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The Effects of Recent Climate Change on Spring Phenology, With a Special Focus on Patterns of Bee Foraging

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THE EFFECTS OF RECENT CLIMATE CHANGE ON SPRING PHENOLOGY, WITH A SPECIAL FOCUS ON PATTERNS OF BEE FORAGING

by

Michael Stemkovski

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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ABSTRACT

The effects of recent climate change on spring phenology, with a special focus on
patterns of bee foraging

by

Michael Stemkovski, Doctor of Philosophy

Utah State University, 2023

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Department: Biology

Phenology, the seasonal timing of life-history events, is a major determinant of the abiotic environment and ecological interactions that species experience. Phenological plasticity, or the responsiveness of phenology to differences in inter-annual climatic conditions, is one of the ways that species cope with environmental variability and climatic shifts. Shifts in spring plant phenology are one of the clearest biotic signals of recent anthropogenic climate change, as temperatures have increased in much of the world, and many plant species have been documented to bloom and leaf-out earlier. While these patterns have been well documented, much less has been understood about the phenological plasticity of pollinators that depend on flowering plants, such as bees. Here, I investigate several aspects of bee phenology and the effect of climate change on phenological variability broadly.

This dissertation is composed of six chapters, with four manuscripts bookended by introductory and concluding chapters. Chapter 2 examines the drivers of bee phenology in a subalpine bee community, quantifying the relative effects of inter-annual climate variability, topography, and species traits on the emergence, peak, and senescence timing of several dozen bee species over a decade. Using the same dataset and a complementary long-term flower phenology monitoring dataset, Chapter 3 quantifies the degree to which bee and flower phenological distributions are skewed toward early- or late-season abundance. Synthesizing work from Chapters 2 and 3, Chapter 4 presents a mechanistic model of bee phenology that is based on demographic rates and is parameterized using *Halictus rubicundus* abundance data collected at a fine temporal scale. Expanding the scope of inquiry, Chapter 5 investigates the degree to which the spring phenology of over a thousand species of plants, insects, and birds is becoming more or less variable across years as a result of climate change.

(263 pages)

PUBLIC ABSTRACT

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Michael Stemkovski

The date on which plants flower and on which bees begin to pollinate varies year-to-year depending on differences in weather. This seasonal timing is known as phenology, and it is already clear that climate change has pushed the spring phenology of many species earlier by increasing temperatures. This is particularly clear in flowering plants, but studying how and why the phenology of pollinators is shifting is more difficult. Most flowering plants rely on pollinators such as bees for their reproduction, and most bees rely on flowers for their sustenance, so bee and flower phenology has to overlap for the crucial interaction of pollination to happen, and understanding the phenology of both is important to predicting how climate change will affect pollination in the future.

Using new and existing data on bee and flower phenology from the Colorado Rocky Mountains, I examined what drives phenology and developed a mathematical model to relate bee phenology to basic demographic rates. Taking a global view, I also tested whether the phenology of plants, insects, and birds is becoming less predictable due to rising temperatures. In general, this dissertation shows that while the drivers of phenology are complex and interrelated, we can predict their outcomes as climate change progresses.

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The data collection for Chapters 2, 3, and 4 was conducted at the Rocky Mountain Biological Laboratory in Gothic, CO, which is located on the ancestral land of the Tabeguache band of the Ute people. My work on this dissertation was funded by a National Science Foundation Graduate Research Fellowship (grant number 1745048). The research presented in Chapter 2 was supported by NSF grants ABI-1759965, EF-1802605, DEB-0922080, DEB-1354104, USDA Forest Service agreement 18-CS-

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Michael Stemkovski

CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

CHAPTER 1

GENERAL INTRODUCTION

The global climate has been experiencing noticeable effects of elevated anthropogenic greenhouse gas emissions since close to the beginning of the industrial revolution (Abram et al., 2016). The most unambiguous, widespread effect has been increasing temperatures (IPCC, 2021). In recent decades, this warming has accelerated as the human population has exploded and greenhouse gas emissions have followed (IPCC, 2021). In fact, just between when I started working on this dissertation in 2018, and the date of the completion of this dissertation, 400 million people were born in the world – a number greater than the population of the United States (United Nations, 2022). In the same time, global temperatures have continued their alarming rise. These past four years have all been in the top ten warmest years ever recorded (NOAA, 2022). Concentrations of carbon dioxide have increased by around 10 parts per million during this time, from 407 ppm in 2018 to 417 ppm in 2022 (Friedlingstein et al., 2022).

This is a critical time in our history as our society grapples with the implications of this rapid climate change and people work to avert its worst outcomes. Ecologists are (or aught to be) playing a key role in anticipating and adapting to changes in ecosystems in terms of services and biodiversity. The “natural” experiment of changing climate also provides an unprecedented opportunity for basic scientific insight for ecologists to exploit.

The ecological effects of climate change range in timescale (Williams et al., 2021). Some will take decades and centuries to play out, while others are observable on a annual basis or even faster (i.e. consequences of extreme weather events). Phenological plasticity (the phenomenon of species shifting the timing of seasonal life-history events in response to abiotic conditions) and the phenological shifts (changes in phenology across years) that are a result of plasticity are a relatively fast ecological consequence of climate change (Badeck et al., 2004). This, together with the fact of many phenological effects being conspicuous and easily studied, has led to phenology research becoming one of the main areas of investigation for ecologists that focus on global change. Phenological shifts are one of the clearest biotic indicators of climate change.

Beyond serving as an indicator of abiotic conditions, phenology is worthy of study in the context of species interactions. Most of ecology rests on the co-occurrence of species in space and time. If there are changes in either dimension, ecological relationships necessarily change. Much work on phenological shifts has been motivated by the match-mismatch hypothesis (Renner et al., 2018). At its core, the idea is that if interacting species have different phenological sensitivities, the timing of their activity will shift at different rates over time as climate change progresses, and they will become temporally decoupled. This possibility is expected to result in some positive fitness consequences if antagonistic relationships (e.g. predation, competition) are disrupted, or negative consequences if synergistic interactions (e.g. pollination, facilitation) cannot occur due to temporal mismatch. The present dissertation examines some of the ways that climate change is affecting phenology, and focuses particularly on the pollination interactions of wild bees and flowering plants.

Phenological plasticity

What are the fundamental causes of phenological plasticity? On one hand, phenological plasticity can be viewed as an adaptive trait, but on the other hand it can be viewed as a neutral product of physiology and vital rates that is not a result of natural selection. These are extreme cases of a continuum, with reality likely lying somewhere between, and phenological plasticity is probably more adaptive in some species than in others. To organize this discussion, I will consider the distinct ways in which phenological plasticity is adaptive and ways in which it is a neutral process.

Trait plasticity is expected to arise as an adaptive strategy (in place of bet-hedging strategies or adaptive tracking) in cases when environmental predictability is sufficiently high, but the time-scale of environmental variation is short (Botero et al., 2015). In the context of phenology, plasticity as an adaptation is expected when conditions early in development are predictive of those during the reproductive phase of a species (or those periods that influence fecundity) and when there is substantial variation in climate conditions year-to-year or in different parts of a species' range. Practically, the ability for species to change the seasonal timing of their activity allows them to track favorable abiotic conditions such as periods of water availability (Singh et al., 2005) and light availability (Augspurger et al., 2017), and avoid hazards such as frost damage (Pardee et al., 2018). Further, species with close interspecific associations, such as obligate mutualists, have strong fitness pressures to track their interacting partners' phenology (Rafferty et al., 2015). In summary, there are definite fitness outcomes of phenological plasticity, and multiple evolutionary ecology studies support this (Anderson et al., 2012;

Gauzere et al., 2020; Kingsolver et al., 2018). While the present research does not directly measure fitness outcomes, phenological matching between bees and flowers is discussed in Chapters 2 and 3.

To understand the fundamental causes of phenological plasticity, it is important to remember that even if we can imagine a logical mechanism by which plasticity benefits a species or even observe plastic responses correlating with fitness outcomes, the trait may not be adaptive (Gould et al., 1979). Does a plant leaf-out in the spring to optimize photosynthesis, or is it only capable of producing leaves under warm spring conditions? The physiological processes that govern phenology are, after all, constrained by thermodynamics (Buckley, 2022). In the context of pollination, apparent matching between a certain bee species' foraging phenology and a plant species' flowering phenology does not necessarily imply coevolution, interaction as a source of adaptive plasticity, or even sensitivity to the same environmental cues; the temporal match may simply be a product of coincidental alignment in developmental schedules. Traits that are not directly rated to phenology may nevertheless influence phenology and the degree of its sensitivity to climatic variation. This is discussed at length in Chapter 2. Further, phenological abundance distributions (the temporal spread of a species abundance over a season) are products both of phenological onset plasticity and demographic rates such as mortality that are not traditionally thought of as drivers of phenology. Chapter 3 examines phenological abundance distributions in bees and flowers, and Chapter 4 presents a model that attempts to synthesize phenological plasticity and demographic processes.

Climate change effects on phenology

Climate change is affecting both temperature and precipitation patterns. While temperature is projected to increase almost everywhere in the world, precipitation is likely to increase in some areas and decrease in others (IPCC, 2021). Phenology in some species is known to respond to precipitation magnitude and timing (e.g., Danforth, 1999), but temperature is, broadly speaking, the strongest predictor of phenology across taxa (Thackeray et al., 2016). Chapter 2 discusses some of the interplay of temperature and precipitation sensitivity in bee phenology, but Chapter 5 focus exclusively on temperature sensitivity. In montane systems with seasonal snowpacks, snowmelt timing is typically a strong predictor of phenology (Inouye, 2008), and Chapters 2 and 4 discuss snowmelt timing acting on phenology through its control over the temperatures that species experience.

There are multiple dimensions and nuances to the general prediction that temperatures will rise and precipitation patterns will change. Extreme weather events are changing in frequency, intensity, and location due to changes in the water cycle (IPCC, 2021), and individual weather events can affect regional phenology (Jentsch et al., 2009).

Another dimension of the changing climate is variability. While most public attention and research effort goes to overall, mean changes in climate, temperature and precipitation variability is also likely to change (IPCC, 2021). And these changes in variability have substantial, sometimes unintuitive, ecological effects (Mulder et al., 2017). It is important to recognize that variability can change in both space and time. For example, the spatial variability of precipitation globally is sure to increase because some areas will receive more water and some will receive less (IPCC, 2021). The effect of climate change on temporal climate variability is perhaps less certain. At the sub-continental scale, temperature and precipitation levels have become more variable across years in some areas but less variable in other areas (Liu et al., 2020). Further, there are multiple timescales of variability changes with different ecological implications. Most phenology studies that analyze the effects of temperature variability do so within-seasons, intra-annually. Chapter 5 is devoted to the question of whether inter-annual temperature variability is changing, and how phenology is or is not responding.

Particulars of bee phenology

Whether and to what degree plant flowering and bee foraging phenology will shift as a result of climate change is central to anticipating the future of pollination interactions (Rafferty et al., 2015). The worry that species might decouple in time is partially rooted in the observation that different biological mechanisms determine flower and bee phenology. The obvious bears emphasizing here: plants and animals are fundamentally different. Phenological sensitivities and phenological abundance distributions that appear similar across bees and flowers must necessarily arise from distinct mechanisms. Because most phenology work is done on plants, it is worthwhile here to highlight the ways in which bee phenological plasticity differs from that of plants.

First, the vital rates that shape phenological distributions are different between flowers and bees. Annual plants produce flowers after a sequence of germination and growth, and perennials produce flowers from existing buds with minimal new growth needed before reproduction. In contrast, wild bees that are solitary (not forming colonies) and univoltine (having a single generation per year), must overwinter in nests and then emerge and begin the behavior of foraging. Bee species overwinter in multiple different stages of development, nest in a variety of substrates, and have different nest structures, all of which may influence phenological sensitivity (Bartomeus et al., 2011). The processes that determine phenological cessation are also distinct. Flowers experience tissue senescence, while bee foraging phenology ends through mortality, behavior switching, or relocation. Chapter 4 examines these vital rates and formalizes their effects on phenological distributions using a mathematical model. Finally, the ability to select a habitat distinguishes the phenology of plants and bees. While plants are limited to the location in which they are rooted, bees may travel sometimes long distances in search of floral resources (Greenleaf et al., 2007). While movement in search of floral resources poses a challenge for studying bee phenology, it also has consequences for pollination and competition in the field (Ogilvie et al., 2016). Chapter 4 also discusses the effect of local floral abundance on observed bee abundance via habitat selection.

Dissertation outline

There are countless unanswered questions about the effects of climate change on phenology, and the study of bee phenology is only starting to hit its stride. The research topics presented in the subsequent chapters were chosen through consideration of interest, importance, feasibility, and happenstance. Though work on these distinct research projects happened often in tandem, the chapters form a progressive sequence. Chapter 2 inspired the questions that led to Chapters 3 and 4, and Chapter 5 grew out of a desire to answer a large-scale question in terms of geography, taxonomy, and time.

Chapter 2 is a community-level study that explores the drivers of bee phenology using a long-term monitoring project at the Rocky Mountain Biological Lab in Colorado, USA. Using data from thousands of professionally identified specimens across dozens of species, this chapter picks apart the effect of snowmelt timing, precipitation, temperature, elevation, topography, body size, nest location, and overwintering life stage on determining bee phenology. This chapter also investigates whether traits affect phenological sensitivity to climate and whether different factors are responsible for different parts of bees' phenological abundance distributions. The next two chapters delve into questions about the shape of these abundance distributions.

Chapter 3 examines whether bee phenological abundance distributions tend to be skewed in time, testing whether individuals tend to be concentrated in the early or late part of species' active periods. Similar studies have been done on skewness in flower phenology, but this chapter expands our understanding by comparing skewness and bee and flower phenology. While Chapter 2 used a phenomenological approach (generalized additive models) to characterize phenological distributions, Chapter 4 attempts to model these distributions mechanistically based on vital rates.

Finally, Chapter 5 looks beyond bees, flowers, and the Colorado Rocky Mountains to ask whether climate change is making phenology more or less variable across the Northern Hemisphere. This broader scope incurred methodological tradeoffs, so this chapter focused just on phenological onset rather than on whole phenological distributions.

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CHAPTER 2

BEE PHENOLOGY IS PREDICTED BY CLIMATIC VARIATION AND FUNCTIONAL TRAITS

Abstract

Climate change is shifting the environmental cues that determine the phenology of interacting species. Plant-pollinator systems may be susceptible to temporal mismatch if bees and flowering plants differ in their phenological responses to warming temperatures. While the cues that trigger flowering are well-understood, little is known about what determines bee phenology. Using Generalized Additive Models, we analyzed time-series data representing 67 bee species collected over nine years in the Colorado Rocky Mountains to perform the first community-wide quantification of the drivers of bee phenology. Bee emergence was sensitive to climatic variation, advancing with earlier snowmelt timing, while later phenophases were best explained by functional traits including overwintering stage and nest location. Comparison of these findings to a long-term flower study showed that bee phenology is less sensitive than flower phenology to climatic variation, indicating potential for reduced synchrony of flowers and pollinators under climate change.

Introduction

Ecological relationships break down when the synchrony of interacting species is disrupted. Climate change is altering the phenology (timing of life-history events) of species, with spring events generally happening earlier (Bell et al. 2015, Cohen et al. 2018) and fall events later (Gallinat et al. 2015). Crucially, the rate of phenological shift varies among co-occurring species and guilds (Thackeray et al. 2016, König et al. 2018). This is of particular concern for species within cross-guild associations, such as plants and their pollinators, because the two groups may have different sensitivities to environmental cues (Forrest and Thomson 2011, Rafferty et al. 2015). Positively interacting species that experience a phenological mismatch due to different directions or rates of response to climate change are likely to suffer reduced fecundity or increased mortality (Visser & Gienapp 2018). Mismatches due to climate change have been observed in consumer-resource systems (Kharouba et al. 2018) and mutualistic interactions (Petanidou et al. 2014). In the short term, mutualist species that experience a phenological mismatch are expected to suffer fitness losses, followed by adaptation to reestablish synchrony (Visser & Gienapp 2018). If climate change outpaces the rate of adaptation, however, mutualists may experience irreparable de-coupling. Thus, it is critically important to understand the drivers of phenological shifts and compare their magnitudes for interacting species.

In plant-pollinator systems, phenological mismatch due to earlier spring events has been reported for early-season flowers and their pollinators (Kudo et al. 2004, Kudo & Ida 2013). As spring events such as snowmelt timing are projected to occur earlier under climate change (IPCC 2014), these mismatches are expected to become more common and pronounced. Phenological mismatch in a pollination system could have negative fitness consequences for plants through pollen limitation (Rafferty & Ives 2012, Kudo & Ida 2013), and pollinators through a lack of floral resources (CaraDonna et al. 2018, Schenk et al. 2018). At the community level, mismatches can lead to a collapse of the mutualism (Warren and Bradford 2014), and may reduce crop yield in agricultural systems if pollinator species richness is low (Bartomeus et al. 2013). While phenological responses to climate change have been well documented for plants (Parmesan & Yohe 2003, CaraDonna et al. 2014, König et al. 2018), less is known about the responses of pollinators, especially insect pollinators such as bees (Bartomeus et al. 2011). Even if bee and flowering phenologies are both responsive to temperature (Hegland et al. 2009, Forrest and Thomson 2011, Renner & Zohner 2018), they may not be equally sensitive to variation in temperature, potentially leading to a future mismatch under climate change (Ellwood et al. 2012, Ovaskainen et al. 2013, Petanidou et al. 2014, Olliff-Yang & Mesler 2018). The few studies that have examined the phenological response of bees to environmental cues have been limited by practical constraints mostly to small subsets of the total bee community (e.g., Kehrberger & Holzschuh 2019, Slominski & Burkle 2019). To understand the full effects of climate change on plant communities, it is imperative to determine the community-level drivers of bee phenology given the role of bees as the primary pollinators in most ecosystems (Klein et al. 2007).

From the perspective of pollination, the most important bee activity is the flight period in which adults transfer pollen. The flight period can be described by three points in time (hereafter phenophases): emergence from nests (the beginning of adult foraging, rather than the time of eclosion), timing of the peak abundance of foragers, and senescence (the end of foraging). These phenophases may be driven by different environmental cues, but may also be linked by developmental time (Donnelly et al. 2011, Keenan & Richardson 2015, Ettinger et al. 2018). Differences in temperature (Forrest & Thomson 2011), soil moisture (Danforth 1999, Olliff-Yang & Mesler 2018), and snowmelt timing along elevation gradients in montane regions (Pyke et al. 2011) may shift bee emergence phenology. Snowmelt timing may be particularly influential in areas where the growing season is limited by many months of persistent snowpack. Given these sensitivities, bee phenology has advanced, on average, due to climate change (Bartomeus et al. 2011). Certain functional traits (those that influence fitness) may shape bee phenology (Diamond et al. 2011, Forrest 2016), including variable thermal tolerance due to body mass (Stone & Wilmer 1989), nest location (Bartomeus et al. 2011), and the life stage in which bees overwinter (Fründ et al. 2013). Species that nest above ground are expected to be more responsive to climatic variation, as air temperature is more variable than soil temperature (Parton & Logan 1981), and the stage in which bees overwinter may interact with climate to determine when they can emerge from nests because prepupae-overwintering species must undergo additional development before emergence (Forrest 2016). While these drivers of phenology have been described in isolation, understanding their relative importance and potential interactions is impossible without a comprehensive study that examines them simultaneously at the community level.

Here, we present findings on the drivers of bee phenology using nine years of time-series data from a study of solitary bees along an elevation gradient. To make phenology estimates from a sparse time-series dataset and to avoid the biases of first-observation dates (Miller-Rushing et al. 2008, Lindén 2018, Inouye et al. 2019), we introduce an approach based on generalized additive models that calculates the first 5%, middle, and last 5% of a distribution (van Strein et al. 2008), corresponding to the three phenophases of foraging bee populations. We used these estimates to determine the drivers of bee phenology at the community level, including climate, topography, and bee traits, by comparing phenological variation among years. Specifically, we investigated the predictions that earlier phenophases are more strongly affected by climate variation compared to late phenophases (Forrest 2016), and that snowmelt timing is the primary driver of bee phenology in the sub-alpine ecosystem of this study, as it is for flower phenology (Inouye 2008). We also predicted that species that overwinter as adults emerge earlier than those that overwinter as pre-pupae, because they are less constrained by development time in the early growing season (Fründ et al. 2013). Motivated by the idea that species' phenological plasticity to climatic variation may be mediated by their traits (Diamond et al. 2011), we tested for an interaction between two traits (nest location and overwintering stage) and snowmelt timing. Finally, to explore whether bee phenology will track flower phenology under climate change (Ogilvie et al. 2017), we compared rates of advance in bee phenology in response to earlier snowmelt timing to published rates in flowering phenology at nearby study sites (CaraDonna et al. 2014). By providing the first community-level assessment of the drivers of bee phenology, our findings give insight into the future of plant-pollinator systems under forecasted climate change.

Methods

Study system

We gathered data at 18 sites around the Rocky Mountain Biological Laboratory (RMBL) in the Elk Mountains of western Colorado, USA from 2009 to 2017 (Table S2). Sites were located along an elevation transect (2456-3438 meters above sea-level) in montane and sub-alpine habitats dominated by a diverse mixture of perennial flowering species (CaraDonna et al. 2014). The area is highly seasonal, with snowpack typically persisting from November until May. The short growing season of only a few summer months results in predominantly univoltine bee life cycles, although some bee species may exhibit parsivoltine life cycles (Forrest et al. 2019). The European honey bee *Apis mellifera* and other non-native bees were absent during the study period.

Bee data collection

We sampled bees in habitat types that were representative of dominant vegetation types: wet meadows dominated by *Veratrum tenuipetalum*, those dominated by *Salix* spp., rocky dry meadows, and *Artemisia* spp. steppe. We conducted biweekly bee abundance surveys at each site using pan traps (following LeBuhn et al. 2003). We set out 10 each of white, fluorescent yellow, and fluorescent blue pan traps along two approx. perpendicular 45-meter transects at intervals of 3 meters, an array that passively attracts bees by mimicking a display of flowers. We deployed pan traps between approx. 0800 and 1700 (the period of maximum bee activity) only on warm, calm, sunny days and removed traps when these conditions changed drastically. Further details of the bee sampling are provided by Gezon et al. (2015). Specimens were identified to the lowest taxonomic resolution possible using a variety of resources (Michener et al. 1994, Michener 2000, Gibbs 2010, Scott et al. 2011). We excluded the pollen-foraging genera *Anthidium*, *Ashmeadiella*, *Atoposmia*, *Eucera*, *Diadasia*, and *Dianthidium* and all cleptoparasites (*Coelioxys, Epeolus*, *Holcopasites*, *Nomada*, *Stelis*, *Sphecodes*, and *Triepeolus*) because we were unable to identify them to species or they were very rare (together, individuals from these genera made up 4% of the collection). We were unable to identify most species of the diverse genus *Andrena*, so only four species in this genus are included in the analysis (this omission represents 3% of the total collection). The list of species included in the analysis is presented in Table S3. The population estimates at each sampling date were calculated as *bees captured/hour of sampling*, to account for variable sampling effort, including females and males (with the exception of *Lasioglossum* spp. for which we were only able to identify females). Because pan traps over-represent small bees such as halictids and under-represent large bees (Cane 2000), we excluded the large-bodied genus *Bombus* from analyses (3% of pan-collected specimens).

Climate, topographic, and trait data

To explain variation in bee phenology, we gathered data on yearly climate variation, topographic data associated with sites, and bee functional traits. We selected snowmelt timing, summer temperature, and summer rainfall as climate variables, elevation and solar incidence as topographic variables, and body mass, nest location, and overwintering stage as functional traits. Full details on the methods for gathering these data and justifications for their inclusion in the analyses are available in Appendix A.

Phenophase estimation

To bypass the problems of first-occurrence measures of sparse time-series data for many taxa including bees, take into account variable uncertainty, and estimate emergence, peak, and senescence dates from distributions of unknown form, we developed a novel application (validated in Appendix A) of Generalized Additive Models (GAMs; Wood 2006). For each species/site/year combination, we fit a GAM with day-of-year as the explanatory variable and abundance as the response using a cubic spline smoothing basis with a Gaussian distribution family and performed Generalized Cross-Validation to avoid over-fitting. We set the dimension of the smoothing basis to 4 when there were <5 observations, and 5 for ≥5 observations. For each model fit, we determined the peak timing by calculating the predicted date of the maximum of the model fit and found the first and last occurrence of 5% of the maximum to determine dates of emergence and senescence, respectively. We did not record estimates of emergence or senescence in cases where sampling began too late or ended too early to observe the tails of the distribution below 5% of the maximum. We also did not record estimates of peak abundance when we did not unambiguously observe the “crest” of the abundance curve, though we were able in some cases to estimate emergence or senescence but not peak by identifying the transition from zeroes to positive abundances. Due to this conservative approach, we were able to make emergence estimates for 47% of the total time-series, 40% for peak, and 53% for senescence. We calculated confidence intervals as twice the standard error at each phenophase. GAMs were implemented using the *mgcv* R-package (Wood 2012).

Modeling drivers of phenology

We created three candidate models by modeling emergence, peak, and senescence timing as functions of climate, topographic, and species trait variables, accounting for pseudo-replication at the site and species level by modeling these as random effects according to the equation

$$DOY_{phase} \sim \theta_{clim} + \theta_{topo} + \theta_{trait} + e_{site} + e_{sp}$$

where DOY_{phase} is the estimated day-of-year (*DOY*) of each phenophase, θ_{clim} are the climate variables (snowmelt date, summer temperature, and summer precipitation), θ_{topo} are the topographic variables (elevation and solar incidence), θ_{trait} are species traits (body mass, nest location, and overwintering stage), e_{site} are sites, and e_{sp} are species. θ terms represent fixed effects, while *e* terms represent random effects, forming a mixed effects model (Bates et al. 2014). All terms were modeled as additive effects, with no interactions in this top model. Due to heterogeneity in the frequency of sampling, population numbers, and shape of the abundance curves, phenophase estimates have heterogeneous confidence intervals. To propagate this uncertainty through our analysis, we weighted the estimates based on the inverse of their standard errors. To generate directly comparable standardized effect sizes, we scaled and centered explanatory variables (Gelman & Hill 2007). To make categorical variables comparable to continuous ones, we scaled the continuous variables by 0.5 standard deviations (Gelman 2008).

Because it is not known which of the proposed variables determine bee phenology at the community level, we employed a model averaging protocol, following Burnham & Anderson (1998), to determine which variables were influential. We fit models with each possible combination of predictor variables and averaged coefficients from models within 4 AIC units of the best one. Because model averaging can bias estimates (Cade 2015), we compared the averaged coefficients to the coefficients from the top model for each phenophase, finding very tight correlations (Pearson $r > 0.999$ for all three models, Figure A.5). Additionally, we tested for multicollinearity, finding sufficiently low variance inflation factors for each predictor (Appendix A).

To investigate whether climate would more strongly affect emergence timing, while other variables would be more influential for later phenophases, we calculated marginal and conditional R^2 values based on the single best model in the top model set and investigated variance partitioned between climate and trait variables by calculating the proportion of variance explained by models fitted with just climate and trait variables versus the top model. Due to small sample sizes for some species/predictor variable combinations, we were unable to estimate independent parameter values for every species, and treated species as a random effect in the full model. To provide a visual aid of some species-specific responses to advancing snowmelt and to compare with reported flower phenology shifts, we performed a reduced analysis with the most common species (those that had ≥10 species/site/year estimates for two or more phenophases), modeling species responses as $DOY_{phase} \sim \theta_{snowmelt} * species + e_{site}$. This analysis was conducted for 10 species: three from the Andrenidae, one from the Colletidae, four from the Halictidae, and two from the Megachilidae. We did not control for phylogeny in the analyses because we did not seek to describe the evolution of the present traits. To investigate whether certain traits influence the phenological responsiveness of species to climate, we modeled phenophase estimates as functions of snowmelt (for other climatic variables, see Appendix A) interacting with nest location and overwintering stage, with variable intercepts and slopes, holding all else equal, modeled as $DOY_{phase} \sim \theta_{snowmelt} * \theta_{trait} + e_{sp} + e_{site}$. We did not include interaction terms in the top model due to the difficulty of estimating many additional parameters with limited data and complications with model averaging (Galipaud et al. 2014). We also tested for the presence of phenological sequences (Keenan & Richardson 2015, Ettinger et al. 2018) by modeling peak and senescence as linear functions of emergence. Model averaging and R^2 calculation (*r.squaredGLMM* function) were done using the *MuMIn* package (Barton 2015). We tested for significance of interactions using the *lmerTest* package (Kuznetsova et al. 2017), and all analyses were run in R version 3.4.4 (R core team 2018).

Results

The bee monitoring study yielded 1606 time-series of at least 4 abundance measures for 67 species at 18 sites (Table S2) in 9 years (2009-2017), representing 23,742 collected specimens across 751 sampling periods. The mean maximum species-specific catch rate across all time-series was 1.48 bees/hour, ranging from 0.11 to 35.14 bees/hour per sampling period. We were able to estimate 519 emergence, 438 peak, and 584 senescence dates. The mean emergence day-of-year across all years, sites, and species was 24 June ± 25 days, mean peak was 10 July ± 21 days, and mean senescence was 30 July ± 23 days. Responses to snowmelt, measured as the slope coefficient, fell generally between 0 and 1 days of phenological advance per day of snowmelt advance for most species (Figure 2.1; Table S4). Five phenophases across four species (*Halictus* *virgatellus* emergence and peak, *Lasioglossum sedi* senescence, *Panurginus ineptus* emergence, and *Pseudopanurgus bakeri* senescence) delayed in response to advanced snowmelt, though these effects were not significant. *Hoplitis fulgida* exhibited the greatest response in emergence to variation in snowmelt timing, while *Hoplitis robusta* had the greatest peak response (Figure 2.1). As an illustrative example, in the severe drought year of 2012, snowmelt occurred 25 days earlier than in other years, the median emergence phenology advanced by 34 days, peak by 15 days, and senescence by 4 days.

Each candidate predictor variable was represented in the model set (Figure 2.2). Bees emerged (11.52 ± 2.68), peaked (12.82 ± 2.42), and senesced (7.81 ± 2.44) later in years with later snowmelt date, and snowmelt timing had the largest absolute effect size among the climate variables for each phenophase. Elevation had the largest effect of the topographic variables, with bees at higher elevations emerging (13.57 ± 3.23) and peaking later (7.76 ± 3.65), but senescing earlier (-5.92 ± 4.05). Of the species traits, nest location had the largest effect on emergence timing; compared to bees that nest above ground, those that nest below ground emerged (11.21 ± 4.30) later but peaked (-4.57 ± 3.84) and senesced earlier (-9.82 ± 4.29). Overwintering stage had the largest effects on peak and senescence timing; bees that overwinter as adults emerged (1.91 ± 3.52), peaked (11.20 ± 3.23), and senesced earlier (20.91 ± 3.59) than those that overwinter as pre-pupae. Each phenophase model was roughly equally able to predict the variation in yearly phenology (Figure 2.3a). When phenophases were predicted with subsets of the predictor variables, climate variables explained a higher proportion of the total variation for earlier phenophases, while species traits explained more variation in later phenophases (Figure

2.3b). Full numerical details including significance are provided in Tables S5-S6.

There was a significant interaction between nest location and snowmelt timing for emergence (t_{433}=-3.278, p<0.01) and peak phenology (t_{360}=-2.861, p<0.01) (Figure 2.4), and the difference in slope decreased across the phenophases. The interaction between snowmelt timing and overwintering stage was greatest for peak timing and smallest for senescence timing, but these interactions were not statistically significant (emergence: t_{441}=-0.867, p>0.05, peak t_{368}=-1.565, p>0.05, senescence t_{470}=-0.481, p>0.05). Lastly, we found that emergence significantly predicted peak timing ($F_{1,212}$=201.2, p<0.0001) and senescence timing ($F_{1,104}$=29.63, p<0.0001) but that emergence described less variation in senescence (R^2=0.22) than in peak timing (R^2=0.49) (Figure A.6).

Discussion

We analyzed time-series abundance data from a nine-year bee monitoring project to provide the first community-wide assessment of the main predictors of bee emergence, peak, and senescence phenology. While yearly climatic variation, topography, and species functional traits all shaped bee phenology, the emergence and peak phenophases were particularly sensitive to climate. Following patterns in early-season flowering phenology (Inouye 2008), the timing of early snowmelt, which is a determinant of how much thermal energy is received by bee nests in this montane study area, was particularly influential in advancing the early phenophases. The later, senescence phenophase was determined to a greater extent by functional traits including nest location and the life stage in which bees overwinter (Fründ et al. 2013). Nest location also disposed certain species to respond more dynamically to climatic variation. Contrary to predictions

(Forrest 2016), we did not find that adult-overwintering species responded more dynamically to climatic cues despite being less limited by development time prior to emergence. These findings lead us to predict that under increasing temperatures and earlier snowmelt due to climate change, the bee community foraging season will begin earlier and increase in overall duration. However, certain species may be less able to shift their phenology due to variable responses (Figure 2.1) on the basis of functional traits (Figure 2.4).

Bee phenology is determined by climate, topography, and species traits

Snowmelt timing was the main climatic driver of bee phenology, with earlier dates of snowmelt advancing emergence and peak in particular (Figure 2.2, panel 1). Snowmelt in this system is a major determinant of how much thermal radiation is received by bee nests (for species that nest below ground), so this finding supports previous work suggesting that adult bee emergence has thermal requirements (Kemp and Bosch 2005, White et al. 2009, Forrest and Thomson 2011). Thus, we expect bee species in areas without persistent snowpack to similarly adjust their phenology on the basis of thermal energy. Higher summer temperatures and lower summer rainfall resulted in significantly earlier bee emergence but not peak or senescence, resulting in longer community-wide flight periods. Spring events that shape the onset of a phenological process can have cascading effects on later phenophases, leading to phenological sequences, but this cascade can become less pronounced due to variation in developmental time and the influence of other cues (Keenan & Richardson 2015, Ettinger et al. 2018). We found that emergence timing did predict peak and senescence timing, but that emergence timing described less variation in senescence than in peak timing (Figure A.6). Thus, the earlier phenophase of bee foraging influences, but does not determine, the later phenophases. Sites at higher elevations experienced later bee emergence and peak times, but earlier senescence time (though the senescence effect was not significant), resulting in a shortened foraging season (Figure 2.2, panel 2). These findings support studies that found a phenological shift in bumble bee abundance based on elevation (Pyke et al. 2011) and are in line with findings on flower phenology (Theobald et al. 2017). We note that because we calculated climatic variables as constant across sites within each year, the elevation effect may be driven by local variation in snowmelt timing, which is determined in part by solar incidence and elevation in montane regions.

