niche centroids are more associated with optimal abundance than the range centroid (Martínez-Meyer et al., 2013).

A key question that arises is to what extent observed changes in species distributions match changes in modeled shift of suitable bioclimatic space, or if the shift of bioclimatic niche conditions predicts the change of observation-based distribution. The assumption is that modeled environmental suitability is positively related to actual species abundance (VanDerWal et al., 2009; Gutiérrez et al., 2013; Weber et al., 2017).

Our goal here was to examine the spatial relationship between the direction and velocity of the model predicted distribution shifts versus observed distribution shifts of 250 bird species across the contiguous United States from 1969 to 2011. We compared the distribution centroids based on abundance data across each species' range versus those based on climate suitability. Both the abundance- and climate suitability-based centroid data outputs and the methodologies have been published in previous publications (VanDerWal et al., 2013; Huang et al., 2016; Bateman et al., 2016a,b). We compared the results of these approaches and correlated both the direction and the velocity of the two types of distribution shifts over four decades and examined if ecological traits related to climate change exposure and adaptative ability affected the velocity of shifts.

Specifically, we tested the following six hypotheses:

- H1. The modeled distribution shifts are correlated with the observed shift in terms of their direction and velocity because climate suitability is positively correlated to species abundance.

- H2. Habitat generalist birds shift their distribution faster than other birds because they can utilize a wide spectrum of resources and thereby adapt to changing climate.
- H3. Temperate migratory (short-distance migratory) birds have higher distribution shift velocity because they effectively respond to changing climate by being able to migrate to suitable habitats.
- H4. Neotropical migratory birds have lower velocity in distribution shift than other birds because they are not exposed to severe winter conditions in their wintering grounds.
- H5. Boreal forest-associated birds have a higher velocity in range shift than other bird species because high-latitude areas experience a higher magnitude of climate change.
- H6. Grassland birds and wetland birds have higher range shift velocity than other bird species because their obligate habitats have low topographic variation, which increases the necessary travel distance to locate suitable habitats during changing climates.

2. Method & data

2.1. Abundance-based distribution centroids

For our analyses, we selected breeding landbird species with occurrence data in both North American Breeding Bird Survey (BBS) and Global Biodiversity Information Facility (GBIF) datasets in the conterminous United State between 1950 and 2011. We excluded species whose breeding range is exclusively or primarily north or south of the conterminous US border, and species nesting offshore. A total of 250 bird species were included in the analysis, covering a variety of migratory and habitat specializations guilds (Table S.1).

We quantified changes in the observed species distribution shifts with abundance-based distribution centroids using data produced by Huang et al. (2016, 2017a,b). Methods are described in detail in Huang et al. (2016, 2017a,b) and briefly summarized here. We analyzed BBS data from 1969 to 2011 (Sauer et al., 2013) for the contiguous United States for this analysis, which ensured consistent spatial and temporal coverage with the analysis for bioclimatic range centroids. We delineated strata as the basic spatial units for estimating regional population abundance. Strata are homogeneous regions with consistent geographic characteristics and the number of routes surveyed. Strata are the smallest unit where the abundance can be estimated within the hierarchical Bayesian framework while accounting for factors such as observer and year effect that influence likelihood of detection and, consequently, abundance (Sauer et al., 2013; Huang et al., 2017a). We defined strata here as the intersection of states and Bird Conservation Regions (BCRs) (Sauer et al., 2003), resulting in 130 strata for the contiguous United States. We delineated the range of each species as all strata with more than four survey routes along which the species was encountered to ensure sufficient sample size.

We parameterized a hierarchical Bayesian model to calculate a stratum-specific annual abundance index for each species (for details, see Link and Sauer (2002) and Huang et al. (2016, 2017a,b)). Briefly, the hierarchical Bayesian model is structured as an overdispersal Poisson regression model; the model takes into consideration stratum (i), year (t), and observer/route effects. The year, observer, and overdispersion effects are all specified to have a normal distribution with mean of zero, the rest of the hyperparameters used non-informative priors (Link and Sauer, 2002; Huang et al., 2016, 2017a). We used the R2winbugs package (Sturtz et al., 2005) in the R language for statistical computing and graphics (R Core Team, 2020) to call the Winbugs program (Lunn et al., 2000; Spiegelhalter et al., 2003) to fit the hierarchical models. Ultimately model estimates the stratum-specific annual abundance index N_{it}. We calculated the coordinates of annual centroids (X_{it} and Y_{it}) of abundance-based distribution for each species as the mean strata centroid coordinates (x_i and y_i) weighted by corresponding N_{it} of the year (Huang et al., 2016, 2017a). We then generated posterior distributions of the estimated centroid coordinates using Markov Chain Monte Carlo simulations (Link and Sauer,

2002). We aggregated the posterior samples by calculating the average annual centroid coordinates for each species based on 10,000 collected posterior samples, a sample size that is sufficient for quantifying changes in distribution shifts (Huang et al., 2016, 2017a).

