



# Significant shifts in latitudinal optima of North American birds

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Changes in climate can alter environmental conditions faster than most species can adapt. A prediction under a warming climate is that species will shift their distributions poleward through time. While many studies focus on range shifts, latitudinal shifts in species' optima can occur without detectable changes in their range. We quantified shifts in latitudinal optima for 209 North American bird species over the last 55 y. The latitudinal optimum ( $m$ ) for each species in each year was estimated using a bespoke flexible non-linear zero-inflated model of abundance vs. latitude, and the annual shift in  $m$  through time was quantified. One-third (70) of the bird species showed a significant shift in their optimum. Overall, mean peak abundances of North American birds have shifted northward, on average, at a rate of 1.5 km per year ( $\pm 0.58$  SE), corresponding to a total distance moved of 82.5 km ( $\pm 31.9$  SE) over the last 55 y. Stronger poleward shifts at the continental scale were linked to key species' traits, including thermal optimum, habitat specialization, and territoriality. Shifts in the western region were larger and less variable than in the eastern region, and they were linked to species' thermal optimum, habitat density preference, and habitat specialization. Individual species' latitudinal shifts were most strongly linked to their estimated thermal optimum, clearly indicating a climate-driven response. Displacement of species from their historically optimal realized niches can have dramatic ecological consequences. Effective conservation must consider within-range abundance shifts. Areas currently deemed "optimal" are unlikely to remain so.

climate change | species distributions | abundance shifts | non-linear species-environment models

Climate change has profound impacts on biodiversity, affecting local environmental conditions and altering species' interactions (1). A concerning aspect of recent climate change is the rise in global average temperature. Over the past two decades, Earth's surface temperatures have been 0.99 °C higher, on average, than in pre-industrial times (2). Each species lives within a specific envelope of biotic and abiotic conditions that constrains its spatial distribution (3, 4). With rising temperatures, sites once suitable to sustain a given species may no longer be suitable. Some species may undergo local or global extinction, while others may adapt (5). For many species, the pace of climate change outstrips the time required for evolutionary adaptations (6); however, populations may shift temporally and/or spatially toward realized niches that permit survival (1, 7).

Species may adapt to climate change by shifting their range to higher latitudes and/or elevations (8). In a recent global meta-analysis, Lenoir et al. (9) found an overall poleward expansion of  $6.02 \pm 1.77$  km  $y^{-1}$  in the leading-edge range of marine taxa accompanied by a southward contraction of  $6.49 \pm 2.13$  km  $y^{-1}$  in the trailing edge, both shifts linked to climate warming (9). For terrestrial species, they found an upslope shift in the trailing and leading edges of  $2.34 \pm 0.67$  and  $2.15 \pm 0.60$  m  $y^{-1}$ , respectively, although overall there was no significant latitudinal shift detected (9). By focusing on the edges of species' spatial distributions (ranges) or only on presence/absence data, important changes in either total or relative abundances within species' ranges can be missed (9, 10). Furthermore, measures of changes in spatial distributions that focus on shifts in species' modal positions along gradients are more likely to detect smaller shifts and are less susceptible to errors caused by differences in sampling effort over time (11).

Species may show a change in total abundance (population size), or a spatial shift in peak mean abundance along latitude or elevation gradients (i.e., their "optimum") in response to climate change, without necessarily showing a shift of the range limits (12, 13). Population declines have been documented and projected for a wide range of taxa (14), but climate-driven shifts in species' optima along broad-scale spatial gradients are comparatively less well-studied. Species are expected to reach peak mean abundances where biotic and abiotic conditions are optimal for them (15–18). Shifts in elevational or latitudinal optima can provide an important ecological signal of either changing environmental conditions, or displacement of species into sub-optimal environments. For example, Lenoir et al. (19) demonstrated upward shifts in estimated optimal elevations

## Significance

We estimate that the latitudinal optimum (peak mean abundance) of 209 North American birds has shifted northward at an average rate of 1.5 km/y over the past 55 y. We also show that birds from eastern and western North America have distinct trends, with birds in the western region experiencing stronger poleward shifts. Our results directly implicate climate-induced increases in temperature as the primary driver, with birds' thermal optima being the strongest predictive trait of inter-specific differences in rates of latitudinal change through time.

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of mountainous forest plants associated with a warming climate. We consider detection and quantification of climate-related shifts in abundance optima to be critical, as precursors of broad-scale potential range shifts and population declines (12).

The propensity and rate at which species respond to climate change by shifting their spatial distribution depends on a host of intrinsic and extrinsic biological and environmental factors (20, 21). First, climate change is a complex phenomenon that is not spatially homogeneous. Elevation and latitude can interact in their effects on species (21, 22); indeed, sites at higher latitudes are more strongly affected by global temperature increases (10, 23). Furthermore, local and regional topography affect climatic conditions, so populations separated by significant geographical barriers may differ in their responses (24). Superimposed on these extrinsic factors are species' intrinsic traits, particularly those associated with capacity for movement, proliferation, emigration, and establishment in new surroundings (25). For example, vagile ecological generalists are expected to readily colonize new areas, whereas poor dispersers with specialized resource requirements are more likely to experience population declines as ecosystems change (26, 27). However, our understanding of which traits may result in greater resilience *via* spatially adaptive responses to climate change remains limited (28).

Birds are the most speciose clade of terrestrial vertebrates. They are found in virtually every ecosystem, performing essential functions and services, including nutrient cycling, seed dispersal, pest control, and pollination (29). Current declines in total abundances of many bird populations are well documented (30–32). One in every eight species of bird is currently threatened with extinction, with climate change playing a prominent role (32). Quantifying responses of birds to climate change is essential for their conservation and for the maintenance of terrestrial ecosystems.

Several broad-scale multi-species studies have demonstrated shifts in geographical ranges or range limits for bird species over the last two to five decades, across many regions of the world (21, 33–35). However, the use of presence-absence (or presence-only) data—although standard for most species distribution models (SDMs) in ecology (36)—can mask shifts in population densities (10). In addition, sightings of species in areas of low mean abundance are more sporadic than in areas where mean abundances are high (37). Thus, not surprisingly, results obtained regarding shifts at range boundaries are more variable than those measured at their center of abundance (38). Inconsistencies in the results of studies focused on range boundaries—e.g., for north–south vs. east–west directions (39–41), and across different regions of the world—has generated debate regarding the relative roles of climate change vs. changes in land-use and other factors potentially affecting bird distributions (13, 34, 39).

