

## **ABSTRACT**

WEPPRICH, TYSON MATTHEW. Effects of Climatic Variability on a Statewide Butterfly Community. (Under the direction of Nicholas M. Haddad.)

Predicting how organisms will respond to anthropogenic climate change and other human impacts on the environment has become a key goal of ecological research, with the ultimate aim of informing conservation management decisions to reduce extinction rates and maintain ecosystem function. Long-term monitoring of organisms has provided evidence that climate change is already impacting ecosystems and that temperature can dictate how species respond to environmental change. Butterflies have generally accelerated their lifecycle as higher temperatures speed up development, expanded their ranges poleward to track optimal climate conditions, and added generations in lengthened growing seasons. However, it is still unknown if these biotic responses to climate change will increase the long-term viability of butterfly species.

This dissertation examines how differences in species' responses to climatic variability impact population viability using a volunteer-collected, 20-year monitoring data set from the Ohio Lepidopterists. First, I present a new population modeling approach to estimate an abundance index and phenology for separate generations of insects with complex lifecycles. Second, I test what environmental cues induce butterflies to add an extra generation late in the growing season and whether these generations have consequences for population growth rates. Third, I compare annual variation in butterfly phenology with plant phenology, estimated with remote sensing, to analyze if mismatches in phenological responses across trophic levels impact butterfly population growth rates. Finally, I evaluate how species respond to temperature variability across space and time and whether the land cover composition around monitoring sites affects their responses.

Species within the butterfly community demonstrate a diversity of population responses to climatic variability, which could indicate which species will be vulnerable to declines with ongoing anthropogenic climate change. In general, more species have declining statewide population trends than increasing trends. Adding an extra generation, which is an evolved response to photoperiod cues, increases annual population growth rates. Butterfly phenology is less variable than plant phenology and population growth rates are higher when butterfly phenology peaks occurs later in the season. Land-use has little effect on annual population growth rates, which are influenced by density dependence across all species and temperature variability in different ways between species. This dissertation contributes to the understanding of complex insect responses to the direct and indirect effects of climate variability and tests how these responses impact population growth rates, which will determine long-term changes in species' distributions and abundances.

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Effects of Climatic Variability on a Statewide Butterfly Community

by  
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## **DEDICATION**

I dedicate this dissertation to people who contribute to science by recording natural history observations, coding open-source software, and supporting research at government agencies.

## BIOGRAPHY

I don't remember a specific period when studying nature became fascinating as a child, but when my Mom recently asked me to sort through her archive of my elementary school artwork I found that many of the pieces portrayed my future self as a scientist, probably because I thought that was what smart people did. None of the artwork featured butterflies, unfortunately.

Two things I did as a kid that, in hindsight, predicted me becoming an ecology quant:

1. I kept a long list of animals with their scientific Latin names which I added to whenever I checked out new books from the library or received a new Zoobooks. Again, I think I had no idea what scientists did.
2. I acted out entire seasons of various sports with 10 plastic figurines, which isn't that strange. I also recorded box scores and kept elaborate statistics for these imaginary games, which is strange.

## ACKNOWLEDGMENTS

This dissertation would not exist without the immense effort by volunteers with the Ohio Lepidopterists long-term butterfly monitoring program. I thank Jerry Wiedmann, Barbara Coleman, Linda Romine, Rob Liptak, and others for working with me and supporting this project. Leslie Ries is organizing all statewide monitoring programs under one network ([www.nab-net.org](http://www.nab-net.org)). I thank her for inviting me to participate in a SESYNC working group, which inspired much of the research questions in this dissertation.

I thank my advisor Nick Haddad. When I was a prospective student visiting the lab, I was disconcerted when all of the students I met with could not say a bad thing about Nick. I took this to mean that he was either a great guy with no flaws or a tyrant that everyone feared. It's the former, obviously. I appreciate all of the times eating cookies, getting chiggers, talking science, paddling slowly, and competing for oxygen in an enclosed closet office with friends in the Haddad lab and across NCSU.

Funding for this project was provided in part by the Southeast Climate Science Center, which has provided a wonderful community for students at NCSU and supported me through their fellowship program. The National Socio-environmental Synthesis Center (SESYNC) supported me with access to their computing cluster as part of the Models for Citizen Science Insect Data venture. Thanks to Mike Carter, George Nichols, and the Graduate School dissertation completion grant and support network. Taxpayer-funded public datasets I used in this dissertation come from the USGS, NASA, and NOAA.

The biggest thanks goes to Anna and Sasha.

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# **CHAPTER 1: Estimating abundance indices and phenology for separate insect generations from repeated monitoring**

## **ABSTRACT**

Monitoring butterfly communities provides estimates of abundance and phenology that are used to track biotic responses to habitat changes and climate change. The predominant long-term monitoring protocol, weekly Pollard walks at volunteer-selected sites, is widely used because it records all species in the community with simple guidelines. I reviewed criticisms of Pollard walks and the existing statistical methods, typically tailored to European butterfly monitoring programs, used to estimate abundance and phenology. I propose modifications to the existing methods that add covariates to account for observer effort during the survey, spatial correlation among sites, and scaling of the growing season by thermal time rather than ordinal date to account for the physiological requirements of butterfly development. This new approach estimates abundance and phenology for separate generations of butterflies in multivoltine species. I validated my approach by comparing long-term trends estimated from the existing methods and with my modifications.

## **INTRODUCTION**

Estimates of abundance and distribution of organisms, generally by inference from samples, form the base of ecology and conservation biology (Morris and Doak 2002; Royle and Dorazio 2008). When these estimates are biased or inaccurate, it reduces the ability to apply scientific research for conservation policy decisions. For example, if abundance trends

cannot accurately be classified as increasing or decreasing we cannot detect species at risk of extinction (Wilson et al. 2011). Butterflies are one of the most common targets of population monitoring due to their popularity and their sensitivity to environmental changes including anthropogenic climate change (Thomas 2005; Parmesan 2006). A wide range of methods are used to sample butterfly populations and estimate abundance (Nowicki et al. 2008).

However, the existing methods do not adequately account for variation in the observation process or the temperature-dependent life history of insects. In this chapter, I review the sampling methods and statistical models used to analyze citizen-science observations of insects in structured monitoring programs. I propose and validate a new method for estimating abundance and phenology that accounts for the challenges in large-scale monitoring data and the variety in insect life histories.

Insect life history challenges the assumptions of many sampling designs and statistical models that estimate abundance. Ideally, sampling of animal populations will be designed to estimate detection probability, or the chance of missing an individual in a census when it is actually present, using replicated counts (Royle et al. 2005). The number of individuals counted is the product of actual abundance and the detection probability, so variation in detection probability between species, sites, or observers can bias abundance estimates when assumed to be constant (Royle et al. 2005; Nowicki et al. 2008). However, insect populations rarely adhere to the modeling assumption of population closure due to high mobility, short lifespans, and new individuals entering the adult population continuously as they emerge from pupa (Nowicki et al. 2008). Additionally, butterflies often cluster in groups at floral resources or mud puddles, which violates the assumption of independent

detection of individuals (McCarthy et al. 2013). With these challenges in mind, studies of single butterfly species, often rare or of conservation concern, with Capture-Mark-Recapture or distance sampling provide unbiased abundance estimates when methods are tailored to the species' life history and habitat (Haddad et al. 2008; Henry and Anderson 2016). The commitment of effort, resources, and training for these more intensive sampling techniques limits their use despite their benefits in terms of accuracy of abundance estimates (Taron and Ries 2015).

In addition to abundance estimates that inform conservation management, monitoring has revealed changes in the timing of butterfly lifecycles that have provided a key indicator of the effects of anthropogenic climate change (Parmesan 2006). As development is temperature-dependent, many species have emerged earlier in the year as climate warms over time (Forrest 2016). Warmer temperatures and expanded growing seasons will also increase the number of generations (voltinism) insects may attempt in a year (Altermatt 2010). Quantifying these phenological shifts in butterfly populations rely on repeated estimates of abundance made throughout the flight period to track the short-lived adult life stages. Estimates of phenology can be made without modeling abundance through comparisons of the date of first observations each year, but these are demonstrably biased by population size and variation in observer effort (van Strien et al. 2008; Moussus et al. 2010). Using repeated temporal estimates of abundance, the peak or mean of the distribution of counts is less biased and better represents the phenology of the population than first observation dates. The distribution of counts over the season describes the flight period of adult butterflies, which is a function of the timing of emergence from pupae, the lifespan of adults, and the total

population size (Zonneveld 1991). However, it is rarely possible to separate estimates of abundance, emergence phenology, and lifespan from count surveys (Nowicki et al. 2008; Calabrese 2012).

Widespread anthropogenic, environmental changes have led to volunteer-based monitoring programs focusing on entire communities of organisms to track populations through time and across regions (Dickinson et al. 2010; Tulloch et al. 2013). For spatially-extensive butterfly monitoring, the previously described intensive sampling methods do not scale up (van Swaay et al. 2008; Taron and Ries 2015). Butterfly monitoring programs typically use less rigorous sampling with Pollard walks, developed originally for the UK Butterfly Monitoring Scheme (Pollard and Yates 1994). In this method, volunteers set up fixed paths spanning different habitat types at monitoring sites of their choosing. The observer walks the path weekly from spring to fall and counts each individual butterfly and records the species if they fall within an imaginary, 5-meter-sided cube centered in front of the observer. Surveys are only performed under favorable weather conditions at certain times of the day to maximize the likelihood of butterfly activity. This standardized protocol has been adopted by many monitoring programs due to its ease and adaptability to different sites and climates (van Swaay et al. 2008; Taron and Ries 2015).

There are concerns that the reduced effort in Pollard walks reduce the validity of abundance and phenology estimates (Nowicki et al. 2008; Pellet et al. 2012). Pollard walks do not account for detection probability as in distance sampling methods, which also use transect walks, or as in replicated counts, as populations are not closed during weekly survey intervals. Volunteer selected sites are often clustered around population centers and favor

protected areas, which may bias regional estimates of trends compared to systematic or random placement of sites (Roy et al. 2015b). These concerns have led to comparisons of abundance estimates from Pollard walks with distance sampling (Isaac et al. 2011), Capture-Mark-Recapture surveys (Haddad et al. 2008; Pellet et al. 2012), and stratified random placement of surveys (Roy et al. 2015b). Counts from Pollard walks are generally correlated with the true abundance, but researchers should cautiously accept that Pollard walks provide a population index and limit their comparisons to relative population changes (van Swaay et al. 2008; Taron and Ries 2015).

I briefly review different strategies for analyzing data from Pollard walks and summarize these in Table 1-1. The UK Butterfly Monitoring Scheme uses a flexible generalized additive model (GAM) to model seasonal phenology to impute missing counts, with variation and how phenology varies across regions (Rothery and Roy 2001; Dennis et al. 2013; Schmucki et al. 2016). The imputed counts are then combined with raw counts to estimate a collated index that accounts for site and yearly variation in abundance (Dennis et al. 2013). Dennis et al. (2016a) recognize that different species' life-history traits should guide which modeling approach to use and provide three options of varying complexity. Species with complex flight periods with overlapping generations are modeled with splines or GAMs, as in the first step of the UK Butterfly Monitoring Scheme method. Species with separate generations can be modeled with Gaussian mixture models to estimate abundance and phenology separately for each generation, or can use the mechanistic stopover model introduced by Matechou et al. (2014) that estimates additional parameters, such as detection

probability, lifespan, and emergence phenology, while separating generations with a mixture model.

I adapt the approach of Dennis et al. (2016a) to create a more general analysis that could be readily applied across regional efforts and across insect species. I have difficulty applying the existing methods to a long-term monitoring program in Ohio due to fewer sites and a greater number of generations in multivoltine species compared to the UK, requiring updates to the methods presented in Dennis et al. (2016a). I add new features to model sampling effort at each survey, incorporate spatial variation in seasonal phenology, and scale the monitoring season according to the thermal requirements for butterfly development using growing degree days (Table 1-1). My three-step modelling approach estimates a site x year population index and phenology of each generation for species producing one to five generations each monitoring season. First, I fit a GAM to all observations for each species using covariates, similar to Hodgson et al. (2011). Second, I use simulated counts from the GAM to estimate Gaussian mixture models to assign counts to separate generations within the growing season, similar to Dennis et al. (2016a). Third, the simulated counts for each site x year x generation are fit with a normal distribution to describe a population index and phenology.

I validate my modeling approach by comparing its estimates of relative population indices (from all generations combined within a site and year) and statewide trends to those derived from the established methods. I expect high correlations between the existing methods and my methods, as this is a check to ensure that my modeling process works. The key difference is that my modeling approach estimates abundance and phenology for separate

generations while including additional covariates for the sampling process and butterfly temperature-dependent development.

## **METHODS**

### *Monitoring data*

The Ohio Lepidopterists have organized statewide monitoring since 1995, including about 80 sites per year sampled with weekly Pollard walks ([www.ohiolepidopterists.org](http://www.ohiolepidopterists.org)). I used 21,223 Pollard walks (mean duration of 76 minutes with a mean 8.2 species observed) at 143 sites with a mean 7.1 years of participation from 1996-2014. Of the 122 species recorded, I modeled populations for 40 resident species with at least 10 unique site x year observations, excluding species with widely overlapping generations, idiosyncratic life-history, or flight periods near the boundary of the monitoring season. For these 40 species, I use my new approach to estimate described below to estimate abundance and phenology for separate generations. An additional 39 species were modeled for analysis in Chapter 4 using the generalized additive models described below without the following steps to estimate generations separately (Dennis et al. 2016a).

### *Environmental and survey covariates*

Each monitoring site was assigned geographic coordinates for the transect start or the address of the monitoring site reported by volunteers and verified using Google Earth. For each survey date, I calculated the cumulative growing degree days since January 1 using the daily average method with a 10°C minimum temperature threshold (Moore and Remais 2014). Daily minimum and maximum temperature for degree-day calculation came from 1-

km<sup>2</sup> gridded interpolations from the Daymet data set available from the Oak Ridge National Laboratory (Thornton et al. 1997; Thornton et al. 2014).

Volunteers report the time of day, duration, temperature, wind speed, and cloudiness of each survey. The number of species recorded during each survey (list length) also provides information on the site's habitat quality, observer effort, and suitability of the weather during the survey (Szabo et al. 2010; Breed et al. 2013). After evaluating correlations between the survey covariates, I included survey duration scaled by the site (as transects are different lengths between sites), relative temperature scaled by the week and region, and relative list length scaled by the week and region. I scaled these covariates to account for systematic, spatiotemporal variation that affects temperature and the number of species flying. Scaling covariates by one standard deviation also minimized correlations between them before including them in the models.

#### *Generalized additive models*

I used counts from all monitoring years in separate models for each species. For each species, I filtered the data to exclude site x year observations in the lowest 10<sup>th</sup> percentile of number of weekly surveys and number of individual butterflies counted. Data filtering in this manner removes sites with the lowest sampling effort and reduces the amount of data for common species with computationally-intensive models. All data preparation, statistical analysis, and visualization were performed in R 3.3.2 (R Core Team 2016). Code is archived in a public repository (<https://github.com/tysonwepprich/counting-butterflies>).

Generalized additive models are generalized linear models that use smooth functions of predictor variables, with smoothness determined by the data (Wood 2006). All were fit

using the *mgcv* R package (Wood 2011). The flexibility of GAMs makes them especially good for predicting insect phenology over time while accounting for missing surveys, spatial correlation, and highly variable insect counts (Hodgson et al. 2011; Schmucki et al. 2016). In the models, the expected count as a site x year (Figure 1-1A) was a function of:

1. Cumulative growing degree-days, to scale time in thermal units for temperature-dependent insect development (Roff 2002). The response to growing degree days varied by latitude and longitude to account for local adaptation in development rate, voltinism, and spatial correlation between sites. The interaction between these three variables was modeled with tensor product smooths (Wood 2006). All years were modeled together, but phenology could vary across years due to variation in the growing degree day accumulation.
2. Ordinal date modeled as a cyclic cubic regression spline, as inclusion captures the end of season declines in abundance after degree-days slow in accumulation.
3. Random effects of a site x year indicator using factor smooth interactions.
4. Survey covariates (temperature, duration, and list length scaled as described above) in thin plate regression splines.

Butterfly counts typically show overdispersion and were best modeled with a negative binomial link function, as noted in Dennis et al. (2016a), with the scale parameter estimated from the data (Wood 2006). Restricted maximum likelihood was used to select the degree of smoothness in the different parameters. Additional observations of zero counts were added in the months outside of the monitoring season to aid in curve fitting (Schmucki et al. 2016).

Alternative parameterizations of the GAM, such as grouping observations by region rather than latitude and longitude, showed similar results with slightly worse model fit. The tensor product interactions and random effects are computationally costly to include, and with larger data sets a simpler spline may suffice (Dennis et al. 2016a).

#### *Gaussian mixture models*

Using the species' GAM, I simulated weekly population counts for all sites and years 500 times from the posterior distribution of the parameters to account for uncertainty (Wood 2006). For each simulation, I classified all counts by generation, with respect to growing degree-days, with Gaussian mixture models in the *mclust* R package (Fraley et al. 2012). The assumption of Gaussian distributions for each generation is simplistic but computationally efficient for multivoltine butterflies (Dennis et al. 2016a). The potential number of generations was constrained based on visualization of flight curves to avoid overfitting generations that did not match the biology of the species. The best number of generations for each simulation was selected by BIC (Fraley et al. 2012). The simulated observations, after being classified to generation, were disaggregated to estimate abundance and phenology at a particular site x year with a Gaussian distribution (Figure 1-1D). The 500 simulated distributions for each site x year x generation were summarized using linear combination for the final estimate of the population index and the mean and standard deviation of the phenology (Winkler 1981).

My modeling approach is outlined in Figure 1-1 with an example from one site and year and two simulations. This approach was necessary due to the noisy data within each year. If the mixture model were applied to a single year, often unreasonable generation

phenology was estimated due to irruptions or very low counts. Lumping all years together classified the observations into generations more consistently by distinct ranges of physiological time and had fewer outlier classifications. A larger data set might be able to use mixture models on individual years or regions, or ideally, include parameters for each generation's phenology, abundance, detection probability, and covariates in a more mechanistic model as in Matechou et al. (2014).

#### *Comparison with other methods*

I imputed missing counts with each species' GAM and then estimated the population index for each site x year with the trapezoid rule (which is an integration by parts of the area under the curve of counts by date) with weekly raw or imputed counts, similar to the UKBMS method in Schmucki et al. (2016). As raw counts are limited by variation in detection probability and overdispersion, I also derived population indices using all imputed weekly counts from the GAM. I compared site x year population indices from these two methods and my new approach using Kendall's correlation statistic, which evaluates the rank order of observations.

For each method, I calculated annual collated indices with a generalized linear model with site and year categorical covariates (Brereton et al. 2011). Statewide temporal trends were modeled linearly using these annual collated indices. I included an interaction between year and modeling method in three pairwise linear models to test whether the species' temporal trends differed with the modeling approach. I compared the temporal trends for 32 multivoltine species with the abundance of all generations summed together or for the first generation abundance only.

## RESULTS

Sample sizes, GAM fit, temporal trends, and correlations between methods for 40 species are summarized in Table 1-2. Generalized additive models fit the highly variable butterfly count data well, with species' models explaining an average of 81% (standard deviation of 10%) of the total deviance in the observations. Twenty-seven species' models show overdispersion greater than one, which is accounted for with a negative binomial error distribution. List length is the most important covariate accounting for sampling effort and weather on a survey's count, as it is statistically significant ( $p < 0.05$ ) in 39 of 40 species' models and generally contributes much more to the model fit according to the chi-squared estimates for each parameter in the model. For comparison, temperature is significant in 14 and survey duration is significant in 16 species' models. As an example of the GAM fit, Figure A1 shows model predictions plotted against raw counts for four sites in different regions of the state over all years for the Spicebush swallowtail.

The mixture model used to classify simulated species observations into generations performs well on visual inspection of results. I show an example in Figure A2 for the Spicebush swallowtail, where the estimated size of each generation (scaled by the total population size) at each site x year is plotted against the estimated mean growing degree day of the Gaussian distribution representing each generation in the mixture model. For multivoltine species, this method captures the regional and annual variation in relative generation sizes and the local adaptation between regions for the growing degree days at peak phenology (Figure A2). However, this step had to be adjusted and reanalyzed based on the data visualizations, as some species' models have better classification of separate

generations with homogenous or heterogeneous standard deviations of the Gaussian distributions in the mixture model. For one species, the Baltimore Checkerspot, the mixture model has unreasonably high estimates of population counts which trace back to the simulations from the GAM parameter posteriors. The uncertainty in this GAM is high for the univoltine species, leading to simulations with estimated counts orders of magnitude higher than those observed.

The three methods show similar temporal trends for all 40 species. Even though a few species' trends are statistically significant in one method and not the others, the magnitudes of the trend estimates are similar (Table 1). In pairwise comparisons in linear models for each species with an interaction term for method, no interaction terms are significant ( $p > 0.05$ ). When all species trends are averaged for each method, the UKBMS and GAM methods are slightly more pessimistic, with an average annual trend estimate 0.015 lower than the average trend estimated by the GAM + mixture model method.

Correlations for the site x year population indices show less agreement. Across species, the GAM and GAM + mixture model methods have an average correlation of 0.92, whereas these two methods have average correlations of 0.72 and 0.68 with the UKBMS population indices, respectively.

For multivoltine species, temporal trends estimated using collated indices derived from all broods or the first brood generally show agreement. Of the 32 species, only the Carolina Satyr, Horace's Duskywing, and Red-banded Hairstreak have significant differences between trends (results not shown).

## DISCUSSION

I propose a new method to analyze butterfly monitoring data derived from Pollard walks and verify its results against the established method. This new approach is tailored to the Ohio butterfly monitoring data set, but could potentially be applied to other insect monitoring data. The key features I add to existing approaches in Dennis et al. (2016a) and Schmucki et al. (2016) are separating up to five generations with mixture models for abundance and phenology estimates, scaling the monitoring season by physiological time using growing degree days, incorporating survey covariates to account for effort and weather, and accounting for spatial variation in flight patterns between sites. These new features make possible analyses of population indices and phenology separated by generation (Chapters 2 and 3). When compared to the established method to estimate population trends, there is no significant difference between the statewide trends estimated with this new method and the established approach, which provides validation against errors in the modeling process.

The existing methods for modeling population counts have been developed for the particularly well-monitored and long-term UKBMS, with over 1000 sites monitored annually over 40 years. The Ohio butterfly monitoring data set is smaller, which limits my ability to use the most parameter rich, mechanistic approaches to modeling butterfly abundance and phenology (Matechou et al. 2014). Whereas previous studies use relatively simple GAMs to account for seasonal phenology, I use a variety of smoothing parameters available in the *mgcv* R package to account for different aspects of spatiotemporal variation in butterfly counts (Wood 2006). My modeling approach makes simplifying assumptions, such as that seasonal phenology at a particular location is driven by growing degree days in a similar

manner across different years, in order to fit these relatively complicated GAMs. My inclusion of survey covariates is consistent with other approaches, admitting that counts are confounded in part by detection probability due to observer, site, and weather variation. The lower correlation between population indices at the site x year level between my method and the UKBMS method might be a consequence of my inclusion of these covariates. Rather than take raw counts as the best representation of the population size on a particular day, my method adjusts volunteer counts based on survey covariates, with list length being notably important in the model fits (Szabo et al. 2010; Breed et al. 2013). This does not estimate detection probability and true abundance, which would require a replicated sampling design and a hierarchical analysis (Royle and Dorazio 2008; Fiske and Chandler 2011).

The particular climate in the UK means that most butterflies have generations that can be separated easily and are often limited to two generations annually. The life history of species in my data set have more complex patterns of voltinism, many of which are flexible across space and between years, making mixture models developed for the UKBMS difficult to fit for multivoltine species in Ohio. My approach using mixture models as a separate step incorporates model uncertainty from the GAM using simulation of the posterior distribution of parameters (Wood 2006). This is likely not as optimal as fitting mixture models in one integrated approach to allow uncertainty to be accounted for at different levels of the model simultaneously (Dennis et al. 2016a; Dennis et al. 2016b). However, my approach of post-hoc mixture models permitted fitting GAMs with multiple parameters for survey effort and spatiotemporal phenology variation, which explained a high proportion of the deviance in the count data (Table 1-2). A future effort could compare this approach with (Dennis et al.

2016a) in a simulation of bivoltine species with variation in detection probability and regional variation in phenology. My approach could also be tested on less structured monitoring data, such as those in opportunistic field trips (Breed et al. 2013). Since GAMs could be fit to opportunistic data at geo-located sites, it is possible that separate generations could be analyzed using mixture models as I have done here.

Scaling the monitoring season by growing degree days is another new feature of this method compared to the existing approaches. Although it is recognized that insect development rate is temperature-dependent and can be approximated with growing degree days (Moore and Remais 2014; Cayton et al. 2015), most analyses of Pollard walks describe phenology by the week or ordinal date of the count. Based on visualizations of the GAM predictions for each species, scaling by physiological time with growing degree days generally synchronizes generations across annual temperature variation even if phenology does not align on an absolute timescale (Hermann et al. 2016). Scaling time by growing degree days tends to lengthen the flight curves at the beginning and end of the season when fewer degree days accumulate between weekly samples. It is unclear how butterfly lifespan depends on absolute time versus physiological time, which would need to be resolved in order to estimate true abundance from Pollard walks (Nowicki et al. 2008; Matechou et al. 2014). The fact that growing degree days plateau in their accumulation late in the monitoring season makes them less informative as a model parameter, which is why I included ordinal date in the GAMs to limit the start and end of butterfly flight periods.

Despite the valid criticisms of monitoring with Pollard walks (Nowicki et al. 2008; Pellet et al. 2012), some of their limitations can be accounted for in the statistical analysis of

the data. The goal with extensive butterfly monitoring networks is generally to detect long-term trends rather than providing estimates of true abundance, which could be provided with more intensive sampling methods (Henry and Anderson 2016). In this chapter, my new modeling approach and the established UKBMS approach differ in certain respects, as illustrated by the lower correlations between the species' site x year population indices. More work should focus on this discrepancy in site x year population indices, as these indices are often used as the basis of ecological research and management decisions at finer scales. In spite of these differences, the 18-year, statewide trends of all 40 species in this study were not significantly different when estimated with the different methods. This may provide evidence that the choices in the modeling approach to account for noise in the data do not affect the long-term signal in the underlying population changes at large scales.

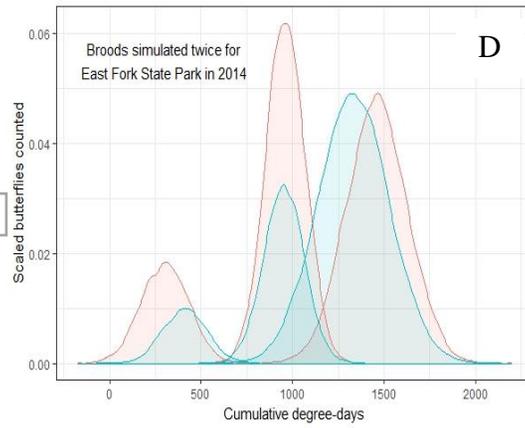
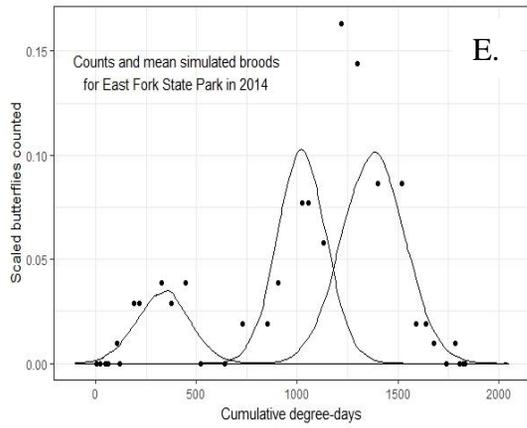
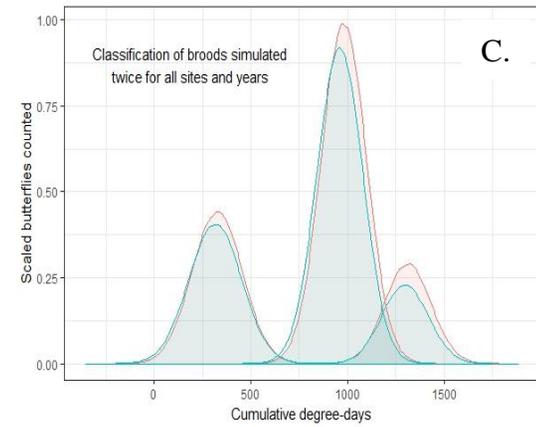
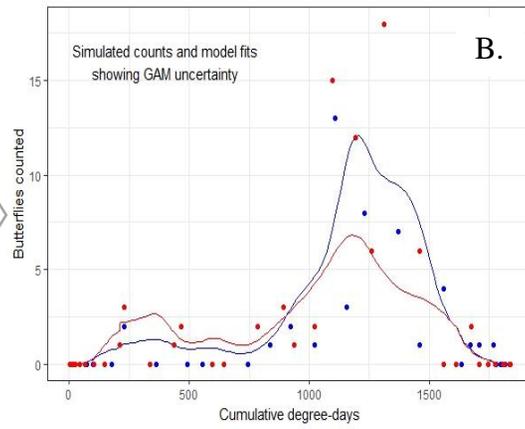
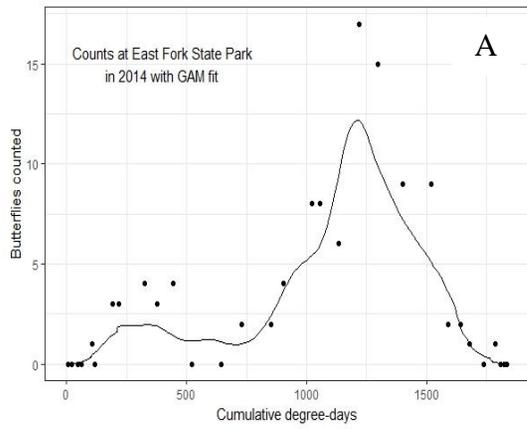
Table 1-1: Comparison of different methods used to analyze population monitoring data from Pollard walks.