2.2. Bioclimatic-based distribution centroids

To quantify the modeled distribution shifts based on climatic suitability, we used previously published species distribution models on an annual time scale for birds in North America (Bateman et al., 2016b) and previously published bioclimatic distribution centroids data in Bateman et al. (2016a,b). These data were derived using established methodologies for modeling short-term species distribution (Reside et al., 2010) and deriving bioclimatic distribution centroids at an annual scale (VanDerWal et al., 2013), which are not obtainable from traditional long-term climate-based species distribution models. Methods are described in detail in Bateman et al. (2016a,b) and briefly summarized here. Bateman et al. analyzed the same list of 250 bird species using occurrence data within breeding season archived by the Global Biodiversity Information Facility (GBIF, accessed 2012-08-02, gbif.org), which include a variety of avian records (see Bateman et al., 2016a,b for a full list of datasets included). All data were collected between 1969 and 2011 in the contiguous United States, to maintain consistency and comparability with the aforementioned abundance-based analysis. The occurrence record of all birds within the breeding season in the original dataset were also used as target-group background points to address temporal and spatial biases in the database while ensuring that the background region of the species distribution models are accessible to studied species (Barve et al., 2011; Merow et al., 2013). Bateman et al. (2016a,b) used monthly total precipitation and temperature maxima and minima from the PRISM dataset (4-km resolution, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu), and aggregated the monthly data into eight BIOCLIM variables, i.e., mean annual temperature, temperature seasonality, the maximum temperature of the warmest period, minimum temperature of the coldest period, annual precipitation, precipitation in the wettest quarter, precipitation in the driest quarter, and precipitation seasonality. Bateman et al. (2016a,b) calculated climate variables for three time periods: 6, 12, and 36 months prior to the survey month of the occurrence record to capture short- to long-term climatic conditions. For the 6-month period, they excluded two precipitation metrics (precipitation of the wettest and driest quarter) because they are not meaningful for half-years; the mean annual temperature/precipitation was replaced by mean temperature/precipitation over the 6 months preceding the observations. The process resulted in 22 (6 + 8 + 8) climate variables (Bateman et al., 2016a). For each bird species, they used Maximum Entropy (Maxent) modeling (Phillips et al., 2006; Hijmans et al., 2015) to predict each species' suitable climatic conditions for each month of the breeding season (April through July) from 1969 to 2011. The process resulted in monthly gridded maps of bioclimatic suitability during the breeding season between April and July at 4 km resolution across the contiguous United States. They then calculated the centroid of the suitable bioclimatic space (center of gravity of the bioclimatic suitability map) based on the methodology of VanDerWal et al. (2013) and using R package SDMTools (VanDerWal et al., 2011). The center of gravity of bioclimatic space is defined as the geometric center of all pixels in the studied area weighted by their bioclimatic suitability index values (VanDerWal et al., 2013). Bateman et al. (2016a,b) calculated the annual centroid coordinates by averaging the coordinates of the monthly centroids within the breeding season (between April and July) of a given year. All species distribution models' performance was evaluated by AUC scores using both tenfold cross-validation and against an independent bird dataset within North American Breeding Bird Survey. The majority of the species model exhibited high area-under-the-curve (AUC) scores from both cross-validation evaluation (average AUC > 0.85) and were able to accurately predict presence and absence from independent data (average AUC > 0.89), suggesting high model performance, see Bateman et al. (2016a) for details.

2.3. Direction and velocity of distribution shifts

For both types of centroids, and for each species, we regressed the latitudinal and the longitudinal coordinates of the annual centroid respectively against year in two linear models. The slope of the regression lines quantified the rate of centroid change (km·yr^{-1}) by longitude or latitude. We considered shifts in longitudinal and latitudinal direction as two vectors (with their own velocity and angle) perpendicular to each other, and summing (the resultant) of the two vectors resulted in a new vector representing the velocity and direction of species' shifting distribution.

2.4. Correlation between observed and modeled distribution shifts

To compare the directions of the observed and modeled distribution shifts, we computed the circular correlation coefficient (Jammalamadaka and Sengupta, 2001) between the directions of distribution shifts computed by the two methods. As the angle between two vectors increases, the two measurements periodically oscillate between ma*x*imum and minimum similarity. Circular statistical methods account for such periodicity. The circular correlation coefficient (Eq. (1)) is defined so that Xi and Yi are i_{th} elements of two paired circular variables, and $\overline{X}$ and $\overline{Y}$ are their respective mean. It is similarly to the Pearson's correlation coefficient, but $X_i - \overline{X}$ and $(Y_i - \overline{Y})$ are replaced by $\sin\left(X_i - \overline{X}\right)$ and $\sin\left(Y_i - \overline{Y}\right)$.

$$r_c = \frac{\Sigma_i \sin\left(X_i - \overline{X}\right) \sin\left(Y_i - \overline{Y}\right)}{\sqrt{\Sigma_i \sin^2\left(X_i - \overline{X}\right) \Sigma_i \sin^2\left(Y_i - \overline{Y}\right)}} \tag{1}$$

We calculated the circular correlation coefficient and the significance test between the two angular variables using the 'circular' package (Agostinelli and Lund, 2011) in R (R Core Team, 2020).

We calculated the correlation between the velocity of observed and model distribution shifts among all 250 species, as well as among guilds of species defined by ecological traits using the guild classification system of the State of North American Birds Report (North American Bird Conservation Initiative, 2014) (detailed information about the selected guilds were in the next section). We also computed Spearman's rank correlation coefficient and conducted significance tests between the two types of velocity with a significance level of $\alpha = 0.1$.

The directional difference between the two types of centroids was measured by angular differences (direction of the modeled shift minus the direction of the observed shift) ranging between $-180°$ and $180°$.