Few large-scale multi-species studies of birds have examined shifts in species' latitudinal optima within species' ranges at a continental scale. Most have been restricted to a modest number of species and/or to narrow geographical regions, such as Finland (10, 42, 43), Great Britain (44), New York State (33), and the Sierra Nevada (7). Measures used to quantify abundance-based species' optima also have varied; these include weighted averages of latitude (10, 38, 42, 45), estimates from generalized additive models (GAMs) (12, 35, 44, 46) or abundance estimates at spatial scales much larger than the scale of observations (e.g., strata averaging 59,000 km<sup>2</sup>) (41, 47). Unfortunately, neither weighted averages of latitude nor GAMs will necessarily accommodate asymmetrical mean responses of species along gradients (48), along with the over-dispersion (49) and zero-inflation (50) inherent in broad-scale observational data (51). Some studies have included a species-specific measure of detectability in abundance-based models of species' latitudinal optima

(44, 52, 53) but many zeros can occur (even at a species' optimum position along a given gradient) due to a wide variety of other (measured or unmeasured) limiting factors unrelated to detection (54). We aim here to achieve a rigorous overall estimate of the mean shift in birds' latitudinal optima over recent decades of rapid climate change at a continental scale.

Potential factors driving inter-specific differences in the direction and magnitude of shifts in latitudinal optima for birds require investigation. Some traits, such as body mass, migratory behavior, territoriality, population size, and habitat associations, have been shown to affect bird species' responses to climate change (45, 46, 55). We regard species-specific thermal preference (i.e., their optimal temperature) and thermal tolerance as traits of particular interest, as species from colder, more exposed regions and with narrower climatic ranges are more likely to be negatively affected by climate change (26, 56).

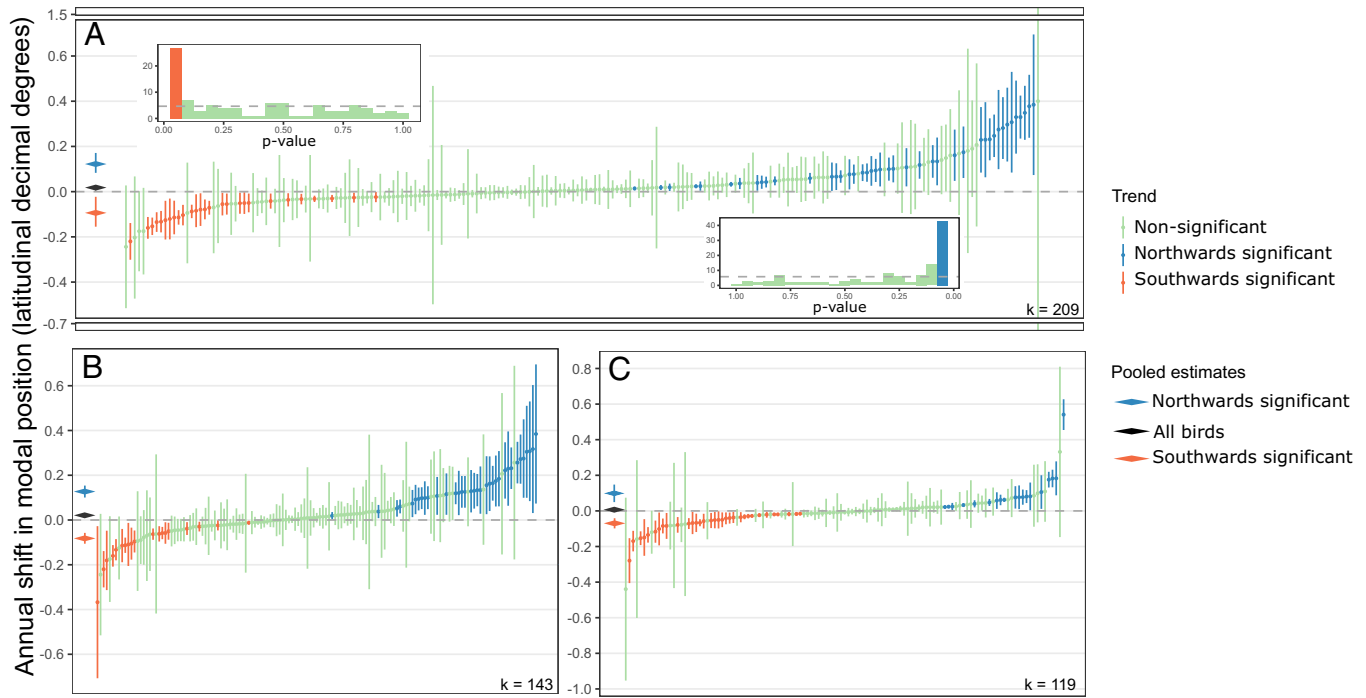
In this study, we created and implemented an improved modeling approach to answer the following questions: 1) Overall, have the bird species of North America shifted their latitudinal optima significantly over the past 5.5 decades? 2) If so, has this shift been northward, in accordance with climate-change predictions? 3) What is the size of the overall estimated shift? and 4) Are shift magnitudes linked to species' traits—in particular, to species' thermal optima?

We estimated the optimum latitude (i.e., the latitude at which mean abundance is maximized) for each of 209 North American bird species annually, over a period of 55 y, using the North American Breeding Bird Survey (BBS) dataset. Analyses were done at a continental scale, and, separately, for eastern and western regions. We examined directional changes (north or south) in individual species' latitudinal optima through time, and explicitly quantified, in meta-analyses, the overall shifts across all species. We hypothesized that, overall, there would be a significant poleward shift (northward) in latitudinal optima across all bird species, and that this would be consistent at the continental and regional scales. We also hypothesized that variation across species in the absolute magnitude of their shift in optimum would depend on bird traits. Specifically, we examined and quantified the extent to which a given bird species' dispersal capability, migration strategy, territoriality, habitat generality, preferred habitat density, and/or thermal optimum could explain the shift in its latitudinal optimum.

## Results

**Shifts in Species' Latitudinal Optima Over Time.** The distribution of *p*-values obtained from individual tests for a trend in latitudinal optimum (*m*) over time for every species was clearly non-uniform (Fig. 1). Using a significance level of  $\alpha = 0.05$  (and assuming independent tests), we would expect 5% of the *p*-values to be less than 0.05 by chance alone. However, one-third of North American bird species (70 out of 209) demonstrated a significant shift in their latitudinal optimum ( $P < 0.05$ ), with 61% of these shifting northward (Table 1; combined dataset). At a continental scale, the pooled estimated mean shift in latitudinal optimum across all species at the continental scale was 1.5 km northward per year ( $\pm 0.58$  SE), corresponding to a total distance moved, on average, of 82.5 km ( $\pm 31.9$  SE) over the last 55 y ( $m = 0.0134^\circ$ , CI = {0.0033°, 0.0236°},  $P = 0.0095$ ; Fig. 1A and *SI Appendix, Table S1*). In terms of absolute shift (i.e., regardless of the direction north or south), the estimated mean size of the latitudinal shift in absolute value was  $|m| = 0.0463^\circ$  per year (95% CI = {0.0309°, 0.0616°},  $P < 0.001$ ; *SI Appendix, Table S2*).