Turning to species traits, nest location and overwintering stage, but not body mass, had significant effects on phenophases (Figure 2.2, panel 3). Ground-nesting bee species emerged later than those that nest above ground, but senesced earlier, indicating that below-ground nesting bee species have shorter average foraging periods. While our finding that adult-overwintering bees have earlier phenology supports the idea that overwintering stage has a large effect on insect phenology broadly (Fründ et al. 2013, Forrest 2016), we were surprised to find that the effect was larger on peak and senescence timing than on emergence timing, which deviates from our initial expectation that overwintering stage would primarily dictate emergence phenology. It may be that there is an evolutionary trade-off between adult mortality rate and the fast development rate that allows certain species to overwinter as adults (see Wright et al. [2010] for an example in plants) or simply that adult-overwintering species have shorter effective foraging lifespans because they spend more time in the adult phase. More long-term studies are needed to understand if this is a general trend, and mechanistic studies would provide insight on the physiological underpinnings of the pattern.

While climatic variation, topography, and species traits determine the date of bee phenophases when viewed separately, bee species' functional traits mediate their climate sensitivities (i.e., our models support an interaction between functional traits and environment). Above-ground nesting species are more sensitive to snowmelt timing (Figure 2.4, top panel) and average summer temperature (Appendix A) than those that nest below ground. This finding is slightly counter-intuitive when we consider that ground-nesting bees are buried by snow. The discrepancy may be explained by recognizing that snowmelt timing is correlated with other potential phenological cues such as spring temperature. We would expect above-ground nesting bees to be more sensitive to temperature fluctuations, as above-ground temperature varies more than below-ground (Parton and Logan 1981), and their nests are not insulated by snowpack. This suggests that above-ground nesters may suffer less phenological mismatch with plants under increased variability due to climate change. Surprisingly, we did not find a significant interaction between bee overwintering stage and snowmelt timing (Figure 2.4, bottom panel). Bees that overwinter as adults require less developmental time before emerging in the spring, so we expected their phenology to be more responsive to snowmelt timing. The finding that adult-overwintering bee species do not take advantage of this shorter developmental time suggests that there may not be a benefit to greater phenological sensitivity, or that other factors limit their sensitivity.

Different drivers of emergence and senescence phenology

The effect of snowmelt timing on emergence was nearly 50% greater than it was on senescence, and the absolute effects of temperature and rainfall on emergence were nearly an order of magnitude higher than on senescence, indicating that the onset of foraging is timed by external cues, while the end is less dynamic. These results match plant phenology findings that showed a reduction in the effect of snowmelt timing on later phenophases (Wipf 2010). Similarly, in butterflies, early phenophases have been shown to advance more frequently in response to recent climate change (Roy & Sparks 2000). Summer temperature and rainfall span the entirety of the active bee foraging season and also had larger effects on emergence than on later phenophases (Figure 2.2, panel 1), indicating that the pattern of a greater climate influence on early phenology is not entirely a byproduct of spring-specific climate variables. Late season phenology may be less sensitive to climatic fall events such as the date of first frost because adult bees – particularly those that nest below ground – are insulated from cold nights in their nests.

Although the predictive power of our models was similar for all phenophases (Figure 2.3a), climate variables explained more variance for early phenophases, and traits explained more variance for later phenophases (Figure 2.3b, Appendix A). The effect of snowmelt on senescence is diluted by inherent inter-specific variation in foraging flight period. In other words, the effect of the phenological sequence becomes reduced in later phenophases (Figure A.6). Some plants exhibit stronger climatic control of spring phenology (Menzel 2003) but stronger genetic control of autumn phenology (Fracheboud et al. 2009), and our results hint at a similar pattern in bees. The drivers of senescence phenology in insects may be particularly complex due to variation in life-history strategies (Gallinat et al. 2015). For example, univoltine insect species are expected to advance their fall senescence in response to warming, while multivoltine species may delay the end of their active period by producing additional generations. Lastly, our finding that spring and fall phenophases are determined by different drivers points to the necessity of studying the whole phenological distributions rather than focusing on the onset of an active period.

Climate change implications

Two of the main effects of climate change in montane regions are an advance of snowmelt timing and increased temperatures (Ogilvie et al. 2017). Bee phenology at the community level is tied to snowmelt but does not precisely track it, and phenophases exhibit different responses to climatic variation. As climate explained more variation and produced larger shifts in early phenophases (Figure 2.2b), we expect that emergence and peak timing in areas of the world with increasing temperatures and decreasing precipitation will shift at greater rates than senescence, extending the active flight period of adult solitary bees. This could lead to additional generations during the growing season (Altermatt 2010), or potentially a developmental trap in which species produce a maladaptive second generation that is ill-prepared for autumn conditions (Van Dyck et al. 2014). An extended active bee foraging season may have positive pollination outcomes, allowing pollen-limited plants to reproduce for longer periods of time, though this effect may be tempered by phenological mismatches or declining populations (Hedhly et al. 2009, Vanbergen et al. 2013).

Given observed trends and projections for earlier snowmelt timing, it is relevant to compare variation in bee phenology to that of flowers. A 39-year study of flowering phenology at the RMBL documented that the date of first flowering has advanced by 0.89±0.083 days per day of snowmelt advance (Caradonna et al. 2014). The flowering community in this subalpine region shows two distinct peaks in total floral abundance (Aldridge et al. 2011) which have shifted at different rates (first peak: 0.74±0.056 days per day of snowmelt; second peak: 0.53±0.095 days). We found that bee emergence timing shifted by 0.49±0.11 days per day of snowmelt advance (peak 0.49±0.09 days, and senescence 0.28±0.1 days). Thus, bee phenophases are potentially less sensitive than flowering phenophases to shifts in snowmelt timing, with bee emergence advancing at 55% the rate of first flowering, and bee peak advancing at 67% and 93% the rate of the two flower peaks. The discrepancy in the rates of shift of bee emergence and first flowering may be partially due to differences in the metric of onset, as first occurrence data may be biased and are inherently different from our measure of the first 5% of the foraging population (van Strien et al. 2008). We also note that the flower phenology study comprised a narrow elevation band at separate sites in the middle of the present study's roughly 1000m elevation transect, and patterns of phenological shift may vary across elevation. Nevertheless, this difference in the sensitivities of bee and flowering phenology indicates the potential for a community-wide mismatch in this plant-pollinator system due to climate change. While the ability of both bees and flowering plants to respond to climatic cues is a promising sign for future synchrony under climate warming, the difference in rates of shift suggests at least short-term mismatches, which may become chronic if the interacting species are not able to adapt or shift their ranges to match the rate of climate change (van Asch et al. 2007).

Conclusions

Community-level bee phenology is shaped primarily by climatic cues, elevation, nest location, and overwintering stage. Early phenology is particularly sensitive to climatic variation while later phenology is determined more by functional traits, suggesting that climate change will affect emergence more than senescence, potentially lengthening the active foraging period of bees. And while more long-term and species-level studies are needed, the present results suggest that the responsiveness of bee phenology may lag behind that of flowers.

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Figures

Figure 2.1. Common species vary in their responses to snowmelt timing, with most phenophase shifts falling between no response (0, dashed line) and perfect tracking (1, dotted line) of snowmelt. Points to the left of zero represent advances in response to advanced snowmelt timing, and those to the right represent delays. Blue points represent emergence shifts, green points represent peak, and brown points represent senescence. The width of bars represents twice the standard errors around the estimates of response.

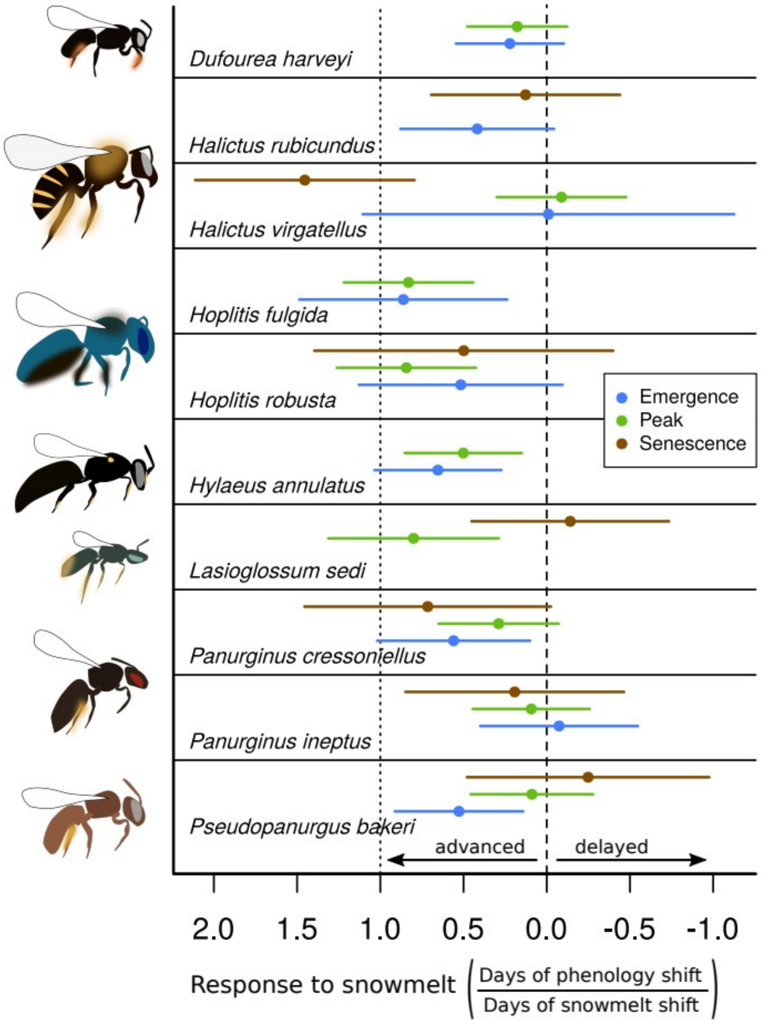


Figure 2.2. Bee phenology is determined by inter-annual climatic variation, topography, and several species traits. The drivers vary in their relative effect across the phenophases, with the effect of climate variables generally lower for later phenophases. The first panel shows the standardized effect sizes of climate variables, the second topographic variables, and the third species traits on emergence (blue), peak (green), and senescence timing (brown) with standard errors around the estimates shown as brackets. Values greater than 0 represent later phenology, and those less than 0 represent earlier phenology. Standardized effect sizes are defined as the slope coefficients derived from scaled and centered explanatory variables.

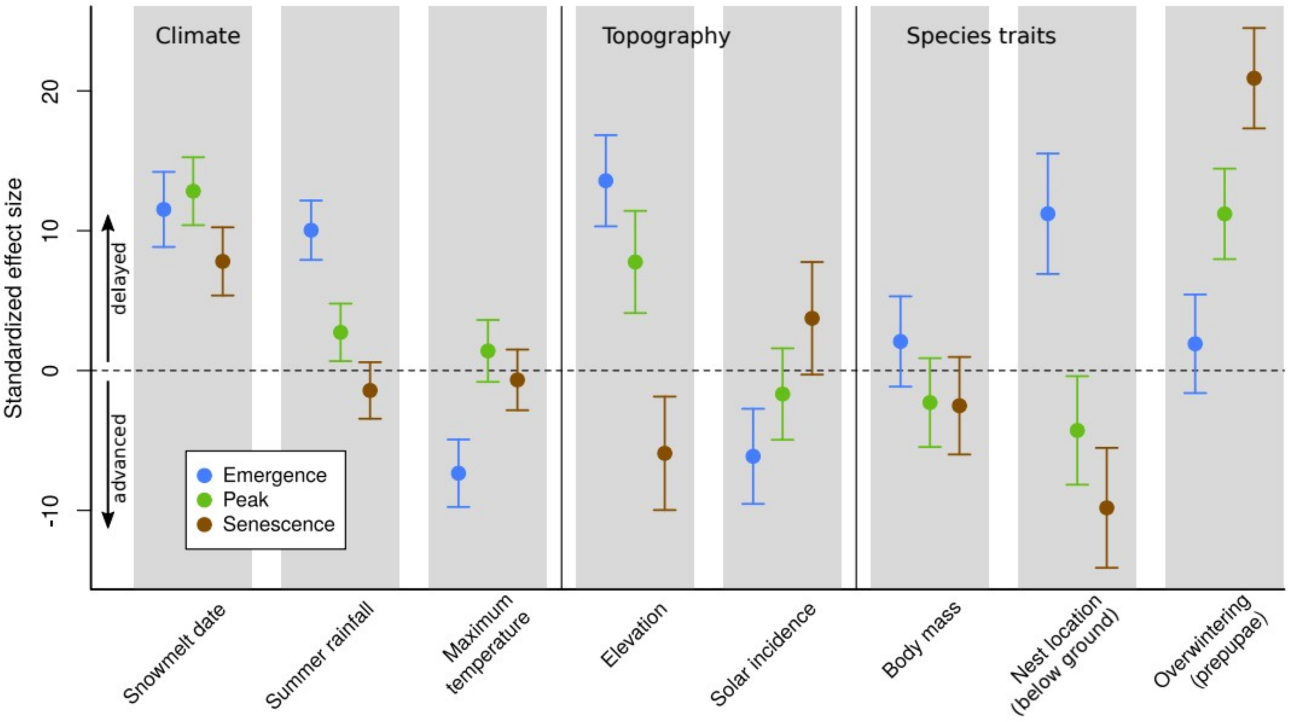


Figure 2.3. While the models were roughly equal in their ability to predict phenological shifts across all phenophases (panel a), early phenophases were predicted more strongly by climate variables and late phenophases by species traits (panel b). Panel a compares the marginal and conditional R^2 values across the top models for each phenophase, and panel b shows the ratio of variance explained by reduced models of only climate and trait variables versus the variance explained by the top model. The ratio of variance in panel b was calculated as R^2_{subset}/R^2_{total} where R^2_{subset} is the marginal R^2 of a model containing just climate or just species trait variables and R^2_{total} is that of the top model containing all variables.

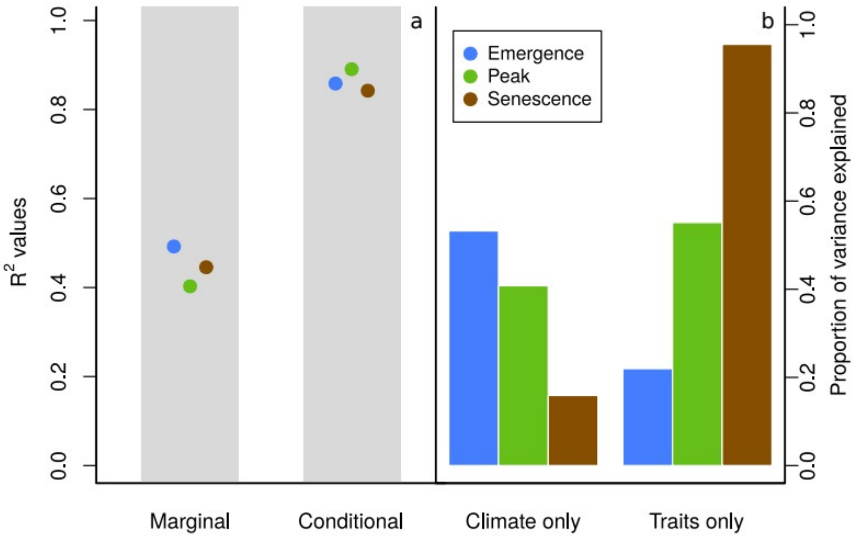
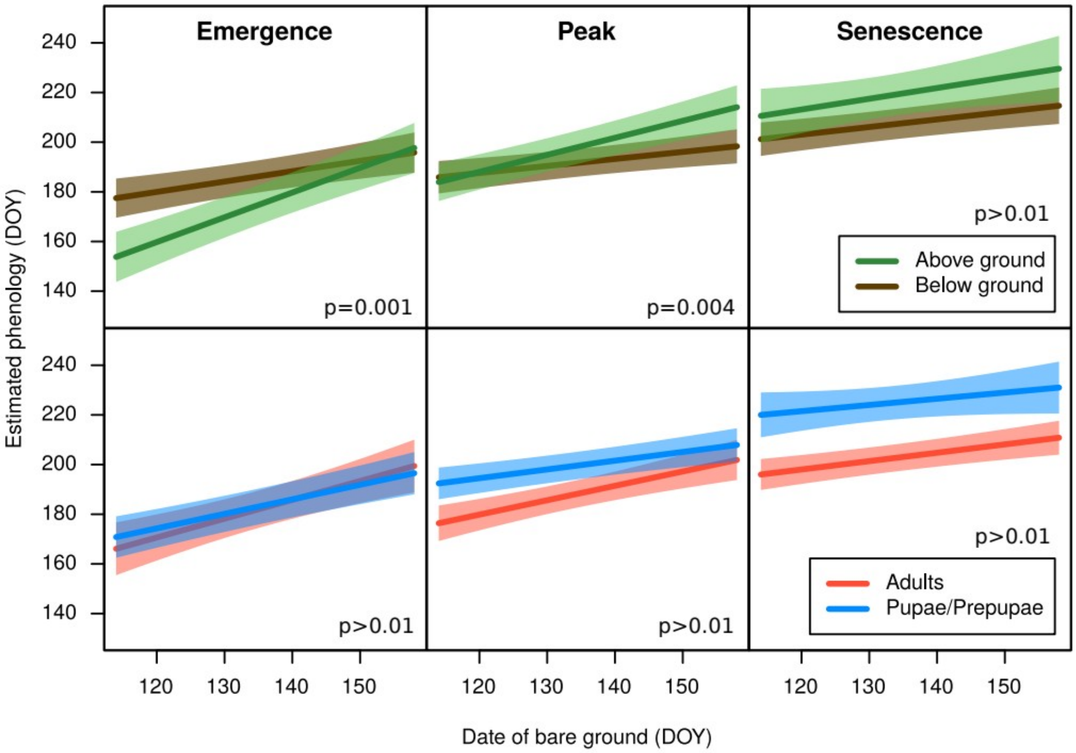


Figure 2.4. Bee species that nest above ground and those that overwinter as adults are more sensitive to variation in snowmelt timing than species that nest below ground and that overwinter as pupae or prepupae. The top three panels show predicted phenophase responses to snowmelt based on nesting location, and the bottom panels show the same based on overwintering stage. The slope of the lines represents the sensitivity of each phenophase to snowmelt timing. P-values are presented for the two significant differences in slope at the α=0.05 level.



CHAPTER 3

SKEWNESS IN BEE AND FLOWER PHENOLOGICAL DISTRIBUTIONS

Abstract

Phenological distributions are characterized by their central tendency, breadth, and shape, and all three determine the extent to which interacting species overlap in time. Pollination mutualisms rely on temporal co-occurrence of pollinators and their floral resources, and while much work has been done to characterize the shapes of flower phenological distributions, similar studies including pollinators are lacking. Here, we provide the first broad assessment of skewness, a component of distribution shape, for a bee community. We compare skewness in bees to that in flowers, relate bee and flower skewness to other properties of their phenology, and quantify the potential consequences of differences in skewness between bees and flowers. Both bee and flower phenologies tend to be right-skewed, with a more exaggerated asymmetry in bees. Early-season species tend to be the most skewed, and this relationship is also stronger in bees than in flowers. Based on a simulation experiment, differences in bee and flower skewness could account for up to 14% of pair-wise overlap differences. Given the potential for interaction loss, we argue that difference in skewness of interacting species is an under-appreciated property of phenological change.

Introduction

Timings of seasonal life-history events (phenology) are often characterized by single points in time (e.g., first-appearance date), but in reality, these events are typically distributed processes (Carter et al., 2018; Inouye et al. 2019). Species phenological distributions are characterized by their central tendency, their breadth, and their shape (e.g., mean, standard deviation, and skewness) (Rathcke et al., 1985). Ecological interactions usually require temporal co-occurrence, where the population performance of any species is dependent on phenological overlap with resource availability. In the case of pollination and other mutualistic interactions, interacting species benefit from maximizing temporal overlap with one another, while dealing with the fitness costs of changing their phenology (Visser et al., 2012). The degree of overlap between interacting species is determined by the mean, breadth, and shape of both species' phenological distributions (Fig. 3.1), with differences in any one of the three properties being enough to reduce overlap. While the shape of phenological distributions has been recognized as an important component of species interactions (Thomson, 1980), studies of phenological match/mismatch in plants and pollinators have focused primarily on how first or mean dates of seasonal activity shift in response to varying cues (Inouye et al., 2019) and how the temporal breadth of their activity stretches or contracts. The importance of skewness differences in determining mismatch in pollination interactions remains unclear. This is in part because there has not been a systemic analysis of skewness in phenological distributions across many species of pollinators and flowering plants together.

Flower phenological distributions are often right-skewed, with a long, trailing tail after the peak of flowering in prairie (Rabinowitz et al., 1981) and montane (Thomson, 1980) ecosystems. Within populations, the degree of skewness can vary among years

(Blionis et al., 2001; Forrest & Thomson, 2010). Phenological distribution shape may also be affected by local resource competition that reduces plant size, which is in turn correlated with floral phenology skewness (Schmitt, 1983). It has also been suggested that the right-skewness of flowering phenologies may be a product of selective pressure for early flowering (Forrest & Thomson, 2010) and that recent climate change has affected the shapes of flower phenological distributions (CaraDonna et al., 2014). While the typical patterns of flower phenological skewness are well understood, we do not know if these patterns are also similar for pollinators. There is reason to suspect that phenological sensitivity differs between plants and pollinators and that the seasonal onset and end of activity in pollinators (such as bees) shift at different rates (Stemkovski et al., 2020). Thus, a community-wide assessment to compare bee and flower phenological skewness is warranted.

In this study, we quantified phenological skewness for multiple bee and flower species within a montane community. We determined the relative prevalence of right-skewed, left-skewed, and symmetrical distributions, and examined the differences between bees and flowers in how skewness relates to other properties of their phenological distributions. *A priori*, we predicted that bee phenologies would be similarly skewed to those of flowers, but that bees active in the early season would have phenologies more strongly right-skewed than those in the late season due to a hard limit on activity before snowmelt in the study system. Lastly, we performed a simulation study to gain perspective on the potential consequences that variation in skewness in this community may have on phenological overlap between bees and flowers.

Methods

Data sources

We used flower phenology data from a long-term monitoring program spanning from 1974 to 2019 at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA, a mountainous location with a short summer growing season set ~2890 m above sea level (CaraDonna et al., 2014; Inouye, 2008). The total number of flowers was counted approx. three times per week for the extent of the growing season for all flowering species in 4 m^2 fixed plots. This dataset includes mainly long-lived perennial forb species. Further details on this program are reported by CaraDonna et al. (2014) and Inouye (2008), and all data are available through Open Science Framework (Inouye et al., 2022). For our analysis, we included 35 flower plots aggregated into 8 sites by proximity to agree with the spatial scale of the bee phenology sites. We obtained bee phenology data from a companion study to the flower phenology project which tracked bee abundance from 2009 to 2020 at the RMBL (Ogilvie et al., 2017; Stemkovski et al., 2020). Bee abundance was measured using pan traps approx. every two weeks across the growing season at 18 sites spaced across an elevation gradient (Gezon et al., 2015). Because pan traps are biased toward collecting smaller-bodied bees, hand netting was used for bumble bees (*Bombus* spp.). Additional details on bee data collection and all data are available through Open Science Framework (Irwin et al., 2018). All data processing steps and analyses for this study can be viewed and reproduced using code available online (https://doi.org/10.5281/zenodo.6561297; Stemkovski et al., 2022).

Data processing

We formatted and standardized flower and bee data to make them directly comparable. For all data, we excluded records with uncertain identifications and those that were identified only to genus. We excluded all grass and sedge species, but included shrubs. The bee abundance data were derived from multiple pan traps or netters, so we aggregated flower and bee counts across plots/traps/netters per site. For the bee data, we included only female bees because female specimen identifications were more fully resolved and because combining females and males could lead to inaccurate estimates of skewness because males often emerge later than females in social species. We distinguished queen and worker castes of bumble bees (*Bombus* spp.) to avoid biasing skewness estimation by confounding an early-season queen peak in abundance and a later peak in worker abundance. Because bumble bees were sampled explicitly by netting and due to difficulties of combining sampling effort between netting and pan traps, we excluded pan-trapped *Bombus* and net-trapped non-*Bombus* bees. To ensure that we only included sampling periods that consistently captured representative samples of abundance, we excluded sampling days when traps were deployed for less than three hours and excluded netting days with less than one hour of effort (excluding 17 of 778 trap sampling days and 21 of 809 net sampling days). Lastly, to ensure adequate sample size and robust skewness estimation, we only considered time-series with at least 10 individual bee records per year and at least 100 flower records per year. Thus, we excluded 1,932 of 18,710 bee records (10.3%) and 126,659 of 3,943,796 flower records (3.2%).

Skewness calculation and predictors

We calculated skewness as the Fisher-Pearson standardized third-moment coefficient of skewness (g_1), as implemented in the *moments* R-package (Komsta et al., 2015), for each site/year/species phenological abundance distribution (i.e., frequencies of bee and flower abundance by date). This approach uses only the data and avoids making assumptions about functional form necessary for more complex model fitting. We tested whether skewness in individual time-series was different from zero (corresponding to a symmetrical distribution) using D'Agostino's K^2 test (D'Agostino, 1970). We used a one-sample t-test to assess whether skewness across flower time-series was significantly different from zero, and a two-sample t-test to test whether bee skewness was significantly different from flower skewness.

To examine whether and how skewness in bees and flowers was related to other properties of their phenological abundance distributions, we calculated the means and standard deviations of each distribution. To test whether the phenological position of species (how early or late they are active in a season) predicted their skewness, we modeled skewness as a mixed-effects model with phenological mean interacting with guild (flowers vs. bees) as fixed effects, and accounted for repeated measures with species, site, and year as variable-slope random effects. We note that, statistically, means are shifted by skewness, so the two are necessarily linked to a certain extent. To test whether species with longer active seasons tended to be more skewed, we modeled skewness as a mixed-effects model with distributions' standard deviation interacting with guild as fixed effects, and the same random effects structure as in the previous model.

Overlap calculation

To demonstrate the potential phenological match/mismatch consequences of skewness differences between bees and flowers, we simulated the maximum possible overlap of distributions with different skews. To do this, we repeatedly generated pairs of skew-normal density distributions (Azzalini, 2020) with two different skewness parameters, representing the phenological distributions of one flower species and one bee species. To find the maximum possible overlap, we perturbed the mean and standard deviation of one distribution in 2000 total parameter combinations. This was a somewhat coarse discretization, so slightly distorted results are expected at a fine scale of comparison. For each pair of perturbed distributions, we then calculated the overlap coefficient (Inman et al., 1989) by integrating to find the area encompassed by both probability density curves (as illustrated in Fig. 3.1), and recorded the largest of the resulting overlap coefficients. We repeated this procedure for every pairwise combination of 50 skewness values sequenced evenly between -5 and 5, resulting in 2500 (i.e., 50^2) total comparisons. In other words, we calculated the largest possible overlap of paired distributions by keeping skewness constant and allowing mean and standard deviation to vary freely. A visual representation of this simulation process is provided in Appendix B: Section B.4. To provide perspective, we calculated the bounds of the middle 95% of skewness values from the empirical datasets and overlayed these onto the simulated overlap estimates.

Results

We estimated skewness for 2,754 flower time-series and 480 bee time-series. The time-series represented 92 plant species across 71 genera, and 49 bee species/castes across 14 genera. In time-series with sufficient data to calculate skewness, the average flowering period (across all years, sites, and species) was centered on July 10, and bee foraging on July 2. The typical phenological breadth across time-series, measured as one standard deviation on either side of center, was 14 days in flowers and 39 days in bees. Flower time-series were significantly right-skewed (g_1 = 0.33, t_{3232} = 20.05, $p < 0.01$), and bee time-series were also right skewed (g_1 = 0.89), significantly more so than flowers (t_{3232} = 13.84, $p < 0.01$). Viewed individually, 48.7% of flower time-series were significantly right-skewed, only 13.6% were significantly left-skewed, and 37.7% were not significantly different from symmetrical. Of bee time-series, 48.5% were right-skewed, 9.4% were left-skewed, and 42.1% were not significantly different from symmetrical (Fig. 3.2). Skewness was somewhat affected by data truncation, though both bees and flower curves were still right-skewed regardless of truncation type (Appendix B: Section B.1).

Skewness in plants was significantly predicted by how early or late in the season a species flowered, with early season species being more strongly right-skewed (mean-to-skew slope significantly different from zero; $t= -8.32$, $p < 0.01$). This relationship was more pronounced in bees (mean-to-skew slope significantly steeper in bees than in flowers; $t =-13.01$, $p < 0.01$), with early season bees being right-skewed, and later-season bees being left-skewed (Fig. 3.3, top panel). Plants with longer flowering periods tended to be more right-skewed ($t = 7.03$, $p < 0.01$), while bees with longer active periods tended to be more symmetrical ($t = -10.06$, $p < 0.01$) (Fig. 3.3, bottom panel).

Simulated overlap losses between interacting species ranged from 0% at perfectly matched skewness values to 25% for distributions where one has $g_1 = 5$ and the other $g_1 = -5$ (Fig. 3.4). The maximum overlap loss for the central 95% of bee and flower skewness values found in our datasets was 14% overlap loss. We do not directly compare bee and flower distribution breadth because the frequency of bee data collection inherently discounted species with short active periods. Comprehensive species lists and summary statistics are provided in Appendix B: Section B.3.

Discussion

We found that both bee and flower phenological distributions tend to be right-skewed (Fig. 3.2), suggesting that similar processes are acting on bees and plants to determine the shape of their phenological distributions. Multiple explanations have been offered for skewness in flowering time, including selection for skewed flowering driven by pollinators and resources (Forrest & Thomson, 2010; Thomson, 1980), by-products of intraspecific competition (Schmitt, 1983), and simple geometrical necessity because daily survival probabilities are cumulative and inherently skewed (Blionis et al., 2001). Multiple distinct scenarios that may lead to skewed phenological distributions can be examined by focusing on onset rates (e.g., flower opening, bee emergence) and cessation rates (e.g., floral senescence, bee mortality). First, differences in the intra-annual dispersion of onset and cessation rates may produce phenological skewness. Second, variable phenology among individuals with unequal representation (e.g., different numbers of flowers per individual plant) may produce skewed aggregate distributions even when the component onset and end rates are equally dispersed. Third, onset and/or cessation distributions themselves may be skewed. Further, combinations of these processes may influence the shapes of phenological distributions in complex ways. In the context of our findings, the prevalence of right-skewness in bee phenological distributions suggests that, on average, bees emerge with more synchrony than with which they cease foraging. Drawing conclusions about the processes behind the observed skewness in flower phenology is more difficult due to flower counts being aggregated across individual plants in our data.

While demographic data (i.e., tracking individual plants and insects) beyond what we present here are needed to determine the mechanistic causes of the differences in onset/end variance that produce skewed phenology, some information can be gleaned by comparing skewness with other phenological properties. We found that bees that were active closer to the beginning of the growing season tended to be more right-skewed (Fig. 3.3). For example, the early season sweat bee *Lasioglossum sedi*, with an average capture date of June 16 across all sites and years, was strongly right-skewed (g_1 = 1.94), while the later-season masked bee *Hylaeus annulatus*, with a capture date of August 5 on average, tended to be left-skewed (g_1 = -0.27). A similar but weaker pattern was seen in flowers, though flowers did not tend to flip to left-skewness at the end of the season. In the snowy sub-alpine environment of the present study, the onset of activity is strongly limited for flowers (Inouye, 2008) and bees (Stemkovski et al., 2020) by the timing of snowmelt. Because species closer in time to this unambiguous onset cue tended to be more strongly right-skewed, we can reasonably infer that this cue, or at least the phenological response of species to this cue, is less intra-annually variable than the processes that lead to flower senescence and the end of bee foraging (e.g., frost events, precipitation, inherent lifespan/persistence, etc.). By extension, these findings suggest that later-season onset cues, or species' phenological responses to them, are more variable than the early snowmelt cue.

Our finding of right-skewness in flowering phenology was broadly similar to previously published results, though we found that average flowering skewness in the present study (g_1 = 0.33) was less positively skewed than in a previous study in the same area (g_1 = 0.46; Thomson, 1980) and a prairie community (g_1 = 0.41, Rabinowitz et al., 1981). While this comparison is useful, we caution against over-interpretation due to differences between the studies such as frequency and duration of monitoring and size of sampling plots. Turning to insects, we lack other studies focused specifically on phenological skewness in other insect groups, but individual abundance time-series indicate that right-skewness may also be found in univoltine butterflies (Dennis et al., 2017; Zonneveld, 1991), flies (Haab et al., 2019; Judd et al., 1991), and hemipterans (Gamarra et al., 2020; Ma et al., 2008). Comparisons with multi-voltine species in areas with longer growing seasons are difficult, and further research is needed to compare uni- and multi-modal phenological distributions, especially as climate change creates opportunities for additional generations in some insects (Dyck et al., 2015; Hodgson et al., 2011). Given the apparent prevalence of skewness in phenological distributions, we encourage researchers to use modeling methods that are designed to capture asymmetry (Belitz et al., 2020). We advise caution when closely comparing skewness values between bees and flowers because there is inherently more uncertainty in the bee dataset due to the methodological challenges of tracking wild insects.

