

# Winter range shifts and their associations with species traits are heterogeneous in eastern North American birds

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## ABSTRACT

Many species' distributions are shifting in response to climate change. Many distributional shifts are predictably poleward or higher in elevation, but heterogeneity in the rate and direction of shifts both within and between species appears to be common. We found high heterogeneity in the trajectory of winter range shifts for 65 species of birds across eastern North America and in the different traits and trait interactions associated with these shifts across the spatial scales we examined. We used data from the Christmas Bird Count to quantify the trajectory of winter latitudinal center of abundance range shifts over 4 decades (1980–2019) for 65 species of songbirds and woodpeckers in North America, both across eastern North America (ENA) as a whole and for the Atlantic (ATL) and Mississippi (MISS) flyways separately. We then used linear models and Akaike's Information Criterion with small-sample size correction (AIC<sub>c</sub>) model selection to test whether species traits could explain variation in range shifts or flyway discrepancies. Across ENA, most species showed northward latitudinal range shifts, but some showed no latitudinal shift while others shifted southwards. Amongst ATL and MISS, we documented both within- and between-species differences in the rate and direction of latitudinal shifts, complicating the results from across ENA. No single trait emerged as a dominant driver of range shift differences at the ENA and flyway scales. Migration strategy interacted with insectivory to explain variation at the largest spatial scale (ENA), whereas frugivory and mean winter latitude explained much of the variation in ATL and MISS, respectively. Exploring heterogeneity in range shifts within and between species, and in the associations between range shifts and life history traits, will help us better understand the mechanisms that mediate differing responses to environmental change and predict which species will be better able to adapt to those changes.

**Keywords:** climate change, diet flexibility, distributional shifts, migration strategy, species traits, winter diet

## How to Cite

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## LAY SUMMARY

- Species are shifting their distributions due to recent climate change, but variation in these shifts, and the influence of species traits, are not well understood.
- We quantified the rate and direction of recent winter range shifts for 65 species of eastern North American birds and compared within- and between-species variation.
- Additionally, we explored if species traits (migratory strategy, winter diet, and winter geography) can explain variation in range shifts across different spatial scales.
- Most species moved northward during this 40-year time period, but there was wide variation both between species and within species between the eastern flyways.
- We found that across eastern North America, short-distance migrants tended to shift at higher rates than residents and moderate-distance migrants, but the level of insectivory was also important.
- At the flyway level, frugivory and migration strategy were important variables explaining shifts along the Atlantic flyway, whereas winter geography and migratory strategy were more important in the Mississippi flyway.

## Los desplazamientos en el rango invernal y sus asociaciones con las características de las especies son heterogéneos en las aves del este de América del Norte

## RESUMEN

Muchas distribuciones de especies están cambiando en respuesta al cambio climático. Muchos desplazamientos de distribución ocurren predeciblemente hacia el polo o hacia mayores altitudes, pero la heterogeneidad en la velocidad y dirección de los desplazamientos tanto dentro de una misma especie como entre especies parece ser común. Encontramos una alta heterogeneidad en la trayectoria de los

desplazamientos del rango invernal para 65 especies de aves en todo el este de América del Norte y en las diferentes características e interacciones de las características asociadas con estos desplazamientos en las escalas espaciales que examinamos. Utilizamos datos del Censo de Aves de Navidad para cuantificar la trayectoria de los desplazamientos latitudinales invernales en el rango del centro de abundancia durante 4 décadas (1980–2019) para 65 especies de aves canoras y pájaros carpinteros en América del Norte, tanto a través de todo el este de América del Norte (EAN) como en las rutas migratorias del Atlántico (ATL) y del Mississippi (MISS) por separado. Luego utilizamos modelos lineales y el Criterio de Información de Akaike con corrección para muestras pequeñas (CIAc) para seleccionar modelos y probar si las características de las especies podrían explicar la variación en los desplazamientos del rango o las discrepancias en las rutas migratorias. A través del EAN, la mayoría de las especies mostraron desplazamientos del rango latitudinal hacia el norte, pero algunas no mostraron cambios latitudinales mientras que otras se desplazaron hacia el sur. Entre las rutas migratorias de ATL y MISS, documentamos diferencias tanto dentro como entre especies en la velocidad y dirección de los cambios latitudinales, lo que complica los resultados a través del EAN. Ninguna característica individual surgió como un factor dominante en las diferencias en los desplazamientos del rango a las escalas del EAN y de las rutas migratorias. La estrategia de migración interactuó con la insectivoría para explicar la variación a la escala espacial más grande (EAN), mientras que la frugivoría y la latitud media en invierno explicaron gran parte de la variación en las rutas migratorias de ATL y MISS, respectivamente. Explorar la heterogeneidad en los desplazamientos del rango dentro y entre especies, y en las asociaciones entre los desplazamientos del rango y las características de la historia de vida, nos ayudará a entender mejor los mecanismos que intervienen en las diferentes respuestas al cambio ambiental y a predecir qué especies serán capaces de adaptarse mejor a esos cambios.

**Palabras clave:** cambio climático, características de las especies, desplazamientos de distribución, dieta invernal, estrategia migratoria, flexibilidad de la dieta

## INTRODUCTION

Shifts in species distributions are one of the most widespread and visible biological effects of recent climate change (Parmesan and Yohe 2003, Chen et al. 2011). Most avian range shifts in the northern hemisphere appear to be northward (or higher in elevation), in line with predictions based on warmer temperatures (e.g., Hitch and Leberg 2007, La Sorte and Thompson 2007, Auer and King 2014 for birds in North America), especially in the breeding season (e.g., Potvin et al. 2016 for birds in Finland). However, variation between species in the rate and direction of range shifts appears to be common (Tingley et al. 2012, Gillings et al. 2015), and some poleward and upslope shifts might not necessarily correlate within species (DeLuca and King 2017). Variation in distributional shifts within species is much less studied (but see McCaslin and Heath 2020) but comparing the rate and direction of shifts among regions within a species' range can help in identifying the nuanced drivers of these shifts.

Heterogeneity in temperature and precipitation change exists at regional scales (Melillo et al. 2014), and there is growing evidence that this heterogeneity is associated with differences in range shifts among and within species (Rapacciuolo et al. 2014, Vanderwel et al. 2014, McCauley et al. 2017). In addition, multiple drivers can influence range shifts and potentially increase regional or among-species heterogeneity. Widespread changes in land use including forest cover (Guo et al. 2018) and urbanization (Zuckerberg et al. 2011), supplemental bird feeding (Greig et al. 2017), and biotic factors (Pearson and Dawson 2003) can drive abundance and distributional shifts. Moreover, these factors can interact to influence range shifts across large scales (Oliver et al. 2014, Saunders et al. 2022).

Less is known about species traits associated with, and potentially driving how individual species distributions shift in response to environmental change (Estrada et al. 2016, MacLean and Beissinger 2017), particularly on the wintering grounds. For example, if climate change is causing changes in the distribution, abundance, and seasonality of food sources, but not all food sources are affected in similar ways, then species with different diets may show differing responses. Differing degrees of dietary specialization might also be associated with different capacities to adapt to climate change through distribution shifts (Buckley and Kingsolver 2012, Auer and King 2014, Monaco et al. 2020).

Similarly, species with different migratory strategies ranging from year-round residency to long-distance migration might be expected to differ in their responses to heterogeneity in climate change. Short-distance and facultative migrants have less fixed migratory schedules and may be able to respond to localized environmental cues better than medium- and long-distance migrants, which tend to show higher site fidelity to over-wintering sites (Cresswell 2014). Other studies have shown that year-round residents have shifted their distributions poleward (Rushing et al. 2020) or higher in elevation (Zuckerberg et al. 2009) to a greater degree than short-distance migrants, at least on the breeding grounds.

Species whose winter distributions lie farther north or south (or higher in elevation) may be expected to shift at lower rates due to the restrictions of their historical range limit. Lack of available habitat north of a species range may preclude its ability to shift northward, and mountaintop species are necessarily restricted in their ability to shift upwards in elevation (Moritz et al. 2008). One of the traits that consistently explained variation in range shifts across taxa in a recent meta-analysis was the historic range limit of a species (MacLean and Beissinger 2017). Specifically, for a wide range of taxa, those with higher latitudes tended to shift at lower rates compared with species occupying lower latitudes, despite greater warming at higher latitudes in the northern hemisphere (Rantanen et al. 2022).