For the subset of bird species in the combined dataset that shifted significantly northward, the overall estimate was  $m_{north} = 0.1171^\circ$  (CI = {0.0889°, 0.1452°},  $P < 0.001$ , Fig. 1A and *SI Appendix,*



**Fig. 1.** Model pathway for estimating the latitudinal optimum and temporal trends in the latitudinal optimum for bird species. (A) Obtain the raw abundance data for each combination of data subset (East, West, or Combined; Table 1), species, and year. As an example, we show the raw continental abundance data of Eastern Wood-Pewee (*Contopus virens*) for the year 2001. (B) Use the Modskurt modeling framework outlined in Appendices 1 and 2 to estimate the latitudinal optimum (modal position) ( $m$ ) for each year. (C) Run generalized least squares (GLS) models to estimate the temporal trends in the latitudinal optimum ( $m$ ) for each combination of species and data subset. In the example, we show the continental poleward trend of the Eastern Wood-Pewee. Image credit: Eastern Wood-Pewee by Andy Reago & Chrissy McClarren, licensed under CC BY 2.0 <https://creativecommons.org/licenses/by/2.0>, via Wikimedia Commons.

Table S3), corresponding to ca. 13 km/y ( $\sim 715$  km in 55 y). This was 1.6 times higher than the overall estimated shift for the subset of birds moving significantly southward ( $m_{south} = -0.0781^\circ$ , CI =  $\{-0.1432^\circ, -0.0130^\circ\}$ ,  $P < 0.001$ , Fig. 1A and *SI Appendix, Table S4*), which was ca. 8.7 km/y ( $\sim 478.5$  km in 55 y).

At the regional scale, there was a higher proportion of significant northward shifts in latitudinal optima in the West and a higher proportion of significant southward shifts in the East (Table 1,  $\chi^2_1 = 7.38$ ,  $P < 0.01$ ). For the West, the estimated average overall northward shift was  $m_{West} = 0.0202^\circ$  (CI =  $\{0.0041^\circ, 0.0362^\circ\}$ ,  $P = 0.0137$ , Fig. 1B and *SI Appendix, Table S5*), approximately 2.2 km/y. For the East, however, results were more variable across species, and the overall estimate did not differ significantly from zero (Fig. 1C and *SI Appendix, Table S6*).

For each species and data subset, we divided the rate of change for individual species ( $\beta$ ) by its SE, giving us a measure to identify species exhibiting stronger and more consistent latitudinal shifts (Dataset S3). Those with the highest  $\beta/SE(\beta)$  ratios shifting northward were: Cassin's Sparrow (*Peucaea cassinii*) in the East ( $60.02 \pm 4.9$  km/y), Brown Creeper (*Certhia americana*) ( $19.54 \pm 2.50$  km/y), and Eastern Wood-Pewee (*C. virens*) ( $6.93 \pm 0.65$  km/y). Those with the highest  $\beta/SE(\beta)$  ratios shifting southward were Mississippi kite (*Ictinia mississippiensis*) ( $17.07 \pm 2.19$  km/y), northern harrier (*Circus cyaneus*) ( $12.68 \pm 1.82$  km/y), and Baltimore oriole (*Icterus galbula*) in the West ( $3.14 \pm 0.40$  km/y).

Significant shifts in latitudinal optima were detected for four out of the nine "near threatened" bird species examined in our study. In the East, the wood thrush (*Hyllocichla mustelina*) displayed a significant southward shift of  $5.54 \pm 2.35$  km/y, while significant northern shifts were detected for the common grackle (*Quiscalus quiscula*) ( $4.41 \pm 1.13$  km/y) and the loggerhead shrike

(*Lanius ludovicianus*) ( $7.37 \pm 1.12$  km/y). In addition, significant northward shifts were observed for the eastern meadowlark (*Sturnella magna*) in both the West ( $6.72 \pm 1.75$  km/y) and in the East ( $8.93 \pm 2.05$  km/y).

**Relationship between Shifts in Optima and Species' Traits.** There was no qualitative difference between the model that included all bird species and the model excluding species that lacked precise estimates of thermal range. Therefore, the final continental-scale model was built using all predictor variables and all species (except for three species that had no values for SSI, *Materials and Methods*).

We found the absolute value of the shift in latitudinal optimum at the continental scale was significantly related to four traits: thermal optimum, territoriality, habitat specialization, and dispersal capability (*SI Appendix, Table S7*). However, the direction of the shift (northward vs. southward) was also significant, as were its interactions with species' traits (*SI Appendix, Table S7*). Therefore, we conducted separate analyses for species that exhibited southward trends (*SI Appendix, Table S8*) and species that exhibited northward trends (*SI Appendix, Table S9*). For species showing a southward shift, the global test (across all predictors) was not statistically significant (see *SI Appendix, 3*, although the individual predictor of the hand-wing index was marginally so, see *SI Appendix, Table S8*). Therefore, we focus our attention here on the results of the model for species with northward trends (*SI Appendix, Table S9*).

At the continental scale, northward shifts in latitudinal optima ( $m$ ) per year were significantly related to (in order of importance): a bird species' thermal optimum, its territoriality, and its degree of habitat specialization (*SI Appendix, Table S9*). Bird species with colder optimal temperatures had significantly higher northward

**Table 1. Data subset used for each geographical analysis and descriptive summary of results concerning the number (and percentage) of significant shifts in latitudinal optima for bird species**

Geographical subset	Data subset	Number of species in subset	Number of Significant trends	Significant northwards	Significant southwards
East	Eastern birds + Eastern distribution of widespread birds	119	52 (~44%)	19 (~37%)	33 (~63%)
West	Western birds + Western distribution of widespread birds	143	54 (~38%)	35 (~65%)	19 (~35%)
Combined	Eastern birds + Western birds + Intermediate birds + Widespread birds	209	70 (~33%)	43 (~61%)	27 (~39%)

annual shifts (Fig. 2B). More specifically, we estimated that the magnitude of their annual optimum shift decreased by  $-0.003$  latitudinal degrees (CI =  $\{-0.0043^\circ, -0.0017^\circ\}$ ,  $P < 0.0001$ ), or about  $0.33$  km, for every  $1^\circ\text{C}$  increase in a species' thermal optimum (Fig. 2B and *SI Appendix, Table S9*). Non-territorial species had significantly greater northward shifts in their latitudinal optima than either weakly territorial or strongly territorial species (Fig. 2A). In addition, habitat generalists shifted more, on average, than habitat specialists; that is, annual shifts were negatively linked to the degree of habitat specialization (SSI slope estimate =  $-0.0193$ ; CI =  $\{-0.0333, -0.0053\}$ ,  $P = 0.0068$ , Fig. 2C and *SI Appendix, Table S9*).