The consequences of variable skewness in flower and pollinator distributions for phenological match/mismatch in natural populations are not well understood and require further study. When considering simulated pair-wise interactions, the skewness of phenological distributions alone has the potential to cause up to 14% loss in overlap in the species that we studied (Fig. 3.4). We note that this analysis encompassed only phenological differences, and in reality there are other barriers to pollination such as specialization or morphological limitations. It is also important to consider that loss of overlap does not necessarily translate to fitness losses, as pollen limitation is not ubiquitous (Knight et al., 2005) and many bees and flowering plants are generalists (Waser et al., 1996). Beyond pollination interactions, differences in skewness have the potential to affect other mutualistic interactions, predator-prey and host-parasite interactions, and to alter patterns of inter- and intra-specific competition within guilds. As both flowers and bees tend to be right-skewed, individuals may compete most strongly with their conspecifics in the early part of their activity. Future studies should examine how phenological skewness translates into fitness consequences through changes in inter- and intra-specific interactions throughout species' active periods.

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Figures

Figure 3.1. Conceptual diagram of the causes of phenological mismatch. Differences in the phenological mean timing (top panel), breadth (center panel), and skewness (bottom panel) of species determine the extent to which interacting species overlap in time. The purple and gold curves represent phenological distributions of two species, and the hatched areas are times of phenological overlap.

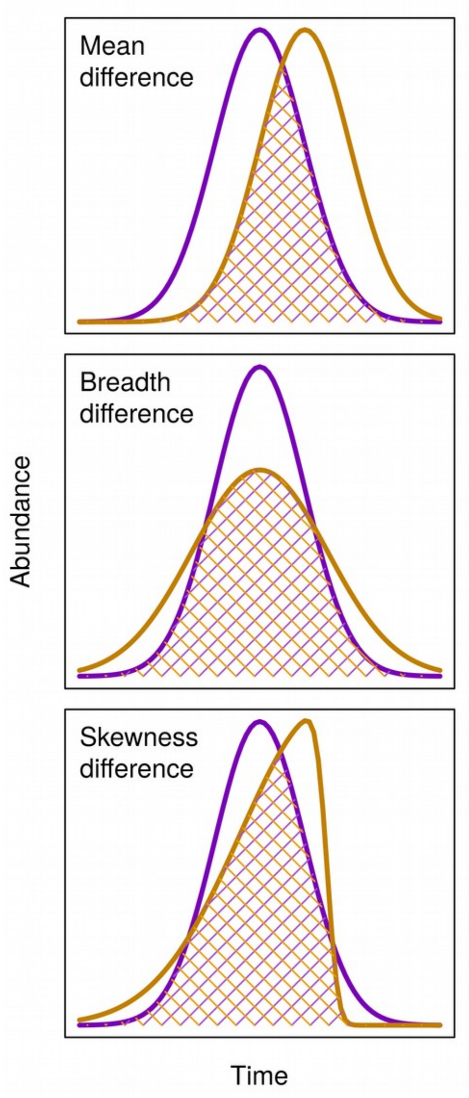


Figure 3.2. Flower (top panel) and bee (bottom panel) phenological skewness. Both flower and bee species tend to have right-skewed phenological distributions, though there is substantial variation in shape, and many distributions in both groups are not significantly different from symmetrical (white shaded bars). Skewed distribution icons give the percent of individual time-series that are significantly left- and right-skewed.

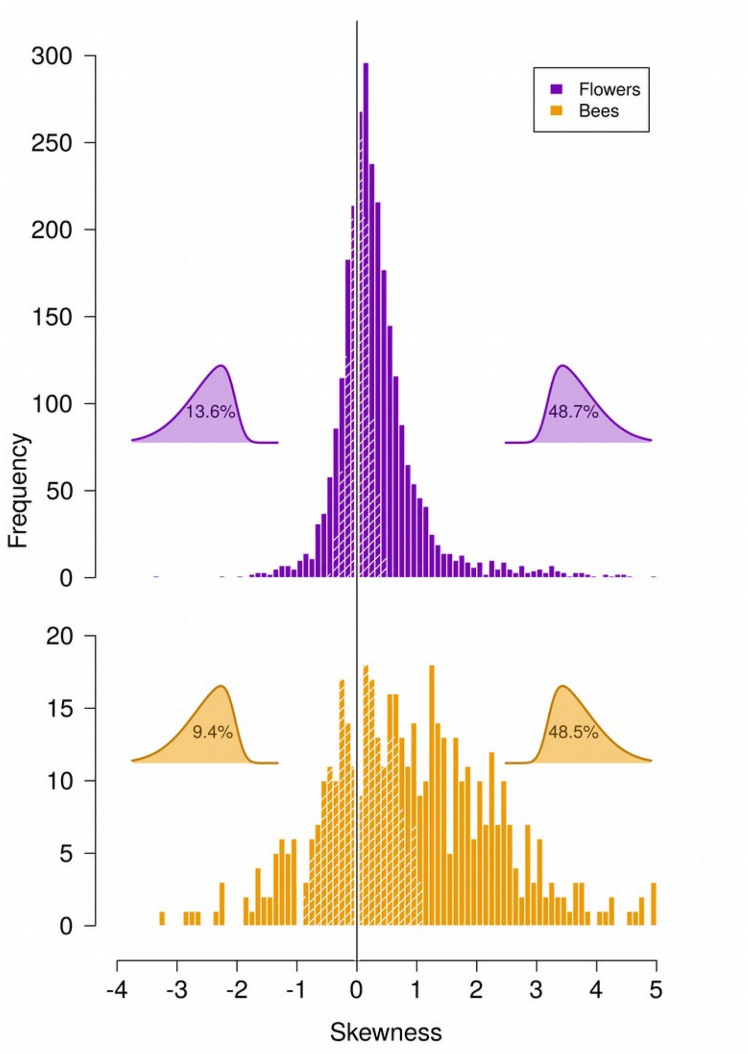


Figure 3.3. Skewness is predicted by mean and breadth. Early-season bees and flowers tended to be more heavily right-skewed (top panel), thought the effect was more pronounced in bees than in flowers. Flowers with broader phenological distributions tended to be more skewed, while bees with broader phenology tended to be less skewed in either direction (bottom panel).

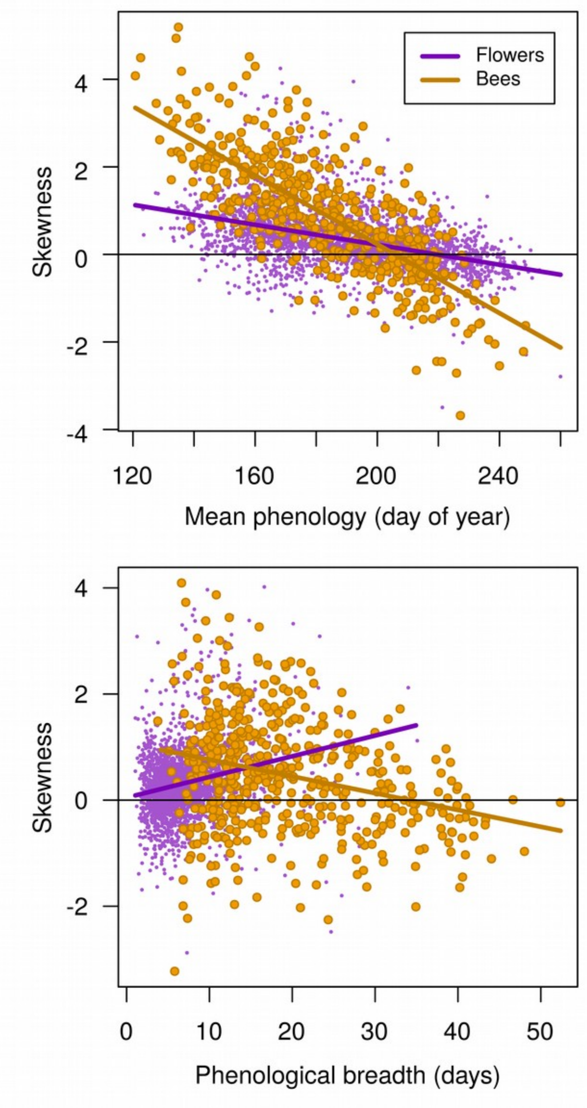
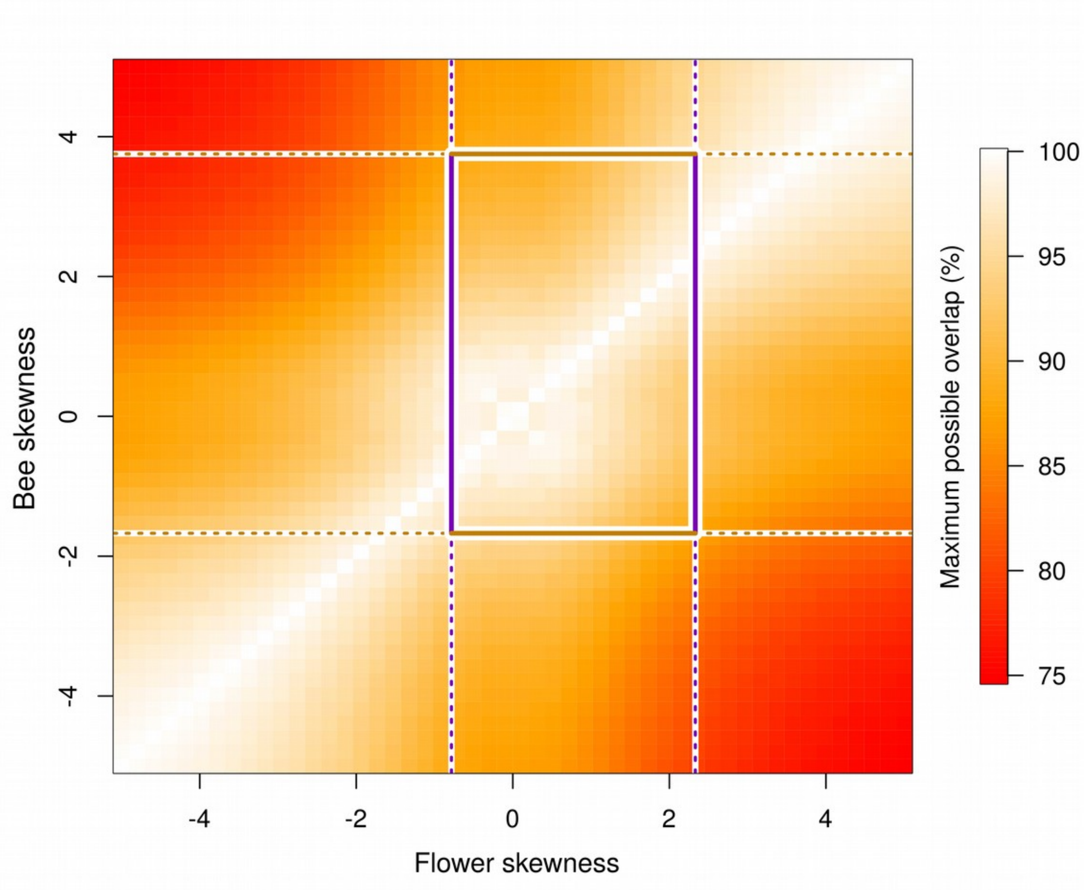


Figure 3.4. Skewness constrains the degree to which phenological distributions can overlap. The maximum possible overlap of pair-wise interacting species with different hypothetical skewness values is shown as colors, with red depicting the lowest overlap, and white depicting perfect overlap. Bounds for 95% of the actual observed skewness values are shown with purple lines for flowers, and gold lines for bees. The resulting box in the middle of the figure therefore depicts the potential loss of phenological overlap in pair-wise interactions between bees and flowers due to differences in skewness alone, isolated from the effects of mean and breadth changes.



CHAPTER 4

PREDICTING BEE PHENOLOGICAL DISTRIBUTIONS MECHANISTICALLY WITH DEMOGRAPHIC RATES

Abstract

The ability of bees to shift the timing of their seasonal activity (phenology) to track favorable conditions influences the degree to which bee foraging and flowering plant reproduction overlap. While bee phenology in natural settings has been shown to shift due to interannual climatic variation, over time as a signal of anthropogenic climate change, and in response to experimental temperature manipulation, the underlying causes of these shifts are poorly understood. Most studies of bee phenology have been phenomenological and have only examined shifts of point-estimates such as first-appearance or peak timing. While such cross-sectional measures are convenient for analysis, pollination interactions occur over whole phenological abundance distributions. Here, we make simultaneous inferences about interannual shifts in the bee phenology, emergence and senescence rates, population size, and the effect of floral abundance on observed bee abundance. We accomplish this by developing a mechanistic mathematical model implemented in a hierarchical Bayesian framework and parameterizing it with fine-scale time-series of the sweat bee *Halictus rubicundus* in a natural setting. We find that *H. rubicundus* phenological onset cueing was highly sensitive to the timing of snowmelt, but that emergence rate, mortality rate, and population size did not differ

greatly across years. We discuss the limits of inference about these potentially correlated rates and our ability to make predictions about unobservable bee life stages.

Introduction

Phenology (the seasonal timing of life-history events) shifts year-to-year in response to climatic variation, with implications for ecology of interacting species. Due to the fast (annual) time-scale of phenological sensitivity, advancing spring phenology over the past several decades and across many taxa is one of the most conspicuous biotic indicators of recent anthropogenic climate change (Parmesan et al., 2003; Pau et al., 2011; Thackeray et al., 2016). While the trend toward earlier activity in the spring has been nearly ubiquitous and largely predictable, the potential mechanistic causes of these shifts are numerous and challenging to isolate. Accumulated temperature is usually highly predictive of phenological onset (Cayton et al., 2015), though other factors affect phenology and limit the degree to which phenology can respond to climate, as some species have winter chilling requirements (Fu et al., 2015), photoperiod plays a role (Way et al., 2015), and some species time their activity to precipitation events (Danforth, 1999). More generally, the mechanistic causes of observed phenological plasticity can be divided into two groups: adaptations to track favorable conditions, and byproducts of physiological rates that are not actually adaptive. Species may evolve to delay development until a temperature threshold is met, or development rates may be delayed by insufficient heat energy. Phenological stages progress in a sequence (Ettinger et al., 2018), so rate limitation in early stages may result in apparent phenological plasticity year-to-year but not serve to match with favorable climate conditions or species interactions later in the season.

While the adaptive and neutral drivers of phenological plasticity have been examined extensively in plant flowering and leaf-out, less attention has been given to pollinator phenology. It is important to understand if and why phenological sensitivity varies among plants and their pollinators so that we can anticipate how cross-guild interactions will change (Hegland et al., 2009) and how community interaction networks will rewire due to phenological mismatches as climate change progresses (Ibáñez et al., 2010). Long-term phenology studies of bees – the most important group of animal pollinators (Potts et al., 2016) – have only begun to uncover the drivers of their phenological sensitivity (Bartomeus et al., 2011). Similarly to plants, temperature is predictive of bee phenology both in the winter (Fründ et al., 2013) and spring/summer (Pyke et al., 2016). Species that are active earlier in the season are more sensitive to temperature variation than those that are active later in the season (Forrest, 2016). Further, inter-annual variation of early-season phenology (such as emergence) is mostly predicted by climate variables, while inter-specific variation in the phenology of later stages have more to do with species traits such as nest location and the life stage in which bees overwinter. (Stemkovski et al., 2020). These insights give us a coarse, heuristic sense of the drivers of phenological plasticity in wild bee populations, but we lack a mechanistic model of bee phenology that incorporates both phenological plasticity and variable emergence and mortality rates. For the purposes of this research, phenological plasticity can be thought of as the shift in the onset of bee emergence in response to variation in the timing of climatic cues. The rate of emergence, on the other hand, determines the time between the onset of emergence and peak abundance. The emergence rate, together with the rate at which individuals cease foraging, are vital rates that are henceforth refered to as demographic rates. Both phenological plasticity and variable demographic rates shape the patterns of bee abundance that we see distributed over parts of the season. Some studies have explained interspecific differences in phenological sensitivity with functional traits, which is a step closer to a mechanistic understanding of bee phenology (Diamond et al., 2011; Slominski et al., 2019). But, observable traits often serve as proxies for more fundamental physiological and demographic processes such as emergence and mortality rates.

Bee foraging phenology – the focus of this study – is a process in which abundance is distributed over time (Inouye et al., 2019), and the timing of this process, its duration, and the shape of this distributed abundance (Stemkovski et al., 2023) are products of adaptive plasticity and variation in demographic rates that is not necessarily adaptive. Most studies have focused on cross-sections of the whole phenological abundance distribution, such as onset, peak, or end timing (Belitz et al., 2020). These cross-sections make convenient units for comparison, but considering the entirety of phenological distributions allows us to more precisely investigate phenological overlap (Edwards et al., 2021). Beyond furthering the pursuit of fundamental understanding, there are practical reasons to move beyond cross-sectional approaches. Bees, like many insects, have cryptic life stages that cannot, realistically, be observed in natural settings. A mechanistic approach to modeling phenology can be used to make inferences about these cryptic stages (e.g. unemerged adults and prepupae) from the observable data, greatly expanding the scope of potential inquiry. Also, building a mechanistic model allows us to generalize across multiple datasets and studies by mathematically formalizing the demographic processes that are shared across species.

Here, we take a mechanistic modeling approach to describe the phenological abundance distributions of a wild bee species in the Colorado Rocky Mountains. We collected fine-scale abundance data for the whole active period of *Halictus rubicundus* over two years to examine the relationships between the adaptive and neutral drivers of their phenology which can be inferred from observational data alone. Using a difference equation approach in a Bayesian modeling framework, we simultaneously quantify inter-annual onset phenology shifts, differences in emergence and senescence rates, population size, and the effect of local floral abundance on the observed abundance of this species over time. We find that *H. rubicundus* phenology is sensitive to snowmelt date, but that beyond this other demographic rates and processes are remarkably consistent across the two study years. We hope that the model developed here and this general approach will enable new work that integrates phenology and demographics.

Methods

In this study, we collected fine-scale time-series data on the abundance of *Halictus rubicundus* in order to parameterize a mechanistic model of its phenological abundance distribution. The study was located in a pair of subalpine meadows in the Colorado Rocky Mountains and involved non-lethal bee population sampling in the field. We developed a piecewise, two-compartment difference equation model that simultaneously estimates phenological onset shifts and demographic rates. We fit this model to data in a Bayesian framework.

Study system

We collected bee and flower abundance data over two years (2019 and 2021) in two subalpine meadows in the East River valley of the Elk Mountains in Colorado, USA. The sites – "Trail" and "Waterfall" – were southwest-facing, located at 2960 m and 2990 m above sea level and were approx. 33,000 m^2 and 25,000 m^2 in area, respectively, and 1.3 km apart (Fig 1). We selected the sites for their similar flora and abiotic conditions, containing areas of ground-nesting substrate for bees, and delineated their boundaries based on natural features (streams, tree stands, and willow thickets). Both meadows contained a diversity of flowering plants, but were dominated mainly by *Taraxacum officinale* in the early season and *Potentilla pulcherrima* in the remainder of the season. The growing season in this area is limited by snow with persistent cover from roughly November to May each year, meaning that most bee species in the area are univoltine and solitary. Annual snowmelt timing is a strong predictor of bee and flower phenology (Stemkovski et al., 2020). Cattle are driven through much of the area in the early autumn, disturbing vegetation and maintaining areas of bare trampled ground.

We selected *Halictus rubicundus* (orange-legged furrow bee) as the focal species for its adequate abundance and identifiability in the field without lethal sampling. *H. rubicundus* is a widely-distributed halictid (sweat bee), and is a generalist most often observed on plants of the families Asteraceae and Rosaceae (Soucy, 2002); in this study, we almost exclusively observed them foraging on *Taraxacum officinale*. They are facultatively social in warm climates, overwinter as emerged adults, and commonly form nest aggregations on south-facing slopes in loose soil (Potts et al., 1997). In cold climates, such as the present study area, *H. rubicundus* is solitary, producing one reproductive brood in each season (Eickwort et al., 1996), though they still commonly nest in aggregations. *H. rubicundus* phenology appears to track climatic cues closely, with individuals from the same aggregation emerging in close synchrony (Cane, 2021).

Data collection

To obtain fine-scale time-series data on bee phenological distributions, we sampled bee and flower abundances along transects at each site three days per week, weather permitting. On each sampling day, we (re)placed 5 randomly located 20m-long transects within the boundaries of the site, and placed a sixth transect in an area of perceived high floral density to account for bee selective foraging behavior. We walked along each transect and scanned for bees for 10 minutes within a 2m band, netted any observed bees, identified them using a hand lens, marked them with non-toxic paint on the thorax, released them, and recorded floral association. We paused the 10 minutes of sampling time while handling insects and recording data. We repeated this procedure at each transect once in the morning and once in the afternoon, resulting in 120 minutes of netting effort per day. We quantified floral abundance in each transect by counting the number of flowering plants and number of flowers on 10 plants in four evenly spaced 1m-by-1m quadrats along the transect in 2019, and by counting the total number of flowers (not distinguishing plants) in the four quadrats in 2021. We also noted flowering plants that were found in the transects but outside of the quadrats.

Most bees cannot be reliably identified to species in the field without lethal collection and microscopy. While we recorded taxon information for all bees we caught (usually to genus), we focused on *H. rubicundus* in part because they can be reliably identified in the field. To confirm the validity of our field identification, we collected reference specimens throughout the season and confirmed their species identities under magnification in the lab.

The winter of 2018/19 had a deep snow pack relative to other recent years, with 967cm of total snowfall and a June 6 date of bare ground at a nearby weather station (Barr, 2022). By comparison, the winter of 2020/2021 was much drier, with 561cm of total snowfall and a May 8 date of bare ground. This contrast between 2019 and 2021 provided a natural experiment to examine the phenological consequences of climatic variability. In 2019, we continued our sampling campaign for the entirety of the summer in order to capture any unexpected late-season population dynamics and track other identifiable species, but in 2021 we ended data collection in July. In 2019, we sampled at the Trail site 32 times from June 12 to September 4 for a total of 3,360 netting minutes, and we sampled the Waterfall site 27 times from June 24 to September 3 for a total of 2,760 netting minutes. In 2021, we sampled at the Trail site 25 times from May 14 to July 21 for a total of 2,330 netting minutes, and we sampled the Waterfall site 22 times from May 15 to July 23 for a total of 2,160 netting minutes. Sampling was not done in the summer of 2020 due to the Covid-19 pandemic.

Mathematical modeling

The number of mature bees of a species that are actively foraging at a given time is a product of the total number of individuals in that location, the rate at which they appear (through development from earlier life-stages and through emergence), and the rate at which they disappear (through mortality or nest reentry). Practically, the number of bees observed at a given location is also mediated by the availability of desirable floral resources, and abiotic factors such as temperature and precipitation. The observed population number can thus be modeled as

$$O_{t,s,y}=v\left(u_{s,y},a_y,b_y,m_y,h_y,t\right)+f\left(t,s,y\right)+\epsilon$$

where O is the observed number of bees foraging at time *t*, site *s*, and year *y*. The underlying phenological trajectory of the species is represented by *v*, which is a function of the total number of individuals before any have emerged $u_{s,y}$, the maximum emergence rate *a*, a friction parameter *b* which influences the actual rate of emergence, and the mortality rate *m*. The parameters *a*, *b*, and *m* are assumed to be fundamental demographic rates for a species that are constant across sites. The effect of floral abundance on observed bee numbers at time t and site s is represented by the linear function *f*.

Specifically, the function *v* is a system with two compartments,

$$v\left(B_{t=0,s,y},a_y,b_y,m_y,h_y,t\right)\begin{cases}\begin{cases}B_{t,s,y}=u_{s,y}\\ P_{t,s,y}=0\end{cases} & for\, t<h_y\\ \begin{cases}B_{t,s,y}=B_{t-1,s,y}-a_y B_{t-1,s,y}+b_y B_{t-1,s,y}^{2}\\ P_{t,s,y}=P_{t-1,s,y}+a_y B_{t-1,s,y}-b_y B_{t-1,s,y}^{2}-m_y P_{t-1,s,y}\end{cases} & for\, t\geq h_y\end{cases}$$

with B representing the unobserved bank of yet-to-emerge individuals, and P representing the observed population of foraging adults. *B* flows into *P* as a logistic decay process using the original formulation of the logistic growth equation by Verhulst (1838) which – in contrast to the typical formulation used in ecology that involves a “carrying capacity” parameter – allows for negative growth (Gabriel et al., 2005). The flow from *B* to *P* depends on the maximum emergence rate a and the friction parameter b. The friction parameter (following the nomenclature of Gabriel et al.) controls the shape of the emergence curve. Individuals then leave P at the mortality rate m. The system of equations is piecewise around the parameter h, which models phenological onset. The effect of floral abundance of observed bee abundance f is modeled linearly as

$$f(t,s,y)=\beta_F F(t,s,y)$$

with β_F being the slope of flower to bee abundance, and F being the observed number of flowers at time t site s, and year y. An intercept term is not included in this equation because the baseline abundance count v serves as the intercept. To study the phenological effects of climate differences between the two study years, we allowed the parameters a, b, m, and h to vary by year, denoted with the subscript $_y$. The parameter u was allowed to vary for each time-series (across years and sites), and the floral abundance parameter β_F was assumed to remain consistent over all years and sites.

Model fitting

We implemented the model described above in a Bayesian hierarchical framework with Stan in R (version 4.1.1) using the *rstan* package. We treated a, b, m, and h as hierarchical parameters by year, u as hierarchical by both year and site (different for each timeseries), and β_F as a global parameter that is independent of year and site. The decision to allow the rate parameters (a, b, and m) to vary by year and not by site reflects the assumption that there are not fine spatial-scale differences in phenophase transition rates within a given bee species but that those rates might be affected by climatic variation. Similarly, we assumed that phenological onset cueing (h) would be the same across sites but would be sensitive to climatic variation across years. Consequently, we assumed that the only cause of differences in observed phenological abundance curves within years would be different population sizes (u) across sites. Because the phenological curve function is modeled using discrete difference equations at a resolution of 1 day for each timestep, we interpolated the model linearly to generate continuous predictions to estimate the onset parameter, h. We implemented non-centered reparametrization for the a, b, and m parameters to aid in parameter space exploration and model convergence. We used uninformative or weakly informative priors for all parameters based on prior knowledge about the study system and model dynamics. Full model specifications are provided in Appendix C, which we encourage readers to consult alongside the model code that is provided in the accompanying data release. We fit the model using the NUTS sampling algorithm, 10,000 iterations (5000 for warmup and 5000 for sampling) in 4 Markov chains, with the target acceptance probability in the warmup period (the ‘adapt_delta’ argument) set to 0.95. We checked for parameter estimate convergence and chain mixing by examining trace plots, checking parallel coordinate plots, and ensuring that $\hat{r}$ values were close to 1. Finally, we performed posterior predictive checks to verify that the functional form of the model was appropriate for the data.

Results

We caught 110 total *Halictus rubicundus* females, on 39 sampling days across all sites and years, with 31 caught in 2019 and 41 in 2021 at the Trail site, and 18 in 2019 and 20 in 2021 at the Waterfall site. The onset of flowering and bee foraging phenology shifted markedly between the two years. In 2019 at the Trail site, we observed the first open *Taraxacum officinale* flower and the first foraging *H. rubicundus* female on June 20, but in 2021 at the same site we observed the first *T. officinale* flower nearly a month earlier on May 30 and the first *H. rubicundus* on May 26. The end of flowering and foraging phenology was similarly earlier in 2019 than in 2021, with *H. rubicundus* caught for the last time on July 19 in 2019 and for the last time on June 18 in 2021. We counted a total of 137 *T. officinale* flower heads at the Trail site and 54 at the Waterfall site in 2019, and 281 and 84 at those sites in 2021.

This shift between years is reflected in onset parameter (*h*) estimates. The mean onset estimate for 2019 was 175.93 day-of-year (DOY) (~ June 25) (CI 163.35-180.68) and 141.76 DOY (~ May 22) (CI 137.06-145.85) for 2021. Abundance was predicted to have peaked on July 4 and July 2 at the Trail and Waterfall sites respectively in 2019, and on June 1 and May 31 in 2021. Population size parameter estimates were similar across sites and years, with mean *u* estimates of 27.13 (CI 10.97-46.79) and 27.40 (CI 10.36-47.19) in 2019 and 24.42 (CI 5.02-47.81) and 26.21 (CI 8.31-47.05) in 2021. The emergence, mortality and emergence friction rates changed little between years. In 2019, mean emergence, mortality, and friction parameter estimates were 0.18 (CI 0.112-0.24), 0.36 (CI 0.15-0.87), and 0.0041 (CI 0.0017-0.0077) respectively, and in 2021 the parameter estimates were 0.16 (CI 0.11-0.24), 0.35 (CI 0.14-0.79), and 0.0046 (CI 0.0017-0.0077). This resulted in similarly shaped phenological curves between 2019 and 2021, though shifted and with somewhat different magnitudes (Figure 2). Local flower abundance had a slight effect on observed bee abundance, with a mean β_f estimate of

0.03 (CI 0.004-0.061) across all timeseries.

The mean absolute error of the model prediction was similar between the years and sites, with 0.58 at the Trail site and 0.65 at the Waterfall site in 2019, and 0.87 at the Trail site and 0.50 at the Waterfall site in 2021. $\hat{r}$ values for all parameter estimates were <1.01, indicating mixing across MCMC chains. Examination of parameter trace plots indicated model convergence and mixing across chains (Figs. C.1, C.2, C.3, C.4). Posterior predictive checks also indicate that the model is appropriate to characterize the data (Fig S5). All Bayesian Credible Intervals (CI) represent 95% of the posterior parameter distributions.

Discussion

We collected fine-scale abundance time-series of wild *Halictus rubicundus* populations to parameterize a mechanistic model that synthesizes the phenological onset plasticity and demographic processes to predict bee phenological abundance distributions. In summary, we found that while onset shifted in concert with different snowmelt timing between the two study years, emergence and senescence rates did not change greatly. This was evidenced by similarly shaped abundance distributions and similar inferred population sizes. We argue that out approach avoids some of the pitfalls of previous similar modeling efforts and that the present model can be applied beyond the data to which it was parameterized.

Phenological cueing vs. demographic rates

The difference in climatic conditions between 2019 and 2021 provided a natural experiment to examine the patterns and causes of bee phenological plasticity. There was nearly a month disparity in the timing of snowmelt, with the snowpack near our sites disappearing on June 6 in 2019 but on May 8 2021. The shift in *Halictus rubicundus* phenology was similarly striking, and was apparent through visual inspection of the data, even without mathematical modeling (Fig 2). Was this shift in observed phenology a product of plastic phenological onset or of different emergence rates between the two years? Our model was able to shed light on the answer to this question. We estimated a shift in *H. rubicundus* foraging phenology onset between the two years that was complementary to the shift in snowmelt date, with phenological onset estimated as occurring on June 28 in 2019 and on May 23 in 2021, supporting previous observations of phenological plasticity in this species (Cane, 2021). By contrast, the rate of emergence of overwintering bees did not differ greatly between the two years, with only a 54% probability that emergence was faster in 2019 than in 2021 (compared with a >99% probability that the onset was earlier in 2021 than in 2019). The other transition rates also did not differ greatly between the two years, with emergence (55:45 odds that it was faster in 2019) and senescence (65:35 odds that it was faster in 2019) rates essentially indistinguishable from perfect 50:50 odds (no difference) as calculated from the posterior probabilities. Therefore, we can conclude that phenological cueing rather than changes in distribution shape accounted for the observed shift in *H. rubicundus* phenology between the two years. With the obvious caveat that this is a two-year case-study of a single species, our results suggest that bee phenophase transition rates may not be strongly affected by climatic variation. Consequently, we propose that this model structure is appropriate to use in other contexts without needing to estimate year-specific phenophase transition rates. Year-specific demographic rates could, of course, be estimated in the future if that is the direct object of study.

The shape of phenological distributions is determined by the interaction of emergence and senescence rates (Zonneveld, 1991). Fast emergence relative to senescence results in right-skewed distributions, whereas the converse results in left-skewed distributions (Stemkovski et al. 2022). While the proportional values of these rates can be inferred from observational data, this is not the case for every parameter in the present model. For example, senescence rate and population size are strongly, inherently correlated (Fig 3). A large population that senesces quickly can result in a nearly identical phenological abundance distribution to that of small population that senesces slowly. This multicollinearity that could impede statistical inference (McElreath, 2019) is detected by our Bayesian approach, and may be obscured by models that do not take into account parameter correlations. Changes in population size have been recognized as complicating factors when measuring phenology (Miller-Rushing et al., 2008). Our results add another dimension to this difficulty, and we caution against inference about population size and mortality/senescence rates in isolation using an approach like ours that relies on observation data alone.

Fine-scale spatial variation in floral resource availability appears to play a small but significant role in predicting local bee abundance. On average, we observed 2.7 additional bees per 100 flowers of *Taraxacum officinale* in a given transect, and there was a 95% chance that the relationship between flower and observed bee abundance is indeed positive. This finding is evidence that the present study species makes informed foraging decisions at the local scale (within a site), in line with previous findings that bees select foraging areas based on flower displays (Heinrich, 1979), and remain in resource rich areas longer than in resource poor ones (Waddington, 1980). The present data cannot inform estimates of foraging distance or site fidelity, however. Finally, we did not observe obvious phenological mismatch between *H. rubicundus* and floral resources in either year because *T. officinale* shifted its phenology in roughly equal measure, providing another example of maintained synchrony between pollinators and their floral resources (Renner et al., 2018).

Comparison to existing mechanistic models

This study is not the first that has attempted to model phenological abundance distributions mechanistically, though we are not aware of another such model that has been applied to bees. Zonneveld (1991) proposed a model to describe the phenological abundance curves of butterflies gathered from transect counts. That model jointly estimated butterfly maximum emergence rate, dispersion of the emergence rate, mortality rate, and total population size. Notably, the formulation of the Zonneveld model is similar to what is presented here, and the second piecewise component of Eq. 2 is a Eulerian approximation of that model. Though initially proposed and used as a method to estimate population size after accounting for detection probability (Gross et al., 2007), this model has been criticized for not being robust to departures from assumptions about emergence and death rates (Calabrese, 2012). The present model departs from and advances the Zonneveld model in three crucial ways: estimating phenological onset, incorporating covariates, and implementing model fitting in a Bayesian framework which addresses some of the earlier criticisms of Zonneveld’s model and provides for flexibility in parameter estimation (e.g., addressing the colinearities outlined above, and using hierarchical estimation to overcome data limitations).

