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Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change

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Over the past half century, migratory birds in North America have shown divergent population trends relative to resident species, with the former declining rapidly and the latter increasing. The role that climate change has played in these observed trends is not well understood, despite significant warming over this period. We used 43 y of monitoring data to fit dynamic species distribution models and quantify the rate of latitudinal range shifts in 32 species of birds native to eastern North America. Since the early 1970s, species that remain in North America throughout the year, including both resident and migratory species, appear to have responded to climate change through both colonization of suitable area at the northern leading edge of their breeding distributions and adaption in place at the southern trailing edges. Neotropical migrants, in contrast, have shown the opposite pattern: contraction at their southern trailing edges and no measurable shifts in their northern leading edges. As a result, the latitudinal distributions of temperate-wintering species have increased while the latitudinal distributions of neotropical migrants have decreased. These results raise important questions about the mechanisms that determine range boundaries of neotropical migrants and suggest that these species may be particularly vulnerable to future climate change. Our results highlight the potential importance of climate change during the nonbreeding season in constraining the response of migratory species to temperature changes at both the trailing and leading edges of their breeding distributions. Future research on the interactions between breeding and nonbreeding climate change is urgently needed.

Breeding Bird Survey | species distribution modeling | occupancy modeling | range shifts | migration

Over the past half century, North America's avifauna has experienced widespread and sustained declines, with an estimated net loss of nearly 3 billion birds (1). Although these declines have occurred across most major biomes and taxonomic groups, there has been a notable difference in population trajectories of migratory and resident species, with the former experiencing a net loss of nearly 2.5 billion individuals while the latter has slightly increased (1). This stark difference suggests that these groups face different threats or differ in their ability to adapt to changing environmental conditions (2, 3).

The causes of the population declines documented by Rosenberg et al. are only partially understood, especially for migratory species, but the primary threats to North American birds are thought to include habitat loss (4), invasive species (5), and direct and indirect anthropogenic mortality (6–8). Although these threats are likely the primary drivers of declines in North America's avifauna, evidence that climate change is affecting the distribution and demography of plant and animal populations is pervasive (9–12). Continued climate change will likely act as a threat multiplier, exacerbating declines caused by other factors (13–15) and complicating management and restoration efforts to reverse declines (16–18).

To date, most attempts to assess climate change vulnerability in birds have used climate envelope models to project species distributions under different emissions scenarios and quantify the degree to which future distributions will overlap with current distributions (19, 20). These methods, however, assume that species will track climate change in space and therefore do not account for adaption in place (21) or constraints on the ability to colonize newly created habitats (22). An alternative approach to assessing vulnerability, which explicitly aims to determine the degree to which species or groups of species respond to climate change, is to quantify the degree to which species have already shifted their distributions in response to recent climate change.

For avian species, climate-driven changes in distributional centers have been documented during both the breeding and nonbreeding seasons (23, 24), and the speed of these shifts has been positively linked to both population trend (25) and body size (26). Expansion and contraction along range margins, however, has been relatively understudied, despite evidence that the effects of climate change will be most severe in these peripheral regions (27). In this paper, we used a newly developed dynamic species distribution model (28) to quantify breeding range dynamics of 32 species of eastern North American birds using 43 y of monitoring data from the North American Breeding Bird Survey (BBS). We quantified the rate and direction of latitudinal range shifts at each species' breeding range center and range margins and then tested how species' traits, including winter geography, population trend, and body size, influenced the rate of range shifts. We restricted our analysis to eastern North America to reduce the influence of factors other than

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Significance

Over the past half century, populations of neotropical migratory birds in North America have plummeted while populations of resident species have largely remained stable. We show that resident and migratory birds in eastern North America have responded differently to climate change over this period, with the ranges of resident species expanding along their northern margin while the ranges of migratory species have contracted at their southern margin. These results suggest that the ability to colonize newly suitable areas may make resident species resilient to future climate change but that climate-induced range contractions may make neotropical migrants vulnerable to these changes.