2.5. Hypotheses testing

To test our hypotheses that there are systematically different velocities among different avian guilds, we obtained the habitat and migration guild assignment from the State of North American Birds Report (North American Bird Conservation Initiative, 2014). We classified each of our 250 species according to six binary indices to indicate whether they are part of the following non-exclusive guilds: habitat generalist (47 species), neotropical migrant (85), temperate migrant (short-distance migrant) (116), boreal forest birds (41), grassland birds (29), and wetland birds (55) (Table S.1). Generalists are species that are adaptable and can utilize multiple habitats, whereas the boreal, grassland, and wetland species primarily use one type of habitat. Neotropical migrants regularly breed in the continental U.S. or Canada. They can be found in Mexico, Caribbean Basin, Central or South America during the non-breeding season, whereas temperate migrants occur mostly in the U.S. and Canada during the non-breeding season. To measure velocity differences related to climate change exposure and adaptability, we compared the velocity of the bird species within a specific guild to all other species using the one-tailed two-sample Wilcoxon test (Bauer, 1972). The significance level was set at $\alpha = 0.1$. We assessed the differences in the velocity among guilds for both observed and modeled distribution shifts.

To examine the influence of shared evolutionary history of species on our comparisons, which can potentially undermine the assumption that species are independent, we also compared estimates from phylogenetic generalized least squares models (pgls) with generalized least squares models (gls). We fit two sets of pgls and gls models to determine if adding phylogenetic correlation structure substantially changes the model results, one set with abundance-based velocity of distributions shifts as the response variable and one with bioclimatic-based velocity as the response. Within each set of models, we examined whether the binary guild indices (predictive variables) significantly influenced the measure of velocity (dependent variable). The pgls models include a phylogenetic correlation structure derived from the variance-covariance matrix. Many models can be used in the pgls to test the variance-covariance matrix, here we used the default Brownian motion model of evolution. Phylogenetic relatedness of species was based on a large-scale phylogenetic tree for extant birds (Jetz et al., 2012). We calculated Pagel's λ to separately quantify phylogenetic signal in the model and in the response variable. We also conducted likelihood ratio tests to determine if Pagel's λ was significantly different from zero. We fit pgls and gls models in the R statistical environment using the nlme and ape packages (Paradis et al., 2004).

2.6. Range-size robustness test

In our prior work, we examined both the raw velocity (average distance shifted per year by the distribution centroid) and the standardized velocity index to account for range size (the raw velocity divided by the range size, to quantify the velocity of distribution shifts because the size of the range can limit the upper limit of the velocity captured by the centroid methods) (Huang et al., 2017a). However, the influence of range size on the centroid velocity is not clear, and because our analysis included a large number of species with a wide spectrum of range sizes, we conducted a test to evaluate the impact of range size on centroid velocity to assess the robustness of our centroid-based methods.

We examined the relationship between range size and velocity of distribution shifts of the two centroid methods by regressing the raw velocity against the area (km^2) of each species' range. We then computed the slope of the linear model and tested the level of significance of the slope. Species' range sizes were calculated as the summed area of all strata where a species was recorded in the BBS dataset. We used the same range size measurement for both centroid metrics.

Data and the R script used in our analyses were made available on open source repository Figshare (https://doi.org/10.25573/data.21266037.v1).

3. Results

3.1. H1. Correlation between observed and modeled distribution shifts

We found large differences between the observed and modeled distribution shifts, contrary to our hypothesis that shifts in climate suitability are correlated with the observed shifts of population abundance in terms of both their direction and velocity.

The angular correlation coefficients between the directions of the observed and modeled distribution centroids were, in general, not significantly different from zero (*p*-value = 0.33). Among all birds, the coefficient was $r_c = -0.060$ (Table 1). The majority of the observed shifts were in westward or eastward directions, while most modeled shifts were in westward and northward directions (Fig. 1). The directions of the two distribution shifts for different guilds were largely uncorrelated, with angular correlation coefficients ranging between 0.23 and -0.20 (Table 1). The guild with the highest absolute angular correlation coefficient was grassland birds ($r_c = 0.23$), followed by boreal forest birds ($r_c = 0.22$), and wetland birds ($r_c = -0.20$), but none of them were significantly different from zero (all *p*-values > 0.05; Table 1).

The direction of individual species' distribution shifts was quantified in degrees ranging between 0° and 360°, with 0° being straight north. The average direction of the observed distribution shift was 176 ± 6°, and

Table 1
Mean velocity and direction of the two centroid methods and the mean minimum angular difference between the direction of the two methods.

Guild	Means and standard errors Abundance-based velocity (km·yr^{-1})	Means and standard errors Bioclimatic velocity (km·yr^{-1})	Cor. of velocity	P-value (velocity cor.)	Means and standard errors Abundance-based shift dir. (degree)	Means and standard errors Bioclimatic shift dir. (degree)	Means and standard errors Min. angular diff. (degree)	Angular cor.	P-value (angular cor.)
All	5.03 ± 0.31	2.26 ± 0.09	0.12	0.05*	176 ± 6	139 ± 5	13 ± 7	−0.06	0.33
Boreal forest	4.57 ± 0.73	2.61 ± 0.22	0.01	0.97	208 ± 17	106 ± 12	64 ± 15	0.22	0.18
Grassland	5.02 ± 0.63	2.25 ± 0.20	0.03	0.87	178 ± 15	186 ± 16	8 ± 20	0.23	0.27
Generalist	6.85 ± 1.02	2.42 ± 0.26	0.13	0.39	169 ± 17	152 ± 14	−10 ± 15	−0.12	0.43
Neotropical migrant	4.38 ± 0.48	2.33 ± 0.16	0.07	0.55	185 ± 10	136 ± 10	6 ± 12	−0.07	0.50
Temperate migrant	5.98 ± 0.53	2.32 ± 0.13	0.17	0.08*	178 ± 10	142 ± 8	17 ± 10	−0.09	0.34
Wetland	7.88 ± 0.99	2.51 ± 0.23	0.20	0.15	171 ± 15	161 ± 13	9 ± 15	−0.20	0.13

* indicates significant correlation coefficient. The significance level was set at α = 0.1.