Beyond models applied to insect studies, relevant models have been developed for unimodal populations in general. Joliceur and Pontier (1989) proposed a model that generalizes population growth and decline as a continuum between the exponential and logistic cases. While not developed exclusively to describe insect abundance phenology, such a model could be applied to cases where mortality (or senescence) rates are not exponential. Condit et al. (2007) took a similar approach to ours to characterize elephant seal colony size as a function of migratory arrival rates and tenure lengths (though not phenological onset), demonstrating the generality of this kind of approach to many study systems.

Potential applications

We have demonstrated that our model can describe bee phenological distributions under different climatic conditions and suggest that phenophase transition rates do not vary greatly in response to climatic differences. Given this, our model can be applied to other datasets of bee phenology (Gezon et al., 2015; Kammerer et al., 2020; Kazenel et al., 2020; Ogilvie et al., 2017) and other taxa (Crimmins et al., 2017; Ovaskainen et al., 2020; Templ et al., 2018) that have similar onset and senescence dynamics. Future studies can exploit the functional form proposed here to extract estimates of phenophase transition rates from datasets that do not have the same fine-scale temporal resolution as the present time-series. For example, emergence rates could be compared across different bee species and different climate regions. Functional traits can be used to explain variation in emergence rates. For example, we might expect species that nest above ground to have faster emergence rates than those nesting below ground because those above ground are not subject to patchy persistent snow cover in the spring. This approach can help us better understand how climate change is affecting species' fundamental demographic rates, and so improve predictive power as we move into regions of climate space where statistical extrapolation from historical patterns may no longer be expected to perform well.

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Figures

Figure 4.1. Observations of *Halictus rubicundus* were made across two sites in the East River valley of Colorado, USA. Points denote transect locations across every sampling date in the sites. Gray points represent transects in which *H. rubicundus* was not detected, and colored points represent those where *H. rubicundus* was detected in 2019 (orange) and 2021 (blue). In total, we performed 336 transect sampling bouts at the Trail site in 2019, 276 at the Waterfall site in 2019, 233 at the Trail Site in 2021, and 216 at the Waterfall site in 2021.

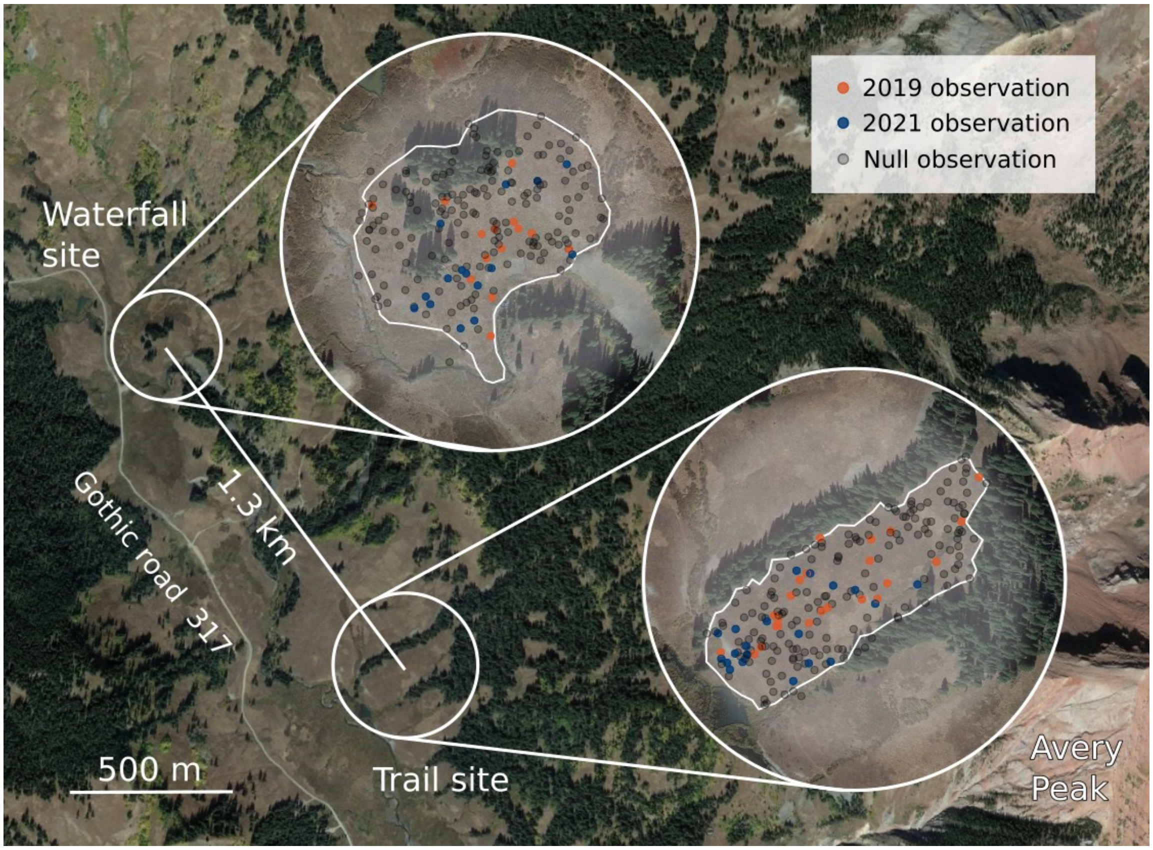


Figure 4.2. The phenological abundance distribution of H. rubicundus at two sites over two years is accurately predicted by a mechanistic model based on phenophase transition rates. Points represent observed bee counts (emerged abundance) in 2019 (orange) and 2021 (blue). Solid curved represent the mechanistic model predictions of emerged abundance, and dashed curves represent predictions about unemerged abundance which was not observed directly. Vertical lines on the solid curved represent model predictions with the added effect of floral abundance on observed bee abundance. Mean parameter estimates are reported in the top right corners of both panels and follow the same color scheme as the curves. Day-of-year is abbreviated as DOY.

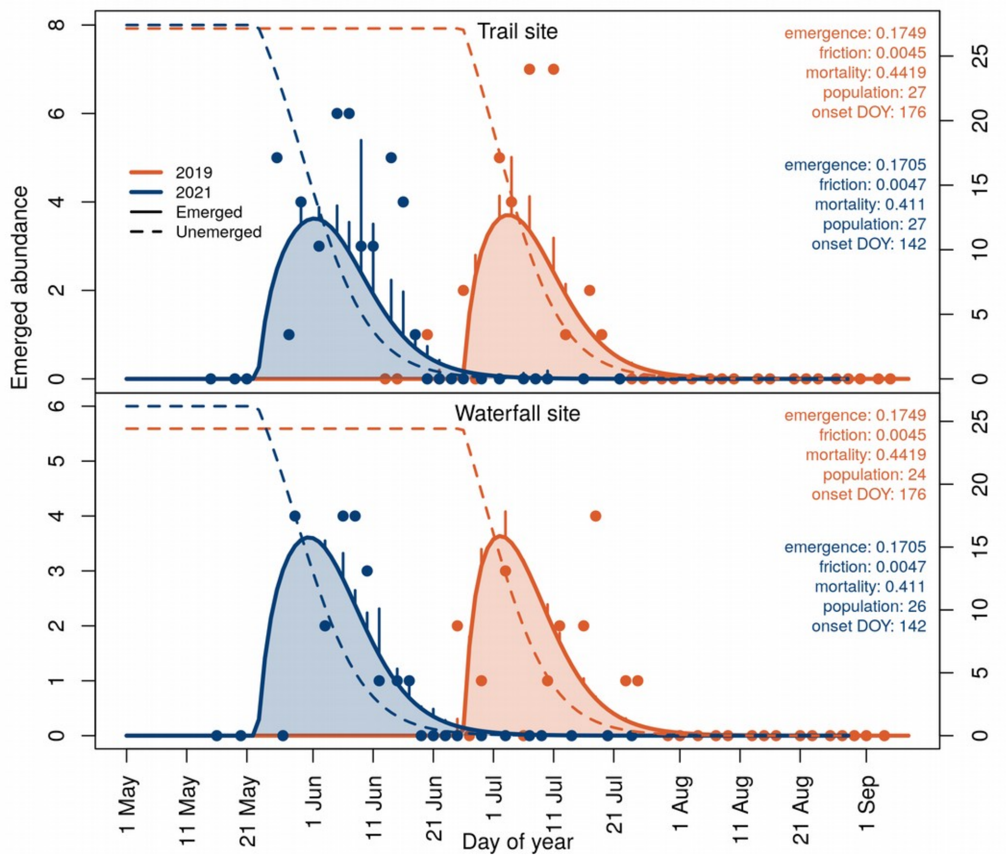
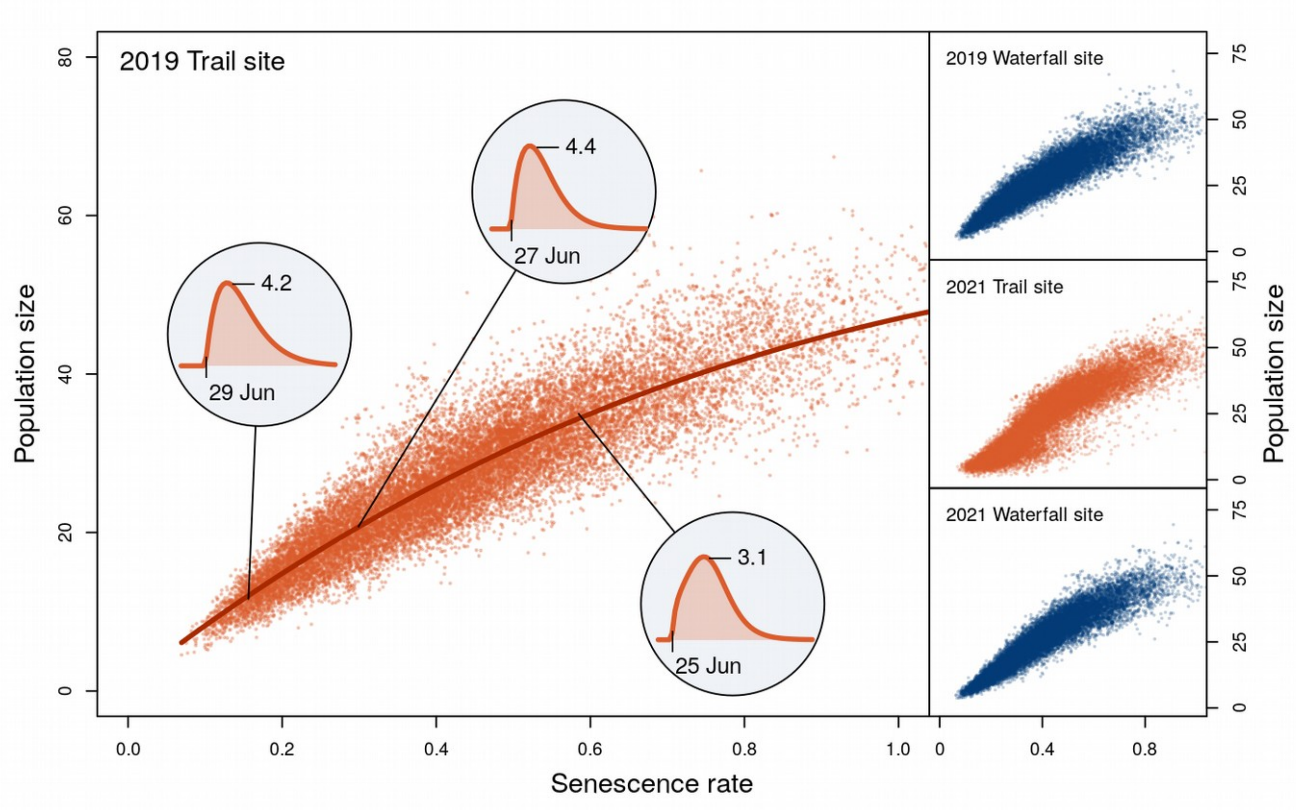


Figure 4.3. Different combinations of certain parameters yield similar model predictions due to parameter non-identifiability. In this example, similar phenological abundance curves (orange curved in light blue circles) are predicted both when senescence rate and population size are low and when these parameters are high. Each point represents a draw from the posterior distribution. This pattern is similar across years and sites (panels).



CHAPTER 5

DISORDER OR A NEW ORDER: HOW CLIMATE CHANGE AFFECTS PHENOLOGICAL VARIABILITY

Abstract

Advancing spring phenology is a well-documented consequence of anthropogenic climate change, but it is not well understood how climate change will affect the variability of phenology year-to-year. Species' phenological timings reflect adaptation to a broad suite of abiotic needs (e.g. thermal energy) and biotic interactions (e.g. predation and pollination), and changes in patterns of variability may disrupt those adaptations and interactions. Here, we present a geographically and taxonomically broad analysis of phenological shifts, temperature sensitivity, and changes in inter-annual variability encompassing nearly 10,000 long-term phenology time-series representing over 1,000 species across much of the northern hemisphere. We show that the timings of leaf-out, flowering, insect first-occurrence, and bird arrival were the most sensitive to temperature variation and have advanced at the fastest pace for early-season species in colder and less seasonal regions. We did not find evidence for changing variability in warmer years in any phenophase groups, though leaf-out and flower phenology have become moderately but significantly less variable over time. Our findings suggest that climate change has not to this point fundamentally altered patterns of inter-annual phenological variability.

Introduction

Shifts in phenology (seasonal timing of life-cycle events) have occurred as a result of changes in climate, and while there has been a general trend of species in seasonal regions advancing their spring phenology over the last few decades due to anthropogenic climate warming (Parmesan & Yohe, 2003), species vary in their phenological responses to inter-annual climatic variation. Species' phenological sensitivity varies based on trophic level (Thackeray et al., 2016), and insects are thought to be able to track climatic cues more closely than other groups of animals and plant (Cohen et al., 2018). Species' traits can influence phenological sensitivity within taxonomic groups including plants (Konig et al., 2018), insects (Diamond et al., 2011), and birds (Butler, 2003). Phenological shifts have been more pronounced in early season species (CaraDonna et al., 2014; Mulder et al., 2017) occupying colder regions (Roslin et al., 2021) and higher latitudes (Parmesan, 2007), likely due to the faster pace of climate change in the upper northern hemisphere (Burrows et al., 2011) and stronger selection for plasticity (Lindestad et al., 2019) in those areas. Some species have also shown decreases in phenological sensitivity to temperature variation in warmer years as they reach the limits of their historical climate conditions, producing non-linear temperature-phenology relationships (Iler et al., 2013; Meng et al., 2020; Mulder et al., 2017). While these complexities alone make it difficult to predict how species' phenologies will change in the future, it is also unclear whether climate change is making phenology inherently more or less variable and predictable. Such changes in variability are not just of academic concern, particularly if they affect the reliability of species' interactions that drive key ecosystem services such as pollination for agriculture (Klein et al., 2007).

The majority of phenological research has focused on changes in the mean of events such as onset and peak over time (phenological shifts) or in response to yearly climatic variation (phenological sensitivity). Some studies have also shown changes in within-season (*intra*-annual) variability due to climate change (Ma et al., 2018; Prevéy et al., 2017; Zohner et al., 2018), but few have investigated whether, or in what ways, the variability of phenological events across years (*inter*-annual) is being affected by climate change. Most studies have assumed constant inter-annual deviation, and some have checked and accounted for heteroscedasticity in time-series residuals (e.g., Bartomeus et al., 2011; Wadgymar et al., 2018) but have not made it a focus of study. There is reason to think that inter-annual variability in phenology might be changing, as there have been recent, geographically heterogeneous changes in inter-annual temperature variability (Liu et al., 2020). Further, decreased sensitivity to temperature variation (Mulder et al., 2017), chilling requirements in plants (Fu et al., 2015; Vitasse et al., 2018), and physiological development time requirements between phenophases (Ettinger et al., 2018; Primack, 1987) may produce patterns of phenological variability that are different from the variability of their cues. The studies that have examined inter-annual phenology variability on a broad scale, using citizen science data (Pearse et al., 2017) and satellite imagery (Liu et al., 2020), have found increases in variance over time, though such changes might also be influenced by changes in monitoring schemes or community composition over time (de Keyzer et al., 2017).

The relative scarcity of research attention does not reflect a lack of importance, as changes in phenological variability can have consequences for the temporal synchrony of interacting species. An increase in phenological variability may hamper the ability of dependent species to track the moving target of other species' changing phenology if the species track different climatic cues or have different sensitivities to the same cues. Variation in phenological overlap affects the strength of interactions between co-occurring species (Tiusanen et al., 2020), so there might be immediate consequences for species' fitness and coexistence. Extreme inter-annual phenological variation in the overlap of interacting species may even lead to local extirpation (Patterson et al., 2020). While phenological mismatches resulting in short-term fitness losses may be followed by evolutionary adaptation in plasticity that corrects the mismatch (Visser & Gienapp, 2019), this adaptation may be less likely to occur if the phenological fitness landscape becomes less predictable (Leung et al., 2020). If environments become extremely unpredictable, species may even adapt bet-hedging strategies rather than maintain plasticity (Botero et al., 2015). Beyond predictability, changes in variability can even influence mean shifts in phenology by interacting with lagged effects of temperature on leaf and flower primordia in previous years (Mulder et al., 2017). From a human standpoint, changes in phenological variability could affect foraged (Anderson et al., 2018) and hunted (Brinkman et al., 2016) food supply and the feasibility of planning for cultural events (Allen et al., 2014).

In the present study, we examine nearly 10,000 time-series datasets of plant, insect, and bird phenology to determine the general patterns of how climate change is affecting both phenological means and variability. To do this, we specify four metrics of change (Fig. 5.1): mean change over many years (mean shift), inter-annual mean changes due to climate variability (mean sensitivity), variability change over years (deviation shift), and inter-annual variability changes due to climate variation (deviation sensitivity). We compare patterns in shifts in variability to determine how phenology is changing in response to climate change and whether it is becoming more or less variable across years. Further, we identify the regional climatic drivers of shifts and sensitivity, the effect of phenological position (how early in the season a phenophase occurs), and differences between taxonomic groups. Finally, we examine the influence of functional traits on shifts and sensitivity within groups.

Methods

In order to determine how phenological means and deviations are shifting over time and how sensitive they are to inter-annual climate variation, we pooled data from eight long-term monitoring schemes, calculated four phenology metrics (Fig. 5.1) for individual time-series within these datasets, and modeled the resulting trends using regional climate and species characteristics. All analyses were done in R version 3.6.3 (R Core Team, 2020). Data management was done using the R-package *data.table* (Dowle & Srinivasan, 2021), quantile regression was done using *quantreg* (Koenker, 2021), and data visualization was aided by *visreg* (Breheny et al., 2015), *rnatualearth* (South, 2017), *sf* (Pebesma, 2021), and *cowplot* (Wilke, 2020). Scripts to reproduce analysis are available online (DOI: 10.5281/zenodo.5593484) and in the supplementary materials.

Phenology data

We performed a broad search of long-term phenological datasets across terrestrial taxa. We included datasets with time-series spanning longer than 10 years, extending at least past the year 2000, and for which measurements were made repeatedly by experts at fixed locations. We included eight sources: Korean meteorological stations (Ibáñez et al., 2010; Kim et al., 2021), Japanese meteorological stations (Doi & Katano, 2008; Ibáñez et al., 2010), the NECTAR network (Cook et al., 2012), the Rocky Mountain Biological Lab (RMBL; CaraDonna et al., 2014; Inouye, 2008), the Manomet Observatory bird monitoring station (Lloyd-Evans et al., 2004; Stegman et al., 2017), the Rothamsted Insect Survey trap network (Bell et al., 2015), the Chronicles of Nature Calendar (Ovaskainen et al., 2020), and the Pan-European Phenology network (Templ et al., 2018). Further details on these data sources are provided in Table S7.1.

We focused our analysis on plant leaf-out, the onset of plant flowering, the first appearance of adult insects, and the first arrival of migratory birds. We refer to these four groups henceforth as phenophase groups. We used first-observation dates as the measure of phenological onset for most datasets due to the unavailability of continuous abundance records and in most of the datasets. The Manomet and RMBL datasets include seasonal abundance time-series, so we were able to more precisely estimate phenological onset using a Weibull estimator (Pearse et al., 2017). We note that first-occurrence dates may not reflect shifts in the peak or duration of phenophases (Inouye et al., 2019), but we did not investigate these due to limitations of the present datasets. We performed systematic quality assurance and excluded time-series based on the following five conditions that were likely to lead to erroneous shift and sensitivity calculations. Of the 15,930 total time-series that we evaluated, we (1) excluded 10 that contained gaps in observations that made up more than three quarters of the time-series range. (2) We excluded 30 time-series that were unusable due to ambiguous data recording schemes in which some phenophases were recorded in January and some in December, but the year was unclear. (3) 89 time-series were excluded due to potentially unreliable estimates flagged by the Weibull method implementation, with estimates not matching up to their confidence interval range (see Smith, 1987). (4) Unresolvable data entry errors were identified in 170 time-series when there were extreme outliers or discontinuous data clusters that might have been caused by swapping days and months in data entry. These cases were flagged using model-based clustering (Fraley et al., 2012) with a conservative model selection threshold of *BIC=25*, and potential cases of clustering were checked visually. Lastly (5), 618 time-series with a total range of observations greater than three months were excluded due to likely aseasonal dynamics. Much of the NECTAR data was removed due to fewer than 10 years of recent observations at most sites. To avoid problems with pseudoreplication due to co-located or spatially clustered sites in the CNC and PEP datasets, we picked the co-located CNC sites with the most records, and in the PEP data selected the sites with the most records for each decimal coordinate rounded to the nearest whole (which is c. 55km apart in Europe). This selection process left 288 of the 354 sites in the CNC data and 360 of the 15,183 locations in the PEP data.

Climate data

We obtained geographically precise historical climate data from the TerraClimate product (Abatzoglou et al., 2018), which provides monthly maximum temperature estimates at a ~4km resolution globally from 1958 to 2018. To match this data product, we did not consider data earlier than 1958 or after 2018. To calculate a series of relevant yearly temperatures for each species/phenophase/site time-series, we identified the median month in which the phenophase occurred across the entire time-series, and extracted the mean daily maximum temperature in that month and the one preceding across all years of the time-series. We note that using the temperature at these two months (median and preceding) may produce conservative estimates compared to approaches characterizing entire climate sensitivity profiles (Thackeray et al., 2016), though by using a fixed integration period length of two months, we ensure comparability across datasets (following Keenan et al., 2020). We also note that temperature sensitivity is often calculated using degree-day models, though a comparison of these models against a simple linear regression approach (similar to what we implemented) showed that they provide similar results (Basler, 2016). We summarized the regional climate of sites with two metrics: seasonality and mean temperature. We defined seasonality as the mean annual temperature range (following Cook et al., 2012) in every year between 1958 and 2018, and mean temperature simply as the mean of monthly temperatures across all months in all years.

Trait data

We obtained data on plant traits from the BIEN database (Maitner et al., 2018). We limited our selection of plant traits to those for which we had over 50% coverage and those which we hypothesized could be influential to leaf or flower phenology (Díaz et al., 2004): whole plant growth form, height, specific leaf area (SLA), and seed mass. We grouped whole plant growth form into five categories: trees, shrubs, herbs, grasses, and dependents. Herbs contained plants classified as forbs, ferns, hemicryptophytes, and geophytes, while dependents contained vines, epiphytes, hemiepiphytes, lianas, parasites, and other climbing plants. We excluded aquatic plants and cacti: rare groups in the present datasets. We obtained data on bird body-mass and diet from the EltonTraits database (Wilman et al., 2014). In order to maximize the generality of the bird trait analysis and to create groups with comparable representation, we grouped herbivores, granivores, and frugivores into one “herbivore” group and combined those feeding primarily on invertebrates, vertebrates, and scavengers into one “carnivore” group. This resulted in three broad diet groups of herbivores, omnivores, and carnivores. We note that, in addition to these traits, migration distance may explain trends in bird phenology (Butler, 2003; Miller-Rushing et al., 2008) but this is not included in the present study due to limited data availability.

Calculation of shifts and sensitivities

We calculated the rates of phenological mean shift for each species/site time-series by modeling the day-of-year (DOY) on which a phenophase was recorded as a linear function of year. Mean sensitivity was similarly calculated with DOY as a linear function of the monthly temperature associated with that observation. We calculated deviation shifts and sensitivities by estimating the variance function using absolute residuals (following Davidian & Carroll, 1987). To estimate change in the standard deviation of the error function, we computed the absolute value of the residuals ($|R_i|$) from the mean shift and sensitivity models and modeled the absolute residuals as a function of year and temperature, respectively, using quantile regression (Koenker et al.,

2001) with $\tau \approx 0.6827$ (corresponding to the proportion of the absolute residual distribution found within one standard deviation of zero). Calculation of standard errors and significance testing for the quantile regressions were done using bootstrapping with the default xy-pairs method and 200 replicates. The calculation of the four metrics is visualized in Fig. 5.1, and we performed a simulation study to confirm that the absolute residual approach is unbiased at detecting deviation shifts (Appendix D: Section D.1). We also tested for the effects of potential non-linearity on mean and deviation change calculations (Appendix D: Section D.2).

Analysis of trends

In order to determine the drivers of phenological mean shifts, temperature sensitivity, and variability changes, we performed several analyses on the estimated rates of shifts. First, we investigated whether regional climate (long-term seasonality and mean annual temperature) and phenological position (how early in the season a species' phenophase typically occurs relative to others at the same site) predicted the magnitude of shifts, and whether different phenophase groups (leaves, flowers, insects, and birds) have all shifted similarly. To do this, we constructed four linear mixed effects models (Bates et al., 2020) with seasonality, mean temperature, phenological position, and phenophase group as additive fixed effects, and species and sites within datasets as categorical random effects. To propagate uncertainty of shift estimates due to variable time-series lengths and correlation strength, we weighted the regressions by the inverse of the standard errors of the μ and σ coefficients. In order to compare the effects of continuous and categorical predictors and to assess the relative importance of coefficient estimates, we centered and scaled the predictor variables by 0.5 standard deviations (Gelman, 2008), and tested for fixed-effect term statistical significance (i.e., coefficients different from 0) using the *lmerTest* R-package (Kuznetsova et al., 2017).

To determine whether traits played a role in mean or deviation shifts, we performed three secondary analyses on subsets of the flower, leaf, and bird data, each with the same random effects structure as in the model above. First, we tested whether four plant traits predicted shifts in flower phenology, with whole plant growth form, height, seed mass, and SLA as additive fixed effects. We conducted this analysis only for flowering phenology data because we obtained sparse data on leaf phenology for every growth form except shrubs and trees. In this and all subsequent models (Appendix D), we estimated a reference intercept (dependents in the plant traits model, shrubs in the plant phenophase model, and carnivores in the bird traits model) and compared groups as contrasts from that intercept because we were interested in whether shifts varied significantly between groups. We then investigated whether flower and leaf phenology exhibited different shifts and whether there was an interaction with growth form for a subset of the data from shrubs, trees, and herbs, with growth form and phenophase as interacting fixed effects. Lastly, we analyzed the effect of body-mass and diet type (herbivore, omnivore, and carnivore) on phenological trends in birds by modeling the four metrics as functions of diet type interacting with the $\log_e$ body-mass of each bird species.

Results

We analyzed 9,705 time-series with a median length of 36 years, representing

349,969 total phenological onset observations. The data were comprised of 2,388 leaf-out, 5,368 first flowering, 985 bird arrival, and 964 insect first-occurrence time-series. These data represented 1,037 species across 423 unique sites, with 790 plant, 168 bird, and 79 insect species (Fig. 5.2b). The study sites were widely distributed across 21 countries in the temperate regions of the Northern Hemisphere and encompassed a wide climatic range, with mean annual temperature ranging from -1.9°C to 30.8°C, and the strength of seasonality ranging from a 3.5°C to 54.1°C difference between summer and winter temperature (Fig. 5.2a).

We observed substantial variability in the strength and direction of mean shifts, mean sensitivity, deviation shifts, and deviation sensitivity. Across all phenophase groups, phenology advanced by 1.63 day/decade (mean shift; $t_{9704} = -39.65$, $p < 0.001$) and phenology was earlier in warmer years by 3.19 days/°C (mean sensitivity; $t_{9704} = -128.4$, $p < 0.001$; Fig. 5.3a). Phenology was not significantly more or less variable in warmer years (deviation sensitivity; 0.01 days/°C, $t_{9704} = -0.556$, $p = 0.58$; Fig. 5.3b) but became less variable by 0.24 days/decade overall (deviation shift; $t_{9704} = -9.54$, $p < 0.001$). There was substantial variation in deviation changes between species, however. For example, the deviation of bigleaf hydrangea (*Hydrangea macrophylla*) flowering onset decreased by 0.96 days/°C on average across 86 sites, while that of the black alder (*Alnus glutinosa*) increased by 0.64 days/°C across 50 sites, and the flowering deviation of European blueberry (*Vaccinium myrtillus*) decreased by 1.28 days/decade across 23 sites. The degree of mean temperature sensitivity significantly predicted the shift in mean phenology over time ($t_{9703} = 45.144$, $p < 0.001$, $R^2 = 0.17$; Fig. 5.4), with greater mean sensitivity to temperature resulting in greater shifts toward earlier phenology over time.

Variation in mean shifts and mean sensitivities were predicted significantly by climatic variables and phenological position (Fig. 5.5 top panel). Early-season species (phenological position) and those in colder regions advanced their phenology the most over time and in warmer years. Of the continuous variables, seasonality was the strongest predictor of mean sensitivity, with less seasonal areas showing the greatest effect of warm years on advancing phenology. Phenophase groups varied in the degree of their means shifts and sensitivities, with insects advancing more than plants, and birds being the least sensitive (Fig. 5.5 bottom panel). No phenophase groups showed significant deviation sensitivity, though deviation decreased over time in leaves and flowers but not in insects and birds. The effects of all predictors were less pronounced on deviation changes than they were on the corresponding mean changes. Full model coefficients and statistical results are available in Appendix D: Table D.1, and are summarized in Fig. 5.5.

Shifts in first flowering phenology and deviation were not significantly predicted by the growth form of plants, height, seed mass, or SLA (Appendix D: Section D.4). Rates of shift in flower and leaf phenology also did not differ significantly and did not interact with growth form (Appendix D: Fig. D.12). Neither diet nor mass predicted phenological shifts or sensitivities in birds (Appendix D: Fig. D.13). Plant trait model coefficients and statistical results are available in Appendix D: Table D.2, those for the phenophase model are in Appendix D: Table D.3, and those for bird traits are in Appendix D: Table D.4. All model results are elaborated and visualized in Appendix D: Section D.3.

Discussion

Climate change has not resulted in a uniform shift of spring phenology across all species or all parts of the world. Phenological responses have varied across trophic levels (Thackeray et al., 2016) and regional climates (Li et al., 2019; Roslin et al., 2021). Even closely related, co-occurring species can differ in their phenological responses based on their traits (Bell et al., 2015; Diamond et al., 2011; Konig et al., 2018) and their phenological position in the season (Cook et al., 2012; Menzel et al., 2006). While numerous factors determine rates of phenological shifts and sensitivity, some trends are general and predictable. Making predictions based on these patterns is crucial to anticipating phenological mismatches between interacting species (Renner & Zohner, 2018) and minimizing their negative consequences on ecosystems through management (Olliff-Yang et al., 2020). Here, we confirm that even when viewed across major climatic gradients and monitoring programs in the Northern Hemisphere (Fig. 5.2), there are consistent patterns in which species are most responsive to climate change. Moreover, we did not find evidence that climate change is making phenology inherently more variable across years. Rather, we found that the timings of leaf-out and flowering onset have actually become modestly but significantly less variable over time, suggesting that the novel, warmer conditions presented by climate change may not fundamentally change patterns of variability in phenology between years.

Predictors of phenological mean shifts and mean sensitivity

Some places have experienced greater changes in phenology than others due to regional climate differences. Mean phenology has advanced most rapidly and is most sensitive to inter-annual temperature variation in colder regions (Fig 5.5 top panel). Growing seasons are shorter in areas with colder climates, so plants, insects, and birds must time their activity more precisely to occur within favorable abiotic conditions (Pau et al., 2011; Roslin et al., 2021). This greater sensitivity in the colder regions of plant species distributions may lead to more connectivity and gene flow across climate gradients by reducing geographic variability within years (Ma et al., 2018; Prevéy et al., 2017). In contrast to this pattern, phenology has shifted the least and is the least sensitive in the most seasonal areas after accounting for differences in the regional mean climate. In areas where temperatures change relatively little between winter and summer, species may evolve to be more sensitive to smaller inter-annual temperature differences and to track them more precisely. Viewed another way, this may simply be a product of the proportionality of phenological advance relative to temperature changes: 1°C of additional warming will have a larger relative effect on phenology in areas where the difference between winter and summer is just 10°C than in areas where the difference is 50°C.

Inherently different physiology and life-histories between taxonomic groups also determine phenological sensitivity and shifts. While all phenophase groups advanced their phenology in warmer years and over time, some were more sensitive than others (Fig. 5.3a), with insects being the most sensitive to inter-annual temperature variation. This difference supports previous work that has found insect phenology to be more sensitive than that of plants and perhaps birds (Cohen et al., 2018; Thackeray et al., 2016). We emphasize, however, that we present less data on insects and birds than on plant phenophases, and that observed phenological trends of migratory birds are largely dependent on conditions in the region from which they are traveling, while insects are dependent on the environment at or closer to their location. Despite these differences between groups, there are also commonalities, with early-season species being the most sensitive and shifting their phenology earlier (Fig. 5.4). This finding supports the idea that species on the edge of their environmental tolerance have evolved to more precisely track tolerable conditions because plasticity is most consequential on the margins of climatic niches (Duputié et al., 2015). The consequences of premature leaf-out, for example, are greater in the early season (Inouye, 2008; Pardee et al., 2018) and species have evolved mechanisms such as chilling requirements to prevent leafing-out too early (Vitasse et al., 2014).