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climate (e.g., land use) on our conclusions. We further excluded from consideration species that are not well sampled by the BBS (e.g., waterfowl, nocturnal species, and shorebirds) and species with northern distributions that extend beyond the BBS sampling area (e.g., boreal species). Computational demands prevented an exhaustive analysis of all species that met these criteria, so instead we selected a representative sample of species (Table 1).

We predicted that after controlling for the effects of body size and population trend, the northern leading range margins of resident species would be shifting northward at a faster rate than that of neotropical migratory species because warming temperatures should relax winter limitation of residents, allowing peripheral populations to grow and expand into newly suitable habitat. Relaxation of winter limitation should also benefit migratory species that winter in North America (hereafter temperate-wintering migrants), allowing these species to expand their northern margins in a similar fashion to residents. Northern populations of neotropical migrants, in contrast, may be constrained in their ability to expand northward by increased migration distance and decreasing winter habitat quality (29, 30). Trailing range margins, on the other hand, have generally been found to be more stable than northern margins (31, 32), and therefore, we predicted that neither migrants nor residents would show evidence of breeding range contractions along their southern trailing range margins.

Results

Across all 32 species included in this analysis, we found evidence of northward shifts in mean breeding latitude, southern trailing range margins, and northern leading range margins (Fig. 1). The average rate of change among all species and across the entire study period was 0.003°/y (95% credible interval [CI] = 0.001 to 0.004) for the southern range margin, 0.007°/y (95% CI = 0.005 to 0.01) for the range center, and 0.005°/y (95% CI = 0.001 to 0.009) for the northern range margin. In general, indices were relatively stable between the start of the study period (1972) and the mid-1980s but began to shift northward at an increasing rate starting in approximately 1985 (Fig. 1 and Table 2).

Species-level traits were important predictors of range shifts, although the effects of the traits differed among indices (Table 3). At the southern range margin, the rate of northward shift was positive for species that winter in the neotropics and negatively associated with population trend and temperate-wintering migratory species, indicating that the southern range margins of neotropical migrants and species with declining population trends were shifting northward faster than those of resident species and species with increasing population trends (Table 3). In contrast, these traits had the opposite effect on

Table 1. Species attributes

Common name	Latin name	Trend (%/y)	Size(g)
Resident			
Red-bellied woodpecker	*Melanerpes carolinus*	1.02 (0.90, 1.15)	63.0
Fish crow	*Corvus ossifragus*	0.48 (0.04, 0.92)	280.0
Carolina chickadee	*Poecile carolinensis*	−0.38 (−0.56, −0.20)	10.5
Tufted titmouse	*Baeolophus bicolor*	1.08 (0.90, 1.24)	21.5
Brown-headed nuthatch	*Sitta pusilla*	−0.55 (−1.06, −0.10)	10.0
Carolina wren	*Thryothorus ludovicianus*	1.04 (0.85, 1.21)	21.0
Northern mockingbird	*Mimus polyglottos*	−0.46 (−0.62, −0.31)	49.0
Temperate migrants			
Black vulture	*Coragyps atratus*	4.77 (4.09, 5.36)	2, 000.0
Red-headed woodpecker	*Melanerpes erythrocephalus*	−2.35 (−2.68, −2.05)	72.0
Eastern bluebird	*Sialia sialis*	1.50 (1.30, 1.71)	31.0
Brown thrasher	*Toxostoma rufum*	−1.04 (−1.18, −0.92)	69.0
Eastern towhee	*Pipilo erythrophthalmus*	−1.34 (−1.48, −1.21)	40.0
Field sparrow	*Spizella pusilla*	−2.33 (−2.60, −2.17)	12.5
Neotropical migrants			
Blue-gray gnatcatcher	*Polioptila caerulea*	0.54 (0.26, 0.81)	6.0
Louisiana waterthrush	*Parkesia motacilla*	0.60 (0.14, 1.03)	20.5
Summer tanager	*Piranga rubra*	0.22 (0.00, 0.41)	29.0
Acadian flycatcher	*Empidonax virescens*	−0.26 (−0.51, 0.01)	13.0
White-eyed vireo	*Vireo griseus*	0.62 (0.41, 0.81)	11.5
Yellow-throated vireo	*Vireo flavifrons*	0.98 (0.73, 1.23)	18.0
Wood thrush	*Hylocichla mustelina*	−1.91 (−2.08, −1.76)	47.0
Prothonotary warbler	*Protonotaria citrea*	−1.10 (−1.55, −0.64)	16.0
Worm-eating warbler	*Helmitheros vermivorum*	0.38 (−0.31, 1.09)	13.0
Kentucky warbler	*Geothlypis formosa*	−0.90 (−1.26, −0.51)	14.0
Hooded warbler	*Setophaga citrina*	1.36 (0.94, 1.79)	10.5
Indigo bunting	*Passerina cyanea*	−0.73 (−0.82, −0.64)	14.5
Orchard oriole	*Icterus spurius*	−0.87 (−1.13, −0.63)	19.0
Prairie warbler	*Setophaga discolor*	−1.85 (−2.16, −1.53)	7.7
Yellow-throated warbler	*Setophaga dominica*	0.98 (0.52, 1.46)	9.4
Swainson's warbler	*Limnothlypis swainsonii*	1.20 (−0.12, 2.31)	19.0
Golden-winged warbler	*Vermivora chrysoptera*	−2.28 (−3.08, −1.47)	8.8
Cerulean warbler	*Setophaga cerulea*	−2.63 (−3.43, −1.73)	9.3
Dickcissel	*Spiza americana*	−0.36 (−0.86, 0.05)	27.0