139 ± 5° for the modeled shifts (The uncertainty was estimated here and hereon with standard error of the mean) (Table 1, Fig. 1). The angular differences between the two types of shifts were relatively uniform (Fig. 1). Among all 250 species, the average angular difference between the two shifts was 13 ± 7° (Table 1).

Among all studied species, the Spearman's rank correlation coefficient between the velocity of two distribution shifts was weak but significantly so, at ρ = 0.12 (p-value = 0.05) (Table 1). The average velocity of the shift measured of the observed shifts was 5.03 ± 0.31 km·yr^{-1}, faster than that of the modeled shifts at 2.26 ± 0.09 km·yr^{-1}.

The correlation between observed and modeled shift velocity for individual guilds was mostly low and insignificant. Correlation coefficient of the velocity ranged from ρ = 0.01 (boreal forest guild) to ρ = 0.20 (wetland guild). Temperate migrants were the only guild for which the correlation coefficient of the velocities was significant, albeit the strength of the coefficient was still relatively weak (ρ = 0.17, p-value = 0.08) (Table 1). The direction and velocity of individual species centroid movements can be found in Table S.1.

3.2. Velocity and direction of shifts between guilds

Among our guilds, wetland birds had the highest average velocity in the observed distribution shifts at 7.88 ± 0.99 km·yr^{-1}, followed by habitat generalist species at 6.85 ± 1.02 km·yr^{-1}, and temperate migrant species at 5.98 ± 0.53 km·yr^{-1}. Neotropical migrants had the lowest velocity at 4.38 ± 0.48 km·yr^{-1}, followed by boreal forest birds at 4.57 ± 0.73 km·yr^{-1} (Table 1).

Similarly, the wetland and habitat generalist guilds had also a relatively high velocity of their modeled distribution shifts at 2.51 ± 0.23 and 2.42 ± 0.26 km·yr^{-1} respectively, only surpassed by the boreal forest guild at 2.61 ± 0.22 km·yr^{-1}. Grassland birds, neotropical migrants, and temperate

migrants had the lowest modeled distribution shift velocities at 2.25 ± 0.20, 2.33 ± 0.16, and 2.32 ± 0.13 km·yr^{-1} respectively (Table 1).

The averaged angular differences between the observed shift and the modeled shift for the different guilds ranged from −10 ± 15° (habitat generalist guild) to 64 ± 15° (boreal forest guild) (Table 1). The guild with the smallest angular difference was neotropical migrants, followed by grassland, and then wetland birds, with averaged differences of 6 ± 12°, 8 ± 20°, and 9 ± 15° respectively (Table 1).

3.3. Hypotheses on adaptability (H2, H3) and climate change exposure (H4, H5, H6)

We hypothesized that generalist birds (H2), temperate migratory birds (H3), would have higher range-shift velocity than the rest of the selected species because their foraging strategies and migratory ability make them more adaptable when their environment changes. Indeed, our result in terms of observed distribution shifts showed these two guilds had significantly higher velocity than their counterparts (Fig. 2).

We also hypothesized that neotropical migratory birds would have lower distribution shift velocity than their counterparts because they are exposed to less severe winter conditions in their wintering range in the tropical regions (H4) and that wetland birds would show significantly greater range-shift velocity than their counterparts because of the greater magnitude of climate change taking place in the flat ecoregion (H6). The observed distribution shifts based on abundance did support these two hypotheses (Table 2, Fig. 2).

In comparison, our results in modeled distribution shift only supported the H5 hypothesis related to climate change exposure in high latitude areas: boreal forest birds exhibited greater shift velocity in bioclimatic space than the other birds (Fig. 2). For the other guilds, there were no significant differences of modeled velocity based on climate suitability between selected guilds and their counterparts.
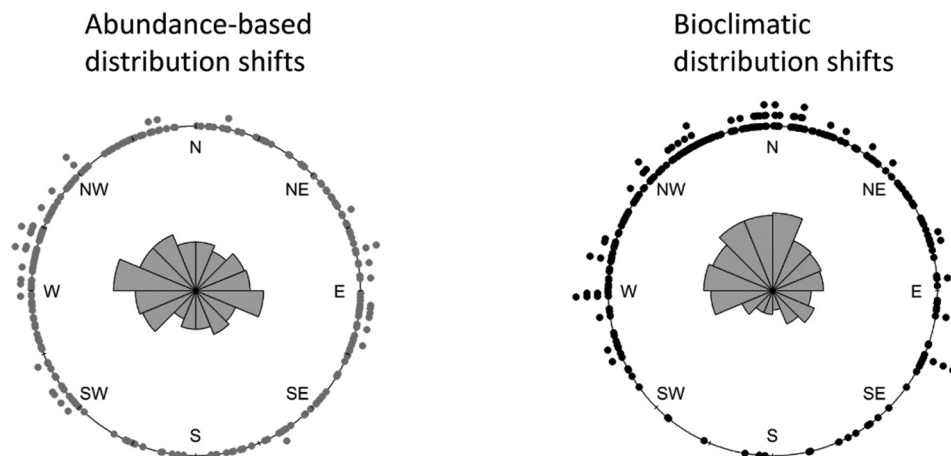
Abundance-based distribution shifts

