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Spatial Nonstationarity in Phenological Responses of Nearctic Birds to Climate Variability

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ABSTRACT

Climate change is shifting the phenology of migratory animals earlier; yet an understanding of how climate change leads to variable shifts across populations, species and communities remains hampered by limited spatial and taxonomic sampling. In this study, we used a hierarchical Bayesian model to analyse 88,965 site-specific arrival dates from 222 bird species over 21 years to investigate the role of temperature, snowpack, precipitation, the El-Niño/Southern Oscillation and the North Atlantic Oscillation on the spring arrival timing of Nearctic birds. Interannual variation in bird arrival on breeding grounds was most strongly explained by temperature and snowpack, and less strongly by precipitation and climate oscillations. Sensitivity of arrival timing to climatic variation exhibited spatial nonstationarity, being highly variable within and across species. A high degree of heterogeneity in phenological sensitivity suggests diverging responses to ongoing climatic changes at the population, species and community scale, with potentially negative demographic and ecological consequences.

1 | Introduction

Shifting phenology is the most frequently observed biological response by which animals exhibit behavioural plasticity to variability in weather or climate (Beever et al. 2017). In birds, the advancement of migration timing with ongoing climate change has been shown to be widespread across species and continents (Knudsen et al. 2011; Romano et al. 2022), resulting in a range of downstream ecological consequences, including temporal decoupling across trophic levels (Hipfner 2008; Mayor et al. 2017; Thackeray et al. 2016), changing community assemblages

(Ovaskainen et al. 2013) and altered demographic rates (Both et al. 2009; Cruz-McDonnell and Wolf 2016; Saino et al. 2011; Youngflesh et al. 2023). The ability of birds to adjust the timing of migration and breeding to match short- and long-term climatic fluctuations is critical to minimising mortality and maximising breeding success (Brown and Brown 2000; Costa-Pereira et al. 2022; Verboven and Visser 1998; Youngflesh et al. 2023).

While previous studies have unequivocally demonstrated the advancement of bird phenology, especially in response to warming temperatures (Horton et al. 2023; Sparks et al. 2005),

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short time series or limited spatial and taxonomic sampling have made it difficult to simultaneously disentangle the relationships between arrival timing and a suite of potentially causal environmental covariates across species and space (Gordo 2007). Temperature, precipitation and snowpack regimes on the breeding grounds are shifting under climate change, each of which has been shown to influence breeding phenology and success among birds by altering food availability and mortality risk (DeSante and Saracco 2021; Hendricks 2003; Horton et al. 2023; Saracco et al. 2019; Zuckerberg, Ribic, and McCauley 2018). In addition to conditions on the breeding grounds, weather patterns on the wintering grounds brought on by climate oscillations have also been shown to influence bird migration timing, although with varying direction and magnitude of effects (Gordo 2007; Haest, Hüppop, and Bairlein 2018; Horn, Rimmel, and Stutchbury 2021; Lawrence et al. 2022; Marra, Hobson, and Holmes 1998; Rockwell, Bocetti, and Marra 2012).

Critically, the relative importance of environmental factors on arrival timing, mortality and breeding success have been shown to vary across species, space and habitats (Husby et al. 2010; Newton 2007; Sanz 2003; Saracco et al. 2019; Zuckerberg, Ribic, and McCauley 2018). This evidence suggests that the relationship between environmental conditions and bird arrival exhibits spatial nonstationarity—in that the strength, relative importance, direction and/or shape of the response varies over space (Rollinson et al. 2021). Nonstationarity in phenological plasticity is likely a result of local adaptation to selection pressures that act on breeding populations experiencing very different ecological conditions (Hendry 2017), especially the varying influence of mortality-causing weather events that limit early arrival and the phenology of invertebrate prey during the breeding period (Newton 2007; Youngflesh et al. 2023). Plasticity in arrival phenology within and across species is likely to be greatest where interannual variation in the timing of selection-inducing events is greatest (i.e., more variable environments) or, non-exclusively, where these pressures have larger fitness consequences (e.g., more extreme environments). Quantifying and explaining potential nonstationarity in phenological responses to a diverse set of environmental conditions across the annual cycle is necessary to understand the mechanisms underpinning plasticity in migration timing, to assess the adaptive capacity of species and populations and to inform related management actions (Thurman et al. 2021).

To disentangle the potential relevance of local climatic conditions and large-scale climate oscillations on arrival timing and how this varies across space and species, we leveraged a set of large-scale community-sourced data using a hierarchical Bayesian approach. We derived 88,965 prebreeding arrival estimates for species populations within equal-area hexagonal grids (hereafter, ‘populations’) from millions of birdwatcher checklists submitted to the citizen-science platform eBird from 2002 to 2022, representing phenological metrics on 222 bird species that breed in the Nearctic. We compared arrival dates at the breeding grounds to local climatic conditions during the arrival period—defined as a 29-day range centred at the mean arrival date of each species at a given location—and to winter (December–February) El-Niño/Southern Oscillation

(ENSO) and North Atlantic Oscillation (NAO) indices. Our flexible hierarchical Bayesian approach allowed us to estimate population- and species-specific sensitivities to each of these factors simultaneously. We compared inter-species differences in how temperature, precipitation and snowpack influence phenology, and how intraspecies variation in sensitivity is explained by the experienced climatic niche position of a given population.

2 | Methods

2.1 | Site-Specific Arrival Estimates

Our method for estimating spatially explicit arrival dates was adapted from Youngflesh et al. (2021) and is briefly summarised here. We downloaded bird occurrence data as checklists from eBird (Sullivan et al. 2009) within the Nearctic (between 170°W and 50°W, and north of 24°N) from 2002 (when eBird launched) to 2022 and then filtered to include only complete checklists with <11 observers, between 5 min to 24 h in duration, with a distance of less than 5 km or an area less than 500 ha, and before ordinal date 200 (i.e., July 19 in non-leap years). Because of differences in sampling across this area, the vast majority of checklists included were from the United States and Canada, limiting inference on species in Mexico. We then grouped checklist data spatially through the use of equally sized hexagonal cells (hereafter ‘sites’) with an equal-area 285-km spacing using the R package dggridr (Barnes and Sahr 2017). Our choice of cell size was balanced to be large enough to fulfil data requirements for precisely estimating arrival dates and to be small enough to make inference on heterogeneity of phenology at finer spatial resolutions. As a result, there may be within-site variation in phenology that is not captured using a 285-km cell size. For each species at each site (hereafter, population) in each year, we fit logistic generalised additive models (GAMs) to our detection-nondetection data in order to estimate arrival timing; specifically, we estimated the date in each year where the probability of detection (i.e., the probability of a complete checklist registering a presence for the species) reached half of the first local maximum value (i.e., half-maximum date, $\bar{H}M$). The half-maximum date measure is a low-bias estimate of phenological events across seasonal taxa, in contrast to metrics such as first arrival dates (Youngflesh et al. 2021). Furthermore, our method here controls for and propagates uncertainty resulting from heterogeneity in detection probability or survey effort within individual spatial units. Our logistic GAMs estimate the probability of detection (p_i) while accounting for effort and elevation of each checklist,