Species are grouped by winter geography (year-round residents, temperate North America, or neotropics). Trend estimates from ref. 52. Values in parentheses are 95% CIs. Body size from Rodewald (54).
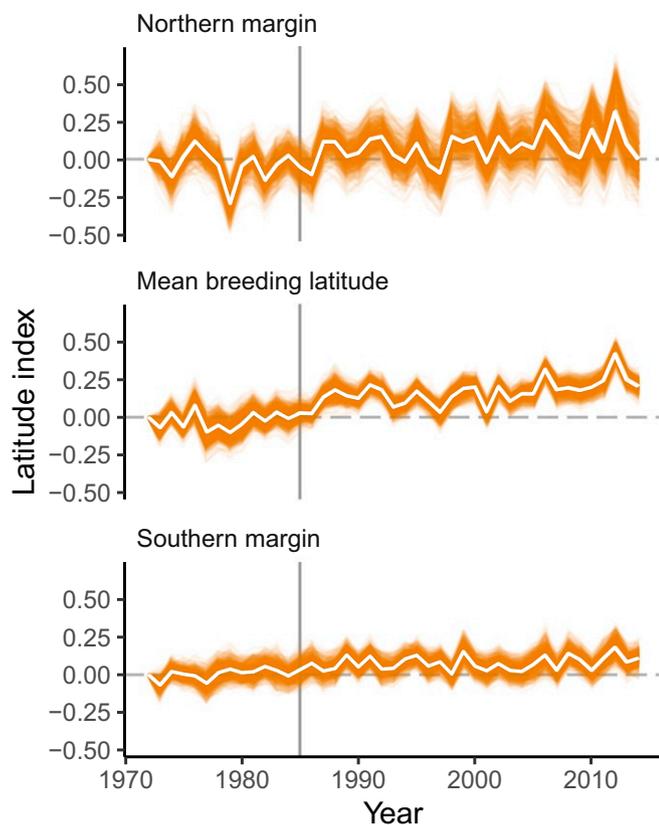
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Fig. 1. Composite range shifts for all 32 species included in our analysis. Orange lines are the posterior estimates of the annual latitudinal indexes, and white lines are the posterior means for each index. Vertical gray line indicates the year 1985, before which none of the indices showed significant directional shifts and after which all but the southern range margin showed significant northward movements.

shifts at the northern range margin. Body size had a small but positive effect on the rate of range shifts at the southern range margins ($p = 0.9$) but no effect on the rate of change at mean breeding latitude or northern range margin. Both neotropical migrants and resident species included in our analysis showed significant northward shifts in their mean breeding latitude, but temperate-wintering migrants did not (Table 3).

