



RESEARCH ARTICLE

Potential for bird–insect phenological mismatch in a tri-trophic system

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Abstract

1. Climate change is altering the seasonal timing of biological events across the tree of life. Phenological asynchrony has the potential to hasten population declines and disrupt ecosystem function. However, we lack broad comparisons of the degree of sensitivity to common phenological cues across multiple trophic levels. Overcoming the complexity of integrating data across trophic levels is essential for identifying spatial locations and species for which mismatches are most likely to occur.
2. Here, we synthesized over 15 years of data across three trophic levels to estimate the timing of four interacting phenological events in eastern North America: the green-up of forest canopy trees, emergence of adult Lepidoptera and arrival and subsequent breeding of migratory birds.
3. We next quantified the magnitude of phenological shift per one unit change of springtime temperature accumulation as measured by accumulated growing degree days (GDD). We expected trophic responses to spring temperature accumulation to be related to physiology, thus predicting a weaker response of birds to GDD than that of insects and plants.
4. We found that insect and plant phenology indeed had similarly strong sensitivity to GDD, while bird phenology had lower sensitivity. We also found that vegetation green-up and bird arrival were more sensitive to GDD in higher latitudes, but the timing of bird breeding was less sensitive to GDD in higher latitudes. Migratory bird species with slow migration pace, early arrivals and more northerly wintering grounds shifted their arrival the most.
5. Across Eastern Temperate Forests, the similar responses of vegetation green-up and Lepidoptera emergence to temperature shifts support the use of remotely sensed green-up to track how the timing of bird food resources is shifting in response to climate change. Our results indicate that, across our plant–insect–bird system, the bird–insect phenological link has a greater potential for phenological

Robert P. Guralnick and Casey Youngflesh contributed equally to this work.

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mismatch than the insect–plant link, with a higher risk of decoupling at higher latitudes.

KEYWORDS

asynchrony, birds, data synthesis, growing degree days, insects, mismatch, phenology, plants

1 | INTRODUCTION

Phenology—the seasonal timing of ecological events—is highly sensitive to environmental change and thus serves as an indicator for the impacts of global change on species and communities (Parmesan & Yohe, 2003). Phenological changes can also potentially trigger consequences for ecosystems via temporal decoupling of interactions between species (Beard et al., 2019). Such phenological decoupling occurs because the magnitude and direction of phenological responses to environmental change vary among interacting species, which can lead to suboptimal outcomes across trophic levels, such as reduced prey availability for predators or reduced seed-set for plants due to low pollination services (Damien & Tougeron, 2019; Kudo & Ida, 2013). Additionally, responses to phenological drivers may vary spatially for species (Burgess et al., 2018), potentially exacerbating the risk of phenological mismatches, which refer to the demographic consequences of these asynchronies (Cushing, 1990; Durant et al., 2007).

Vegetation green-up, insect emergence and the arrival and subsequent breeding of migratory birds are key vernal events in many seasonal systems that are linked via trophic interactions. Most North American birds are primarily or partially insectivorous, and even species that generally do not feed on insect prey as adults (e.g. granivores, nectarivores) still rely heavily on insects to feed offspring (Capinera, 2010; Hurlbert et al., 2021). Lepidoptera larvae (i.e. caterpillars) represent the primary component of this insect prey base for these birds (Holmes et al., 1979; Jones et al., 2003) and caterpillar biomass has been demonstrated to influence avian density (Graber & Graber, 1983), reproductive success (Rodenhouse & Holmes, 1992; Visser et al., 2006) and the number of broods produced in a given year (Nagy & Holmes, 2004, 2005). While the larvae of nocturnal adult Lepidoptera (as opposed to butterflies) are considered particularly important due to their greater abundance and diversity as forest herbivores, all Lepidoptera, regardless of diurnality, exhibit similar phenological shifts in response to climate drivers (Belitz et al., 2023). As ectothermic herbivores, Lepidoptera are sensitive to both temperature and the timing of vegetation green-up as they rely on external heat and palatable leaves for growth (van Asch & Visser, 2007). The degree of phenological synchrony between caterpillars and their host plants has been linked to insect outbreak dynamics (Ekholm et al., 2020) and the decline of butterfly biomass (Larsen et al., 2024), both of which could impact ecosystem function.

Climate change threatens to disrupt tri-trophic interactions among plants, Lepidoptera and birds because the phenology of lower trophic levels, such as primary producers, may respond

more strongly to changing temperatures than higher trophic levels (Thackeray et al., 2016). For plants and insects, spring phenologies are physiologically tied to temperature, with plants and insects maturing faster in warmer environments (Buckley, 2022; Mirth et al., 2021; Piao et al., 2015), although other drivers such as photoperiod also play a regulatory role (Bradshaw & Holzapfel, 2007; Piao et al., 2015). While an association between temperature and the timing of bird migration and breeding phenology is apparent (Bowers et al., 2016), the mechanism by which this association arises is currently unknown (Caro et al., 2013). Food availability is likely to play a role in these phenological events (Cooper et al., 2015) which may itself be regulated by environmental factors such as temperature and precipitation (Raimondo et al., 2004). Conversely, there may be energetic constraints on producing and incubating eggs that could be imposed by temperature, which will impact the breeding phenology of birds (Shutt et al., 2019).

Recent broad-scale research demonstrates that phenological sensitivity to temperature varies across space and among taxa. Temperature-driven phenological advances, where phenology is occurring earlier in the year, in plant leaf out and flowering are greater in colder locations, compared to warmer locations (Prevéy et al., 2017). In birds, radar data have shown that the timing of peak bird migration has advanced 0.6 days per decade on average over 24 years across the United States and that these advances are stronger at higher latitudes (Horton et al., 2020). Youngflesh et al. (2021) found a similar result using eBird data.

As well, life-history traits have considerable impacts on phenological sensitivity to changes in temperature. The overwintering life stage of Lepidoptera is one such trait that is important in determining Lepidopteran phenological sensitivity to temperature. Species that overwinter in later life stages (such as pupa or adult) have greater phenological sensitivity to temperature than species that overwinter in earlier life stages (Roy et al., 2015). In birds, a variety of traits have been shown to influence the timing of bird migration and breeding, with a global meta-analysis indicating diet generalists, primary consumers and larger birds display greater advancements of pre-breeding migration (Romano et al., 2023). Additionally, birds that migrate slower, arrive earlier and overwinter further north are better able to track changes in spring green-up (Youngflesh et al., 2021).

While it is well documented that phenological sensitivities vary across space, taxa and traits, broad-scale studies comparing sensitivities among three trophic levels to a single phenological cue are limited. Broad-scale studies determining phenological synchrony between two of these trophic levels, primarily green-up and birds, are more common (Robertson et al., 2024; Youngflesh et al., 2021).

In the eastern United States, it has been documented that although migratory birds are shifting their arrival dates earlier in more recent years, these shifts are not keeping pace with rapidly changing vegetation green-up, and that the lag between the arrival of migratory birds and green-up is increasing over time (Mayor et al., 2017). The timing of landbird breeding has also not kept up with shifts in the timing of vegetation green-up, with consequences for bird demographics. Across North America, birds produced fewer young in years when the timing of breeding was asynchronous with vegetation green-up (Youngflesh et al., 2023). While studies taking a tri-trophic approach, including lepidopterans, plants and birds, are needed for understanding the consequences of phenological asynchronies, most have occurred on a relatively limited spatial scale and in systems with relatively limited plant and lepidopteran diversity such as the Netherlands (e.g. Both et al., 2009) and the United Kingdom. In the United Kingdom, Burgess et al. (2018) documented that the phenology of oaks, caterpillars and birds is later at high latitudes, but this effect is strongest for oaks. Tri-trophic studies have also documented asynchrony between peak caterpillar biomass and peak nestling demand for birds, with the strongest asynchrony in warmer springs (Burgess et al., 2018; Franks et al., 2018).