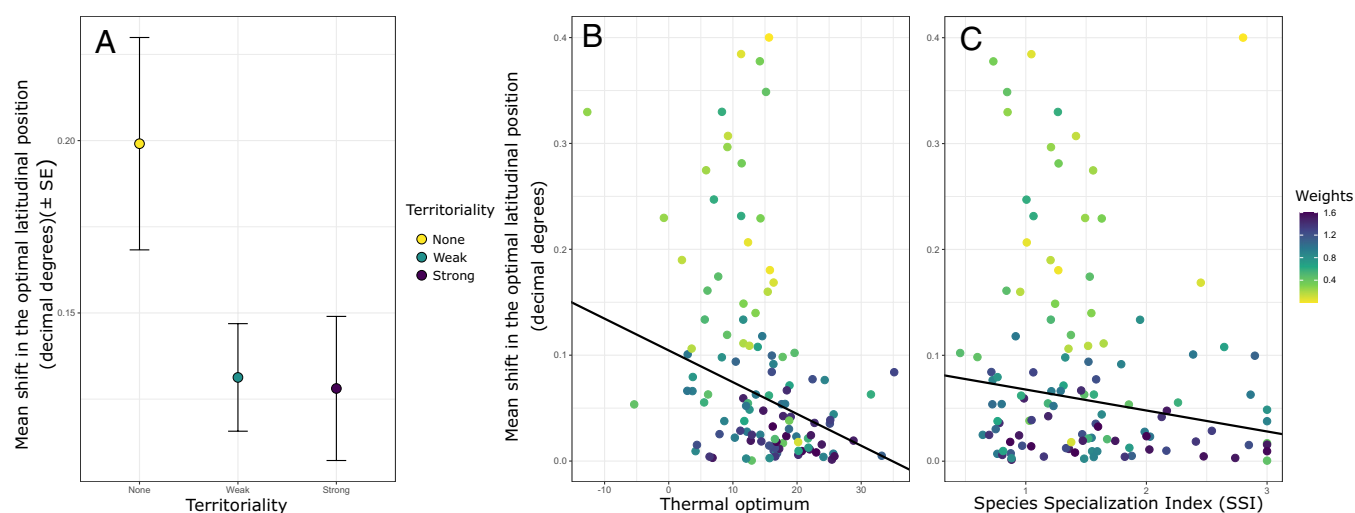
At the regional scale, the relationships between shifts in the absolute value of latitudinal optima and the species-specific traits investigated here were only statistically significant for the West (*SI Appendix, Table S10*). (In the East, although thermal range appeared initially to be significant, it did not remain so once we removed species without precise thermal range estimates; *SI Appendix, 3*). Furthermore, unlike the continental-scale analysis, the direction of the shift (northward vs. southward) was not significant for either the West or East regional-scale models (*SI Appendix, 3 and Table S10*). As for the continental-scale models, no qualitative differences attended results obtained for the western region when species with less precise thermal tolerances were omitted, so the final

model for the West was built using the full set of predictor variables and with all bird species. The absolute value of the shift in the latitudinal optimum per annum for birds in the West was negatively related to (in order of importance): estimated thermal optimum, preferred density of habitat, the degree of habitat specialization, and the degree of territoriality (Fig. 3 and *SI Appendix, Table S10*). In other words, in the West, a bird species showed a greater latitudinal shift, on average, if they i) prefer colder temperatures; ii) prefer denser habitats; iii) are not habitat specialists; iv) and/or are not territorial.

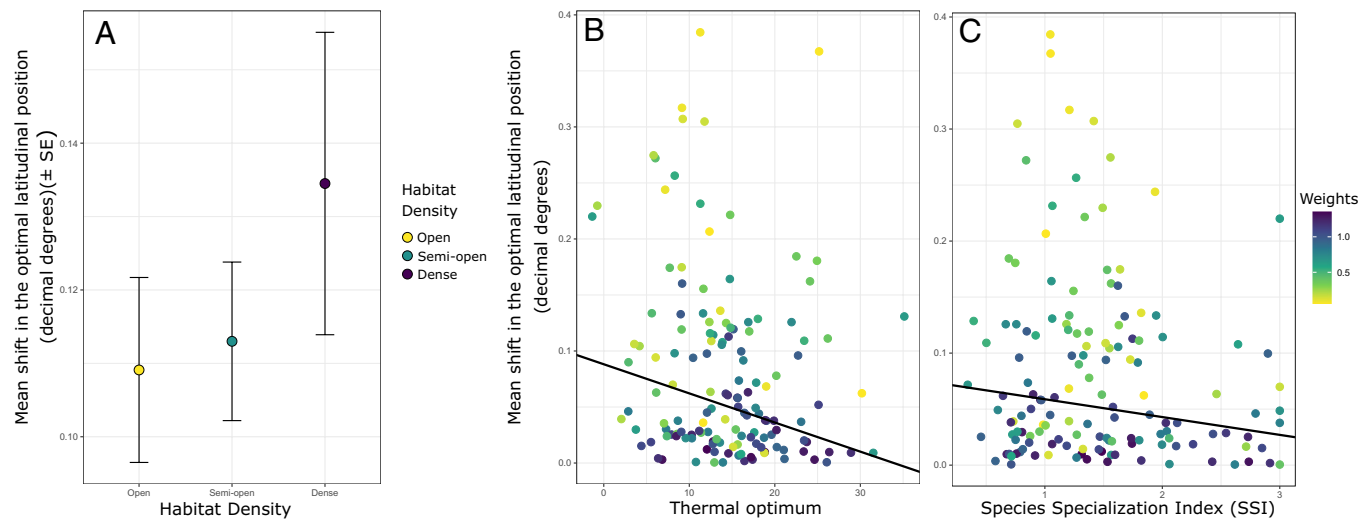
Phylogenetic relatedness among species accounted for very little of the inter-specific variation in shifts of latitudinal optima. The non-phylogenetic component of inter-specific variation was estimated to be 13 times the size of the phylogenetic component at the continental scale (*SI Appendix, Table S9*), and 15 times the size of the phylogenetic component for birds in the West (*SI Appendix, Table S15*).

## Discussion

One-third of the 209 North American bird species investigated here demonstrated significant shifts in their latitudinal optima over the past five-and-a-half decades. Birds shifted significantly northward, on average, at a rate of  $1.5$  km ( $\pm 0.58$  SE) per year,



**Fig. 2.** Meta-analysis plot of the estimated shift in latitudinal optimum per year (in decimal degrees) for each bird species (with 95% CI, ordered in increasing value from left to right), with colors indicating statistical significance toward either the north or south ( $P < 0.05$ ), and with three overall estimates shown at the far left of each panel: one for the subset of species shifting significantly northward (blue), one for the subset of species shifting significantly southward (orange) and one for all birds (black). Results are shown for each of three datasets (as outlined in Table 1): (A) the combined dataset (all of North America,  $n = 209$  species), (B) the West ( $n = 143$  species), and (C) the East ( $n = 119$  species). Insets show the frequency distribution of  $P$ -values for the test of  $H_0$ : no shift in latitudinal optimum, with the dotted line showing the expected (uniform) distribution of  $P$ -values under a true null hypothesis.