Composite indices of range shifts by residents, temperate-wintering migrants, and neotropical migrants largely confirm the results of the regression analysis (Fig. 2). Neotropical migrants showed consistent northward shifts in their southern range limits (0.004°/y, 95% CI = 0.002 to 0.007) and mean breeding latitude (0.007°/y, 95% CI = 0.005 to 0.01) but no evidence of shifts at their northern range margin (0.002°/y, 95% CI = −0.003 to 0.007). In contrast, resident species shifted their northern range limit northward at a rate of 0.014°/y (95% CI = 0.008 to 0.019), but there was no evidence of shifts in their

southern range limits (0.0007, −0.002 to 0.003). Temperate-wintering migrants shifted northward at their northern margins at a rate of 0.007°/y (95% CI = 0.004 to 0.01) and at their mean breeding latitudes at a rate of 0.0027 (95% CI = 0.001 to 0.004), roughly half the rate of resident species. Similar to residents, temperate-wintering migrants did not shift their southern margins (−0.0001, −0.003 to 0.003). As a result, the latitudinal distribution (difference between the northern and southern range margins) of neotropical migrants shrunk over the time period from 1972 to 2014 while the distribution of temperate-wintering migrants and residents increased. Interestingly, the northern range margin of migratory species showed more annual variation (neotropical migrants, coefficient of variation [CV] = 7.19; temperate-wintering species, CV = 7.93) than the northern range margin of residents (CV = 3.55, 95% CI = 0.54 to 19.01).

None of the three groups have kept pace with temperature changes across their ranges. Despite significant northward shifts at their range margins, mean annual temperature at the northern range margin of resident species has increased at a rate of 0.007°/y (95% CI = 0.002 to 0.011). The rate of temperature change at the northern range margin of migratory species was even greater (temperate-wintering migrants, 0.021°/y, 95% CI = 0.017 to 0.024; neotropical migrants, 0.023°/y, 95% CI = 0.019 to 0.029). Along their southern range margins, residents have experienced a temperature increase of 0.013°/y (95% CI = 0.009 to 0.017) compared to 0.016°/y (95% CI = 0.013 to 0.018) for neotropical migrants and 0.032°/y (95% CI = 0.028 to 0.035) for temperate-wintering migrants.

Discussion

Using 43 y of monitoring data, we found evidence that the distributions of 32 species of eastern North American birds have shown measurable responses to recent climate change. Averaged across species, we detected significant northward shifts in mean breeding latitudes and range margins, with a notable increase in the rate of northward shifts at the mean breeding latitudes and northern range margins beginning in the mid-1980s (Table 2). This pattern of little to no directional change throughout the 1970s and early 1980s followed by rapid shifts beginning in the mid-1980s closely matches temperature changes over this same time period (33), supporting the hypothesis that latitudinal distributions of North American birds are strongly influenced by temperature (34). These overall patterns, however, mask notable differences in the responses of species that remain in North American throughout the entire year (residents and temperate-wintering species) and neotropical migrants. Consistent with our predictions, resident species and temperate-wintering migratory species have shifted their northern range margins northward by nearly half of a degree latitude but have shown no directional change at their southern margins. Neotropical migrants have shown the opposite pattern, with measurable northward shifts in their southern trailing range margins but no directional shifts at their northern margins. These opposing patterns have resulted in an expanding latitudinal distribution of species that remain in North America year-round and a contracting latitudinal

Table 2. Estimated rate of range shifts before 1985 and after 1985

	Pre-1985		Post-1985	
Index	Rate (°/y)	Pr (Rate > 0)	Rate (°/y)	p
Mean breeding latitude	0.0015 (−0.004, 0.0081)	0.65	0.0058 (0.0036, 0.0083)	1.00
Northern margin	−0.0038 (−0.0132, 0.0063)	0.21	0.0039 (−0.0005, 0.0102)	0.94
Southern margin	0.0042 (−0.0025, 0.0111)	0.89	0.0014 (−0.0002, 0.0032)	0.96

Values in parentheses are 95% CIs, and Bayesian *P* values indicate the proportion of posterior samples greater than or less than 0.