The prevalence of within-species variation in range shifts is not well-studied, despite the spatial variation in climatic changes across terrestrial landscapes over the last several decades. In North America, climate warming is known to be proceeding more rapidly across the midwestern plains (Wuebbles et al. 2017) and in the northeast (NOAA 2023) than in adjacent regions at similar latitudes. Additionally, parts of the inland U.S. south lie in what is known as a “warming hole”, an area that has not undergone the same increases in winter temperatures as the rest of the country (Partridge et al. 2018). If environmental changes are causing shifts in animal distributions, and if these changes are heterogeneous, we might expect to see heterogeneity in range shifts across different portions of a species' range (e.g., some portions shifting north, others shifting south or not shifting). However, if shifts are synchronous range-wide, despite geographic variation in environmental changes, it could indicate that those changes are not the sole driver of the range shift. A better understanding of how distributional shifts are occurring within different areas across

species ranges will help us predict which species, and populations within species, are most at risk from future environmental change. Further, understanding synchrony or asynchrony of within-species range shifts in a context of heterogeneous environmental change can also be advanced by comparing range shifts to traits and trait interactions that link species to their environment, such as diet and migratory strategy.

In this study, we quantified the rate and latitudinal direction of winter range shifts in eastern North America (ENA) for 65 species of songbirds and woodpeckers from 1980 to 2019. We compared these shifts between the two major eastern North American flyways—Atlantic (ATL) and Mississippi (MISS)—to estimate synchrony in range shifts and tested whether species traits could explain variation in range shifts at these spatial scales. We chose species that have broad population distributions in eastern North America during the winter, and that collectively represent a variety of winter diets, migratory strategies, and mean winter range latitudes. We asked the following questions: (1) How much between-species variation exists in the latitudinal rate and direction of winter range shifts for these 65 species across eastern North America? (2) How much within-species variation exists in the winter range shifts between the two eastern flyways, and how does within-species variation compare to between-species variation? And (3) can species traits such as mean winter latitude, migratory strategy, and winter diet, explain any of this variation? We expected that (1) most species would show northward shifts but at different rates, while some species would not shift at all and some would show southward shifts; (2) due at least in part to geographic differences in recent climatic changes, there would be within-species differences in the rate of range shift between flyways; specifically, we expected northward shifts in ATL would be higher than in MISS due to the higher rate of temperature change in the northeast and the winter warming hole in the lower MISS flyway; and (3) short-distance migrants would show stronger northward shifts than residents and medium-distance migrants; diet specialists would show weaker northward shifts compared to those with a more generalist diet; and lower-latitude species would shift at higher rates than higher-latitude species, especially in ATL.

## METHODS

### Species and Flyway Selection

We chose to focus solely on songbirds and woodpeckers to minimize potential confounding effects of more extreme variation in body size, life history, and habitat association (e.g., terrestrial/aquatic; Angert et al. 2011). We chose species that (1) have significant populations in ENA during the winter and across both eastern flyways (e.g., not restricted to coastal habitats); and (2) collectively represent a variety of diets, migratory strategies, and latitudinal distributions across the study area. We followed Waller et al. (2018) and delineated ATL and MISS by state and provincial boundaries (Figure 1).

### Christmas Bird Count Data

We requested Christmas Bird Count (CBC) data from 1980 to 2019 from the National Audubon Society for 65 species (Supplementary Material Table 1) that met the above criteria. We chose 1980 as a starting point based on data from Vose et al. (2017) and Rushing et al. (2020) that indicated that breeding distributional shifts of North American birds and

temperatures started to change most noticeably in the mid-1980s. The CBC is an annual survey during a 2-week window centered on 25 December. Surveys occur within 24.14-km diameter circles centered on the same point each year, with locations across North America (Figure 1). We truncated this dataset to only those circles located in the MISS and ATL flyway states and provinces (shaded regions, Figure 1). To avoid potential spatial-temporal bias that may arise when new CBC circles are initiated each year, we limited our analysis to only those circles that participated in at least 36 out of the 40 years (90%) of data collection during the study period. Thus, of the 1,961 CBC circles in the two flyways that collected data during any years of the study period, we used data from 629 circles. The spatial distribution of CBC circles is biased towards the north and east of the study area (Figure 1) (Meehan et al. 2019). This sampling bias may influence the static location of a species' latitudinal center of abundance (LCA), but it affects species similarly, and temporal changes in LCA location (our principal concern) arise only from differential abundance changes across sites over time, not from the static spatial sampling distribution.

### Latitudinal Center of Abundance Calculation

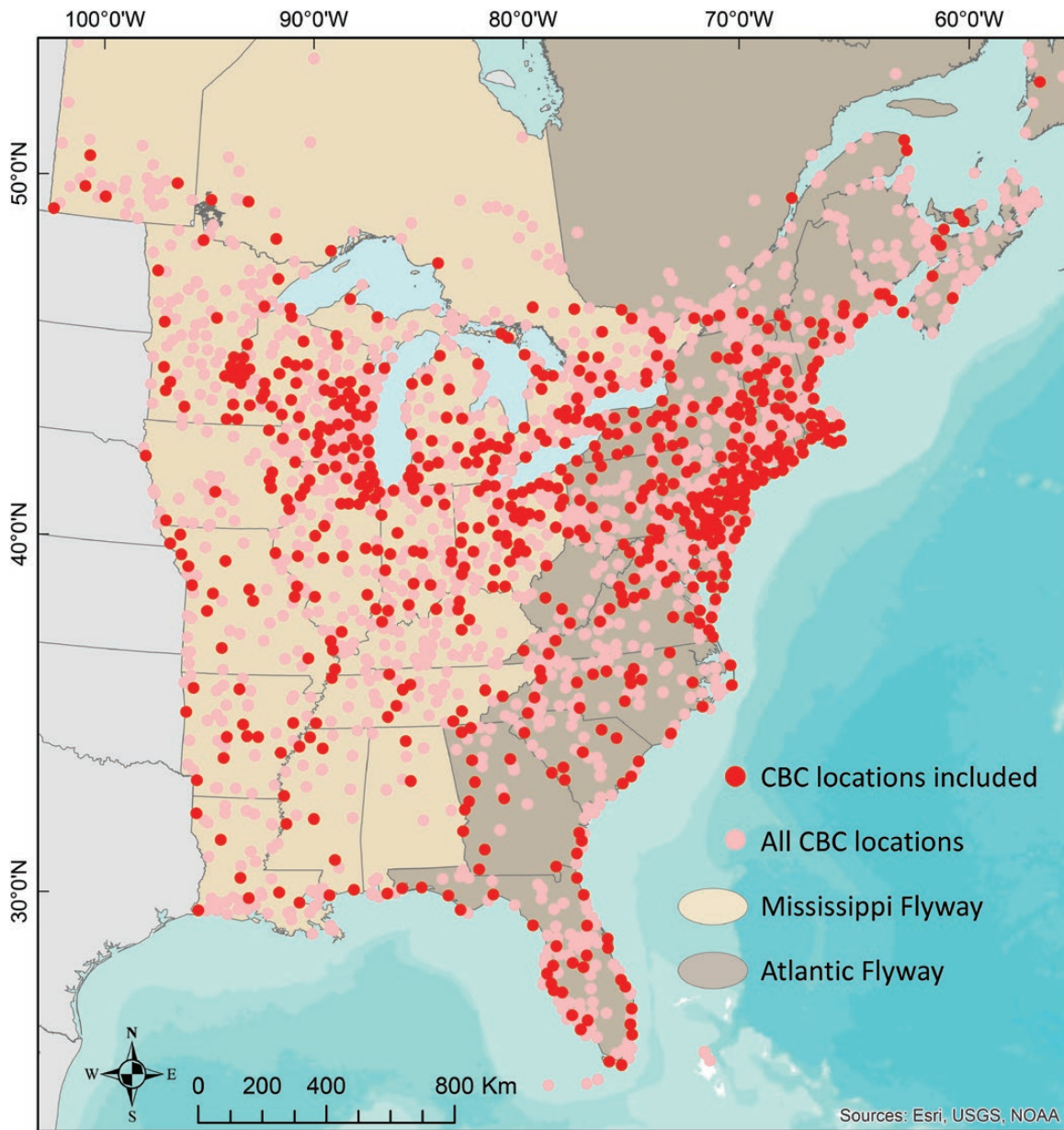
Latitudinal center of abundance is a standard expression of mean geographic range location, and LCA changes over time have been used to quantify range shifts (La Sorte and Thompson 2007, Paprocki et al. 2014). To calculate the LCA of each species for each year and flyway, we calculated the geographic mean of all CBC circles with that species present that year, weighted by the relative abundance of that species in each circle, using the R package *geosphere* (Hijmans et al. 2019). Because survey effort varies between circles and years, we used the number of birds per party-hour as an index of relative abundance for the weighted average to account for this variation in effort (Koenig and Liebhold 2016, Curley et al. 2020).