$$y_i \sim \text{Bernoulli}(p_i) \quad (1)$$

$$\text{logit}(p_i) = \alpha_{\text{GAM}} + \beta_{\text{GAM}} * \text{Effort}_i + \theta_{\text{GAM}} * \text{Elevation}_i + f(\text{Day}_i) \quad (2)$$

where y_i is the record of whether a species was recorded on a checklist (detection/nondetection), α_{GAM} is the intercept, β_{GAM} is the effect of effort and θ_{GAM} is a categorical effect representing variation in arrival across elevational levels binned by 500 m increments (<0.5, 0.5–1, ..., 2.5–3, >3 km). Because we were interested in the timing of latitudinal migration and

not elevational movements, we only used estimates for arrival in each cell for the elevational range with the most checklists across all years for downstream analyses. This filtering effectively limits our dataset to relatively low-elevation areas within each spatial unit. The final term, $f(\text{Day}_i)$, is a smoothing penalised regression spline for day of year, which characterises how detection probability changes over a given year, particularly as a function of a species' migratory arrival into a cell. We fit GAMs where enough data were available to calculate precise estimates of arrival (see Youngflesh et al. 2021 for details on data and model fit requirements). To avoid using considerable computational resources associated with increasing data volume over time, we made two additional filtering steps. First, for sites with much more data than needed to precisely estimate arrival dates (assessed as approximately 5000 records), we subsampled (without replacement) down to 5000 records per site/year. Second, we only estimated GAMs for cells where the focal species was present on at least 1% of all checklists for landbirds and 0.5% for waterbirds. We implemented a lower threshold for waterbirds to include species that are relatively abundant but may be confined spatially (e.g., on lakes or coastlines).

2.2 | Filtered Dataset and Species Inclusion

We considered all diurnal, obligate migratory species that breed in the Nearctic for our analysis. We excluded nocturnal species because of low data density and low detectability. For each species, we attempted to estimate arrival dates for all cells that fit the data requirements and then filtered our dataset to include only species-cell combinations with estimated arrival dates later than January 31 to avoid capturing wintering movements. We only included arrival estimates within the Nearctic breeding range of species, classified using eBird Status and Trends (eBird ST) polygons (Fink et al. 2020). We then filtered to species-cell combinations with >2 yearly arrival estimates and included species with >3 sites represented. We then filtered to species with at least 50 species-cell-year estimates. Included species were primarily songbirds (Passeriformes, $n=128$), though 12 other avian orders were also represented, including shorebirds (Charadriiformes, $n=29$), waterfowl (Anseriformes, $n=22$) and woodpeckers (Piciformes, $n=3$).

2.3 | Arrival Window

For each species at each site, we calculated an 'arrival window'—defined as the 29-day period centred at the mean arrival date across all years to isolate the temporal range in which environmental conditions are likely to influence arrival timing. We chose to identify population-specific arrival windows to avoid potential biases when using a broader and generalised time window (e.g., March–May) that would fail to account for the wide variation in arrival timing of species across the continent. The 29-day window length (the mean arrival day plus 2 weeks on either side) was chosen to encompass the period during which arrival was likely (incorporating 98.8% of all individual arrival estimates) and capture environmental conditions over a biologically meaningful time scale.

2.4 | Weather Covariates

We downloaded minimum temperature, precipitation and snow water equivalent at a daily, 1-km resolution from Daymet (Thornton et al. 2022). We used minimum temperature because it may serve as a proxy for a physiological limit to bird survival (Newton 2007). To match environmental variables with arrival estimates, we calculated the average daily minimum temperature, precipitation and snowpack during each 29-day arrival window for each cell, species and year combination. We calculated how anomalous conditions were for each environmental variable in each year by normalising yearly estimates (i.e., subtracting each by the mean and then dividing by the variance of all estimates during the study period). Environmental anomalies were only weakly correlated with each other (Pearson's r : temperature and snowpack = -0.25 ; temperature and precipitation = 0.04 , precipitation and snowpack = 0.07).

2.5 | Variation Across Species' Ranges

To test whether the sensitivity to climate variables varied predictably across species' ranges, we used the average minimum temperature, average daily precipitation and average snow water equivalent experienced by each species across each site within its range. We then calculated z -scores within species to provide an index that represents the niche position of each site on a hot–cold, wet–dry and high snowpack–low snowpack scale for each species.

2.6 | Climate Oscillations

NAO and ENSO are most strongly correlated with weather during the winter months and have variable effects across space (Clarke 2008; Hurrell et al. 2003). As a result, climate oscillations can have opposite effects on wintering weather experienced by species depending on where they spend their winter (Figure S2). To account for this, we explicitly estimate and incorporate the effect of each climate index on the weather conditions in the nonbreeding range of each species into our models. To do this, we probabilistically drew 10,000 points from the eBird ST nonbreeding range map for each species, filtering points to include only those within the Western Hemisphere. We applied this filtering step to include only those wintering areas likely to be used by birds breeding in the Nearctic. We then took the average of the correlation at all points for both ENSO and NAO effects on precipitation and temperature averages during the months of December–February using data from 2002 to 2021. Temperature and precipitation data come from ERA5 reanalysis (Hersbach et al. 2020) and ENSO and NAO data are from the National Weather Service Climate Prediction Center (available via www.cpc.ncep.noaa.gov). Because the effects of climate indices on temperature and precipitation across species ranges are highly correlated, we collapsed species-level values to a single axis using a principal component analysis (PCA), representing a cold and wet to warm and dry axis for both ENSO and NAO correlations. The first PCA axis explained 99.5% and 93.7% of the variation in ENSO temperature and precipitation, and 99.9% and 10.7% of the variation in NAO temperature and precipitation, respectively.