Table 3. Effects of species' traits on the estimated rate and direction of range shifts

| | Winter geography | | | | | | Trend | | Body size | |
| | Resident | | North America | | Neotropics | | | | | |
Index	Intercept	p	Intercept	p	Intercept	p	Slope	p	Slope	p
Southern margin	0.0004 (−0.004, 0.004)	0.6	−0.007 (−0.02, 0.002)	0.94	0.003 (0.0005, 0.006)	1.0	−0.002 (−0.004, −0.0003)	0.998	0.00003 (−0.00003, 0.0001)	0.9
Mean breeding latitude	0.02 (0.01, 0.02)	1.0	−0.0005 (−0.004, 0.003)	0.60	0.009 (0.006, 0.01)	1.0	0.002 (0.0003, 0.003)	1.000	−0.00005 (−0.0001, 0.00001)	0.7
Northern margin	0.01 (0.004, 0.02)	1.0	0.005 (−0.002, 0.01)	0.90	0.002 (−0.003, 0.008)	0.7	0.004 (0.001, 0.007)	1.000	0.00006 (−0.00001, 0.0002)	0.7

Intercepts for each wintering geography represented the average annual rate of change (degrees latitude/y) at each latitudinal range index. Values in parentheses are 95% CIs, and Bayesian *P* values indicate the proportion of posterior samples greater than 0.

distribution of Neotropical migrants, underscoring potentially important differences in climate change vulnerability between the two groups.

As temperatures across North America have warmed over the past century, many species that were historically restricted to the southeastern and mid-Atlantic United States have been increasingly common in the northeast United States and southern Canada (35–38), although quantifying the rate and magnitude of range shifts is challenging due to the low-density and often stochastic nature of peripheral populations. Our study, which provides a quantitative assessment of the rate and magnitude of these northern limit expansions using methods that account for imperfect detection, provides compelling evidence that these leading-edge range shifts have primarily occurred in species that winter in temperate areas. These shifts may be due to increasing winter temperatures allowing species to survive at higher latitudes, although these species are also generally tolerant of urban/suburban habitats, which could explain some of their expansion (36).