Mechanisms affecting phenological variability

There are many plausible, potentially conflicting mechanisms that may have led to our observation of reduced phenological variability over time in leaf-out and flower timing (Fig. 5.5, bottom panel). First and perhaps most obviously, inter-annual phenological variation is tied to inter-annual variation in temperature. If spring temperatures become more variable between years, spring phenology should also become more variable (Appendix D: Fig. D.20). But the expectation of more climatic variability may not be borne out broadly in observations, as changes in inter-annual temperature variance have been geographically heterogeneous (Liu & Zhang, 2020), and we found an overall slight reduction in inter-annual spring temperature deviation at the sites represented in this study (Appendix D: Fig. D.18). The observation that climate change leads to more extreme weather events within seasons does not necessarily mean that we should expect more extreme years when the overall, mean trends of climate change are accounted for (Ummenhofer & Meehl, 2017). Population size can also affect phenological first-observation dates (Lee et al., 2011; Miller-Rushing et al., 2008), with decreasing populations resulting in later and more variable appearance observations (Appendix D: Fig. D.16). Many insect populations are declining (Hallmann et al., 2017), and birds that depend on insects are following suit (Bowler et al., 2019), so these declines might have counteracted decreasing inter-annual temperature variability to produce no observable deviation shift or change in deviation sensitivity in insects and birds (Fig. 5.5). We were unable to directly investigate the effects of population declines due to a lack of abundance information in most of the present data sources, but we encourage future research into the influence of population changes on phenological variability.

Beyond technical considerations, phenological mean shifts themselves may affect deviation shifts. When spring phenology shifts earlier in the season, species may become subject to novel environmental constraints that affect the shape of their phenological distributions and consequently their inter-annual variability. Because the early season presents adverse conditions such as frost (Inouye, 2008; Pardee et al., 2018) and may increase the dominance of constraining phenological cues such as photoperiod (Meng et al., 2021), species' phenological onset can become more abrupt and less variable year-to-year (Appendix D: Fig. D.17). These sorts of constraints may also be evidenced by nonlinear phenological responses to temperature, with species being more sensitive in colder years (Fu et al., 2015; Mulder et al., 2017). In fact, non-linear responses can present themselves with reductions in variance when data are fit with linear models (Wolkovich et al., 2021), though we did not find major differences after accounting for potential non-linearity (Appendix D). In contrast to observed patterns of no change in variation *across* warmer years, phenological variation between individuals within seasons has been shown to increase *within* warmer years (Zohner et al., 2018), suggesting that the *intra*-annual variability of phenology does not directly translate into its *inter*-annual variability. Due to these multiple, potentially counteracting mechanisms, patterns of phenological variability may change going forward, and further studies are needed to investigate the relative strengths of the above mechanisms.

Implications for future phenology

Our findings of little-to-no change in phenological variability over time and in warmer years have implications both for the future of biotic interactions that depend on temporal overlap and for our ability to forecast phenology as climate change progresses. As species are increasingly subjected to the extremes of the historical climate conditions to which they are adapted (Butt et al., 2015), we might observe fundamental changes in biological processes such as phenological plasticity. While there have been some recent indications of species phenological responses approaching the limits of their plasticity (Mulder et al., 2017; Vitasse et al., 2018), we did not find evidence of the pronounced changes in the inter-annual phenological variability that might result from species failing to track climatic variation. We found that, on average, phenological variability did not differ between warmer and cooler years (Fig. 5.5, bottom panel). And while there was substantial variation in deviation sensitivity and deviation shifts between species (Fig.

5.3b), this variation was not well explained by the regional climatic variables (Fig. 5.5, top panel) or species traits (Appendix D: Sections D.4-D.6). From a forecasting perspective, it is important to know whether the responses to environmental variation that we have observed in the past will be informative under novel conditions. We have not found evidence of broad changes in the inherent predictability of phenology as climate change has progressed in the present study period. This is an encouraging sign for forecasting and management. If phenological mean shifts due to climate change outpace species' plasticity or abilities to adapt their strategies for phenological synchrony (Richardson et al., 2017), active management such as diversifying genotypes by relocating individuals (Olliff-Yang et al., 2020) may be needed to avoid the worst consequences of phenological mismatches for ecosystem services. The maintenance of predictability in inter-annual phenology that we have observed offers hope for mitigation efforts that utilize phenological understanding (Enquist et al., 2014). Phenological plasticity is, of course, only one way in which species acclimate to environmental change; it is one of the many factors shaping species interactions, and inter-annual variability is only one component of phenology.

Conclusion

Shifts in phenological means in warmer years and over time are only part of the story of how climate change is affecting phenology. In this study, we examined another part of the story: whether inter-annual variation in the timing of leaf-out, start of flowering, insect first-occurrence, and bird first-arrival has changed over time or in response to warmer years. We found that, across all phenophase groups, phenology was not significantly more or less variable in warmer years, and that plant phenophases have actually become somewhat less variable over time. While regional climate and the phenological position helped explain differences in mean shifts and mean sensitivities between timeseries, they did little to explain deviation shifts and deviation sensitivities. Taken together, our findings suggest that climate change will not necessarily lead to increasingly unpredictable, disorderly inter-annual phenology. Multiple conflicting factors including inter-annual temperature variability, population size, environmental constraints, non-linear temperature responses, and changing intra-annual variability may be shaping phenological variability. We hope that testing the prevalence and relative importance of these mechanisms will provide avenues for further investigation and that future studies of phenology will examine changes both in inter-annual means and deviations.

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Figures

Figure 5.1. Conceptual demonstration of the four phenology shift and sensitivity metrics. Phenological mean shift and mean sensitivity (top panels) are defined as the slope of the relationship between the day of year on which a phenophase was observed and the year or temperature, respectively, associated with that observation. Deviation shift and sensitivity (bottom panels) are then computed as the slope of the absolute residuals versus the year/temperature. Teal points represent yearly data, and orange ones represent data relating to inter-annual temperature variation. Red lines indicate positive residuals, blue lines represent negative residuals, and dashed lines represent absolute residuals. The middle, pop-out subfigures highlight the intermediate process of taking the absolute value of the residuals from the mean regression in the top panels in order to compute deviation changes in the bottom panels. This hypothetical example demonstrates a case in which mean phenology is shifting earlier (top-left), is earlier in warmer years (top-right), deviation is not shifting over time (bottom-left), but deviation is greater in warmer years (bottom-right).

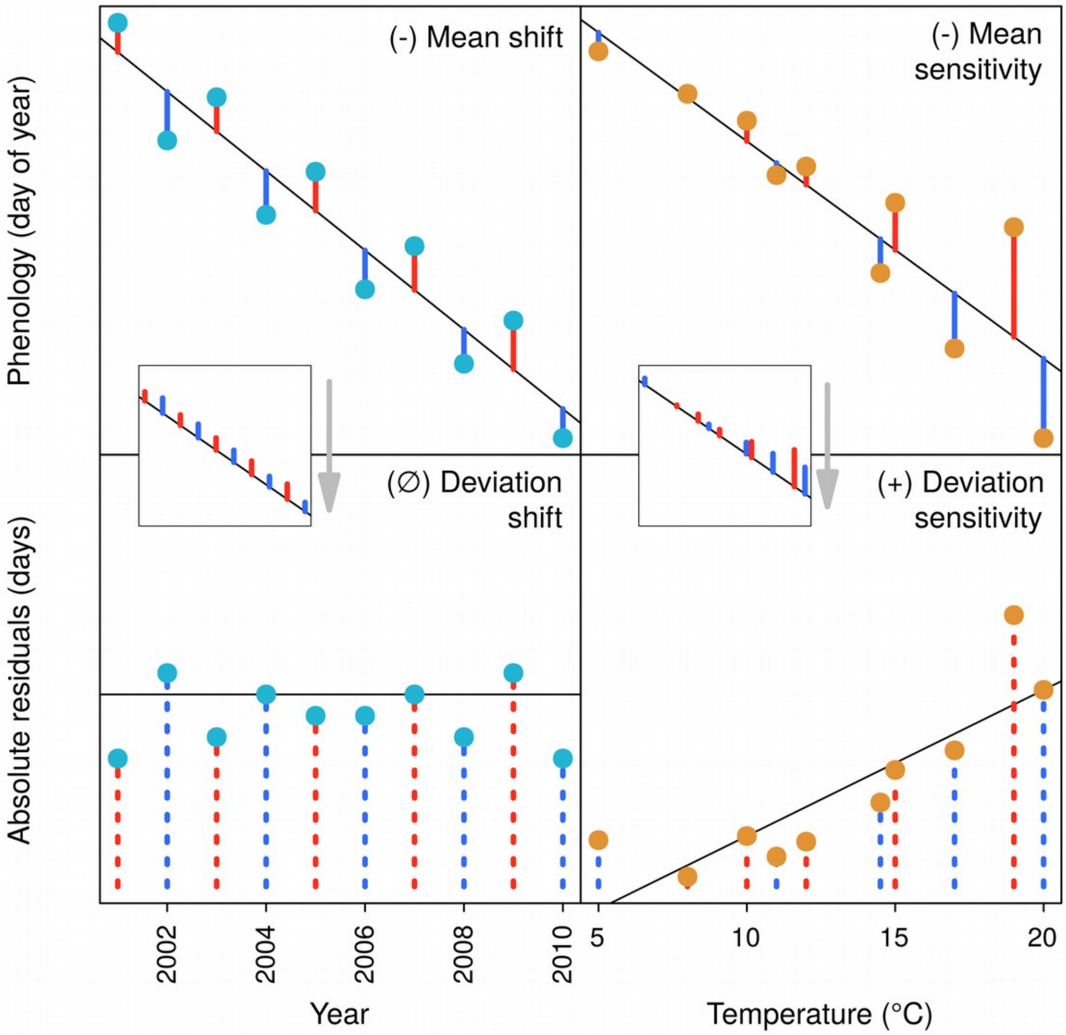

(-) Mean shift
(-) Mean sensitivity
(∅) Deviation shift
(+) Deviation sensitivity
Phenology (day of year)
Absolute residuals (days)
2002
2004
2006
2008
2010
Year
5
10
15
20
Temperature (°C)

Figure 5.2. Spatial distribution of phenological data sources. Long-term phenological observation data has mostly been conducted in the temperate and boreal parts of the northern hemisphere, but the data used in this study are widely distributed and span a large gradient of regional climates (left panel). Yellow points represent sites with the least pronounced seasonal temperature differences, while purple ones represent the most seasonal sites. Seasonality is calculated as the annual mean temperature (°C) difference between the warmest and coldest months at each location. Most of the available phenological data is on plant phenophases, but the duration of time-series in the present dataset is roughly equal across taxonomic groups (right panel). Vertical bold lines represent the median duration of time-series for each phenophase group, with horizontal dashes representing the median start and end dates. The shaded bars around the horizontal dashes represent the first and third quartiles of the start and end years of the time-series.

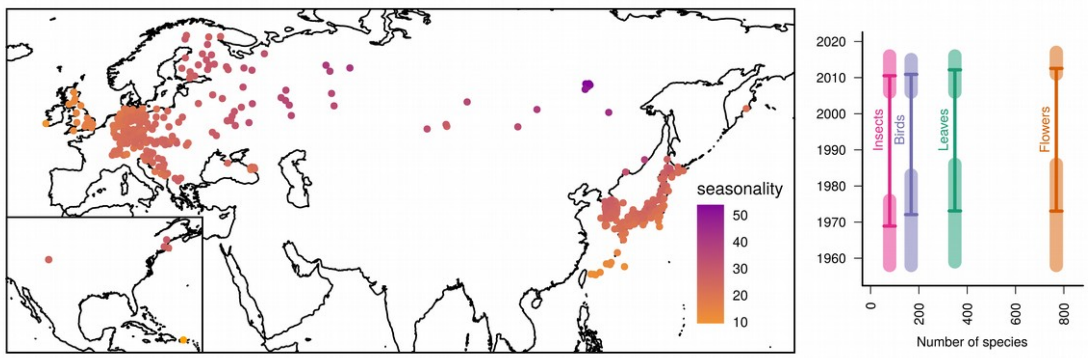


Figure 5.3. Phenological onset dates tend to be earlier and less variable in warmer years. The majority of all phenophase groups (95% of flowers, 97% of leaves, 78% of birds, and 80% of insects) advanced their mean spring phenology in response to increased temperature (panel a). By contrast, phenology did not become more or less variable in warmer years for any phenophase group (panel b). Time-series with individual slope estimates not significantly different from zero are shaded with white, and some of the data are obscured due to overlapping histograms. The plotting range is narrowed slightly to show the distributions more clearly, so 5 (<0.1%) points are excluded on the left of panel a, 2 (<0.1%) points on the right of panel a, 97 points (1%) on the left of panel b, and 57 points (0.6%) on the right of panel b.

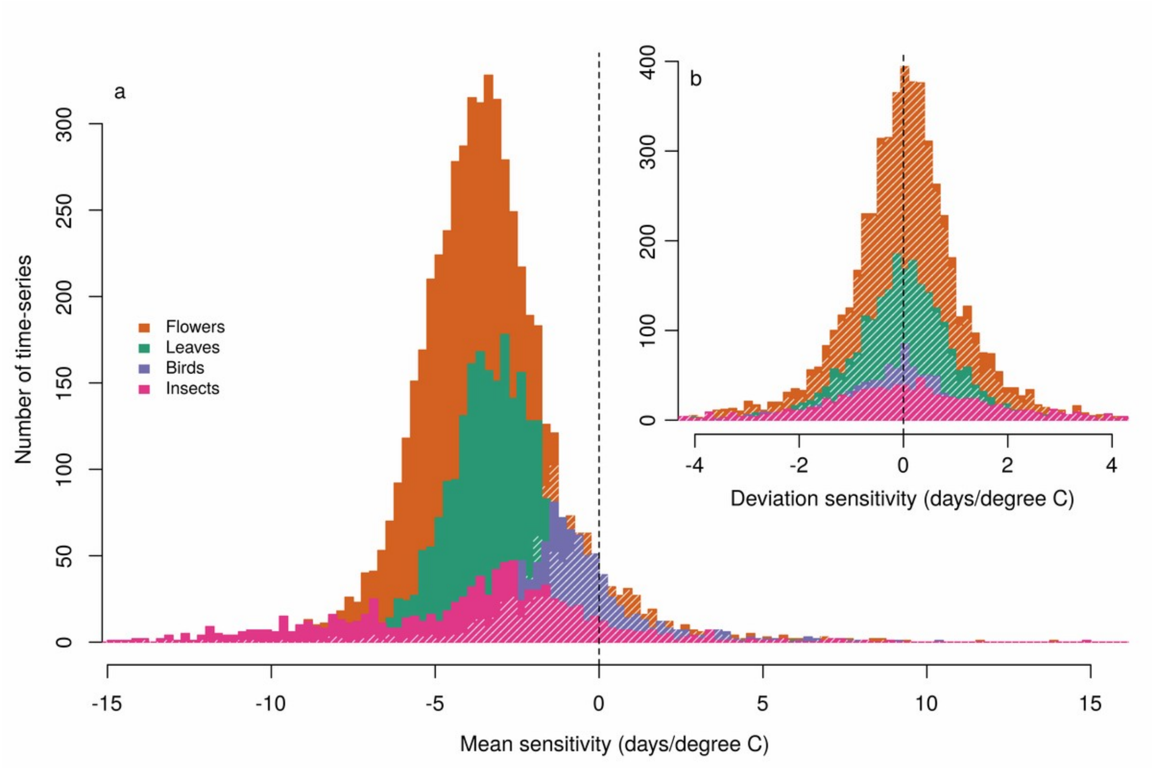

a
Number of time-series
0
50
100
150
200
250
300
Flowers
Leaves
Birds
Insects
-15
-10
-5
0
5
10
15
Mean sensitivity (days/degree C)
b
0
100
200
300
400
-4
-2
0
2
4
Deviation sensitivity (days/degree C)

Figure 5.4. The mean sensitivity of phenology to temperature variation predicts observed shifts over time. The phenological position of species relative to others at the same sites (point and contour color; color legend on the right) is also a strong predictor of temperature sensitivity. Species whose phenophases occur on average earlier in the spring season (blue points) are more sensitive to temperature than those close to the middle (pink points) or end (red points) of spring. Most time-series exhibited both an advance in spring phenology over time and with increased temperature (bottom left), though some delayed over time but advanced with increased temperature (top left). Relatively few time-series showed a delay with increased temperature (right). Contour lines are colored by the mean phenological position of points within 0.5 mean sensitivity units and 0.25 mean shift units around the contours.

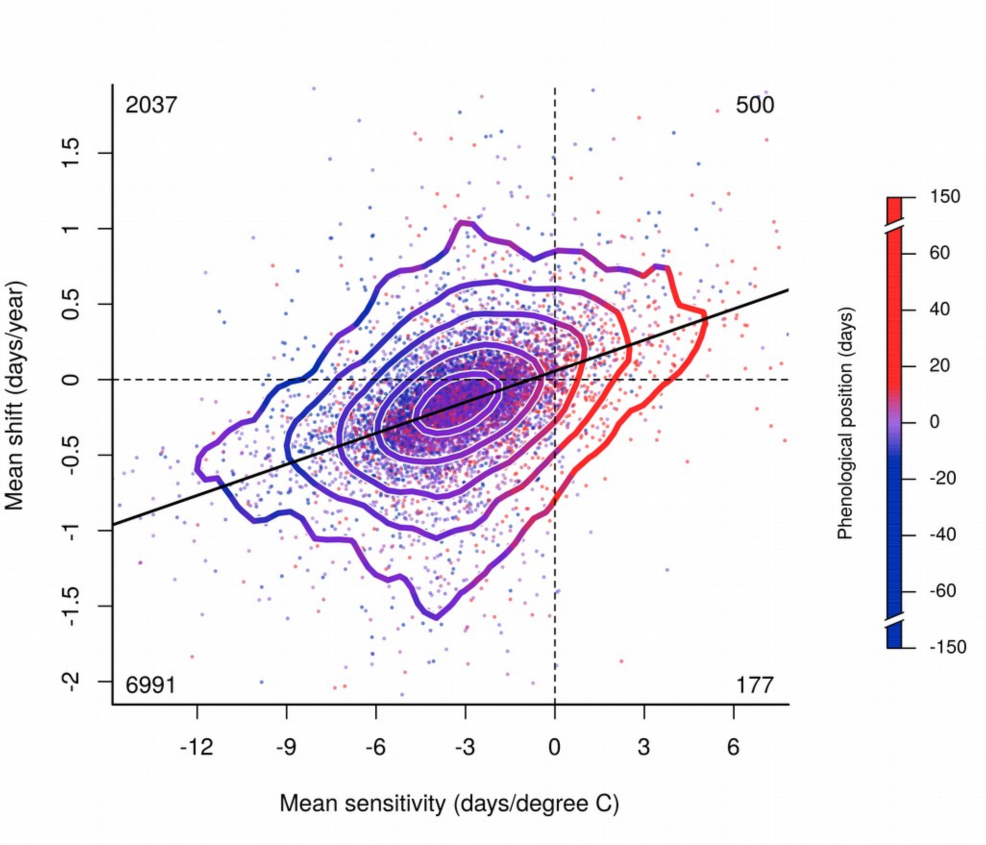
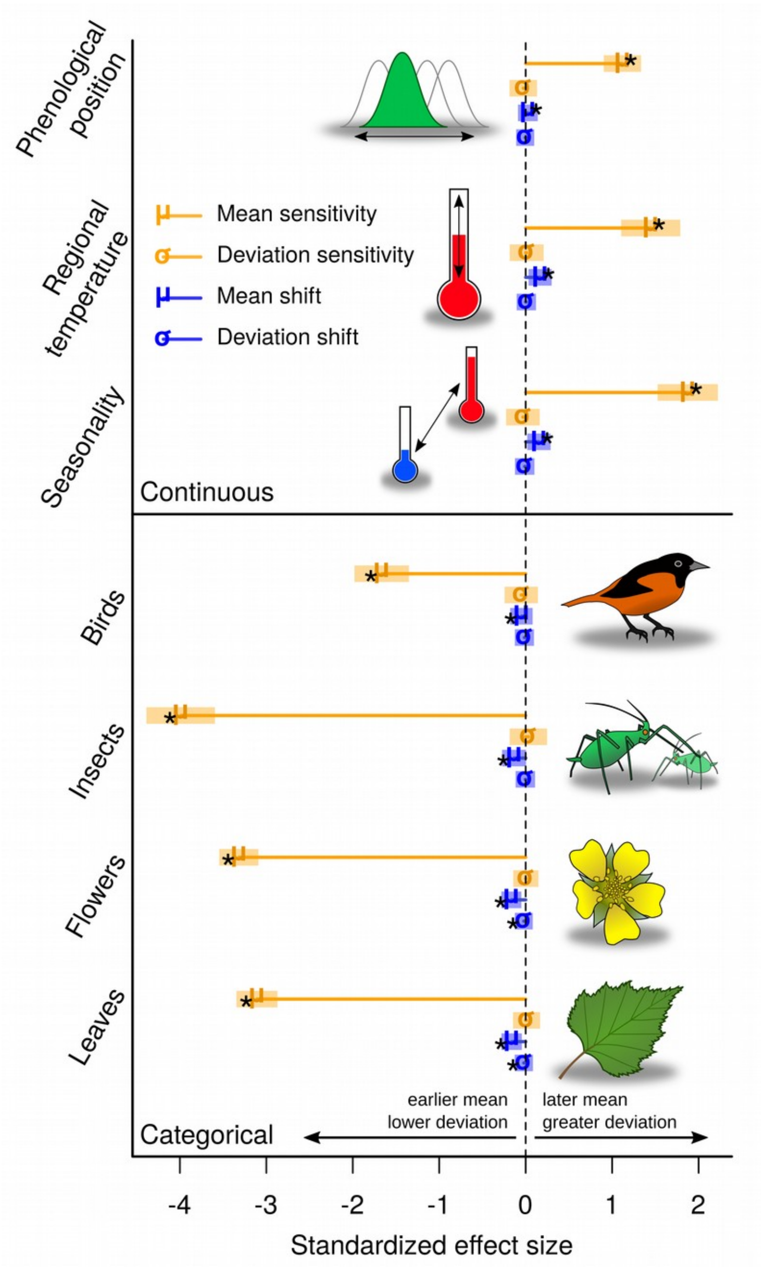


Figure 5.5. Phenological shifts and sensitivities vary by taxonomic group, regional climate, and the phenological position of species. Earlier-season species in the coldest and least seasonal areas have advanced their spring phenology and are the most sensitive to temperature variation (top panel). All phenophase groups advanced their mean phenology over time and in warmer years, with insects being the most sensitive (bottom panel). While deviation sensitivity remained unchanged in warmer years for all phenophase groups, deviation shifted in flowers and leaves, decreasing over time. The standardized effects of each predictor variable on the four phenological response metrics are grouped together in rows. Orange lines represent sensitivities with respect to yearly temperature variation, and blue lines represent shifts over time. Mean coefficients are represented with a μ and deviation coefficients with a σ. For continuous variables, coefficients are slope parameters, and for categorical variables, coefficients are contrasts from zero. Asterisks indicate significant effects ($p < 0.01$), and the shaded bars represent 2×standard error around the coefficient.


Phenological position
Regional temperature
Seasonality
Continuous
Birds
Insects
Flowers
Leaves
Categorical
μ Mean sensitivity
σ Deviation sensitivity
μ Mean shift
σ Deviation shift
earlier mean
lower deviation
later mean
greater deviation
-4
-3
-2
-1
0
1
2
Standardized effect size

CHAPTER 6

GENERAL CONCLUSIONS

While this dissertation has at various points delved into specific nuances of phenology and their responses to climate change, I have tried to approach every question with an eye toward generality and synthesis. Taking a wide view, there are several key themes and findings that are worth highlighting and expanding on here. First, phenological responses to climate change are predictable once sufficient groundwork is done. Second, bee foraging and plant flowering phenology respond similarly to climate change. And finally, the field of phenology research is, at present, methodologically diverse and may benefit from standardization to improve applicability of findings across systems. This research has opened up many new lines of inquiry, and here I discuss some potentially fruitful future directions.

Bee/flower mismatch

This dissertation, and much of the recent phenology research, particularly in pollination systems, is motivated by the possibility of novel phenological mismatch of interacting species due to climate change. Mismatches in plant and insect phenology have thus far not been documented in many studies (Renner et al., 2018). What does this dissertation have to say about the trajectories of bee and flower pollination interactions?

Chapter 2 showed that bee phenology is sensitive to climatic variables, including snowmelt timing, temperature, and precipitation. Further, bee phenology differs based on elevation. Broadly speaking, these patterns are similar to what has been observed about flower phenology. Chapter 2 compared the snowmelt timing sensitivity of bee phenology to that calculated in a related study of flower phenology (CaraDonna et al., 2014), finding that bee phenology advances slower than flower phenology. Since Chapter 2 was published in 2020, it appears that this particular finding has been one of the main takeaways for readers based on citations and press coverage. Here, I would like to caution against over-interpretation of this particular finding. As noted in the Discussion of Chapter 2, the calculated rates of snowmelt sensitivity, while in the same units, may differ in substantive ways between the studies. First, the flower phenology study comprises data from a narrow elevation band, while the bee phenology study spans a broad elevation gradient (though elevation is accounted for in the model). Second, phenological onset is calculated differently between the two studies. Third, the other climatic variables besides snowmelt timing are calculated differently. Consequently, it is unclear how alarmed we should be about the apparent difference in bee and flower phenological sensitivity to snowmelt timing.

Chapter 3 showed that bee foraging and plant flowering phenological distributions are similarly skewed in time. Bees tend to exhibit abundance concentrated in the early part of their activity and trail off in abundance more slowly than they appeared, and flowers tend to open with more synchrony than they senesce. While Chapter 3 did not investigate whether phenological skewness changes substantially due to climate change, it does suggest that bee and flower phenology is similar in terms of distribution shape. Phenological skewness has the potential to affect temporal overlap, but based on the present research, there is not reason to thing that bee and plant species will decouple due to changes in skewness. Overall, I believe that the research presented in this dissertation does indicate that phenological mismatch will not be among the main challenges facing pollination systems as climate change progresses.

Predictability of phenology

There are many sources of uncertainty that go into predicting the future of ecosystems under climate change, ranging from greenhouse gas emission scenarios to the ability of species to disperse to newly suitable habitats (Felton et al., 2022). How much does phenology contribute to this uncertainty? Of the various mechanisms by which ecosystems acclimate to novel conditions, I argue that phenology is among the most predictable. Phenological plasticity plays out on a fast time-scale relative to processes such as natural selection and community turnover. This has allowed ecologists to gain deep insights about how phenology responds to climatic variation and how it will respond in the future.

With less than a decade of data, Chapter 2 was able to make inferences about not only the additive effects of traits, climate, and topography on phenology, but also interactive effects. With only two years of data, Chapter 4 was about to make inferences about vital rates and unobservable bee life stages. This level of nuanced understanding is much more difficult to attain for slower ecological processes.

A critical question about the future under climate change is how informative the past will be about the future. Will climate change fundamentally change ecological processes so that our accumulated knowledge becomes irrelevant? One way to look at this is to test whether variability in a certain process in increasing over time or is greater in warmer years. In terms of phenology, there is evidence based on citizen-science data that the inter-annual variability of plant phenology is increasing (Pearse et al., 2017). Chapter 5 looked at this question at a larger scale, but found no evidence for variability increases over time or in warmer years, and no major differences between taxonomic groups or based on regional climate. Of all of the results in this dissertation, this (null) result is perhaps the most surprising. When I have presented this work at a MacArthur Academy conference in 2022, I polled the audience (mainly late-career, established ecologists) for their a-priori expectations about whether phenology is getting more or less variable over time. The overwhelming majority expected variance increases, and were surprised by the null result. While this was not a rigorous poll, I think the results are reflective of the dominant narrative about climate change effects. While it is true that climate change will make a great many processes less predictable, the present research does not suggest that this will be the case for phenological processes.

Methods of phenology estimation

The etymology of “phenology” corresponds to the way in which it has been studied by ecologists. The Greek “phaino” (as in “phenomenon”) has to do with light and appearance, itself based on the Proto-Indo-European root “*bha-” which means to “to shine” (OED Online, 2022). So, phenology can be though of as the study (“-logia”) of the act of appearance. Correspondingly, ecologists have primarily studied the beginning (rather than the end) of seasonal events (Gallinat et al., 2015). But ecological interactions happen over the entire range of phenological distributions, and the field is shifting its focus from single dates to entire processes (Inouye et al., 2019). This transition is statistically complicated because there are many ways to go from discrete to continuous. Many methods exist that are applicable to phenology datasets, and the phenology literature is full of disparate approaches.

Just in this dissertation, I have employed first-observation dates, distribution tail estimates, quantile regression, empirical moment calculation, generalized additive models, and mechanistic difference equations to characterize different aspects of phenology. So perhaps it is hypocritical to call for standardization of statistical methods in phenology research, but I believe that the field would benefit from more common practices to make studies more comparable. Great work has been done recently to compare phenology estimation methods (Belitz et al., 2020; Roberts, 2012), so I have hope for coalescence. There will always be a diversity of statistical tools because they have different areas of applicability, but we can at least work to use the same tools for the same purposes.

Future directions

For as much as this dissertation has been motivated by uncertainty about the future of pollination and ecosystems under climate change, it is notable that nowhere do I perform a forecast of future phenological responses. While the inference in these chapters about phenological drivers is statistical and rigorous, the implications about future phenology are heuristic. This should not be surprising, as ecology has always primarily been a descriptive rather than a predictive (out of sample; in the future) science. Ecological forecasting has only recently emerged as a discipline, and early attempts are being made to forecast phenology (Taylor et al., 2020; White et al., 2006). A logical next step is to apply the knowledge about bee phenology that has been collected here to near- and long-term statistical forecasts of bee phenology. Such forecasts would not only give concrete estimates about future plant-pollinator interactions complete with uncertainty quantification, but would also constructively test our understanding of pollinator systems by forcing us to make out-of-sample predictions (Houlahan et al., 2017). Developing such forecasts is likely to be more difficult for bees than for plants because real-time or automated data collection is much easier to do with plants, but this challenge should not stop us from trying.

Another logical next step to take based on this dissertation is to apply the model that was developed in Chapter 4 to answer other ecological questions. Most obviously, the model can be applied to more temporally coarse bee abundance datasets, such as the one used in Chapters 2 and 3. The burden of functional form validation has been done by the fine-scale dataset of Chapter 4, so subsequent studies can apply this form more confidently. Further, this model is general: nowhere is there a specific “bee” term, parameter, or mechanism. So, it can be applied to characterize the phenological distributions of other insects or plants that share similar emergence and senescence dynamics. Beyond expanding the taxonomic scope, the model can be used to link phenophase transition rates to phenological overlap and fitness outcomes. How do bee emergence rates vary based on functional traits? Are mortality rates a function of yearly variation in floral resource availability? Does the ratio of emergence to senescence rate vary by regional climate conditions? These are just some of the questions that could be answered using this model.

Lastly, the bee abundance dataset collected for Chapter 4 could be further exploited. While only data on *Halictus rubicundus* was analyzed for the purpose of developing the present model, I collected data on all bees that were caught while performing transect counts. The identifications in the rest of the data are almost all genus-level because species-level bee identification without lethal collection is impossible for most groups, but there are plenty of questions that could be answered using the genus-level data. The data collection scheme would also be conducive to exploring the spatial scale-dependence of the effect of floral abundance on observed bee abundance. The scheme contains three levels: sites that are spaced about a kilometer apart, transects that are spaced between ten and a hundred meters apart, and quadrants within the transects that are spaced meters apart. The two lower spatial levels are simply aggregated in the present analysis. While the locations of transects are used to visualize the spatial distribution of *H. rubicundus* presences (Figure 4.1), the quadrant level is not used at all. Another spatial analysis that should be done is on fine-scale habitat selection within sites. The precise locations shown in Figure 4.1 could be coupled with landcover data to infer where different species or genera tend to forage. Future studies could also explore finer-scale temporal patterns of bee foraging. I recorded precise timings of each transect sampling period and collected hourly air and soil temperature data, but none of these data made it into the final analysis. These fine temporal- and spatial- analyses would be easy pickings for subsequent studies.

Chapter 2 was published in Ecology Letters in 2020 (Stemkovski et al., 2020), Chapter 3 was published in Ecology in 2022 (Stemkovski et al., 2023), Chapter 4 is in preparation to be submitted for review at The American Naturalist, and Chapter 5 was published in Ecology in 2022 (Stemkovski et al., 2023)

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APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER 2:

BEE PHENOLOGY IS PREDICTED BY CLIMATIC VARIATION AND FUNCTIONAL TRAITS

Section A.1: Climate, topography, and trait data gathering

Climate data

We used data from a weather station at the RMBL operated by long-time resident, billy barr. We selected this data source because it was consistently collected throughout the duration of our study with no missing days, and because it provides a direct measure of snowmelt timing. In addition, this weather station was closer to the majority of our study sites than any other weather stations with data available.

For the climate variables, we made *a priori* selections of snowmelt date (first date of uncovered ground in a year), average monthly summer rainfall, and average monthly summer maximum temperature. We defined summer as the period between April 1 and September 30, the typical flight period for the bee community at the RMBL (Gezon et al. 2015). We did not include total snowfall or snow water content, because they were highly correlated with snowmelt date ($r=0.82$ and $r=0.86$, respectively). We predicted that snowmelt date in particular would be a major driver of bee phenology, with earlier snowmelt driving earlier occurrences of all phenophases, because the persistent snowpack greatly limits the growing season in the study area and strongly affects flowering phenology (Inouye 2008) and bumble bee catch rates (Ogilvie et al., 2017). We calculated temperature and rainfall values over the entirety of the active bee season because bee foraging phenophases are distributed throughout the season. The flight periods of individual, univoltine species are thought to be short (just a few weeks), so many senescence events are expected to occur before many emergence events, and vice versa.

Topographic data

We assessed the effects of elevation and solar incidence on bee phenology. The elevation of our sites ranged from 2456 to 3438 meters above sea level (Table S2). Bee phenology has been shown to shift based on elevation in the study area (Pyke et al. 2011). Solar incidence was calculated as the hourly average angle to the sun from 0900 to 1800 on July 1 of each year using the *insol* R-package (Corripio 2014). We included this variable on the premise that sites with a more direct angle of incidence to the sun would experience warmer temperatures and receive more accumulated solar energy over the course of a season, which could advance some phenophases (Jackson 1966, Weiss et al. 1993, Allen et al. 2014). To calculate the degree of solar incidence, we obtained elevation, slope, and aspect data from a digital elevation map, and we verified slope and aspect data at each site using a clinometer and compass.