	UKBMS method in Dennis et al. (2013); Schmucki et al. (2015)	Splines from Dennis et al. (2014)	Mixture models from Dennis et al. (2014)	Stopover model from Matechou et al. (2014)	GAM + mixture model from this study
Abundance	Index of “butterfly-days” for each site x year, using trapezoid rule of raw counts and missing counts imputed with GAMs	Relative abundance index for year averaging across sites, accounting for seasonal phenology with splines	Relative abundance index for year averaging across sites, accounting for seasonal phenology with mixture model of generations	True abundance of super population of butterflies for each site and year, by estimating lifespan	Relative abundance index for each site x year, accounting for seasonal phenology with GAM
Detection probability	Assumed to be constant within a species	Assumed to be constant within a species	Assumed to be constant within a species	Estimates detection probability, but can be confounded with abundance if covariates not independent	Covariates to account for sampling effort for each survey included in GAM
Phenology metrics	Quantiles, first observations based on combined raw and imputed counts	None derived in study	Mean and standard deviation of modes in mixture model estimated for generations	Mean and standard deviation of modes in mixture model estimated for generation emergence	Mean and standard deviation of modes in mixture model estimated for generations
Multiple generations	Not separated, often split manually post-hoc	Not separated	Mixture model	Mixture model	Mixture model estimated from GAM
Flight curve variation	Not modeled for raw counts, regional variation in GAM for imputed counts	Seasonal phenology uses same spline across space, varies by year	Covariates for multiyear mixture model allow variation across space and time	Covariates for emergence, lifespan, and detection probability for single year model	Covariates included in GAM for space, annual temperature variation, and site x year deviations
Scaling of time	Week, ordinal date	Week, ordinal date	Week, ordinal date	Week, ordinal date	Growing degree days and ordinal date

Table 1-2: Comparison of species' population model fit and estimated trends with different methods. Summary of count data used, GAM fit, temporal trends in collated indices, and correlations between three modeling methods.

Species	Counts used after filtering			GAM fit		Mixture model of broods			GAM (all imputed)			UKBMS (Raw + imputed)			Correlation for Site x year index		
	# Site x Year	Surveys present	Total # counted	Deviance explained	θ (over-dispersion)	Annual trend estimate	Standard error	P-value	Annual trend estimate	Standard error	P-value	Annual trend estimate	Standard error	P-value	Brood versus GAM	Brood versus UKBMS	GAM versus UKBMS
Acadian Hairstreak	41	123	693	0.936	2.566	-0.010	0.031	0.759	-0.035	0.044	0.440	0.047	0.058	0.425	0.910	0.720	0.756
American Copper	226	1488	8007	0.831	1.403	<b>-0.106</b>	<b>0.039</b>	<b>0.015</b>	<b>-0.135</b>	<b>0.054</b>	<b>0.023</b>	<b>-0.145</b>	<b>0.066</b>	<b>0.041</b>	0.964	0.789	0.805
Appalachian Eyed Brown	82	356	1606	0.899	4.807	-0.026	0.027	0.364	-0.043	0.041	0.310	-0.045	0.041	0.294	0.965	0.863	0.873
Baltimore	49	115	782	0.955	5.459	<b>-0.098</b>	<b>0.045</b>	<b>0.044</b>	<b>-0.222</b>	<b>0.056</b>	<b>0.001</b>	<b>-0.247</b>	<b>0.065</b>	<b>0.001</b>	0.398	0.362	0.883
Banded Hairstreak	216	365	753	0.713	0.666	-0.009	0.009	0.318	-0.012	0.010	0.235	<b>-0.057</b>	<b>0.026</b>	<b>0.043</b>	0.917	0.512	0.523
Black Swallowtail	659	3617	9859	0.750	1.954	<b>-0.034</b>	<b>0.009</b>	<b>0.002</b>	<b>-0.035</b>	<b>0.010</b>	<b>0.002</b>	-0.025	0.014	0.080	0.961	0.727	0.753
Broad-winged Skipper	40	134	4250	0.987	5.326	<b>-0.123</b>	<b>0.057</b>	<b>0.049</b>	-0.123	0.062	0.070	-0.117	0.069	0.113	0.754	0.703	0.867
Cabbage White	704	13383	236301	0.912	3.755	-0.027	0.013	0.065	-0.026	0.014	0.071	-0.026	0.017	0.150	0.982	0.856	0.860
Carolina Satyr	35	149	495	0.802	1.378	0.008	0.037	0.834	-0.003	0.036	0.930	-0.040	0.051	0.457	0.950	0.728	0.758
Coral Hairstreak	106	209	432	0.787	1.501	-0.012	0.006	0.057	<b>-0.018</b>	<b>0.006</b>	<b>0.008</b>	-0.025	0.014	0.093	0.801	0.420	0.496
Crossline Skipper	189	411	915	0.597	0.254	<b>-0.010</b>	<b>0.005</b>	<b>0.047</b>	-0.033	0.020	0.107	-0.028	0.015	0.078	0.943	0.552	0.543
Eastern Comma	600	2605	4800	0.575	0.975	-0.015	0.007	0.066	-0.015	0.008	0.066	-0.015	0.011	0.208	0.941	0.627	0.663
Eastern Tiger Swallowtail	700	6178	22909	0.812	2.621	-0.006	0.016	0.721	-0.005	0.016	0.765	0.007	0.020	0.748	0.970	0.737	0.750
European Skipper	384	1273	44285	0.954	0.834	<b>-0.063</b>	<b>0.017</b>	<b>0.002</b>	<b>-0.091</b>	<b>0.022</b>	<b>0.001</b>	<b>-0.105</b>	<b>0.030</b>	<b>0.002</b>	0.946	0.760	0.783
Giant Swallowtail	223	598	941	0.612	1.872	-0.001	0.008	0.871	-0.005	0.007	0.482	-0.004	0.017	0.817	0.930	0.579	0.603
Great Spangled Fritillary	649	4599	25800	0.879	2.571	<b>-0.062</b>	<b>0.019</b>	<b>0.004</b>	<b>-0.089</b>	<b>0.031</b>	<b>0.010</b>	<b>-0.085</b>	<b>0.036</b>	<b>0.030</b>	0.971	0.810	0.819
Hackberry Emperor	314	1670	8474	0.854	1.392	<b>0.052</b>	<b>0.019</b>	<b>0.017</b>	<b>0.054</b>	<b>0.019</b>	<b>0.013</b>	<b>0.043</b>	<b>0.017</b>	<b>0.025</b>	0.966	0.762	0.780
Hobomok Skipper	392	1315	6253	0.868	1.125	-0.019	0.011	0.083	-0.044	0.022	0.057	-0.030	0.019	0.123	0.935	0.652	0.677
Horace's Duskywing	244	777	1918	0.715	0.827	<b>-0.043</b>	<b>0.020</b>	<b>0.044</b>	<b>-0.071</b>	<b>0.031</b>	<b>0.035</b>	-0.085	0.043	0.067	0.935	0.611	0.638
Juvenal's Duskywing	291	772	2764	0.848	1.083	<b>-0.058</b>	<b>0.026</b>	<b>0.036</b>	<b>-0.086</b>	<b>0.040</b>	<b>0.045</b>	-0.075	0.044	0.102	0.935	0.713	0.727
Least Skipper	550	3939	22974	0.844	1.409	-0.008	0.040	0.851	-0.033	0.055	0.552	-0.034	0.058	0.568	0.971	0.768	0.779
Leonard's Skipper	76	190	1104	0.922	1.843	-0.026	0.023	0.258	-0.028	0.025	0.288	-0.043	0.032	0.205	0.779	0.657	0.803
Little Glassy Wing	413	1375	7341	0.877	0.949	0.010	0.013	0.464	-0.014	0.025	0.590	-0.017	0.027	0.520	0.949	0.680	0.706
Little Wood Satyr	634	3956	63653	0.940	1.573	0.040	0.022	0.079	0.038	0.021	0.084	<b>0.034</b>	<b>0.014</b>	<b>0.028</b>	0.941	0.813	0.831
Long Dash	151	346	1224	0.856	0.842	<b>-0.029</b>	<b>0.012</b>	<b>0.031</b>	<b>-0.053</b>	<b>0.018</b>	<b>0.009</b>	<b>-0.060</b>	<b>0.026</b>	<b>0.032</b>	0.856	0.542	0.608
Meadow Fritillary	317	1161	4409	0.781	0.744	<b>-0.090</b>	<b>0.021</b>	<b>0.001</b>	<b>-0.096</b>	<b>0.022</b>	<b>0.000</b>	<b>-0.066</b>	<b>0.021</b>	<b>0.007</b>	0.946	0.754	0.782
Northern Broken-Dash	332	1028	4973	0.869	0.982	-0.012	0.012	0.340	-0.031	0.021	0.159	-0.005	0.022	0.830	0.939	0.650	0.686
Northern Cloudywing	107	200	345	0.622	0.600	<b>-0.032</b>	<b>0.010</b>	<b>0.004</b>	<b>-0.034</b>	<b>0.008</b>	<b>0.001</b>	<b>-0.059</b>	<b>0.022</b>	<b>0.016</b>	0.905	0.441	0.481
Northern Pearly-Eye	246	880	2269	0.770	1.376	-0.013	0.018	0.472	-0.037	0.029	0.214	-0.035	0.033	0.301	0.954	0.756	0.776
Pearl Crescent	723	10867	138847	0.863	1.764	-0.005	0.015	0.763	-0.004	0.015	0.772	-0.001	0.019	0.963	0.977	0.805	0.808
Peck's Skipper	621	4173	20324	0.829	1.388	-0.014	0.020	0.472	-0.041	0.032	0.224	-0.037	0.034	0.293	0.968	0.741	0.754
Red-banded Hairstreak	64	127	305	0.755	0.809	0.077	0.039	0.071	0.069	0.042	0.125	0.062	0.053	0.262	0.902	0.530	0.584
Red-spotted Purple	605	2616	5139	0.681	2.421	<b>-0.043</b>	<b>0.011</b>	<b>0.001</b>	<b>-0.069</b>	<b>0.021</b>	<b>0.004</b>	<b>-0.068</b>	<b>0.025</b>	<b>0.014</b>	0.948	0.626	0.655
Sleepy Duskywing	83	213	635	0.815	0.849	0.001	0.019	0.945	0.000	0.020	0.983	-0.017	0.019	0.373	0.943	0.739	0.767
Southern Cloudywing	89	225	446	0.740	1.491	-0.018	0.010	0.107	-0.034	0.021	0.122	-0.006	0.026	0.810	0.940	0.578	0.584
Spicebush Swallowtail	582	3948	19998	0.874	3.427	0.017	0.015	0.280	0.018	0.016	0.260	0.021	0.019	0.289	0.972	0.792	0.808
Tawny-edged Skipper	294	913	1797	0.650	0.884	<b>-0.033</b>	<b>0.009</b>	<b>0.003</b>	<b>-0.060</b>	<b>0.019</b>	<b>0.005</b>	<b>-0.067</b>	<b>0.017</b>	<b>0.001</b>	0.945	0.556	0.582
Viceroy	560	3275	12834	0.859	3.874	<b>-0.052</b>	<b>0.015</b>	<b>0.003</b>	<b>-0.080</b>	<b>0.030</b>	<b>0.014</b>	<b>-0.085</b>	<b>0.032</b>	<b>0.017</b>	0.968	0.807	0.823
Wild Indigo Duskywing	333	1882	12677	0.857	1.121	<b>0.091</b>	<b>0.022</b>	<b>0.001</b>	<b>0.099</b>	<b>0.022</b>	<b>0.001</b>	<b>0.102</b>	<b>0.024</b>	<b>0.001</b>	0.970	0.798	0.812
Zabulon Skipper	497	2490	8860	0.803	1.461	<b>0.043</b>	<b>0.017</b>	<b>0.021</b>	<b>0.046</b>	<b>0.018</b>	<b>0.021</b>	<b>0.062</b>	<b>0.023</b>	<b>0.017</b>	0.961	0.749	0.767

Figure 1-1: Outline of modeling approach for abundance and phenology of separate generations. Example is given using one site x year of Spicebush swallowtail counts. Species' counts are modeled over all years and sites (A). Uncertainty in the GAM is simulated 500 times (B). Mixture model of simulated weekly counts classifies generations over all years (C). Simulated counts are disaggregated to site x year with assigned generations (D). Site x year simulated generations summarized (E).



## APPENDIX

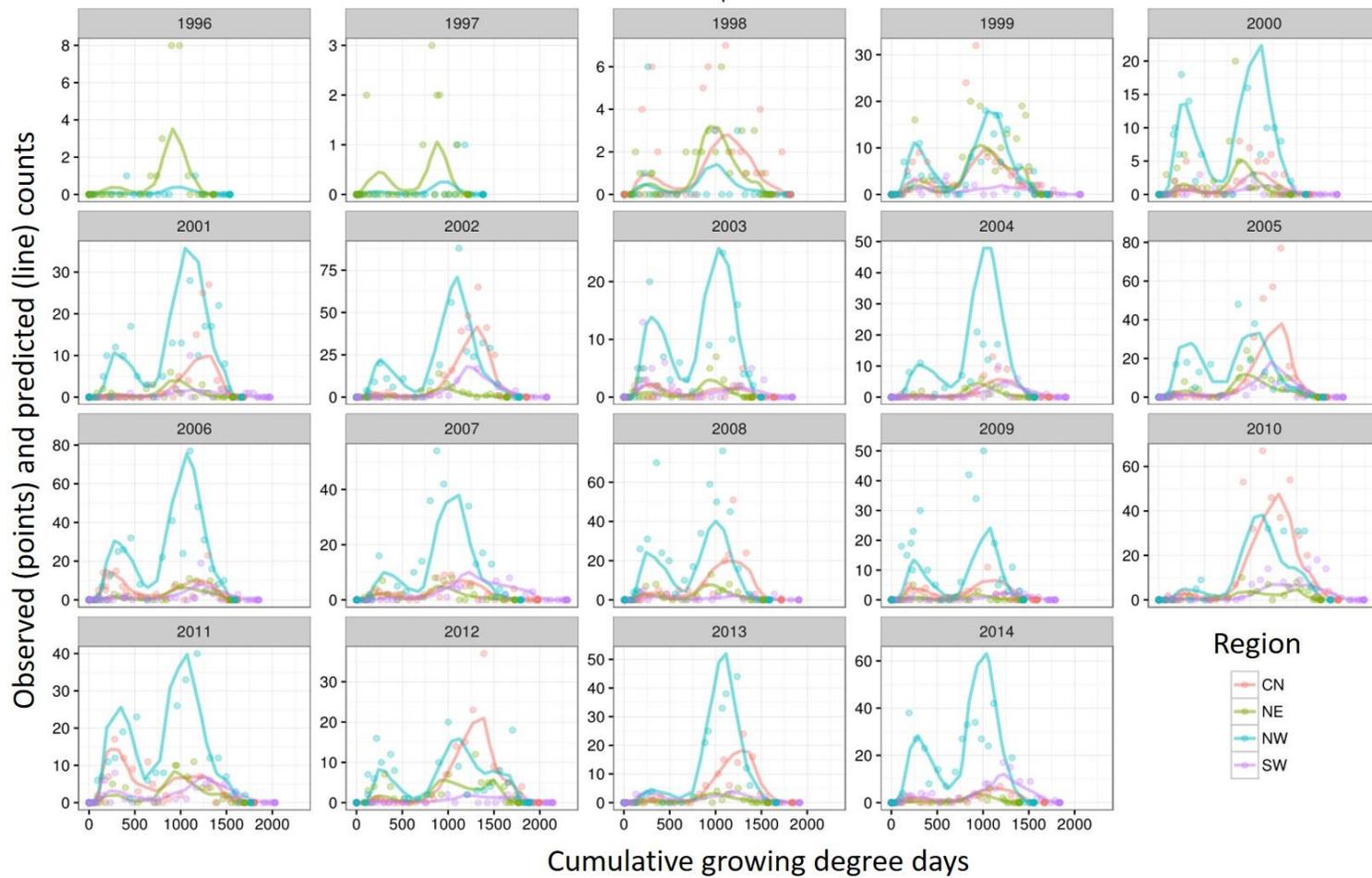


Figure 1-A1: Butterfly counts versus model predictions in different years and regions. Example predictions from a generalized additive model versus the observed Spicebush Swallowtail counts from 4 sites in different regions across years.

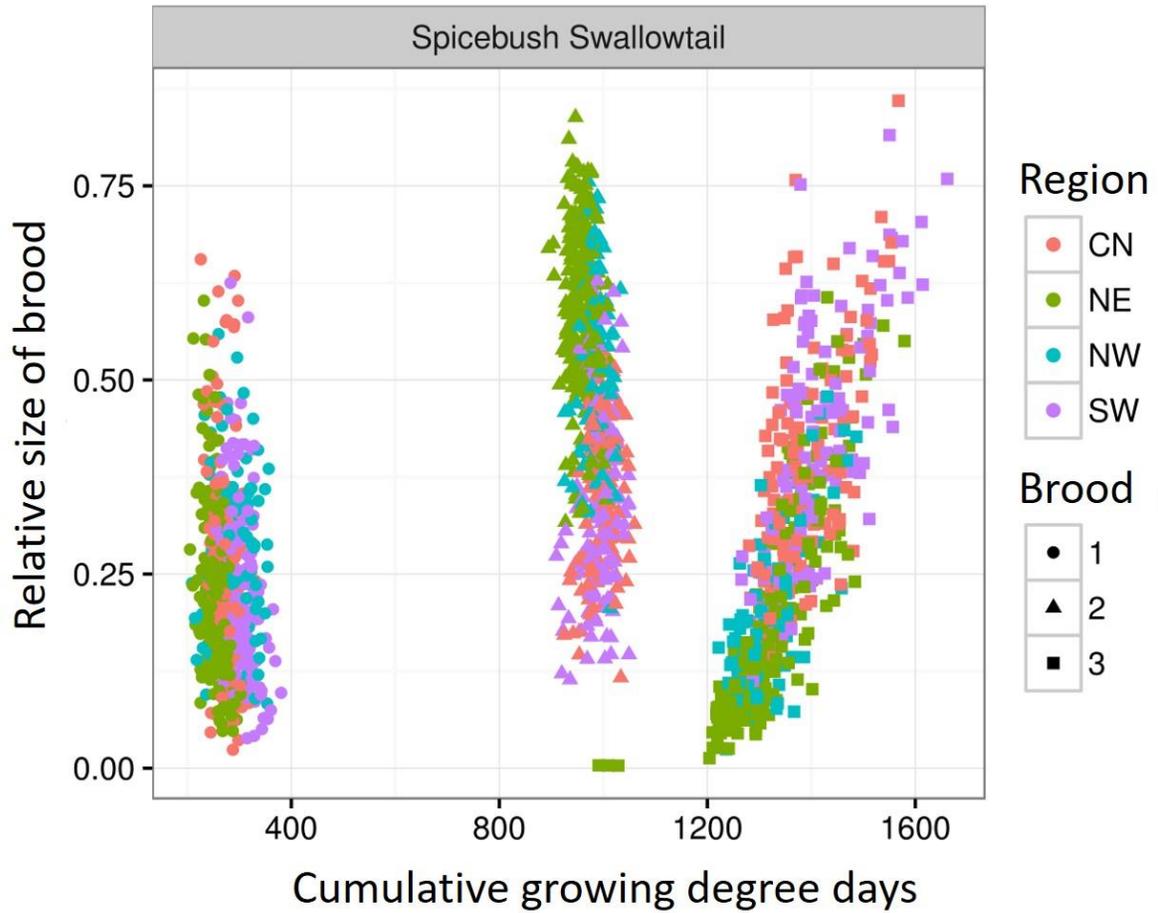


Figure 1-A2: Estimated size and phenology of separate generations in different regions. Mean phenology of Spicebush swallowtail generations, scaled by growing degree days, plotted against their relative size for each site x year estimated from the mixture models.

## **CHAPTER 2: Facultative, late-season generations increase population growth rates for butterflies with flexible voltinism**

### **ABSTRACT**

Rapid environmental change may cause mismatches in species' evolved responses to informative cues required for developmental decisions, with negative fitness consequences in evolutionary traps. For insects relying on stationary photoperiod cues to initiate diapause, warmer temperatures can change development rates and exposure to cues, leading to direct development into another generation before the onset of winter. It is hypothesized that this last generation may experience high mortality if it does not have sufficient time to complete development to the appropriate life stage before overwintering, creating a lost generation with severe consequences for population growth. I test this lost generation hypothesis in 20 butterfly species that show plasticity in their voltinism, or number of generations per year, in response to climatic variability across space and time. I use long-term, citizen science monitoring of butterflies to estimate the phenology and abundance index for each species' generation. The size of the last generation varies with exposure to environmental cues during the previous generation, principally through locally-adapted responses to photoperiod. Annual population growth rates depend on the interaction between winter severity and the size of the last generation in nearly all species, with interspecific variation in the importance of different winter variables. A simulation of population growth rates across the observed range of climatic variability with different sizes of the last generation shows that 13 of 20 species increase population growth rate in response to increased voltinism, while only one

species has a negative response. This study suggests that evolutionary traps for insects with flexible voltinism are rare, although the lost generation hypothesis may explain population crashes in species with mismatched responses to cues in parts of their range.

## INTRODUCTION

Successful conservation of biodiversity under anthropogenic climate change requires better predictive models of organismal responses to climatic variability (Urban et al. 2016). We can predict some responses, such as shifts in geographic range limits and springtime phenology, relatively well due to the direct relationship between temperature and physiological traits in poikilothermic organisms (Kingsolver 1989; Crozier and Dwyer 2006; Parmesan 2006). In other traits, informative cues control whether organisms with plastic traits respond appropriately to stochastic, seasonal, or trending climatic changes (Robertson et al. 2013; Sgrò et al. 2016). If optimal responses to cues evolved in an environment that differs from the current one, then mismatches between evolved life history and the rapidly changing environment can reduce fitness in an evolutionary trap (Schlaepfer et al. 2002; McNamara et al. 2011; Robertson et al. 2013). A population tracks environmental change through a number of evolutionary strategies, such as phenotypic plasticity in response to predictable changes in seasonal environments (Roff 2002). Models indicate that extinction probability increases when the optimal strategy changes due to the rate of environmental change, a species' adaptive potential, or a decoupling of cues from the optimal responses (Botero et al. 2015). A recent study suggests that an evolutionary trap has contributed to a drastic range collapse of a European butterfly, as evolved cues used to select developmental

pathways now result in “lost generations” with high overwinter mortality (Van Dyck et al. 2015). In this chapter, I test the lost generation hypothesis in butterflies with plastic life-history responses to climatic variability.

Both environmental conditions and evolved cues drive insect voltinism, or the number of generations produced during suitable conditions in a seasonal environment (Tauber and Tauber 1981). As temperature controls development rate, insects are limited in the number of generations completed within the growing season by time scaled by physiological rate rather than days, often expressed in cumulative degree days (De Réaumur 1735; Roff 2002; Moore and Remais 2014). Based on long-term monitoring in Europe, voltinism of butterflies and moths have increased in response to warmer temperatures and longer growing seasons (Altermatt 2010; Pöyry et al. 2011). Climate-driven changes in voltinism may impact management of agricultural pests, biocontrol predators, and forest defoliators (Tobin et al. 2008; Jönsson et al. 2013; Bentz et al. 2014; Grevstad and Coop 2015). Increased voltinism is presumably beneficial due to the increased rate of molecular evolution when generation time decreases (Thomas et al. 2010), although on a macro-ecological scale more generations may constrain body size (Zeuss et al. 2017). However, not all insects change their life cycle to use the expanded growing season, which may influence which species will persist through climate warming. It will be a challenge to predict changes in voltinism, which vary across species’ geographic ranges depending on the interaction between cues, life history, and temperature changes (Tobin et al. 2008; Levy et al. 2015; Van Dyck et al. 2015).

In temperate climates, insects with more than one annual generation use cues during sensitive life stages to determine whether to develop directly from egg to adult or to undergo diapause to delay normal development until after winter (Danilevskii 1965; Tauber and Tauber 1976). Diapause, an alternative development pathway, arrests normal development and prepares for poor growing conditions by increasing cold hardiness and conserving energy reserves (Tauber and Tauber 1976; Denlinger 2002; Bale and Hayward 2010). The most common environmental cue that induces diapause in insects is decreasing photoperiod, or hours of daylight, which indicates predictable seasonal declines in suitable temperatures, food resource quality, and the approach of winter (Danilevskii 1965; Tauber and Tauber 1976). Species are locally adapted both in the photoperiod cue and in voltinism, with diapause induced earlier in the growing season in regions with shorter growing seasons and generally with fewer generations at higher latitudes (Danilevskii 1965; Bradshaw et al. 2004; Levy et al. 2015). Transplanted insects across latitudes illustrate the consequences of maladapted voltinism caused by local adaptation to seasonal. Transplanting pitcher-plant mosquitoes to new latitudes reduces fitness both in Northern-adapted insects responding to shorter Southern photoperiods due to early induction of diapause and in Southern-adapted insects foregoing diapause entirely when longer Northern daylength does not reach the triggering cue during their sensitive stage (Bradshaw et al. 2004). Similarly, a mechanistic model predicts that an introduced biocontrol beetle may counterintuitively attempt too many generations at Northern latitudes and become univoltine at Southern latitudes as developmental rates in different temperature regimes desynchronize sensitive life stages with the diapause-inducing photoperiod cues (Grevstad and Coop 2015). Although we expect

local adaptation to photoperiod cues to affect insects transplanted across large latitudinal distances, one concern is that cue-response mismatches will emerge in stationary populations due to anthropogenic climate change and its effect on temperature means and variability (Vázquez et al. 2017).

In a predictable seasonal environment, natural selection will drive insects to switch between direct-developing and diapausing offspring to maximize expected fitness (Cohen 1970; Roff 2002). However, climatic variability makes the optimal switching time uncertain, and both diapausing and nondiapausing offspring should be produced simultaneously over a window of time that broadens with greater uncertainty of the time remaining in the growing season (Roff 2002). The gradual increase in the proportion of diapausing offspring with decreasing photoperiod is demonstrated by experiments (Danilevskii 1965) and observations that voltinism shifts gradually over a species range with partial generations produced in transition zones (Välimäki et al. 2013). Variability in temperature, precipitation, and host plant quality that affects the development rate may shift the date of photoperiod response if cue sensitivity requires a threshold body size, leading to differences in voltinism between years within the same population (Danilevskii 1965; Roff 2002). The size of a facultative, extra generation made up of direct developing individuals at a particular site and year will be a function of local adaptation to photoperiod variation across space and phenotypic plasticity in response to variation in photoperiod exposure between years.

The optimal time to switch to diapausing individuals may occur at a time delay from the photoperiodic cue, in which case the reliability or predictive power of the cue, in addition to environmental variability, determines whether fitness is maximized under uncertainty

(McNamara et al. 2011). Insects use multiple cues, in addition to the relatively stationary photoperiod, to inform diapause decisions. Temperatures experienced during the sensitive stage modify diapause decisions, such that cool or warm temperatures can override photoperiod cues to produce direct development or diapause, respectively (Danilevskii 1965). Multiple cues improve the ability to predict future conditions and increase plasticity in a system that mainly relies on the stationary photoperiod cue evolved to predict the optimal timing for the average year (Roff 2002; McNamara et al. 2011; Robertson et al. 2013). If climate conditions shift, adaptation in the photoperiod response to track the optimal timing is required to avoid a mismatch with negative fitness consequences, or an evolutionary trap (McNamara et al. 2011; Robertson et al. 2013). For example, pitcher-plant mosquitoes have evolved rapidly to use a shorter photoperiod cue more typical of Southern latitudes to track the expanded growing season (Bradshaw and Holzapfel 2006). On the other hand, snowshoe hare coat color change tracks photoperiod inappropriately in warmer autumns, leading to heavy predation on white hares mismatched with snowless habitat (Zimova et al. 2016). Developmental traps describes special cases of evolutionary traps: an organism chooses a maladaptive developmental pathway, such as diapause versus direct development into an additional generation, as a result of a cue response adapted to past conditions (Van Dyck et al. 2015). A key driver of conditions that could lead to a developmental trap is unequal climate warming between seasons, which is happening as annual temperature variability flattens with asymmetric warming (Robeson 2004; Wang and Dillon 2014).

A recent study suggests that a range collapse of the Wall Brown butterfly (*Lasiommata megera*) in Europe results from a developmental trap related to climate

warming (Van Dyck et al. 2015). Its populations have declined in central Europe, where the species transitions between bivoltinism in Scandinavia to 3 to 4 overlapping generations in southern Europe. However, populations at cooler sites along the coast have not declined as much as at warmer, inland sites where a third generation is more abundant late in the growing season. In an experimental transplant of second-generation larva between warmer, inland sites and cooler, coastal sites at similar latitudes in Belgium, all butterflies reared at warmer, inland sites developed into a late season third generation compared to 57.5% of coastal-reared caterpillars that entered diapause for winter (Van Dyck et al. 2015). Van Dyck et al. (2015) proposed the lost generation hypothesis to explain the concurrent patterns of population declines and diapause decisions: if the facultative, late-season generation does not have sufficient time to develop before temperatures cool, it could result in high overwinter mortality with ramifications for its long-term population viability (Van Dyck et al. 2015). A vulnerability assessment of European butterflies did not predict declines in widespread Wall Brown butterflies based on their broad thermal niche and availability of suitable habitat under climate forecasts (Settele et al. 2008).

The lost generation hypothesis could explain the rapid decline of a common butterfly species, but it is unknown if developmental traps are widespread in insects. In this chapter, I test whether adding facultative, late-season generations have population consequences when developmental decisions confront variation in winter severity, as proposed by the lost generation hypothesis (Van Dyck et al. 2015). I use 19 years of citizen science monitoring to track the phenology of 20 butterfly species with flexible voltinism in response to spatial and temporal temperature variability. I test how different cues may determine the size of

facultative generations and whether local adaptation to photoperiodic cues varies across species. I test whether the size of facultative generations interacts with winter weather to affect population growth rates. For all species, I simulate the population consequences for smaller and larger facultative generations across a range of winter conditions that varies over space and time. Finally, I test whether life-history traits predict the interspecific differences in the population consequences of increased voltinism.

## **METHODS**

### *Butterfly monitoring and species selection*

Volunteers recorded butterfly observations in a 20-year monitoring program across the state of Ohio, USA. Volunteers with the Ohio Lepidopterists sample fixed transects according to the Pollard walk protocol and count all species within an imaginary 5-meter moving box around the observer (Pollard and Yates 1994). I used 21,223 Pollard walks at 143 sites with a mean 7.1 years of participation from 1996-2014.

I selected 20 common species that produce an extra generation in response to temperature variation across space and time. To do this, I fit a generalized additive model (GAM) to annual butterfly counts for all resident species to assess phenology variation with data visualizations (Hodgson et al. 2011). I did not include species with ambiguous generations or life-history traits, such as summer aestivation, that suggest that separate flight peaks may contain butterflies from the same generation (Iftner et al. 1992). I show examples of phenological variation in different regions and years for three species in Figure 2-1.

### *Estimates of phenology and abundance by generation*

Previous studies documenting increased voltinism in Lepidoptera do not estimate population sizes or annual variation in voltinism (Altermatt 2010; Pöyry et al. 2011). My population modeling approach allows for analysis of the annual and spatial variation in the size of the last generation and population growth rates to test for demographic consequences of increased voltinism (Chapter 1). For each species, I model an abundance index and time of peak phenology in growing degree days for each generation (Chapter 1).