The lack of leading-edge expansion by neotropical migrants and the slow rate of expansion by temperate-wintering migrants raise important questions about what determines range limits in migratory species. The observed range expansions by resident species suggest that range limits of migratory species are not the result of physical boundaries or dispersal limitation. Instead, these results suggest that migration itself may constrain populations from colonizing newly suitable habitat. Migratory individuals breeding along the northern margin of their distribution must undertake long migrations to reach these locations, which could impose survival costs not experienced by resident species and hinder the ability of individuals to colonize new habitats. The lack of observable range expansion by neotropical migrants, however, indicates that these species may face additional constraints not experienced by temperate-wintering migrants. One hypothesis for this difference is that the northern distribution of neotropical migrants is determined, at least partially, by conditions experienced during the tropical winter. Specifically, winter climate has been shown to negatively
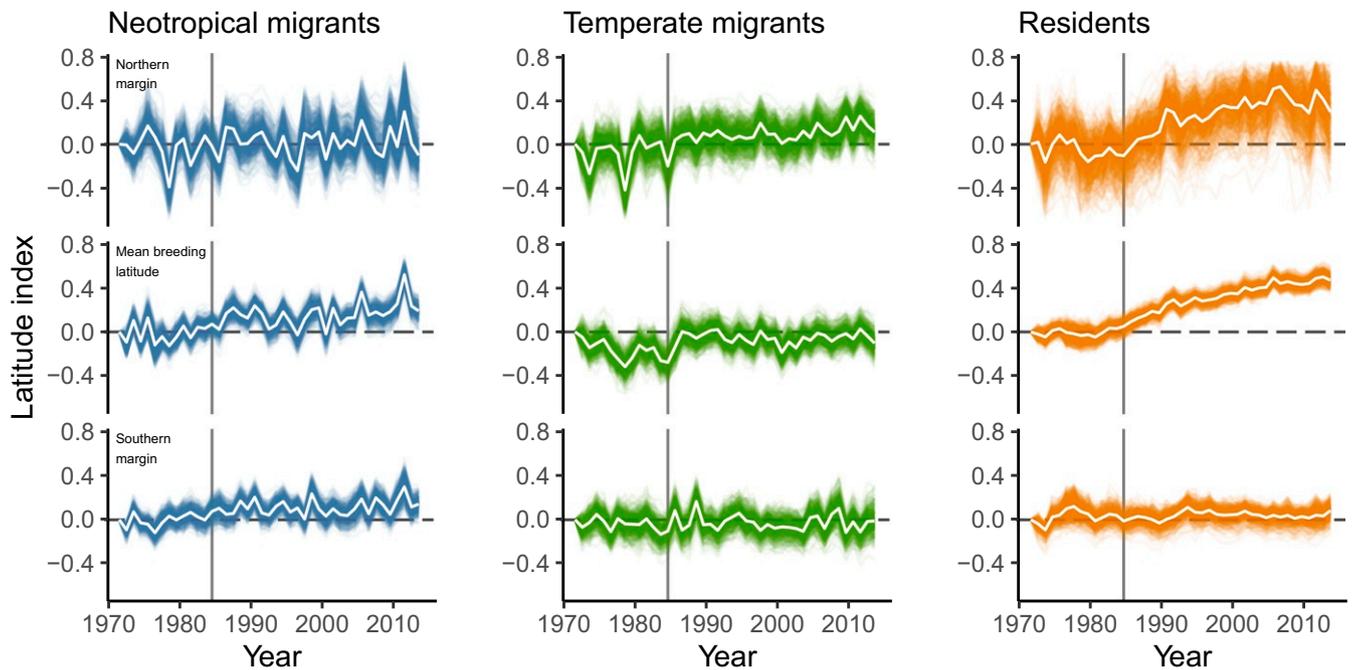

Fig. 2. Composite range shifts for neotropical migrants, temperate migrants, and year-round resident birds in eastern North America. Blue, green, and orange lines are the posterior estimates of the annual latitudinal indexes, and white lines are the posterior means for each index. Vertical gray line indicates the year 1985, before which none of the indices showed significant directional shifts and after which all but the southern range margin showed significant northward movements.

affect survival of neotropical migrants (39), and long-term drying trends in the tropics (29) may be preventing neotropical migrants from expanding their distributions during the breeding season. The high degree of annual variability in the northern range margin of neotropical migrants, which would be expected if the locations of these margins are influenced by winter climate, lends support to this hypothesis. Drying trends have not been uniform across the tropics, and further research exploring the effects of winter geography (e.g., Caribbean vs. Central America vs. South America) and winter habitat preferences on breeding season range shifts is needed. These results also underscore the limits of predicting the future distributions of migratory species using climate envelope models (19, 20) and highlight the need for more mechanistic species distribution models.

At the trailing edges of their ranges, neither resident species nor migratory species that winter in North America have shown directional shifts despite significant warming temperatures in these regions (33). The lack of contraction at the trailing edge suggests that these species may be adapting in place, likely by shifting the timing of breeding activities to track shifts in resource phenology (21, 40). In contrast, because arrival of neotropical migrants on the breeding grounds is often constrained by endogenous routines (41, 42) and winter conditions (43), these species may have less opportunity to respond to climate change via phenological shifts in breeding activities (3, 44). These constraints are likely to be most severe at the southern trailing edge of the breeding range because these areas will be the first to experience spring green-up. By the time individuals reach the southern edge of the breeding distribution in spring, resource phenology may have already advanced beyond the conditions required to successfully nest and raise offspring. For individuals that breed along the southern margin of the distribution, migrating farther north may be the only option for responding to temperature-induced changes to resource phenology (45, 46). These constraints are likely less severe in temperate-wintering migrants due to more flexible migration behaviors (47, 48) or because the southernmost breeding populations remain resident throughout the year (49).