2.7 | Bayesian Hierarchical Model

To calculate the effect of weather conditions at the breeding grounds on arrival for all populations and species simultaneously, we constructed a hierarchical Bayesian model that estimates the effects of each weather variable while accounting for uncertainty. This model uses a hierarchical random slopes and intercepts structure to provide population-specific estimates while also providing species and 'global' (i.e., all species) estimates for the relationships between arrival and climate across all species.

We considered the posterior mean of the GAM-estimated half-max ($\widehat{HM}_{i,c,t}$) as an imperfectly observed estimate of the true arrival date ($Arr_{i,c,t}$) with uncertainty derived from the posterior of the halfmax estimate ($\sigma_{\widehat{HM}_{i,c,t}}$):

$$\widehat{HM}_{i,c,t} \sim N(Arr_{i,c,t}, \sigma_{\widehat{HM}_{i,c,t}}) \quad (3)$$

This process allows us to propagate site- and species-level uncertainty in arrival dates that may arise due to low local data availability, or differences in species detectability (e.g., in areas where a species is rarer) into downstream models of environmental sensitivity. Taking into account the varying degree of uncertainty for each arrival date, we then modelled the (latent) true arrival date as a linear function of a priori covariates:

$$Arr_{i,c,t} \sim N(\alpha_{i,c} + \beta_{1,i,c} * T_{i,c,t} + \beta_{2,i,c} * I_{i,c} * S_{i,c,t} + \beta_{3,i,c} * P_{i,c,t} + \phi_{1,i,c} * E_{i,t} + \phi_{2,i,c} * N_{i,t}, \sigma_i) \quad (4)$$

Arrival of species i in site c in year t is modelled as a function of z -scored minimum temperature (T), snow water equivalent (S) and precipitation anomalies (P). The effects of each of these three variables are represented with β_{1-3} . E and N represent the ENSO and NAO index during the winter (December–February) preceding arrival, with effects of each represented by ϕ_{1-2} . We did not estimate the population-level effect of snowpack when mean snowpack during the arrival period was less than 0.1 kg/m^2 and therefore unlikely to be biologically relevant. We did this by including an indicator variable, $I_{i,c}$, which evaluates to either 1 (mean snowpack $> 0.1 \text{ kg/m}^2$) or 0 (mean snowpack $< 0.1 \text{ kg/m}^2$). To improve model fit, we centred arrival dates by subtracting the mean arrival date across all data points and then back-calculated the arrival date for model interpretation.

Each parameter at the population level was modelled hierarchically to estimate species-level effects, with the mean arrival of each population described by:

$$\alpha_{i,c} \sim N(\mu_{\alpha_i} + \zeta_i * L_c, \sigma_{\alpha}) \quad (5)$$

where μ_{α_i} represents the mean arrival date of each species at the latitudinal centre of its range and ζ_i represents the species-level effect of latitude (L) on mean arrival date in each cell. The effects of temperature, snowpack and precipitation at the population level are modelled as a function of the niche position of each population within a species' range:

$$\beta_{1,i,c} \sim N(\mu_{\beta_{1,i}} + \theta_{1,i} * \widehat{TN}_{i,c}, \sigma_{\beta_1}) \quad (6)$$

$$\beta_{2,i,c} \sim N(\mu_{\beta_{2,i}} + \theta_{2,i} * \widehat{SN}_{i,c}, \sigma_{\beta_2}) \quad (7)$$

$$\beta_{3,i,c} \sim N(\mu_{\beta_{3,i}} + \theta_{3,i} * \widehat{PN}_{i,c}, \sigma_{\beta_3}) \quad (8)$$

where $\widehat{TN}_{i,c}$, $\widehat{SN}_{i,c}$ and $\widehat{PN}_{i,c}$ represent the mean temperature, snowpack and precipitation during a given species-specific arrival period—raw means are transformed into z -scores across all populations within a species. The effect of niche position on sensitivity is represented by θ for each of T , S and P , while the parameter μ_{β_1} represents the species-level effect of T at $\widehat{TN}$ (and similarly for S and P). Parameters $\sigma_{\beta_{1-3}}$ represent process error at this level. The species-level effects of ENSO and NAO are represented by hierarchical normal distributions with means $\mu_{\phi_{1,i}}$ and $\mu_{\phi_{2,i}}$ and process errors $\sigma_{\phi_{1-3}}$ and $\sigma_{\phi_{1-2}}$.

$$\phi_{1,i,c} \sim N(\mu_{\phi_{1,i}}, \sigma_{\phi_1}) \quad (9)$$

$$\phi_{2,i,c} \sim N(\mu_{\phi_{2,i}}, \sigma_{\phi_2}) \quad (10)$$

Residual variance is likely to vary among species, so we modelled process variance at the species-level (σ_i), derived from a lognormal distribution with estimated parameters ($\mu_{\sigma}, \sigma_{\sigma}$):

$$\sigma_i \sim \text{Lognormal}(\mu_{\sigma}, \sigma_{\sigma}) \quad (11)$$

Finally, we modelled the species-level intercept and slope parameters above (Equations 6–8) hierarchically to get the global effects indicating the effects of each covariate across all species. The cross-species mean arrival dates at the latitudinal centre of species' ranges were modelled as γ with process error $\sigma_{\mu_{\alpha}}$:

$$\mu_{\alpha_i} \sim N(\gamma, \sigma_{\mu_{\alpha}}) \quad (12)$$

The cross-species mean effect of latitude on arrival date was modelled with a hierarchical normal:

$$\zeta_i \sim N(\mu_{\zeta}, \sigma_{\zeta}) \quad (13)$$

where the cross-species mean intraspecies effect of latitude on arrival is represented by μ_{ζ} , with process error σ_{ζ} . The cross-species means of $\mu_{\beta_{k,i}}$ and $\theta_{k,i}$ are represented by η_k and ν_k respectively, and Σ_{β_k} are 2×2 covariance matrices.