Bioclimatic distribution shifts

Fig. 1. Comparison of the directions of the observed (abundance-based) and the modeled (bioclimatic-based) distribution shifts. Area of petals represent proprotion of species with indicated directional shift, dots indicate species.
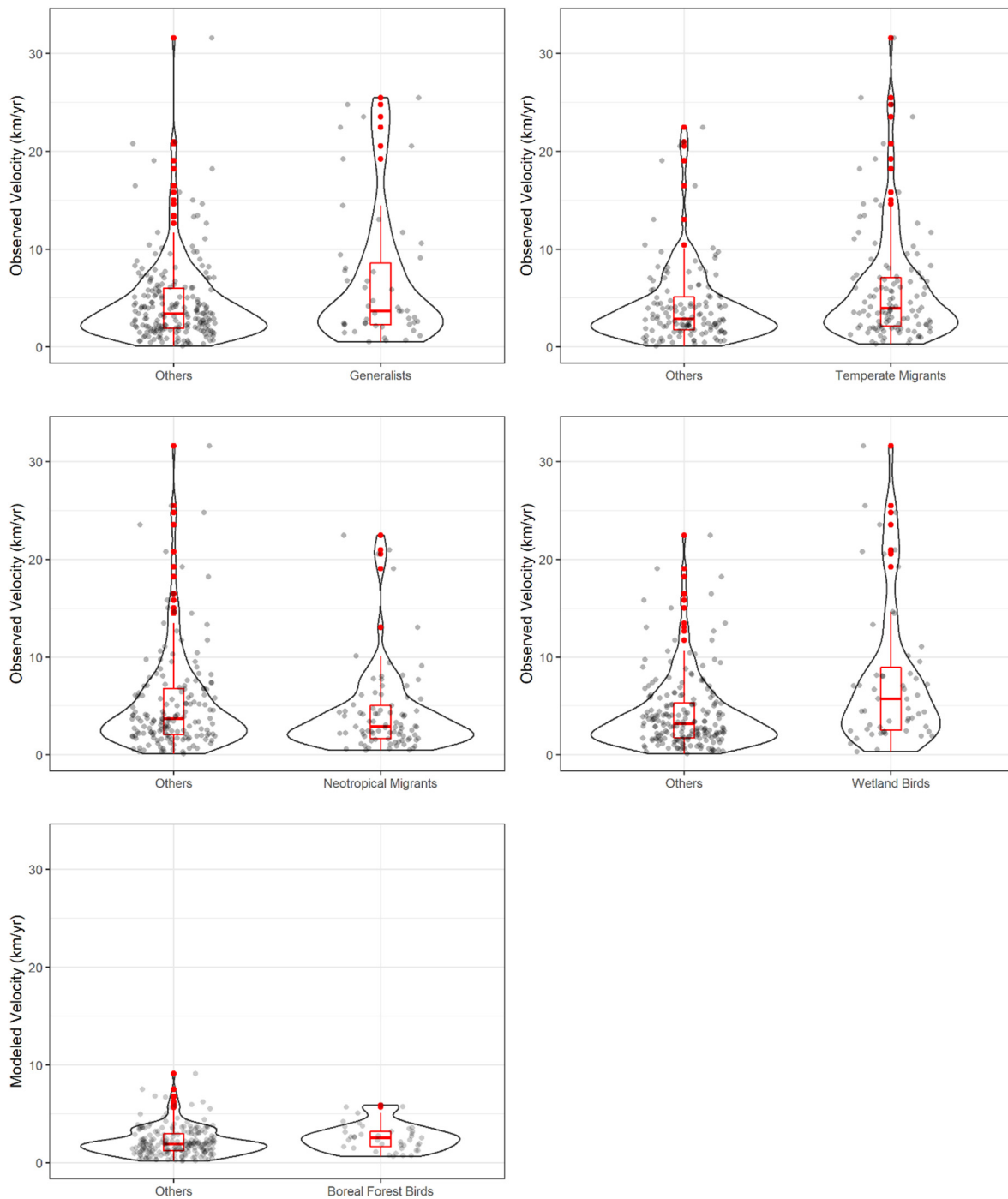
Fig. 2. Contrasting velocity of centroid shift between guilds. Top two rows: violin plots of the observed distribution shift velocity for habitat generalist, temperate migrant, neotropical migrant, and wetland guilds in comparison to their counterparts. The bottom panel: the modeled distribution shift velocity for boreal forest guild and all other species at the bottom left.

Neither of the velocity measures supported the hypothesis related to the grassland ecosystem (H6), and the velocity of grassland birds was not significantly faster than that of the other guilds.

The plgls models accounting for the shared evolutionary history between studied species showed qualitatively similar results to the gls models without phylogenetic structure, suggesting that including the phylogenetic similarity into the model does not substantially change the hypotheses test results. We included the detailed results in the Appendix C. For all bioclimatic models, Pagel's λ was not significantly different from 0. For all abundance-based models, Pagel's λ was significant,

although the values are low (λ = 0.21–0.30) indicating weak phylogenetic signal.