Expanding the spatial and taxonomic scope of tri-trophic phenology studies is essential for understanding the drivers of phenological mismatch and identifying where, and for which taxonomic groups, these mismatches are most likely to occur. Here, we quantified the degree to which changes in spring accumulated growing degree days (GDD)—a measure of energy accumulation based on temperature—shifts the timing of forest canopy trees, Lepidoptera which are primary consumers on that canopy, and birds which utilize caterpillars as a key food source. We co-located data for all three trophic groups across eastern North America and estimated the sensitivity of green-up of new vegetation, emergence of adult butterflies (as a proxy for caterpillar availability), migratory bird arrival and bird breeding to spring accumulated GDD. Based on physiological ties of plant and insect phenology to temperature (Buckley, 2022; Mirth et al., 2021; Piao et al., 2015), we predict that local plant and Lepidoptera phenology will be more tightly coupled to interannual variation and trends in GDD compared to bird arrival and breeding phenology (Burgess et al., 2018; Franks et al., 2018). Furthermore, using the dense set of data resources collated here, we examine whether the signal of phenological asynchrony varies spatially across regions and trophic levels. We expect greater sensitivity to GDD in more northerly locations for all three of our trophic levels given the results of previous studies (e.g. Burgess et al., 2018; Youngflesh et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Estimating phenological metrics

We estimated the timing of vegetation green-up, initiation of adult butterfly flight period, bird arrival and bird breeding for the years 2002–2017. Our study scope was restricted to the area of North

America east of 95°W and north of 24°N, which bounds the Eastern Temperate Forest ecoregion. This study area was chosen because it has a high density of bird and butterfly observations in our datasets and is a seasonal biome where plant and insect phenologies are known to be regulated by temperature (Larsen et al., 2022; Neupane et al., 2022). We aggregated satellite-derived canopy green-up with butterfly and migratory bird data within 74 equal-sized hexagonal cells (area of ~70,000 km²) created with the R package *dggridR* (Barnes, 2017). This aggregation was done to balance typical data densities for butterflies and bird arrival within spatial bins where climate variation is much lower within cells compared to between cells (following Youngflesh et al., 2021; Figure 1). Bird breeding was estimated at individual bird banding locations.

We estimated vegetation green-up from the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Dynamics MCD12Q2 v.6 data product, provided at 500m spatial resolution (Friedl & Sulla-Menashe, 2019). This product has been shown to be reliable for estimating vegetation phenology (Purdy et al., 2023; Zhang et al., 2006). These data were first filtered by land cover, to only those classified as ‘forest’ in the year 2017, as provided by the MCD12Q1 product (following Youngflesh et al., 2021). Additionally, green-up values were only extracted from those pixels as having data quality ‘good’ or ‘best’. Mid-green-up, the estimate of the day of the year at which the Enhanced Vegetation Index reaches its half-maximum, was selected as the specific metric to represent green-up (see Youngflesh et al., 2021) as inflection points are more reliable than other quantiles used to estimate a tail of a distribution (Belitz et al., 2020). Green-up for a given cell and year was calculated as the mean of the green-up values for all pixels within a cell meeting the above requirements. Cell-level green-up estimates were estimated for 1184 year/cell combinations.

Phenology of Lepidoptera was based on the start of the adult butterfly flight period as a proxy for caterpillar phenology, because adult butterfly phenology has been shown to covary with caterpillar phenology (Di Cecco et al., 2023) and broad scale caterpillar data remain scarce, despite recent efforts expanding structured caterpillar surveys conducted by citizen scientists (Hurlbert et al., 2019). Estimates of Lepidopteran flight phenology were derived from Larsen et al. (2024). Their approach estimated Lepidopteran flight phenology using adult butterfly occurrence records from three citizen science platforms: iNaturalist (GBIF, 2021), eButterfly (Prudic et al., 2017) and the North American Butterfly Association's ‘Butterflies I've Seen’ and ‘Recent Sightings’ programs (Taron & Ries, 2015). Species that overwinter as adults or are migratory were excluded, as we were interested in Lepidoptera in terms of their availability as caterpillars, a key food resource for birds. The remaining butterfly observations were aggregated by overwintering stage (egg, caterpillar, pupa). Aggregating across platforms increases precision through greater data volume and mitigates program-specific biases (Belitz et al., 2020), while trait-level aggregation captures different observed phenological dynamics not strongly correlated with phylogenetic relatedness (Larsen et al., 2024). Phenological metrics

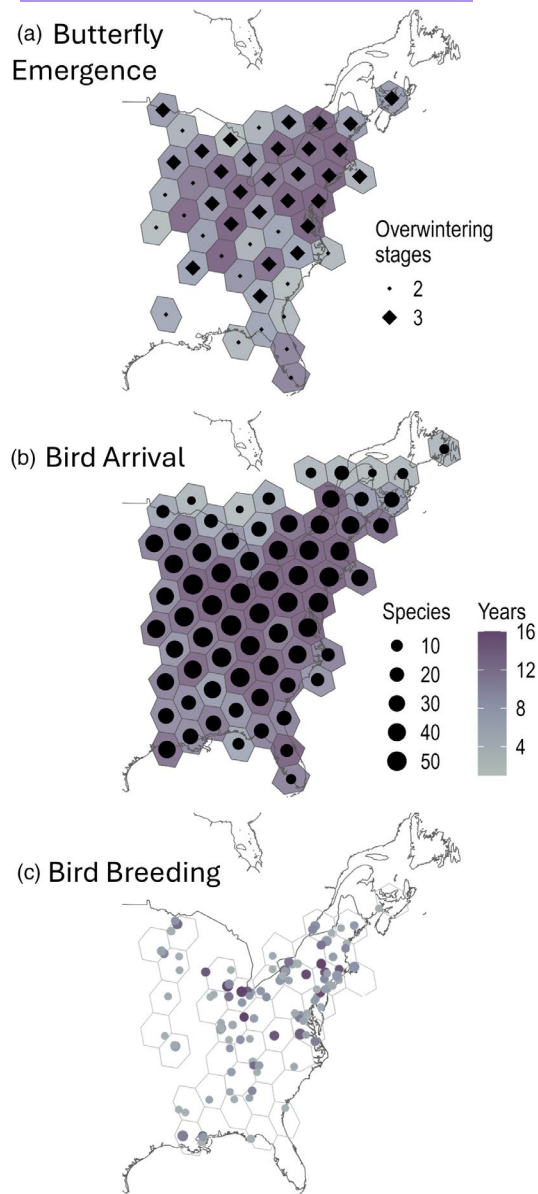


FIGURE 1 Summary of data sources used in this study. The timing of vegetation green-up, (a) butterfly emergence and (b) bird arrival was estimated at the resolution of the cell, while the (c) timing of bird breeding was estimated at individual survey sites. The number of years with phenology estimates is denoted by purple shading, while the number of bird species or butterfly overwintering stages with phenology estimates are represented by the size of points. Green-up estimates were produced for all 16 years at all cells.

were estimated for each group of butterflies (egg, caterpillar, pupa) pooled by overwintering stage for each year and cell combination when at least 15 total occurrences were observed on at least eight unique days. The timing of adult butterfly emergence of each overwintering stage was estimated as the 5th percentile of all butterfly observations across the flight season for each year-cell-overwintering stage combination following Larsen et al. (2024). In total, we estimate butterfly emergence for 1018 year/cell/overwintering stage combinations.

Estimates of the arrival dates of migratory birds were derived from Youngflesh et al. (2021). Their approach used generalized additive models in conjunction with intrinsic autoregressive spatial models in a Bayesian framework to estimate arrival from citizen science data from Project eBird (Sullivan et al., 2014). Estimates of arrival phenology were available for 56 migratory forest or near-forest dwelling birds that breed in eastern North America. We restricted estimates to cells within a species' breeding and migratory range, excluding cells where they overwinter, using range maps from BirdLife International (Data Zone BirdLife International, 2019). A full description of this approach can be found in Youngflesh et al. (2021). In total, we estimated arrival dates for 20,168 year/cell/species combinations for 56 bird species.