### *Response variables*

For each species x site x year, I quantify the size of the last, facultative generation as a proportion ranging between zero and one, calculated by dividing the abundance estimate of the last, facultative generation by the sum of it and the obligate, penultimate generation (Aalberg Haugen and Gotthard 2015). I transformed this zero-inflated variable using the cube root in order to use linear models for analysis (Harrell 2015).

For each species and site, I calculated the annual population growth rate as the natural logarithm of the difference between the first generations of consecutive years for a metric that is comparable between species with different voltinism (Bradshaw et al. 2004). I repeated analyses with an overwinter population growth rate from the penultimate generation to the first generation in the next year, but will only present those results when the conclusions diverge from those obtained with annual population growth rates.

### *Environmental variables*

I derived environmental variables used as potential cues by insects around time windows relative to the peak phenology of the penultimate generation. Photoperiod was

derived from the ordinal date at the peak and site latitude using the *geosphere* package (Hijmans et al. 2012). Temperature and precipitation were calculated as the mean daily observations in the 30 days after the generation peak compared to the expected mean during those 30 days for the site from 1980-2015. Temperature and precipitation values were obtained from the Daymet product from the Oak Ridge National Laboratory, which has interpolated daily weather at 1-km grid cells across North America from 1980-2015 (Thornton et al. 1997; Thornton et al. 2014).

I used a principal components analysis (Jolliffe 2002) to quantify the spatial and temporal variation in winter severity that may impact insect overwinter mortality, such as extreme cold, snow, and early onset of cold temperatures (Bale and Hayward 2010). Winter severity was measured using variables derived from the Daymet climatic data set (Thornton et al. 2014). First, minimum daily temperatures from fall to spring were modeled as a smooth function of ordinal date using GAMs (Wood 2006). *Winter onset*, *winter end*, and *winter length* were estimated from the dates that the predicted temperature crossed 0°C in these models. *Minimum temperature* was the coldest temperature recorded that winter. *Cumulative temperature* was the sum of degree days spent below 0°C during the winter. Mean daily *snow cover* and *precipitation* during the season were estimated averaging daily Daymet values between winter onset and end. Butterfly phenology responses to urban warming depend on the spatial variation in temperature across Ohio (Diamond et al. 2014). In order to separate the spatial and temporal aspects of variability in winter severity, each of the seven variables was split into the site mean value and the annual variation about the site mean. In all, 14 variables were used in the principal components analysis employed to create

orthogonal variables from correlated weather variables and to gauge whether spatial or temporal variation accounts for a greater proportion of winter variability. I selected the first seven principal components ranked by proportion of variance explained (Jolliffe 2002).

In order to summarize spatial variation in species' voltinism and population responses in analyses and figures, I group observations by region. To classify monitoring sites into regions of the state with common environmental conditions, I used the *mclust* package to determine the best number of groups delineated by latitude, longitude, and mean annual growing degree days (Fraley et al. 2012). I refer to the resulting four clusters as the Northeast, Northwest, Central, and Southwest regions.

#### *Statistical analysis*

All statistical analyses were performed in R 3.3.2 (R Core Team 2016). Code is archived in a public repository (<https://github.com/tysonwepprich/multivoltine>).

#### *Model of facultative generation size in response to cues*

I tested how the size of the last generation, indicating how many larva choose direct development over diapause, responds to different environmental cues. The proportional size was modeled as a response to photoperiod, temperature, precipitation, latitude and all two-way interactions. I included site latitude to account for local adaptation in the response to the predictor variables and the size of the last generation, which varies regionally for different species (Danilevskii 1965). Predictor variables were centered and scaled by one standard deviation. I checked correlations between predictor variables and VIF to avoid redundant, collinear parameters (Harrell 2015).

All species were modeled at once using linear mixed effects models in the *lme4* package (Bates et al. 2014). As species variation is of key interest in this analysis, intercepts and slopes were allowed to vary by species. The mixed effects model estimates the community wide response as well as the individual species variation around it for each parameter in the model (Nice et al. 2014). All fixed and random effects were included in the final model (Gelman and Hill 2006).

I also modeled species individually in order to see how well different cues contributed to the model fit to gauge their relative importance in controlling the last generation size. The relative importance of the predictors were measured using the *relaimpo* package to compare their contribution in terms of the model  $R^2$  (Grömping 2006). As temperature and precipitation are more flexible cues than photoperiod, species using them may have more reliable information about environmental conditions (McNamara et al. 2011). I compared the combined importance of photoperiod, latitude, and their interaction against the combined importance of temperature, precipitation, and all interactions including them.

#### *Model of local adaptation to photoperiod cue*

I focused on the dominant cue, photoperiod, to compare the contributions that local adaptation and phenotypic plasticity make to species' responses. For each species and monitoring site, photoperiod exposure was re-parameterized as two variables: the mean photoperiod for the site and the annual variation in photoperiod at the site. Within-group centering in this manner separates the response to photoperiod into spatial and temporal components whose slopes can be compared to test if phenotypic variation between sites shows local adaptation (van de Pol and Wright 2009; Phillimore et al. 2010; Roy et al.

2015a). Local adaptation to a stationary cue like photoperiod could be a contributing factor to developmental traps, as evolutionary change may not adequately track the changing climate (Bradshaw et al. 2004; Van Dyck et al. 2015).

After observing that this analysis resulted in some species showing atypical responses if their penultimate generation occurred closer to the summer solstice, I reanalyzed these models using ordinal date instead of photoperiod. Photoperiod is the cue that insects use to gauge seasonal time, but daylength changes its trend from increasing to decreasing at the summer solstice (Danilevskii 1965). Using ordinal date is more typical in phenological studies of local adaptation (Phillimore et al. 2010; Roy et al. 2015a), even though other variables correlated with date, such as photoperiod or growing degree days, may be the main drivers behind phenological patterns.

#### *Population models of last generation size and winter severity*

The lost generation hypothesis predicts that overwinter mortality is higher for direct-developing individuals forming the last generation compared to those that diapaused from the previous generation (Van Dyck et al. 2015). Higher mortality could result from early onset of winter or from cold temperatures if the overwintering stage does not complete metabolic preparations for winter (Bale and Hayward 2010). To test if increased voltinism leads to lower survival and which aspects of winter variability may correlate with lost generations, I modeled population growth rate in response to the size of the last generation, seven principal components describing winter severity, and their two-way interactions. Density dependence was included as the previous generation's population index scaled by site and species to account for unmeasured site differences in habitat quality and sampling effort.

Exploratory analysis revealed nonlinear responses to winter severity in some species. Thus, each species was modeled separately with a GAM to allow for flexible response curves and their interactions with tensor product smooth terms in the *mgcv* package (Wood 2006). The optimal amount of smoothing was determined by generalized cross validation. An extra penalty was added so that parameters would be removed automatically if they had little effect (Wood 2006). In this way variable importance was assessed by counting the number of species for which a variable was included in the model. I compared nested models of increasing complexity, with the simplest model just including density dependence, to assess whether including the size of the last generation, and its interactions with weather variables, improved model fit ( $R^2$ ) or changed the estimated effect of different winter severity parameters. For each species the models were ranked by generalized cross validation scores, which generally correspond to model ranking with AIC (Wood 2006).

One downside to GAMs is that there is not a single slope estimate to summarize the effect of the predictor variable and test its statistical significance. The effective degrees of freedom provide one measure of how important a variable may be, but the p-values have inflated significance because model selection has been performed on the variables (Wood 2006). Partial residual plots were used to visualize species responses to density dependence, last generation size, and the winter severity principal components if they were selected in the species models. I plot predicted values for population growth rates for each species across the range of winter principal components and last generation size in order to visualize interactions which may be judged by the 95% confidence intervals and their overlap. These plots include predictions from the species' GAM without the extra generation size included

as a variable to see if growth rate responses to climate differ when the extra generation is ignored.

#### *Population consequences of facultative generations*

I performed simulations across the observed range of winter variability to summarize the potential population consequences of increasing voltinism. For each species and region, I simulated realistic values of density dependence and variability in the winter severity principal components. With these values and either a smaller (10<sup>th</sup> percentile) or larger (90<sup>th</sup> percentile) last generation size (tailored to the species and region), I predicted annual population growth rates from each species' GAM. I simulated the annual population growth rate either 500 times for each region in Ohio or weighted by the number of regional observations to quantify the overall statewide effect. The simulated annual population growth rates for the two sizes of the last generation were averaged by their geometric mean, which accounts for variability in stochastic growth rates (Morris and Doak 2002). The geometric mean population growth and its 95% confidence intervals were estimated with the *DescTools* package (Signorell et al. 2015). If a species had non-overlapping confidence intervals in the simulated geometric mean population growth rates for the two different generation sizes, then the population consequence of increased voltinism was considered significant.

#### *Effect of species traits on population consequences*

I modeled the population consequences of increased voltinism as a response in linear models to test if life-history traits could predict the interspecific differences. The traits were derived from previous steps in the analysis and from Iftner (1992) and Cech & Tudor (2005). I used larval host category (forb, graminoid, or woody plant), overwintering stage (egg,

larvae, or pupae), maximum number of generations in a year, average size of the last generation, ordinal date of the penultimate generation peak, relative variable importance of different cues, magnitude of the species' response to photoperiod, local adaptation in the species' photoperiod response, and spatiotemporal variability in the last generation size. I selected traits that have been suggested to influence phenological responsiveness or cue mismatches: host plant, overwinter stage, voltinism in Diamond et al. (2014); ordinal date of phenology peak in Valtonen et al. (2011); reliance on stationary or multiple cues in Robertson et al. (2013); and local adaptation versus phenotypic plasticity in Roy et al. (2015a). I performed univariate linear regressions on each trait separately (Pöyry et al. 2009), as with only 20 species model overfitting was a concern.

## RESULTS

### *Phenology and abundance estimates*

Generalized additive models for each species performed well, explaining a median 0.83 (range 0.60 - 0.95) of the deviance in counts (Chapter 1). After separating generations with mixture models, the average size of the last generation for different species had a median of 0.26 (proportion of total counts across all generations, range 0.10 - 0.56). Species differences in the mean and spatiotemporal variation in the size of the last generation are reported in Table 2-1.

### *Environmental variables*

The principal components analysis created orthogonal variables that represent spatial and temporal variability in winter severity (Table 2-A1). The principal components

describing spatial variability between site means or temporal variability from annual site anomalies each explain about half the total variance. The first two principal components have variable loadings that describe spatial (32% variance explained) and temporal (27% variance explained) differences in winter severity (encompassing longer, colder, and snowier season). Other principal components describe different aspects of winter, such as onset timing, extreme temperatures, and precipitation (Table 2-A1).

*Model of facultative generation size in response to cues*

The multi-species model shows that longer photoperiod exposure in the penultimate generation leads to a larger size of the facultative last generation (Table 2-2). Last generation size decreases at higher latitude and increases when the month after the previous generation peak experiences higher temperatures. Photoperiod interacts with temperature and precipitation to modify the size of the last generation. When photoperiod is shorter (indicating later phenology), higher temperatures increase the size of the last generation more so than when photoperiod is long (indicating earlier phenology). Higher precipitation increases the size of the last generation but only when photoperiod is shorter. The multi-species model fits well, with a marginal  $R^2$  of 0.33 (representing the contribution of the fixed effects) and a conditional  $R^2$  of 0.90 (including the contribution of the random effects). Although photoperiod has the strongest effect across species on the size of the last generation, species vary in their response and some have a negative relationship between photoperiod exposure and last generation size (Figure 2-2).

In individual species models, the analysis of relative variable importance of different cues demonstrates that photoperiod exposure and latitude are more important than

temperature and precipitation (Table 2-1). Individual species models generally explain the size of the facultative last generation well, with a median  $R^2$  of the linear models of 0.76 (0.10-0.89 range), with a median 0.08 (0.02-0.26 range) of the total  $R^2$  coming from variables of temperature, precipitation, and all interactions including them (Table 2-1).

#### *Model of local adaptation to photoperiod cue*

Most species have locally-adapted phenotypic change in the last generation size in response to either photoperiod exposure (13 of 20, Figure 2-A1) or ordinal date (14 of 20, Figure 2-A2) of the penultimate generation peak. For the analysis of photoperiod cues, nine species show positive co-gradient local adaptation for the photoperiod cue, with both local adaptation and phenotypic plasticity correlated with larger last generation sizes with longer photoperiods. Three species, which are typically univoltine, with generation peaks near the summer solstice (European Skipper, Little Glassy Wing, and Northern Broken-dash) show negative co-gradient local adaptation, with longer photoperiods between sites leading to smaller last generation sizes and little effect of within-site temporal variation. For the analysis of ordinal date, all co-gradient local adaptation is negative, as later ordinal dates leading to smaller last generation sizes. Counter-gradient local adaptation is rare, occurring in one species in the photoperiod analysis (Figure 2-A1) and two species in the ordinal date analysis (Figure 2-A2).

#### *Population models of last generation size and winter severity*

Models of population growth rate had improved fit when the size of the last generation was included with its interactions with winter severity variables. Generalized cross validation selects the most complex models (with density dependence, last generation

size, seven winter severity principal components, and the two-way interactions between generation size and the principal components) over simpler models in 19 out of 20 species (Table 2-1). The median  $R^2$  for best-fitting species models of annual population growth rates is 0.49 (range 0.28 – 0.73, Table 2-1). Population models of annual growth rate with a single term for density dependence fit well for their simplicity, with a median  $R^2$  of 0.39 (range 0.21 – 0.57, Table 2-1). When overwinter population growth rate is modeled instead of annual growth rate, models have similar fits to those of annual population growth rates, with a median  $R^2$  change of 0.02 (range -0.14 – 0.11).

Variable selection of principal components of winter severity suggests that temporal variation impacts annual population growth more than spatial variation (Figure 2-A4). The most important variables, judged by the number of times they were included in species models, are density dependence (20 species), PC3: Colder Winters (19 species), PC2: Warmer/Shorter Winters (18 species), and last generation size (15 species). Density in the previous year had a consistent negative relationship with population growth rate across all species. Years with a late onset and colder, snowier winters (PC3) have lower annual growth rates. Warmer years (PC2) with shorter winters and less snow generally showed negative relationships with growth rate. The size of the last generation had idiosyncratic responses across species, with many nonlinear relationships (Figure 2-A5).

Interactions between the last generation size and winter severity variables, which may indicate different overwinter mortality by development decision, are commonly selected as important variables in species models. For one interaction term, PC3 x last generation size, five species (Eastern Tiger Swallowtail, Meadow Fritillary, Northern Broken-dash,

Spicebush Swallowtail, and Tawny-edged Skipper) show lower growth rates with increased voltinism when winter starts late with colder extreme temperatures, but not with smaller last generations (Figure 2-3). Other species specific patterns emerge in interaction plots (Figure 2-A3), but there are no general patterns across species that suggest clear mechanisms that explain how increased voltinism may have population consequences.

#### *Population consequences of facultative generations*

The majority of species (13 of 20) have significantly higher simulated, statewide population growth with increased voltinism than with smaller last generations in response to the observed variability in winter severity (Table 2-1). One species, the European Skipper, has significantly lower simulated population growth with increased voltinism. Species have regional variation in the simulated population consequences (Figure 2-4).

#### *Effect of species traits on population consequences*

Univariate linear regression models of species' traits on the statewide population consequences of increased voltinism showed weak or no significant effects. Including marginally significant results ( $P < 0.10$ ), species that benefit more from increased voltinism are those with larger mean size of the last generation, greater temporal variation in last generation size, and non-egg overwintering stages (Table 2-A3).

## **DISCUSSION**

The lost generation hypothesis proposes that a developmental trap, where evolved cues trigger maladaptive decisions that increase overwinter mortality, links patterns of increased voltinism and population declines in the Wall Brown butterfly (Van Dyck et al.

2015). In this first test of the lost generation hypothesis, I evaluated the effect of cues on voltinism, the interaction of last generation size and winter severity on population growth rates, and simulated the population consequences of increased voltinism across 20 butterfly species. Locally-adapted photoperiod exposure determines the size of the last, facultative generation. The size of the last generation interacts with overwinter weather in the best-fit models of population growth rate, with some species' responses suggesting that overwinter mortality increases when the last generation confronts severe winters. Simulated population growth rates, across a range of observed winter severity and regional variation in voltinism, suggest that larger sizes of the last generation increase mean population growth rates for the majority of species in this study.

This study demonstrates that the mechanisms for insect diapause decisions, well-known from experiments, explain the interspecific variation in voltinism observed in long-term, citizen-science monitoring across a range of climatic conditions. A rich body of experimental work shows that photoperiod is the principal cue regulating diapause induction for insects (Danilevskii 1965; Tauber and Tauber 1976; Denlinger 2002; Kostal 2006). Previous studies have documented increased voltinism over decades of climate warming (Altermatt 2010; Pöyry et al. 2011) and over spatiotemporal variation in degree days (Hodgson et al. 2011). I show that increased voltinism, defined by the proportional size of the last generation, is linked to longer photoperiod exposure during the peak of adult phenology across space and time (Table 2-2, Figure 2-2). If photoperiod cues for making diapause decisions become unreliable, using multiple cues could be important for maintaining the ability to track the changing climate (McNamara et al. 2011; Robertson et al. 2013). I found

that temperature and precipitation in the month after the peak of adult phenology had an effect on voltinism, but did not play as large of a role in predicting the size of the last generation as photoperiod in both the community and species models. These cues may influence diapause decisions indirectly by altering temperature-dependent growth rates and host plant quality, which would change phenology and photoperiod exposure (Roff 2002; Grevstad and Coop 2015).

Most species in this study had co-gradient local adaptation in the size of the last generation, with a larger response to spatial variation than temporal variation in photoperiod exposure or ordinal date of the penultimate generation (Figures 2-A1, 2-A2). With co-gradient phenotypic variation, the last generation size is a result of synergistic responses to genetic (between-site local adaptation) and environmental (within-site phenotypic plasticity) variation, leading to more divergent responses across the gradient (Conover et al. 2009; Phillimore et al. 2010). Counter-gradient local adaptation is more commonly reported in insect traits, such as faster development rates in colder environments that synchronize springtime phenology across latitudes (Conover et al. 2009; Roy et al. 2015a). It is interesting that early-season and late-season butterfly phenology do not show similar patterns in local adaptation, which could be explained by the observation that temperature-dependent development rates drive early-season phenology while photoperiod controls late-season phenology in insects (Bradshaw et al. 2004; Valtonen et al. 2011). Insect phenotypes do not always respond to environmental gradients linearly, as local adaptation in development rates may form sawtooth patterns across latitudes depending on the interaction between voltinism and growing season length (Levy et al. 2015).

In general, species have larger population growth rate responses to interannual variability in winter severity than to spatial differences between sites, based on which variables were selected in population models (Figure 2-A3). Overwinter conditions play key roles in temperate insect lifecycles, by synchronizing growing season phenology, determining metabolic energy losses while in diapause, and directly impacting mortality through extreme temperatures (Bale and Hayward 2010; Williams et al. 2012; Stålhandske et al. 2015). It is difficult to analyze which winter conditions have the largest impacts on an insect's overwintering life stage and population growth rate (Roland and Matter 2016). In this study, orthogonal variables from the principal components analysis each account for some proportion of the variance in winter conditions observed across space and time. Years with colder, longer winters (PC2, 27% of variance) increased population growth rates for many species (Figure 2-A4), possibly due to energy conservation with lower metabolic rates (Sinclair 2015). Counterintuitively, colder years with a late winter onset and colder extreme temperatures (PC3, 11% of variance) also had a negative effect on population growth rates across species (Figure 2-A4), possibly due to a lack of cold hardiness (Bale and Hayward 2010). It is difficult to generalize how different aspects of winter severity impact different species, as many population responses show nonlinear patterns. It is an open question as to whether inclusion of many variables is necessary to capture the complexity of population dynamics, but highly-parameterized population models have been successful at predicting species responses to climate variability when analyzed in a machine learning framework (Roland and Matter 2016).

The principal mechanism for population declines suggested by the lost generation hypothesis is higher overwinter mortality for extra, late-season generations compared to the previous diapausing generation (Van Dyck et al. 2015). I found that the size of the last generation changed the population responses to winter covariates, as these interaction terms improved fit of population models in all but one species (Table 2-1). Five species show decreased population growth rates in years when they have larger last generations followed by colder winter extremes (PC3, Figure 2-3). This pattern suggests that late generations may be less prepared for severe winter temperatures, although the later onset of winter in these years does not fit with the idea that a lack of time for development causes higher overwinter mortality. Potential mechanisms hypothesized from these population responses should be tested in an experimental framework to confirm how changes in the timing of diapause influences overwinter metabolism, cold hardiness, and mortality as components of the population responses to winter severity.

My simulation demonstrates that increased voltinism is generally beneficial, as 13 of 20 species have larger population growth rates with larger last generation sizes (Table 2-1). Only one species, the European Skipper (*Thymelicus lineola*), had significantly smaller population growth rates with increased voltinism. When I simulated population responses by region, there were no general patterns across species that suggested increased voltinism is more detrimental in places with harsher winters (Figure 2-4). This finding fits with the results in the species' models of population growth rates, where principal components representing spatial variation between sites were not as important to the models as temporal variation. If increased voltinism is beneficial for insects, it may make management of agricultural and

forest-defoliating pests more costly (Porter et al. 1991; Jönsson et al. 2009). At the same time increased voltinism may prevent negative impacts of climate change on insects, such as phenological mismatches, as multivoltine species are predicted to be less vulnerable to negative population impacts in any one generation (Knell and Thackeray 2016).

The European skipper is a notable species to have negative consequences of increased voltinism. The negative population consequences only occur in the Northeast region, where the skipper is most abundant and rarely has extra generations. Other regions show higher simulated population growth rates when the extra generation is larger. This observation fits with my analysis of species' traits, where the only trait that significantly predicted higher population growth rate with increased voltinism was a larger mean size of the last generation. The European skipper is one of two non-native species in this study (the other being the Cabbage White), which could explain why it is susceptible to an evolutionary trap due to a mismatch between its evolved cues and the current temperature regime (Robertson et al. 2013). In Europe, it is univoltine and typically emerges in July after the summer solstice. In Ohio, which is warmer and at a lower latitude than the UK, it frequently emerges in June with its distribution split by the solstice. This special case suggests that introduced species with sensitive life stages near the solstice may be especially vulnerable to disruption of diapause decisions. Other skippers show similar responses in last generation size to variation in photoperiod exposure, which differ from the majority of species' patterns and could be worth further investigation of these species' cues and diapause decisions (Figures 2-A1).

This study provides evidence that developmental traps causing lost generations are not widespread in butterflies with flexible voltinism. One lesson from the Wall Brown

butterfly is that regional temperatures interact with life history to control diapause decisions, and possibly population trends, across a species' range (Van Dyck et al. 2015). Even if the temperature regime over the last two decades has not caused developmental traps for most of the 20 species in this study, there is no guarantee that increased voltinism will continue its benefit in the future. The degree to which developmental decisions and voltinism are determined by local adaptation and phenotypic plasticity matters for the long-term persistence of organisms in response to environmental change (Chevin et al. 2010).

This study does not support widespread negative consequences of increased voltinism. The proxy we use for diapause decisions, the size of the facultative last generation, is well predicted by photoperiod and other cues for most species and fits with theoretical and experimental knowledge of diapause in multivoltine insects. Including the size of the last generation improves models of annual population growth in response to overwinter conditions. Population models show that annual variation in winter severity has a stronger effect on population growth rate than spatial variation between sites. A simulation study of the population consequences of diapause decisions demonstrates that the majority of species have higher population growth when the last generation size is larger. This is encouraging for their persistence in the face of climate change and the likely increase in voltinism, but does not preclude that future climate warming will have different effects or that new developmental traps will arise.

Table 2-1: Species' voltinism and summary of model results. *Variation in voltinism* shows proportional sizes of the last, facultative generation and its standard deviation across sites and across years. *Model of cues* describes the relative variable importance of photoperiod and latitude versus temperature and precipitation from linear models for each species. *Population growth models* compares the fit ( $R^2$ ) of three generalized additive models of increasing complexity, with the best model in bold selected by generalized cross validation. *Simulation* shows the population consequence of increased voltinism versus a smaller size of the last generation for statewide variation in winter severity.

Species	Variation in voltinism			Model of cues			Population growth models				Simulation
	Mean size of last generation	Spatial: SD across site means	Temporal: mean SD within sites	Sample size	R <sup>2</sup> : photo. + lat.	R <sup>2</sup> : temp. + prec.	Sample Size	R <sup>2</sup> : Density	R <sup>2</sup> : Density + winter	R <sup>2</sup> : Density + winter + generation	Impact of larger last generation
American Copper	0.458	0.147	0.084	226	0.295	0.062	157	0.248	0.354	<b>0.405</b>	<b>0.140</b>
Black Swallowtail	0.402	0.138	0.162	659	0.615	0.156	475	0.485	0.536	<b>0.575</b>	<b>0.254</b>
Cabbage White	0.455	0.199	0.165	699	0.719	0.100	561	0.572	0.716	<b>0.726</b>	<b>0.057</b>
Crossline Skipper	0.167	0.071	0.044	188	0.677	0.071	96	0.383	<b>0.458</b>	0.512	-0.017
E. Tiger Swallowtail	0.160	0.140	0.068	699	0.320	0.069	553	0.504	0.569	<b>0.601</b>	<b>0.089</b>
European Skipper	0.127	0.177	0.094	382	0.418	0.016	257	0.213	0.242	<b>0.280</b>	<b>-0.041</b>
Giant Swallowtail	0.207	0.094	0.123	223	0.584	0.257	134	0.392	0.612	<b>0.695</b>	-0.004
Horace's Duskywing	0.466	0.124	0.113	244	0.010	0.090	128	0.294	0.399	<b>0.472</b>	<b>0.123</b>
Least Skipper	0.285	0.195	0.147	546	0.754	0.062	409	0.379	0.407	<b>0.433</b>	<b>0.056</b>
Little Glassy Wing	0.100	0.134	0.047	412	0.827	0.035	283	0.346	0.381	<b>0.411</b>	0.000
Meadow Fritillary	0.417	0.216	0.125	313	0.805	0.075	144	0.299	0.357	<b>0.410</b>	<b>0.043</b>
Northern Broken-Dash	0.104	0.122	0.062	332	0.530	0.048	211	0.330	0.356	<b>0.410</b>	<b>0.101</b>
Northern Pearly-Eye	0.496	0.167	0.176	246	0.495	0.053	153	0.376	0.520	<b>0.588</b>	<b>0.141</b>
Pearl Crescent	0.308	0.177	0.167	709	0.796	0.091	561	0.512	0.605	<b>0.626</b>	<b>0.084</b>
Peck's Skipper	0.206	0.137	0.149	611	0.693	0.096	451	0.432	0.500	<b>0.514</b>	-0.007

Table 2-1 Continued

Species	Variation in voltinism			Model of cues			Population growth models				Simulation
	Mean size of last generation	Spatial: SD across site means	Temporal: mean SD within sites	Sample size	R <sup>2</sup> : photo. + lat.	R <sup>2</sup> : temp. + prec.	Sample Size	R <sup>2</sup> : Density	R <sup>2</sup> : Density + winter	R <sup>2</sup> : Density + winter + generation	Impact of larger last generation
Red-spotted Purple	0.320	0.156	0.105	605	0.757	0.091	440	0.390	0.440	<b>0.460</b>	-0.001
Spicebush Swallowtail	0.228	0.114	0.128	582	0.593	0.139	437	0.435	0.494	<b>0.529</b>	<b>0.143</b>
Tawny-edged Skipper	0.171	0.100	0.078	293	0.590	0.079	174	0.416	0.447	<b>0.519</b>	<b>0.029</b>
Viceroy	0.559	0.147	0.120	559	0.602	0.112	404	0.359	0.403	<b>0.418</b>	<b>0.024</b>
Wild Indigo Duskywing	0.109	0.095	0.069	333	0.721	0.064	227	0.392	0.484	<b>0.507</b>	0.020

Table 2-2: Effect of environmental cues on the size of the facultative last generation. Linear mixed effects model of the scaled size of the facultative last generation for 20 species modeled together with random intercepts and slopes for each parameter. These estimates represent the community wide fixed effects (model estimate B, its standard error, and approximate p-value) and the variation in the model estimate by species (Random standard deviation).

	<i>B</i>	<i>std. error</i>	<i>p</i>	<i>Random SD</i>
(Intercept)	0.621	0.051	<.001	0.223
Photoperiod	0.187	0.033	<.001	0.144
Latitude	-0.048	0.013	<.001	0.054
Temperature	0.031	0.006	<.001	0.026
Precipitation	0.001	0.002	.684	0.008
Photoperiod X latitude	0.006	0.017	.733	0.071
Photoperiod X temperature	-0.026	0.004	<.001	0.015
Photoperiod X precipitation	-0.007	0.002	<.001	0.006
Latitude X temperature	0.002	0.002	.246	0.005
Latitude X precipitation	-0.002	0.002	.263	0.004
Temperature X precipitation	0.000	0.002	.847	0.009

Figure 2-1: Examples of spatial and temporal variation in voltinism. Modeled relative abundance (scaled phenology) of three species for the three warmest and three coolest sites with more than 10 years of data. Each line represents a different year, colored by the variation in cumulative growing degree days compared to the site's mean.