$$\begin{bmatrix} \mu_{\beta_{k,i}} \\ \theta_{k,i} \end{bmatrix} \sim \text{MVN} \left(\begin{bmatrix} \eta_k \\ \nu_k \end{bmatrix}, \Sigma_{\beta_k} \right), k = 1, 2, 3 \quad (14)$$

The species-level effects of the average winter indices of the climatic oscillations ENSO and NAO ($\mu_{\phi_{1,i}}, \mu_{\phi_{2,i}}$) are in turn modelled as a function of the average cross-species effect of each climate oscillation when either oscillation is uncorrelated with weather at the species wintering grounds and the effect of each climate oscillations correlation (κ_1, κ_2) with a PCA of

temperature and precipitation effects at the wintering grounds ($\widehat{EW}_i, \widehat{NW}_i$) with process error $\sigma_{\mu_{\phi_1}}$ and $\sigma_{\mu_{\phi_2}}$.

$$\mu_{\phi_1 i} \sim N(\omega_1 + \kappa_1 * \widehat{EW}_i, \sigma_{\mu_{\phi_1}}) \quad (15)$$

$$\mu_{\phi_2 i} \sim N(\omega_2 + \kappa_2 * \widehat{NW}_i, \sigma_{\mu_{\phi_2}}) \quad (16)$$

2.8 | Percent Variance Explained

We calculated to what degree climate during the arrival period and climate oscillations explained variation in arrival timing. We did this by calculating how much variance each weather covariate ($\beta_{1-3, i, c}$) and climate oscillation ($\phi_{1-2, i, c}$) explained variation in arrival at each cell for each species (Equation 4) using a Bayesian R^2 (Gelman et al. 2019) that computes the variance in predicted arrival explained by each coefficient-covariate pair ($\beta_{1-3, i, c}, \phi_{1-2, i, c}$), analogous to the frequentist coefficient of determination (R^2):

$$g_{rep, i, c, t} = \beta_{i, c} * X_{i, c, t} \quad (17)$$

$$\epsilon_{i, c, t} = Arr_{i, c, t} - g_{rep, i, c, t} \quad (18)$$

$$\frac{\sigma_{g_{rep}}^2}{\sigma_{g_{rep}}^2 + \sigma_{\epsilon}^2} \quad (19)$$

where β represents the model coefficient of interest, X represents the covariate of interest and g_{rep} represents the predicted response. $Arr_{i, c, t}$ is the estimated arrival date, and ϵ is the difference between the true arrival date and the predicted arrival date. The variance of the metrics of interest is represented by σ^2 . To calculate species-level variance metrics (i.e., the degree to which arrival of each species is explained by each environmental covariate), we took the mean of these population-specific estimates.

2.9 | Model Fits and Checks

All models were fit using the package rstan version 2.21.8 (Stan Development Team 2021) to interface with stan (Stan Development Team 2020) using R version 4.2.3 (R Core Team 2023). We analysed our models using MCMCvis version 0.15.5 (Youngflesh 2018). Our model fit objects, summary of parameter estimates and posterior predictive checks for our model are included as Data S3.

3 | Results

3.1 | Effect of Temperature on Arrival Phenology

We found that warmer average minimum air temperatures (hereafter, ‘temperatures’) during the arrival period had a pervasive advancing effect on arrival across species, with the average species arriving 1.07 days earlier in years when temperatures were one standard deviation (+1SD) warmer than the mean (89% credible interval [CrI] = -1.18 to -0.97, $\Pr(\eta_1 < 0) = 1$ [Equation 14]; Table S1; Figure 1). The vast majority (92.4%) of populations (i.e., individuals of a given species within a spatial cell) advanced arrival timing in years with warmer temperatures during the arrival window ($\beta_1 < 0$

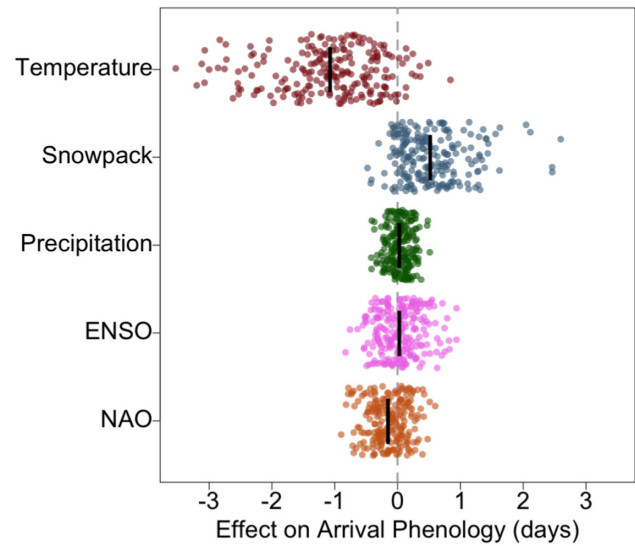


FIGURE 1 | Effects of temperature, snowpack, precipitation, the El-Niño/Southern Oscillation and the North Atlantic Oscillation on arrival of 222 Nearctic bird species. Species-level effects (dots represent posterior medians) of a +1SD increase in temperature, snowpack and precipitation, and a +1 index value of ENSO and NAO on spring arrival phenology. Solid black bars represent median cross-species effects for each climate variable (credible intervals are reported in Table S1).

[Equation 6], $n = 9393$), averaging an advancement of 0.65 days per 1°C (Figure 2). Within species, the effect of temperature on arrival was more strongly negative in parts of the species' range with the coldest average minimum temperatures during the arrival window ($\nu_1 = 0.14$ [Equation 14], 89% CrI = 0.10–0.17, $\Pr(\nu_1 > 0) = 1$; Table S1; Figure 3). Due to both consistent intraspecific spatial variation and species-level differences, the median effect of anomalously warm conditions was strongest among breeding communities further north (Figure 4A).