3.4. Impact of range size on velocity

We did not find that range size was related to velocity, and the slopes of the linear models using range size to predict the observed and modeled velocity were both small ($|p\text{-}value| < 0.0001$). The p-values were 0.50 and 0.89 for the observed shift model and modeled shift model, respectively, indicating that both slopes were not significantly different from zero. The

Table 2
Comparison of distribution shift velocity between bird guilds. We classified each of our 250 studied species into 6 non-exclusive guilds using six binary indices according to the classification of the State of North American Birds Report: habitat generalist (n = 47), neotropical migrant (85), temperate migrant (short-distance migrant) (116), boreal forest birds (41), grassland birds (29), and wetland birds (55). With each index, we classified all studied species in the guild member (n) or non-guild member (250-n). We tested six hypotheses using observed distribution shift velocity and modeled distribution shift velocity. We performed a single-tailed Wilcoxon test to compare the mean velocity of the shift of a specific guild with that of all other species. ∗Indicates significant results which support the hypotheses. The significance level is set at α = 0.1.

Hypotheses	Observed distribution shifts	p-Value	Modeled distribution shifts	p-Value
	W statistics		W statistics	
H2. Generalist birds had greater velocity than the other selected birds	4092	0.06∗	4588	0.34
H3. Temperate migratory birds had greater velocity than the other selected birds	6276	<0.01∗	7244	0.18
H4. Neotropical migratory birds had less velocity than the other selected birds	7937	0.04∗	6610	0.77
H5. Boreal forest birds had greater velocity than the other selected birds	4851	0.91	3408	0.02∗
H6. Grassland birds had greater velocity than the other selected birds	2810	0.14	3016	0.30
H6. Wetland birds had greater velocity than the other selected birds	3571	<0.01∗	4832	0.13

range size is thus not a significant factor contributing to the velocity of both range centroid shifts.

4. Discussion

We examined the relationships between the direction and velocity of the modeled and observed distribution shifts of 250 bird species across the contiguous United States. We found large differences between the two types of centroid distribution shifts among all the studied bird species and within habitat and migratory guilds. This was contrary to our prediction that the direction and velocity of bioclimatic distribution shifts are correlated with the abundance-based distribution.

4.1. H1. Disagreement of shifting climatic conditions and abundance distribution

We found that the directions of the observed and modeled centroid shifts over the past four decades were uncorrelated when analyzing all selected bird species and for most ecological guilds. The velocity of the observed abundance-based shift is faster and more variable than the modeled centroid shift (e.g., Figs. 3, S.1).
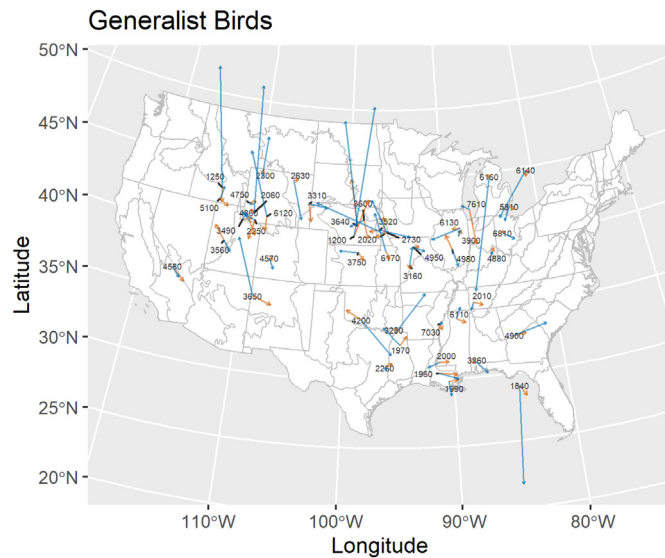

Fig. 3. Difference in observed and modeled centroid shifts. The direction and velocity of generalist bird species distribution shifts based on abundance-based centroid (blue arrow) and bioclimatic-based centroid (orange arrow). The species are labeled with American Ornithological Union (AOU) number. See Appendix Table B.1 to correspond species name with AOU number. The length of the vectors is computed as the number of years (42) × the velocity of the centroid movement (km. year^{-1}) reported. Therefore, the length indicates the total distance (km) the centroid shifted over the studied period, proportional to the velocity (km. year^{-1}) reported. More visualization of the centroid shifts for other guilds is in Appendix Fig. A.1.

Our results thus highlight a major mismatch between projected shifts of bioclimatic based-distribution centroids and the observed shifts of avian distribution centroids (Table S.1, Fig. S.1), suggesting shifts in the spatial arrangement of bird abundance overtime did not align with the change in bioclimatic suitability. Accordingly, our results suggest that shifts of the distribution of birds in the continental U.S. were rarely in alignment with shifts of the bioclimatic niche defined by the center of climatic suitability. These findings were consistent for both the direction and the velocity of the range shifts.

4.2. H2–H6. Driving mechanism of range shift velocity

Our hypotheses that were based on species' adaptability, specifically their ability to migrate and to utilize multiple habitat types, were largely supported by our results.

However, among the guilds of birds that we had hypothesized to experience higher climate change exposure, only wetland birds exhibited significantly faster velocity in abundance distribution than the rest of the studied species. This may be attributed to that coastal wetlands are subject to substantial environmental changes, including rising sea level, changing patterns of hurricane frequency, intensity, as well as changes in wetland hydrology and geomorphology (Michener et al., 1997). Freshwater wetlands are also quite vulnerable to climate change due to the sensitivity of shallow water bodies to changes in precipitation, water volume, and duration of hydroperiods (Kundzewicz et al., 2007; Johnson et al., 2010). Both freshwater and coastal wetlands have undergone dramatic habitat loss and degradation in the past few decades (Brinson and Malvarez, 2002; Davidson, 2014), not all of which are due to climate change. The rapid distribution changes we observed in wetland species abundances might be related more to the sensitivity of wetland habitat to changing hydrology and development rather than greater climate change exposure per se. This is supported by the fact that in our analysis of the modeled climate suitability, the velocity of change for wetland bird guild was no faster than that of other bird species.