Estimates of the timing of bird breeding were derived from the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante et al., 2004). MAPS is a long-term bird-banding effort conducted during the breeding season, with systematic, constant-effort protocols and stations located across North America (DeSante et al., 2004). Bird breeding phenology was calculated as the mean date of capture across all juvenile (defined as a bird hatched in that year) birds of a particular species at a given banding location in a given year (following Saracco et al., 2019; Youngflesh et al., 2023). Repeat captures of the same individual after its initial capture were excluded in our calculation of breeding bird phenology. Estimates of bird breeding phenology were made at the level of individual banding stations for each species, while predictor variables were calculated at the larger cell level to coincide with metrics used for our other phenological measures. In total, we estimated bird breeding phenology for 1641 year/station/species combinations for 30 bird species, all of which were also included in the arrival analysis. No ethical approval was required for this data synthesis study.

2.2 | Climate data

We used climate data to calculate spatially explicit measures of spring accumulated growing degree days (GDD), a metric that approximates the amount of heat available to ectotherms such as plants and insects for growth. GDD is calculated based on each day's minimum and maximum temperature over a fixed time (Bonhomme, 2000). Yearly spring accumulated GDD was calculated at the resolution of the cell using daily temperature data provided at 0.5 degree latitude × 0.5 degree longitude resolution by NOAA Physical Sciences Laboratory's Climate Prediction Center (NOAA PSL, 2021). First, we averaged daily minimum and maximum temperature values across all pixels within each cell. Next, for each year, we summed the total GDD values of each cell using a single-sine approximation of daily temperature curves within thermal limits of (10, 33°C) (Abarca et al., 2024; Cayton et al., 2015) for all days between the Northern Hemisphere spring equinox (mid-March) and summer solstice (mid-June). Although these thermal limits were informed by Lepidoptera-specific studies,

these thresholds are similar to those used in plant-focused studies (Dethier & Vittum, 1967).

2.3 | Statistical analysis

We used a hierarchical Bayesian approach to estimate the phenological sensitivity of green-up, butterfly emergence, arrival of migratory birds and bird breeding phenology to our abiotic metric of interest, spring accumulated growing degree days (GDD). We define sensitivity as the magnitude of phenological change per one unit change in GDD. In each case, we modelled phenology as a function of GDD and further estimated if this sensitivity varied across latitudes. For butterfly phenology, we quantified the sensitivity to GDD of adult butterfly emergence for each of the three different overwintering stages (egg, larvae and pupae). We estimated sensitivity for bird arrival and breeding at the species level and further quantified the relationship that life-history traits had on sensitivity.

The date (day of year) of vegetation green-up (y) in year i at cell j was modelled as normally distributed, as a function of GDD

$$y_{ij} \sim N(\mu_{ij}, \sigma)$$

$$\mu_{ij} = \alpha_j + \beta_j \times \text{GDD}_{ij},$$

where σ is the process error at this level of the model, α is the intercept (mean green-up date at mean GDD) for each cell and β is the effect of GDD on green-up. Parameter α was modelled as normally distributed,

$$\alpha_j \sim N(\mu_\alpha, \sigma_\alpha),$$

where μ_α represents the mean green-up date for each cell and σ_α is the standard deviation. Parameter β was itself modelled as normally distributed as a function of latitude,

$$\beta_j \sim N(\mu_{\beta_j}, \sigma_{\beta_j})$$

$$\mu_{\beta_j} = \gamma + \theta \times \text{Lat}_j,$$

where parameter γ represents the effect of GDD on green-up at the mean latitude across all cells, θ is the degree to which latitude mediates the effect of GDD and σ_{β_j} is the process error at this level of the model. GDD values were centred within each cell (mean=0), while latitude values were centred across all cells. Similar models were used for each of the phenological metrics, with slight modifications that are described in detail below.

The date of butterfly emergence (y) in year i , at cell j , for overwinter stage k , was modelled as normally distributed as a function of GDD and number of occurrence records,

$$y_{ijk} \sim N(\mu_{ijk}, \sigma)$$

$$\mu_{ijk} = \alpha_{jk} + \beta_{1jk} \times \text{GDD}_{ijk} + \beta_{2jk} \times \text{Obs}_{ijk},$$

where α is the intercept for each cell/overwintering stage combination and β_1 is the effect of GDD. β_2 is the effect of the distinct number of days with occurrence records used to generate butterfly emergence phenology metrics, which was included because unique observation days are known to be important model predictors when using presence-only data (Belitz et al., 2023). Parameter α was modelled as normally distributed,

$$\alpha_{jk} \sim N(\mu_\alpha, \sigma_\alpha),$$

where μ_α represents the mean emergence date for each cell/overwintering stage and σ_α is the standard deviation. Parameter β_1 was modelled as normally distributed,

$$\beta_{1jk} \sim N(\mu_{\beta_{1jk}}, \sigma_{\beta_1})$$

$$\mu_{\beta_{1jk}} = \gamma_k + \theta_k \times \text{Lat}_{jk},$$

where parameter γ represents the effect of GDD on butterfly emergence at the mean latitude for each overwintering stage, and θ is the degree to which latitude mediates the effect of GDD for each overwintering stage. GDD values were mean centred within each cell/overwintering stage combination. Latitude values were mean centred within each overwintering stage. The number of unique days with occurrence records used to generate butterfly emergence estimates was mean centred across all year/cell/overwintering stage combinations.

The date of migratory bird arrival (y) in year i , at cell j , for species k , was modelled as a normally distributed function of GDD,

$$y_{ijk} \sim N(\mu_{ijk}, \sigma)$$

$$\mu_{ijk} = \alpha_{jk} + \beta_{jk} \times \text{GDD}_{ijk},$$

where α is the intercept for each cell/species combination and β is the effect of GDD. Parameter α was modelled as normally distributed,

$$\alpha_{jk} \sim N(\mu_\alpha, \sigma_\alpha),$$

where μ_α represents the mean date for migratory bird arrival of each species/cell and σ_α is the standard deviation. Parameter β was modelled as normally distributed,

$$\beta_{jk} \sim N(\mu_{\beta_{jk}}, \sigma_{\beta_j})$$

$$\mu_{\beta_{jk}} = \gamma_k + \theta_k \times \text{Lat}_{jk},$$

where parameter γ_k represents the effect of GDD on migration arrival at the mean latitude for each species, and θ_k is the degree to which latitude mediates the effect of GDD for each species. Parameter γ_k was modelled as normally distributed,

$$\gamma_k \sim N(\mu_{\gamma_k}, \sigma_{\gamma_k})$$

$$\mu_{\gamma_k} = \kappa + \varphi \times \text{Traits}_k,$$

where κ represents the effect of GDD on arrival at mean *Traits* value, and ϕ represents the effect of migratory traits on species-level GDD effect. *Traits* represents the first axis of a principal component analysis describing correlated migratory traits for which positive values are associated with faster migration pace, later arrival dates and more southerly overwinter latitudes (derived from Youngflesh et al., 2021). GDD values were mean centred within each cell/species combination. Latitude values were mean centred within each species. Traits values were mean centred across species. The date of bird breeding was modelled using the same approach as migration arrival, but phenology data were collected and modelled at the station level, rather than the cell level. GDD values were mean centred within each station/species combination. Latitude values were mean centred within each species. Traits values were mean centred across species.

We tested phylogenetic autocorrelation in the residuals of the top level of both bird phenology models (i.e. migratory arrival and breeding). We did so by first generating a phylogenetic covariance matrix using the phytools package in R (Revell, 2012). This matrix was calculated for the individual bird species included in each model from each of 100 consensus phylogenetic trees obtained from BirdTree (Jetz et al., 2012). We calculated the γ residual by subtracting γ_k from μ_{γ_k} . We used Pagel's lambda (Pagel, 1999) to test for phylogenetic signals in these residuals based on the phylogenetic covariance of the bird species included in each model. No evidence of phylogenetic signal in the γ parameter was detected in either model.

Analyses were run using R version 4.2.3 (R Core Team, 2023), relying on the R packages MCMCvis (Youngflesh, 2018) and cmdstanr (Gabry et al., 2024) to interface with Stan (Carpenter et al., 2017). Our models were run using four chains and 4000 iterations with a warmup of 2000 iterations. All parameters were given weakly informative priors. No models had divergent transitions, and Rhat values were below 1.02 for all parameters. We used graphical posterior predictive checks to ensure the models were similar to the data (Gabry et al., 2019). Data estimated from the posterior predictive distribution were similar to the observed data.