Temperature explained 15.7% of the interannual variation in arrival phenology for the average species after controlling for variation in mean arrival date between sites (species-level range = 0.8%–58.3%, Table S2; Figure 5). The explanatory power of temperature varied taxonomically. Arrival of certain groups, including wood-warblers (Parulidae, $n = 39$) and waterfowl (Anatidae, $n = 22$), was particularly well-explained by temperature, accounting for an average of 22.3% and 21.7% of the total variation in arrival dates within these groups, respectively (Figure S1). Comparatively, temperature explained less variation in arrival dates of groups such as sparrows (11.8%; Passerellidae, $n = 16$) and swallows (4.1%; Hirundinidae, $n = 7$; Figure S1). Substantial variation was often observed even among closely related species. For example, the explanatory power of temperature in determining arrival of the three ‘Solitary Vireo’ species varies by an order of magnitude (Blue-headed Vireo *Vireo solitarius*: 34.2%; Plumbeous Vireo *Vireo plumbeus*: 2.9%; Cassin's Vireo *Vireo cassinii*: 2.5%; Table S2).

3.2 | Effect of Snowpack on Bird Arrival Timing

Greater snowpack levels at breeding grounds—measured as the average weight of snow per square meter—had a delaying effect on arrival, with species arriving 0.52 days later on

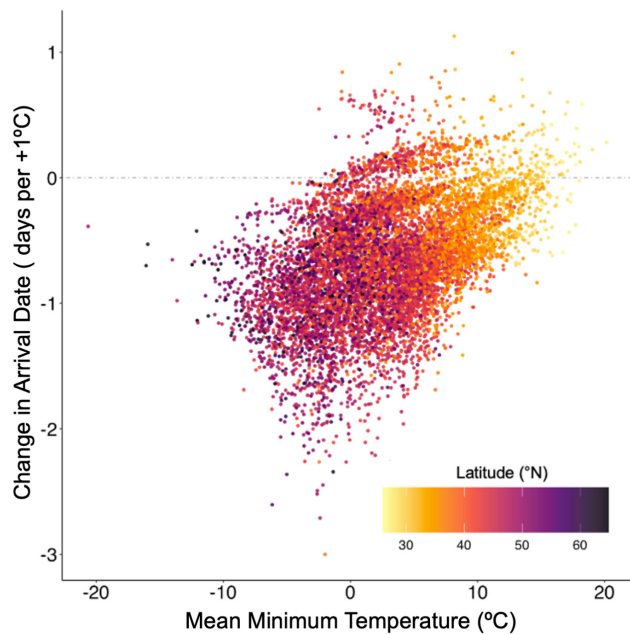


FIGURE 2 | Populations breeding in colder areas exhibit greater sensitivity in arrival timing to interannual variation in temperature. Predicted change in arrival timing for each population per 1°C change (sensitivity) is represented by a dot, with the mean minimum temperature during the arrival period at the breeding grounds from 2002 to 2022 represented on the x-axis. The colour ramp represents the mean latitude of each site, with darker points representing higher latitude.

average when snowpack levels were 1SD above the mean (89% CrI = 0.44–0.61, $\Pr(\eta_2 > 0) = 1$ [Equation 14]; Table S1). This effect was observed while simultaneously controlling for temperature and was largely consistent across species, with 88% of species predicted to arrive later when snowpack levels were greater than normal (median estimates of species-level effects, $\mu_{\beta_2} > 0$ [Equation 7], 196/222). Within species, the delaying effect of snowpack is the greatest in areas with on-average higher snowpack during the arrival window ($v_2 = -0.08$ [Equation 14], 89% CrI = -0.12 to -0.05, $\Pr(v_2 < 0) = 1$; Table S1), and strongest among communities in the Prairie Potholes and Great Plains regions (Figure 4B).

Across species, snowpack explained a moderate amount of the variation in arrival (mean = 4.5%, species-level range = 0%–21.8%; Figure 5; Figure S1). Snowpack explained a larger amount of the variance among waterfowl species (mean = 10.3%; order Anseriformes, $n = 22$), but less for some songbird groups like the tyrant flycatchers (mean = 2.1%; family Tyrannidae $n = 18$) and cardinal-grosbeaks (0.6%; family Cardinalidae, $n = 10$; Figure S1).

3.3 | Effect of Precipitation on Bird Arrival Timing

In contrast to the strong and consistent effects of temperature and snowpack, the effect of precipitation (measured as the mean daily accumulation during the arrival window, in millimetres) was much weaker, with the average effect of a 1SD increase in precipitation leading to an average 0.04 day delay in arrival (89% CrI = -0.0003 to 0.08, $\Pr(\eta_3 > 0) = 0.94$ [Equation 14]; Table S1; Figure 1). Species-level effects of precipitation were