For each species, we used linear regression to determine the strength and direction of the shift in LCA. We used year as the explanatory variable and LCA as the response variable, and the resulting regression slope estimated the rate of shift over the 40-year time period (see Figure 2). For our initial descriptive summaries of range shifts across species and flyways, we used only those slopes that were significantly different from zero as evidence for a range shift. However, all slopes were used unaltered for further statistical analysis (see below). To better illustrate effect sizes, we converted the regression slope from degrees latitude per year to cumulative distance (in kilometers) during the study period using the conversion of  $1^\circ = 111$  km multiplied by 40 years. We performed these regressions for each species in eastern North America (ENA) as a whole, and for each flyway (ATL and MISS) separately to quantify variation in the direction and magnitude of range shifts between the flyways. We quantified flyway synchrony for each species by calculating Pearson's correlation coefficient  $r$  between the flyway-specific LCA time series. This metric provides a quantitative comparison of the relative rate and direction of range shift between flyways for each species (see Figure 2).

### Within- vs. Between-species Variation

To compare between-species variation in the rate and direction of range shifts to within-species variation between flyways, we created and compared 2 indices. Our index of





**FIGURE 1.** Map showing the ENA study area, consisting of the ATL and MISS flyways, CBC survey locations (all pink and red circles) and those used in the analysis (red circles). Only locations with data for at least 90% of years during 1980–2019 were included in analysis.

within-species variation was the absolute value of the difference between flyway regression slopes, for each species:

$$\sigma_{\text{within}_i} = |\text{ATL\_slope}_i - \text{MISS\_slope}_i| \quad (1)$$

For a comparable index of between-species variation, for each species we calculated the absolute value of the difference between the ENA regression slope of that species ( $\text{ENA\_slope}_i$ ) to the mean of all other species' slopes ( $\text{ENA\_slope}_k$ ) in the ENA dataset:

$$\sigma_{\text{between}_i} = |\text{ENA\_slope}_i - \frac{1}{n} \sum_{k=1}^{63} (\text{ENA\_slope}_k)| \quad (2)$$

We converted slopes to cumulative distance (km) across the 4-decade study period, as above. These two indices allowed us to more directly compare within- and between-species variation in range shifts for a given species, because they are on

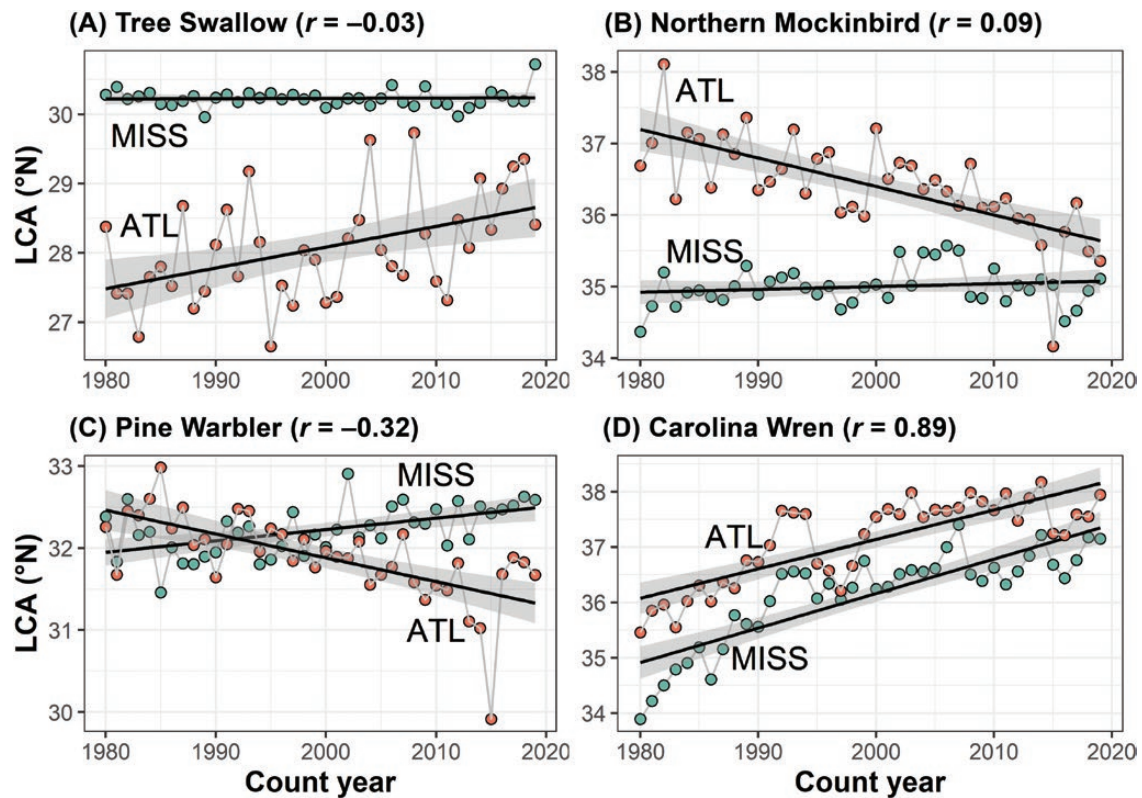
the same scale. In particular, the between-species variation provides a meaningful benchmark against which to judge the importance of the within-species variation.

### Species-level Traits

We tested if species-level traits could explain variation in the strength and direction of winter range shifts in the study area as a whole, within flyways, and between flyways. We included the following species-level traits in our analysis:

#### Winter latitude (continuous variable).

We calculated the mean LCA for each species during the first 3 years of the study period (1980–1982). The LCA during the first 3 years provides a baseline mean latitude for each species, prior to shifts occurring over the subsequent four decades. We



**FIGURE 2.** LCA and flyway synchrony (Pearson's  $r$ ) results for 4 species showing range shift differences between ATL and MISS flyways. **(A)** Tree Swallow (*Tachycineta bicolor*) shifted norward in ATL but remained steady in MISS and had a low flyway synchrony value. **(B)** Northern Mockinbird (*Mimus polyglottus*) shifted southwards in ATL but remained steady in MISS, and also had low flyway synchrony. **(C)** Pine Warbler (*Setophaga pinus*) shifted northwards in MISS but southwards in ATL and had negative flyway synchrony. **(D)** Carolina Wren (*Thryothorus ludovicianus*) had high flyway synchrony and shifted similarly northward in ATL and MISS.

included this variable to test whether more northerly species were shifting at different rates than more southerly species.

#### Migration strategy (categorical variable).

We placed each species into 1 of 4 migration strategy categories: residents, short-distance migrants, moderate-distance migrants, and irruptive migrants. We removed the three irruptive species, Cedar Waxwing (*Bombycilla cedrorum*), Pine Siskin (*Spinus pinus*), and Red-breasted Nuthatch (*Sitta canadensis*) from the trait-based models (see below) due to small sample size for the category (three species), but we included them in the initial descriptive statistics.

#### Winter diet (continuous variable).

Using data from Billerman et al. (2020), we quantified winter diet by estimating insects, fruit, and seeds taken in the winter for each species as a percentage of the total. To simplify this analysis, we did not include carnivorous (e.g., Loggerhead Shrike [*Lanius ludovicianus*]) or piscivorous species (e.g., Belted Kingfisher [*Megasceryle alcyon*]) in this study.