**Fig. 3.** Significant relationships identified in the meta-regression analysis between the estimated annual shift in latitudinal optimum (in decimal degrees per year) and: (A) territoriality, (B) thermal optimum (in °C), and (C) the species specialization index (SSI), for  $n = 206$  individual bird species across North America at the continental scale (combined dataset). Weights from the meta-analysis are shown using a color gradient in (B) and (C), with bird species having less variability in their estimated latitudinal optimum being weighted more heavily.

amounting to a total average distance moved of 82.5 km ( $\pm 31.9$  SE) in 55 y. Species from western North America had stronger poleward shifts than species from the eastern region, where no overall latitudinal trends were found. The strongest predictor of inter-species variation in the sizes of shifts found here was a physiological trait—namely, thermal optimum. Bird species with colder optimal temperatures had significantly higher annual shifts in their latitudinal optima, indicating that these shifts are directly linked to increasing temperatures from climate change. Thus, this key physiological trait has hereby been directly linked to widespread multi-species climate-driven movement responses of bird species at a continental scale. Ornithologists interested in particular species can refer directly to the results we provide in [Dataset S3](#), where estimated trends are documented for every species.

Our results are consistent with the general expectation that species will move to higher latitudes to track suitable climate conditions as average global temperatures rise (8, 57). The estimated size of the overall shift in latitudinal optima (1.5 km/y) is substantial. It exceeds an estimate obtained in a study of North American birds completed 15+ years ago (1.03 km/y) (38) and the estimated trend obtained for 94 bird species in Finland completed 9 + years ago (1.26 km/y) (10). More recently, Lehtikoinen et al. (43) estimated a shift of 1.95 km/y for 31 bird species in Great Britain over 39 y (1970 to 2009) and 0.84 km/y for 21 bird species in Finland over 27 y (1981 to 2008). Although Huang et al. (41) documented centroid shifts of 5.89 km/year, this was for a subset of just 36 species showing significant shifts in any direction. Their study also was based on large-scale models of abundance for spatial strata averaging 59,000 km<sup>2</sup> in size (rather than at the scale of individual BBS routes). McCaslin and Heath (47) examined 73 species of migratory birds in North America over a 23-y period (1994 to 2017) and estimated a northward shift of 3.67 km/y, but this was based on essentially the same large-scale (strata) approach of Huang et al. (41) and was restricted to birds demonstrating a northward shift. By comparison, if we similarly restrict our estimate to reflect only those species showing a significant northward shift (43 species, Table 1), the estimated latitudinal shift is 13 km/y ( $\pm 1.6$  SE), indicating literally hundreds of kilometers of movement for these species over the past half-century.

Despite the overall northward trend, we also found a high level of variability across species, with some species moving southward and others not exhibiting any significant latitudinal shift through time. Variability in the direction of shifts has been reported often (40, 41, 57) and can be caused by a variety of factors, including sensitivity to supplemental cues (such as vegetation green-up) (47), disturbance-driven release from competition (58), and potentially opposing effects of climate change and land-use changes (9). Some species may be unable to move due to dispersal limitation, geographical barriers, inter-specific interactions, or the availability of suitable habitats (59, 60), hence may experience population declines (31). Some may have relied on climatic refugia in microhabitats (61) or have undergone adaptive phenological shifts (5), while others may be shifting their optimum simultaneously along other spatial axes, such as altitude or longitude (13). Potential explanations clearly warrant more detailed investigations at the individual species level.

We also found distinct differences in eastern vs. western trends. In the West, latitudinal optima shifted poleward on average (at a rate of 2.2 km/y), while in the East the overall shift was not significant. This could be due to different rates of warming in the two regions; climate simulation models show greater warming in the West vs. the East, where there appears to be a lack of warming or even a cooling tendency over some areas (the so-called “warming hole”) (62, 63). Furthermore, species may be limited by different climatic variables in the two regions. North America is divided into an arid west and a humid east resulting from large-scale atmospheric circulation and moisture transport processes (62, 64). Species in the West may be more affected by temperature changes, while eastern species may be more limited by precipitation (65). In addition, there is decreasing environmental variation and habitat heterogeneity along with increasing primary productivity along a longitudinal gradient from west to east, which can reduce the effects of deterministic environmental filtering (66). Finally, species tend to shift toward directions that offer low resistance to dispersal (67). The generally north-south orientation of the Pacific coastline, the Rocky Mountains, and the Cascade Range together form north-south corridors that can facilitate latitudinal shifts in the western region. Although none of the above explanations are mutually exclusive, the significant association between optimum

shifts and species thermal optimum indicates that the difference in rates of warming in the two regions is among the most likely explanations. Due to the warming hole, species inhabiting the eastern region may not need to shift poleward to keep pace with their temperature optima.

Inter-specific variation in the size and direction of shifts in latitudinal optima was not well explained by phylogenetic relationships among species. This accords with previous findings that suggest traits can be poor predictors of species' responses to climate change (68–70). However, traits that are not necessarily phylogenetically (or taxonomically) conserved, or that are not easily measured, can nevertheless play an important role in climate adaptation. Closely related species can differ markedly in their climate sensitivities, niche optima, and tolerances, which in turn can influence how climate change will affect their fitness (69, 71).

We found a physiological trait (thermal preference) to be a strong predictor: larger latitudinal shifts were associated with a preference for colder environments. This may be linked to latitudinal differences in the rate of climate warming. Species that prefer cooler environments likely inhabit higher latitudes, where climate warming tends to be greater (23). For example, Virkkala and Lehikoinen (10) found that poleward density shifts were greater among birds in northern Finland, where temperatures have risen more rapidly, than among southern species. There may be physiological limitations associated with living in colder environments, with a substantial reduction in the fitness of cold-acclimated individuals when exposed to warmer temperatures (72).

Birds have been found to track their climate niche through time, and our results support earlier studies demonstrating that habitat-generalist bird species are more likely to do so than habitat specialists (7, 46). Habitat availability can outweigh the importance of climate for specialist species. Additional characteristics, such as the ability to overcome anthropogenically altered landscapes (73) and exploit novel resources (74), may make habitat generalists better at following optimal environmental conditions and colonizing new environments.

We found that bird species lacking territorial behavior demonstrated greater shifts in their latitudinal optimum through time alongside a changing climate. This contrasts somewhat with previous studies on birds, where territoriality was positively associated with climate matching (46, 75). Although a species exhibiting territorial behavior may possess greater competitive abilities for defending their climate niche in altered environmental circumstances, territorial species also generally have lower dispersal capability and relatively sedentary lifestyles which would limit their overall ability/tendency to shift geographically (76).

Finally, we found in the West that bird species primarily inhabiting denser, more forested environments demonstrated greater shifts in their latitudinal optima through time compared to those preferring more open habitats. This result was the opposite to what we had predicted; we expected denser habitats might buffer the effects of climate change on species (77). Viana and Chase (46), for example, found that birds in open habitats were better adapted to their climatic niche. However, the use of macroclimatic data to model species' responses to climate change can lead to misleading conclusions, as broad-scale data may not necessarily match well with smaller-scale environmental conditions experienced by organisms (78). For instance, Haesen et al. (78) found that SDM models that used macroclimate data overestimated species' tolerances, given the buffering effects of forests.