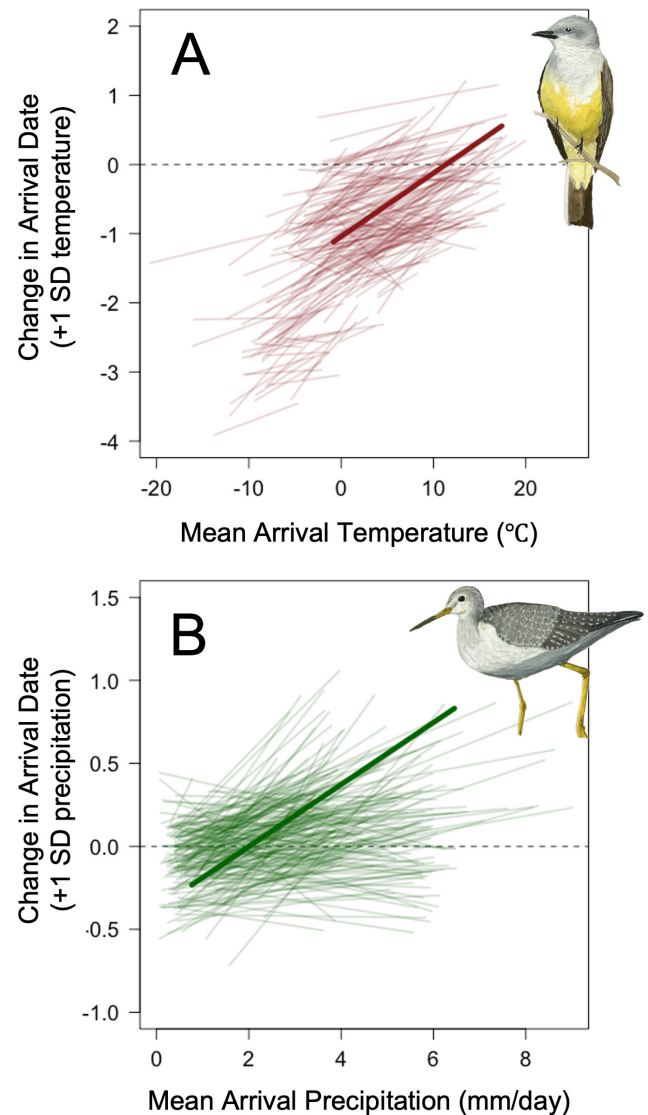


FIGURE 3 | Sensitivity to temperature and precipitation at the breeding grounds exhibits spatial nonstationarity at the intraspecies level. Each line represents the model-estimated sensitivity to temperature (A) or precipitation (B) on bird arrival timing across the range of environmental conditions experienced within a species' range. Slopes of lines that differ from zero (i.e., non-flat lines) represent spatial nonstationarity, where environmental gradients have spatially varying effects on arrival timing. Representative species exhibiting different directionality of effects across the species' range (i.e., earlier arrival in some parts and delayed arrival in others) are shown with bold lines (A: Western Kingbird *Tyrannus verticalis*; B: Greater Yellowlegs *Tringa melanoleuca*).

balanced between delaying (59.9%) and advancing (40.1%; median estimates of species-level effects, μ_{β_3} , $n = 222$; Figure 1). Within species the effect of precipitation was more consistently explained by niche position, with high precipitation leading to more delayed arrival in wetter parts of a species' range (i.e., areas with higher average precipitation during the entire study period) and earlier arrival in drier parts ($v_3 = 0.08$ [Equation 14], 89% CrI = 0.04–0.11, $\Pr(v_3 > 0) = 1$; Figure 3). These relationships translated spatially to an association of increased precipitation with arrival delays along the Pacific Coast and in New

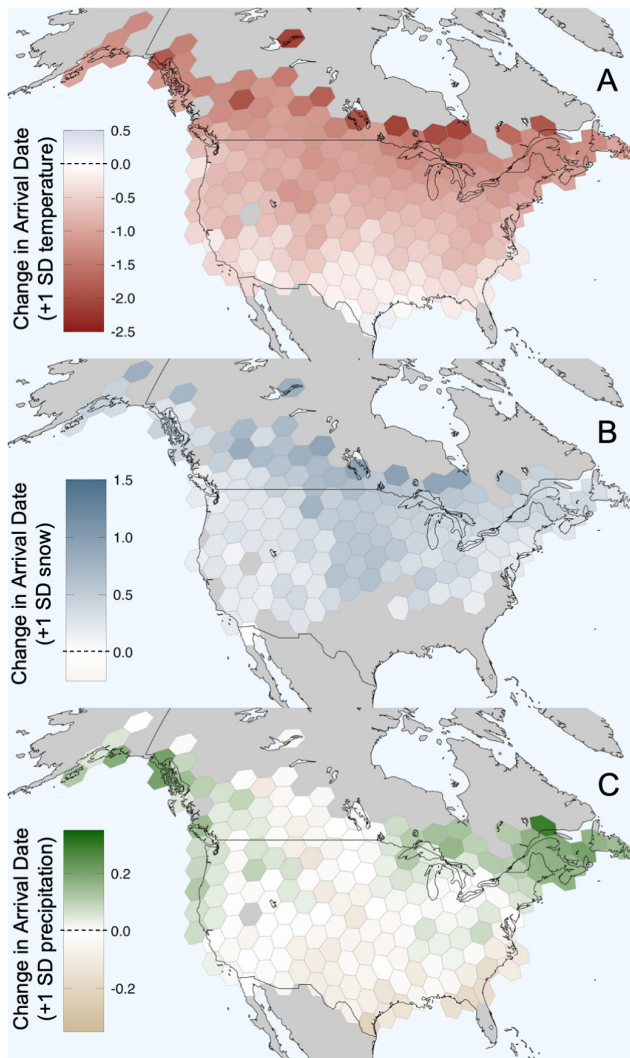


FIGURE 4 | Sensitivity of spring arrival date to climate variability varies across space. Median population-level effects at each site (hexagons) represent the predicted change in arrival date with a one standard deviation increase in temperature (A), snowpack (B), and precipitation (C). Sites are included where at least 10 species are evaluated. Sites with no data or < 10 species evaluated are not plotted. Note different colour scales across panels.

England, and advancements in the American South and Great Plains (Figure 4C). Compared to temperature and snowpack, precipitation explained a very small average percent of the variance in arrival across species (mean = 1.2%, range = 0.2%–5.8%; Table S2; Figure 5; Figure S1).

3.4 | Effects of ENSO/NAO

We found consistent but relatively weak effects of December–February ENSO and NAO indices on the arrival of birds in the following spring. The effect of ENSO on species' arrival varied greatly depending on how El Niño/La Niña affects weather at a species' wintering grounds (median $\kappa_1 = 0.50$ [Equation 15], 89% CrI = 0.33–0.66, $\text{Pr}(\kappa_1 > 0) = 1$; Table S1; Figure 1). Species that spend Northern Hemisphere winters (hereafter, 'winter') in regions where a high ENSO index is associated with high

temperatures and low precipitation (e.g., Alder Flycatcher *Empidonax alnorum*) tended to arrive later following a winter El Niño event (i.e., positive ENSO index). For species spending the winter months in an area where a high ENSO index is associated with cool temperatures and higher precipitation (e.g., Rufous Hummingbird *Selasphorus rufus*), arrival tended to be earlier following winter El Niño events (Figure S2). Taken together, this suggests that hot and dry conditions brought on by the El Niño/Southern Oscillation in wintering grounds generally led to later arrival on breeding grounds. Despite the consistency of this result across species, ENSO still explained a relatively small amount of variation in species' arrival (mean = 2.2%, range = 0.2%–16.7%; Table S2).