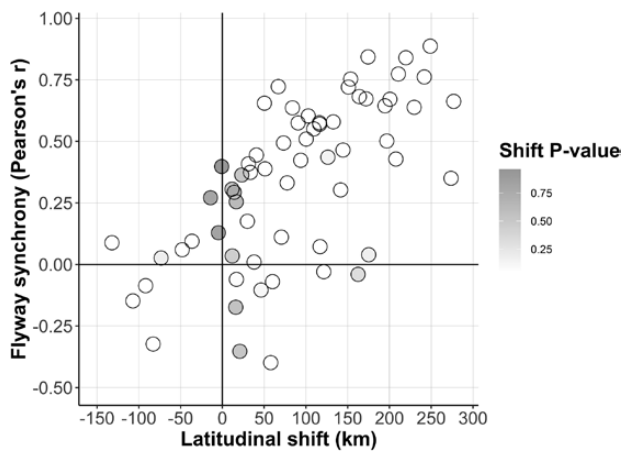
#### Trait-based Range Shift Models and Model Selection

We created generalized linear models (GLMS) using the cumulative magnitudes of LCA range shift (km) in ENA, ATL, and MISS as the response variables and species traits as explanatory variables, with interaction terms. For the flyway discrepancy response variable  $\sigma_{\text{within}}$ , we created GLMS with Gamma error distribution to account for the log-normal distribution of this variable.

We used all LCA regression slopes for the response variables rather than converting non-significant slopes to 0, which would have created a non-normal response variable, violating the assumptions of the linear models. In practice, most non-significant slopes were near 0 (Figure 3).

We used Akaike's Information Criterion with small-sample size correction ( $AIC_c$ ) to evaluate models with and without interactions (Burnham and Anderson 2002, Burnham et al. 2011). We performed model selection separately for ENA, ATL, MISS, and for  $\sigma_{\text{within}}$ , examining the same set of models in each case. The model set included all combinations of the trait variables winter latitude, migration strategy, and winter diet. Models that included latitude or % fruit in diet also included a quadratic component for those variables, based on unimodal (hump-shaped) relationships with range shifts suggested in preliminary scatter plot visual assessments (Supplementary Material Figure 1). Winter diet was represented by three continuous variables (% insects, % fruit, and % seeds) but only 1 of these was included in any given model to avoid collinearity. Additive and interaction models were included for each variable combination, resulting in a total of 26 models including an intercept-only model (Supplementary Material Table 2). Model selection and assessment of overall variable importance [i.e., the summed Akaike weights ( $\sum w_i$ ) of all models that included the variable] were performed using the *MuMIn* package in R (Barton 2022). The GLMS and all other numerical analyses described above were performed in R version 4.0.5 (R Core Team 2021).





**FIGURE 3.** Relationship between rate of LCA shift (km) for ENA and the Pearson's correlation coefficient ( $r$ ) between flyways, estimating flyway synchrony, for each species ( $n = 64$ ). White-filled circles indicate significant ENA range shift regression slopes (49 of 64 species) and shaded circles indicate non-significant slopes (16 of 64 species), filled according to the  $P$ -value of the linear regression. Most of the non-significant slopes (shaded circles) fall along the  $x$ -axis near zero, indicating small rates of range shift for ENA. In general, north-shifting species showed positive synchrony between flyways, but not always.

## RESULTS

### Shifts In LCA Across ENA and Between Eastern Flyways

Of the 65 species included in this study, 43 (66.2%) underwent significant northward shifts across ENA during the 40-year study period. Sixteen species (24.6%) did not undergo a significant latitudinal shift across ENA, and 6 species (9.2%) underwent significant southward shifts (Figures 3 and 4; Supplementary Material Table 1). For the species that shifted northwards, the average LCA shift was 143.7 km (SD = 113.3 km) during the 40-year study period in ENA, and across all species was 87.4 km northward (SD = 123.7 km). There was a positive relationship between the magnitude of the LCA shift in ENA as a whole and LCA shift synchrony (Pearson's  $r$ ) between flyways for each species ( $F = 44.4$ ,  $df = 62$ , adj.  $R^2 = 0.41$ ,  $P < 0.001$ , Figure 3). Species with larger range shifts across ENA tended to have synchronous shifts in both flyways.

In ATL, 36 species (55.4%) shifted northward, 7 (10.8%) shifted southward, and 22 (33.8%) did not shift significantly during the study period. In MISS, 46 species (70.8%) shifted northward, 4 (6.2%) shifted southward, and 15 (23.1%) did not shift significantly. There was no difference ( $P = 0.54$ ) between the mean LCA shift in ATL ( $\bar{x} = 82.6$  km, SD = 135.5 km) and MISS ( $\bar{x} = 96.0$  km, SD = 112.5 km), despite MISS having 10 more northward-moving species than ATL (Figure 4).

### Within-species Variation between Flyways

Though most species underwent northward shifts across ENA, we documented compelling within-species variation between the 2 eastern flyways (Figures 2 and 4). Of the 65 species included in the study, only 31 (47.7%) underwent a significant northward winter range shift in *both* ATL and MISS, whereas 20 species (30.8%) underwent a northward shift in one flyway but no LCA shift or a southward shift in the other. For 15 of these 20 species, the northward shift took place in

MISS. Eleven species (16.9%) did not undergo a shift in either flyway when quantified separately, and 10 species (15.4%) underwent a significant southward shift in one flyway but no LCA shift or a northward shift in the other. Importantly, none of the 65 species underwent significant southward shifts in both flyways when analyzed separately. For all species with a significant southward shift across ENA, the shift was driven by a southward shift in only a portion of its range. The flyway synchrony values (Pearson's  $r$ ) varied from  $-0.4$  to  $0.89$  and had a median value of  $0.40$  (Figures 2 and 3).

### Comparison of Within- vs. Between-species Variation

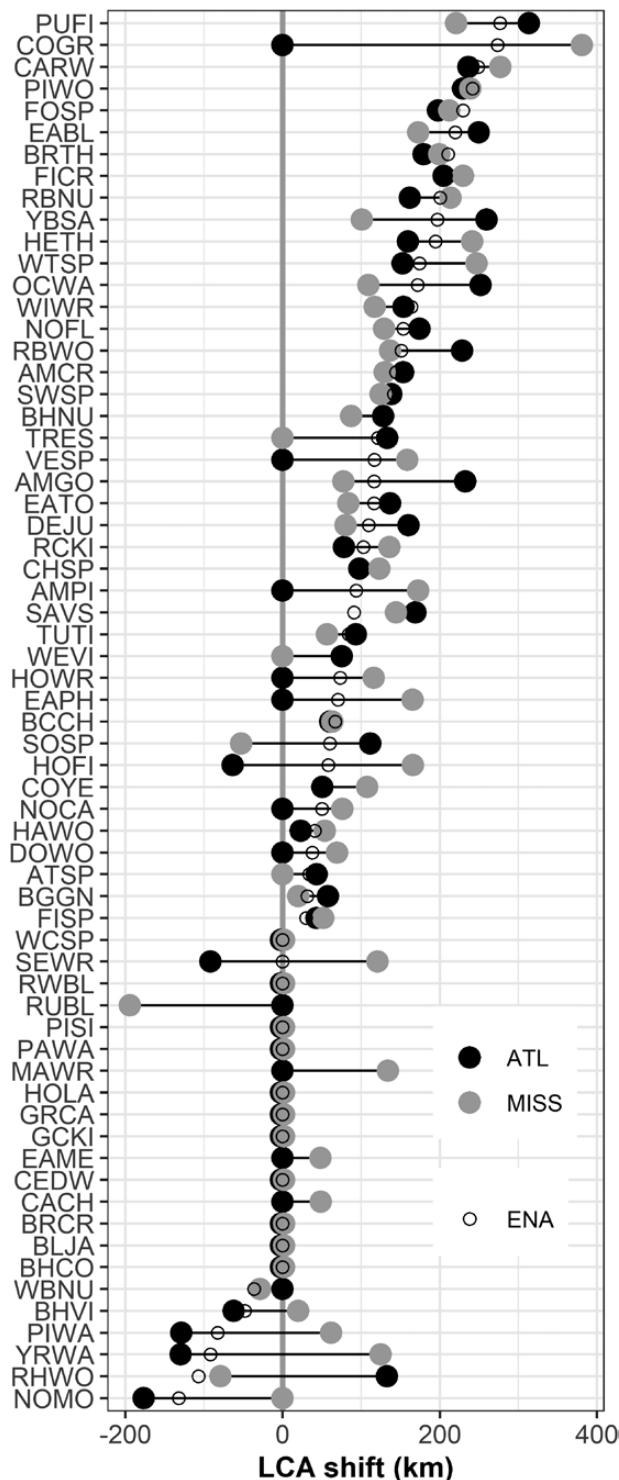
We compared the within-species variation in range shifts between the flyways ( $\sigma_{\text{within}}$ ) to between-species variation in range shifts across ENA ( $\sigma_{\text{between}}$ ), quantified for each species. Although the median  $\sigma_{\text{within}}$  was lower than the median  $\sigma_{\text{between}}$  (Figure 5A), the mean  $\sigma_{\text{within}}$  (94.3 km) was higher than the mean  $\sigma_{\text{between}}$  (79.3 km) but not significantly so ( $t = 1.1$ ,  $P = 0.272$ ). There was a positive relationship between  $\sigma_{\text{between}}$  and  $\sigma_{\text{within}}$  ( $t = 2.7$ ,  $df = 61$ ,  $P < 0.01$ ), indicating that those species with higher deviation from the mean ENA shifts (in either direction) also have higher variation between the flyways. Further, 34 species (53.1%) had higher  $\sigma_{\text{within}}$  values than  $\sigma_{\text{between}}$  values, indicating that in more than half of the species we examined, the within-species difference in range shifts between flyways outpaced the between-species difference in ENA range shifts between the species and other species (Figure 5B).