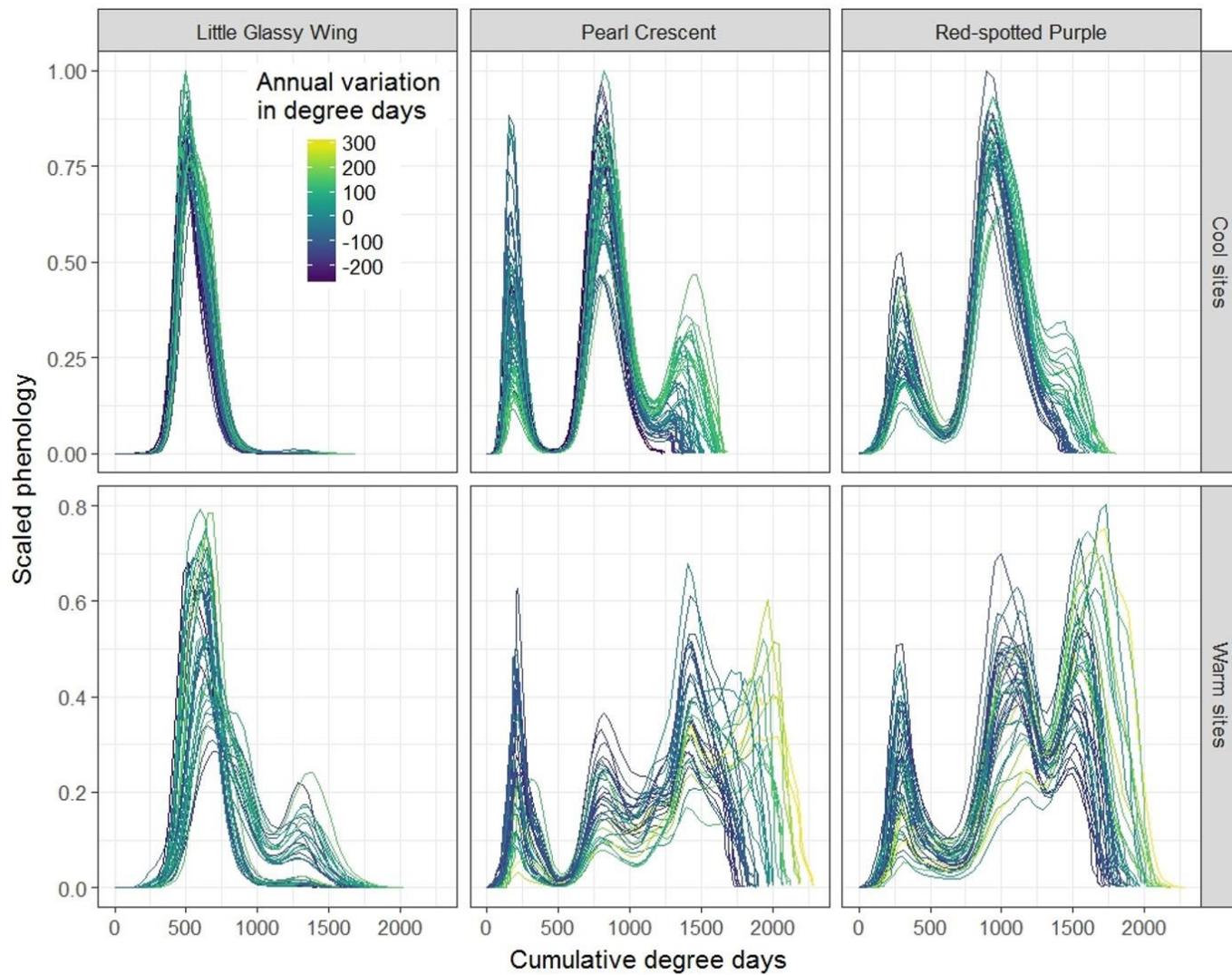


Figure 2-2: Species' variation in the size of the last generation in response to photoperiod cues. The size of the last generation is predicted by photoperiod of the previous generation peak with variation by latitude and timing of the summer solstice. Each data point represents a summary of the mean observation for each region x year, in order to ease visualization. Photoperiod is not simply a chronological axis, as it varies over time, latitude, and in relation to the summer solstice.

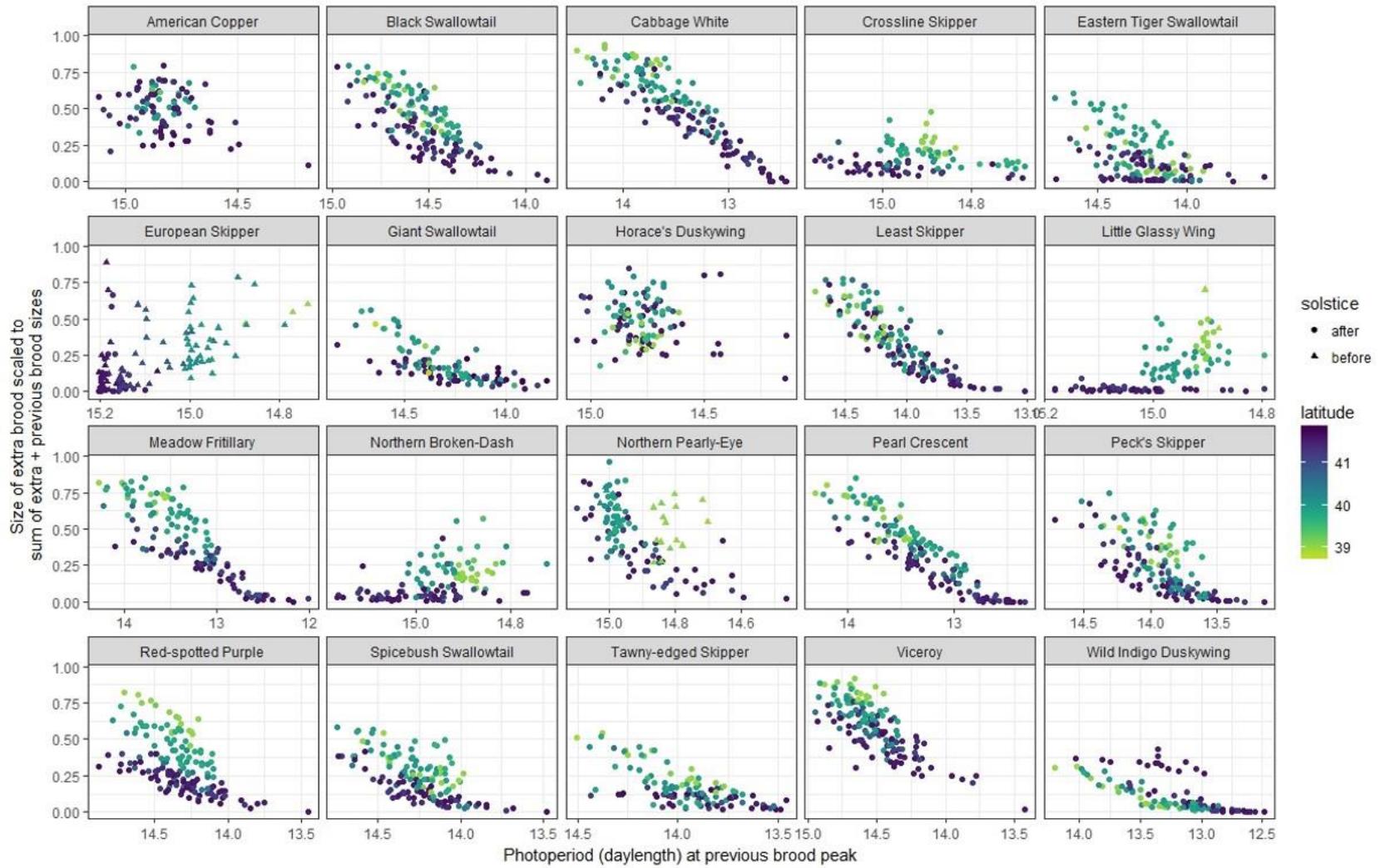
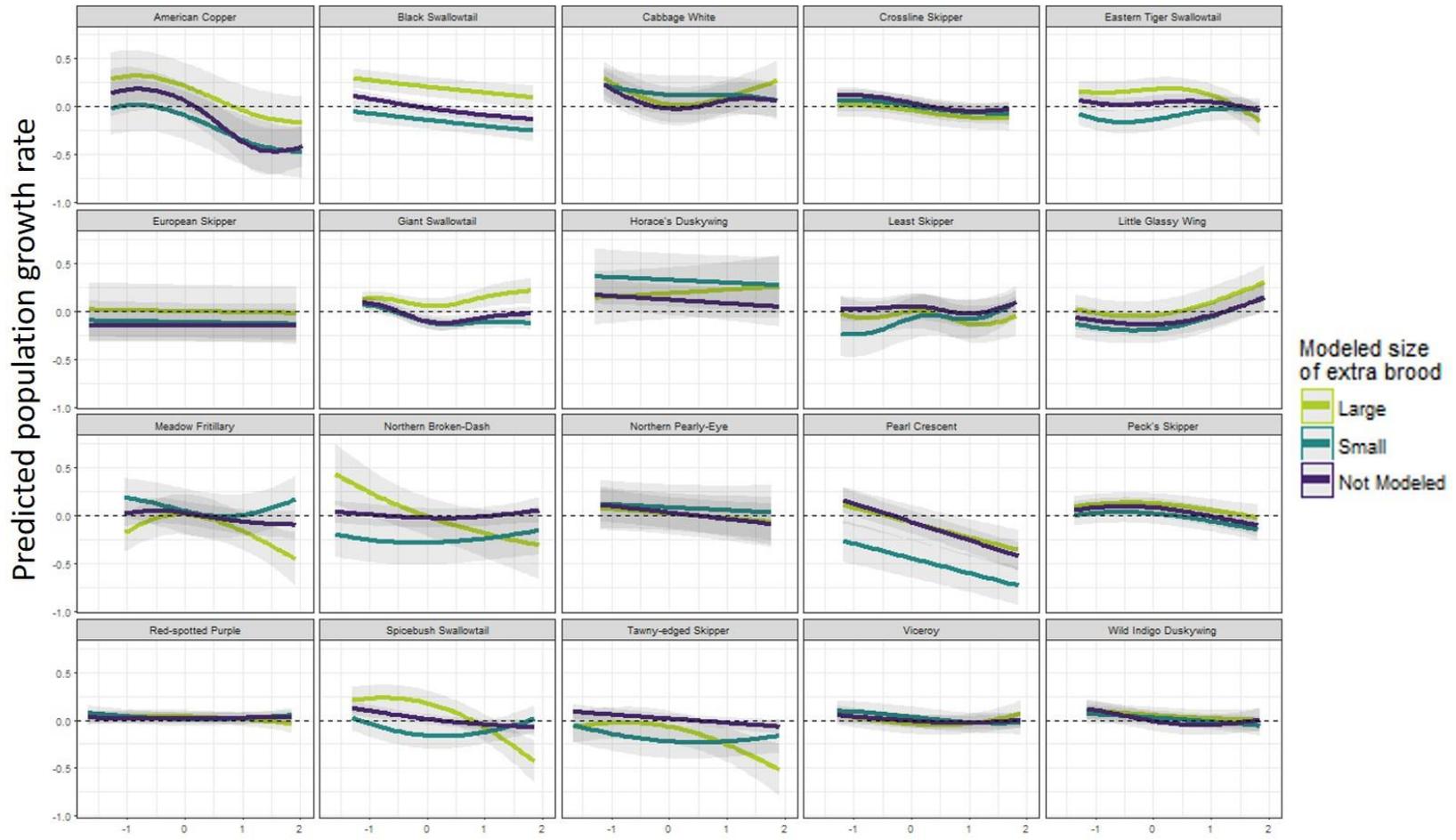


Figure 2-3: Population growth rates respond to the interaction of colder winters and last generation size. The effects of the last generation size (green and blue lines for larger and smaller, respectively) and PC3 (larger values indicate late onset, colder, and snowier years) interaction on the annual population growth rate for the 20 species' generalized additive models. PC3 values were selected as the middle 80<sup>th</sup> percentile of observed values for each species. For comparison, the purple line shows the effect of PC3 on annual growth rate if last generation size is not included in the model at all.



PC3: Larger values indicate late onset, colder, and snowier years

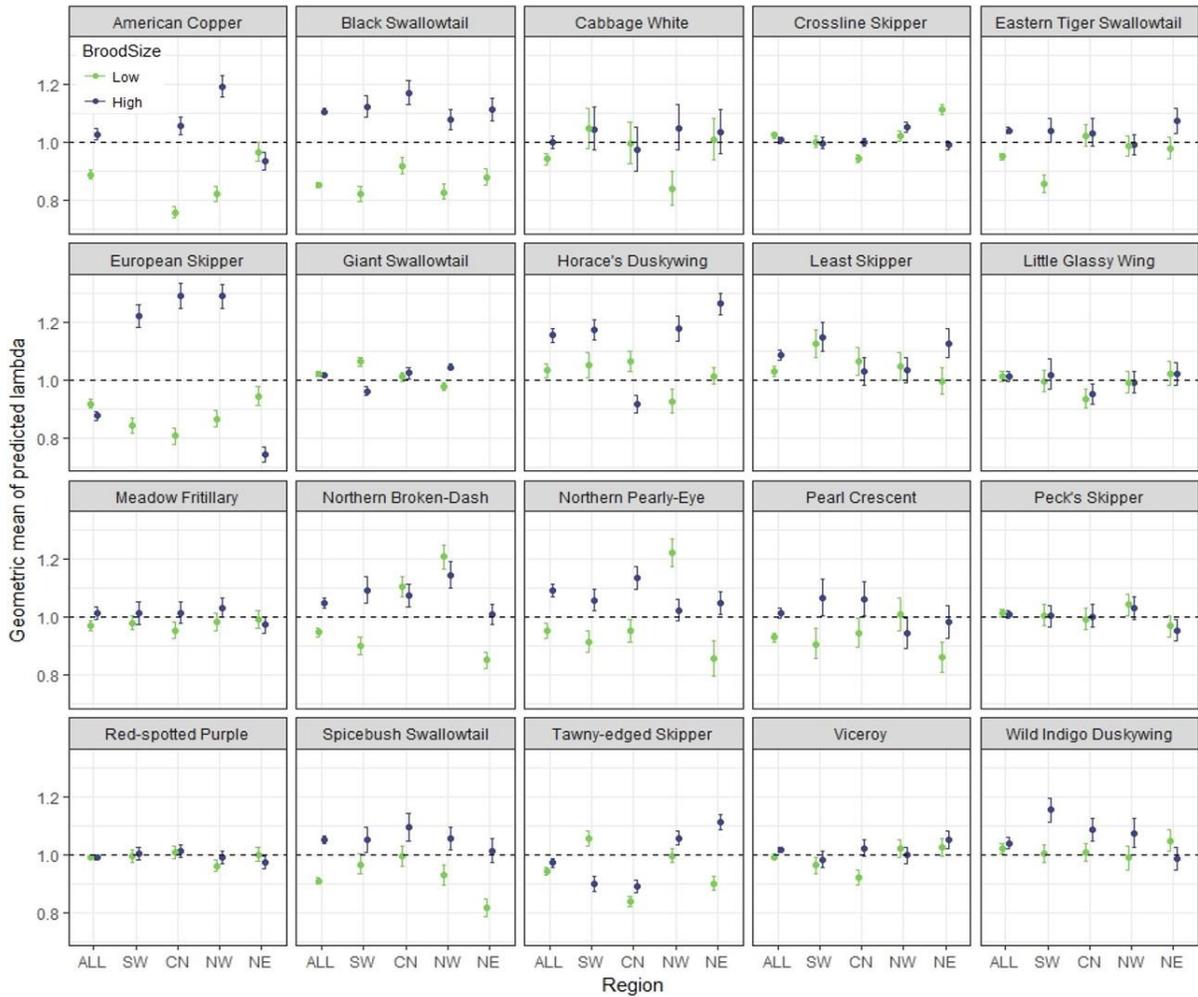


Figure 2-4: Simulated population consequences of increased voltinism. The geometric mean of annual growth rate modeled in response to winter variability across the entire state and by region (Southwest, Central, Northwest, and Northeast Ohio) when the size of the last generation (Generation Size) is larger or smaller than species-specific, regional average. Confidence intervals (95%) were calculated with the *DescTools* package (Signorell et al. 2015).

## APPENDIX

Table 2-A1: Principal components analysis to quantify winter severity. Variables of winter timing, temperature, and precipitation split into spatial and temporal variability. Numbers in bold show variable loadings that are greater than half the absolute value of the maximum loading for any principal component, which indicates important loadings (Jolliffe 2002).

Predictor	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Annual Variation Season Onset	0	<b>0.36</b>	<b>0.39</b>	0	0	0.35	<b>-0.58</b>
Annual Variation Season End	0	<b>-0.41</b>	-0.18	0	0	0.05	<b>-0.67</b>
Annual Variation Season Length	0	<b>-0.45</b>	<b>-0.35</b>	0	0	-0.20	0.02
Annual Variation Min. Temp.	0	<b>0.33</b>	<b>-0.57</b>	0	0	0.19	0.11
Annual Variation Cum. Temp. <0°C	0	<b>0.45</b>	<b>-0.31</b>	0	0	0.22	0.07
Annual Variation Snow	0	<b>-0.30</b>	<b>0.44</b>	0	0	<b>0.45</b>	<b>0.44</b>
Annual Variation Precipitation	0	<b>-0.30</b>	<b>-0.29</b>	0	0	<b>0.74</b>	0.00
Site Mean Season Onset	<b>-0.27</b>	0	0	0.09	<b>0.81</b>	0	0
Site Mean Season End	<b>0.43</b>	0	0	0.12	0.33	0	0
Site Mean Season Length	<b>0.46</b>	0	0	0.03	-0.21	0	0
Site Mean Minimum Temperature	<b>-0.43</b>	0	0	-0.30	-0.05	0	0
Site Mean Cum. Temperature <0°C	<b>-0.45</b>	0	0	-0.21	-0.04	0	0
Site Mean Snow	<b>0.35</b>	0	0	<b>-0.43</b>	<b>0.42</b>	0	0
Site Mean Precipitation	0.14	0	0	<b>-0.81</b>	-0.07	0	0
Standard deviation	2.13	1.95	1.23	1.17	0.99	0.89	0.73
Proportion of variance	0.32	0.27	0.11	0.10	0.07	0.06	0.04
Cumulative proportion of variance	0.32	0.60	0.70	0.80	0.87	0.93	0.97

Table 2-A2: Species' life-history traits. Species, host plant, and winter stage are from Iftner et al. (1992). Sample sizes, maximum number of generations, and the mean date of the penultimate generation peak come from this analysis.

Common name	Species	# Site x Year	Surveys present	Total # counted	Max # gen.	Host plant	Winter stage	Mean penult. gen. peak
American Copper	<i>Lycaena phlaeas americana</i>	226	1488	8007	3	forb	pupa	16-Jul
Black Swallowtail	<i>Papilio polyxenes asterius</i>	659	3617	9859	3	forb	pupa	23-Jul
Cabbage White	<i>Pieris rapae</i>	704	13383	236301	5	forb	pupa	24-Aug
Crossline Skipper	<i>Polites origenes</i>	189	411	915	2	gram	larva	4-Jul
E. Tiger Swallowtail	<i>Papilio glaucus</i>	700	6178	22909	3	woody	pupa	2-Aug
European Skipper	<i>Thymelicus lineola</i>	384	1273	44285	2	gram	egg	18-Jun
Giant Swallowtail	<i>Papilio cresphontes</i>	223	598	941	3	woody	pupa	30-Jul
Horace's Duskywing	<i>Erynnis horatius</i>	244	777	1918	3	woody	larva	14-Jul
Least Skipper	<i>Ancyloxypha numitor</i>	550	3939	22974	3	gram	larva	8-Aug
Little Glassy Wing	<i>Pompeius verna</i>	413	1375	7341	2	gram	larva	2-Jul
Meadow Fritillary	<i>Boloria bellona</i>	317	1161	4409	5	forb	larva	26-Aug
Northern Broken-Dash	<i>Wallengrenia egeremet</i>	332	1028	4973	2	gram	larva	5-Jul
Northern Pearly-Eye	<i>Enodia anthedon</i>	246	880	2269	2	gram	larva	27-Jun
Pearl Crescent	<i>Phyciodes tharos</i>	723	10867	138847	4	forb	larva	28-Aug
Peck's Skipper	<i>Polites peckius</i>	621	4173	20324	3	gram	larva	12-Aug
Red-spotted Purple	<i>Limenitis arthemis astyanax</i>	605	2616	5139	3	woody	larva	30-Jul
Spicebush Swallowtail	<i>Papilio troilus</i>	582	3948	19998	3	woody	pupa	2-Aug
Tawny-edged Skipper	<i>Polites themistocles</i>	294	913	1797	3	gram	pupa	10-Aug
Viceroy	<i>Limenitis archippus</i>	560	3275	12834	3	woody	larva	25-Jul
Wild Indigo Duskywing	<i>Erynnis baptisiae</i>	333	1882	12677	4	forb	larva	29-Aug

Table 2-A3: Effects of species' traits on population consequences of increased voltinism. Each trait was modeled as an univariate predictor of 20 species' simulated population consequences of increased voltinism. Categorical traits came from the literature and continuous traits came from the analysis in this study.

	<b>Estimate</b>	<b>Std. error</b>	<b>F-stat.</b>	<b>P-value</b>
Host plant (vs. Forb)			1.529	0.245
Graminoid	-0.067	0.038		
Woody	-0.037	0.041		
Winter stage (vs. Egg)			2.651	0.099
Larva	0.088	0.070		
Pupa	0.142	0.072		
Local adaptation in photoperiod	0.214	0.165	1.677	0.212
Total response to photoperiod	0.039	0.248	0.025	0.876
Cues: photoperiod and lat.	-0.125	0.079	2.511	0.131
Cues: temperature and precip.	0.225	0.330	0.464	0.504
Max # generations	0.004	0.019	0.041	0.842
Ordinal date of penultimate generation	0.000	0.001	0.021	0.886
Mean size last generation	0.217	0.103	4.439	0.049
Spatial variation in voltinism	0.161	0.448	0.129	0.723
Temporal variation in voltinism	0.673	0.380	3.132	0.094

Figure 2-A1: Local adaptation in the effect of the photoperiod cue on last generation size. For each species, the *combined effect* is the estimate from the linear model of scaled photoperiod on last generation size. *Between site means* represents the spatial effect of photoperiod variation across sites. *Within site variation* represents the temporal effect of annual photoperiod variation within sites. *Between – within* represents a test of the difference between the previous two photoperiod effects. Error bars represent 95% confidence intervals of the parameters.

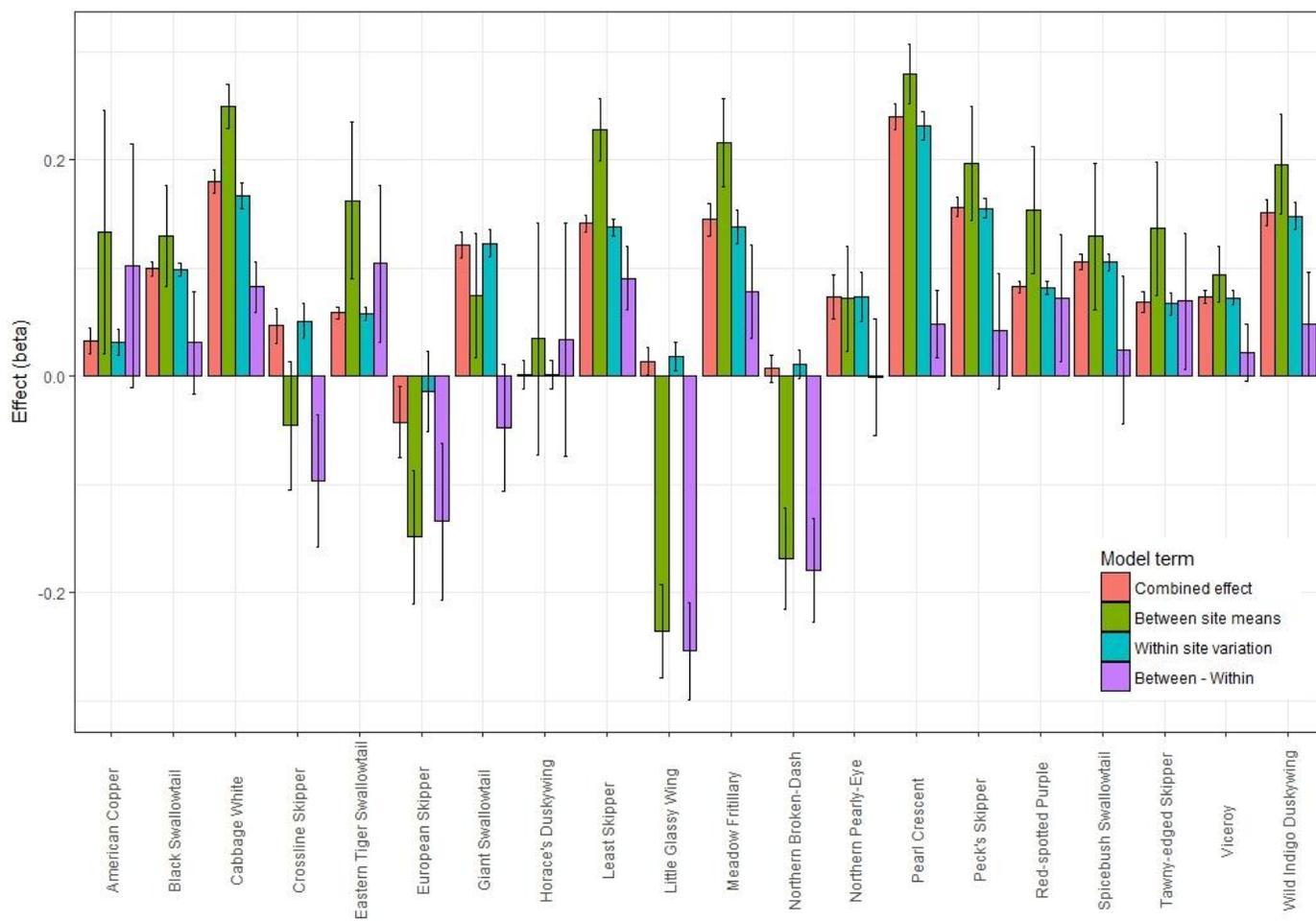
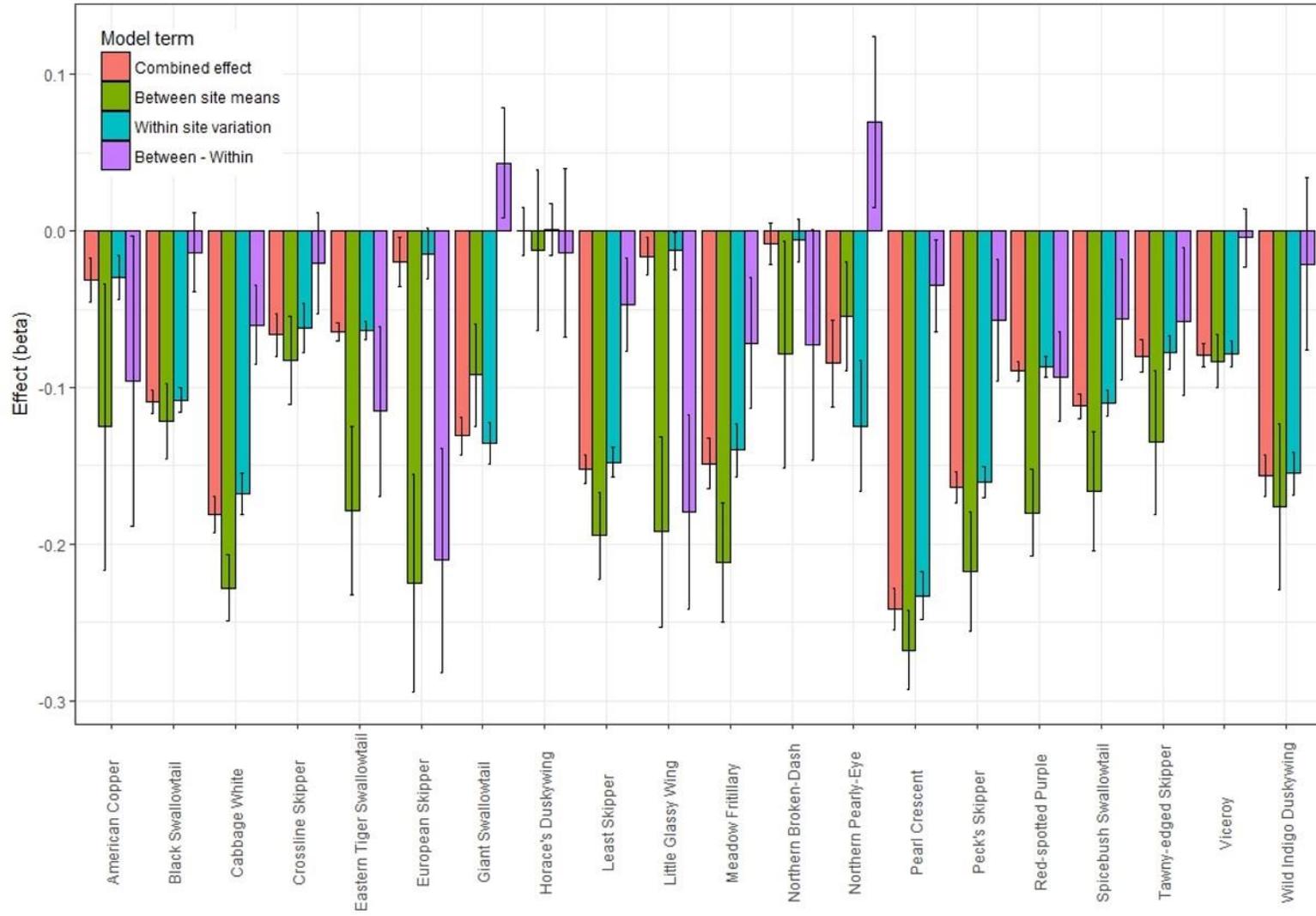


Figure 2-A2: Local adaptation in the effect of ordinal date on last generation size. For each species, the *combined effect* is the estimate from the linear model of scaled date on last generation size. *Between site means* represents the spatial effect of date of peak phenology variation across sites. *Within site variation* represents the temporal effect of annual date of peak phenology variation within sites. *Between – within* represents a test of the difference between the previous two effects. Error bars represent 95% confidence intervals of the parameters.



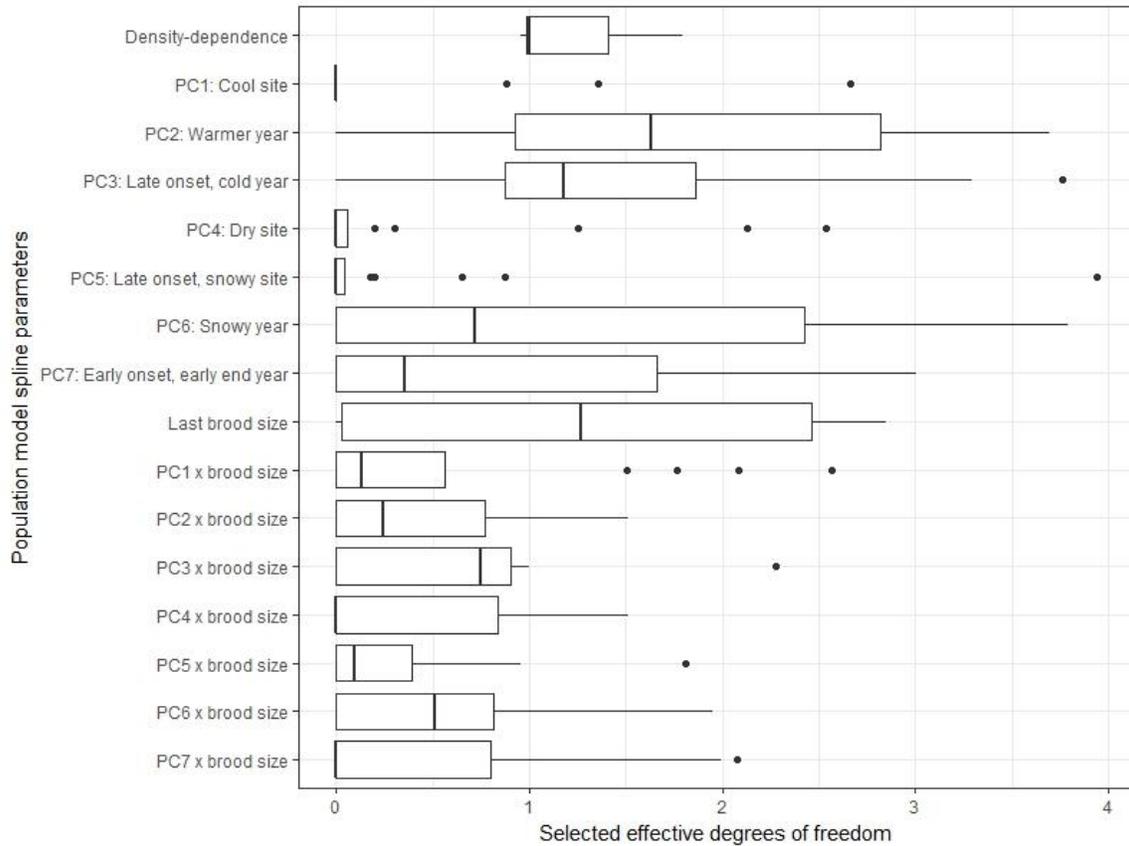


Figure 2-A3: Variable importance in species' models of population growth. For 20 species models, modeled variables were assigned effective degrees of freedom to describe their smooth terms, with zero being assigned for variables that were unimportant in the model. This box plot describes the importance of the variables from the 20 species models, with the vertical line with in the box representing the median effective degrees of freedom.