The observed effect of a positive NAO index across species was negative (median $\omega_2 = -0.14$ [Equation 16], 89% CrI = -0.20 to -0.08, $\text{Pr}(\omega_2 < 0) = 1$; Table S1; Figure 2) but not related to how NAO affects climate on species' wintering grounds (median $\kappa_2 = -0.01$ [Equation 16], 89% CrI = -0.41 to 0.45, $\text{Pr}(\kappa_1 > 0) = 0.52$; Table S1; Figure 2). This finding suggests that when the NAO index is high—a condition associated with warmer temperatures in most of the United States and Southern Canada during spring migration—birds tend to arrive earlier. NAO explained a slightly smaller amount of variation in arrival across species compared to ENSO (mean = 1.8%, range = 0.2%–11.6%; Table S2; Figure 5).

4 | Discussion

The phenological advancement of migratory birds is a canonical example of the ongoing effects of climate change, but disentangling the relative importance of multiple climatic factors on arrival across species and space has remained challenging. Looking across a continent at a wide range of species, from waterfowl to warblers, we found spatial nonstationarity in the sensitivity of avian phenology to environmental conditions, with some populations, species and communities better tracking rising temperatures, diminishing snowpack and more variable precipitation patterns. Spatial nonstationarity in phenological responses to interannual environmental variation suggests widespread diversity in population-level responses to local conditions, highlighting the enhanced importance of environmental factors near the climatic extremes of species' ranges. Greater levels of plasticity in some migratory populations may indicate more intense selective pressures due to local environmental factors, while lower levels of plasticity may suggest the opposite. Alternatively, lower levels of plasticity either at the species or population level may indicate a weaker capacity to respond to environmental conditions, potentially due to physiological limitations or the unavailability of reliable cues. These results stress the need to monitor and measure the wide variation in phenological sensitivity to multiple environmental factors across ecological levels of organisation and spatial scales to accurately forecast ecosystem-level responses to climate change.

Within species, we found spatial nonstationarity in the responses of populations to temperature, snowpack and precipitation. The intraspecific effects of temperature and snowpack on arrival varied predictably across populations, such that effects were strongest in colder and snowier parts of a species'

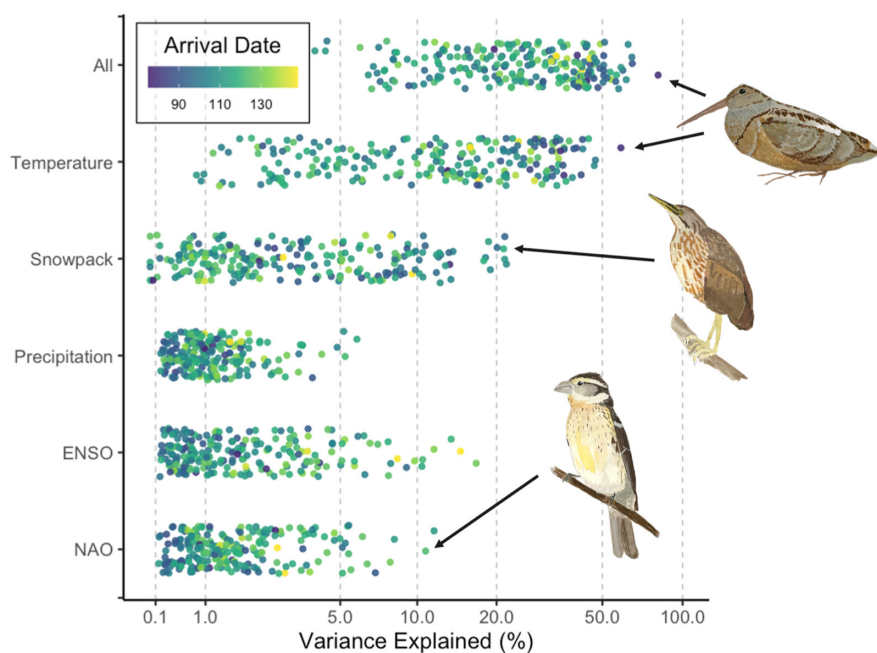


FIGURE 5 | Temperature and snowpack explain more variance in arrival timing when compared to precipitation and climate oscillations. Percent variance explained by all covariates, and for each covariate individually, with each point representing a species. Mean arrival date for each species is represented on the colour axis. Example species with high levels of variance explained by one or more covariates are highlighted (American Woodcock *Scolopax minor*, American Bittern *Botaurus lentiginos*, Black-headed Grosbeak *Pheucticus melanocephalus*).

range. A similar, but weaker, effect was observed with precipitation where the delaying effect of higher precipitation tended to be stronger towards the wetter extreme of a species' range. As climate regimes change across the continent, our results suggest that populations located on either extreme of their experienced niche are likely to diverge in their arrival timing. For example, more phenologically sensitive populations breeding in cold, northern areas may advance arrival as the climate warms while populations at the warmer, southern edge of their range may not—a pattern similarly observed in the response of birds to green-up (Youngflesh et al. 2021). Intraspecific variation in sensitivity of phenology to climate may then have divergent consequences for survival or breeding success across a species' range, with population persistence or growth favoured in more phenologically sensitive populations. Furthermore, responsiveness to environmental conditions may be particularly important for persistence near the edge of a given species' climatic niche due to physiological constraints (Hardie and Hutchings 2010). If increased phenological sensitivity among northern populations compared to southern ones leads to divergent demographic trends, range shifts may result. In support of this hypothesis, southern range contractions but stable northern range limits have been observed among some neotropical migrants (Rushing et al. 2020). The substantial variation and consequences of phenological responses within species across space is increasingly being recognised as an important factor to account for when predicting species- and community-level responses to global change (Border et al. 2024; Diez et al. 2012; Kovach et al. 2015).

Wide variation in species-level sensitivity to fluctuations in environmental conditions may be one cause for divergent population trajectories. The risk of encountering dangerous conditions after arrival at the breeding grounds have been demonstrated

to cause substantial mortality across species (Lerche-Jørgensen et al. 2018; Newton 2007). Presumably, the ability to plastically respond to these interannual fluctuations can mitigate the risk of encountering late storms or other unfavourable conditions. Species or groups that are less sensitive to climatic fluctuations therefore may be the most at risk. Across species, our model explained an average of 28% of site-level variation in arrival timing but varied widely among species, from 4% to 81%. While some groups showed substantial phenological flexibility, others were largely unresponsive—a pattern that may have demographic consequences. For example, waterfowl were the taxonomic group most responsive to climate fluctuations at the breeding grounds (Figure S1), suggesting that this flexibility likely mitigates the risk of encountering events like late spring storms that prohibit feeding by covering the ground with snow and refreezing lakes (Barry 1968; Newton 2007). Similarly at risk, but inflexible by contrast, aerial insectivores—the least responsive group to environmental conditions in our analysis—may be unable to mitigate the risks of encountering cold snaps that limit insect prey activity and cause mass-mortality events due to a strong genetic control of migration timing (Bazzi et al. 2015; Brown and Brown 2000; Newton 2007). Identification of the various biological or physiological constraints that lead to the differential abilities of species and groups to respond to environmental variation—such as heritability of migration timing, the distance and route of migration, or favorability of conditions on the nonbreeding grounds and en route (Justen and Delmore 2022; Paxton et al. 2014; Rockwell, Bocetti, and Marra 2012)—could help elucidate specific pressures on migratory birds.