3 | RESULTS

The effect of yearly spring accumulated GDD (a measure of temperature accumulation) on phenology was stronger for vegetation green-up and butterfly emergence than for bird arrival and breeding (Figure 2a). For each additional GDD accumulated during the spring of a given year, green-up advanced approximately 0.07 days (posterior median = -0.075, 95% CI: -0.081, -0.070). Butterflies responded similarly to spring GDD (posterior median = -0.082), although this phenological event had the least precise posterior distribution (95% CI: -0.168, 0.002). Migratory bird arrival and bird breeding phenology were similarly influenced by spring GDD, both advancing phenology by approximately 0.01 days for each additional GDD accumulated during the spring (bird arrival posterior median = -0.011, 95% CI: -0.013, -0.008; bird breeding posterior median = -0.011, 95% CI: -0.019, -0.003).

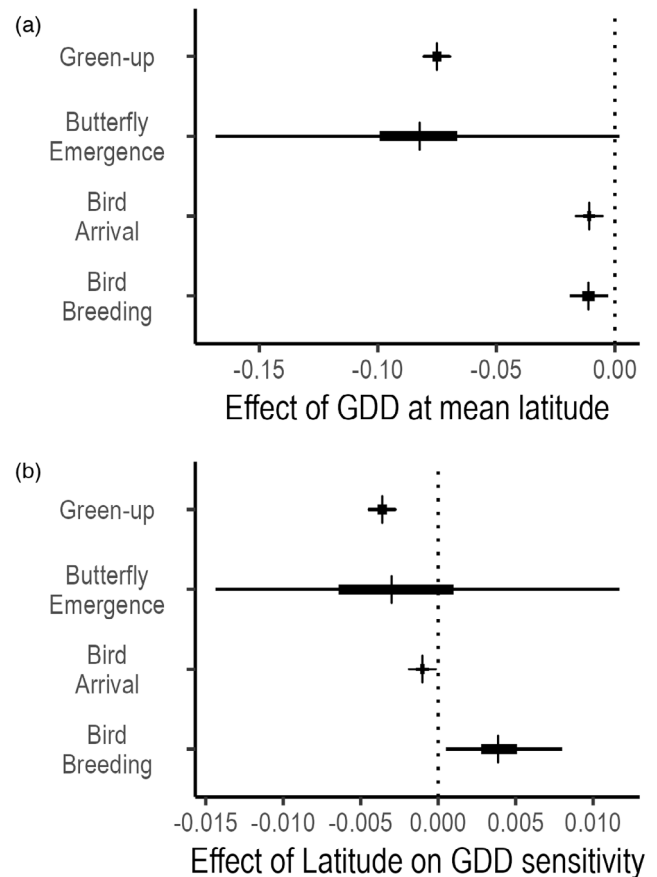


FIGURE 2 (a) The effect of spring accumulated growing degree days (GDD) at mean latitude for vegetation green-up, Lepidoptera emergence, bird arrival and bird breeding. (b) The effect of latitude on GDD sensitivity for vegetation green-up, Lepidoptera emergence, bird arrival and bird breeding. Each vertical line represents the posterior median, thin error bars represent 95% credible interval (CI) and thick error bars represent 50% CI.

The sensitivity of phenological events to spring GDD differed across space (Figure 2b; Figure 3), with vegetation green-up and bird arrival being more affected by GDD accumulated during the spring in higher latitudes. The effect of latitude on phenological sensitivity was stronger for vegetation green-up (posterior median = -0.004, 95% CI: -0.004, -0.003) than bird arrival (posterior median = -0.001, 95% CI: -0.001, -0.001; Figure 2b). The degree to which latitude mediates the effect of spring GDD on butterfly emergence was similar to its effect on green-up given their posterior medians; however, both the 95% and 50% CI encompass zero for the butterfly emergence model (Figure 2b). The direction of the effect of latitude on GDD sensitivity for bird breeding phenology was the opposite of green-up, butterfly emergence and bird arrival (Figure 2b). Bird breeding phenology was less sensitive to spring GDD in higher latitude locations (posterior median = 0.003, 95% CI: 0.000, 0.008), meaning breeding phenology changed less in response to changes in GDD in more northerly cells (Figure 3).

There was greater variation among bird species in sensitivity to spring GDD at mean latitude for the arrival of migratory birds

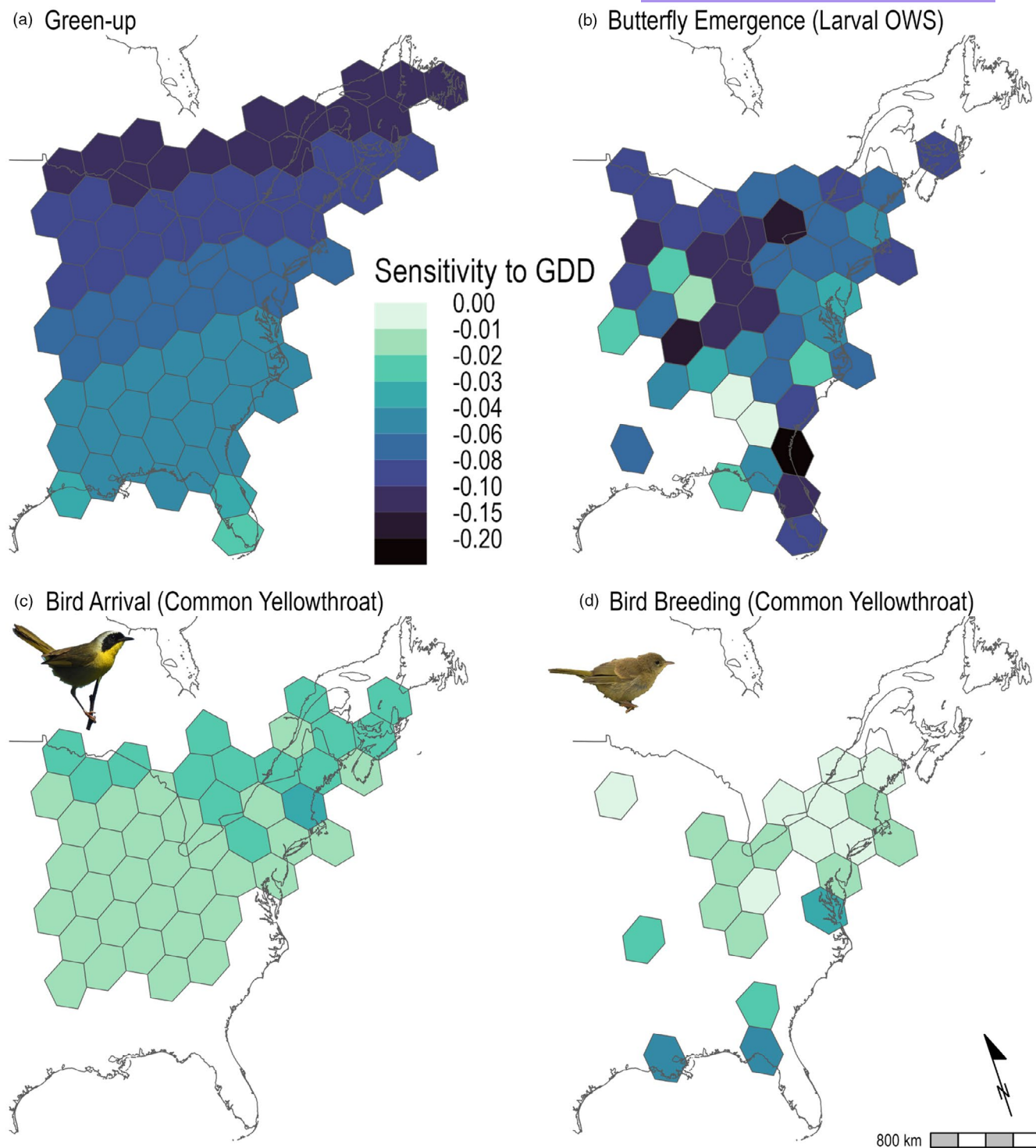


FIGURE 3 (a) Spatial variation in phenological sensitivity of green-up to spring accumulated growing degree days (GDD). (b) The effect of spring GDD on Lepidoptera emergence for an example group of species with larval overwintering strategy (OWS). (c) The effect of spring GDD on spring arrival of an example species, the common yellowthroat, *Geothlypis trichas*, and (d) the effect of spring GDD on the breeding phenology of common yellowthroat across space. Common yellowthroat photos by iNaturalist users @insectology and Steve Holmes @holmesfras.