After controlling for body size and migratory status, we found that species with increasing population trends were more likely to be expanding at their northern margin, whereas species with declining population trends were more likely to be contracting at their southern margin. These results are consistent with previous research on North American birds (25) and provide strong evidence of a positive link between recent population trends and the ability to cope with climate change. In light of the divergent trends of resident and neotropical migrants found by ref. 1, our results suggest that climate change may have contributed, at least in part, to the observed changes in North American avifauna over the past half century. In particular, the ability of temperate-wintering species to cope with climate change at both the trailing and leading edges of their ranges suggests that as a group, these species may be resilient to future climate change, although the extent to which birds in eastern North America are representative of birds in other biomes requires additional research. We also note that even resident species have not kept pace with the rate of temperature change, suggesting these species may still face negative consequences of climate change. Neotropical migrants, in contrast, have shown patterns of range shifts that suggest these species may be particularly vulnerable to future climate change. Of particular concern is the role that climate change in the neotropics, specifically long-term declines in precipitation, may play in limiting the ability of migratory species to cope with temperature changes experienced on the breeding grounds. Although the effects of winter climate on survival and migration phenology are well documented (30, 43, 50), our results suggest that winter climate may constrain migratory

species from responding to phenological changes at the trailing edge of their distribution and from range expansion at their leading edge.

Materials and Methods

Data for this analysis came from the North American BBS, a large-scale citizen science program consisting of over 5,500 roadside survey routes of which approximately 3,100 are surveyed each May or June by highly skilled birders and professional biologists (51). The BBS was initiated in 1966, although we chose to use BBS data collected from 1972 to 2015 due to sparse coverage of routes in the early years of the program (52). Following a rigorous sampling protocol, the observers conduct 3-min counts at 50 regularly spaced stops along each approximately 39.4-km-long route. See ref. 51 for more details regarding the BBS survey protocol.

To ensure that our analysis was able to document dynamics at both the northern and southern extents of each species breeding range, we chose species with range boundaries that are completely within the BBS survey area (Table 1). We further restricted the analysis to species that are well sampled by the BBS protocol (e.g., nocturnal species were excluded from consideration) and species that breed in eastern North America. We purposely selected a suite of species with variation in winter geography and movement strategies (year-round residents, migrants/partial migrants that winter within North America, and neotropical migrants), population trends, and body size to understand how these factors influence range dynamics. Winter geography classifications were based on ref. 53, and average body size was taken from ref. 54.

Species Distribution Model and Indices of Range Dynamics. We modeled the annual distribution of each species using the methods described by ref. 28. Briefly, we converted the raw BBS counts to stop-level presence/absence data (summarized at the 10-stop level) and used a spatially explicit dynamic occupancy model to estimate annual occurrence probability at each BBS route. For each route and year, we model occupancy probability as a function of five climate covariates and used a spatially explicit smoothing function to capture spatial variation in occupancy probability not accounted for by the climate covariates. The smoothing function is composed of basis functions and their corresponding regression coefficients, which were allowed to vary over time as temporally correlated random effects. Because BBS routes are surveyed a single time each year, we used the 10-stop presence/absence data to estimate the probability of detecting each species given that it is present within the 10-stop interval (28, 55, 56). In the observation model, we included wind speed, novice observer effects, and a random observer effect as covariates on detection probability. Models were fit using Just Another Gibbs Sampler (JAGS) (57) called from R using the jagsUI package (58). For additional information on model structure, prior distributions, and Markov chain Monte Carlo details, see ref. 28.