Interestingly, North American wetland birds are the only habitat guild that had a net gain in abundance since the 1970s (Rosenberg et al., 2019). This is likely due to conservation efforts and resources committed to wetland restoration and protection (Rosenberg et al., 2019). The increase of wetland bird abundance resulting from habitat rehabilitation may be a confounding factor in assessing our hypothesis that the wetland birds shifted their distribution due to the higher magnitude of climate change within relatively flat wetland habitats. Furthermore, we caution that the BBS has limitations in its ability to monitor wetland species because it is primarily a roadside survey.

4.3. Non-climatic impact on distribution shifts

Our results support prior findings that climate change is unlikely to be the only driver of abundance shift (Lehikoinen and Virkkala, 2016). Habitat change and climate change both affect species distributions (Warren et al., 2001), and for some species, habitat loss and other aclimatic variables may

outweigh the impact of climate warming at the local level (Warren et al., 2001). Climate change serves indirectly to influence species' distribution by modifying biotic interactions and the degree of habitat fragmentation. Species' sensitivity to climate change is also more pronounced at the range margins than at the centroids (Anderson et al., 2009), and species are buffered to some extent from climate change within the interior of their range. As we are comparing centroid shifts here, it is possible that the mismatch between abundance and bioclimatic centroid range shifts is a factor of this interior buffering effect. Distribution centroids that comprehensively account for information over the entire range, including multiple fronts at the margin of the distribution range, and the high suitability areas might see a delayed response even when consistent changes of climate suitability occur regionally.

Landscape-level biophysical properties of habitat can also alter microclimate and buffer the temperature increase associated with climate change (Latimer and Zuckerberg, 2017) and habitat availability can be a constraint for range expansion (Mair et al., 2014). The complex interactions of climate, habitat, and distribution shifts (La Sorte and Jetz, 2012; Gillings et al., 2015; Bateman et al., 2016a; Huang et al., 2017a) may be the reason why the directions of centroid shifts were not correlated with the direction of climate shift. Particularly, biotic interaction with plant and animal species that support or limit (e.g., via specialized food source, prey, predator) species distribution is a key factor that is not included in the climate-based species distribution models (Brooker et al., 2007; Araújo and Luoto, 2007). The misalignment between the distribution of biotic factors and the climatic niche of the modeled species can contribute to the discrepancy that we observed.

Another reason for the differences between observed and modeled distribution could be lagging in species' responses to changing climate conditions. Such a lag can occur when there is considerable physiological tolerance to changing climate conditions within the existing range, or when there are local refugia where suitable microclimates persist, or when barriers prevent dispersal (Khaliq et al., 2014; Robillard et al., 2015; Latimer and Zuckerberg, 2017). Among the habitat guilds that we studied, boreal forest birds can barely expand their distribution within the conterminous United States: much of their habitat on alpines are by nature fragmented; in New England, boreal birds are bounded by the Atlantic Ocean, and in the Midwest by the Great Plains to the west and Great Lakes to the east. Interestingly, boreal forest birds were the only guild in our analysis that had a significantly faster velocity of their bioclimatic suitability than the rest of the species, suggesting an elevated risk that changing climate might outpace the ability of the species in this guild to adapt or relocate.

Intraspecific variation in response to multiple attributes of environmental change can also be a source of low correlation between observed and modeled centroid velocity. Even within the same guild where a single ecological trait was controlled, the observed distribution change pattern could still be influenced by many genetic and phenotypic attributes that define phenotypic plasticity (Valladares et al., 2014). Species characteristics within ecological guild can often vary greatly (Blaum et al., 2011), particularly many life-history and morphological traits have been shown to link closely with large scale species distribution, abundance, and responses to climate change (Viana and Chase, 2022). Our approach to account for the shared evolutionary characteristics is a way to control for similarity in evolutionary history. However, methods to control for more phenotypic factors could be adopted in the future to rule out the influence of other confounding factors that can be quantified individually across large number of species. Global databases on species morphology and foraging attributes (Wilman et al., 2014; Tobias et al., 2022) can potentially provide valuable resources for facilitating future research in examining the impact of finer scale species attribute on distribution change velocity.

4.4. Relationship of climatic suitability and species abundance

The differences in the shifts of observed and modeled species distributions provide empirical evidence to the debate over the relationship between environmental suitability and species abundance. The common assumption is that environmental suitability resulting from species distribution models is positively correlated to species abundance because suitability determines the upper limit of abundance (VanDerWal et al., 2009; Gutiérrez et al., 2013; Weber et al., 2017). Although a positive relationship between abundance and suitability has been observed for many species, the magnitude of the correlation varied widely (Weber et al., 2017). Furthermore, many factors can influence the strength and shape of abundance-suitability relationships, including the choices of the species distribution models, the selection of aclimatic variables, and if habitat fragmentation and species traits are accounted for (Basile et al., 2016; Weber et al., 2017; Jiménez-Valverde et al., 2021). It is, therefore, challenging to make direct inferences about empirical abundance based on climatic suitability (Dallas and Hastings, 2018; Jiménez-Valverde et al., 2021; Sporbert et al., 2020). Our analysis is distinct from previous studies in that instead of analyzing local abundance-suitability relationships at sampled locations at one time, we characterized and compared the shifting velocity and direction of suitability and abundance across their range in the contiguous U.S. over forty years. Our results further suggest that it is not possible to predict the direction and velocity of long-term abundance change based on the pattern of shifting bioclimatic centroids.