compared to breeding phenology (Figure 4; Figure S1). Bird species with traits associated with slower migration pace, earlier arrival and a more northerly overwintering range shifted the timing of their migration arrival more than species associated with faster migration,

later arrival and a more southerly overwintering range (posterior median = 0.004, 95% CI: 0.002, 0.006; Figure 4a). However, traits associated with migration distance and breeding timing did not show a strong relationship with how sensitive a bird species' breeding

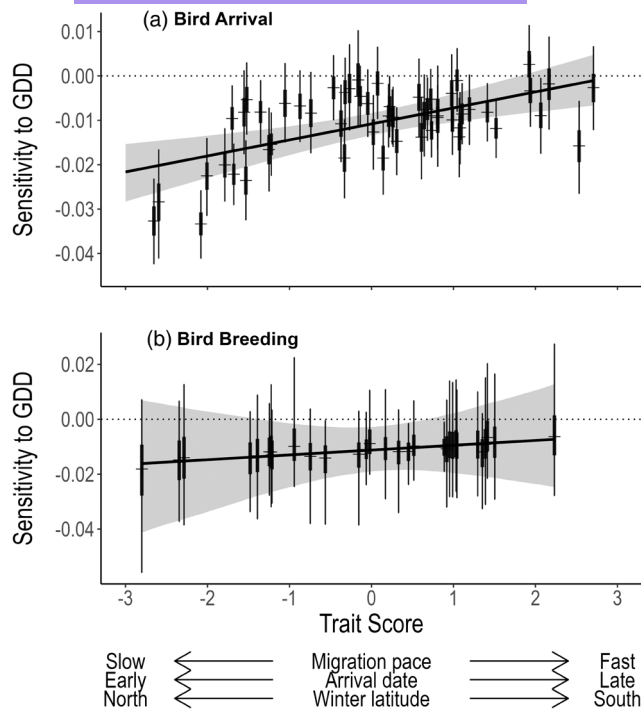


FIGURE 4 Sensitivity of bird arrival (a) and bird breeding (b) phenology to spring accumulated growing degree days (GDD) across trait scores related to correlated migration traits. Positive trait scores for the bird arrival model are associated with species with a faster migration pace, later arrival dates and more southerly overwinter latitudes. Each point represents one species, thin error bars represent 95% CI and thick error bars represent 50% CI. The black line represents the median community effect of PC1 on sensitivity to spring GDD, and the grey ribbon represents the 95% CI.

phenology was to spring GDD (posterior median = 0.002, 95% CI: -0.006, 0.010; Figure 4b).

The effect of spring GDD at mean latitude was similar for butterfly assemblages regardless of overwintering stage (Figure S2). Although the posterior median response was largest for butterflies that overwinter as eggs (posterior median = -0.091, 95% CI: -0.172, -0.038), the 50% and 95% CIs overlapped those for butterflies that overwinter as pupae or larvae (Figure S2). Latitude influenced the sensitivity of butterfly emergence to GDD accumulated during the spring for species that overwinter as pupae, with these species having emergences more sensitive to GDD in higher latitudes (Figure S3; posterior median = -0.008, 95% CI: -0.017, -0.000). However, our model did not provide evidence that latitude affected GDD sensitivity of butterfly emergence for species that overwinter as a larva or egg (Figure S2).

4 | DISCUSSION

Synthesizing a diverse set of co-located data under a unified framework, we quantified how multi-trophic phenological responses to climate change vary across broad spatial and temporal extents.

We provide evidence supporting the hypothesis that ectotherms exhibit stronger sensitivity to changes in temperature than endotherms (Cohen et al., 2018). In line with our prediction, butterflies and vegetation green-up had similarly strong sensitivity to spring GDD (a metric of temperature accumulation in a given year), while birds had lower sensitivity. GDD is known to directly regulate the timing of both vegetation green-up and the development of ectothermic insects (Cayton et al., 2015; Neupane et al., 2022; Piao et al., 2015), but bird phenology is likely only indirectly related to heat accumulation and instead is presumed to be proximally driven by food resource availability (Bison et al., 2020; Shutt et al., 2019; Visser et al., 2012), though the mechanisms behind this temperature phenology relationship for birds are still not fully understood (Caro et al., 2013). Still, we found that the arrival and breeding of migratory birds were earlier in warmer years and later in cool years, in line with our expectations (DeSante & Saracco, 2021; McDermott & DeGroot, 2016; Socolar et al., 2017). Given the differences in sensitivity across trophic levels, our results indicate that birds are not adjusting to the changing phenology of lower trophic levels that are directly influenced by temperature changes (Youngflesh et al., 2021). Because breeding productivity declines when these bird species fail to breed during optimal periods of time (Youngflesh et al., 2023), it is likely that some constraint on their phenological sensitivity exists.

Our work provides a needed basis for identifying potential locations and taxonomic groups most at risk of phenological asynchrony and the potential associated demographic consequences over a latitudinal gradient spanning more than 24 degrees. We particularly highlight the potential for mismatch (i.e. demographic consequences resulting from temporal asynchronies), including the production of fewer young, as highlighted by Youngflesh et al. (2023), as bird sensitivity to spring accumulated GDD is weaker than that of plants and Lepidoptera. Our result that vegetation green-up and bird arrival were more sensitive to spring GDD in higher latitudes aligns with previous studies (Prevéy et al., 2017; Youngflesh et al., 2021). However, the effect of latitude on spring GDD sensitivity has rarely been compared across trophic levels. Here, we show that not only is spring GDD sensitivity higher at lower trophic levels but also the degree to which this sensitivity changes across a latitudinal gradient is greater at lower trophic levels. In plants, our finding of greater sensitivity at higher latitudes might be due to the fact that small changes in temperature represent relatively larger increases in thermal budgets for plants in cold environments (Prevéy et al., 2017). Migratory birds, which cannot assess local climate conditions at breeding grounds prior to arrival, may be better able to adjust behaviour during migration based on immediate environmental conditions, likely by shifting stopover duration (Schmaljohann & Both, 2017). Birds that migrate to more northerly cells have the opportunity to track plant growth across greater distances (Thorup et al., 2017), though these adjustments are not enough to perfectly track changes in the timing of green-up. More work is still needed to understand mechanisms determining sensitivity across environmental gradients and taxa. Here, we use temperatures across a static window for the calculation of

spring accumulated GDD, but this time period may be more relevant for some trophic levels or cells than others (e.g. at more northerly cells compared to more southerly cells).

Contrary to our expectation, we found that bird breeding phenology was less sensitive to spring GDD in higher latitudes. These results contradict a study that found the date of hatching of a long-distance migrant, the European pied flycatcher *Ficedula hypoleuca*, in Sweden has advanced more in northern locations than in southern areas (Vega et al., 2021). It may be that some phenomena studied across smaller spatial extents in colder regions do not apply broadly across larger extents in warmer ones. The effect of latitude on GDD sensitivity for insect phenology is also relatively unknown, although it likely mirrors plant responses with greater sensitivity to GDD in higher latitudes. Our median posterior distribution estimate suggests such a response, with higher spring GDD sensitivity in more northerly cells for butterfly emergence, but this parameter estimate has high uncertainty. Butterfly species that overwinter as pupae, the latest overwintering life stage included in this study, displayed the greatest effect of latitude increasing spring GDD sensitivity, aligning with other studies that found earlier season insects are more responsive to spring conditions (Buckley, 2022). Among the three overwintering groups examined in our study, pupae overwintering species will emerge as adults on the landscape before egg or larva overwintering species (Belitz et al., 2023).