To estimate the annual distribution of each species, we created a 2°-buffered convex hull around all routes where the species was detected at least once. Within this area, we next created a 0.5° raster layer and extracted location and annual climate data for each 0.5° cell. Posterior distributions of the predicted annual occupancy probability in each cell were then estimated using the posterior samples for each model parameter. From these predicted occupancy probabilities, we created three indices of range dynamics: mean breeding latitude and northern and southern range limits. Annual estimates of the mean breeding latitude of each species were estimated as the sum of the cell latitudes weighted by their occupancy probabilities, divided by the total occupancy probability across all cells (59). Annual indices of the northern/southern core latitudes were estimated by sorting the map cells by latitude and then using a smoothing spline function to predict the latitudes below/above which 50% of the total occupancy probability was located (28). Northern and southern range limits were estimated using the same smoothing spline method but using the latitudes below/above which 99.9% of the total occupancy probability was located. Although not an absolute measure of the northern and southern range limits, this index provided a time series of relative change in the northern and southern range boundaries.

Estimating the Rate of Range Shifts and Influence of Species' Traits. We used the annual indices of range dynamics to test predictions about how species traits influence their response to climate change. First, we estimated the rate and direction of shifts in each index for each species by fitting a linear model with latitude as the response and year as the predictor. The slope coefficient from this model therefore measures the annual rate at which the index changed (a slope of 0 means the index remained at the same latitude throughout the study period, whereas positive/negative values indicate

the index moved northward/southward). We fit this model to each posterior trajectory of 43 yearly values of each index and summarized the rates using the mean and 2.5/97.5% quantiles (i.e., 95% CIs) of the 1,500 posterior slope estimates. We considered 95% CIs that did not include 0 as evidence of directional range shifts.

To determine how species' traits influence the rate and direction of range shifts, we fit linear models using the species-specific slope coefficients for each index as the response variable and trend, migratory status, and body size as predictors (Table 1). Again, we fit these models for each posterior sample and summarize the results using the mean and 2.5/97.5% quantiles of the slope estimates and considered 95% CIs that did not include 0 as evidence that a trait influenced the rate and direction of range shifts.

Composite Indices of Latitudinal Range Limits. In addition to estimating range dynamics for each species, we created composite latitudinal indices for groups of species. These composite indices are useful for making inferences about whether species that share specific traits have collectively shown evidence of climate-induced range shifts. To create composite indices, we first scaled the indices for each species by subtracting the starting latitude for each index. Scaling in this way removed interspecific differences in the starting latitude of each index and improved interpretability of the indices (final values greater than 0 indicate northward range shifts, and values less than 0 indicate southward shifts). Composite indices were then created by taking the mean of the scaled indices in each year for a predefined group of species. For our analysis, we created these composite indices for all species combined and for resident vs. migrant species.

Have Species Kept Pace with Climate Change? To determine whether range shifts occurred at the same rate as relevant climate variables, we extracted

the mean annual temperature for all cells within each species breeding range at the estimated latitude for each species/index. We then took the mean temperature of those cells as an estimate of the climate conditions that each species experienced at a given latitudinal index in each year. As for the composite indices described above, we next scaled the annual temperature indices by subtracting the initial temperature and then took the mean temperature indices for all species within a given focal groups (all species, long-distance migrants, and resident/short-distance migrants). Finally, we regressed the mean temperature values against year to determine the rate of climate change experienced by each group at each index. If groups tracked conditions to maintain a constant climate niche, we expected the slope from these models to be 0, whereas if climate changed faster than species distributions, we expected a positive slope. As for range shifts, we fit these models for each posterior trajectory of 43 yearly values and summarize the results using the mean and 2.5/97.5% quantiles. We considered 95% CIs that did not include 0 as evidence that climate conditions shifted faster than range indices.

Data Availability

All data used as part of this analysis are freely available through the North American BBS (https://www.pwrc.usgs.gov/BBS/RawData/) and University of East Anglia Climate Research Unit (http://www.cru.uea.ac.uk/data). For code used to fit distribution models and estimate, see Rushing et al. (28).

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