Species abundance was observed to reduce as the distance from the niche centroid increases (Martínez-Meyer et al., 2013). However, such a relationship is often not linear, suggesting that areas with optimal niche suitability sustain much higher abundance than most occupied areas (Martínez-Meyer et al., 2013). Such a non-linear pattern might retain a stronger and more linear abundance-suitability relationships only in limited regions, such as the fundamental niche with a positive growth rate (Holt, 2009; Soberón, 2010). Future studies could examine the spatial relationship of centroid shifts only in such high suitability areas.

4.5. Assumptions & limitations

We analyzed 250 bird species whose ranges are centered in the contiguous U.S. Our selection criteria favored inclusion of species with large ranges due to our minimum strata requirement (species must be sufficiently sampled in at least 10 physiographic strata (Huang et al., 2017a)). Consequently, most of the bird species included in our study are widespread species and neither threatened nor endangered. Both climate and non-climatic stressors may have stronger effects on rare and endangered species that have limited or fragmented distributions (Walther et al., 2002; Songer et al., 2012). In general, rare species are more likely to be specialists, highly dependent on specific habitats (Davies et al., 2004), or have limited dispersal ability (Rocca and Milanesi, 2020). These factors make them more likely to have a prominent lag in tracing shifts in their climatic niche, resulting in slower and more idiosyncratic distribution shifts. However, evaluating how the abundance of species with limited ranges changes in response to climate change requires new methodologies.

Here, we examined two groups of mechanisms that potentially can determine the velocity of climate-induced distribution change: adaptability and climate change exposure. We tested five hypotheses that fall within the two mechanisms. We found that species adaptability to migrate and to adapt multiple habitat types were significant predictors of higher velocity of the observed shifts, whereas the effect of climate change exposure is not prominent. However, alternative hypotheses, considering a combination of ecological traits and environmental factors, can also be tested. For instance, low-latitude organisms may be more strongly affected by temperature change due to their proximity to their thermal maxima and exposure to a narrow thermal range (Amano et al., 2020). Warm-adapted southerly birds can be more likely to thrive under warming winter conditions and colonize new regions (Princé and Zuckerberg, 2015). Body size, associated with thermoregulatory cost during winter, may also affect species distributions in response to climate change (Gaston, 2003; Dalby et al., 2013). Particularly, hypotheses examining the influence of continuous variables such body size can potentially provide new insight by accounting for more intraspecific variations than our approach that groups species into guilds.

Our hypotheses were based on an implicit assumption that current climate change conditions are well within the physiological tolerance of the species that we studied (Khaliq et al., 2014), and that specialist species did not experience major climate-induced population declines. However, if the limits of their physiological tolerances have been reached, then any additional change could cause rapid contraction of distribution and population decline, contrary to what we observed.

In theory, it takes time for species distribution to respond to changing climate and reach equilibrium. The impact of climate on species distribution can therefore be delayed. Based on established methodologies, we used 6-, 12-, and 36-months moving windows to capture short to long term climate conditions prior to the occurrence of species. However, it is possible to adapt alternative temporal windows to quantify climate conditions. Particularly, longer term (e.g., 3–10 years) climate influence could play a role in affecting habitat suitability, fragmentation, and biotic interaction, thus influencing the distribution of specific species whose distribution depends on such mechanism. Future studies can be focused on to compare the model performance between bioclimatic models with short term climate average and long-term climate average. Such comparison can even be used to detect the time required for individual species to reach equilibrium.

5. Conclusion

We compared the observed and modeled species distributions centroids of 250 bird species across the contiguous United States in the past four decades. We found that observed changes did not correlate with the modeled changes in shifting direction or velocity of centroids, likely due to the important role of habitat in influencing bird distributions as well as in temporal lags in bird response to climate change. The relationships were weak for all of the studied species and within most migratory and habitat guilds.

Our climate change adaptability hypotheses, which grouped species based on their ability to migrate and utilize multiple types of habitat, were supported by observed abundance-based centroid movement. Neotropical migratory birds showed slower velocity of observed distribution shift which can be attributed to their low exposure to extreme winter conditions. We predicted a faster shift in flat biomes and found that to be true only for wetland birds. However, habitat restoration and population growth specifically associated with wetland birds were confounding factors. For most habitat and migratory guilds studied in our analysis, the velocity of modeled distribution shifts based on climatic suitability was relatively uniform, not exhibiting significant differences among guilds. The only exception was the boreal forest guild. Boreal forest birds showed a significantly faster bioclimatic distribution shift than other guilds, which suggests an elevated level of climate change risk for high latitude and altitude species within North America.

The distinct velocity and direction of the observed and modeled distribution change patterns highlight that predicting species distribution change based solely on climate suitability is challenging. Accordingly, aclimatic factors such as habitat availability greatly shape species distributions even while climate changes rapidly.

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CRediT authorship contribution statement

Qiongyu Huang: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Brooke L. Bateman: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Writing - review & editing.

Nicole L. Michel: Conceptualization; Methodology; Writing - review & editing.

Anna M. Pidgeon: Writing - review & editing.

Volker C. Radeloff: Writing - review & editing.

Patricia Heglund: Writing - review & editing.

Andrew J. Allstadt: Writing - review & editing.

Justin A. Nowakowski: Formal analysis; Writing - review & editing; Validation.

Jesse Wong: Validation; Visualization.

John R. Sauer: Conceptualization; Writing - review & editing.

Data availability

The data and code has been made available on FigShare

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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