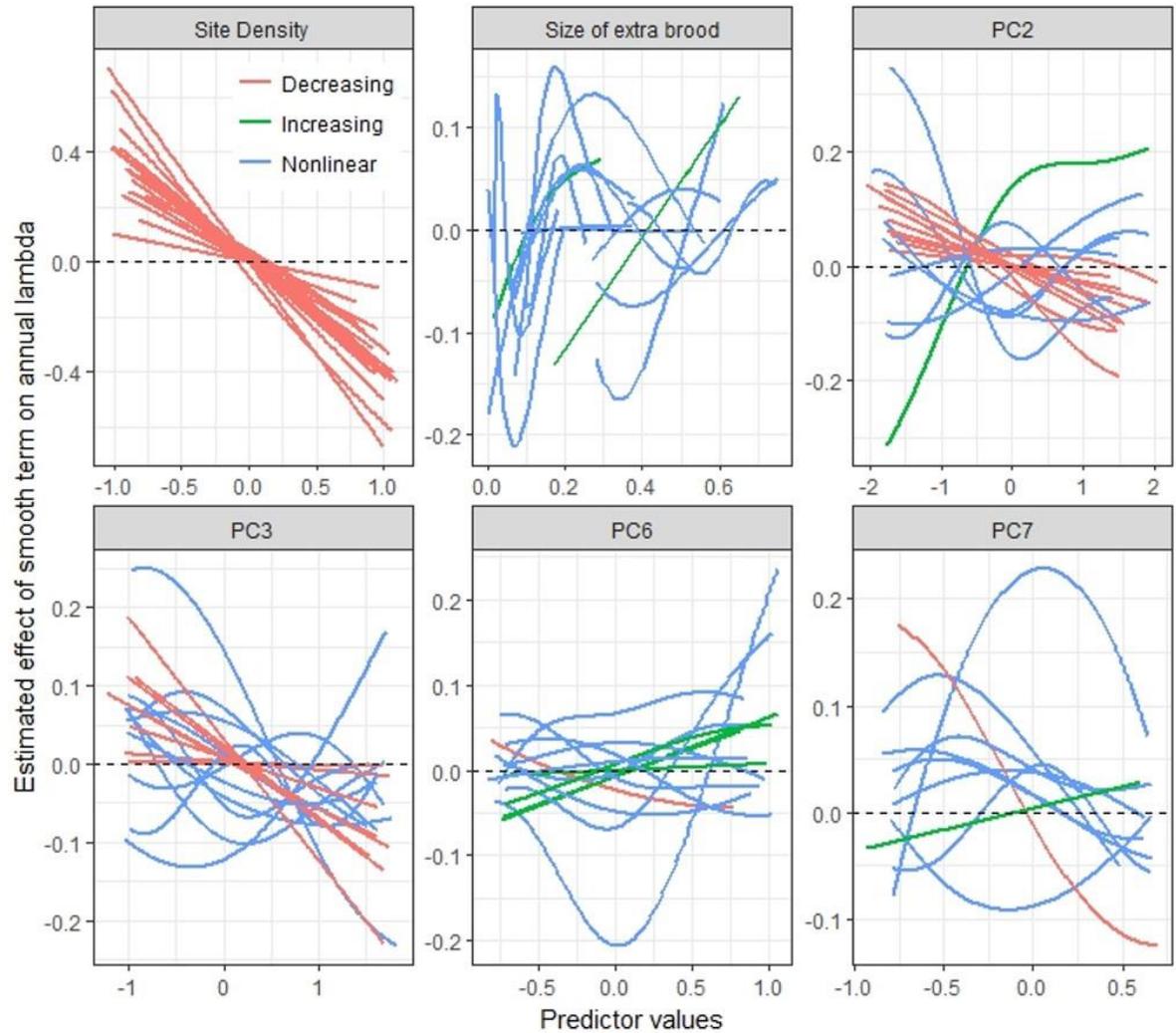


Figure 2-A4: Marginal effects of variables on species' population growth rates. The effects of different smooth terms on the annual population growth rate for the variables selected in the 20 species generalized additive models. Predictor values were selected at one standard deviation from the mean for each species. Colors of the lines indicate whether they are monotonically increasing, decreasing, or nonlinear. These plots do not include interaction terms even though they were potentially in the species model as well.

### **CHAPTER 3: Butterflies have higher population growth rates with later springtime phenology relative to plant green-up phenology**

#### **ABSTRACT**

Climate change may disrupt species interactions if their respective sensitivities to climate variability and environmental cues leads to asynchronous changes in phenology, the timing of life history events. It is often predicted that these phenological mismatches will correspond with negative demographic consequences and evolutionary change to maintain temporal overlap of interacting species. Host plant-insect herbivore interactions are a key system for studying phenological mismatches, as both taxa have responded to climate change with phenological shifts. In this chapter, I compare the rates of change in phenology of springtime plant green-up and 36 butterfly species in response to annual climate variability and landscape characteristics. I then test for demographic changes in butterfly populations in response to plant green-up, phenological mismatches, and density dependence. Plants and butterflies have different sensitivities to spatial and temporal climate variability and land-use around sites. Butterflies showed less annual variation in their phenology than plant green-up and the degree of phenological mismatches varied across years. Butterfly population growth between generations is higher following later plant green-up and when butterfly phenology is later than expected. Much of the variation between species' responses can be explained by voltinism. These results contrast with studies arguing that earlier emergence is beneficial for butterflies or that butterfly population growth is maximized when phenological shifts between trophic levels are synchronized. I conclude that consequences of phenological

mismatches, in terms of population growth rates, are not generally detrimental across a community of butterflies with a range of emergence times.

## **INTRODUCTION**

Global climate change alters the strength of species interactions in addition to its direct effects on species' development, fitness, and range limits (Parmesan 2006; Tylianakis et al. 2008). These indirect effects of climate change may be as important as direct effects in determining species' vulnerability to extinction (Gilman et al. 2010; Cahill et al. 2012). As species interactions require temporal overlap, much of the change in species interaction strength is due to phenological shifts (Yang and Rudolf 2010). Phenological shifts in the timing of life history events are a general effect of climate change common across taxa that respond to the direct effects of temperature on development rate (Fitter and Fitter 2002; Parmesan 2006; Thackeray et al. 2016). If phenological shifts between interacting species or trophic levels are asynchronous, mismatches in timing may have fitness and demographic consequences (Cushing 1990; van Asch and Visser 2007; Reed et al. 2013b). In this chapter, I test how the phenology of plants and butterflies shift in response to climate variability and whether mismatched responses affect butterfly demography in resource-consumer species interactions.

It is difficult to predict how interactions will respond to climate change as each species' phenology responds to temperature-dependent development rates, environmental cues, and winter diapause strength (Visser et al. 2010; Forrest and Thomson 2011; Forrest 2016). Potential for phenological mismatches is often diagnosed by comparing sensitivities to

climate variation, for example, in terms of days of shifted phenology per degree of warming (Thackeray et al. 2010; Polgar et al. 2014; Kharouba and Vellend 2015). Plant phenology generally shifts earlier to a greater degree than insect phenology in response to warming, altering resource availability for the consumer (Forrest and Thomson 2011; Kharouba and Vellend 2015; Thackeray et al. 2016). However, a review of plant-pollinator phenological mismatches concluded that synchrony has been maintained in long-term, observational studies (Forrest 2015). Even if sensitivities can predict the timing of species interactions, multi-species studies show a range of phenological responses within trophic levels (Roy and Sparks 2000; Calinger et al. 2013; Kharouba et al. 2014) and insects are projected to become more sensitive to future warming than plants in the UK (Thackeray et al. 2016). It is still unclear how different sensitivities, averaged across years and sites, relate to variation in temporal overlap between insects and plant resources within a given year or to impacts of phenological mismatches on consumer demography.

Most studies of phenological mismatches assume that greater temporal overlap leads to higher level of species interaction and, in the case of host plant-herbivore relationships, to higher population growth rates for the consumer with negative effects of being either too early or too late (Johansson et al. 2015). Demographic consequences of phenological mismatches have been demonstrated for pairs of interacting species and simple food webs with experiments and long-term studies (Both et al. 2009; Posledovich et al. 2015; Lany et al. 2016; Uelmen et al. 2016). Negative consequences of mismatches often are not as simple as the consumer being early or late, and may depend on how early in the spring interactions take place or on how intraspecific competition for seasonally-varying resources changes with

density-dependent effects (Reed et al. 2013a; Bewick et al. 2016). Not all herbivores benefit from matching their host plant phenology as expected in the basic match-mismatch model (Johansson et al. 2015), as fitness is determined by the product of vital rates which may have different responses to phenological synchrony (Singer and Parmesan 2010). Pairing annual variation in phenological mismatches with corresponding demographic responses could demonstrate how important this mechanism may be for driving species declines compared to the direct effects of climate change (Forrest 2015). Long-term demographic data sets can be combined with landscape-level plant phenology measured with remote sensing to test for consequences of mismatches at larger scales (Foster et al. 2013; Cole et al. 2015).

Although case studies show fitness and demographic costs to phenological mismatches, it is not known how an entire community of insects responds to phenological asynchrony. In this study, I combine long-term monitoring of butterflies with remote sensing phenological observations to test for phenological mismatches and demographic consequences. This approach summarizes annual phenological variation of plant leaf-out phenology and compares it with population-level butterfly phenology and abundance changes for 36 species. I first test whether plant and butterfly phenology differs in their sensitivity to winter and spring climate variability. I then quantify the variation in the mismatch between leaf green-up and peak butterfly phenology between years and across sites. I model the consequences of phenological mismatches in population models of butterfly growth rates. Finally, I test if species' life-history traits predict which species have larger demographic consequences following phenological mismatches.

## METHODS

### *Butterfly abundance and phenology*

Butterfly counts have been collected by volunteers organized by the Ohio Lepidopterists ([ohiolepidopterists.org](http://ohiolepidopterists.org)) since 1996 using weekly Pollard walks (Pollard and Yates 1994). I selected species for which abundance and phenology estimates could be made for separate generations as detailed in Chapter 1. After excluding species with less than 50 site x year population estimates, I used 36 species (16 univoltine, 20 multivoltine) for this analysis. I used all available years in the analysis of butterfly phenological sensitivity, but only 2001-2014 for other analyses where these data were used in conjunction with plant phenology data. Species names and life history traits are followed according to Iftner et al. (1992)

### *Land surface phenology*

I used two different remote sensing products that measure the onset of springtime phenology of plants by tracking spectral changes in light reflected by plants during the onset of photosynthesis (Zhang et al. 2012). From the USGS, I used the “start of season” NDVI metric from the eMODIS remote sensing phenology product with 250-meter resolution ([doi.org//10.5066/F7PC30G1](https://doi.org/10.5066/F7PC30G1)) processed to remove observation noise and smoothed temporally to derive the timing of vegetation change (Swets et al. 1999). From the NASA LP DAAC, I used the “Increase” EVI metric from the V005 MODIS Land Cover Dynamics (MCD12Q2) product with 500-meter resolution downloaded with the MODIS Reprojection Tool (Dwyer and Schmidt 2006). For each product, I extracted the terrestrial raster cells within 250-meter to 8000-meter circular buffers around the 141 butterfly monitoring sites

and took a weighted average of their values to obtain the ordinal date of green up phenology at each site from 2001-2014. I compared these two products, across spatial scales, by the correlations between their estimates for each site x year and the distributions of their estimates for each year.

#### *Land-use/land cover*

Land-use or land cover affects plant and butterfly phenology through changes in species composition and land cover effects on temperature (White et al. 2002; Diamond et al. 2014). It also changes the observation biases in land surface phenology measured with remote sensing, by altering the spectral characteristics of the landscape (Melaas et al. 2016; Zipper et al. 2016). I used the NLCD 2006 product derived from 30-meter resolution Landsat data that classifies land cover into 16 classes (Fry et al. 2011). Raster cells in buffers (250-meter to 2000-meter radius) around each butterfly monitoring site were extracted and summarized as percent cover. I scaled these compositional data by centered log ratios and performed a principal components analysis to reduce the number of variables and determine how land cover classes contributed to differences between sites (Aitchison 1982; Cade 2015). I used the top four principal components accounting for 90% of the variation between sites in subsequent analyses (Table 3-A1).

#### *Climatic variables*

I quantify spatial and temporal variation in winter and spring temperature, and the timing of seasonal change based on 1-kilometer resolution, daily weather interpolations at each monitoring site from the Daymet product produced by Oak Ridge National Laboratory (Thornton et al. 1997; Thornton et al. 2014). I average the mean daily temperature, mean

daily snow fall, and mean daily precipitation over the winter and spring seasons. I estimated the onset and end of winter as the ordinal date when the predicted daily minimum temperature crossed 0°C in a generalized additive model of daily minimum temperatures in response to a smooth variable of ordinal date (Wood 2006). These environmental variables were scaled to account for spatial and temporal variation (between sites and between years) and reduced with a principal components analysis to create new, uncorrelated variables for analysis (Jolliffe 2002). The top five principal components accounting for 77% of the variation across sites and years were used in subsequent analyses (Table 3-A2).

I calculated cumulative degree days using a lower threshold of 0°C from the Daymet daily temperature interpolations for the ordinal dates of estimated plant and butterfly phenology (Moore and Remais 2014). Although growing degree days for butterflies are typically calculated with a higher base temperature (Cayton et al. 2015), plant phenology occurred early in the season so that a lower base temperature was needed to prevent zero truncation of the distributions.

### *Statistical analysis*

All statistical analyses were performed in R 3.3.2 (R Core Team 2016). Code is archived in a public repository ([github.com/tysonwepprich/phenmismatch](https://github.com/tysonwepprich/phenmismatch)).

### *Sensitivities of plant and butterfly phenology*

I analyzed how the observed timing of plant and butterfly phenology responds to climatic variation across space and time and land-use around monitoring sites. I used both ordinal date and degree days in separate models to see if scaling by absolute or physiological time better predicted phenological responses. I used the five climatic variables and four land-

use variables described above. For plant phenology, I modeled green up measured by NDVI and EVI separately in response to these predictors with random intercepts of site and year using linear mixed effects models in the *lme4* package (Bates et al. 2014). For butterfly phenology, I used similar models plus random intercepts and slopes by species to quantify the community wide sensitivity as well as variation between species' responses (Nice et al. 2014). For land-use predictors and the plant phenology response variables, I varied the spatial scale at which they were summarized from satellite products to test whether results were robust to changes in scale.

### *Phenological mismatches*

The observational data measures adult butterfly flight and plant green-up phenology at the landscape scale as a proxy for the species interactions between butterfly larva and their host plants. I assume the annual variation in the species interaction of interest is correlated with the annual variation in the remote-sensing proxy within a growing season. In multiple studies the order of leaf-out phenology among species is consistent in years with early or late phenology (Herms 2004; Morin et al. 2009; Panchen et al. 2014). This means that annual variation in landscape green-up will likely correlate with phenological variation in host plants leaf-out phenology later in the season. However, the reliability of this proxy for leaf-out phenology of individual plant species may change across sites, as remote sensing phenology depends on variation in plant species composition and land cover (Shustack et al. 2009; Melaas et al. 2016). For this reason, I scale plant phenology by site to use annual anomalies to quantify whether plant phenology is relatively early or late in a given year for each site. Mismatches were scaled by both ordinal date and growing degree days for comparison.

Butterfly phenology is correlated between life stages, so adult flight phenology provides a proxy for larva phenology. The sensitivity analysis did not show a community wide response to land-use, so butterflies were not scaled by site as done for plant phenology. The butterfly monitoring data also had gaps in data collection for some sites and years, so I scaled butterfly phenological variation by regional mean rather than by site. This provides a measure of annual anomalies in butterfly phenology that accounts for local adaptation in mean phenological timing of different regions.

I quantified mismatches between the annual responses of plant and butterfly phenology as the residuals from linear regression models of plant phenological anomalies predicting butterfly phenological anomalies for each species (Lany et al. 2016). Using model residuals to quantify the phenological mismatch provided a variable uncorrelated with plant and butterfly phenology, which aids in statistical modeling. An alternative method to quantify mismatch as the absolute difference in plant and butterfly phenology was highly correlated with plant phenology and had high variance inflation factors values when included in population models.

I modeled the community wide effects of winter and spring weather on phenological mismatches between butterflies and plants using a mixed effects model similar to those used for sensitivity. Only the three climate principal components corresponding to annual variation were included because the mismatches were quantified as annual anomalies to remove the effects of spatial variation between sites.

### *Demographic responses to phenological mismatches*

I modeled how butterfly population growth rates respond to plant phenology, mismatches between butterfly and plant phenology, and density dependence. For univoltine species, I calculated the annual population growth rate as the natural logarithm of population estimates between years. Some univoltine species have partial second generations, as detailed in Chapter 2, which could affect the annual growth rate. I excluded the sites and years where species' extra generation sizes exceeded 25% of the total annual estimated size. Univoltine species' demography could be affected by phenology in either the current year or the previous year. I chose to only include the current year mismatch so that the species could be modeled concurrently with multivoltine species. For multivoltine species, I calculated the population growth rate between the first two generations within the same monitoring season as the difference of the natural logarithms of population estimates.

I used a linear mixed effects model using the *lme4* package (Bates et al. 2014) to model population growth rates in response to density-dependence (previous generation size scaled by site and species), annual anomaly in plant phenology, linear and quadratic effects of mismatches, and the interactions between plant phenology and mismatches. Random intercepts vary by site, year, and species. Random slopes for each predictor vary by species, accounting for individual differences while predicting a community wide response (Nice et al. 2014). I performed this analysis with butterfly and plant phenology in terms of either degree days or ordinal date.

### *Species traits*

I used a linear model to test if species' life history traits correlated with estimated responses in the community model of population growth in response to phenological mismatches. I performed a PCA on the estimated coefficients of the community model to identify which coefficients explain the variation in species responses (Diamond et al. 2014). The principal components were then used as a response variable in a linear model with host plant category (graminoids, forbs, or woody), voltinism (univoltine or multivoltine), and mean date of peak butterfly phenology. I used traits in tests of the hypotheses that: (1) temporal windows of higher host plant quality vary between categories, with forb host plants providing higher-quality resources for a longer time to minimize the effect of mismatch (Cizek et al. 2006); (2) mismatches will be more negative for univoltine species (Knell and Thackeray 2016); and (3) the consequence of butterfly phenology being early or late may depend on how early in the season they emerge with potential exposure to mortality-increasing cold temperature (Singer and Parmesan 2010).

## **RESULTS**

### *Sensitivities of plant and butterfly phenology*

Winter and spring climate variability and the surrounding land-use affects the phenology of plants and butterflies with key differences (Table 3-A3 for results of 6 models). In general, warmer sites (PC1), warmer years (PC2), and warmer springs (PC5) cause butterfly phenology to be earlier in terms of ordinal date, but later in terms of degree days (Figure 3-1). Plant phenology, in terms of start of season green-up, has different sensitivities

than the butterfly community and between the two remote sensing products (Figure 3-1). Land-use around monitoring sites has no effect on the average butterfly phenological sensitivity, but a large effect on both measures of plant phenology. Greater agricultural (PC1) or urbanized (PC2) land-use accelerates the green-up phenology measurements.

The two plant phenology products differ in their estimates of green-up phenology and vary depending on the scale used to summarize phenology around each site (Figure 3-2). The two products, EVI and NDVI, have stronger correlations between their estimates for each site  $\times$  year when scaled by degree days compared to ordinal date (0.46 and 0.35, respectively, at 8000-meter buffer scale) and when phenological estimates are derived from larger spatial buffers around each site (0.34 for 500-meter and 0.46 for 8000-meter scaled by degree days). Correlations between the two products greatly improve when site effects are removed by scaling phenology estimates as the annual anomalies from each site mean (0.66 and 0.59 for degree day and ordinal date, respectively, at 8000-meter buffer scale). The EVI phenology estimate for green-up occurs earlier than the NDVI estimate and its distribution was frequently zero truncated on the degree-day scale. For this reason, I present results from the NDVI product at a 2000-meter spatial scale.

Butterfly sensitivity model coefficients did not vary substantially with the spatial scale of land-use buffers. I present results using 500-meter buffers, as models with this land-use scaling have slightly lower AIC than other spatial scales (results not shown).

### *Phenological mismatches*

All butterfly species show less variation in annual phenology than plant green-up phenology in terms of degree days. The best fit linear models of the effect of plant phenology

on butterfly phenology have slopes shallower than the 1:1 line, which would indicate equal annual phenology responses (Figure 3-3). Scaling phenology by ordinal date gives similar results (Figure 3-A1). The relationship between plant and butterfly phenology without scaling is highly dependent on spatial variation (Figures 3-A2 and 3-A3), compared to that derived from annual anomalies of phenology for each site (Figures 3-3 and 3-A1).

The phenological mismatch, defined as the residual from the linear model predicting the anomaly in butterfly phenology from the anomaly in plant phenology, varies with annual climate variability (Table 3-2). There is no effect of years that are warmer and wetter across both winter and spring (PC2), suggesting a similar response for butterflies and plants. A warm winter with the later end (PC4) delays butterfly phenology more than expected and a later winter onset with a cooler spring (PC5) accelerates butterfly phenology more than expected. Models with scaling by degree days or ordinal date show similar results (Table 3-2).

#### *Demographic responses to phenological mismatches*

The butterfly community has higher population growth rates when plant phenology is later and when the phenological mismatch is larger (i.e. butterfly phenology is later than predicted). Nonlinear and interaction terms differ in their statistical significance between the models scaled by degree days and ordinal date, but the overall effects are relatively weak (Table 3-3). In both models, negative density dependence has the strongest effect on population growth rate. Species vary in their estimated model parameters, and some show interactions in which later phenological mismatches lead to higher growth rates only when plant phenology is also late (Figure 3-4).

### *Species traits*

Butterfly voltinism explains most of the variation between species in the population growth model. In the principal components analysis of species' coefficients, differences in the intercept and density dependence explained 93% of the variation between species coefficients. Linear models of traits explaining these principal components showed that voltinism groups the species into univoltine species with smaller intercepts and greater density dependence versus multivoltine species with larger intercepts and less density dependence (Figure 3-4). The coefficient for the linear effect of butterfly mismatches on butterfly growth rates loads onto the third principal component, which explained 6% of the variation. Consuming graminoid host plants correlated with a positive effect of the butterfly mismatch on population growth, with higher population growth when butterfly phenology is later than expected.

## **DISCUSSION**

Different sensitivities of plant and butterfly phenology to climate variability lead to asynchronous shifts in timing, but do not necessarily translate into phenological mismatches with negative consequences. Phenological mismatches do not reduce population growth rates across a community of butterflies with a range of emergence times. These results do not fit with the match-mismatch model where an asynchronous change in either direction negatively impacts resource availability for consumers (Miller-Rushing et al. 2010; Johansson et al. 2015). However, butterfly population growth rates are higher when the start of spring, measured by plant green-up, is later. These negative demographic consequences of earlier

plant phenology, regardless of the extent that butterflies track the change, may also be a concern when predicting potential responses to anthropogenic climate change.

This study differs from others, in that I model population responses across an insect community with a range of life-history traits rather than focusing on species phenology occurring early in the spring (Both et al. 2009; Reed et al. 2013a; Posledovich et al. 2015). Many features of species' life histories may alter the expected predictions of demographic consequences for phenological mismatches (Johansson et al. 2015). Early-season phenology across taxa changes more quickly in response to climate variation (Diamond et al. 2011; Calinger et al. 2013); so these species may be more vulnerable to phenological mismatches and declines due to climate change. Most species in this study are abundant and many are host plant generalists, making phenological mismatches less of a concern (Miller-Rushing et al. 2010). Some species in this study emerge early in the spring, when phenological mismatches are predicted to be consequential, but this species trait did not impact the variation in responses between species in the population models. For some species responses, interactions between plant phenology and expected butterfly phenology fit show that delayed butterfly phenology has more negative impacts on population growth rates when plant phenology is early (Figures 3-4).

Phenological mismatches can cause higher population growth due to intraspecific interactions, diverging from the classic match-mismatch model (Johansson et al. 2015). Even though there may be directional selection for earlier phenology in consumers to match resources, population growth rates may be unaffected by mismatches (Reed et al. 2013a). Density-dependent population regulation may buffer growth rates in years with high

phenological mismatches if limited reproduction due to a lack of resources leads to relaxed competition (Reed et al. 2013a). Models of host plant-butterfly interactions corroborate that intraspecific competition changes with the level of phenological matching with resources (Bewick et al. 2016) and individual butterflies emerging before or after the peak phenology have higher fitness (Revilla et al. 2014). Density dependence has the strongest effect on population growth rate for butterflies (Table 3-3) and may explain the unexpected results that later butterfly phenology is better than matching changes in plant phenology. Strong negative density dependence could benefit butterflies against future phenological mismatches by slowing population declines and increasing the odds of evolutionary change tracking environmental changes (Reed et al. 2015).

Region-specific climate variability and its future changes may play a role in how species interactions become decoupled. Asynchronous phenological shifts are expected if interacting species respond to different cues and seasons have heterogeneous changes in climate, but it is unclear if this is a necessary condition for phenological mismatches (Straile et al. 2015). Because consumers receive imperfect information from cues about resource phenological variation, they are modeled to respond insufficiently to resource phenology changes even under homogeneous warming across seasons (Gienapp et al. 2014). My results suggest that butterfly phenology is less responsive than green-up phenology to annual variation in climate conditions. Models of mismatch magnitude in this study demonstrate larger effects of climate variables that show diverging climate conditions between seasons (PC4 and PC5, Table 3-2) rather than the climate variable representing warmer conditions across both winter and spring (PC2). It is not known if butterflies in this study are using

different cues than plants or have different physiological requirements that lead to different sensitivities to climate variation. When the goal is to predict future synchrony, models of phenological mismatches between interacting species should consider if cues differ and how climate sensitivity across seasons may vary between species (Thackeray et al. 2016).

I found that voltinism divides species responses in population models, with univoltine species having stronger negative density dependence and lower population growth rates. Univoltine species growth rates were modeled on an annual basis between generations, while multivoltine species growth rates were modeled between generations within the growing season. Most multivoltine species in this study are more abundant later in the season, explaining their higher average population growth rates. Host plant category explained a small part of species variation in their population responses to mismatches. Eating graminoid plants correlated with a larger benefit of later butterfly phenology, which does not support the hypothesis that the quantitative plant defenses in graminoids would limit butterfly growth (Cizek et al. 2006). It could be that phenology of graminoids is less correlated with the variation in green-up phenology measured by remote sensing, which could be dominated by the canopy in forests.

Although population growth increases after later butterfly phenology, other unmeasured demographic effects may alter the long-term phenological response that would maximize fitness. For example, phenological mismatches interact with temperature conditions and host plant to drive larval performance (Posledovich et al. 2015). One consequence of later butterfly phenology that is not captured in immediate population growth rate could be decreased likelihood of adding an extra generation late in the season. I have

found that extra generations generally increase population growth rates for butterflies in this study system (Chapter 2). However, if later phenology provides a better match to host plant quality, developmental rates may be optimized and enable an extra generation (Scriber 2002). Negative effects from faster developmental rates enabled by warmer temperatures may emerge at a time lag from the mismatch if subsequent generations have smaller body sizes and lower fecundity (Nylin and Gotthard 1998).

Butterfly monitoring of adult flight and remote sensing of land surface green-up phenology are both imperfect proxies for the host plant-herbivore species interaction that may become mismatched with asynchronous responses to climate change. The correlations between the phenological responses in this study to the actual timing of host plant quality and caterpillar feeding are unknown. Some plant species' leaf-out phenology can be accurately predicted from land surface phenology, but this requires validation with on the ground observations, in person or via camera (Melaas et al. 2016). I take a cautious approach in this study by using annual anomalies at each site for plant and butterfly phenology to avoid unmeasured causes of phenological differences that vary across sites. Future studies should take finer scale approaches to demonstrate the impact of asynchrony in specific butterfly-host plant interactions.

This study combines two modes of data collection that have greatly expanded the extent and resolution of phenological observations: volunteer, citizen science monitoring and remote sensing (Sagarin and Pauchard 2012). This study is one of the first to look at a whole community of insects and their responses to phenological mismatches, which is valuable for demonstrating general patterns. The shared responses across species suggest that synchrony

between trophic levels is not necessary to maximize consumer population growth rates.

However, if butterflies have higher population growth rates when plant phenology is later

and when butterfly phenology is later than expected, there may be negative consequences of

accelerated phenology due to climate change regardless of phenological mismatches.

Table 3-1: Effect of annual climate variation on phenological mismatches. A linear mixed effects model of three climate principal components representing annual variability predicts the size of the mismatch between the butterflies observed and expected phenology. A positive coefficient represents that the variable results in later butterfly phenology than expected.