Additionally, it is possible that decreases in habitat quality over several decades, due to urbanization and deforestation (including increasing frequency and severity of fires in forested areas across the western region) (79, 80), have driven species in denser habitats

to move. For instance, Guo et al. (81) examined elevation shifts for several animal and plant species and found that baseline forest cover and changes in forest cover over time significantly influenced the extent of distribution shifts. Their findings emphasize the importance of considering the simultaneous interplay between climate change and land-use change on species' distributions (81). Species may respond more strongly to the indirect effects of climate change on habitat availability than to direct physiological impacts of small gradual increases in mean temperature, per se (60).

We attribute the overall poleward trend documented here at the continental scale and for the western region to rising temperatures, whether they be a consequence of direct or indirect effects. First, the large spatial extent of our study reduces the possibility that unmeasured factors (such as elevation or inter-specific interactions, that are unlikely to have a consistent relationship with latitude), are primary determinants of our findings. Second, the strong effect of birds' thermal preferences in explaining inter-specific variations in optimal shifts supports the hypothesis that temperature is a major driver. Nevertheless, inconsistencies among species and between western and eastern regions highlight the complexities and multi-directional nature of species' within-range movements (13).

Shifts in species' optima result from spatial changes in meta-population dynamics, including deterministic and stochastic processes affecting birth and death rates within local populations, and the spatial aggregation and dispersal of individuals. Spatial changes in species abundance peaks may reflect shifting fitness gradients whereby some local populations have higher survival rates than others. They may also be due to individuals dispersing and/or aggregating toward optimal environmental envelopes, preferred resources or to find mates. Regardless of the underlying processes, spatial shifts in peak abundances have important ecological and evolutionary consequences, altering community dominance patterns (82), functional diversity (10), and biotic interactions (83). The conservation and sustainability of avian biodiversity requires pro-active management strategies that consider not only future forecasts, but the evidence of rampant changes happening now (20). Shifts in peak abundance are critical to assess regularly, as areas currently deemed "optimal" are not likely to remain so.

## Materials and Methods

**Bird Dataset.** We used annual count data from the North American BBS over a period of 55 y, from 1966 to 2021 (84). Data are collected from thousands of roadside survey routes in 37 Bird Conservation Regions (BCRs) across the United States and Southern Canada. Each route is 40 km long and consists of 50 stops separated by 800 m. Every year, in a single day during the local bird breeding season, a single observer conducts a 3-min point-count at each stop (85, 86). We only used data that fit the official BBS data quality criteria (see ref. 84 for more details).

The complete BBS dataset includes more than 700 avian taxa. For our study, we removed i) taxa not identified to species level; ii) species with fewer than 50 occurrences over 10 or more years; and iii) primarily nocturnal or aquatic species. Subspecies were grouped under their main epithet. In addition, birds were filtered based on how much of their known range was covered by the BBS spatial extent. First, we used all routes to create a geographic concave hull representing the BBS coverage. Next, we obtained independent distributional data for each species from *BirdLife International* and *Handbook of the Birds of the World* (87). We retained all species for whom the BBS coverage covered at least 70% of their total known breeding distribution (for migrant and partial migrant birds) or resident distribution (for resident birds). Some species are naturally rare, despite having most of their range sampled, so we also retained birds with at least 20 occurrences over 10 or more years for whom the BBS coverage included at least 90% of their breeding or resident distribution. Finally, four bird species were excluded from subsequent analyses because our models estimated either that their optimum lay outside the range of latitudes sampled by the BBS (*Contopus cooperi*, *Junco*

*hyemalis*, *Melospiza lincolni*) or their abundance pattern was multi-modal (i.e., showing multiple peaks in mean abundance vs. latitude, *Cathartes aura*).

Our final dataset therefore included counts in at least 10 y for each of 209 bird species from seven orders (Dataset S1): Passeriformes (174), Piciformes (12), Accipitriformes (10), Galliformes (8), Columbiformes (2), Cuculiformes (2), and Falconiformes (1). In terms of conservation status, two species are classified by the IUCN (88) as “vulnerable”: the chestnut-collared longspur (*Calcarius ornatus*) and the pinyon jay (*Gymnorhinus cyanocephalus*). Nine are classified as near threatened: the greater sage-grouse (*Centrocercus urophasianus*), northern bobwhite (*Colinus virginianus*), wood thrush (*H. mustelina*), loggerhead shrike (*L. ludovicianus*), Bachman’s sparrow (*Peucaea aestivalis*), common grackle (*Q. quiscula*), cerulean warbler (*Setophaga cerulea*), eastern meadowlark (*S. magna*), and golden-winged warbler (*Vermivora chrysoptera*). The remaining 198 (out of 209) are considered of “least concern” (SI Appendix, Table S3).

See Dataset S1 for our final list of birds with their migration category based on Tobias et al. (89) and percentage of geographical range covered by the BBS sampling extent. The number of routes sampled by the BBS has increased over time from 1966 (400 routes) to 2021 (2,540 routes). The total number of observation rows (all route-by-year combinations) utilized in our study was 119,567.

**Geographical Subsets.** Eastern and western regions of North America are divided by large-scale topographic barriers (90) and differ in their atmospheric circulation, moisture transport, and bio-physical climatic conditions (64). We expected eastern and western regions to have differing bird communities that would potentially have different responses to broad-scale climate change. To identify an appropriate east-west divide on the basis of bird community composition, we performed a spatially constrained cluster analysis on the basis of Bray-Curtis dissimilarities among BCR units. Dissimilarities were calculated from square-root transformed dispersion-weighted abundance values to decrease the relative importance of highly abundant and/or erratic or flocking bird species (91). We used regionalization with dynamically constrained agglomerative clustering and partitioning (REDCAP) (92, 93) with group-average linkage. Following this, all BBS routes were classified as either eastern or western. Our resulting east-west divide roughly matches the 100th Meridian (SI Appendix, Fig. S1).

We classified each of the 209 bird species as being “eastern”, “western”, “widespread”, or “intermediate” in its distribution. A species was classified as either eastern (32 species) or western (56 species) if it occurred in 50 or more routes in only one of the two regions. A species was classified as widespread (88 species) if it occurred in at least 50 routes in both eastern and western regions. Species not meeting either of these criteria (e.g., with 20 occurrences in the east and 30 occurrences in the west) were classified as intermediate (33 species).