### Effects of Species Traits on Range Shifts and Flyway Differences

In addition to the three irruptive species we removed due to small sample size for this migration category, we also removed American Robin (*Turdus migratorius*) from the trait-based models, because this species was a data outlier. (American Robin shifted northward across ENA at a rate of  $17.8 \text{ km yr}^{-1}$ , a rate more than 8 times that of the average shift for all other species.)

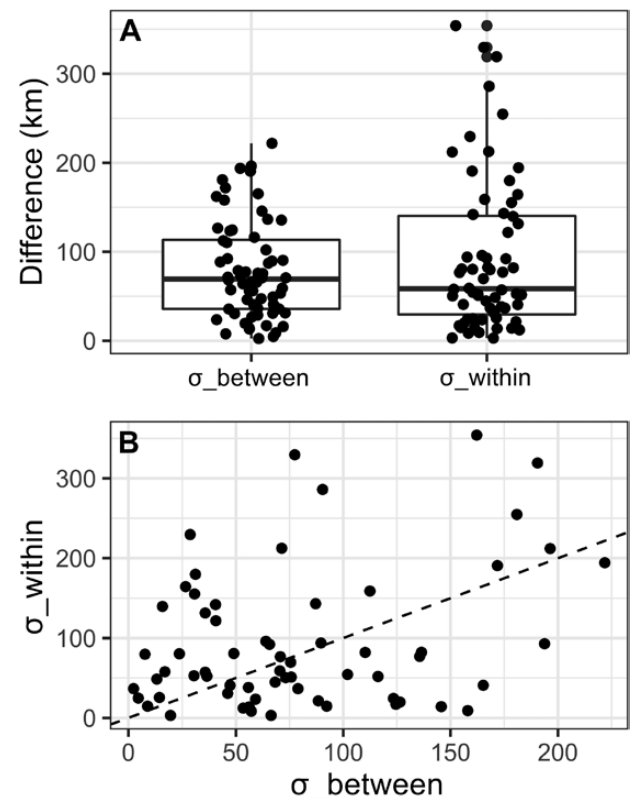
Different traits and trait interactions were associated with the among-species variation in range shifts across ENA, ATL, and MISS (Table 1 and Figure 6). For ENA, the top model in AIC<sub>c</sub> model selection included migration strategy and % insects in the diet, as well as the interaction between these terms. Short-distance migrants shifted northwards at higher rates than moderate-distance migrants and residents (Figure 6A). However, there was an interaction between migration strategy and diet: short-distance migrants with a highly insectivorous diet shifted northward at lower rates than short-distance migrants with fewer insects in their winter diet, whereas resident (non-migrant) insectivores shifted northward at higher rates than resident species with fewer insects in their winter diet (Figure 6B). The variables with the highest importance values across all ENA models were migration strategy ( $\Sigma w_i = 0.68$ ), % insects ( $\Sigma w_i = 0.38$ ), and % fruit ( $\Sigma w_i = 0.34$ ).

The best model for ATL, and the second best for ENA, included migration strategy and % fruit<sup>2</sup> (Table 1). The % fruit<sup>2</sup> variable suggests that those species with low or high percentage of winter fruit shifted minimally or southward, whereas those with a more omnivorous diet including some fruit shifted northward (Figure 6C). The three species with the highest frugivorous winter diet either did not shift at all



**FIGURE 4.** Rate and direction of winter range shift (total km) for each species in each flyway (black-shaded circles are ATL shift, gray-shaded circles are MISS shift) over 4 decades (1980–2019). Species are organized top-to-bottom in order of decreasing overall ENA range shift (total km; small open circles). Negative values are southward shifts. For interpretation of species 4-letter codes, refer to [Supplementary Material Table 1](#).

(Gray Catbird [*Dumetella carolinensis*]), or shifted southward during the study period (Yellow-rumped Warbler [*Setophaga coronata*] and Northern Mockingbird [*Mimus polyglottos*]), suggesting that an all-fruit diet in winter is associated with



**FIGURE 5.** (A) Boxplots comparing  $\sigma_{\text{between}}$  (between-species variation in range shifts across ENA) and  $\sigma_{\text{within}}$  (within-species variation in range shifts between flyways). Every species has a value for both metrics, and each point represents a species. (B) Scatterplot showing  $\sigma_{\text{within}}$  plotted against  $\sigma_{\text{between}}$  with a dashed one-line. Species above the dashed one-line differed more in range shift between flyways than their overall range shift differed from other species (34 of 64 species). To better illustrate effect sizes, we converted slopes ( $\text{km yr}^{-1}$ ) to cumulative distance (km) across the 4-decade study period.

minimal or even southward winter range shifts, at least in ATL. The next best model for ATL ( $\Delta\text{AIC}_c = 1.38$ ) included interactions between migration strategy, latitude<sup>2</sup>, and % fruit<sup>2</sup>. The significant migration:latitude<sup>2</sup> interaction indicates that lower-latitude residents shifted northward at a higher rate than higher-latitude residents, while the reverse is true for short-distance migrants ([Supplementary Material Figure 2](#)). The variables with the highest importance values across all ATL models were % fruit<sup>2</sup> ( $\Sigma w_i = 0.94$ ), migration strategy ( $\Sigma w_i = 0.45$ ) and latitude<sup>2</sup> ( $\Sigma w_i = 0.34$ ).

For MISS, the top model included the interaction between migration strategy and % insects ([Table 1](#)), similar to the top ENA model: short-distance migrants specializing on insects shifted northward at lower rates than short-distance migrants with other diets ([Supplementary Material Figure 3](#)). However, a second top model had a nearly identical  $\text{AIC}_c$  value and included only latitude<sup>2</sup> ( $\Delta\text{AIC}_c = 0.08$ ), and a third, closely competitive model included latitude<sup>2</sup> and migration strategy ( $\Delta\text{AIC}_c = 1.0$ ). In MISS, mid-latitude species shifted northward at higher rates than lower- and higher-latitude species ([Figure 6E](#)). The variables with the highest importance values across all MISS models were latitude<sup>2</sup> ( $\Sigma w_i = 0.63$ ), migration strategy ( $\Sigma w_i = 0.55$ ) and % insects ( $\Sigma w_i = 0.34$ ).