	Scaled by ordinal date			Scaled by degree days		
	<i>B</i>	<i>CI</i>	<i>p</i>	<i>B</i>	<i>CI</i>	<i>p</i>
<b>Fixed effects</b>						
Intercept	0.01	-0.32 – 0.35	.936	-0.00	-0.30 – 0.30	.992
PC2: Cold/wet winter and spring	0.02	-0.02 – 0.07	.328	-0.03	-0.07 – 0.02	.243
PC4: Warm/wet winter with late end	0.08	0.05 – 0.11	<.001	0.07	0.04 – 0.10	<.001
PC5: Late winter onset, cooler spring	-0.11	-0.16 – -0.07	<.001	-0.16	-0.20 – -0.11	<.001
<b>Random effects</b>						
$\sigma^2$		0.353			0.355	
$\tau_{\text{Site}}$		0.042			0.036	
$\tau_{\text{Species}}$		0.006			0.006	
$\tau_{\text{Year}}$		0.404			0.315	
Observations		9287			9287	
Marginal / Cond. $R^2$		0.03 / 0.58			0.05 / 0.54	

Table 3-2: Effects of phenological mismatches on population growth rates. To linear mixed models predict the population growth rates between generations for all species. The fixed effects show the shared responses across species, while the random effects show differences in intercepts for species, sites, and years.

	Scaled by ordinal date			Scaled by degree-day		
	<i>B</i>	<i>CI</i>	<i>p</i>	<i>B</i>	<i>CI</i>	<i>p</i>
<b>Fixed effects</b>						
Intercept	0.25	0.11 – 0.39	<.001	0.26	0.11 – 0.40	<.001
Density-dependence (scaled $N_{t-1}$ )	-0.23	-0.28 – -0.18	<.001	-0.23	-0.28 – -0.18	<.001
Plant anomaly	0.07	0.04 – 0.10	<.001	0.06	0.03 – 0.09	<.001
Mismatch	0.13	0.09 – 0.17	<.001	0.12	0.09 – 0.16	<.001
Mismatch <sup>2</sup>	0.02	0.01 – 0.04	.012	0.01	-0.01 – 0.03	0.255
Plant anomaly x Mismatch	0.03	0.01 – 0.06	.007	0.01	-0.01 – 0.03	0.415
Plant anomaly x Mismatch <sup>2</sup>	-0.00	-0.01 – 0.01	.746	0.00	-0.01 – 0.02	0.516
<b>Random effects</b>						
$\sigma^2$		0.232			0.232	
$\tau_{\text{Site}}$		0.018			0.017	
$\tau_{\text{Species}}$		0.118			0.117	
$\tau_{\text{Year}}$		0.022			0.030	
Observations		9287			9287	
Marginal / Cond. $R^2$		0.11 / 0.50			0.12 / 0.51	

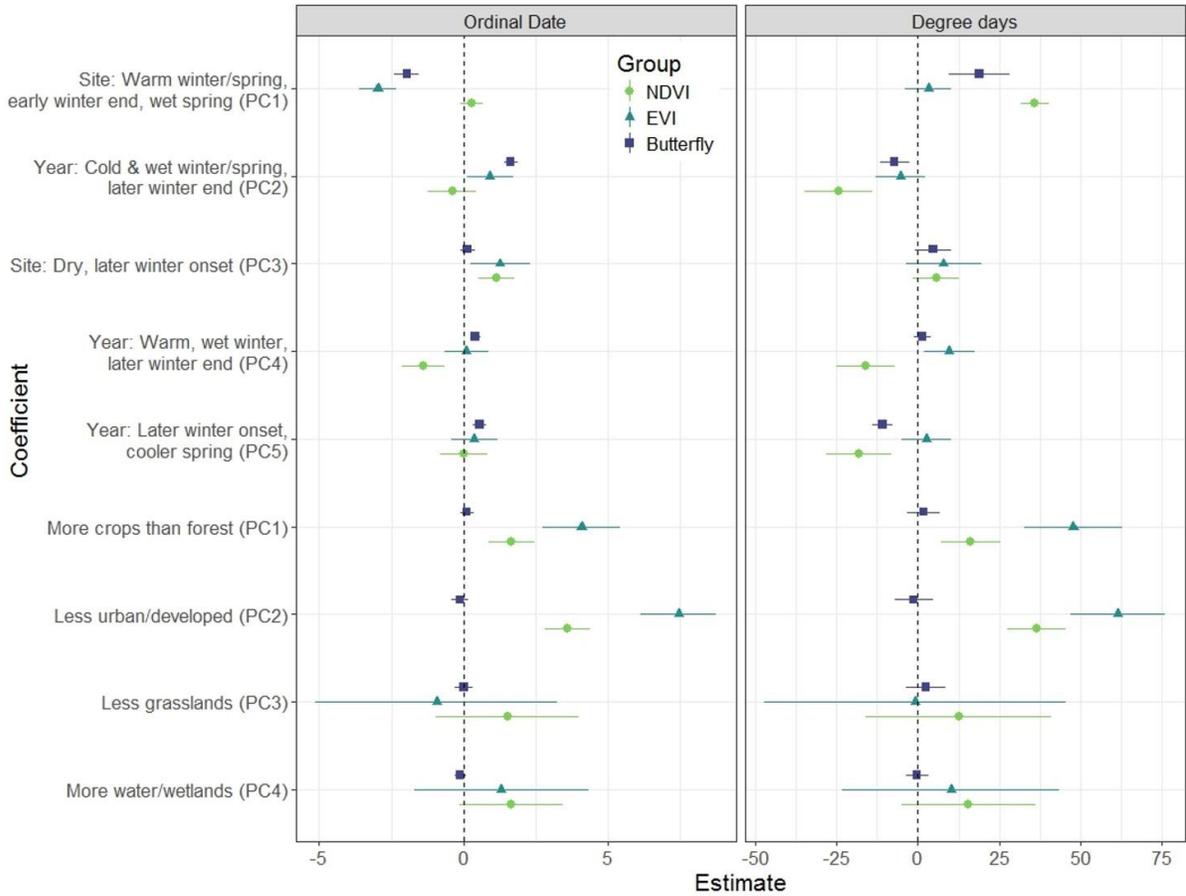


Figure 3-1: Sensitivity of plant and butterfly phenology to climate and land-use. Coefficients estimated from linear mixed effects models of phenology, scaled by ordinal date or degree days, for 36 butterfly species' mean response, NDVI green-up, or EVI green-up. Lines show 95% confidence intervals for the coefficient estimates. Positive estimates correspond to later phenology in response to the listed coefficients.

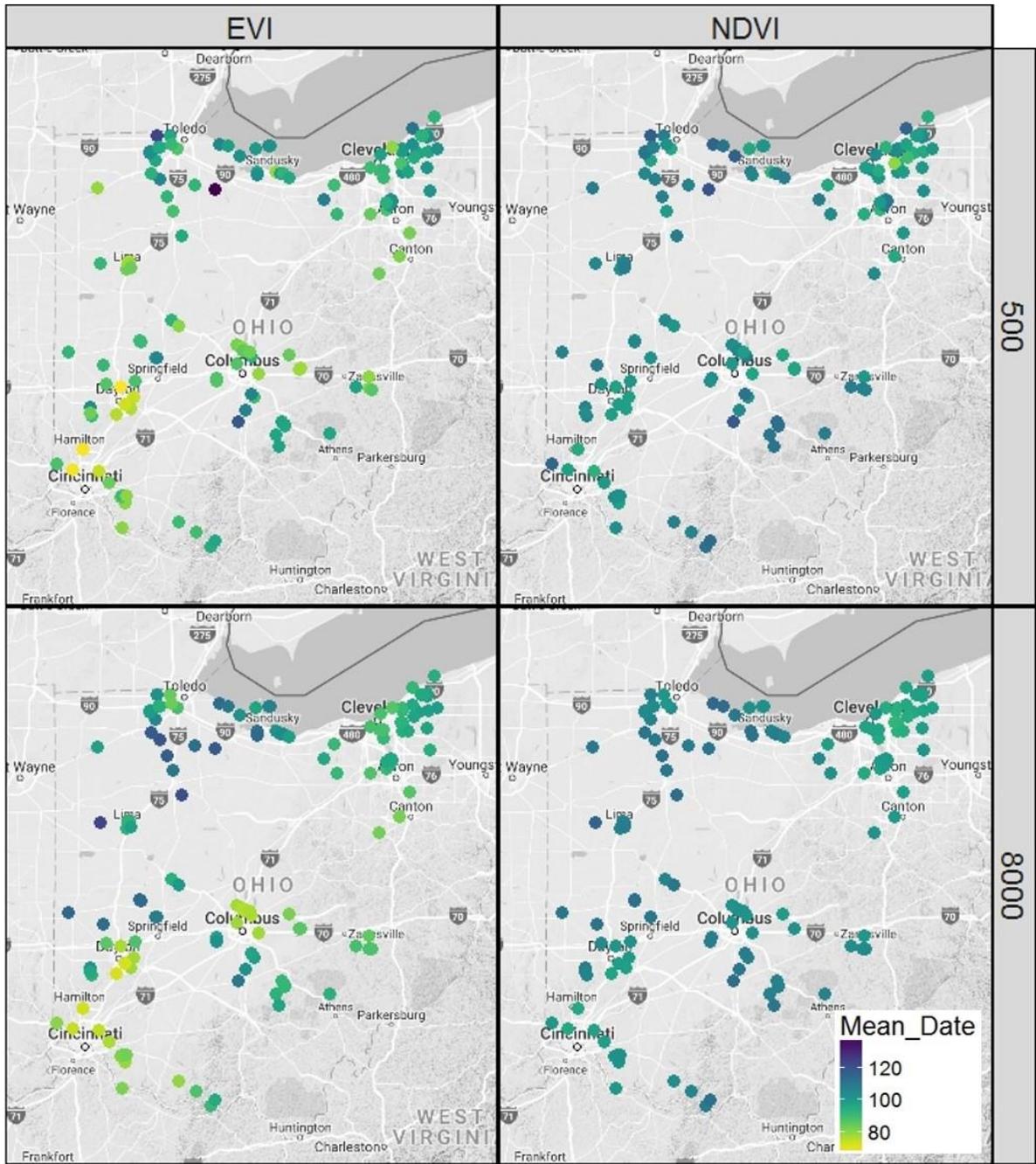
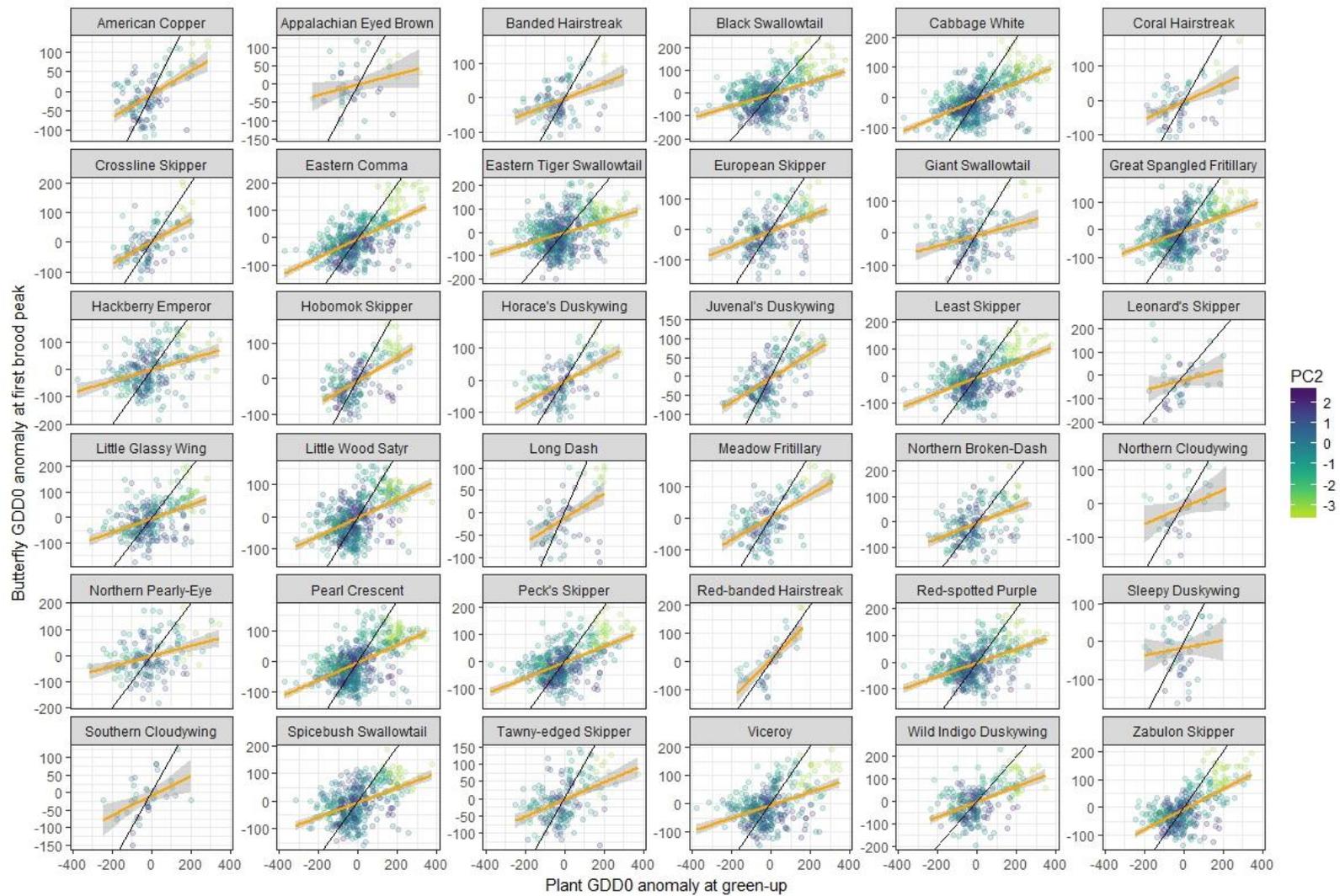


Figure 3-2: Mean estimates of plant phenology by site. The mean date of green-up for each site from 2001-2014 estimated by either EVI or NDVI remote sensing metrics summarized at different spatial scales (either 500-meter or 8000-meter circular buffers around each site).

Figure 3-3: Comparison of plant and butterfly annual phenology variation scaled by degree days. Data points represent a site x year observation and are colored by the climate variable PC2, corresponding to warmer (yellow) to colder (blue) years. The orange line is a linear regression fit, with confidence intervals, predicting butterfly phenology as a response to plant phenology. The black line shows a 1:1 match between changes in phenology, indicating a similar magnitude of response.



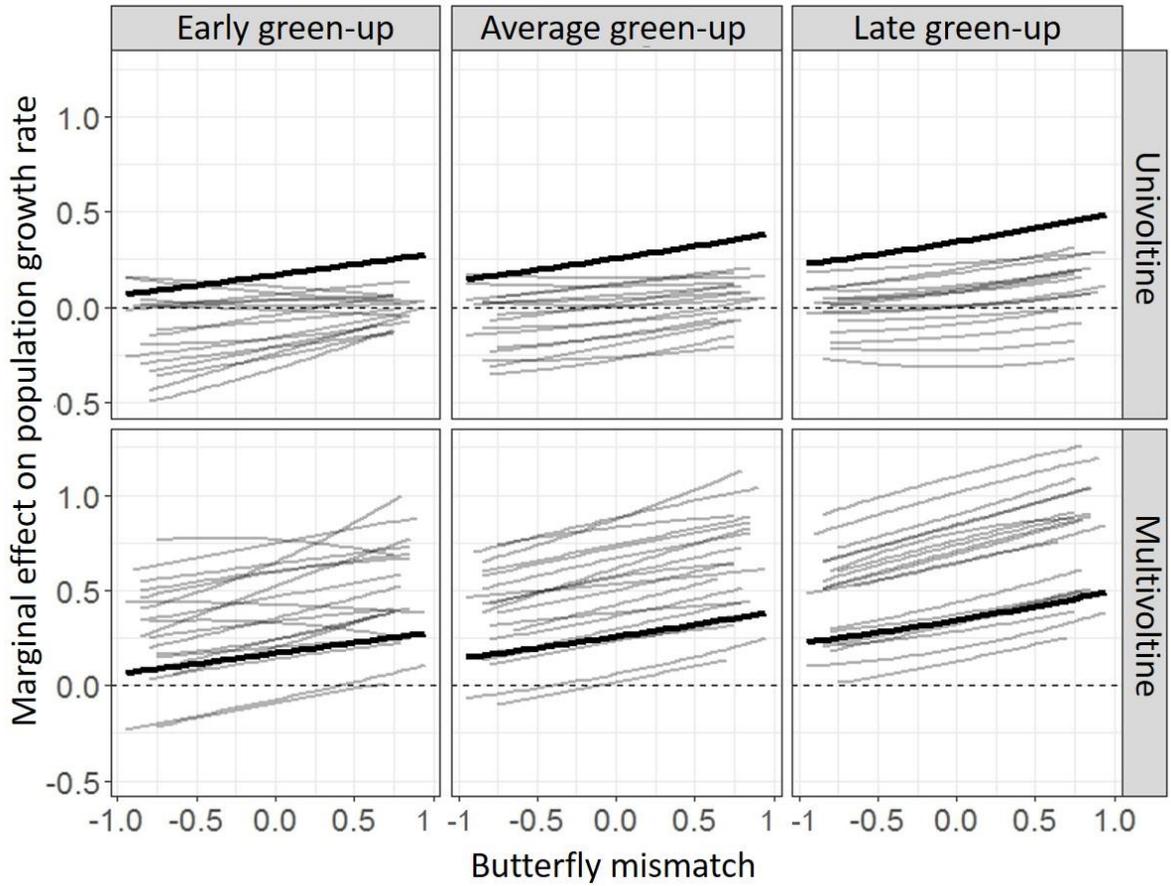


Figure 3-4: Effects of phenological mismatches on population growth rate for butterflies with different voltinism. Higher values for butterfly mismatch represent later butterfly phenology than expected. The black line indicates the shared responses across all species. The light gray lines each represent one species' response. The values come from model predictions from the linear mixed model in Table 3-2.

## APPENDIX

Table 3-A1: Principal components analysis of land cover variables. Loading of land-use variables on the top four principal components. Results were similar when land-use variables were summarized at different spatial scales; this table only shows land-use within a 2000-meter buffer around sites.

<b>Predictor</b>	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>	<b>PC4</b>
Open water	0.00	-0.08	-0.10	<b>0.68</b>
Developed, open space	0.02	-0.29	0.26	-0.29
Developed, low intensity	0.06	<b>-0.45</b>	0.34	-0.22
Developed, medium intensity	0.03	-0.19	0.13	-0.08
Developed, high intensity	0.01	-0.07	0.05	-0.03
Barren land	0.00	-0.02	0.00	0.01
Deciduous forest	<b>-0.75</b>	<b>0.50</b>	0.14	-0.14
Evergreen forest	-0.05	0.03	0.01	0.00
Mixed forest	0.00	0.01	0.00	0.01
Shrub	-0.01	0.00	-0.02	-0.01
Grassland	0.00	-0.11	<b>-0.87</b>	<b>-0.35</b>
Pasture	-0.01	0.06	0.01	0.08
Crops	<b>0.66</b>	<b>0.63</b>	0.12	-0.15
Woody wetlands	0.00	0.01	0.00	0.01
Herbaceous wetlands	0.03	-0.04	-0.07	<b>0.47</b>
Standard deviation	0.06	0.05	0.03	0.02
Proportion of variance	0.46	0.27	0.11	0.06
Cumulative Proportion	0.46	0.73	0.84	0.90

Table 3-A2: Principal components analysis of climate variables. Seasonal climate variables were scaled by mean conditions at each site and annual anomalies within each site. Loadings of these variables on the top five principal components are shown here, with important variables in bold text.

<b>Predictor</b>	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>	<b>PC4</b>	<b>PC5</b>
Site mean: end of winter	<b>-0.48</b>	0.00	-0.17	0.00	0.00
Site mean: onset of winter	-0.13	0.00	<b>0.34</b>	0.00	0.00
Site mean: winter precipitation	0.02	0.00	<b>-0.66</b>	0.00	0.00
Site mean: winter snow	<b>-0.32</b>	0.00	<b>-0.51</b>	0.00	0.00
Site mean: winter temperature	<b>0.49</b>	0.00	-0.11	0.00	0.00
Site mean: spring precipitation	<b>0.40</b>	0.00	<b>-0.39</b>	0.00	0.00
Site mean: spring temperature	<b>0.51</b>	0.00	0.05	0.00	0.00
Annual anomaly: end of winter	0.00	<b>0.48</b>	0.00	<b>0.44</b>	0.25
Annual anomaly: onset of winter	0.00	-0.09	0.00	-0.19	<b>0.68</b>
Annual anomaly: winter precip.	0.00	<b>0.32</b>	0.00	<b>0.39</b>	<b>-0.37</b>
Annual anomaly: winter snow	0.00	<b>0.33</b>	0.00	<b>-0.47</b>	-0.27
Annual anomaly: winter temp.	0.00	<b>-0.36</b>	0.00	<b>0.61</b>	-0.06
Annual anomaly: spring precip.	0.00	<b>0.31</b>	0.00	-0.10	-0.32
Annual anomaly: spring temp.	0.00	<b>-0.57</b>	0.00	-0.10	<b>-0.41</b>
Standard deviation	1.96	1.49	1.46	1.18	1.13
Proportion of variance	0.27	0.16	0.15	0.10	0.09
Cumulative Proportion	0.27	0.43	0.58	0.68	0.77

Table 3-A3: Butterfly and plant phenological sensitivity to climate and land-use in degree days. Summary of linear mixed models of plant and butterfly phenology to climate and land-use principal components corresponding to results shown in Figure 3-1.

	Butterflies			NDVI			EVI		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	1275.638	85.802	<.001	338.470	32.784	<.001	254.401	11.629	<.001
PC1	18.896	4.822	<.001	35.929	2.202	<.001	3.166	3.558	.374
PC2	-7.188	2.274	.002	-24.367	5.220	<.001	-5.416	3.838	.158
PC3	4.652	2.805	.097	5.627	3.641	.122	7.807	5.906	.186
PC4	1.423	1.307	.276	-16.109	4.660	<.001	9.644	3.932	.014
PC5	-10.903	1.599	<.001	-18.231	5.085	<.001	2.529	3.895	.516
zPC1	1.734	2.490	.486	-16.203	4.729	<.001	-47.701	7.674	<.001
zPC2	-1.336	3.010	.657	36.434	4.560	<.001	61.500	7.399	<.001
zPC3	2.414	3.053	.429	-12.488	14.532	.390	0.883	23.580	.970
zPC4	-0.333	1.763	.850	-15.504	10.498	.140	-10.092	17.035	.554
Observations	12896			1904			1904		
R <sup>2</sup>	0.987			0.784			0.697		

Table 3-A4: Butterfly and plant phenological sensitivity to climate and land-use in ordinal date. Summary of linear mixed models of plant and butterfly phenology to climate and land-use principal components corresponding to results shown in Figure 3-1.

	Butterflies			NDVI			EVI		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	161.755	4.254	<.001	102.256	2.096	<.001	93.197	1.477	<.001
PC1	-1.966	0.219	<.001	0.279	0.190	.143	-2.971	0.322	<.001
PC2	1.628	0.118	<.001	-0.399	0.423	.345	0.915	0.412	.026
PC3	0.132	0.131	.314	1.135	0.315	<.001	1.270	0.534	.017
PC4	0.405	0.091	<.001	-1.396	0.382	<.001	0.099	0.390	.800
PC5	0.552	0.112	<.001	-0.000	0.413	.999	0.370	0.408	.364
zPC1	0.111	0.119	.350	-1.659	0.409	<.001	-4.084	0.693	<.001
zPC2	-0.134	0.147	.363	3.593	0.394	<.001	7.443	0.669	<.001
zPC3	-0.001	0.159	.997	-1.514	1.256	.228	0.941	2.131	.659
zPC4	-0.123	0.100	.216	-1.648	0.907	.069	-1.306	1.539	.396
Observations	12896			1904			1904		
R <sup>2</sup>	0.984			0.628			0.788		

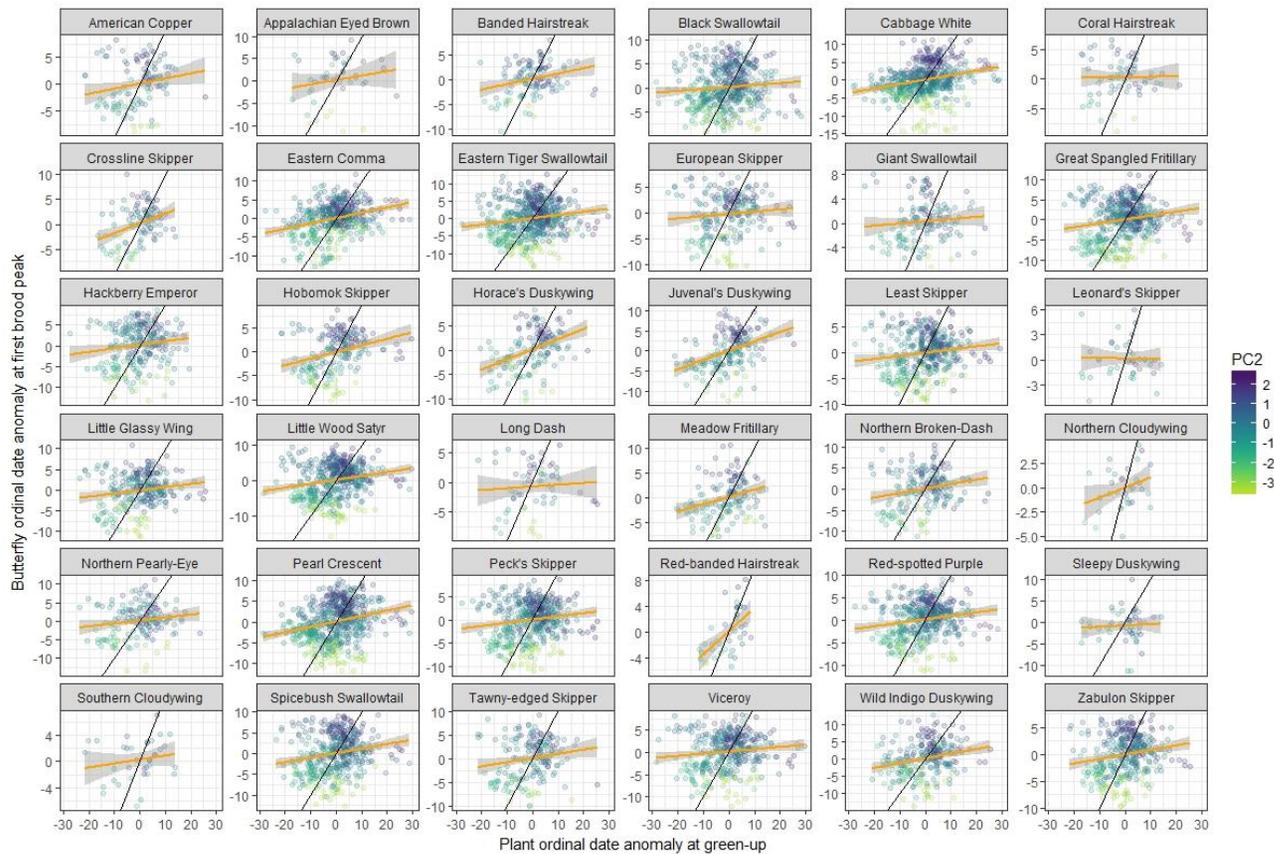


Figure 3-A1: Comparison of plant and butterfly annual phenology variation scaled by ordinal date. Data points represent a site x year observation and are colored by the climate variable PC2, corresponding to warmer (yellow) to colder (blue) years. The orange line is a linear regression fit, with confidence intervals, predicting butterfly phenology as a response to plant phenology. The black line shows a 1:1 match between changes in phenology, indicating a similar magnitude of response.

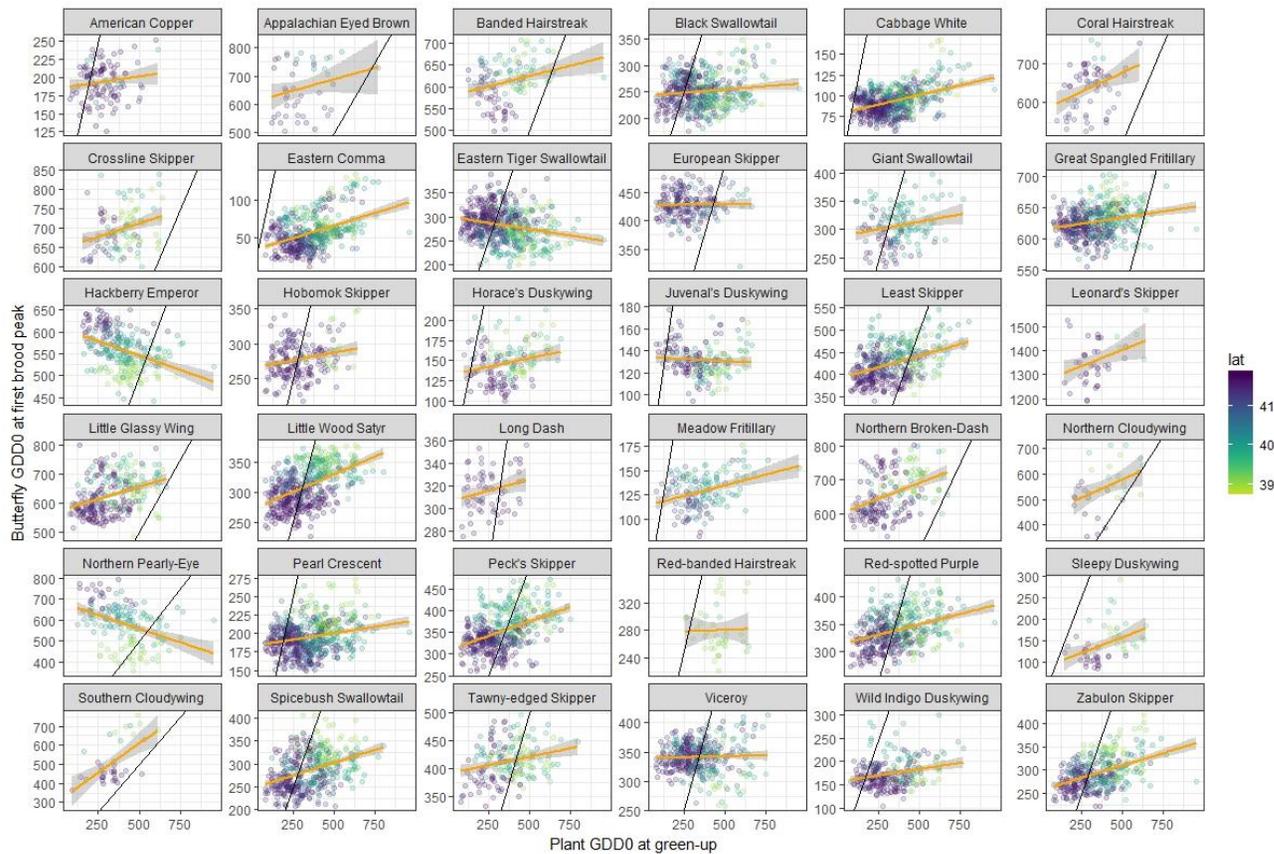


Figure 3-A2: Observed phenology of plants and butterflies scaled by degree days. Data points represent a site x year observation and are colored by the site latitude, corresponding to southern (yellow) to northern (blue) sites. The orange line is a linear regression fit, with confidence intervals, predicting butterfly phenology as a response to plant phenology. The black line shows a 1:1 match between degree days at which plant and butterfly phenology occur, indicating a similar timing of response.