The ability to match arrival timing with favourable environmental conditions may also be limited by the availability of reliable cues. For example, while temperature and snowpack are correlated spatially and temporally (Data S2) and therefore could

act as increasingly reliable cues as birds near their breeding grounds, precipitation is less spatially correlated and potentially harder to predict (Data S2). Despite the demonstrated effects of precipitation on the mortality and breeding success of birds (Fisher et al. 2015; Zuckerberg, Ribic, and McCauley 2018), variation in precipitation was the least explanatory variable included in our analysis (Figure 5). The inability to anticipate or adjust phenology to match important environmental conditions may have demographic consequences. For example, grassland birds—a group in precipitous decline across the United States and Canada (Rosenberg et al. 2019)—have been shown to exhibit higher mortality during periods with extreme precipitation (Conrey et al. 2016; McGowan, Perlut, and Strong 2021; Zuckerberg, Ribic, and McCauley 2018). Alternatively, weak effects of precipitation observed across species may result from precipitation having both negative and positive effects on local populations (e.g., high precipitation may advance invertebrate prey phenology but also cause higher mortality risks). Inflexibility to respond to rainfall events is likely to exacerbate declines among vulnerable species and restructure local bird communities as precipitation patterns become more variable in the future (Boyle, Shogren, and Brawn 2020; Pörtner et al. 2022).

Variation in phenological sensitivity is likely to restructure the composition of communities both spatially and temporally. Divergence in demographic rates resulting from varying degrees of responsiveness to climate change at a given location may restructure the relative abundances of local communities for the reasons outlined above. At the same time, our results suggest that interannual fluctuations in environmental conditions could restructure communities temporally by altering the composition of migratory communities and the relative order of arrival timing. This leads to a change in the temporal overlap of species during the migratory and arrival periods, with potential implications for the co-occurrence or degree of inter-species interactions, with largely unknown consequences to predator–prey, competition and disease dynamics (Cohen and Satterfield 2020; Fuller et al. 2010; Samplonius and Both 2019).

Explicitly accounting for inter- and intraspecific variation in sensitivity can provide insight into questions that might otherwise be difficult to address. For example, the effects of climate oscillations on avian migration phenology are well studied but a general consensus on their importance remains elusive (Gordo 2007; Haest, Hüppop, and Bairlein 2018). Here, we estimated the effects of ENSO and NAO across hundreds of species simultaneously, allowing for variation according to how those climatic oscillations affect species on their wintering grounds. Our results suggest that when ENSO brings warm and dry conditions to birds' wintering areas, birds tend to delay their arrival on breeding grounds. This delay is likely due to either later departure and/or decreased body condition prior to the initiation of migration (Cooper, Sherry, and Marra 2015; González-Prieto and Hobson 2013). In contrast, the effect of warm conditions in much of the United States brought on by a high NAO appear to lead to slightly earlier arrival for most species regardless of the location of their wintering grounds, suggesting that NAO may lead to advanced arrival by improving conditions on route during migration. By accounting for variation in where species spend winter, we find that the impact of these oscillations likely occurs at different points in the annual life cycle.

Future work building on models that account for spatial non-stationary and variation across ecological levels of organisation can lead to better predictions about species' responses to global change at both large and small spatial scales. We found that a high degree of variation in population- and species-level sensitivities manifests as variation in communities across geographical space, with those at higher latitudes (e.g., southern Canada and Alaska) more responsive than those in the southern United States. Increasing minimum temperatures and diminishing snowpack are disproportionately affecting higher latitudes (Pörtner et al. 2022). Together, this suggests that the most extreme shifts in arrival are likely to be observed among communities closer to the poles, a product of both high rates of environmental change and high phenological sensitivity. Integrating phenological models with regional climate projections could be used to explicitly forecast the arrival of migratory birds across the continent in both the short and long term.

By combining arrival forecasts with models of other ecological processes—such as demography (Youngflesh et al. 2023)—arrival estimates could help inform investigations into how diverging phenological trends will affect other ecological phenomena of interest across the continent, including community composition and mismatches in phenology of other taxa, such as plants and insects. Future work could also augment our current model to integrate and investigate other potentially explanatory weather variables (e.g., wind, aridity and temperature extremes) and more complex processes governing phenological shifts, including changes in timing due to genetic inheritance, carry-over effects, response to cue-conflicts and limitations to plasticity (Åkesson and Helm 2020; Both and Visser 2001; Rockwell, Bocetti, and Marra 2012). Explicit tests for the other factors that may drive spatial nonstationarity—including ecoregions, elevation and genetics—may provide insight into the eco-evolutionary feedbacks that facilitate or hamper differentiation of phenotypic plasticity across populations. Models of large-scale phenological processes that span species' ranges and account for intraspecific spatial variation could help reveal important differences in the mechanisms underlying observed phenological shifts and improve our understanding of threats to avian populations in the future.

Author Contributions

B.A.T. conceived the study with the supervision of M.W.T. All authors contributed to the design of the analysis. B.A.T. conducted the analysis with the help of C.Y. and with T.C. contributing data. B.A.T. wrote the manuscript with input and revisions from all authors.

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Data Availability Statement

Code to process data and run analyses is available on GitHub: https://github.com/bentonelli/Nonstationarity_pheno_climate. Code and data are archived on Zenodo: <https://doi.org/10.5281/zenodo.13381533>. The statistical model object is also available separately on Zenodo: <https://doi.org/10.5281/zenodo.13256390>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14526>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.