Birds with fast migration pace, late arrivals and more southerly wintering latitudes may be particularly vulnerable to potential mismatch because the arrival of these species was the least sensitive to spring accumulated GDD (Figure 4a). This result aligns with prior work that showed the arrival of migratory birds of short distance and early arriving species is more sensitive to fluctuations in green-up compared to species that migrate longer distances and arrive later (Youngflesh et al., 2021). However, we did not find evidence that those traits were important in estimating species-specific sensitivity to spring GDD for breeding dates, in contrast to Youngflesh et al. (2023) who found species that migrate shorter distances and breed earlier in the season were more sensitive to green-up fluctuations. This is likely due to the smaller spatial and taxonomic extent of our study compared to Youngflesh et al. (2023), and the use of GDD instead of green-up. These differences highlight the importance of considering geographic scope, taxonomic breadth and the specific environmental variables when interpreting phenological sensitivity across studies.

The differences in how data are aggregated across different monitoring tools cannot be overlooked and represent a key challenge going forward. Here, bird arrival and breeding were the only phenological events measured at the species level. Even with these measures, our measure of bird breeding captures variation in the fledging date of birds, which will be influenced by the survival rate of nests that might vary according to nesting date. That is, it is an imperfect measure of the timing of bird breeding. Our other events—adult butterfly emergence and vegetation green-up—are community-wide proxies rather than species-specific measurements. Furthermore, the diet of most, though not all, nestling birds

also consists not of adult butterflies but of larval moths. Previous work has demonstrated that adult butterfly observations can serve as reasonable proxies for caterpillar onset phenology (Di Cecco et al., 2023). However, it is unclear when these proxies might be inappropriate. The appropriateness of these measures might vary across latitude, across years and exhibit different dynamics during outbreak events that affect only certain caterpillars, which may or may not be preferred by specific bird species. While we expect these factors to add noise to our analyses, we do not expect these to introduce substantial biases into the inference we derive from our results.

Finally, we note that numerous questions well suited for macroecological data synthesis remain unanswered within this, or any, tri-trophic system. For example, although the seasonal abundance of insects has important effects on bird demography (Grames et al., 2023), the importance of an interaction between the abundance and phenology of insects on bird breeding success remains relatively unknown (Weir & Phillimore, 2024). Simply put, is the demography of birds only impacted by asynchrony in years with low resource abundance? Continuing to fill data gaps and integrate diverse workflows is critical given that widespread population declines have been reported in both birds (Pollock et al., 2022; Rosenberg et al., 2019) and Lepidoptera (Forister et al., 2021; Habel et al., 2019; Warren et al., 2021), and phenological mismatch has been proposed as one of the major causes of these declines (Jones & Cresswell, 2010; Larsen et al., 2024; Visser & Gienapp, 2019). Continued sharing of phenological data across trophic levels generated via experimental and observational approaches, along with improved monitoring, promises to play a crucial role in closing the many remaining gaps in our knowledge, particularly how these dynamics vary spatially, temporally and across taxonomic groups.

AUTHOR CONTRIBUTIONS

Michael W. Belitz, Robert P. Guralnick and Casey Youngflesh conceived the ideas and designed methodology based on a framework created by Allen H. Hurlbert, Leslie Ries and Morgan W. Tingley; Michael W. Belitz, Elise A. Larsen, Grace J. Di Cecco, Naresh Neupane and Casey Youngflesh curated aspects of the data; Michael W. Belitz and Casey Youngflesh synthesized and analysed the data; Michael W. Belitz, Robert P. Guralnick and Casey Youngflesh led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study was a synthesis of data collected across the Eastern Temperate Forest. Our authorship team represents locations throughout this region, supporting the appropriate interpretation of data and results used in this study.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code available from Zenodo <https://doi.org/10.5281/zenodo.13968356> (Belitz & Youngflesh, 2024). Raw data sources used in this study are referenced in the Section 2.

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REFERENCES

- Abarca, M., Parker, A. L., Larsen, E. A., Umbanhowar, J., Earl, C., Guralnick, R., Kingsolver, J., & Ries, L. (2024). How development and survival combine to determine the thermal sensitivity of insects. *PLoS One*, 19(1), e0291393. <https://doi.org/10.1371/journal.pone.0291393>
- Barnes, R. (2017). *dgggridR: Discrete Global Grids for R. R package version 0.1.12*.
- Beard, K. H., Kelsey, K. C., Leffler, A. J., & Welker, J. M. (2019). The missing angle: Ecosystem consequences of phenological mismatch. *Trends in Ecology & Evolution*, 34, 885–888. <https://doi.org/10.1016/j.tree.2019.07.019>
- Belitz, M., & Youngflesh, C. (2024). TriTrophicPhenology (1.1). *Zenodo*. <https://doi.org/10.5281/zenodo.13968356>
- Belitz, M. W., Larsen, E. A., Ries, L., & Guralnick, R. P. (2020). The accuracy of phenology estimators for use with sparsely sampled presence-only observations. *Methods in Ecology and Evolution*, 11(10), 1273–1285. <https://doi.org/10.1111/2041-210X.13448>
- Belitz, M. W., Larsen, E. A., Shirey, V., Li, D., & Guralnick, R. P. (2023). Phenological research based on natural history collections: Practical guidelines and a lepidopteran case study. *Functional Ecology*, 37(2), 234–247. <https://doi.org/10.1111/1365-2435.14173>
- Bison, M., Yoccoz, N. G., Carlson, B., Klein, G., Laigle, I., Van Reeth, C., Asse, D., & Delestrade, A. (2020). Best environmental predictors of breeding phenology differ with elevation in a common woodland bird species. *Ecology and Evolution*, 10(18), 10219–10229. <https://doi.org/10.1002/ece3.6684>
- Bonhomme, R. (2000). Bases and limits to using 'degree.day' units. *European Journal of Agronomy*, 13(1), 1–10.
- Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, 78(1), 73–83. <https://doi.org/10.1111/j.1365-2656.2008.01458.x>
- Bowers, E. K., Grindstaff, J. L., Soukup, S. S., Drilling, N. E., Eckerle, K. P., Sakaluk, S. K., & Thompson, C. F. (2016). Spring temperatures influence selection on breeding data and the potential for phenological mismatch in a migratory bird. *Ecology*, 97(10), 2880–2891. <https://doi.org/10.1002/ecy.1516>
- Bradshaw, W. E., & Holzapfel, C. M. (2007). Evolution of animal photoperiodism. *Annual Review of Ecology, Evolution, and Systematics*, 38, 1–25. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110115B>
- Buckley, L. B. (2022). Temperature-sensitive development shapes insect phenological responses to climate change. *Current Opinion in Insect Science*, 52, 100897. <https://doi.org/10.1016/j.cois.2022.100897>
- Burgess, M. D., Smith, K. W., Evans, K. L., Leech, D., Pearce-Higgins, J. W., Branton, C. J., Briggs, K., Clark, J. R., du Feu, C. R., Lewthwaite, K., Nager, R. G., Sheldon, B. C., Smith, J. A., Whytock, R. C., Willis, S. G., & Phillimore, A. B. (2018). Tritrophic phenological match–mismatch in space and time. *Nature Ecology & Evolution*, 2(6), Article 6. <https://doi.org/10.1038/s41559-018-0543-1>
- Capinera, J. (2010). *Insects and wildlife: arthropods and their relationships with wild vertebrate animals*. Wiley-Blackwell. <https://www.wiley.com/en-us/Insects+and+Wildlife:+Arthropods+and+their+Relationships+with+Wild+Vertebrate+Animals-p-9781444332995>
- Caro, S. P., Schaper, S. V., Hut, R. A., Ball, G. F., & Visser, M. E. (2013). The case of the missing mechanism: How does temperature influence seasonal timing in endotherms? *PLoS Biology*, 11(4), e1001517.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, 76(1), 1–32.
- Cayton, H. L., Haddad, N. M., Gross, K., Diamond, S. E., & Ries, L. (2015). Do growing degree days predict phenology across butterfly species? *Ecology*, 96(6), 1473–1479. <https://doi.org/10.1890/15-0131.1>
- Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8(3), Article 3. <https://doi.org/10.1038/s41558-018-0067-3>
- Cooper, N. W., Sherry, T. W., & Marra, P. P. (2015). Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. *Ecology*, 96(7), 1933–1942.
- Cushing, D. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. In *Advances in marine biology* (Vol. 26, pp. 249–293). Elsevier.
- Damien, M., & Tougeron, K. (2019). Prey–predator phenological mismatch under climate change. *Current Opinion in Insect Science*, 35, 60–68. <https://doi.org/10.1016/j.cois.2019.07.002>
- Data Zone BirdLife International. (2019). <http://datazone.birdlife.org/species/requestdis>
- DeSante, D. F., & Saracco, J. F. (2021). Climate variation drives dynamics and productivity of a subalpine breeding bird community. *Ornithological Applications*, 123(2), duab014. <https://doi.org/10.1093/ornithapp/duab014>
- DeSante, D. F., Saracco, J. F., O'Grady, D. R., Burton, K. M., & Walker, B. L. (2004). Methodological considerations of the monitoring avian productivity and survivorship (MAPS) program. *Studies in Avian Biology*, 29, 28–45.
- Dethier, B. E., & Vittum, M. (1967). *Growing degree days in New York state*.
- Di Cecco, G. J., Belitz, M. W., Cooper, R. J., Larsen, E. A., Lewis, W. B., Ries, L., Guralnick, R. P., & Hurlbert, A. H. (2023). Phenology in adult and larval lepidoptera from structured and unstructured surveys across eastern North America. *Frontiers of Biogeography*, 15(1), e56346. <https://doi.org/10.21425/F5FBG56346>
- Durant, J. M., Hjermand, D. Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33(3), 271–283. <https://doi.org/10.3354/cr033271>
- Ekholm, A., Tack, A. J. M., Pulkkinen, P., & Roslin, T. (2020). Host plant phenology, insect outbreaks and herbivore communities—The importance of timing. *Journal of Animal Ecology*, 89(3), 829–841. <https://doi.org/10.1111/1365-2656.13151>
- Forister, M. L., Halsch, C. A., Nice, C. C., Fordyce, J. A., Dilts, T. E., Oliver, J. C., Prudic, K. L., Shapiro, A. M., Wilson, J. K., & Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American west. *Science*, 371(6533), 1042–1045. <https://doi.org/10.1126/science.abe5585>