We tested whether species traits could explain  $\sigma_{\text{within}}$ , the within-species flyway discrepancy variable. The best model

included the interaction between latitude<sup>2</sup> and % insects (Table 1), indicating that lower-latitude insectivores showed higher flyway discrepancy than higher-latitude insectivores (Figure 6E). The next-best model included the interaction between latitude<sup>2</sup> and % seeds. Given that insectivory and granivory were negatively correlated (see Supplementary Material Figure 1), these two models may be expressing the same underlying pattern. The variables with the highest importance values across all  $\sigma_{\text{within}}$  models were latitude<sup>2</sup> (0.89) and % insects (0.63).

In summary, the top predictor variables in terms of overall importance values across models were different for ENA, ATL, and MISS, and interactions among predictors were important across all three. Migration strategy and winter diet were the most important variables in both ENA and ATL, with insectivory more important in ENA and frugivory more important in ATL. Latitude<sup>2</sup> was the most important predictor

in MISS and for  $\sigma_{\text{within}}$ , whereas migration strategy and insectivory were also important for MISS and  $\sigma_{\text{within}}$ , respectively (Table 1).

## DISCUSSION

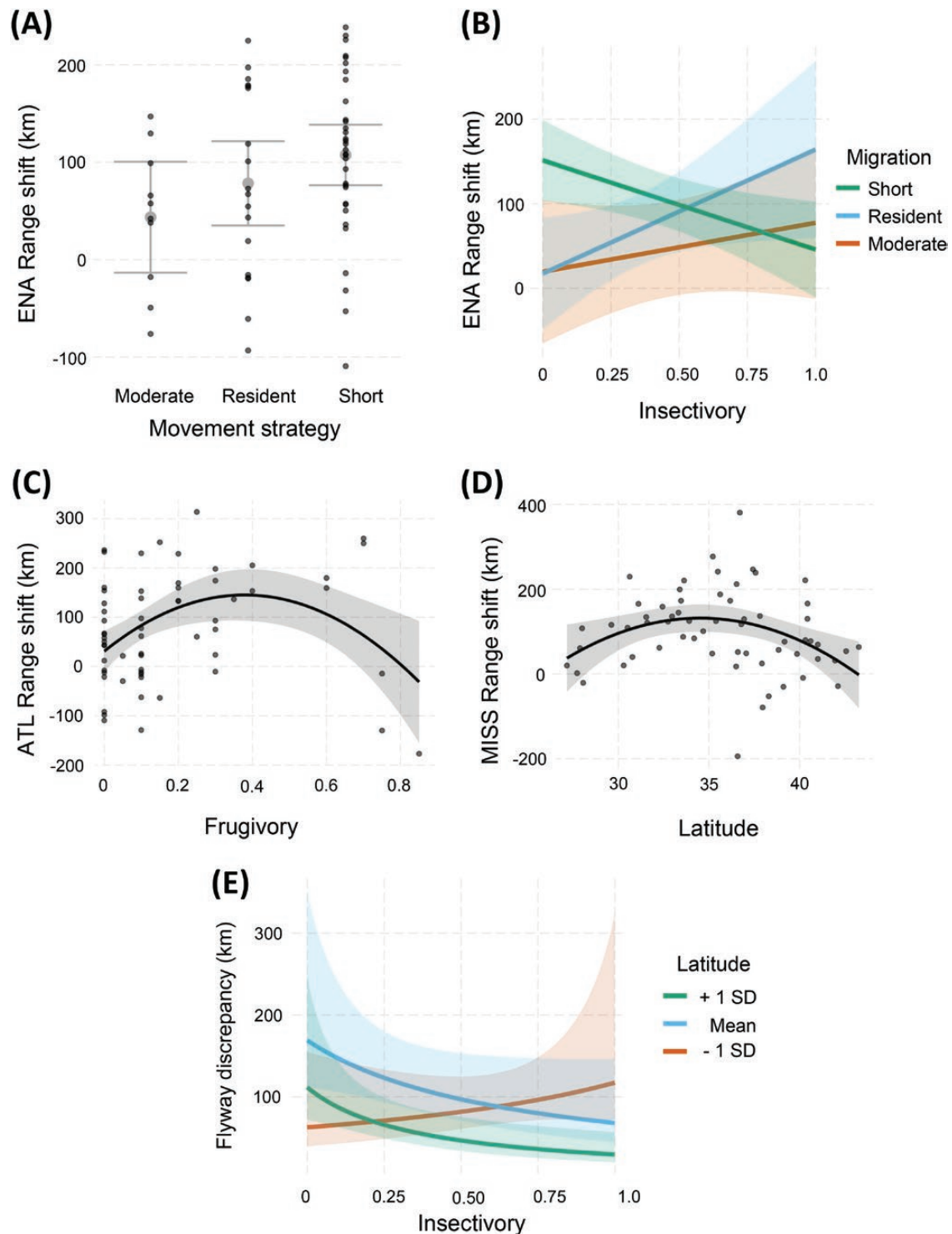
We found that most species shifted their winter distributions northward, but there was strong variation in these shifts, both between species and within species between flyways. Our results indicate that the trajectory of range shifts over large spatial scales (ENA) can mask the trajectory of shifts at smaller spatial scales (the two flyways). Some species, for example, showed overall northward shifts across ENA, but no LCA shift or even a southward shift in one of the flyways. Further, we found that short-distance migrants generally shifted northward at higher rates than residents and medium-distance migrants, and diet specialists generally shifted northward at

**TABLE 1.** Top models up to  $\Delta\text{AIC}_c < 6.00$ , model selection results, and major variable importance values for ENA, ATL, MISS, and  $\sigma_{\text{within}}$ , examining relationships between magnitude of range shifts, within-species variability, and species traits.

Model name	Model selection results				Importance values		
	df	logLik	Adj $R^2$	$\Delta\text{AIC}_c$	$w_i$	Variable	Importance
ENA							
Migration * insects	7	-357.11	0.15	0.00	0.32	Migration	0.68
Migration + fruit <sup>2</sup>	6	-359.70	0.09	2.60	0.09	Insects	0.38
Intercept-only	2	-364.62		3.10	0.07	Fruit <sup>2</sup>	0.35
						Migration * insects	0.32
						Latitude <sup>2</sup>	0.29
ATL							
Fruit <sup>2</sup>	4	-368.69	0.12	0.00	0.42	Fruit <sup>2</sup>	0.93
Migration * lat <sup>2</sup> * fruit <sup>2</sup>	15	-353.47	0.34	2.01	0.15	Migration	0.42
Migration + fruit <sup>2</sup>	6	-367.31	0.13	2.09	0.15	Latitude <sup>2</sup>	0.31
Lat <sup>2</sup> + fruit <sup>2</sup>	6	-367.88	0.11	3.23	0.08	Fruit * migration	0.23
Migration * fruit <sup>2</sup>	8	-365.33	0.16	3.35	0.08	Fruit * latitude	0.18
Migration + lat <sup>2</sup> + fruit <sup>2</sup>	8	-366.27	0.13	5.22	0.03	Lat * migration	0.16
Lat: fruit + lat <sup>2</sup> + fruit <sup>2</sup>	7	-367.67	0.10	5.36	0.03		
Intercept-only	2	-373.76		5.64	0.02		
MISS							
Migration * insects	7	-356.64	0.15	0.00	0.21	Latitude <sup>2</sup>	0.62
Lat <sup>2</sup>	4	-360.44	0.09	0.20	0.19	Migration	0.56
Migration + lat <sup>2</sup>	6	-358.50	0.12	1.15	0.12	Insects	0.35
Lat <sup>2</sup> + seeds	5	-360.38	0.08	2.46	0.06	Insects * migration	0.21
Lat <sup>2</sup> + insects	5	-360.38	0.08	2.46	0.06	Seeds	0.14
Migration	4	-362.05	0.04	3.43	0.04	Fruit <sup>2</sup>	0.12
Migration * fruit <sup>2</sup>	8	-357.06	0.13	3.50	0.04		
Migration + lat <sup>2</sup> + insects	7	-358.43	0.10	3.59	0.03		
Intercept-only	2	-364.41		3.64	0.03		
$\sigma_{\text{within}}$							
Lat <sup>2</sup> * insects	6	-329.93	0.24	0.00	0.53	Latitude <sup>2</sup>	0.90
Lat <sup>2</sup> * seeds	6	-331.34	0.20	2.82	0.13	Insects	0.64
Lat <sup>2</sup>	4	-334.41	0.12	4.11	0.07	Insects * latitude	0.53
Lat <sup>2</sup> + seeds	5	-333.53	0.14	4.74	0.05	Seeds	0.21
Lat <sup>2</sup> + insects	5	-333.54	0.14	4.76	0.05	Seeds * lat	0.13
						Migration	0.11

Adjusted  $R^2$  (Adj  $R^2$ ) values for the  $\sigma_{\text{within}}$  models are McFadden's pseudo  $R^2$  values for GLMS. df = degrees of freedom, Akaike weight =  $w_i$ .