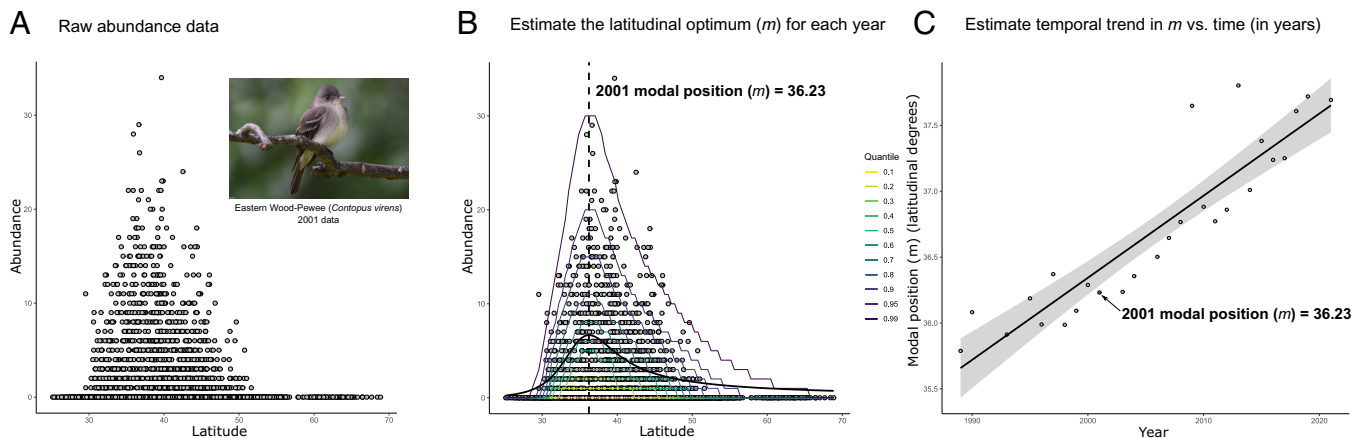
We performed separate analyses for each of three geographical subsets of data (Table 1): i) East (eastern birds and the eastern routes for widespread birds); ii) West (western birds and the western routes for widespread birds); and iii) Combined (all birds at the continental scale). One species (*Passerina caerulea*)

was widespread, but was only analyzed for the combined dataset because its estimated optimum occurred outside the latitudinal range of BBS data in the west.

**Statistical Models of Species’ Latitudinal Optima.** The mean abundance response of a species along a natural broad-scale spatio-environmental gradient (such as latitude, moisture, temperature, etc.) is generally expected to be unimodal (15, 16), although not necessarily symmetric or Gaussian (48, 94, 95). We used species-environment non-linear models (*senlm*) (51) as a flexible parametric framework to characterize the unimodal mean response of each species vs. latitude within each year. Two important parameters from these models include the maximum estimated mean abundance ( $H$ , the height of the mode in the unimodal response), and the position along the gradient of that peak mean abundance ( $m$ , the modal latitudinal position). The estimated value of  $m$  is directly interpretable as the optimal latitude for the species along the gradient. Note that eastern, western, and intermediate species only have one estimated modal position per year, whereas widespread birds have three per year: one for the east, one for the west, and one for the entire dataset.

Here, we extended the *senlm* framework to create a non-linear mean function (called *modskurt*; SI Appendix, 1) that is modular, allowing increasing complexity in the shape of the unimodal response curve to include i) left/right asymmetry, ii) peakedness/flattening, and/or iii) exaggerated tails, via inclusion of relevant additional parameters. A bespoke model-selection procedure was then used to choose an appropriate level of complexity for the abundance-vs-latitude model (mean function + error distribution) for each species-by-year combination (SI Appendix, 2). Importantly, the meaning and interpretation of the *modskurt* function’s core parameters ( $H$  and/or  $m$ ) is not altered by increasing (or decreasing) the complexity of the required mean response shape in individual cases. Thus, estimated values of  $m$  can be validly compared through time and/or across species. In addition, the error component in our *senlm* framework directly models the most vital and well-recognized statistical properties inherent in broad-scale observational species count data (SI Appendix, 1); namely, overdispersion (91, 96), zero-inflation (37, 50), mean-variance relationships (49, 96) and occupancy-abundance relationships (37). Dataset S2 contains the individual estimated values of species’ latitudinal optima ( $m$ ) for all species-by-year combinations for each dataset (East, West, and Combined).

We consider our *senlm modskurt* models to be particularly efficacious at drilling through the “noise” inherent in continental-scale observational data to quantify these key signals. Calculations of mean (or weighted mean) latitude values (i.e., a “center of abundance”) using raw counts or densities, or analyses of mean (or modeled) abundances for broad-scale spatial units will not accommodate the skewed/asymmetric nature of count data that is apparent both within a given latitude (handled here via the use of a zero-inflated negative binomial error distribution), and also across latitudes (handled here by the flexible shape of the *modskurt* non-linear function for the mean response). Unfortunately, asymmetry and zero-inflation can cause even flexible empirical GAMs to yield biased estimates of species optima along gradients (51).



**Fig. 4.** Significant relationships identified in the meta-regression analysis between the estimated annual shift in latitudinal optimum (in decimal degrees per year) and (A) habitat density, (B) thermal optimum (in °C), and (C) the SSI, for  $n = 140$  individual bird species in the West (as per Table 1). Weights from the meta-analysis are shown using a color gradient in (B) and (C), with bird species having less variability in their estimated latitudinal optimum being weighted more heavily.

For each species, we plotted the estimated values of their latitudinal optimum ( $m$ ) vs. time (in years) and estimated the linear slope ( $\beta_m$ ) of this relationship (Fig. 4) using generalized least squares (GLS), with temporal autocorrelation being accommodated by using either first-order or second-order auto-regressive errors (i.e., AR(1) or AR(2), chosen by AIC). All GLS models were fitted using the *gls* function in the R package *nlme* (97). Species classified as eastern, western, or intermediate had one fitted GLS model (hence, one estimated slope parameter), while those classified as widespread had three: one for each regional subset (East and West) and one for their entire distribution across all of North America (Combined). **Dataset S3** contains detailed results from all GLS models (estimates of parameters, associated SE, and  $P$ -values) for each individual bird species and dataset. Each estimated slope parameter provides a direct estimate of the latitudinal shift (per annum) in a given species' peak mean abundance (its optimal latitudinal position) for a particular dataset (East, West, or Combined), with a positive slope indicating a northward shift.

**Meta-Analyses of Regional and Continental Trends.** Slopes (and their SE) from GLS models for each species were used as input into a multi-level random-effect meta-analysis to obtain an overall quantitative estimate of the shift in latitudinal optima across all bird species. A separate meta-analysis was done for each of the three datasets: East, West, and Combined (Table 1). We used the *rma.mv* function in the R package *metafor* (98) and included two random factors associated with individual species' identities: One was an independent species effect, and the other explicitly incorporated phylogenetic correlations among species. Variance components were estimated using restricted maximum likelihood (REML) (99). This approach allows species-level variance in slopes to include an evolutionary component and a component unexplained by phylogenetic relationships (100, 101).