Species trait data

To examine the role of functional traits in determining bee phenology, we assessed the effect of body mass, nest location, and overwintering stage. We did not include sociality as a trait in the analysis because we specifically excluded the eusocial group *Bombus*, and some halcitids in our study system have been shown to exhibit variable solitary lifestyles at high elevations (Eickwort et al. 1996), while bees of the same species may be social at lower elevations. We calculated body mass by measuring intertegular distance (ITD) for up to ten individuals of each species and scaling the measurements according to an established ITD-to-mass relationship (Cane 1987). We chose body mass as a predictor because body mass has been shown to influence thermal tolerance (Stone & Willmer 1989). Thus, it may be that smaller bees have evolved more conservative phenologies (closer to the middle of the season) in order to avoid temperature extremes. We note that the present analysis is limited to smaller bodied bees due to the exclusion of *Bombus* from the analysis. We obtained nest location (above ground vs. below ground) and overwintering stage (adult vs. prepupae) for each species by compiling existing trait information from primary resources (Pardee 2018; Table S3).

Section A.2: Power analysis and method validation

In order to validate the phenophase estimation method presented in this paper and to explore its performance, we conducted a power analysis using simulated data with known parameter values. We drew observations from a normal distribution to generate a simulated population time series. The mean was selected from a uniform distribution ranging from 50 to 200 days of the year, the standard deviation was varied by ten intervals from 7 to 50 days, and points were drawn every 14 days to mirror the actual bee monitoring protocol. These parameter values and sampling frequency were selected to reflect realistic ranges of bee abundance in our study system. The drawn values were rounded to the nearest one-day bin, and true peak timing, emergence, and senescence values were calculated as the maximum observed abundance, and the first and last days on which 5% of the maximum was observed, respectively. To test the efficacy of the phenophase estimation method at different re-sampling regimes, we added different levels of error to the observed values. The error terms were picked from a normal distribution centered at zero and with a standard deviation equal to the standard deviation of the simulated distribution multiplied by a scaling factor. We varied the scaling factor by ten intervals from 0 to 1. We then performed the GAM phenophase estimation method detailed previously on the sampled dataset to estimate phenophase values and generate confidence intervals (illustrated in Figure S1). We performed this procedure 500 times for each combination of standard deviation and error values, resulting in 50,000 total simulations. To test for the effectiveness of the method on skewed distributions, we repeated the above procedure with a skew-normal distribution, generated using the *sn* R-package (Azzalini 2020). For the skew-normal distribution, we varied the degree of skew from 0 to 1.5, applied error as before, and randomly selected the standard deviation for each data simulation.

The power of a statistical test is the probability of rejecting the null hypothesis when the alternative is true (Lehmann and Romano 2006). In the context of the present analysis, power is the proportion of simulations in which confidence intervals around phenophase estimates encompass the true phenophase value. At an α-criterion of 0.05, we would expect 80% of the true values to fall within the estimated confidence intervals. We found that the GAM phenophase estimation method consistently provided reliable estimates of the true phenophase values, though the power decreased as the proportion of added error increased (Figure S2). Power did not decrease as the standard deviation of the sampling distribution increased. As expected, the width of the confidence intervals increased as the proportion of added error and width of the sampling distribution increased. Additionally, we found that the power of the GAM method was higher when estimating peak timing, and the confidence intervals around the peak estimate were smaller than those for emergence and senescence timing across nearly all parameter combinations. This is to be expected, as values on the extremes of distributions are harder to estimate than those toward the center. When comparing actual and estimated phenophase values across all simulations with the proportion of error added < 0.5, the estimates accounted for 95% of the variation in emergence values, 99% for peak, and 83% for senescence. We detected slight bias in the phenophase estimates, with median error in actual versus estimated values being 3.8 days later for emergence, 2 days earlier for peak, and 1.7 days later earlier for senescence timing.

In summary, we found that the GAM method had high power when error rates were small, but gave reasonable estimates even when error was very high. The estimates generated by the method explained the vast majority of the variation in actual values, and the biases were small. We conclude that the GAM method adequately estimates actual phenophase timing within a set of parameters that is representative of the data within this study.

Figure A.1. An illustration of the proposed phenophase estimation method on a simulated dataset where actual phenophase values are known. In this example, points (red filled circles) were drawn at an interval of 14 days from a distribution (black circles) centered at 170 with a standard deviation of 15, with no error added to the observations. The GAM method was applied to the observed time-series dataset, and phenophase estimates were made. These estimates (red lines) are plotted with confidence intervals (light red bars) and compared against actual phenophase values (black lines).

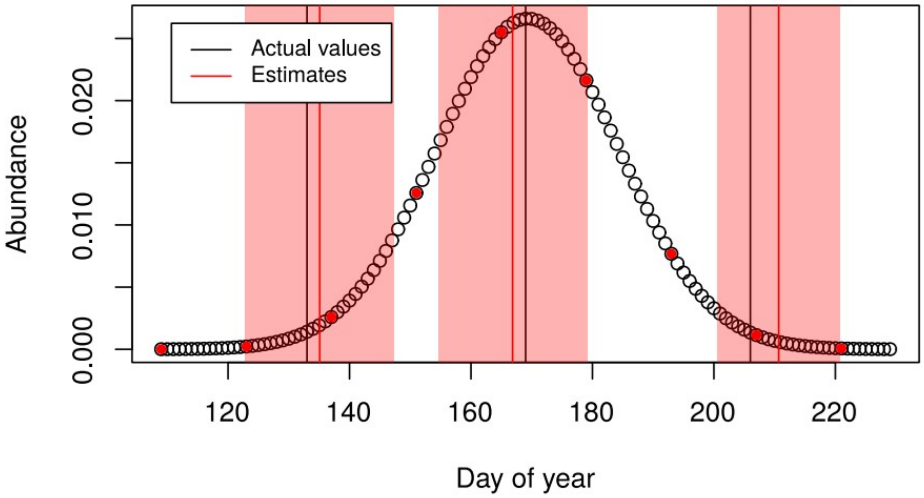


Figure A.2. The phenophase estimation method effectively estimates the actual phenophase values regardless of the spread of the distribution, but is less able to make correct estimates as more error is added to observations. The power of the GAM method (left panels) decreases for each phenophase estimate as there is more error added to sampled points, but not as the standard deviation of the sample distribution increases. The width of the confidence intervals (right panels) increases as more error is added and as the standard deviation of the sample distribution increases.

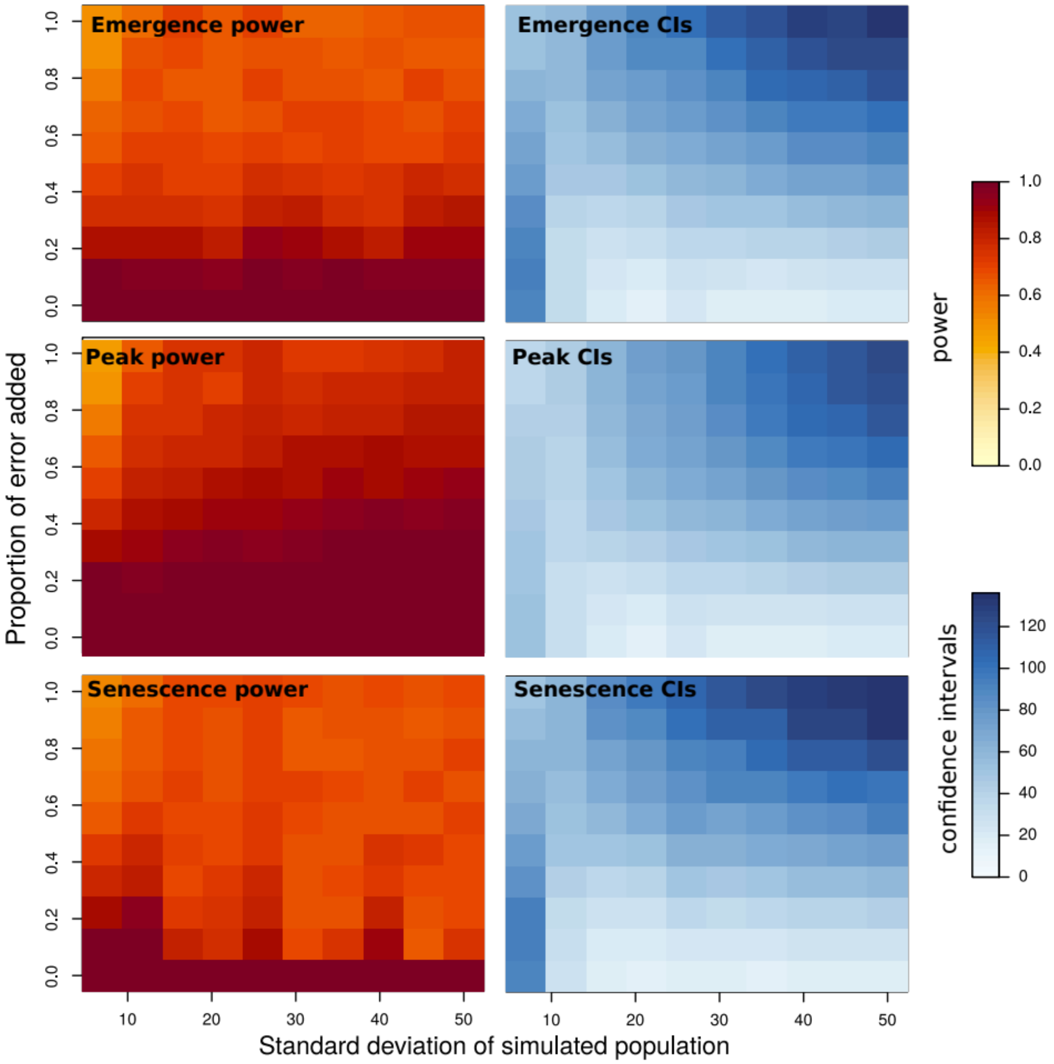
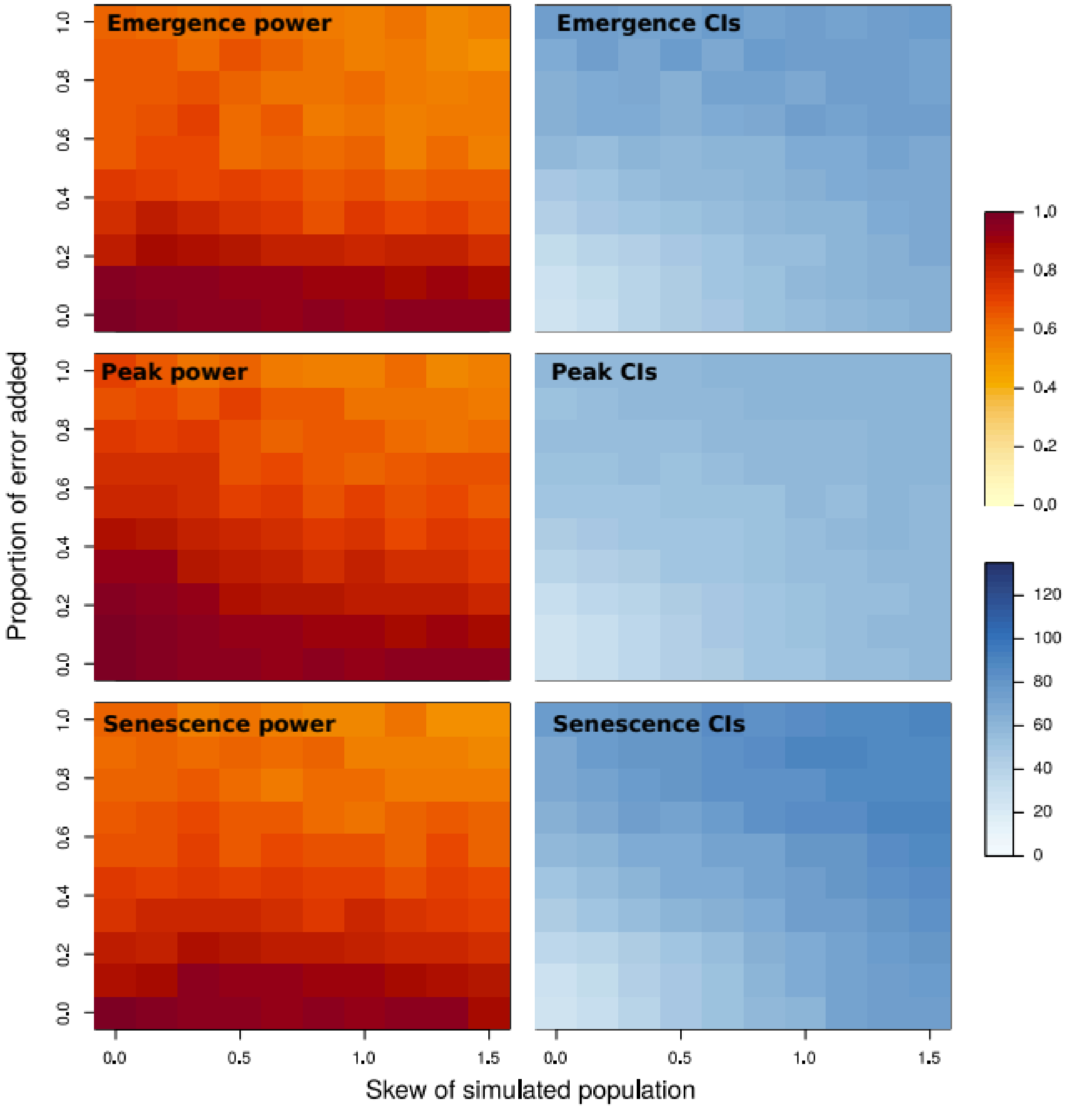


Figure A.3. The phenophase estimation method is effective at estimating phenophases of skewed distributions, though the power decreases as more error is added to observations. The width of the confidence intervals (right panels) increases as more error is added, and the confidence intervals around the long tail of the distribution (senescence) increase at higher levels of skew.



Section A.3: Additional statistical tests

Variance inflation factors

Multicollinearity in predictor variables can lead to erroneous inference using standard linear modeling and model averaging techniques (Cade 2015). To avoid this issue, we examined correlations between all predictors before running models. This led us to exclude some variables such as snow depth and minimum temperature from our list of predictors. As a second step to ensure that our models did not suffer from multicollinearity, we calculated variance inflation factors (VIFs) for each of our top models using the vif function in the car R-package (Fox et al. 2012). We found that VIFs were all near one, with the highest value being 2.18 for temperature in the peak phenophase model. These VIF values were well below the threshold of VIF=5 in which highly correlated variables lead to problematic inference (James et al. 2013), so we concluded that our models did not suffer from mulitcollinearity.

Additional interactions

While we focused on the interactions of snowmelt timing with nest location and overwintering stage, we also tested for interactions between the other climatic variables (average summer maximum temperature and average summer rainfall) and the two functional traits. We found no significant nest location/rainfall or overwintering stage/temperature interactions for any phenophases. We did find a significant interaction between overwintering stage and rainfall but only for the peak phenophase, with species that overwinter as adults slightly advancing their peak with more rain and those that overwinter as prepupae delaying their peak (0.66 ± 0.25, $t_{379} = 2.669$, $p<0.01$). We also found that the emergence and peak timing of species that nest above ground was more sensitive to temperature (emergence: 7.76 ± 2.88, $t_{453} = 2.694$, $p<0.01$; peak: 8.87 ± 2.83, $t_{379} = 3.14$, $p<0.01$), mirroring our earlier findings of a nest location/snowmelt interaction.

Variance of random effects

Another approach to look indirectly at the relative influence of climatic variation, topography, and functional traits on bee phenology is to fit a model without fixed effects that simply predicts phenophases on the basis of year, site, and species treated as random effects. This is represented as the model $DOY_{phase} \sim e_{year} + e_{site} + e_{species}$, where e represents a random effect, and DOY_{phase} represents the estimated day-of-year of a phenophase. This results in three models, one for each of emergence, peak, and senescence. Upon fitting the model, we calculated the proportion of the variance attributed to each random effect by dividing the variance (the square of the standard deviation) by the sum of the variances of the other random effects including the residual variance. The raw variance values are given in Table S1, and the trends are summarized in Figure S4. We found that the variance attributed to years and sites was highest for emergence and decreased with later phenophases, while the variance attributed to species was highest for senescence. This supports our general finding that different bee phenophases are determined by different types of drivers, as well as the specific finding that climate more strongly influences emergence and functional traits more strongly influence senescence.

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Table A.1. The variance attributed to each random effect and residual variance.

Phenophase	**Year variance**	**Site variance**	**Species variance**	**Residual variance**
Emergence	221.14	193.01	74.95	39.03
Peak	64.09	36.61	98.45	20.61
Senescence	21.77	46.24	170.66	42.46

Figure A.4. The proportion of variance attributed to years and sites decreases across phenophases, while it increases across phenophases for species. The proportional residual variance increases slightly across phenophases.

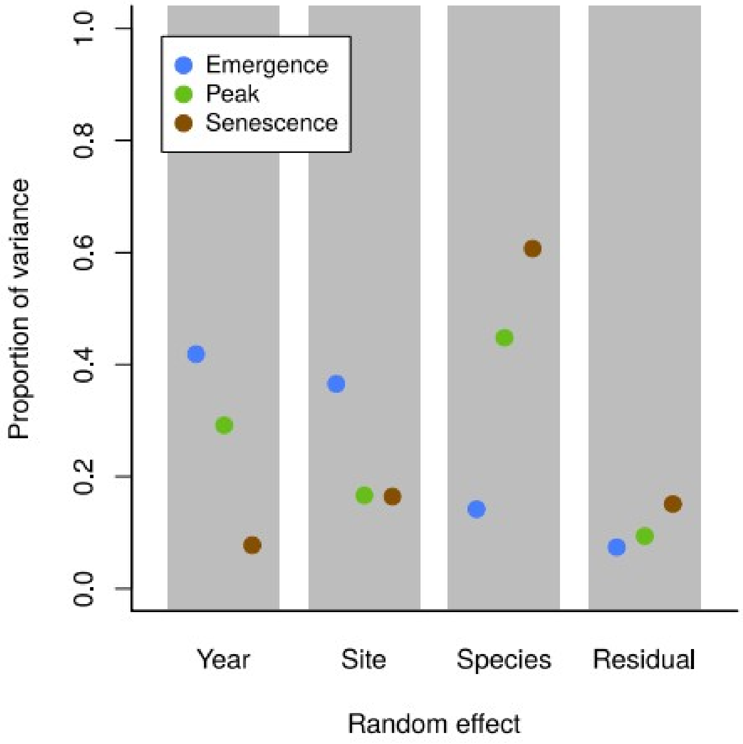

Figure A.5. Model averaging did not bias our calculations of relative effect sizes. The coefficients derived from model averaging are highly correlated with those from the top model for each phenophase. The red lines represent one-to-one relationships, and all points fall very close to these lines.

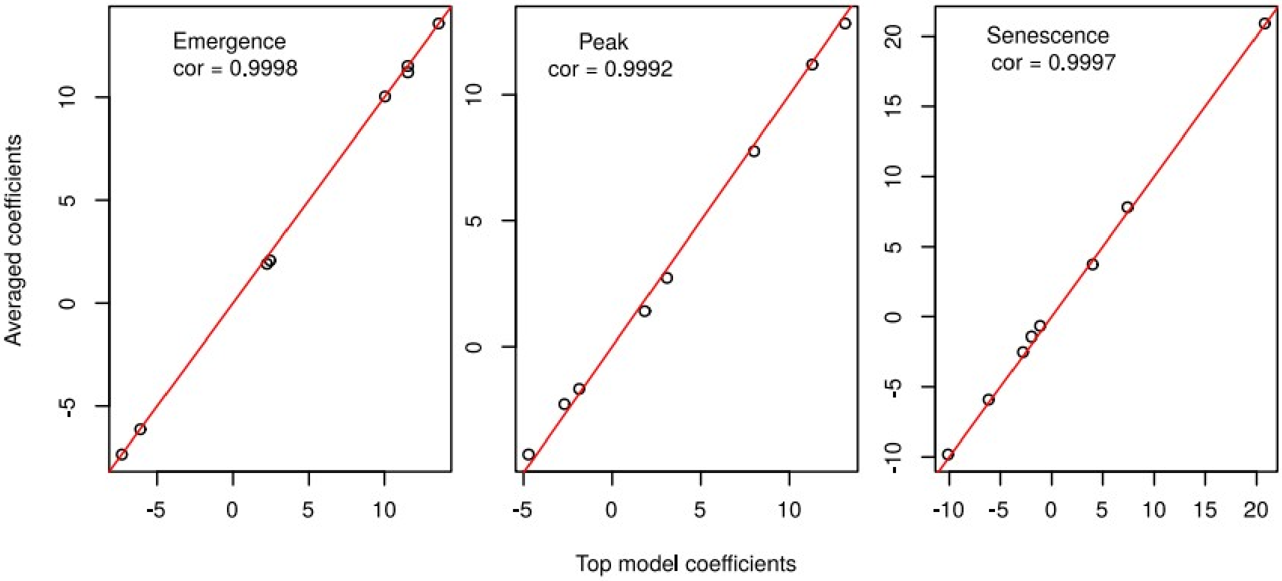

Figure A.6. Emergence significantly predicted later phenophases, with more variation explained in peak timing than in senescence timing.

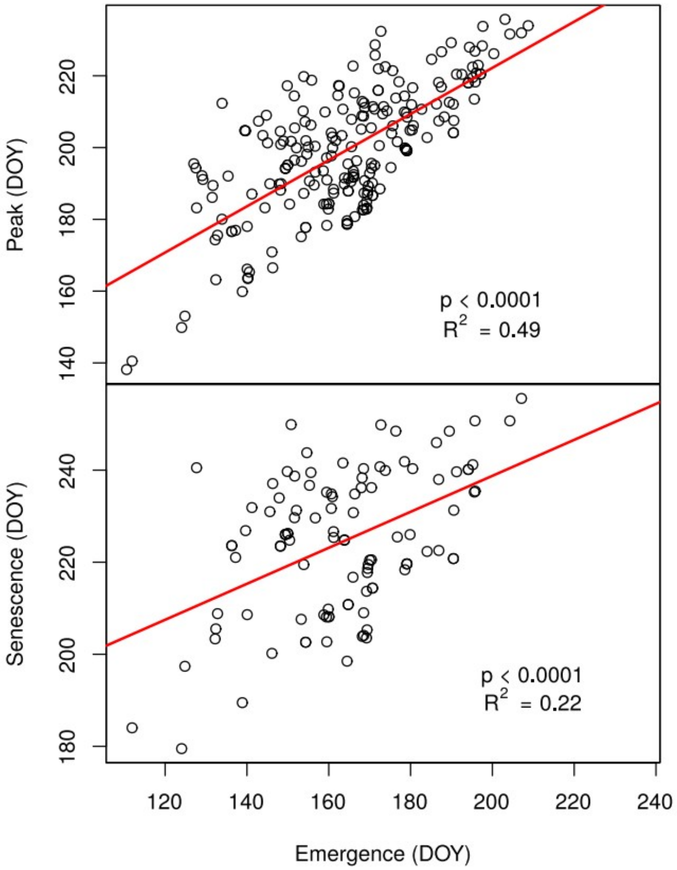

Table A.2. Information on the sites used in the analysis.

Site name	Elevation (m)	Latitude	Longitude	Aspect	Slope
Almont Curve	2456	38.66125	-106.85152	168.69	10.825
Almont	2569	38.65622	-106.86203	111.801	15.07
CDOT	2588	38.78257	-106.87002	243.435	6.37937
Lypps	2639	38.74812	-106.83269	263.66	6.45795
Tuttle	2877	38.954751	-106.988704	243.435	3.1996
Willey	2884	38.955971	-106.988482	261.87	5.05115
Kettle Ponds	2884	38.94435	-106.97174	18.4349	2.26364
Beaver	2921	38.961597	-106.993975	45	5.05115
Seans	2931	38.964099	-106.992616	225	8.04947
Rustlers	2977	38.9885	-107.00512	231.34	9.09464
Davids	2979	38.962124	-106.986896	206.565	12.6044
Gothic	3001	38.963088	-106.994866	71.565	11.18
Little	3061	38.96732	-106.96885	135	8.04947
Hill	3069	38.96677	-106.97009	123.69	19.827
Copper	3072	38.96896	-106.96801	102.529	12.9794
Snodgrass	3224	38.92625	-106.98172	118.74	23.8426
Elko	3230	39.01245	-107.05279	45	1.01275
Mexican Cut	3438	39.02685	-107.06513	51.3402	17.7528

Table A.3. A list of the species, number of individuals, associated traits, number of individuals used in the analysis (#), and the number of phenophase estimates that we were able to make from the time-series data. Abbreviations are as follows: ITD is intertegular distance, Em. is emergence, and Sen. is senescence. Because there have not been species-levels trait studies on every species in the analysis, some nest location and overwintering stage traits have been inferred from other species in the same genera (marked with an * in the references column). We also compared these trait values with those reported in papers summarizing traits by genus (Mitchell 1960, Mitchell 1962, Stephen et al. 1969, Michener 2007, Harmon-Threatt 2020).

Family	Species	ITD (mm)	Nest loc.	Overw. stage	#	Em. points	Peak points	Sen. points	Reference
Andrenidae	Andrena algida Smith 1853	1.91	below	adults	44	0	1	6	(LaBerge 1986)
	Andrena lawrencei Viereck & Cockerell 1914	2.36	below	adults	20	0	0	1	(LaBerge and Ribble 1975)
	Andrena nothocalaidis Cockerell 1905	2.15	below	adults	5	0	0	1	(Thorp 1969; Cane & Love 2016; Gezon et al. 2015)
	Andrena transnigra Viereck 1904	3.17	below	adults	19	0	0	5	(Bouseman and LaBerge 1978)
	Calliopsis coloradensis Cresson 1878	1.65	below	prepupae	4	2	1	1	(Mitchell 1960; Shinn 1967 Jackson 1966; Miliczky 1991; Sheffield et al. 2014)
	Calliopsis teucrii Cockerell 1899	1.41	below	prepupae	319	5	4	1	(Shinn 1967; Hefetz et al. 1982)
	Panurginus cressoniellus Cockerell 1898	1.3	below	prepupae	2269	29	48	29	(Stephen et al. 1969) *
	Panurginus ineptus	1.35	below	prepupae	946	36	38	37	(Gezon et al.

	Cockerell 1922								2015; Stephen et al. 1969) *
	Pseudopanurgus bakeri (Cockerell 1906)	1.12	below	prepupae	569	61	29	13	(Gezon et al. 2015; Stephen et al. 1969) *
	Pseudopanurgus didirupa (Cockerell 1908)	1.3	below	prepupae	102	19	6	3	(Gezon et al. 2015; Stephen et al. 1969) *
Apidae	Anthophora terminalis Cresson 1869	3.17	above	prepupae	10	3	3	1	(Medler 1964)
	Ceratina neomexicana Cockerell 1901	1.37	above	adults	67	1	3	5	(Michener 1936)
	Melissodes confusus Cresson 1878	3.01	below	prepupae	13	5	1	0	(LaBerge 1961; Clement 1973; Hurd et al. 1980)
	Melissodes grindeliae Cockerell 1898	2.72	below	prepupae	2	1	1	0	(LaBerge 1961; Clement 1973; Hurd et al. 1980)
	Melissodes hymenoxidis Cockerell 1906	3.11	below	prepupae	2	1	0	0	(LaBerge 1961; Clement 1973; Hurd et al. 1980)
	Melissodes tristis Cockerell 1894	3.07	below	prepupae	12	0	3	1	(LaBerge 1961; Clement 1973; Hurd et al. 1980)
Colletidae	Colletes consors Cresson 1868	2.19	below	adults	2	1	1	1	(Gezon et al. 2015; Sheffield et al. 2014) *
	Colletes nigrifrons Titus 1900	2.04	below	adults	38	6	8	5	(Gezon et al. 2015; Sheffield et al. 2014) *
	Hylaeus annulatus (L. 1758)	1.28	above	prepupae	353	34	14	6	(Gezon et al. 2015; Stephen et al. 1969) *
	Hylaeus basalis (Smith 1853)	1.85	above	prepupae	57	8	10	4	(Scott 1996)
	Hylaeus modestus Say 1837	1.38	above	prepupae	2	1	1	1	(Packer et al. 2007; Stephen et al. 1969)
	Hylaeus rudbeckiae (Cockerell & Casad 1895)	0.97	above	prepupae	12	1	0	0	(Packer et al. 2007; Stephen et al. 1969)
Halictidae	Agapostemon texanus Cresson 1872	2.22	below	adults	170	3	1	0	(Roberts 1973a; Eickwort 1981)

	Dufourea fimbriata ^ (Cresson 1878)	1.18	below	prepupae	50	8	7	3	Dumesh & Sheffield 2012)
	Dufourea harveyi ^ (Cockerell 1906)	1.18	below	prepupae	221	33	24	7	Dumesh & Sheffield 2012)
	Dufourea maura (Cresson 1878)	1.73	below	prepupae	43	11	6	5	Dumesh & Sheffield 2012)
	Halictus confusus Smith 1853	1.32	below	adults	38	2	1	1	(Dolphin 1971, 1978; Eickwort et al. 1996; Richards et al. 2010)
	Halictus rubicundus (Christ 1791)	1.87	below	adults	496	25	6	13	(Dolphin 1978)
	Halictus tripartitus Cockerell 1895	1.24	below	adults	231	2	8	7	(Dolphin 1978; Gezon et al. 2015; Roberts 1973b)
	Halictus virgatellus Cockerell 1901	1.44	below	adults	1722	10	19	26	(Gezon et al. 2015; Sheffield et al. 2014) *
	Lasioglossum abundipunctum Gibbs 2010	1.01	below	adults	136	3	3	9	(Gezon et al. 2015; Packer et al. 2007)
	Lasioglossum ephialtum Gibbs 2010	1.01	below	adults	4	1	1	1	(Gibbs, 2010)
	Lasioglossum inconditum (Cockerell 1916)	1.25	below	adults	980	6	3	45	(Gibbs et al. 2013)
	Lasioglossum nigrum (Viereck 1903)	1.28	below	adults	1865	4	6	40	(Packer et al. 2007)
	Lasioglossum obnubilum (Sandhouse 1924)	0.89	below	adults	167	5	4	5	(Gibbs 2010; Packer et al. 2007)
	Lasioglossum occidentale (Crawford 1902)	0.96	below	adults	46	3	5	4	(Packer et al. 2007)
	Lasioglossum pacatum (Sandhouse 1924)	1.12	below	adults	643	0	1	4	(Gibbs 2010; Packer et al. 2007)
	Lasioglossum pavoninum (Ellis 1913)	1.06	below	adults	51	3	2	3	(Gibbs 2010; Packer et al. 2007)
	Lasioglossum prasinogaster Gibbs 2010	1.14	below	adults	806	0	2	5	(Packer et al. 2007)
	Lasioglossum ruidosense (Cockerell 1897)	1.05	below	adults	1273	8	8	27	(Gibbs 2010; Packer et al. 2007)

	Lasioglossum sandhousiellum Gibbs 2010	1.08	below	adults	85	13	1	1	(Gibbs 2010; Packer et al. 2007)
	Lasioglossum sedi (Sandhouse 1924)	0.99	below	adults	6161	4	11	63	(Packer et al. 2007)
	Lasioglossum semicaeruleum (Cockerell 1895)	1.03	below	adults	41	3	5	2	(Gibbs 2010; Packer et al. 2007)
	Lasioglossum tenax (Sandhouse 1924)	1.06	below	adults	343	5	1	16	(Packer 1994)
	Lasioglossum trizonatum (Cresson 1874)	2.3	below	adults	359	2	0	13	(McGinley 1986)
Megachilidae	Dianthidium heterulkei Schwarz 1940	2.08	above	prepupae	49	7	3	0	(Krombein 1967; Clement 1976)
	Hoplitis albifrons (Kirby 1837)	2.43	above	prepupae	13	3	2	1	(Fye 1965)
	Hoplitis fulgida (Cresson 1864)	2.04	above	prepupae	88	9	12	4	(Tepedino & Parker 1984)
	Hoplitis robusta (Nylander 1848)	1.39	above	prepupae	156	23	21	14	(Clement & Rust 1975; Müller & Richter 2018; Müller & Mauss 2016)
	Megachile frigida Smith 1853	3.64	above	prepupae	7	2	1	0	(Hobbs & Lilly 1954; Pengelly 1955; Stephen 1956; Jenkins & Matthews 2004)
	Megachile inermis Provancher 1888	4.43	above	prepupae	4	1	1	0	(Stephen 1956; Medler 1958; Sheffield et al. 2008)
	Megachile melanophaea Smith 1853	3.26	below	prepupae	22	8	4	3	(Hobbs & Lilly 1954; Pengelly 1955)
	Megachile montivaga Cresson 1878	2.61	above	prepupae	15	3	3	2	(Hicks 1926; Hobbs & Lilly 1954; Baker et al. 1985)
	Megachile perihirta Cockerell 1898	3.53	below	prepupae	9	2	1	1	(Sladen 1918; Hicks 1926; Hobbs & Lilly 1954; Bohart

									1957)
	Megachile pugnata Say 1837	3.1	above	prepupae	1	1	0	0	(Medler 1964; Hobbs & Lilly 1954; Sheffield et al. 2008)
	Megachile relativa Cresson 1878	2.47	above	prepupae	18	6	5	2	(Medler & Koerber 1958; Sheffield et al. 2008)
	Osmia albolateralis Cockerell 1906	2.23	above	adults	56	5	7	4	(Rightmyer et al. 2013)
	Osmia brevis Cresson 1864	2.3	above	adults	21	2	2	2	(Baker et al. 1985; Cane 2014)
	Osmia bruneri Cockerell 1897	2.1	above	adults	5	0	0	1	(Baker et al. 1985; Cane et al. 2007; Frohlich 1983)
	Osmia bucephala Cresson 1864	3.76	above	adults	93	3	8	13	(Rightmyer et al. 2013) *
	Osmia inermis (Zetterstedi 1838)	2.35	above	adults	5	0	0	1	(Müller 2018; Sheffield et al. 2014)
	Osmia longula Cresson 1864	3.2	above	adults	6	1	1	2	(Cane et al. 2007; Rightmyer et al. 2013)
	Osmia phaceliae Cockerell 1907	1.78	above	adults	8	1	1	1	(Packer et al. 2007) *
	Osmia sculleni Sandhouse 18939	2.32	above	adults	3	0	1	1	(Cane et al. 2007; Sheffield et al. 2014) *
	Osmia simillima Smith 1853	2.53	above	adults	105	7	6	13	(Cane et al. 2007; Sheffield et al. 2014) *
	Osmia tersula Cockerell 1912	2.31	above	adults	6	1	2	2	(Cane et al. 2007; Sheffield et al. 2008)
	Osmia “torchioi” Griswold ms. name	1.82	above	adults	12	0	1	1	(Gezon et al., 2015)

^ *Dufourea harveyi* and *Dufourea fimbriata* may be synonymous in some parts of their range, but we found clear morphological differences between specimens in these groups in the present study area.