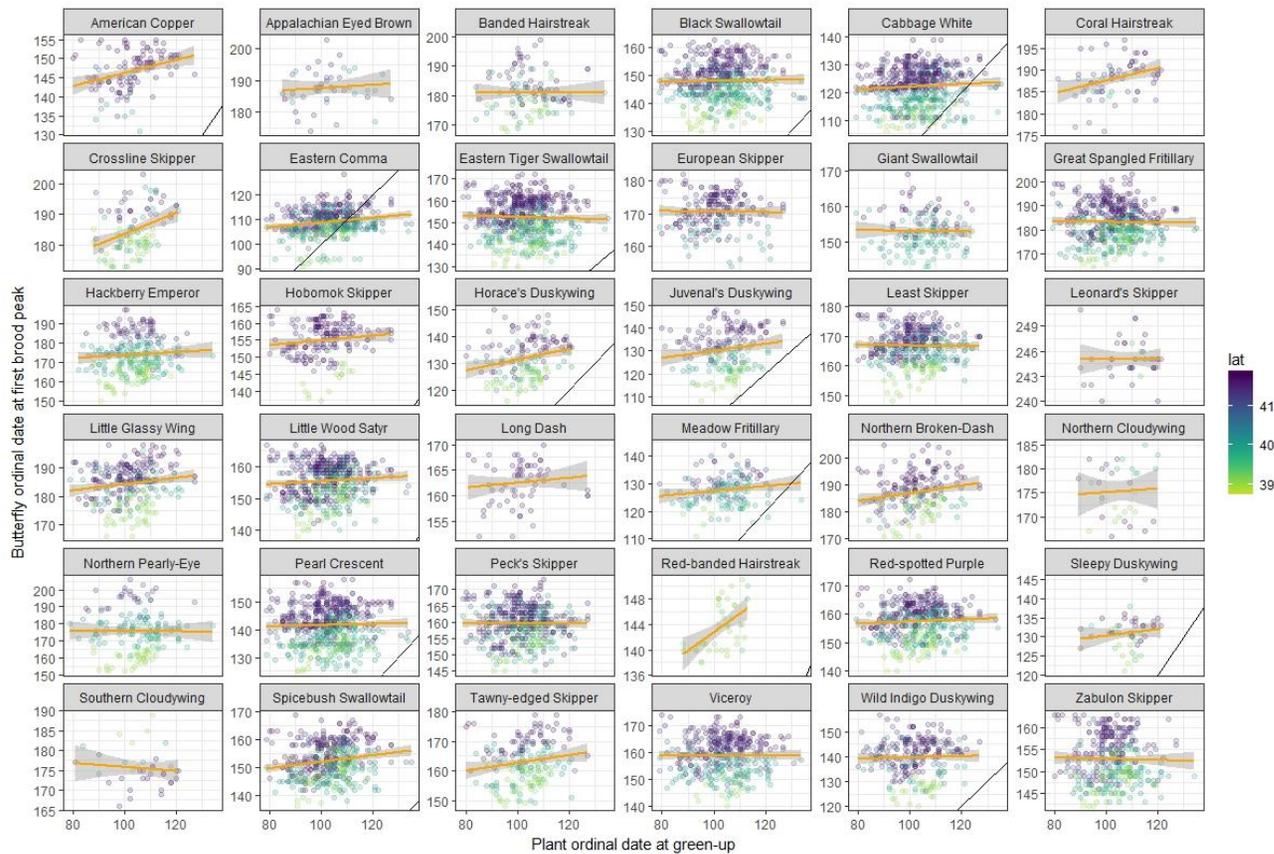


Figure 3-A3: Observed phenology of plants and butterflies scaled by ordinal date. Data points represent a site x year observation and are colored by the site latitude, corresponding to southern (yellow) to northern (blue) sites. The orange line is a linear regression fit, with confidence intervals, predicting butterfly phenology as a response to plant phenology. The black line shows a 1:1 match between ordinal date at which plant and butterfly phenology occur, indicating a similar timing of response.

## **CHAPTER 4: Butterfly responses to spatiotemporal temperature variability generally are not modified by the surrounding land cover composition**

### **ABSTRACT**

Multiple drivers of global environmental change may interact as they alter community composition and ecosystem functioning synergistically. Species' responses to observed environmental changes should be modeled to predict which species will be most vulnerable to future population declines. In this study, I test how temperature variability across space and time interacts with land cover composition to regulate population dynamics in a butterfly community. Species' annual population growth rates demonstrate a range of responses to temperature variability that change between sites that vary in mean temperature. However, land cover has little effect on how temperature variability impacts population growth rates. The diversity of species responses to different aspects of temperature variability could give insight into which species will be vulnerable to ongoing climate change, but interspecific variation was generally not associated with species' life-history traits and did not predict species' differences in statewide population trends across all years of monitoring. Negative density-dependent population regulation is the principal driver of annual population growth rates. Even though land cover does not generally impact short-term butterfly demography, there may still be long-term impacts of land-use change that may drive local extinctions that are not captured in this population modeling approach.

## INTRODUCTION

Habitat loss and degradation from human activities are the primary drivers of biodiversity loss in terrestrial ecosystems (Newbold et al. 2015). The growing impacts of climate change across taxa and biomes suggest that it may surpass habitat loss as the main cause of species extinctions (Parmesan 2006; Scheffers et al. 2016). Vulnerability assessments and conservation actions may underestimate extinction risks if climate change and other environmental stressors are treated as separate, rather than interactive, drivers of biodiversity loss (Brook et al. 2008). Global climate change and habitat degradation from land cover change may increase or decrease the effect (i.e. synergism or antagonism) of the other's impact (Mantyka-pringle et al. 2012; Oliver and Morecroft 2014). Despite the potential link between them, research generally focuses on responses to climate or land-use change separately due to the large data requirements to attribute their separate and joint impacts (Oliver and Morecroft 2014). The interactive effects of climate and land-use change emerge at large spatial and temporal scales, which make citizen-science data collection essential for monitoring complex species responses (Tulloch et al. 2013). I evaluate the effects of temperature variability and land cover on population dynamics in a butterfly community to test if these drivers of biodiversity loss interact in ways that could increase species vulnerability to population declines.

Butterfly communities respond rapidly to climate and land-use changes and can be easily-monitored to assess the biotic impacts of environmental changes (Thomas 2005). Large-scale monitoring of butterflies has demonstrated population responses in abundance to recent climate change (Mair et al. 2012), land-use (Oliver et al. 2010; Dennis et al. 2017),

and their interaction in the specific case of drought and wetland butterflies (Oliver et al. 2015). Changes in species distributions and richness have also been driven by concurrent effects of land-use change and climate warming (Warren et al. 2001; Forister et al. 2010; Casner et al. 2014). Community composition has shifted with multiple environmental changes to favor generalist species, leading to biotic homogenization observed across different biomes (Eskildsen et al. 2015; Melero et al. 2016).

Although the aforementioned effects of climate and land-use are demonstrated by analyzing long-term trends over time, shorter-term demographic responses should also show changes in response to these environmental drivers. Linking environmental variability to demographic processes has the benefit of modeling a mechanistic relationship that can be used to forecast future population trajectories (Morris and Doak 2002; Oliver and Roy 2015). Butterfly population growth rates respond to mean and extreme climate conditions, in both temperature and precipitation (Roy et al. 2001; Roland and Matter 2013). Positive or negative responses to warming can often be explained by the thermal niche of the species and whether warming expands or contracts suitable conditions (Warren et al. 2001). Land-use could alter demographic responses to climatic variability by directly altering the temperatures experienced by butterflies or through indirect effects by altering species interactions. In urban ecosystems, an increase of impervious surfaces warms surrounding areas more than vegetated land-use, created the urban heat island effect (Oke 1982), which has changed butterfly phenology in Ohio (Diamond et al. 2014). Localized urban warming has altered insect interactions with consequences for insect abundance on urban trees (Youngsteadt et al. 2015). A greater diversity of natural habitat or topography creates different microclimates

and resources that insects may use to buffer against extreme climate conditions (Oliver et al. 2010; Fernández-Chacón et al. 2014; Papanikolaou et al. 2016). Land cover associated with more intense human alteration, such as managed agriculture, can negatively affect population trends of butterflies (Hodgson et al. 2010; Gilburn et al. 2015), and would likely also reduce microclimate heterogeneity.

While research has demonstrated butterfly community responses to climate and land-use changes separately, it is unknown whether the interaction of these environmental factors alters the annual population dynamics of butterflies. As multiple environmental changes influence insect populations, it is important to understand interacts between different drivers. For example, if land-use change and climate interact so that some habitat types mitigate population declines in response to extreme temperatures, focusing on restoring habitat quality may compensate for the impacts of a warming climate (Oliver and Morecroft 2014).

In this study, I model the additive and interactive effects of weather variability and land cover composition on annual population changes in butterflies monitored by a long-term citizen science program. I test if ecological traits predict interspecific variation in responses to weather, land cover, and their interaction. I test if species' demographic responses to environmental variables are correlated with the statewide population trends for species estimated in Chapter 1.

## METHODS

### *Butterfly population growth rates*

I estimated population indices for 67 resident species and 12 migratory species using observations from weekly Pollard walks organized by the Ohio Lepidopterists (Pollard and Yates 1994). I used generalized additive models to predict weekly counts for each species, at the sites and years in which they were observed, and calculate the population index for the monitoring season (Chapter 1). For multivoltine species, I did not separate population estimates by generation so that I could use the same modeling approach for all species. I quantify annual population growth rates as the difference between consecutive annual population indices on the natural logarithm scale (Rothery et al. 1997; Roland and Matter 2013). Resident species were classified by family, voltinism, overwintering stage, and ecological specialization for a trait analysis described below (Iftner et al. 1992; Opler and Warren 2002; Cech and Tudor 2005).

### *Environmental variables*

Butterfly population growth can be driven by weather variability in different seasons depending on species' life-history and the timing of more sensitive life stages (Radchuk et al. 2013). I considered the effects of seven seasons on annual population growth rates, from the winter of the previous year to the summer of the current year. I summarized seasonal temperature variability as the mean daily temperature over three months, with data from Daymet, which interpolates daily weather on a 1x1-km grid from North American weather stations (Thornton et al. 1997; Thornton et al. 2014).

Exploratory analysis of climate means, daily extremes, and values exceeding 10/90-percentile cutoffs suggested that mean temperature and extreme temperature occurrences were highly correlated when aggregated over three months. I scaled the seasonal mean temperatures by the mean at each monitoring site to derive two variables: site mean temperatures to compare spatial variation and annual anomalies from the site means to represent temporal variation (van de Pol and Wright 2009). I reduced the number of potential variables and accounted for correlations between them with a principal components analysis of site means and annual anomalies for seven seasons from summer in the current year to winter in the previous year (Jolliffe 2002). I used the first four principal components which accounted for 71% of the total variance for population modeling (Table A4-1). The first principal component represented the site mean temperature across all seasons while the other three represent annual anomalies for different seasons: colder years across seasons (Anomaly PC1), warmer current winter and spring (Anomaly PC2), and colder previous summer and winter (Anomaly PC3).

Land cover surrounding butterfly monitoring sites was characterized with 30-meter resolution raster data from the National Land Cover Database (Homer et al. 2012). Land cover change between 2001 and 2011 was never greater than 5% of pixels between NLCD products, so I used the 2006 NLCD product and ignored changes over time. I extracted the area of different land-use/land cover classes within a 1-km buffer around coordinates for each monitoring site. I reduced the number of land-use covariates with principal components analysis after transforming the compositional data to account for classes with counts of zero (Fry et al. 2000; Cade 2015). I used the first three principal components that together

accounted for 54% of the variance in land-use across monitoring sites (Table A4-2). I refer to these as the UrbanPC, AgriculturePC, and HabitatPC.

### *Statistical analysis*

I modeled population growth rates in response to density dependence, temperature variability, and land cover with multi-species linear mixed effects models that estimate fixed effects parameters shared across species and random effects variation between species (Nice et al. 2014). I analyzed resident and migratory species separately. I used a base model including fixed effects of an intercept and density dependence (natural logarithm of the previous year's population index scaled by species) and random intercepts for species, site, and year. In all models, parameters were allowed to vary by species (random slopes) unless the model estimators did not converge, in which case random effects were deleted until convergence was achieved with a simpler model. I modeled the three temperature anomaly principal components separately, with the following models:

1. Density-dependence:  $\log(N_{t-1})$
2. Linear weather effects: Model 1 + Site Mean + Anomaly + Site Mean x Anomaly
3. Quadratic weather effects: Model 2 + Anomaly<sup>2</sup> + Site Mean x Anomaly<sup>2</sup>
4. Urban x weather effects: Model 2 + UrbanPC + Site Mean x UrbanPC + Anomaly x UrbanPC
5. Agriculture x weather effects: Model 2 + AgriPC + Site Mean x AgriPC + Anomaly x AgriPC
6. Habitat x weather effects: Model 2 + HabPC + Site Mean x HabPC + Anomaly x HabPC

Models were compared with AICc to select the parsimonious model and address the hypotheses that weather has nonlinear effects (comparing models 2 and 3) or that land-use moderates the effects of weather on population growth (comparing models 2 with models 4 through 6). Model fit was assessed with  $R^2$  designed for generalized linear mixed models (Nakagawa and Schielzeth 2013). *P*-values for community wide parameters were approximated with Wald tests to assess statistical significance (Lüdecke 2015). Confidence intervals for the random effects were simulated to see if species' responses differed from the fixed effects parameter shared across species (Knowles and Frederick 2016). I compared interspecific variation in random effects of the three annual temperature anomalies with Pearson's product moment correlation tests to see if species' responses to different temperature anomalies varied independently. I visualized model predictions to interpret interactions and compare species' responses to temperature variability and land cover.

I tested if resident species' responses correlated with traits. The random effects estimates for all parameters varying by species were averaged across models. I performed permutation tests for each parameter against five species traits (voltinism, overwintering stage, host plant type, ecological specialization, and taxonomic family) and adjusted the estimated *P*-values to control for multiple comparisons (Holm 1979; Fay and Shaw 2010).

For the 40 resident species in common between this analysis and Chapter 1, I tested if species differences in responses to the three temperature anomaly principal components predicted statewide trends in population indices with linear regression models.

All analyses were performed in R 3.3.2 (R Core Team 2016), with code available on [github.com/tysonwepprich/Chap1-Bfly-Landuse-Climate](https://github.com/tysonwepprich/Chap1-Bfly-Landuse-Climate).

## RESULTS

For resident species, the best models include quadratic effects of weather for each of the three anomaly principal components (Table 4-A3 to Table 4-A5). These models do not explain a large proportion of the variation, with conditional  $R^2$  values of 0.24. There are few statistically significant shared effects across the community, but species vary in their responses through the modeled random effects (Figure 4-A1 and 4-A2). I visualize examples of species responses to warmer years across all seasons (Anomaly PC1) and to years with a warmer winter and spring (Anomaly PC2) in Figures 4-1 and 4-2. Although they were modeled separately, species responses to the three annual temperature anomaly variables correlate with each other. Comparing linear responses to temperature anomalies, species with higher population growth rates in cooler years (Anomaly PC1) also have lower population growth rates in years with a warm winter and spring (Anomaly PC2,  $r = -0.30$ ,  $P\text{-value} = 0.012$ ) and lower population growth rates when the previous year's winter and summer are cooler (Anomaly PC3,  $r = -0.25$ ,  $P\text{-value} = 0.040$ ). There is no significant correlation between responses to Anomaly PC2 and Anomaly PC3 ( $r = 0.13$ ,  $P\text{-value} = 0.300$ ).

Land cover principal components do not improve population models for resident species (Tables 4-A3 to 4-A5). Few species have responses to the linear effects of land-use that differ significantly from the insignificant fixed effect response shared across species (results not shown). Species share a strong negative response in population growth rate when population size in the previous year is larger.

For migratory species, colder years across seasons (Anomaly PC1) decrease the population growth rates (Table 4-A6). Warmer winter and spring temperatures (Anomaly

PC2) increase population growth rate at cooler sites but decrease it at warmer sites (Table 4-A7). Although the Habitat x Weather model is not the most parsimonious, a greater amount of wetlands and grasslands around the site increases population growth rates and has a marginally-significant interaction with the site mean temperature (Tables 4-A6 to 4-A8). Migratory species' population growth rates are more synchronized than resident species across space and time, with a larger proportion of variation explained by the random intercepts for year and site (standard deviations of 0.35 and 0.13, respectively, for migratory species compared to standard deviations of 0.08 and 0.05, respectively, for resident species in the Density-dependence models). The selected models of migratory species explained more of the total variation in the data than resident species models (conditional  $R^2$  from 0.54 – 0.55 versus 0.22, respectively)

Species' traits have little effect on interspecific variation in responses to weather and land-use. The two significant associations show that species with fewer generations per year (adjusted  $P = 0.046$ ) and more specialized species (adjusted  $P = .003$ ) have a more negative interaction between site mean temperature and urban land cover, indicating lower population growth rates at urban sites in warmer regions of the state.

Statewide population trends are not predicted by interspecific responses to the linear effects of the three temperature anomaly principal components ( $P > 0.10$ , Figure 4-A3).

## **DISCUSSION**

Resident and migratory species differed in their responses to annual weather variation, in their strength of density dependence, and in population synchronization between

years and sites. Whereas migratory species shared a positive relationship between warmer years (Anomaly PC1) and population growth rates, resident species were split between responses favoring warm or cold years (Figure 4-1). Similarly, migratory species shared a positive response to warmer winters and springs (Anomaly PC2) at sites with colder mean temperatures, but resident species show a diversity of responses to the same predictor (Figure 4-2). Negative density dependence for migratory species is stronger than that for resident species, but this effect may be a result of intraspecific competition in the southern portion of their range. Many of the migratory species originate in the southern USA and irrupt in years with favorable conditions (Iftner et al. 1992). The higher synchronization of migratory species corresponds with observations of irruptive species' population dynamics having a stronger dependence on weather conditions (Harrison et al. 2015), but runs counter to observations that specialist species have more synchronized dynamics in grasslands (Franzén et al. 2013).

The weak effects of land cover were surprising as butterfly population trends are lower in urban sites (Dennis et al. 2017), butterfly density and richness declines with agricultural intensification (Hodgson et al. 2010), insect distributions change with long-term changes in land cover (Warren et al. 2001; Fox et al. 2014; Aguirre-Gutiérrez et al. 2016), and more natural habitat around sites promote insect population stability in response to weather variability (Oliver et al. 2015; Papanikolaou et al. 2016). I explore the following potential explanations for this discrepancy: the land cover composition variable does not match the scale at which butterflies interact with the environment, annual population growth

rates may not correlate with long-term trends, and the hierarchical modeling approach may give conservative results.

Scale mismatches between ecological processes and our measurements of them are ubiquitous and can lead to different emergent patterns at different scales (Levin 1992). This study analyzed landscape composition of different land cover classes at the same spatial scale across species, but ideally the environmental variables would be scaled to the dispersal ability of the species to assess how land cover affects population dynamics (Martin and Fahrig 2012). Habitat fragmentation, not quantified in this study, is another important characteristic of the landscape that affects butterfly dispersal, population synchrony, and population recovery from extreme weather events (Leidner and Haddad 2011; Powney et al. 2011; Oliver et al. 2013). Butterfly populations may be regulated by fine-scale habitat quality based on specific resources that are overlooked when analyzing total habitat area (Dennis et al. 2003). Plant resources and nectar resources explain population abundance at the local level for species with different degrees of ecological specialization and dispersal ability (Curtis et al. 2015). In this study, migratory species have higher population growth rates at sites with more wetlands and grassland habitat area. Future studies could test whether these less intensively-managed sites have a wider diversity of nectar resources that attracts migratory butterflies.

Annual population growth rates did not have strong responses to land cover, even though land cover is an important driver of long-term trends in butterfly abundance and richness (Casner et al. 2014; Dennis et al. 2017). Dynamic measures of population changes, such as annual population growth rates, can suggest mechanistic links to environmental

variables that will ultimately determine changes in species' distribution and long-term population viability (Morris and Doak 2002; Selwood et al. 2015). Demographic rates may not show changes with landscape variables over the short term if the species sensitive to land cover have already declined or gone locally extinct. I did not include growth rates where one monitored year had a count of zero in this study. Including zero counts or explicitly modeling the colonization and extinction process between sites with occupancy models could demonstrate effects of land cover on butterfly population dynamics that were missed in this analysis (MacKenzie et al. 2003). Although this study predicts annual population changes based only on the previous year's population size due to turnover in monitoring sites, a time-series approach that forecasts population abundance over time would allow annual prediction errors to compound, as in real-world conservation decisions based on modelling forecasts (Oliver and Roy 2015).

Hierarchical models estimate a shared response across species as well as interspecific variation, but may be more conservative than single species models in estimating significant effects of the predictors (Gelman and Hill 2006; Nice et al. 2014). Estimated coefficients are shrunk towards the community mean response when species' responses are partially pooled together in the model, so extreme parameters estimates are penalized. In addition, species with less data contributing to the model will not be as prone to overfitting as an approach where species are not pooled together (Gelman and Hill 2006). In essence, stronger evidence is required to estimate significant effects for less abundant species, which may obscure real effects of land cover on rarer, more specialized species. Species with different life-history traits have different mean responses to weather variability, and may be better modeled in

groups with similar traits rather than pooled across all resident species (Nice et al. 2014). Phylogenetic meta-analysis approaches would be another way to pool information across species while accounting for the non-independence of responses between closely-related species (Hadfield and Nakagawa 2010; Roy et al. 2015a).

The diversity of species responses to environmental drivers suggests that there will be winners and losers in the race to adapt to anthropogenic environmental changes (Mace et al. 2010). However, this analysis does not suggest that annual population responses to climatic variability provides a way to predict long-term population vulnerability. There is no correlation of species responses to temperature variability with statewide population trends estimated in Chapter 1. Interspecific variation in responses were not frequently associated with species traits. Univoltine and specialized species have lower population growth rates in urban areas in warmer parts of the state, which may suggest a greater vulnerability in the future as a result of these combined stressors acting in synergy. The interaction of urbanization and site mean temperatures also change butterfly phenology, but the species traits that best explained that response are different (Diamond et al. 2014).

Density dependence was by far the most important predictor of population growth rates across all species. One caution when assessing the importance of density dependence is that observation error can create spurious correlations between years that give the appearance of density-dependent population regulation (Freckleton et al. 2006). However, population studies of butterflies using Capture Mark Recapture methods that account for detection probability also demonstrate stronger effects of negative density dependence than environmental variation in models of population growth rates (Nowicki et al. 2009). One

extension of this analysis should be to see how density-dependent factors interact with other covariates in the model, as density-dependent population regulation can vary spatially (Dooley et al. 2013) or after phenological mismatches with resources (Bewick et al. 2016). Other environmental variables may affect population regulation as well, with precipitation or larger-scale periodical weather variation like the El Nino-Southern Oscillation playing a key role in annual butterfly population fluctuations in other studies (Roland and Matter 2013; Harrison et al. 2015).

This study provides an analysis of demographic responses of butterflies to multiple drivers of global change using observational data. Butterflies respond to temperature variability of up to 4°C in Ohio when accounting for spatial differences between sites and annual anomalies. Land cover around monitoring sites generally does not moderate the annual responses to this temperature variability, but this study does not rule out that habitat alteration or fragmentation may play a longer-term role in butterfly population viability. The variety of responses of different species to temperature variability, even when the shared response across the community was weak, suggest that divergent responses to ongoing climate change should be expected. Interspecific variation in responses was not associated with species traits in most comparisons and also did not correlate with statewide population trends. These results caution that different methods for assessing species vulnerability, whether demographic rates or long-term trends, may show different patterns that should be accounted for when making forecasts of species vulnerability to environmental changes for conservation decisions.

Figure 4-1: Interaction effect of warmer years and site mean temperature on population growth rates. These results come from the Quadratic Weather Effects model with fixed effects described in Table 4-A3 and random effects described in Figure 4-A1. I selected the 10 species on either extreme of interspecific variation in the response to warmer years (Anomaly PC1) to show the diversity of response.

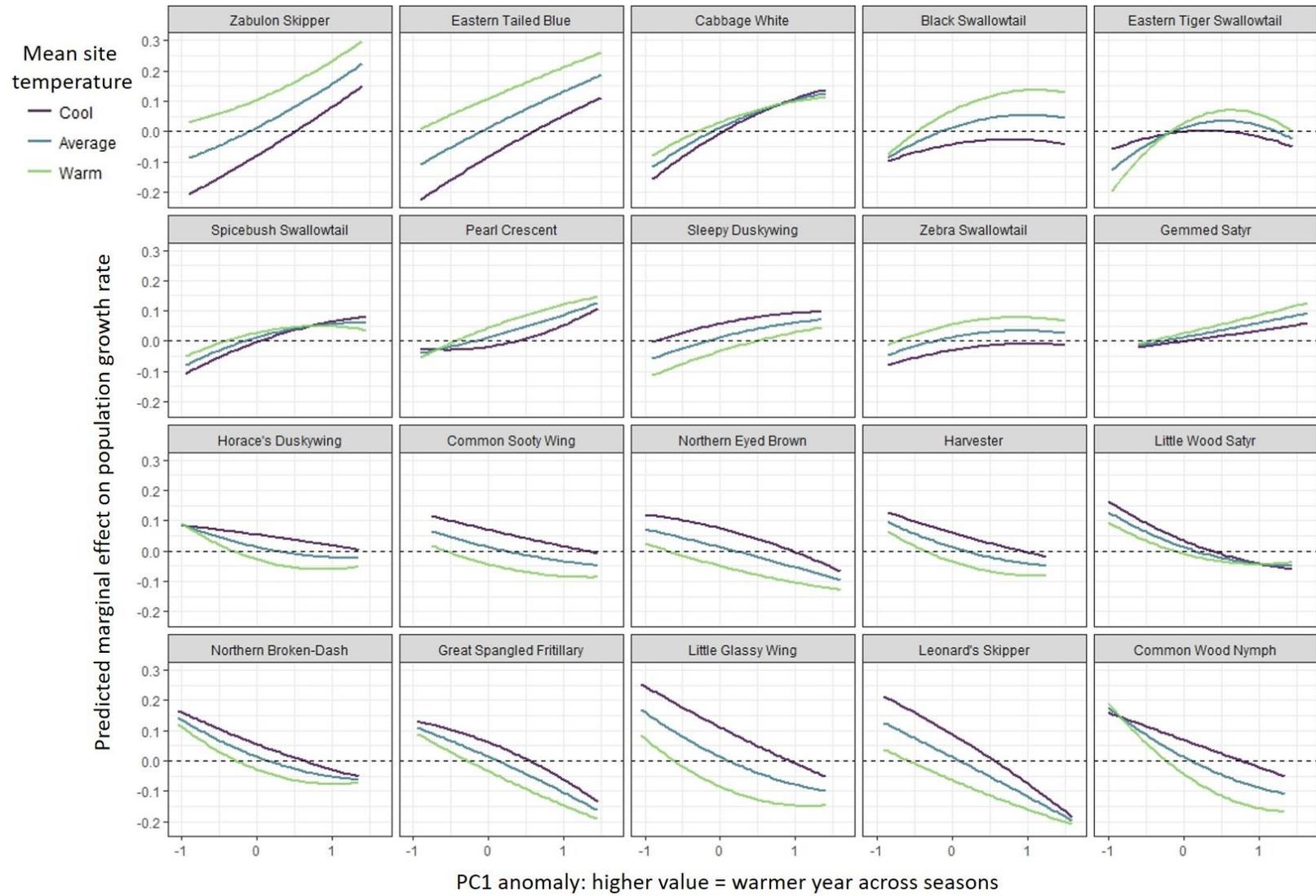
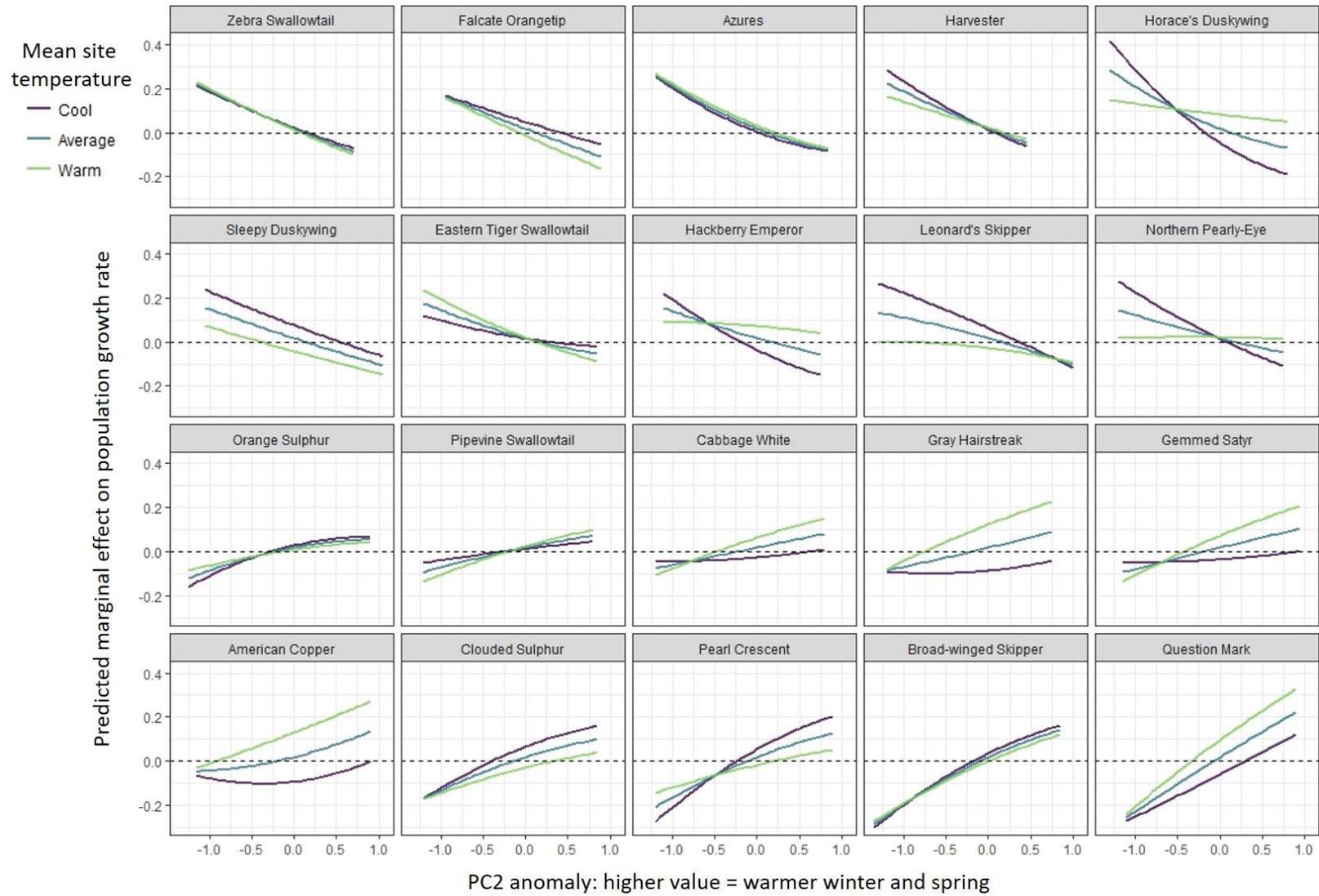


Figure 4-2: Interaction effect of warmer winter/spring and site mean temperature on population growth rates. These results come from the Quadratic Weather Effects model with fixed effects described in Table 4-A4 and random effects described in Figure 4-A2. I selected the 10 species on either extreme of interspecific variation in the response to warmer winter and spring temperatures in the current year (Anomaly PC2) to show the diversity of response.