To create a phylogenetic correlation matrix among species, we first obtained 999 ultrametric phylogenetic trees from the BirdTree project (<http://birdtree.org>) (102) and computed a consensus majority rule phylogenetic tree (103) using the *consensus.edges* function of the *phytools* R package (104). The BirdTree phylogeny was built using an older bird taxonomy (105), so we linked each species in our dataset to its appropriate corresponding position in the phylogenetic tree (**Dataset S3**). Two species in our dataset (*Aphelocoma woodhouseii* and *Troglodytes pacificus*) were absent from the phylogeny, so were added manually to their respective genera. The phylogenetic correlation matrix was calculated assuming a Brownian-motion model of evolution [(104); function *vcv*], and with branch lengths computed using the method of Grafen [(106); function *compute.brlen*] in the *ape* R package (107).

**Linking the Magnitude of Latitudinal Shifts to Species' Traits.** The modulus of individual species' GLS slope estimates was used in a multi-level random-effect meta-regression to investigate and quantify the extent to which several potentially important species' traits might explain inter-specific variation in the absolute sizes of shifts in latitudinal optima. The meta-regression included the same two random-effect components described above to account for phylogenetic relatedness among species. We focused on traits directly or indirectly related to i) temperature optima and/or tolerances, ii) preferred habitat density and/or the degree of habitat specialization, and iii) processes of emigration, vagility, proliferation (e.g., dispersal capability) and/or establishment (25). Information on the following traits: preferred habitat density (an ordered categorical variable with three levels: open, semi-open or dense), migration strategy (three levels: resident, partial migrant, and fully migratory), territoriality (three levels: non-territorial, weakly territorial and strongly territorial) and dispersal capability (the hand-wing index, in mm) were obtained from Sheard et al. (76) and Tobias et al. (89). In addition, we used our bird abundance dataset from the BBS to obtain three more (continuous and quantitative) species-specific traits: thermal optimum ( $^{\circ}\text{C}$ ), thermal tolerance (a range, also in  $^{\circ}\text{C}$ ), and a SSI (108, 109) to measure the degree of habitat specialization. All categorical variables (migration strategy, territoriality, and preferred habitat density) were converted into ranks ranging from one to three and then were standardized along with the continuous variables to ensure comparability of model coefficients for assessing traits' relative importance.

To estimate thermal optima and tolerances, we first obtained monthly mean air temperatures for each BBS route for all of the sampled years in our study by accessing the "GHCN\_CAMS Gridded 2 m Temperature (Land)" dataset provided by the National Oceanic and Atmospheric Administration (NOAA) on the

following website: <https://psl.noaa.gov/data/gridded/index.html> (110). BBS data are collected during the breeding season, and weather conditions during this period are critical to birds' reproductive success (111, 112). Thus, we filtered the temperature data to include only values obtained during the breeding season for each particular species according to Vuilleumier (113) at each route in each year. For each species, the abundance values vs. temperature values across all routes and years were then used to fit a single *modskurt* model to estimate i) its thermal optimum ( $m_{temp}$ ) along the temperature gradient (in  $^{\circ}\text{C}$ ); and ii) its thermal tolerance (a range in  $^{\circ}\text{C}$ ), calculated as the absolute difference between the lower and upper bounds along the temperature gradient generated by the intersection of the 90th quantile curve of the species' unimodal *modskurt* model with a horizontal line corresponding to one-half the height ( $H_{temp}$ ) of the species' peak estimated abundance (*SI Appendix, Fig. S2*). For species whose estimated thermal ranges included temperatures outside the BBS sampling frame, we used the absolute difference between the maximum and minimum temperatures at which a non-zero abundance value was observed for that species within the BBS sampling frame.

To estimate SSI, we obtained measures of land cover for BBS routes using the 2015 land-cover map of North America provided by the Commission for Environmental Cooperation (CEC; <http://www.cec.org/nalcms>). We focused only on BBS routes sampled over the period from 2013 to 2017, to ensure temporal commensurability with the 2015 land-cover map. Given that the geographical coordinates provided in the BBS dataset correspond to the first observation stop of each route, we only used the abundance data from the first two stops to calculate the SSI for each bird species. The map identifies nineteen land-cover classes in accordance with the Land Cover Classification System (LCCS). We combined classes having the same dominant vegetation type (e.g., "temperate or sub-polar needle-leaf forest" and "sub-polar taiga needle-leaf forest" were combined into a single class: "needle-leaf forest"), and ignored five cases that were classified as water or were unclassified. This yielded nine land-cover classes: needle-leaf forest, broad-leaf forest, mixed forest, shrubland, grassland, wetland, cropland, barren, and urban. We estimated the density of each bird species per land-cover class by dividing the number of individuals found in each class by the number of routes in that class. The SSI was then obtained as the coefficient of variation ( $\text{CV} = \text{SD}/\text{mean}$ ) in the estimated densities among land-cover classes (109). The higher the SSI, the higher the variation in abundance across land-cover classes, indicating a more habitat-specialized species (108). It was not possible to obtain SSI measures for sharp-shinned hawk (*Accipiter striatus*), red-tailed hawk (*Buteo jamaicensis*), or Lewis' woodpecker (*Melanerpes lewis*) because they were not recorded in any of the first two stops for any of the routes sampled between 2013 and 2017. As a result, these species were omitted from any trait analyses that included the SSI measure.

A separate meta-regression analysis was performed for each data subset (East, West, and Combined). As some species' thermal ranges were not precisely estimated (i.e., in cases where a species' estimated thermal range landed outside the BBS sampling extent of temperature values), we completed a second set of meta-analyses that omitted these species. We retained the original model (including all species) when omission of these species yielded no qualitative difference in the results (to maximize the information content for the meta-regression); otherwise, we retained the second model to ensure sufficient precision of estimated thermal ranges.

We used the absolute value of each species' shift estimate as the response variable in our continental and regional analyses. Our objective was to identify potential links between species' traits and the magnitude of latitudinal shifts in a given direction. Thus, our full meta-regression model included i) the shift direction as a binary covariate (northward vs. southward), ii) all of the above-mentioned traits, and iii) the interactions between shift direction and every trait. The full model was then simplified using a series of sequential Wald-type tests via the "anova.rmv" function of the "metafor" R package (98). Starting with the term having the highest  $p$ -value, we sequentially removed non-significant terms until all remaining predictors had at least a marginally significant effect on the magnitude of latitudinal shift (i.e.,  $P$ -value  $\leq 0.1$ ). See *SI Appendix, 3* for full details.

**Data, Materials, and Software Availability.** The code used to filter the North American BBS dataset, assess the extent to which the BBS sampling covers each bird distribution (**Dataset S1**), and conduct the primary analysis

has been archived on Figshare (114, 115). All data for the primary analysis are provided as supplementary datasets. Bird Life's (BL) geographic distributions for the birds of the world are available under request from BL website (<https://datazone.birdlife.org/species/requestdis>). Previously published data were used for this work (84, 89).

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