**FIGURE 6.** Results of the top models explaining variation in distributional shifts. For ENA, migration strategy (A) plus the interaction between migration and insectivory (B) were included in the top model. For ATL (C), % fruit<sup>2</sup> was the top model and the variable with the highest importance. For MISS (D), the second-best model by a close margin included latitude<sup>2</sup>, whereas the top model was similar to (B). For  $\sigma_{\text{within}}$  (E), the top model included the interaction between latitude and insectivory.

lower rates than those with more generalist diets. Mid-latitude species, contrary to our expectations, shifted northward at higher rates than either low- or high-latitude species. These trait-based relationships were also scale-dependent, varying between ENA and the two flyways, as well as between flyways.

### Heterogeneity in Range Shifts Across Spatial Scales and Between Flyways

Across ENA, two-thirds of the species we studied shifted their distributions northwards during the study period, while 25% did not shift their LCA significantly, and 9% shifted southwards. These findings are consistent with studies confirming

recent shifts in species' distributions (Thomas and Lennon 1999, Hitch and Leberg 2007, La Sorte and Thompson 2007) that largely follow generalized predictions from climate change-associated rising winter temperatures: many species are shifting their distributions poleward. However, consistent with studies demonstrating strong variation in species responses to climate change (Chen et al. 2011, Tingley et al. 2012, DeLuca and King 2017), we also found that range shifts for many species differed substantially between flyways, and between the two flyways and ENA as a whole. This is consistent with the idea that spatial heterogeneity in climatic changes, and other potential drivers including land use change across eastern North America (Saunders et al. 2022), can lead to heterogeneity in range shifts within species.

Almost 70% of the species we studied shifted their winter distributions northward over the past 4 decades in at least 1 eastern North American flyway, while only half of the species did so in both flyways. For a large number of species we examined, an apparent shift across a large spatial scale (ENA) was driven by a smaller-scale shift within only a portion of the range (1 flyway). For example, 6 species shifted southwards across ENA, but no species shifted southwards in both flyways (Figure 4). Tree Swallows (*Tachycineta bicolor*) have shifted their LCA northwards in ATL by 133.2 km, but their LCA has remained remarkably stable in MISS across the 40-year study period (Figure 2A), perhaps due to winter habitat limitation and the distribution of their winter fruit source, the southern wax myrtle (*Morella cerifera*) (Piland and Winkler 2015). Considering ENA as a whole, their LCA has shifted northward 121.4 km. Similarly, Northern Mockingbird has shifted southwards in ATL by 176.8 km but has not shifted in MISS (Figure 2A), with an overall ENA southward shift of 132.1 km. Pine Warblers (*Setophaga pinus*) have shifted southwards in ATL by 129.0 km, but northwards in MISS by 61.7 km (Figure 2C). This northward shift in MISS would not have been apparent examining ENA as a whole, for which this species showed an overall southward shift of 82.9 km.

Due to climatic changes not occurring evenly across regions (Wuebbles et al. 2017, NOAA 2023), we expected that northward shifts in ATL would be more pronounced than those in MISS, but our results were not in line with these expectations. The average winter range shift for species moving northward in ATL (167.3 km) was slightly higher than for those moving northward in MISS (143.4 km), but this difference was not significant. Further, more species shifted northward in MISS (46 of 65 species) than in ATL (36 of 65 species). The variation in the rate and direction of species range shifts that we documented are in line with predictions that (1) heterogeneous environmental changes among regions will lead to heterogeneity in range shifts and (2) even given exposure to similar environmental change in one region, different species can respond idiosyncratically. The heterogeneity that we document here is likely a result of competing or synergistic global change drivers such as climate change and land use changes including urbanization and forest loss (Zuckerberg et al. 2011, Guo et al. 2018, Saunders et al. 2022). Idiosyncratic responses between flyways also highlight the importance of accurate projection of future climatic changes at these spatial scales in order to anticipate the implications for animal conservation (Carroll et al. 2015). Measuring species-specific drivers of range shifts should be a priority for future studies, and our results indicate that for such studies, analysis at a

variety of spatial scales may reveal important within-species variability.

Our study is one of the first to directly compare within- and between-species variability in range shifts, using quantitative species-specific metrics for both. Both of these metrics (among and within species) highlighted pronounced variability in range shifts relative to the dominant pattern of northward shift for most species. The mean difference between flyway range shifts for individual species ( $\bar{x} \sigma_{\text{within}} = 94.3$  km) was higher than the mean range shift difference among species ( $\bar{x} \sigma_{\text{between}} = 79.3$  km). This further underscores the strongly heterogeneous responses to environmental change among and within species, alongside the simultaneous reality of concerted poleward shifts across species. With such varied geographical responses within and among species, it is no wonder that trait-based correlations with recent range shifts have been hard to predict and to detect (Beissinger and Riddell 2021) and have been variable among studies (MacLean and Beissinger 2017).

### Traits as Predictors of Range Shift

Across ENA, migration strategy was the trait with the highest importance value and interacted with winter diet. In line with our expectations about range shifts in ENA, short-distance migrants were more likely to shift northward than moderate-distance migrants (Figure 6A). These results are consistent with those from other studies showing that longer-distance migrants show high site-fidelity to their over-wintering sites in both Europe (Cresswell 2014) and in southeastern North America (Somershoe et al. 2009). These results also have implications for changes in migration distance: many of the "temperate migrants" in a recent study by Rushing et al. (2020) did not shift their mean breeding season latitude, but a number of these same species did shift their mean wintering latitude in our study, thus potentially reducing migration distance. Examples include Eastern Bluebird (*Sialia sialis*) with a northward winter shift of 219.68 km, Brown Thrasher (*Toxostoma rufum*) with a northward winter shift of 210.74 km, and Eastern Towhee (*Pipilo erythrophthalmus*) with a northward winter shift of 116.22 km. These results are in line with Curley et al. (2020), who found that North American bird species showing decreasing migration distance outnumbered those showing increase, driven by winter shifts. Many residents in our study also shifted their winter range northward in our study, which could reduce competition and enable higher winter survival. Red-bellied Woodpecker (*Melanerpes carolinus*) and Carolina Wren (*Thryothorus ludovicianus*), for example, have not only shifted their breeding season range northward over the same time period, but are also undergoing significant population increases (Rushing et al. 2020), similar to other studies showing positive relationships between climate-driven range shifts and increasing population trends (Ralston et al. 2017).

Perhaps the most striking feature out our trait-based findings was the prevalence of trait interactions. For example, not all short-distance migrants showed strong northward shifts. Migration strategy interacted with winter diet across ENA (Figure 6B), so that short-distance migrants with a more specialized insect diet shifted northward at lower rates than short-distance migratory species with other or more generalist diets. For example, the short-distance migratory insectivores Common Yellowthroat (*Geothlypis trichas*), Golden-crowned

Kinglet (*Regulus satrapa*), and Blue-gray Gnatcatcher (*Polioptila caerulea*) all shifted northward at lower rates than short-distance migrants with more generalist winter diets like Eastern Bluebird and Hermit Thrush (*Catharus guttatus*) (Supplementary Material Table 1). In contrast, resident insectivores, for example, Carolina Wren and Pileated Woodpecker (*Dryocopus pileatus*), shifted northwards at higher rates than residents with generalist diets such as Black-capped Chickadee (*Parus atricapillus*) and Tufted Titmouse (*Baeolophus bicolor*). Variation was high for the residents with non-insect diets, with 3 such species shifting southwards: Northern Mockingbird, Red-headed Woodpecker (*Melanerpes erythrocephalus*), and White-breasted Nuthatch (*Sitta carolinensis*). The idea that diet specialization can interact with migration strategy to explain variation in range shifts has not, to our knowledge, been shown in previous studies and further exemplifies the importance of including interactions in trait-based analyses of range shifts. Trait interactions such as these have not been well-studied in range shift analyses (Beissinger and Riddell 2021). If they are as common as our findings suggest, they could help explain why trait-based range shift studies ignoring potential interactions have often shown negative results (MacLean and Beissinger 2017).