## APPENDIX

Table 4-A1: Principal components analysis of seasonal temperature variables.

Predictor	PC1: Site mean	PC2: Colder year	PC3: Warmer current winter/spring	PC4: Colder previous summer/winter	PC5: Not used	PC6: Not used
Current year summer	0	<b>-0.58</b>	0.02	0.3	-0.24	0.19
Current year spring	0	<b>-0.29</b>	<b>0.43</b>	-0.02	0.14	<b>-0.82</b>
Current year winter	0	-0.24	<b>0.67</b>	-0.17	-0.26	<b>0.44</b>
Previous year fall	0	<b>-0.54</b>	-0.04	0.11	<b>0.35</b>	0.07
Previous year summer	0	-0.18	-0.06	<b>-0.66</b>	0.6	0.2
Previous year spring	-0.01	<b>-0.43</b>	<b>-0.58</b>	0.02	-0.14	-0.07
Previous year winter	0	-0.12	-0.14	<b>-0.66</b>	<b>-0.59</b>	-0.2
Site mean fall	<b>0.52</b>	0	-0.01	0	0	0
Site mean spring	<b>0.51</b>	0	0	0	0	0
Site mean summer	<b>0.49</b>	0	0	0	0	0
Site mean winter	<b>0.48</b>	0	0	0	0	0
Standard deviation	1.87	1.38	1.1	1.09	0.95	0.92
Proportion of variance	0.32	0.17	0.11	0.11	0.08	0.08
Cumulative Proportion	0.32	0.49	0.6	0.71	0.79	0.87

Table 4-A2: Principal components analysis of land cover variables.

Predictor	PC1: Urban	PC2: Agri- culture	PC3: Habitat	PC4: Not used	PC5: Not used	PC6: Not used
Open water	-0.04	-0.04	<b>-0.47</b>	<b>0.37</b>	-0.21	<b>-0.66</b>
Developed, open space	0.08	-0.03	0.06	-0.03	0	0.07
Developed, low intensity	<b>0.36</b>	0.13	0.07	0.07	0.29	0.03
Developed, medium intensity	<b>0.52</b>	0.07	0.20	-0.03	-0.02	-0.1
Developed, high intensity	<b>0.47</b>	0.04	0.22	-0.07	-0.1	-0.1
Barren land	0.08	-0.06	-0.15	-0.13	-0.28	0.12
Deciduous forest	-0.12	-0.14	0.15	-0.03	-0.01	0.1
Evergreen forest	<b>-0.27</b>	-0.33	<b>0.34</b>	0.22	<b>-0.37</b>	0.15
Mixed forest	-0.12	-0.11	-0.03	0.07	-0.01	<b>0.33</b>
Shrub	-0.07	-0.28	-0.02	-0.29	-0.09	0.07
Grassland	-0.16	-0.23	<b>-0.27</b>	<b>-0.66</b>	0.29	-0.22
Pasture	<b>-0.38</b>	0.21	<b>0.48</b>	0.07	0.04	<b>-0.41</b>
Crops	<b>-0.27</b>	<b>0.80</b>	-0.08	-0.18	-0.06	0.16
Woody wetlands	-0.12	-0.12	-0.05	0.4	<b>0.72</b>	0.12
Herbaceous wetlands	0.06	0.09	<b>-0.46</b>	0.24	-0.17	<b>0.34</b>
Standard deviation	7.42	5.85	5.1	4.33	3.96	3.67
Proportion of variance	0.26	0.16	0.12	0.09	0.07	0.06
Cumulative Proportion	0.26	0.42	0.54	0.63	0.71	0.77

Table 4-A3: Effects of colder years and land cover on population growth rates of resident species. These six linear mixed effects models were compared to test for nonlinear effects of temperature anomalies and land cover interactions with responses to temperature variability. These modeled Anomaly PC1.

	Density-dependence			Weather			Weather^2			Urban			Agriculture			Habitat		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	0.018	0.021	.379	0.010	0.021	.640	0.013	0.025	.605	0.006	0.021	.761	0.010	0.021	.638	0.009	0.021	.670
Prev. pop. size	<b>-0.296</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.305</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.304</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.307</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.310</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.311</b>	<b>0.011</b>	<b>&lt;.001</b>
Mean				-0.000	0.006	.968	-0.005	0.006	.424	-0.001	0.007	.828	0.000	0.006	.991	-0.001	0.006	.887
Anomaly				0.003	0.015	.845	0.009	0.016	.569	0.003	0.015	.845	0.005	0.015	.758	0.002	0.015	.887
Mean x Anom.				-0.002	0.003	.607	0.000	0.003	.997	-0.001	0.003	.637	0.000	0.003	.885	-0.001	0.003	.642
Anomaly^2							0.005	0.008	.581									
Mean x Anom.^2							0.004	0.002	.099									
Urban										-0.016	0.011	.142						
Urban x Mean										-0.004	0.006	.495						
Urban x Anom.										-0.000	0.006	.995						
Agriculture													-0.009	0.011	.419			
Agri. x Mean													0.005	0.005	.331			
Agri. x Anom.													0.011	0.006	.057			
Habitat																0.015	0.013	.247
Habitat x Mean																-0.000	0.008	.965
Habitat x Anom.																0.004	0.006	.522
R <sup>2</sup> Marg. / Cond.	0.18 / 0.21			0.19 / 0.23			0.19 / 0.24			0.19 / 0.24			0.19 / 0.24			0.19 / 0.25		
AICc	27688.620			27498.587			<b>27436.646</b>			27521.156			27510.696			27519.226		

Table 4-A4: Effects of colder winter/spring and land cover on population growth rates of resident species. These six linear mixed effects models were compared to test for nonlinear effects of temperature anomalies and land cover interactions with responses to temperature variability. These modeled Anomaly PC2.

	Density-dependence			Weather			Weather^2			Urban			Agriculture			Habitat		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	0.018	0.021	.379	0.017	0.022	.459	0.018	0.026	.496	0.014	0.022	.537	0.017	0.023	.460	0.015	0.023	.506
Prev. pop. size	<b>-0.296</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.295</b>	<b>0.010</b>	<b>&lt;.001</b>	<b>-0.295</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.298</b>	<b>0.010</b>	<b>&lt;.001</b>	<b>-0.301</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.300</b>	<b>0.011</b>	<b>&lt;.001</b>
Mean				0.003	0.006	.562	0.006	0.007	.403	-0.001	0.007	.916	0.004	0.006	.531	0.003	0.006	.580
Anomaly				0.001	0.020	.951	-0.001	0.021	.971	0.001	0.020	.977	0.002	0.020	.904	0.001	0.021	.964
Mean x Anom.				<b>0.010</b>	<b>0.004</b>	<b>.017</b>	<b>0.012</b>	<b>0.005</b>	<b>.008</b>	<b>0.009</b>	<b>0.004</b>	<b>.021</b>	<b>0.009</b>	<b>0.004</b>	<b>.028</b>	<b>0.010</b>	<b>0.004</b>	<b>.015</b>
Anomaly^2							-0.002	0.011	.854									
Mean x Anom.^2							-0.004	0.002	.132									
Urban										-0.011	0.011	.282						
Urban x Mean										-0.008	0.006	.228						
Urban x Anom.										0.001	0.006	.902						
Agriculture													-0.013	0.010	.213			
Agri. x Mean													0.007	0.005	.132			
Agri. x Anom.													-0.007	0.006	.180			
Habitat																0.012	0.012	.335
Habitat x Mean																-0.003	0.007	.616
Habitat x Anom.																0.006	0.008	.417
R <sup>2</sup> Marg. / Cond.	0.18 / 0.21			0.18 / 0.24			0.18 / 0.24			0.18 / 0.24			0.18 / 0.25			0.18 / 0.25		
AICc	27688.620			27448.975			<b>27423.167</b>			27492.068			27472.791			27472.706		

Table 4-A5: Effects of colder previous year winter/summer and land cover on population growth rates of resident species. These six linear mixed effects models were compared to test for nonlinear effects of temperature anomalies and land cover interactions with responses to temperature variability. These modeled Anomaly PC3.

	Density-dependence			Weather			Weather^2			Urban			Agriculture			Habitat		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	0.018	0.021	.379	0.014	0.021	.495	0.011	0.025	.664	0.012	0.021	.572	0.015	0.021	.477	0.013	0.021	.538
Prev. pop. size	<b>-0.296</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.301</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.300</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.305</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.307</b>	<b>0.011</b>	<b>&lt;.001</b>	<b>-0.306</b>	<b>0.011</b>	<b>&lt;.001</b>
Mean				0.002	0.006	.768	0.006	0.007	.361	-0.002	0.007	.767	0.002	0.006	.723	0.001	0.006	.821
Anomaly				0.008	0.018	.683	0.007	0.020	.716	0.007	0.018	.717	0.008	0.018	.663	0.009	0.018	.628
Mean x Anom.				-0.001	0.002	.751	0.000	0.003	.921	-0.002	0.003	.581	-0.002	0.003	.591	-0.001	0.003	.702
Anomaly^2							-0.004	0.011	.724									
Mean x Anom.^2							-0.004	0.002	.100									
Urban										-0.013	0.011	.227						
Urban x Mean										-0.007	0.006	.260						
Urban x Anom.										-0.003	0.006	.615						
Agriculture													-0.011	0.010	.272			
Agri. x Mean													0.007	0.005	.186			
Agri. x Anom.													0.003	0.005	.585			
Habitat																0.012	0.012	.335
Habitat x Mean																-0.003	0.007	.609
Habitat x Anom.																-0.004	0.006	.523
R <sup>2</sup> Marg. / Cond.	0.18 / 0.21			0.18 / 0.23			0.18 / 0.24			0.19 / 0.24			0.19 / 0.24			0.19 / 0.24		
AICc	27688.620			27485.561			<b>27405.418</b>			27507.022			27492.110			27487.769		

Table 4-A6: Effects of colder years and land cover on population growth rates of migratory species. These six linear mixed effects models were compared to test for nonlinear effects of temperature anomalies and land cover interactions with responses to temperature variability. These modeled Anomaly PC1.

	Density-dependence			Weather			Weather^2			Urban			Agriculture			Habitat		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	-0.004	0.086	.959	-0.048	0.089	.587	-0.058	0.099	.559	-0.042	0.088	.634	-0.055	0.090	.538	-0.053	0.089	.553
Prev. pop. size	<b>-0.532</b>	<b>0.057</b>	<b>&lt;.001</b>	<b>-0.538</b>	<b>0.058</b>	<b>&lt;.001</b>	<b>-0.536</b>	<b>0.057</b>	<b>&lt;.001</b>	<b>-0.540</b>	<b>0.059</b>	<b>&lt;.001</b>	<b>-0.554</b>	<b>0.064</b>	<b>&lt;.001</b>	<b>-0.551</b>	<b>0.060</b>	<b>&lt;.001</b>
Mean				0.005	0.021	.795	0.026	0.031	.399	0.001	0.022	.971	0.009	0.023	.696	-0.001	0.023	.969
Anomaly				<b>-0.140</b>	<b>0.066</b>	<b>.033</b>	-0.113	0.066	.087	<b>-0.141</b>	<b>0.064</b>	<b>.028</b>	<b>-0.136</b>	<b>0.065</b>	<b>.038</b>	<b>-0.132</b>	<b>0.065</b>	<b>.043</b>
Mean x Anom.				0.005	0.020	.790	-0.027	0.016	.088	0.003	0.020	.880	-0.009	0.021	.681	0.000	0.020	.990
Anomaly^2							0.020	0.039	.611									
Mean x Anom.^2							-0.023	0.013	.073									
Urban										0.006	0.040	.872						
Urban x Mean										0.001	0.018	.963						
Urban x Anom.										-0.029	0.018	.103						
Agriculture													0.049	0.043	.256			
Agri. x Mean													0.011	0.014	.421			
Agri. x Anom.													-0.024	0.022	.277			
Habitat																-0.041	0.040	.302
Habitat x Mean																<b>0.042</b>	<b>0.019</b>	<b>.027</b>
Habitat x Anom.																0.020	0.032	.522
R <sup>2</sup> Marg. / Cond.	0.30 / 0.48			0.31 / 0.55			0.30 / 0.58			0.31 / 0.55			0.31 / 0.57			0.30 / 0.56		
AICc	3508.688			<b>3459.230</b>			3471.786			3489.800			3481.798			3482.109		

Table 4-A7: Effects of colder winter/spring and land cover on population growth rates of migratory species. These six linear mixed effects models were compared to test for nonlinear effects of temperature anomalies and land cover interactions with responses to temperature variability. These modeled Anomaly PC2.

	Density-dependence			Weather			Weather^2			Urban			Agriculture			Habitat		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	-0.004	0.086	.959	-0.025	0.091	.780	-0.036	0.107	.736	-0.021	0.090	.814	-0.033	0.092	.720	-0.030	0.092	.747
Prev. pop. size	<b>-0.532</b>	<b>0.057</b>	<b>&lt;.001</b>	<b>-0.546</b>	<b>0.066</b>	<b>&lt;.001</b>	<b>-0.529</b>	<b>0.057</b>	<b>&lt;.001</b>	<b>-0.548</b>	<b>0.070</b>	<b>&lt;.001</b>	<b>-0.556</b>	<b>0.074</b>	<b>&lt;.001</b>	<b>-0.550</b>	<b>0.070</b>	<b>&lt;.001</b>
Mean				-0.002	0.019	.907	-0.012	0.024	.621	-0.005	0.021	.825	0.002	0.020	.917	-0.006	0.020	.754
Anomaly				0.003	0.067	.960	-0.024	0.072	.741	0.012	0.067	.860	0.002	0.066	.972	-0.002	0.066	.980
Mean x Anom.				<b>-0.049</b>	<b>0.016</b>	<b>.002</b>	<b>-0.034</b>	<b>0.014</b>	<b>.018</b>	<b>-0.046</b>	<b>0.015</b>	<b>.003</b>	<b>-0.050</b>	<b>0.019</b>	<b>.009</b>	<b>-0.050</b>	<b>0.016</b>	<b>.002</b>
Anomaly^2							0.051	0.044	.252									
Mean x Anom.^2							-0.001	0.014	.959									
Urban										0.060	0.047	.204						
Urban x Mean										-0.013	0.027	.623						
Urban x Anom.										0.012	0.022	.589						
Agriculture													0.041	0.035	.250			
Agri. x Mean													0.012	0.014	.377			
Agri. x Anom.													-0.008	0.035	.820			
Habitat																<b>-0.072</b>	<b>0.030</b>	<b>.017</b>
Habitat x Mean																0.033	0.018	.068
Habitat x Anom.																-0.022	0.033	.512
R <sup>2</sup> Marg. / Cond.	0.30 / 0.48			0.31 / 0.53			0.30 / 0.55			0.31 / 0.55			0.31 / 0.56			0.31 / 0.54		
AICc	3508.688			3482.356			<b>3477.989</b>			3519.609			3521.636			3510.179		

Table 4-A8: Effects of colder previous year winter/summer and land cover on population growth rates of migratory species. These six linear mixed effects models were compared to test for nonlinear effects of temperature anomalies and land cover interactions with responses to temperature variability. These modeled Anomaly PC3.

	Density-dependence			Weather			Weather^2			Urban			Agriculture			Habitat		
	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>	<i>B</i>	<i>SE</i>	<i>p</i>
(Intercept)	-0.004	0.086	.959	-0.022	0.090	.803	-0.144	0.109	.187	-0.018	0.089	.837	-0.026	0.090	.774	-0.020	0.091	.823
Prev. pop. size	<b>-0.532</b>	<b>0.057</b>	<b>&lt;.001</b>	<b>-0.519</b>	<b>0.059</b>	<b>&lt;.001</b>	<b>-0.515</b>	<b>0.054</b>	<b>&lt;.001</b>	<b>-0.524</b>	<b>0.062</b>	<b>&lt;.001</b>	<b>-0.533</b>	<b>0.059</b>	<b>&lt;.001</b>	<b>-0.519</b>	<b>0.059</b>	<b>&lt;.001</b>
Mean				-0.003	0.022	.879	-0.015	0.021	.489	-0.005	0.022	.810	0.000	0.022	.996	-0.008	0.022	.718
Anomaly				-0.008	0.096	.930	-0.057	0.092	.538	0.015	0.082	.856	0.008	0.084	.926	0.005	0.083	.954
Mean x Anom.				-0.007	0.008	.371	-0.008	0.014	.579	-0.010	0.017	.564	-0.012	0.015	.427	-0.010	0.016	.541
Anomaly^2							<b>0.093</b>	<b>0.039</b>	<b>.018</b>									
Mean x Anom.^2							0.008	0.009	.389									
Urban										0.049	0.042	.248						
Urban x Mean										-0.002	0.025	.923						
Urban x Anom.										-0.007	0.016	.669						
Agriculture													0.028	0.033	.391			
Agri. x Mean													0.008	0.013	.511			
Agri. x Anom.													-0.010	0.019	.594			
Habitat																<b>-0.073</b>	<b>0.035</b>	<b>.034</b>
Habitat x Mean																0.031	0.018	.081
Habitat x Anom.																0.016	0.027	.555
R <sup>2</sup> Marg. / Cond.	0.30 / 0.48			0.27 / 0.54			0.29 / 0.56			0.28 / 0.55			0.29 / 0.54			0.28 / 0.54		
AICc	3508.688			<b>3449.857</b>			3470.471			3489.324			3482.991			3472.129		

Figure 4-A1: Species' variation in population response to colder years. The random effects variation in species' responses are shown with their deviation from zero, representing alignment with the shared fixed effects response. Closed dots indicate significant differences where simulated confidence intervals do not overlap zero. These results are from the Quadratic Weather effects model for colder temperature anomalies (Anomaly PC1). Species are arranged by their variation in response to Anomaly PC1, with species on the right showing higher population growth rates in colder years.

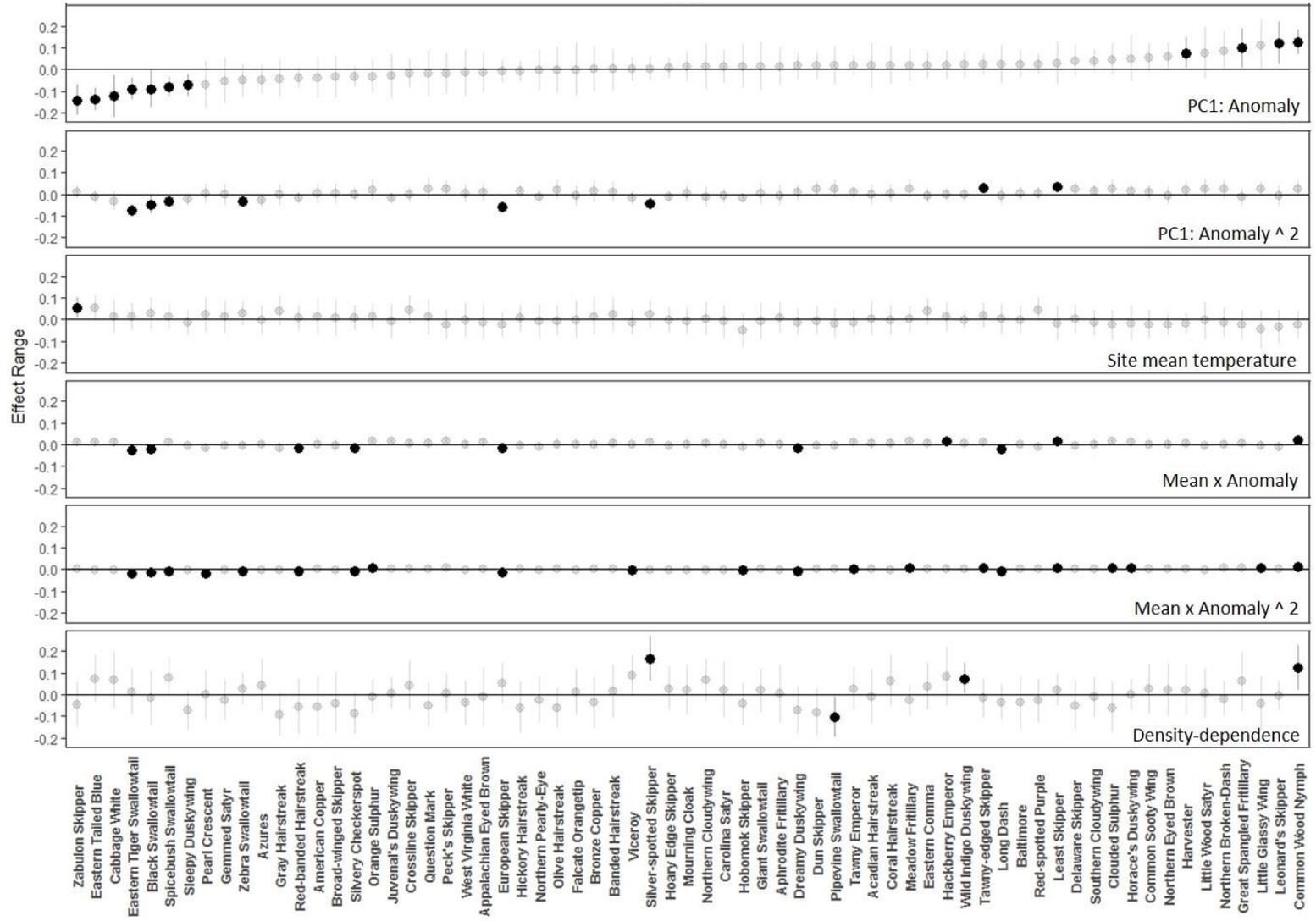
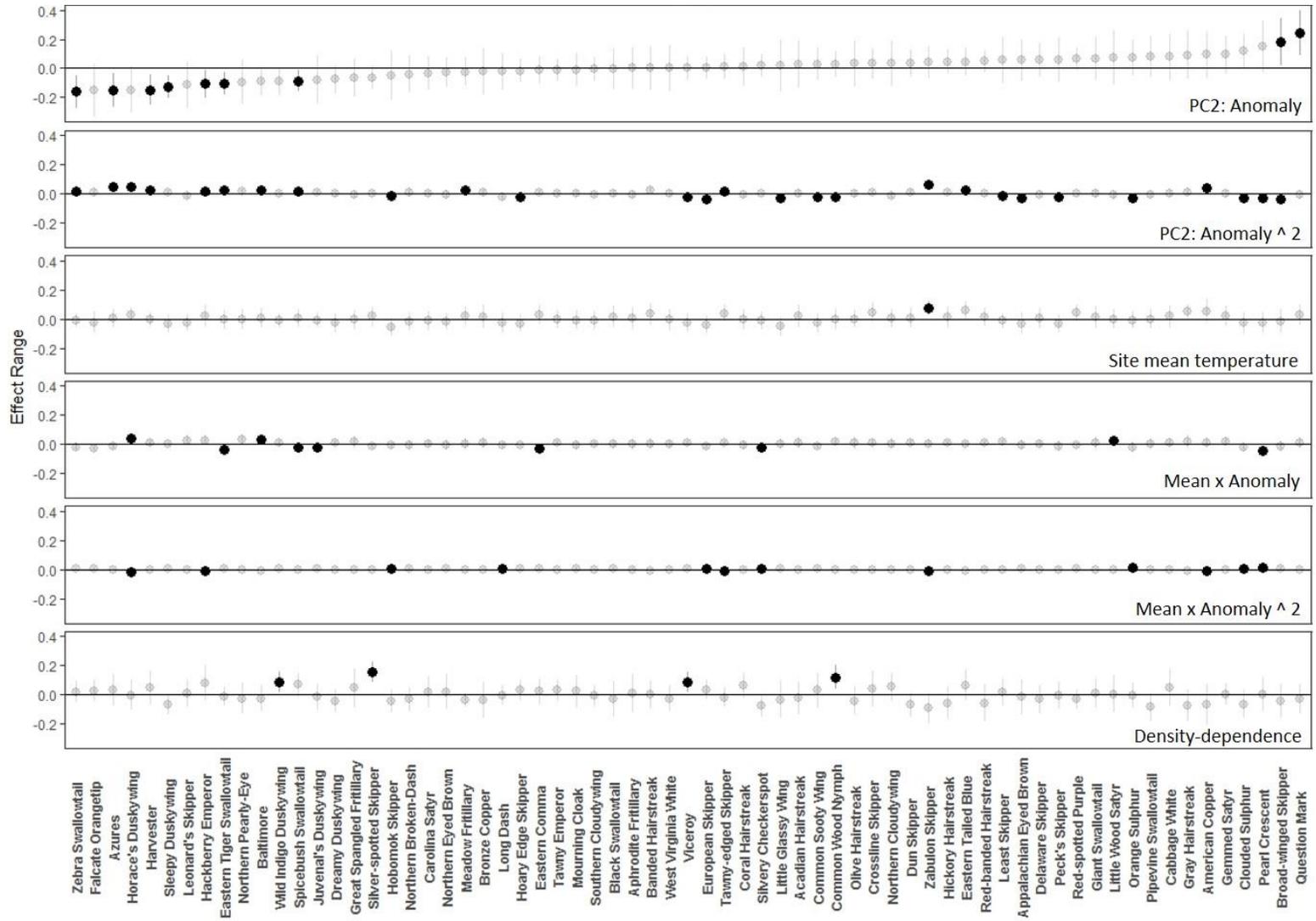


Figure 4-A2: Species' variation in population response to warmer winter/spring in the current year. The random effects variation in species' responses are shown with their deviation from zero, representing alignment with the shared fixed effects response. Closed dots indicate significant differences where simulated confidence intervals do not overlap zero. These results are from the Quadratic Weather effects model for warmer winter/spring temperature anomalies (Anomaly PC2). Species are arranged by their variation in response to Anomaly PC2, with species on the right showing higher population growth rates when the current winter/spring is warmer.



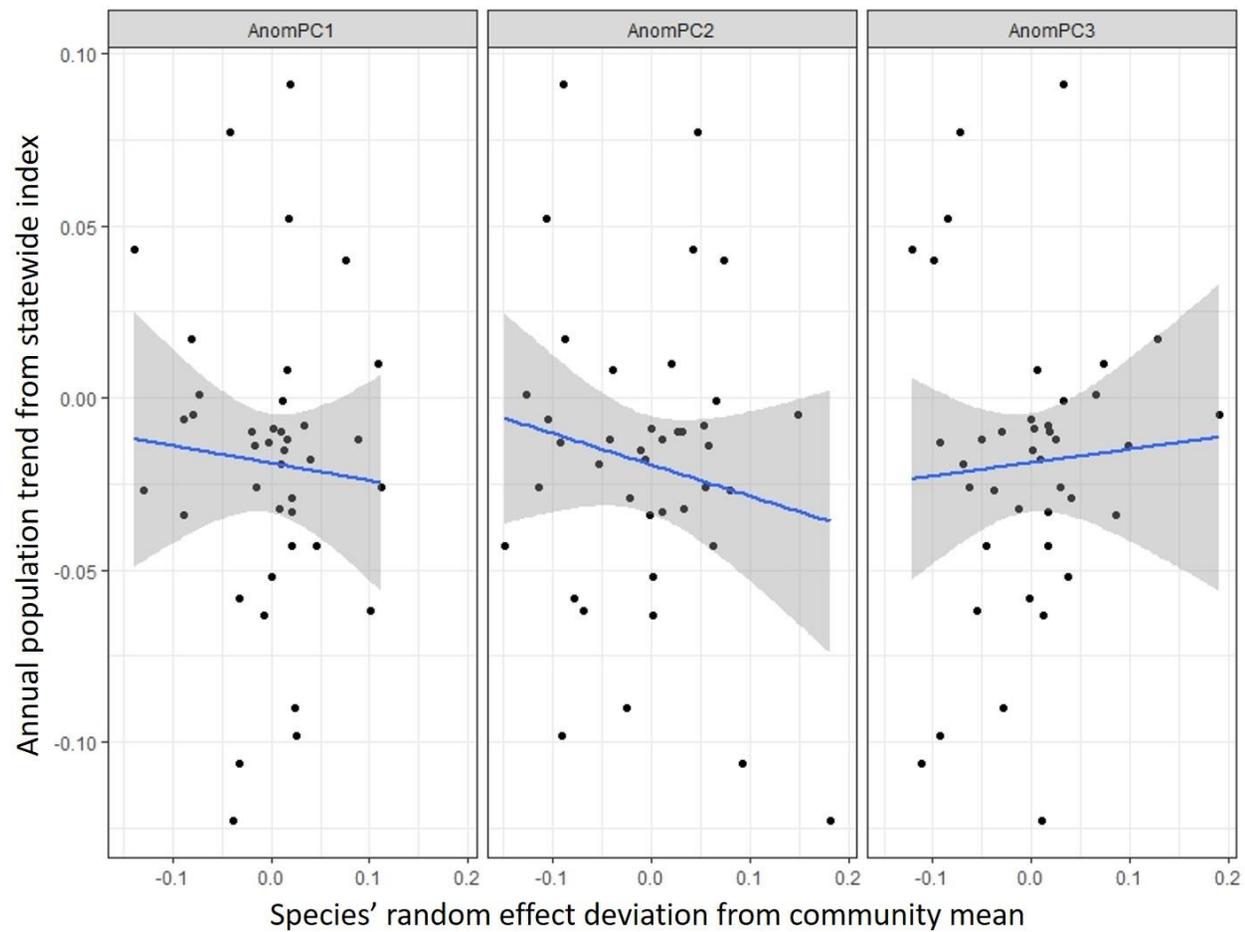


Figure 4-A3: Statewide population trends predicted by species' variation in responses to annual climatic variability. Linear regressions of species' random effects responses to temperature anomalies on statewide trends estimated in Chapter 1. There is no significant relationship between these variables.

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