- Franks, S. E., Pearce-Higgins, J. W., Atkinson, S., Bell, J. R., Botham, M. S., Brereton, T. M., Harrington, R., & Leech, D. I. (2018). The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. *Global Change Biology*, 24(3), 957–971. <https://doi.org/10.1111/gcb.13960>
- Friedl, M., & Sulla-Menashe, D. (2019). MCD12Q1 MODIS/Terra+ aqua land cover type yearly L3 global 500m SIN grid V006. NASA EOSDIS Land Processes DAAC, 10, 200.
- Gabry, J., Češnovar, R., Johnson, A., & Bronder, S. (2024). *cmdstanr*: R Interface to “CmdStan”. <https://mc-stan.org/cmdstanr/>
- Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, 182(2), 389–402. <https://doi.org/10.1111/rssa.12378>
- GBIF. (2021). GBIF occurrence download (2021-09-22). <https://doi.org/10.15468/dl.vm5x8p>
- Graber, J. W., & Graber, R. R. (1983). Feeding rates of warblers in spring. *The Condor*, 85(2), 139–150. <https://doi.org/10.2307/1367247>
- Grames, E. M., Montgomery, G. A., Youngflesh, C., Tingley, M. W., & Elphick, C. S. (2023). The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. *Ecology Letters*, 26(4), 658–673. <https://doi.org/10.1111/ele.14178>
- Habel, J. C., Trusch, R., Schmitt, T., Ochse, M., & Ulrich, W. (2019). Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Scientific Reports*, 9(1), 14921. <https://doi.org/10.1038/s41598-019-51424-1>
- Holmes, R. T., Schultz, J. C., & Nothnagle, P. (1979). Bird predation on forest insects: An enclosure experiment. *Science*, 206(4417), 462–463. <https://doi.org/10.1126/science.206.4417.462>
- Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Climate Change*, 10(1), 63–68. <https://doi.org/10.1038/s41558-019-0648-9>
- Hurlbert, A., Hayes, T., McKinnon, T., & Goforth, C. (2019). Caterpillars count! A citizen science project for monitoring foliage arthropod abundance and phenology. *Citizen Science: Theory and Practice*, 4(1), Article 1. <https://doi.org/10.5334/cstp.148>
- Hurlbert, A. H., Olsen, A. M., Sawyer, M. M., & Winner, P. M. (2021). The avian diet database as a source of quantitative information on bird diets. *Scientific Data*, 8(1), Article 1. <https://doi.org/10.1038/s41597-021-01049-9>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. <https://doi.org/10.1038/nature11631>
- Jones, J., Doran, P. J., & Holmes, R. T. (2003). Climate and food synchronize regional forest bird abundances. *Ecology*, 84(11), 3024–3032. <https://doi.org/10.1890/02-0639>
- Jones, T., & Cresswell, W. (2010). The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology*, 79(1), 98–108. <https://doi.org/10.1111/j.1365-2656.2009.01610.x>
- Kudo, G., & Ida, T. Y. (2013). Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, 94(10), 2311–2320. <https://doi.org/10.1890/12-2003.1>
- Larsen, E. A., Belitz, M. W., Di Cecco, G. J., Glassberg, J., Hurlbert, A. H., Ries, L., & Guralnick, R. P. (2024). Overwintering strategy regulates phenological sensitivity and consequences for ecological services in a clade of temperate north American insects. *Functional Ecology*, 38(5), 1075–1088. <https://doi.org/10.1111/1365-2435.14543>
- Larsen, E. A., Belitz, M. W., Guralnick, R. P., & Ries, L. (2022). Consistent trait-temperature interactions drive butterfly phenology in both incidental and survey data. *Scientific Reports*, 12, 13370.
- Mayor, S. J., Guralnick, R. P., Tingley, M. W., Otegui, J., Withey, J. C., Elmendorf, S. C., Andrew, M. E., Leyk, S., Pearse, I. S., & Schneider, D. C. (2017). Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports*, 7(1), 1–10. <https://doi.org/10.1038/s41598-017-02045-z>
- McDermott, M. E., & DeGroot, L. W. (2016). Long-term climate impacts on breeding bird phenology in Pennsylvania, USA. *Global Change Biology*, 22(10), 3304–3319. <https://doi.org/10.1111/gcb.13363>
- Mirth, C. K., Saunders, T. E., & Amourda, C. (2021). Growing up in a changing world: Environmental regulation of development in insects. *Annual Review of Entomology*, 66, 81–99. <https://doi.org/10.1146/annurev-ento-041620-083838>
- Nagy, L. R., & Holmes, R. T. (2004). Factors influencing fecundity in migratory songbirds: Is nest predation the most important? *Journal of Avian Biology*, 35(6), 487–491. <https://doi.org/10.1111/j.0908-8857.2004.03429.x>
- Nagy, L. R., & Holmes, R. T. (2005). Food limits annual fecundity of a migratory songbird: An experimental study. *Ecology*, 86(3), 675–681. <https://doi.org/10.1890/04-0155>
- Neupane, N., Peruzzi, M., Arab, A., Mayor, S. J., Withey, J. C., Ries, L., & Finley, A. O. (2022). A novel model to accurately predict continental-scale timing of forest green-up. *International Journal of Applied Earth Observation and Geoinformation*, 108, 102747. <https://doi.org/10.1016/j.jag.2022.102747>
- NOAA PSL. (2021). CPC global temperature data. NOAA PSL. <https://psl.noaa.gov/data/gridded/data.cpc.globaltemp.html%0A>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401(6756), 877–884.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>
- Piao, S., Tan, J., Chen, A., Fu, Y. H., Ciais, P., Liu, Q., Janssens, I. A., Vicca, S., Zeng, Z., Jeong, S.-J., Li, Y., Myneni, R. B., Peng, S., Shen, M., & Peñuelas, J. (2015). Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature Communications*, 6(1), Article 1. <https://doi.org/10.1038/ncomms7911>
- Pollock, H. S., Toms, J. D., Tarwater, C. E., Benson, T. J., Karr, J. R., & Brawn, J. D. (2022). Long-term monitoring reveals widespread and severe declines of understory birds in a protected neotropical forest. *Proceedings of the National Academy of Sciences of the United States of America*, 119(16), e2108731119. <https://doi.org/10.1073/pnas.2108731119>
- Prevé, J., Vellend, M., Rüger, N., Hollister, R. D., Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Clark, K., Cooper, E. J., Elberling, B., Fosaa, A. M., Henry, G. H. R., Høye, T. T., Jónsdóttir, I. S., Klanderud, K., Lévesque, E., Mauritz, M., Molau, U., Natali, S. M., ... Rixen, C. (2017). Greater temperature sensitivity of plant phenology at colder sites: Implications for convergence across northern latitudes. *Global Change Biology*, 23(7), 2660–2671. <https://doi.org/10.1111/gcb.13619>
- Prudic, K. L., McFarland, K. P., Oliver, J. C., Hutchinson, R. A., Long, E. C., Kerr, J. T., & Larrivé, M. (2017). eButterfly: Leveraging massive online citizen science for butterfly conservation. *Insects*, 8(2), Article 2. <https://doi.org/10.3390/insects8020053>
- Purdy, L. M., Sang, Z., Beaubien, E., & Hamann, A. (2023). Validating remotely sensed land surface phenology with leaf out records from a citizen science network. *International Journal of Applied Earth Observation and Geoinformation*, 116, 103148.
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Raimondo, S., Liebhold, A. M., Strazanac, J. S., & Butler, L. (2004). Population synchrony within and among lepidoptera species in relation to weather, phylogeny, and larval phenology. *Ecological Entomology*, 29(1), 96–105. <https://doi.org/10.1111/j.0307-6946.2004.00579.x>
- Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 2, 217–223.