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Table A.4. Coefficients for species-specific shifts in phenophases in response to snowmelt timing (Figure 1). The three phenophases (emergence, peak, senescence) are separated by commas.

Species	**Slope**	**SE**	**t**
Dufourea harveyi	0.22, 0.18, NA	0.32, 0.30, NA	0.68, 0.59, NA
Halictus rubicundus	0.42, NA, 0.13	0.46, NA, 0.57	0.42, NA, 0.22
Halictus virgatellus	-0.01, -0.09, 1.45	1.12, 0.39, 0.66	-0.21,-0.68, 2.01
Hoplitis fulgida	0.86, 0.83, NA	0.63, 0.39, NA	1.02, 1.68, NA
Hoplitis robusta	0.52, 0.84, 0.5	0.61, 0.42, 0.9	0.48, 1.59, 0.41
Hylaeus annulatus	0.65, 0.5, NA	0.38, 0.35, NA	1.13, 0.92, NA
Lasioglossum sedi	NA, 0.8, -0.14	NA, 0.51, 0.59	NA, 1.22, -0.45
Panurginus cressoniellus	0.56, 0.29, 0.71	0.46, 0.36, 0.74	0.74, 0.31, 0.79
Panurginus ineptus	-0.07, 0.09, 0.19,	0.47, 0.35, 0.66	-0.62, -0.24, 0.1
Pseudopanurgus bakeri	0.53, 0.09, -0.25	0.39, 0.37, 0.73	0.79, -0.24,-0.52

Table A.5. Coefficients of standardized effect sizes from the full model of bee phenology (Figure 2). The three phenophases (emergence, peak, senescence) are separated by commas. Significant effects at the α=0.05 level are bold, but all effects were determined to be important by the model averaging protocol.

Predictor	**Slope**	**SE**	**z**	**P**
Snowmelt date	**11.52**, **12.82**, **7.81**	2.68, 2.42, 2.44	4.28, 5.26, 3.19	<0.01, <0.01, <0.01
Summer rainfall	**10.04**, 2.73, -1.85	2.12, 2.06, 2.12	4.72, 1.32, 0.87	<0.01, 0.19, 0.38
Maximum temperature	**-7.34**, 1.40, -0.90	2.41, 2.22, 2.47	3.04, 0.63, 0.36	<0.01, 0.53, 0.72
Elevation	**13.57**, **7.76**, -5.92	3.23, 3.65, 4.05	4.15, 2.12, 1.46	<0.01, 0.03, 0.15
Solar Incidence	-6.13, -1.68, 4.03	3.40, 3.27, 4.04	1.80, 0.56, 1.00	0.07, 0.57, 0.32
Body Mass	2.08, -2.58, -2.79	3.23, 3.26, 3.57	0.64, 0.79, 0.78	0.54, 0.43, 0.43
Nest Location (below ground)	**11.21**, -4.57, **-9.82**	4.30, 3.84, 4.29	2.60, 1.19, 2.28	<0.01, 0.24, 0.02
Overwintering stage (prepupae)	1.91, **11.20**, **20.91**	3.52, 3.23, 3.59	0.54, 3.45, 5.81	0.59, <0.01, <0.01

Table A.6. Marginal and conditional R^2 values for the three phenology top models, as well as the proportion of variance explained by subsetted climate and trait models (Figure 3).

Model	**Phenophase**	**Marginal R^2**	**Conditional R^2**	**Proportion of marginal variance explained**
Full model	Emergence	0.49	0.86	
	Peak	0.40	0.89	
	Senescence	0.45	0.84	
Climate only	Emergence	0.26	0.85	0.53
	Peak	0.16	0.88	0.41
	Senescence	0.07	0.84	0.16
Traits only	Emergence	0.11	0.79	0.22
	Peak	0.22	0.85	0.55
	Senescence	0.43	0.82	0.95

APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER 3:

SKEWNESS IN BEE AND FLOWER PHENOLOGICAL DISTRIBUTIONS

Section B.1: Data truncation

Because data collection started after the beginning of activity in some species or ended before the end of activity in some years due to logistical constraints, some bee and flower time-series were truncated. Truncation can artificially bias skewness estimates, so we checked for the potential effect of truncation on the main analyses from this study. To detect potential truncation, we flagged time-series in which the first observation was non-zero (left-truncated), the last observation was non-zero (right-truncated), or both the first and last were non-zero (doubly-truncated). We then examined skewness estimates for each of these truncation groups, and compared them to time-series for which it was certain that truncation had not occurred. We re-ran the analyses comparing mean and standard deviation to skewness for each of the truncation groups. We note that our method of detecting truncation necessarily over-represents the degree to which truncation actually occurred because a lack of a zero-observation does not mean that there would not have a been a zero-observation at the previous time-step if sampling were done. This is especially true for the bee phenology dataset in which sampling was spaced two weeks apart. The beginning and end of sampling for both the bee and flower phenology monitoring projects were designed to be timed to the beginning and end of the growing season.

We found that of the 3,024 flower time-series, 135 were potentially left-truncated, 153 right-truncated, and 18 doubly-truncated. Of the 480 bee time-series, 129 were potentially left-truncated, 105 right-truncated, and 157 doubly-truncated. We found that truncation type affected average skewness, but overall skewness was still positive (right-skewed) for both flowers and bees, regardless of truncation type (Figure S1). The mean-to-skewness relationship varied slightly by truncation type for bees and flowers, but remained negative for all groups with the exception of doubly truncated flower time-series (though this trend was based on just 18 points) (Figure S2). The standard deviation-to-skewness relationship was more variable based on truncation group in bees, with left- and doubly-truncated time-series showing a negative relationship and the other groups showing a positive relationship (Figure S2).

Because both datasets were not strongly biased to left- versus right-truncation, because skewness values were positive despite truncation type, and because the mean-to-skewness results were not strongly affected, we conclude that the findings of this study were not a sole product of data truncation, though truncation may have played some role in the bee phenological skewness results.

Figure B.1. Skewness by truncation type. Frequency refers to the number of time-series represented in each skewness value bin. The red lines show the mean skewness value for each group.

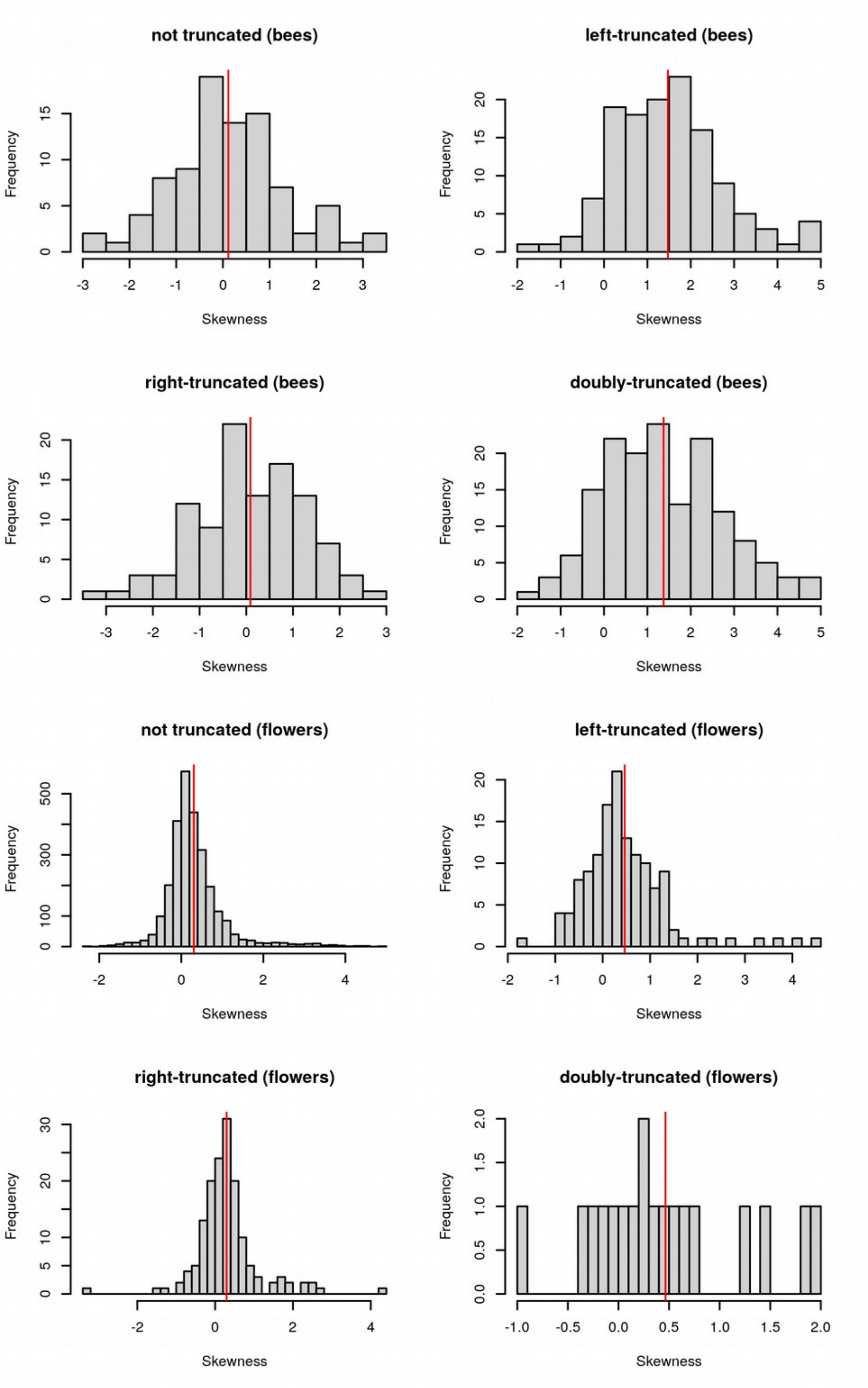
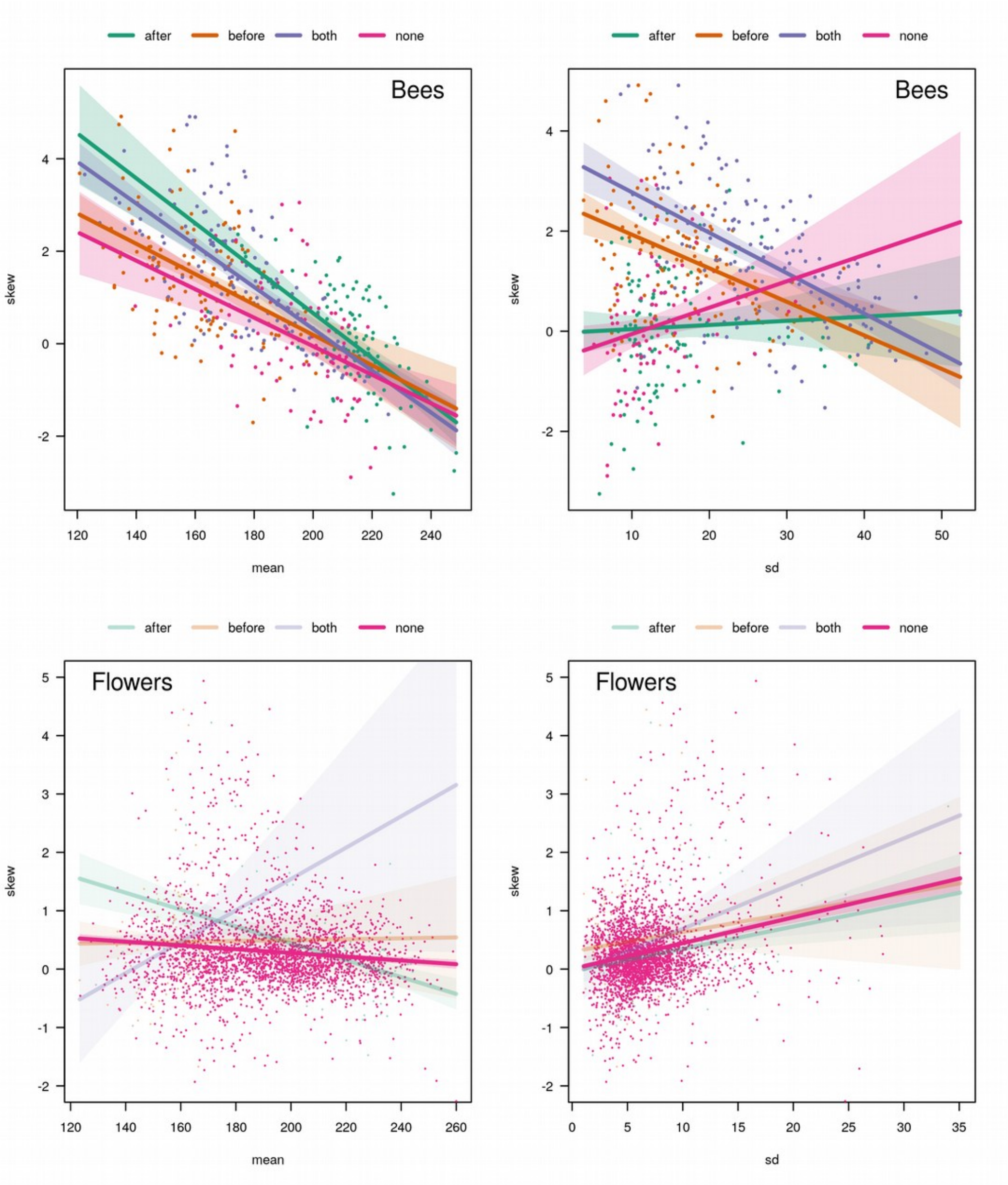


Figure B.2. Mean and standard deviation version skewness by truncation type. The left panels show mean results, and the right panels show standard deviation results. The colors correspond to truncation type, with “after” being right-truncation, “before” being left-truncation, and “both” being double-truncation. For the flower panels, the truncation lines are more transparent because those trends result from a very small number of points relative to the number of non-truncated points.



Section B.2. Abundance effects on skewness

We tested for the effects of abundance on skewness because differences in overall abundance between time-series may artificially influence skewness measures in a number of ways. The flower phenology data is the summed abundance of flowers within plots, sometimes including many individuals. If there are many individual plants grouped into one abundance measure, individual skewed phenological distributions may be superseded by the overall pattern. So, we might expect times-series with lower abundance to show greater skewness and higher variance of skewness estimates. In the bee dataset, there is potential for lethal sampling to affect observed skewness for very small populations. Lethal sampling could have observable consequences for the shape of the abundance curve over time if the sampling itself appreciably drew down populations. If this effect were to appear, we would expect it to happen in smaller populations, in which lethal sampling might have a greater proportional effect. So, if this were happening, we would expect bee time-series with lower overall abundance to appear more right-skewed.

Bee and flower abundances varied widely, with middle 50% of bee time-series representing 15-45 individuals, and the middle 50% of flower time-series representing 33-388 individuals (noting that we excluded time-series with less than 10 total individuals) (Figure S3). We found that for both bees and flowers, skewness was positively correlated with abundance (Figure S4). This is contrary to our predictions that lower abundances would be associated with more right-skewed distributions if skewness were influenced by aggregated flower abundance measures or lethal sampling. So, while it may be that the above-mentioned effects might have tempered observed skewness, they were not enough to reverse the patterns. We encourage future studies to look into skewness at multiple aggregation levels and to investigate further the proportions of bee populations that are removed when lethal sampling is done.

Figure B.3. Bee and flower abundances. Abundances are shown on a log-scale for visualization clarity.

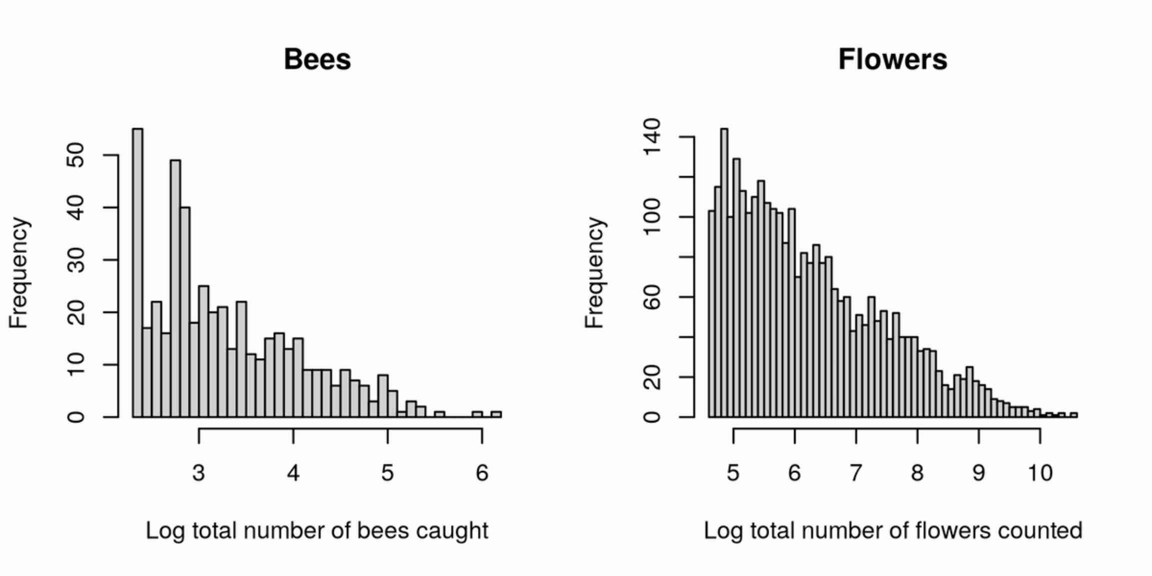
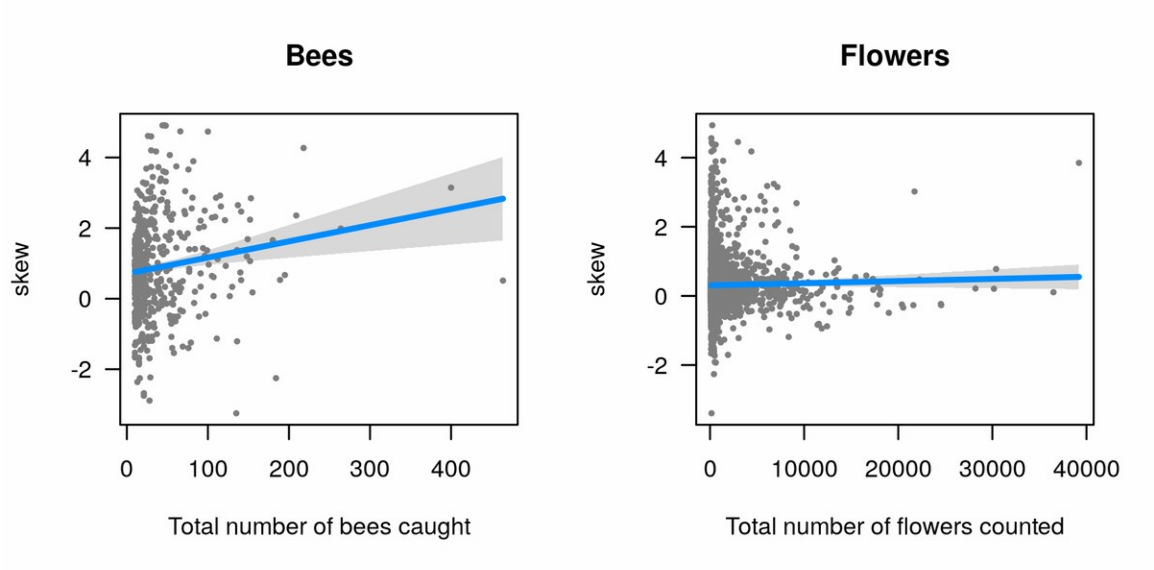


Figure B.4. Skewness predicted by abundance. Each point represents a single time-series.



Section B.3. Species lists and summary statistics

Table B.1. Bee species summary statistics

Family	Species	Mean date	Mean skew	Mean SD	Mean abundance	n time-series	n sites	n years
Andrenidae	Andrena algida	05-29	-0.20	8.71	14	1	1	1
Andrenidae	Andrena cyanophila	07-07	-0.80	16.02	11	1	1	1
Andrenidae	Andrena lawrencei	05-20	0.81	12.89	18	1	1	1
Andrenidae	Andrena medionitens	05-09	2.08	8.79	17	1	1	1
Andrenidae	Calliopsis teucrii	07-29	0.27	12.92	85	3	1	3
Andrenidae	Panurginus cressoniellus	07-20	0.62	12.19	50	20	6	9
Andrenidae	Panurginus ineptus	07-20	0.14	11.98	37	7	6	3
Andrenidae	Pseudopanurgus bakeri	08-06	0.21	13.41	14	3	3	2
Andrenidae	Pseudopanurgus didirupa	08-20	-1.07	13.94	18	1	1	1
Apidae	*Bombus appositus* Q	07-13	0.45	15.85	14	4	4	3
Apidae	*Bombus appositus* W	08-03	-0.34	9.91	18	10	6	5
Apidae	*Bombus balteatus* W	08-02	-0.17	9.72	23	1	1	1
Apidae	*Bombus bifarius* Q	06-14	0.98	16.48	17	12	8	4
Apidae	*Bombus bifarius* W	07-30	-0.12	11.83	36	41	11	7
Apidae	*Bombus fervidus* W	07-29	0.01	14.50	13	1	1	1
Apidae	*Bombus flavifrons* Q	07-06	0.67	17.54	18	11	5	5
Apidae	*Bombus flavifrons* W	08-03	-0.33	11.98	31	21	9	7
Apidae	*Bombus frigidus* W	08-11	1.00	10.06	23	1	1	1
Apidae	*Bombus huntii* W	07-24	0.09	14.01	13	5	3	3
Apidae	*Bombus insularis* Q	07-15	0.54	12.64	16	1	1	1
Apidae	*Bombus rufocinctus* Q	07-27	1.80	9.74	15	1	1	1
Apidae	*Bombus rufocinctus* W	07-27	-0.44	8.76	16	2	2	2
Apidae	*Bombus sylvicola* W	08-01	0.63	11.06	10	1	1	1
Apidae	Ceratina nanula	07-06	0.41	25.50	25	11	4	5

Family	Species	Mean date	Mean skew	Mean SD	Mean abundance	n time-series	n sites	n years
Colletidae	Hylaeus annulatus	08-05	-0.27	13.58	22	10	7	4
Halictidae	Agapostemon texanus	06-12	0.97	25.20	50	9	2	5
Halictidae	Dufourea fimbriata	07-12	0.01	10.42	10	1	1	1
Halictidae	Halictus confusus	06-26	0.33	52.39	24	1	1	1
Halictidae	Halictus rubicundus	06-19	0.51	20.17	17	9	7	4
Halictidae	Halictus tripartitus	07-10	-0.35	19.55	22	9	3	5
Halictidae	Halictus virgatellus	07-04	0.79	25.58	26	51	11	8
Halictidae	Lasioglossum abundipunctum	06-06	0.61	22.04	20	5	4	2
Halictidae	Lasioglossum cooleyi	05-31	1.93	34.95	14	2	2	1
Halictidae	Lasioglossum egregium	07-03	-0.16	16.77	14	2	1	2
Halictidae	Lasioglossum inconditum	06-08	1.98	16.82	31	16	9	5
Halictidae	Lasioglossum nigrum	06-16	2.07	21.44	36	39	13	9
Halictidae	Lasioglossum obnubilum	06-28	0.78	26.11	28	5	2	3
Halictidae	Lasioglossum occidentale	07-17	1.49	12.57	12	1	1	1
Halictidae	Lasioglossum pacatum	06-22	0.69	25.55	155	4	2	3
Halictidae	Lasioglossum prasinogaster	06-19	0.97	23.09	98	10	2	7
Halictidae	Lasioglossum ruidosense	07-03	0.53	30.20	25	44	14	8
Halictidae	Lasioglossum sedi	06-16	1.94	18.26	75	80	17	9
Halictidae	Lasioglossum semicaeruleum	07-04	1.13	14.35	12	3	2	2
Halictidae	Lasioglossum sisymbrii	07-05	0.90	8.59	10	1	1	1
Halictidae	Lasioglossum tenax	06-11	1.73	21.89	29	7	4	4
Halictidae	Lasioglossum trizonatum	05-20	2.15	22.83	52	7	4	3
Megachilidae	Dianthidium heterulkei	08-13	0.80	18.38	10	1	1	1
Megachilidae	Hoplitis fulgida	07-12	0.15	22.28	15	1	1	1
Megachilidae	Osmia proxima	06-21	0.62	16.91	12	1	1	1

Table B.2. Flower species summary statistics.

Family	Species	Mean date	Mean skew	Mean SD	Mean abundance	n time-series	n sites	n years
Apiaceae	Pseudocymopterus montanus	07-05	0.01	9.89	150	5	2	4
Asparagaceae	Maianthemum stellatum	06-22	0.08	3.40	221	6	1	6
Asteraceae	Achillea millefolium	08-17	-0.01	13.09	308	36	3	33
Asteraceae	Antennaria pulcherrima	06-22	0.04	4.49	387	9	1	9
Asteraceae	Cirsium sp	08-03	-0.20	5.29	146	2	1	2
Asteraceae	Dugaldia hoopesii	07-27	0.21	8.37	501	49	5	33
Asteraceae	Erigeron coulteri	08-05	0.31	12.10	193	2	1	2
Asteraceae	Erigeron elatior	08-15	0.19	9.17	144	3	2	3
Asteraceae	Erigeron flagellaris	07-21	0.86	16.07	639	29	1	29
Asteraceae	Erigeron speciosus	08-06	0.28	7.08	2,222	113	4	42
Asteraceae	Gnaphalium uliginosum	06-23	0.44	2.37	254	1	1	1
Asteraceae	Helianthella quinquenervis	07-29	0.18	5.87	334	24	6	12
Asteraceae	Heliomeris multiflora	08-20	0.01	7.24	923	30	4	22
Asteraceae	Heterotheca villosa	08-09	0.24	12.26	5,823	45	1	45
Asteraceae	Ligularia bigelovii	08-11	0.00	5.88	293	33	4	19
Asteraceae	Oligosporus dracunculus	08-19	0.04	6.95	539	43	3	36
Asteraceae	Packera werneriifolia	06-28	-0.23	4.86	418	3	1	3
Asteraceae	Pyrrocoma crocea	08-02	0.43	5.58	264	31	1	31
Asteraceae	Senecio integerrimus	06-26	0.21	5.18	345	28	1	28
Asteraceae	Senecio serra	08-11	-0.12	6.53	750	1	1	1
Asteraceae	Senecio triangularis	07-20	0.34	6.59	126	3	1	3
Asteraceae	Seriphidium tridentata	08-22	0.42	4.63	777	42	1	42
Asteraceae	Solidago multiradiata	08-08	0.27	6.38	746	59	4	34
Asteraceae	Symphyotrichum foliaceum	08-23	0.15	5.85	214	23	4	16
Asteraceae	Taraxacum officinale	06-17	1.22	5.64	195	54	4	34
Berberidaceae	Mahonia repens	06-06	0.16	4.00	624	36	1	36
Boraginaceae	Hackelia floribunda	07-26	0.44	5.67	205	1	1	1
Boraginaceae	Mertensia ciliata	07-11	0.28	7.71	1,398	62	2	37
Boraginaceae	Mertensia fusiformis	06-08	0.27	5.25	1,445	107	4	45
Brassicaceae	Boechera stricta	06-26	1.81	12.85	207	26	3	24

Family	Species	Mean date	Mean skew	Mean SD	Mean abundance	n time-series	n sites	n years
Brassicaceae	Cardamine cordifolia	07-03	0.04	4.45	404	24	2	24
Brassicaceae	Draba aurea	06-28	0.33	6.55	2,405	125	3	44
Brassicaceae	Draba nemorosa	06-08	0.23	4.19	217	2	2	2
Brassicaceae	Erysimum capitatum	07-09	0.55	5.43	320	25	2	24
Brassicaceae	Noccaea fendleri	06-09	0.41	4.89	2,089	58	2	42
Campanulaceae	Campanula rotundifolia	08-09	0.40	7.71	155	8	2	8
Caprifoliaceae	Distegia involucrata	06-28	0.20	4.78	125	1	1	1
Caprifoliaceae	Valeriana edulis	07-19	0.15	14.19	185	28	3	24
Caprifoliaceae	Valeriana occidentalis	06-21	0.17	8.77	556	89	5	44
Caryophyllaceae	Eremogone congesta	07-19	0.85	8.55	7,081	44	1	44
Caryophyllaceae	Stellaria longifolia	07-18	0.11	8.06	130	4	1	4
Chenopodiaceae	Chenopodium album	08-19	-0.80	6.09	521	1	1	1
Crassulaceae	Amerosedum lanceolatum	07-24	0.39	5.22	234	18	1	18
Crassulaceae	Tolmachevia integrifolia	06-27	0.13	4.06	532	18	1	18
Fabaceae	Lathyrus leucanthus	07-05	0.24	5.24	471	79	4	37
Fabaceae	Lupinus argenteus	07-23	0.13	6.05	800	18	2	16
Fabaceae	Lupinus bakeri	07-08	0.31	4.64	2,398	45	4	33
Fabaceae	Lupinus sp	07-11	0.76	5.32	462	7	3	4
Fabaceae	Oxytropis deflexa	06-25	0.71	10.80	167	4	1	4
Fabaceae	Vicia americana	07-17	0.80	6.32	338	35	5	21
Gentianaceae	Frasera speciosa	06-30	0.49	7.27	715	1	1	1
Gentianaceae	Frasera speciosa outside	07-19	0.00	8.58	227	1	1	1
Gentianaceae	Gentianella acuta	08-10	-0.15	7.46	149	1	1	1
Gentianaceae	Gentianopsis thermalis	08-10	0.75	7.37	152	1	1	1
Gentianaceae	Pneumonanthe parryi	08-21	-0.59	5.33	119	4	2	3
Gentianaceae	Swertia perennis	08-07	0.20	6.61	686	16	1	16
Geraniaceae	Geranium richardsonii	07-24	0.09	9.37	331	43	3	31
Hydrophyllaceae	Hydrophyllum capitatum	06-13	-0.56	3.47	401	44	2	42
Hydrophyllaceae	Hydrophyllum fendleri	07-07	0.19	4.62	154	6	1	6
Liliaceae	Erythronium grandiflorum	06-04	0.05	2.30	213	44	2	35
Linaceae	Adenolinum lewisii	07-20	0.85	8.64	1,064	42	2	40
Melanthiaceae	Anticlea elegans	07-22	0.04	5.01	1,443	39	1	39
Montiaceae	Claytonia lanceolata	05-29	0.15	3.78	6,137	81	2	42
Orchidaceae	Limnorchis hyperborea	07-08	0.12	7.05	1,589	18	2	16
Orobanchaceae	Castilleja linariifolia	07-27	0.69	11.87	167	4	1	4
Orobanchaceae	Castilleja sulphurea	07-22	0.16	7.06	195	21	2	21

Family	Species	Mean date	Mean skew	Mean SD	Mean abundance	n time-series	n sites	n years
Orobanchaceae	Orthocarpus luteus	08-18	0.15	6.37	254	4	1	4
Orobanchaceae	Pedicularis bracteosa	07-04	0.21	4.95	323	18	2	18
Polemoniaceae	Collomia linearis	07-28	0.82	12.53	643	28	4	26
Polemoniaceae	Ipomopsis aggregata	07-25	0.62	13.55	360	10	1	10
Polygonaceae	Eriogonum subalpinum	07-15	0.08	6.55	174	23	2	23
Polygonaceae	Eriogonum umbellatum	07-04	0.15	6.27	545	40	1	40
Primulaceae	Androsace septentrionalis	06-18	1.30	10.30	2,988	97	5	41
Primulaceae	Dodecatheon pulchellum	06-29	0.00	3.63	207	20	1	20
Ranunculaceae	Aconitum columbianum	07-28	0.22	6.45	398	59	3	37
Ranunculaceae	Delphinium barbeyi	07-26	0.02	6.13	2,444	102	3	41
Ranunculaceae	Delphinium nuttallianum	06-19	-0.12	4.74	1,893	44	1	44
Ranunculaceae	Ranunculus inamoenus	06-13	1.40	8.54	353	38	3	37
Rosaceae	Amelanchier alnifolia	06-20	0.49	3.97	397	32	1	32
Rosaceae	Erythrocoma triflorum	06-23	0.89	7.24	146	4	1	4
Rosaceae	Fragaria virginiana	06-22	0.99	5.24	315	25	3	16
Rosaceae	Pentaphylloides floribunda	07-19	0.54	9.38	216	23	2	23
Rosaceae	Potentilla hippiana	07-26	-0.04	11.67	387	27	1	27
Rosaceae	Potentilla pulcherrima	07-21	0.17	9.32	1,316	122	6	44
Rubiaceae	Galium septentrionale	08-07	0.02	7.40	263	28	5	21
Salicaceae	Salix brachycarpa	06-08	0.25	2.71	307	11	2	11
Salicaceae	Salix drummondiana	06-04	1.20	3.05	674	1	1	1
Salicaceae	Salix geyeriana	05-28	-0.07	2.88	700	11	1	11
Salicaceae	Salix monticola	06-05	0.35	3.22	5,146	22	1	22
Salicaceae	Salix sp	06-11	-0.06	3.21	739	8	2	8
Salicaceae	Salix wolfii	06-17	0.37	2.93	1,023	9	2	6
Violaceae	Viola praemorsa	06-11	0.25	2.90	355	43	2	41

Section B.4. Additional figures

Figure B.5. Several example phenological distributions on individual time-series. Two examples of negatively and positively skewed distributions are given for different species of bees and plants. The top four panels correspond to bee time-series and the bottom four correspond to flower time-series.