Stronger range shifts in species with mixed diets is consistent with the idea that dietary flexibility enhances adaptability to a changing environment (Angert et al. 2011, Buckley and Kingsolver 2012). It is possible that such an effect would be stronger in one region than another if food resources are a stronger limiting factor in one region, but without detailed information about changing food resource distributions in both flyways, this remains a speculation. Contrary to our findings, Auer and King (2014) found that a more specialized diet led to both greater northward and upward in elevational breeding season shifts for western North American birds, further evidence of contrasting results in trait-based range shift studies.

Our flyway-specific models revealed more nuanced relationships between species traits and range shifts that were not evident at the ENA scale (Table 1). With respect to winter diet, frugivory explained more variation than other diets in ATL, but % fruit had a nonlinear relationship with the rate of range shifts. Supporting our expectations, diet specialists with very high levels of fruit in their winter diet mostly showed negligible or southward range shifts, including Cedar Waxwing, Gray Catbird, and Northern Mockingbird. However, those with mid-levels of % fruit (and therefore a more varied diet) showed more consistent northward shifts, such as Brown Thrasher. It is notable, though, that this nonlinear relationship appeared to be driven by the three most highly frugivorous species in the analysis, without which the relationship could be interpreted as a positive linear association between frugivory and range shift (Figure 6C). Regardless, any interpretation of this model result suggests that species with mixed diets shifted north at high rates in ATL. Future studies of winter fruit availability, especially in the context of global change (Gallinat et al. 2020), will be important to predict responses for many species that rely on soft mass during the nonbreeding season.

Contrary to our expectations, mean winter latitude at the start of the study period (1980–1982) explained more variation in subsequent range shifts among species in MISS than in ATL. This was the most important variable in both the

MISS models and within-species variation models—and these, too, were nonlinear relationships. In MISS, species with mid-latitude winter ranges showed stronger northward shifts than species with higher or lower winter latitudes (Figure 6D). In ATL, however, latitude alone was not an important variable, but was important in interaction with both migration strategy and % fruit. Specifically, higher latitude short-distance migrants shifted northward at greater rates than lower-latitude migrants, but the reverse was true for residents (Figure 6C). Princé and Zuckerberg (2014) found that southerly birds increased in abundance and had a greater impact on changes in winter bird communities than northerly birds in eastern North America, using data from Project FeederWatch (Wells et al. 1998). Our results for MISS are in line with the idea that large range shifts may be precluded for both more northerly species due to lack of habitat availability, and for more southerly species in the winter warming hole where winter temperatures have not risen as fast as elsewhere across North America.

### Other Considerations

We chose to focus on shifts in the latitudinal center of abundance for these species, but earlier studies also examined shifts at the leading (usually northern) edges of species' distributions (Parmesan 1999, Moritz 2008, Angert et al. 2011). LaSorte and Thompson (2007), for example, found a higher shift in the northern winter boundary of North American birds than in their center of abundance, and Thomas and Lennon (1999) found that northern range margins of British birds moved northward, while the southern margin did not. It may be easier to detect a range shift at the leading margin of a species' range (Thomas et al. 2006), but we chose to use the LCA because it is a more general, albeit also more conservative, metric of range shift, potentially sensitive to shifts anywhere in the range (Lenoir and Svenning 2015). It could be, however, that species that showed no LCA shift in this study might still be undergoing range shifts at their (particularly northern) boundaries, but we did not measure this here. Future research should address how shifts at a species' boundary affects the LCA and should measure geographic variation and trait associations in these boundary shifts (e.g., Auer and King 2014).

Similarly, some studies examined longitudinal distribution shifts in addition to latitude. In a study by Bateman et al. (2016), for example, 24% of the species examined shifted westward, whereas most of the other shifts were to the north and northwest. Curley et al. (2020) found stronger latitudinal shifts taking place during winter and variable latitudinal/longitudinal shifts taking place during the breeding season. Clearly, species distributions are not shifting solely along latitude, and this could influence some of our conclusions about latitudinal shifts. For example, if a species in our study increased in abundance within the northwestern part of ENA, this could appear as a westward shift or a shift northward in MISS (but not in ATL), depending on the analysis. This is partly addressed by our analysis of synchrony between flyways for each species, since flyway asynchrony may be associated with longitudinal shift, but further examination would be needed to confirm this.

Potential sources of bias in this study were the spatial distribution of the CBC circles where data were collected (Figure 1)



and the timing of CBC counts during the year. Spatially, winter ranges of many of the species in this study cover nearly all the study area, while others are more restricted. This could lead to differences in the detectability of range shifts because the local abundance changes driving shifts are more likely to be detected in areas with more sampling. Meehan et al. (2019), for example, found that using spatially variable coefficient methods to analyze CBC data for American Robin produced lower uncertainty in their population trend estimates in regions with higher CBC circle density than in areas with lower density. We consider the 40-year shift trajectories to be robust to this bias, since essentially random spatial sampling error differences among species is unlikely to produce strong directional bias for these long repeat-sampling time series. Further, the denser sampling further north in our study area cannot easily explain any particular shift patterns we observed. One way to avoid potential bias might be to limit the analysis to a spatially balanced subsample of CBC circles. We avoided some spatiotemporal bias by only including CBC circles with data from at least 90% of the 40-year study period, similar to Saunders et al. (2022), and we chose not to further limit the number of CBC circles in our analysis. Temporally, the CBC occurs over two weeks surrounding December 25. Our understanding of winter ranges, migration timing, and nonbreeding ecology of birds is changing rapidly, and recent studies indicate that many species show flexibility in their migration timing and winter itinerancy (McKinnon et al. 2013, Thorup et al. 2017). It could be that data from the Christmas Bird Count is revealing changes not only to winter ranges but also migration timing, and future research could shed light on these questions.

## Conclusion

This study is one of the first to compare among-species and within-species variation in winter range shifts across different spatial scales and to include trait interactions to help explain this variation. We document the prevalence of heterogeneity in winter range shifts for eastern North American birds and show that species traits and trait interactions are associated with some of this variation, but these associations are scale-dependent and location (flyway) dependent. The general trajectories of most of these shifts are consistent with expectations under generalized climate change patterns, but finer-scale flyway analyses of range shifts revealed nuances not detected across ENA as a whole. Our results also raise questions about how winter diet may restrict or enable range shifts under future climate change, especially for diet specialists vs. generalists. Future research should examine whether range shift heterogeneity is driven by heterogeneity in recent climate change, other drivers of distributional change, or combinations thereof (e.g., Saunders et al. 2022).

In addition to understanding the drivers of range shifts, it will be important to examine the mechanisms of these shifts as well. For example, are poleward shifts occurring due to higher survival and fecundity in that portion of their range, or through dispersal of individuals from the core of their range moving into these more hospitable habitats? This study adds to the continued impetus to understand how species will respond to ongoing environmental changes, and what traits and trait combinations can serve as important predictors of those responses.

## Supplementary material

Supplementary material is available at *Ornithology* online.

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## Ethics statement

This work is based on observations and bird lists from thousands of community science participants during the Christmas Bird Count in eastern North America, and that data is freely available through the National Audubon Society.

## Conflict of interest statement

The authors declare no conflicts of interest with this publication.

## Author contributions

A.J.L. conceived of the project, collected the raw data, and quantified the range shift results; A.J.L. and L.Y.P. performed the modeling analyses; A.J.L. led the writing of the manuscript; A.J.L. and L.Y.P. edited and revised the manuscript.

## Data availability

The raw community science data we compiled is available from the National Audubon Society through their Christmas Bird Count program. Analyses reported in this article can be reproduced using data provided by Laughlin and Pomara (2023) and found in Supplementary Table S1.

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