- Robertson, E. P., La Sorte, F. A., Mays, J. D., Taillie, P. J., Robinson, O. J., Ansley, R. J., O'Connell, T. J., Davis, C. A., & Loss, S. R. (2024). Decoupling of bird migration from the changing phenology of spring green-up. *Proceedings of the National Academy of Sciences of the United States of America*, 121(12), e2308433121. <https://doi.org/10.1073/pnas.2308433121>
- Rodenhouse, N. L., & Holmes, R. T. (1992). Results of experimental and natural food reductions for breeding black-throated blue warblers. *Ecology*, 73(1), 357–372. <https://doi.org/10.2307/1938747>
- Romano, A., Garamszegi, L. Z., Rubolini, D., & Ambrosini, R. (2023). Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis. *Ecological Monographs*, 93(1), e1552. <https://doi.org/10.1002/ecm.1552>
- Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the north American avifauna. *Science*, 366(6461), 120–124.
- Roy, D. B., Oliver, T. H., Botham, M. S., Beckmann, B., Brereton, T., Dennis, R. L. H., Harrower, C., Phillimore, A. B., & Thomas, J. A. (2015). Similarities in butterfly emergence dates among populations suggest local adaptation to climate. *Global Change Biology*, 21(9), 3313–3322. <https://doi.org/10.1111/gcb.12920>
- Saracco, J. F., Siegel, R. B., Helton, L., Stock, S. L., & DeSante, D. F. (2019). Phenology and productivity in a montane bird assemblage: Trends and responses to elevation and climate variation. *Global Change Biology*, 25(3), 985–996.
- Schmaljohann, H., & Both, C. (2017). The limits of modifying migration speed to adjust to climate change. *Nature Climate Change*, 7(8), 573–576.
- Shutt, J. D., Cabello, I. B., Keogan, K., Leech, D. I., Samplonius, J. M., Whittle, L., Burgess, M. D., & Phillimore, A. B. (2019). The environmental predictors of spatio-temporal variation in the breeding phenology of a passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, 286(1908), 20190952. <https://doi.org/10.1098/rspb.2019.0952>
- Socolar, J. B., Epachin, P. N., Beissinger, S. R., & Tingley, M. W. (2017). Phenological shifts conserve thermal niches in north American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences of the United States of America*, 114(49), 12976–12981. <https://doi.org/10.1073/pnas.1705897114>
- Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., Damoulas, T., Dhondt, A. A., Dietterich, T., Farnsworth, A., Fink, D., Fitzpatrick, J. W., Fredericks, T., Gerbracht, J., Gomes, C., Hochachka, W. M., Iliff, M. J., Lagoze, C., La Sorte, F. A., ... Kelling, S. (2014). The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation*, 169, 31–40. <https://doi.org/10.1016/j.biocon.2013.11.003>
- Taron, D., & Ries, L. (2015). Butterfly monitoring for conservation. In *butterfly conservation in North America* (pp. 35–57). Springer Netherlands.
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), Article 7611. <https://doi.org/10.1038/nature18608>
- Thorup, K., Tøttrup, A. P., Willems, M., Klaassen, R. H. G., Strandberg, R., Vega, M. L., Dasari, H. P., Araújo, M. B., Wikelski, M., & Rahbek, C. (2017). Resource tracking within and across continents in long-distance bird migrants. *Science Advances*, 3(1), e1601360. <https://doi.org/10.1126/sciadv.1601360>
- van Asch, M., & Visser, M. E. (2007). Phenology of forest caterpillars and their host trees: The importance of synchrony. *Annual Review of Entomology*, 52, 37–55. <https://doi.org/10.1146/annurev.ento.52.110405.091418>
- Vega, M. L., Fransson, T., & Kullberg, C. (2021). The effects of four decades of climate change on the breeding ecology of an avian sentinel species across a 1,500-km latitudinal gradient are stronger at high latitudes. *Ecology and Evolution*, 11(11), 6233–6247. <https://doi.org/10.1002/ece3.7459>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3(6), Article 6. <https://doi.org/10.1038/s41559-019-0880-8>
- Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, 147(1), 164–172. <https://doi.org/10.1007/s00442-005-0299-6>
- Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology*, 153(1), 75–84. <https://doi.org/10.1007/s10336-011-0770-6>
- Warren, M. S., Maes, D., van Swaay, C. A. M., Goffart, P., Dyck, H. V., Bourn, N. A. D., Wynhoff, I., Hoare, D., & Ellis, S. (2021). The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2002551117. <https://doi.org/10.1073/pnas.2002551117>
- Weir, J. C., & Phillimore, A. B. (2024). Buffering and phenological mismatch: A change of perspective. *Global Change Biology*, 30(5), e17294. <https://doi.org/10.1111/gcb.17294>
- Youngflesh, C. (2018). MCMCvis: Tools to visualize, manipulate, and summarize MCMC output. *Journal of Open Source Software*, 3(24), 640.
- Youngflesh, C., Montgomery, G. A., Saracco, J. F., Miller, D. A. W., Guralnick, R. P., Hurlbert, A. H., Siegel, R. B., LaFrance, R., & Tingley, M. W. (2023). Demographic consequences of phenological asynchrony for north American songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, 120(28), e2221961120. <https://doi.org/10.1073/pnas.2221961120>
- Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, 5(7), 987–994. <https://doi.org/10.1038/s41559-021-01442-y>
- Zhang, X., Friedl, M. A., & Schaaf, C. B. (2006). Global vegetation phenology from moderate resolution imaging spectroradiometer (MODIS): Evaluation of global patterns and comparison with in situ measurements. *Journal of Geophysical Research: Biogeosciences*, 111, G04017.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Species-specific parameter estimates for the effect of spring GDD at mean latitude for bird arrival and bird breeding.

Figure S2. (A) The effect of spring GDD at mean latitude for butterfly emergence by overwintering stage. (B) The effect of latitude on spring GDD sensitivity butterfly emergence by overwintering stage.

Figure S3. Spatial variation in phenological sensitivity to spring GDD for butterfly emergence for species that overwinter as pupae.

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