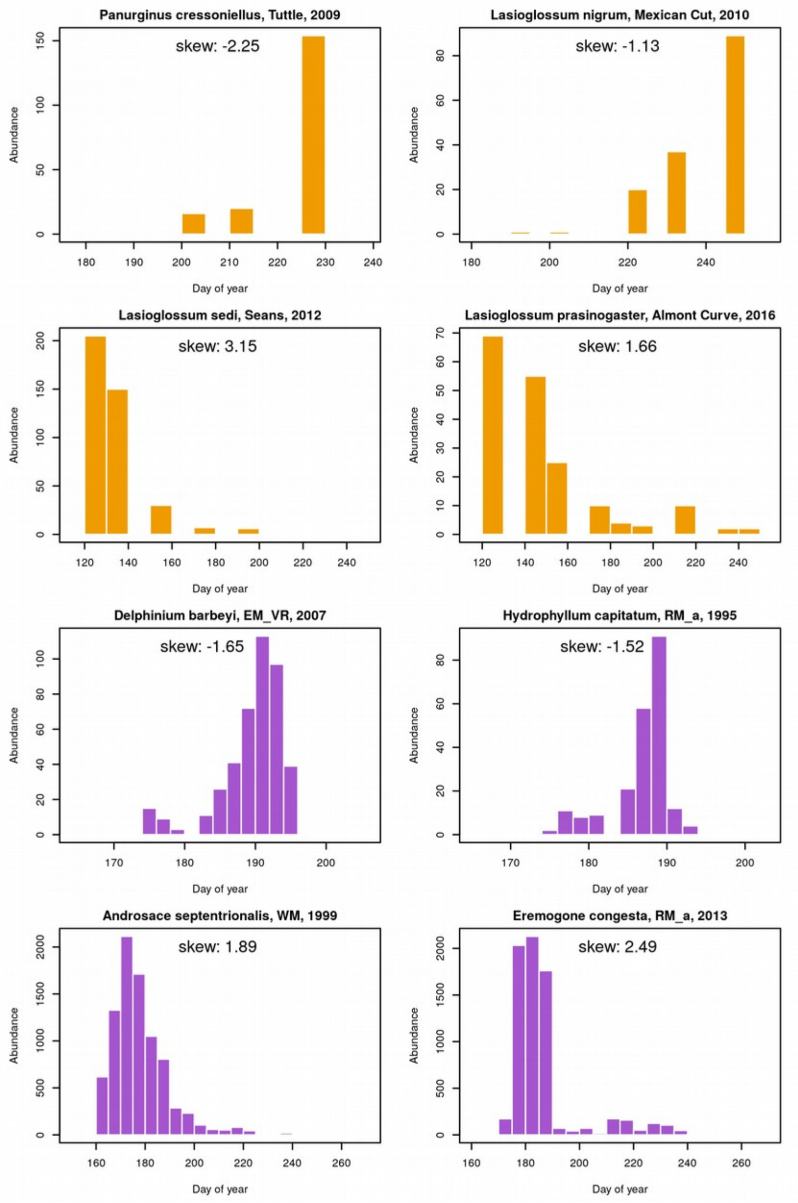
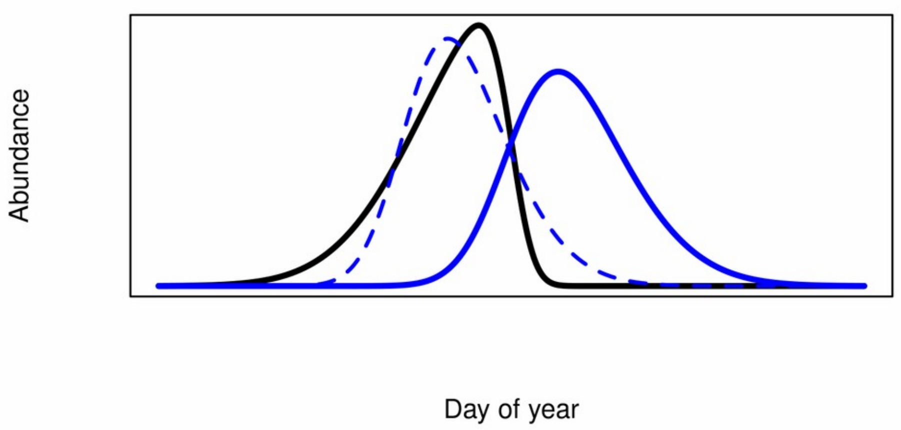


Figure B.6. Illustration of one matched up pair of skewed distributions used to calculate maximum possible overlap in the simulation experiment. The solid black curve represents a distribution with a skewness of -5, and the solid blue curve represents one with skewness of 2. The mean and standard deviation of the blue distribution are perturbed to be higher and lower in 2000 combinations, and the resulting distribution with the greatest overlap with the black distribution is selected (blue dashed curve). Each of the 2500 pixels in Figure 4 from the main text corresponds to one such calculation.



APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER 4:

BEE PHENOLOGICAL DISTRIBUTIONS PREDICTED MECHANISTICALLY BY PHENOPHASE TRANSITION RATES

Section C.1: Model specifications and fitting diagnostics

We specified weakly informative prior parameter distributions based on biological knowledge about the system and model constraints. The prior formulas and justifications are listed here.

Phenology hyperparameters – The center of the μ hyperparameter was set to 160 as the average expected day-of-year (DOY) of the beginning of the growing season at the study location, corresponding to early June. A lognormal distribution was used for the σ hyperparameter, as it was for all standard deviations in the model, because phenology dispersion terms cannot be negative.

$$\mu_h \sim Normal(160,40)$$
$$\sigma_h \sim Lognormal(1,1)$$
$$h \sim Normal(\mu_h,\sigma_h)$$

Population size hyperparameters – The center of the μ hyperprior was set to the expected location population size based on prior knowledge bee populations around the sampling location. The dispersion of this hypoerprior was set to 10 to avoid a truncated distributions, as B_0 must be greater than 0.

$$\mu_u \sim Normal(40{,}10)$$
$$\sigma_u \sim Lognormal(0{,}1)$$
$$u \sim Normal(\mu_u, \sigma_u)$$

Emergence rate – To aid model convergence, non-centered reparametrization (a.k.a. “the Matt trick”) was implemented as follows, implying an emergence prior with mean of 0.2 and dispersion of 0.1.

$$\mu_{\tilde{a}} \sim Normal(0, 1)$$
$$\sigma_{\tilde{a}} \sim Lognormal(0{,}1)$$
$$\tilde{a} \sim Normal(\mu_{\tilde{a}}, \sigma_{\tilde{a}})$$
$$a = 0.2 + 0.1\,\tilde{a}$$

Emergence friction – Non-centered reparametrization was implemented as follows, implying an emergence prior with mean of 0.004 and dispersion of 0.001. This is perhaps the most informative prior because the model predictions quickly go to infinity for *b* values greater than 0.01 (depending somewhat on the corresponding combination of *a* and *u* parameters), greatly reducing fitting efficiency.

$$\mu_{\tilde{b}} \sim Normal(0, 1)$$
$$\sigma_{\tilde{b}} \sim Lognormal(0{,}1)$$
$$\tilde{b} \sim Normal(\mu_{\tilde{b}}, \sigma_{\tilde{b}})$$
$$b = 0.004 + 0.001\,\tilde{b}$$

Mortality rate – Non-centered reparametrization was implemented as follows, implying an emergence prior with mean of 0.2 and dispersion of 0.1.

$$\mu_{\widetilde{m}} \sim Normal(0,1)$$
$$\sigma_{\widetilde{m}} \sim Lognormal(0,1)$$
$$\widetilde{m} \sim Normal(\mu_{\widetilde{m}}, \sigma_{\widetilde{m}})$$
$$m = 0.2 + 0.1\widetilde{m}$$

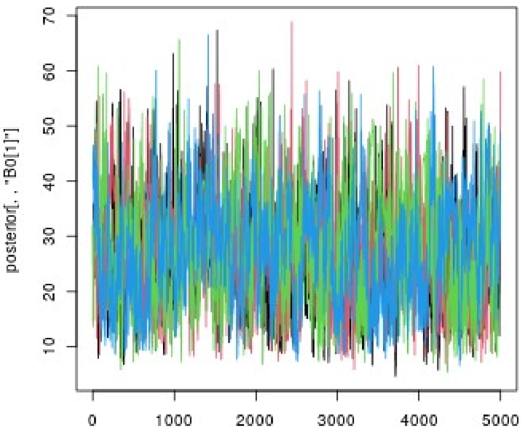
Flower covariate slope – This prior is wide, reflecting our ignorance of its value, and centered at zero to be unbiased.

$$\beta_F \sim Normal(0,5)$$

Error – A lognormal distribution was used because error cannot be less than 0.

$$\epsilon \sim Lognormal(0,1)$$

Figure C.1. Trace plots for the population size parameter, *u*. The left panels represent estimates for 2019, and the right panels represent estimates for 2021. The top panels represent represent estimates for the Trail site, and the bottom panels represent estimates for the Waterfall site. Each color represents one of the four MCMC chains. Parameter values are on the vertical axis, and iterations are on the horizontal axis.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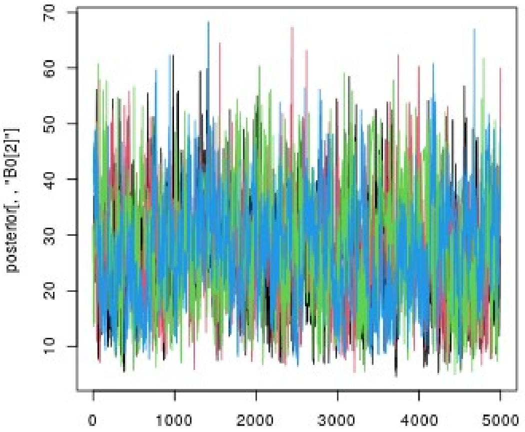
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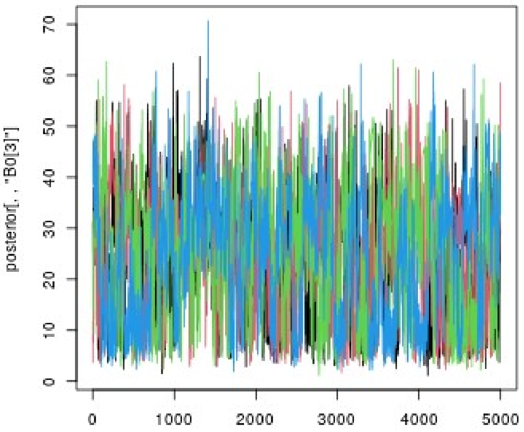
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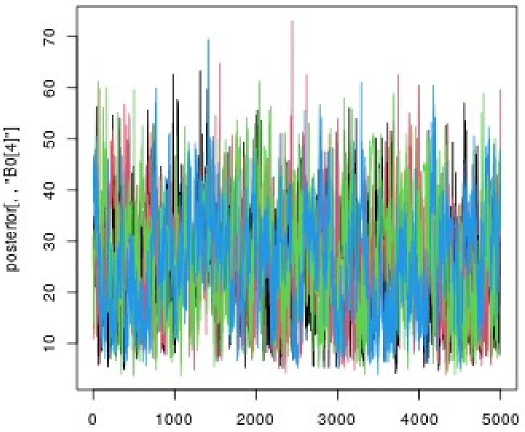
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Figure C.2. Trace plots for the demographic rate parameters. The top panels show estimates of the *a* parameter, the middle panels show estimates of the *b* parameter, and the bottom panels show estimates of the *m* parameter. The left panels correspond to 2019, and the right panels correspond to 2021. Each color represents one of the four MCMC chains. Parameter values are on the vertical axis, and iterations are on the horizontal axis.

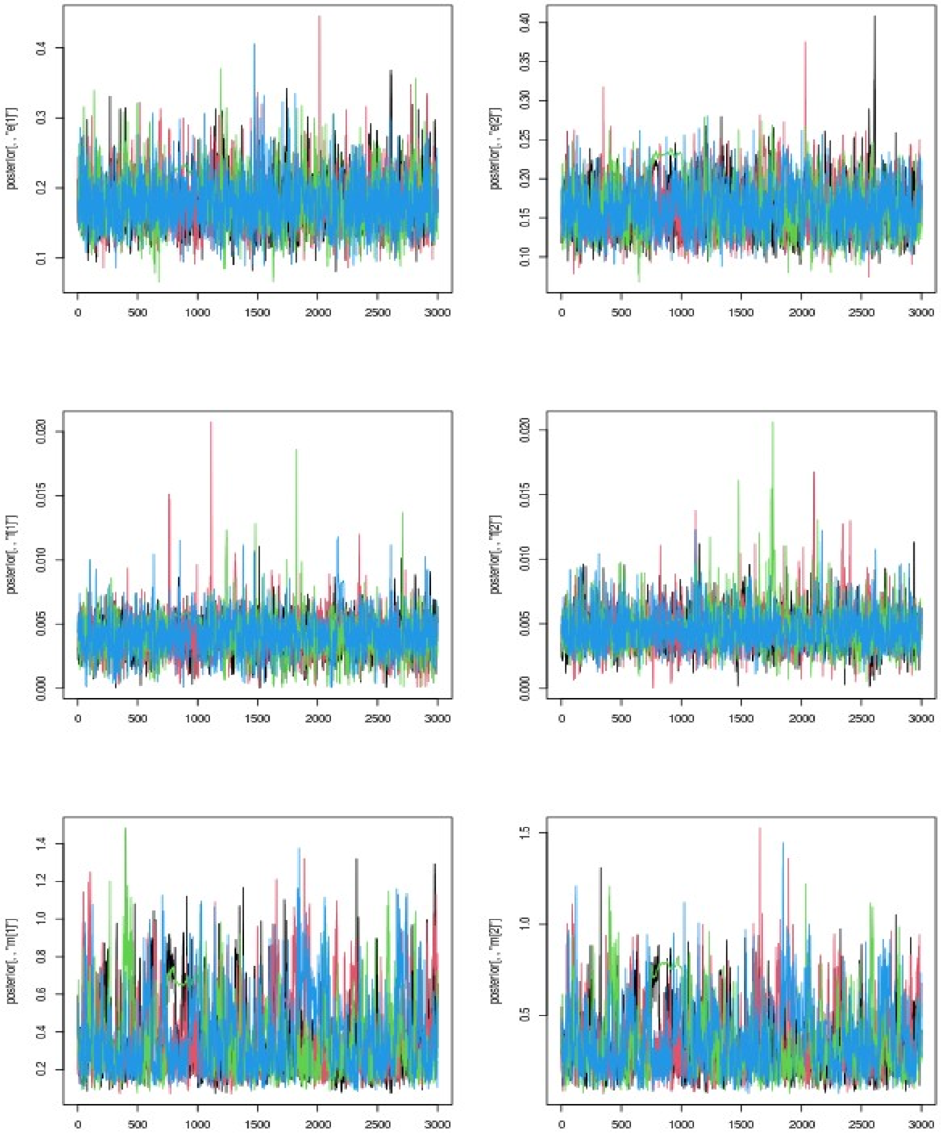


Figure C.3. Trace plots for the onset parameter, *h*. The top panel shows onset estimates for 2019, and the bottom panel shows estimates for 2021. Each color represents one of the four MCMC chains. Parameter values are on the vertical axis, and iterations are on the horizontal axis.

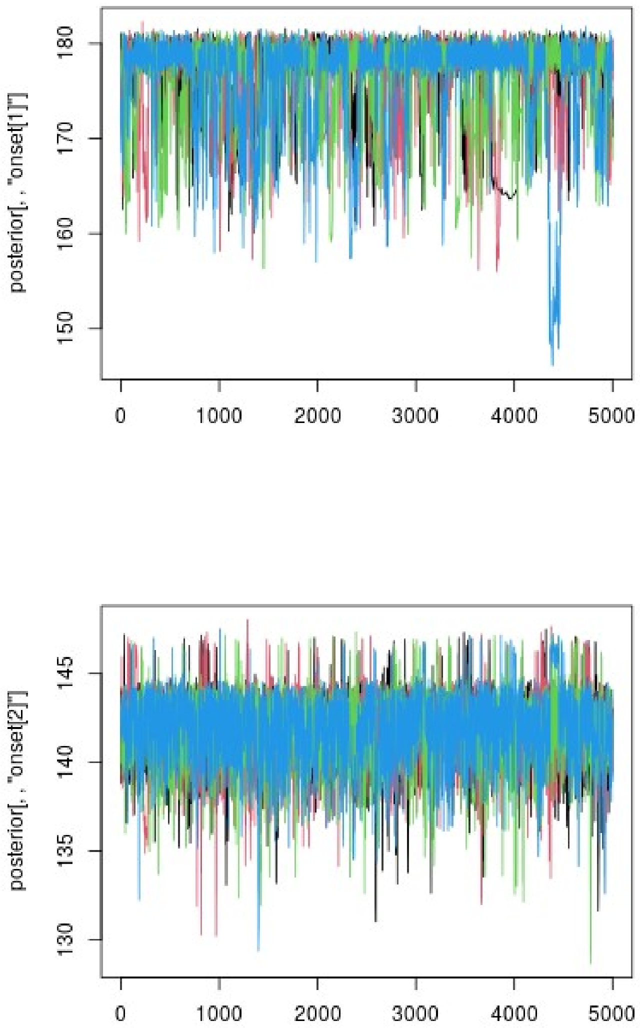
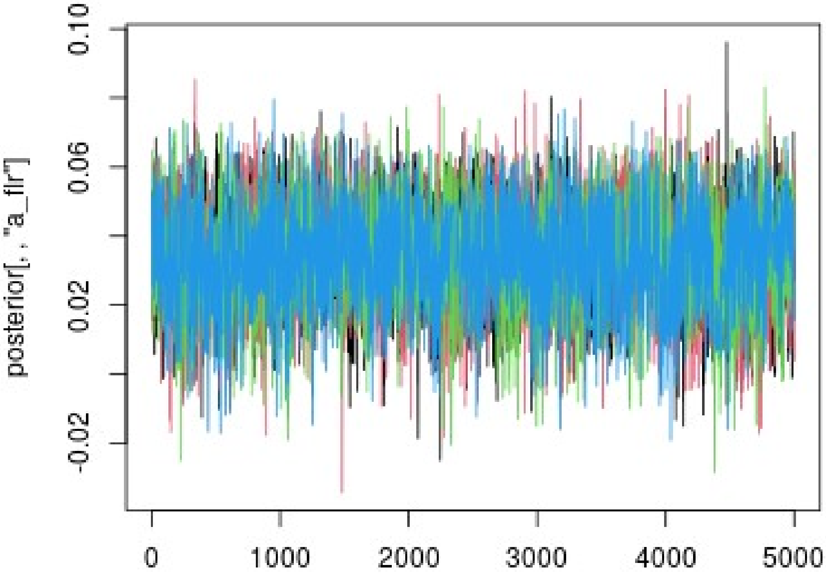


Figure C.4. Trace plots for the flower covariate, β_F (top panel), and error, ϵ (bottom panel), parameters. Each color represents one of the four MCMC chains. Parameter values are on the vertical axis, and iterations are on the horizontal axis.



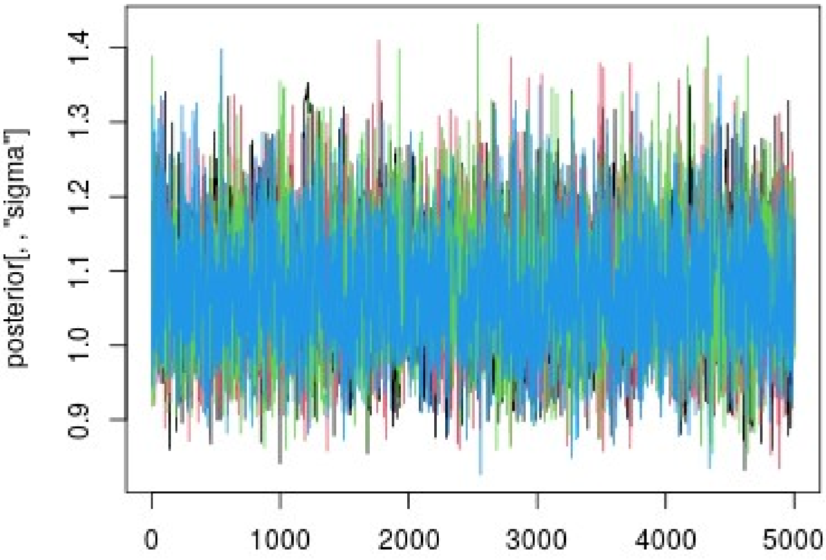
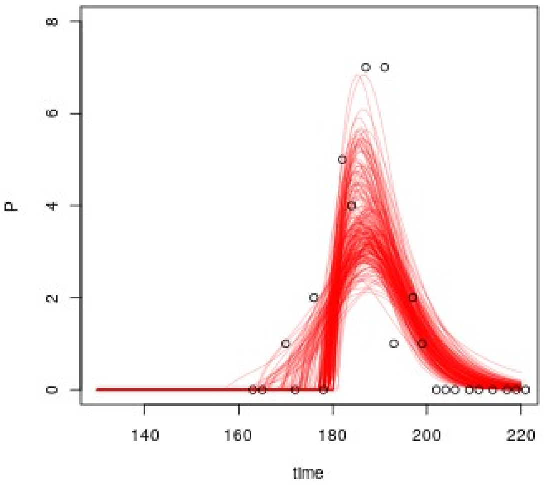


Figure C.5. Posterior predictive checks of model fits to data. For each timeseries, 3000 draws of the posterior are taken to simulate the verhulst function (red lines), not including the flower covariate function. The left panels represent data (black circles) from 2019, and the right panels represent data from 2021. The top panels represent data from the Trail site, and the bottom panels represent data from the Waterfall site.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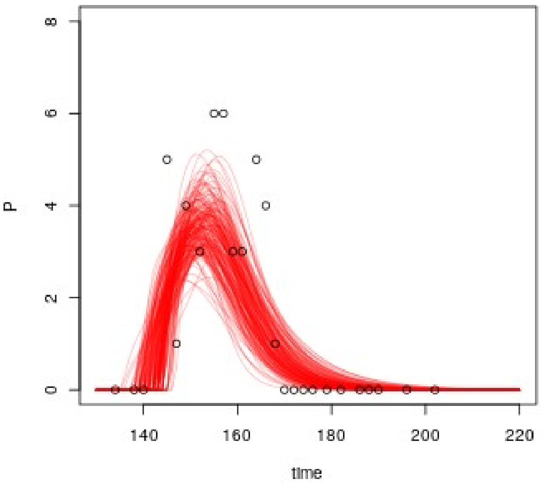
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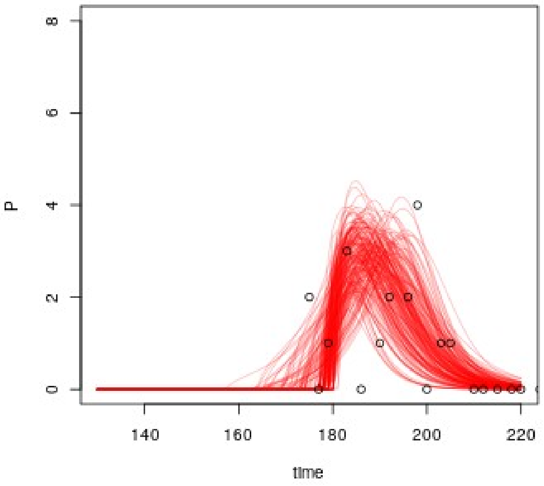
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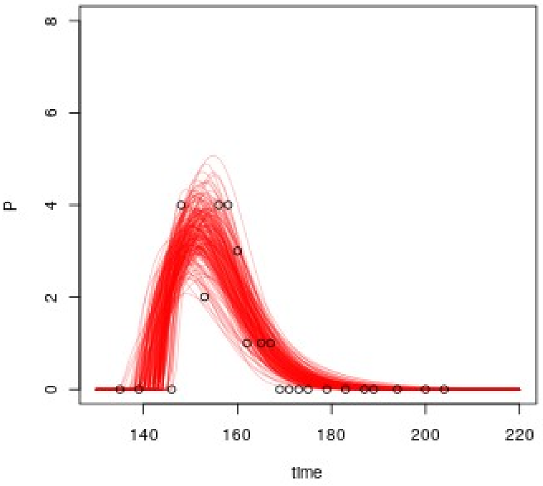
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APPENDIX D

SUPPLEMENTARY MATERIAL FOR CHAPTER 5:

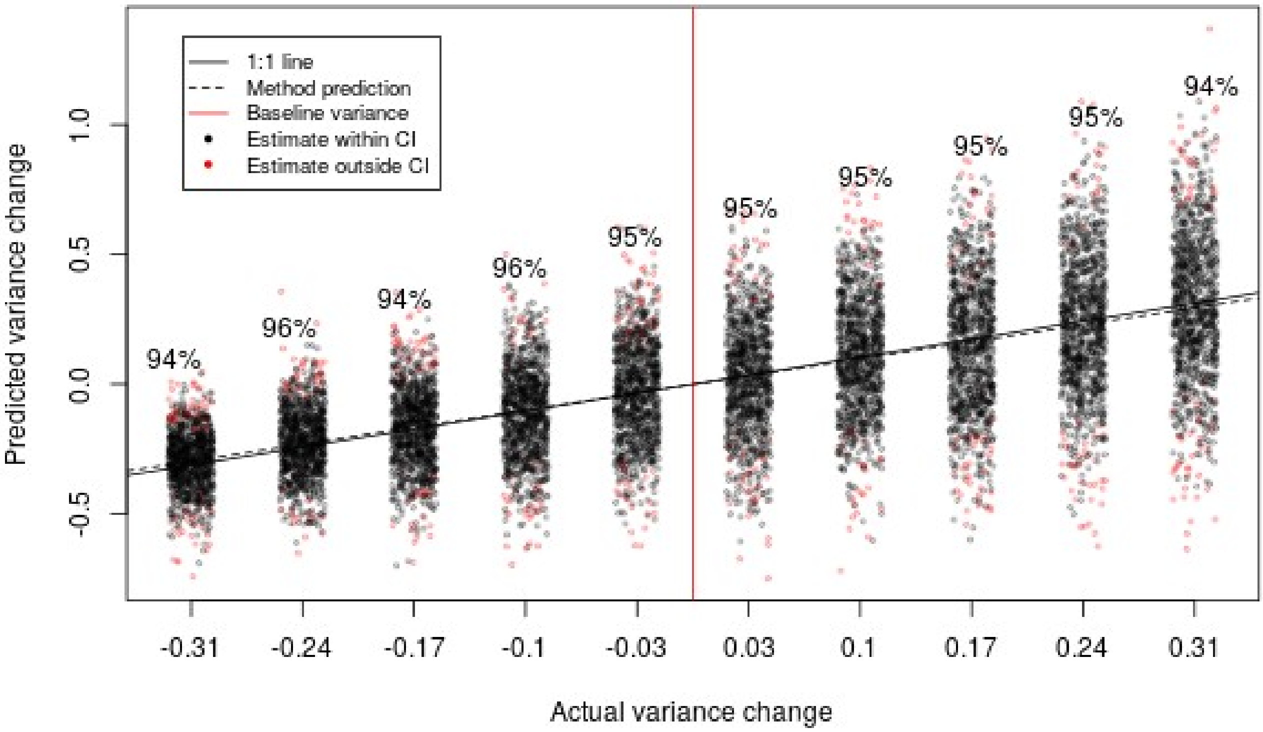
DISORDER OR A NEW ORDER: HOW CLIMATE CHANGE AFFECTS PHENOLOGICAL VARIABILITY

Section D.1: Power analysis

We performed a power analysis in order to determine the efficacy of the residual method in identifying changes in variance. We simulated time-series data by generating 10,000 sequences of 32 years, with the phenological trends varying uniformly within 40 days around the baseline phenology occurring at 100 days-of-year. For each time-series, we added normally distributed error to each time point with a baseline standard deviation of 12 days. We then increased the error term standard deviation by ten increments between -10 and +10 days, resulting in a total error standard deviation range between 2 and 22 days and 1000 replicated per variance change increment. We then performed the residual method test on each time-series and assessed success of the method by testing whether the actual variance change fell within 2 standard errors of the predicted variance change. Actual variance change was calculated as the increase/decrease in the total error SD divided by the number of data points, and the predicted variance change was the slop of the absolute residuals. We then calculated the percentage of successes in each of the 1000 variance change replicates.

We found that the residual method was over 90% successful in correctly detecting variance changes for every variance shift scenario (Fig. S1). We investigated potential biases in the estimation of mean and variance changes, but found that our method accurately predicted both metrics one-to-one. The residual method was equally likely to over-estimate variance change as it was to under-estimate it. We conclude that the residual method of fitting a quantile regression with $\tau \approx 0.6827$ to the absolute residuals accurately predicts the change in the standard deviation of the error term under the present assumptions.

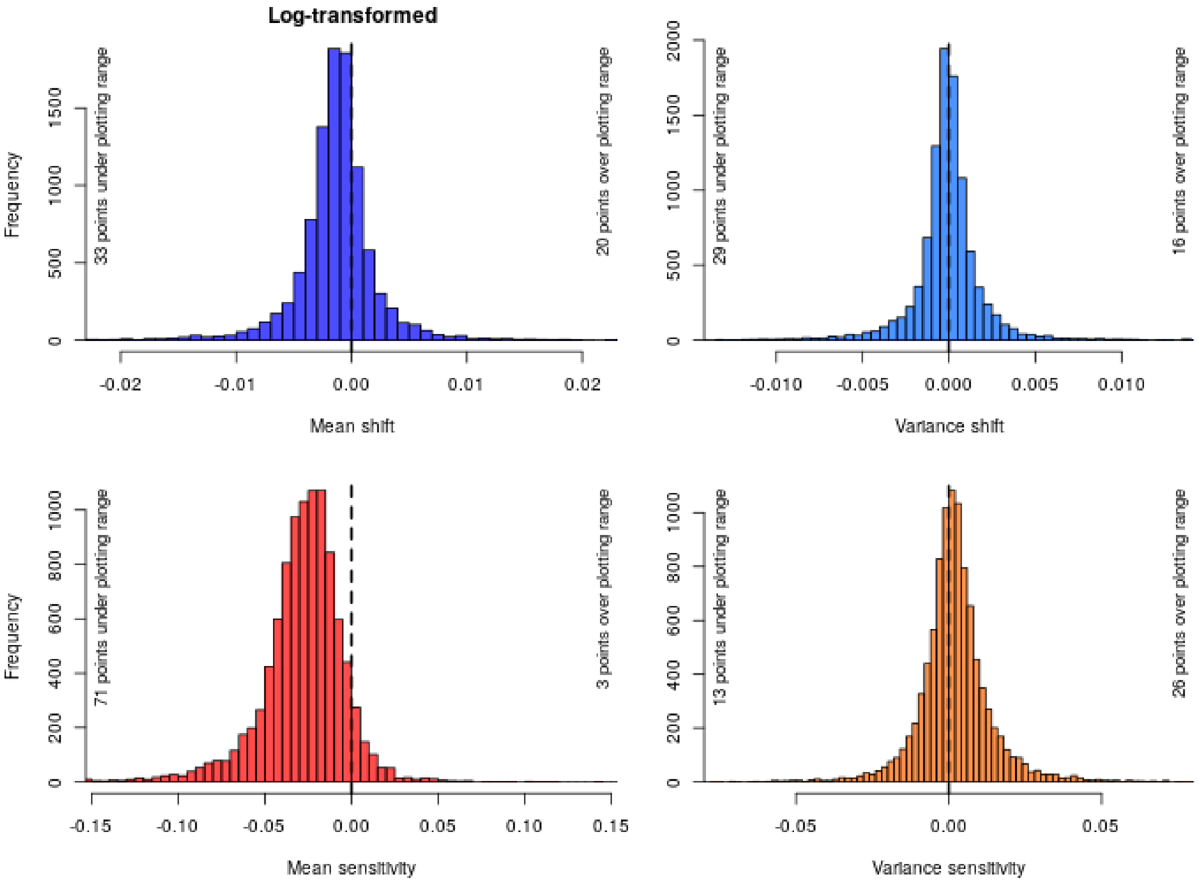
Figure D.1. The power of the residual method for different rates of variance change. Black point indicate simulations for which the method successfully predicted the rate of variance change, and red circles represent those for which it didn't. The ideal 1:1 line is solid black, the actual performance of the residual method is dashed black, and zero variance change is highlighted by the red line.



Section D.2: Accounting for potential non-linearity

It is possible that if phenological responses to increasing temperature are non-linear, as is predicted by a thermal threshold model, that fitting linear models and estimating variance from their residuals might result in biased measures of variance change (Wolkovich et al., 2021). One way to account for the expected non-linearity of a thermal threshold phenological process is to log-transform the response variable when making sensitivity calculations. So, to check whether and to what extend assumptions about linear temperature responses affected our estimates of variance shifts and sensitivity, we $\log_e$-transformed the response variable DOY before calculating the mean and variance metrics. Compared to the effects when DOY was not transformed (Fig. S3), we found that mean shifts and mean sensitivity were still clearly negative overall after this transformation (Fig. S2). There were still overall trends toward modestly negative variance shift, but variance sensitivity became positive with a very small effect size. This indicates that the statistical assumption of a linear relationship between inter-annual temperature and phenology may in part explain the observed variance patterns, but that the results would not change dramatically if the assumption is faulty.

Figure D.2. Overall trends distributions for all phenophase groups when day-of-year is log-transformed to account for potentially non-linear relationships between phenology and temperature. The plotting range is reduced to show detail of the center of the distributions, so some points are not plotted.



Section D.3: Trend visualizations

Figure D.3. Overall trends distributions for all phenophase groups. The plotting range is reduced to show detail of the center of the distributions, so some points are not plotted.

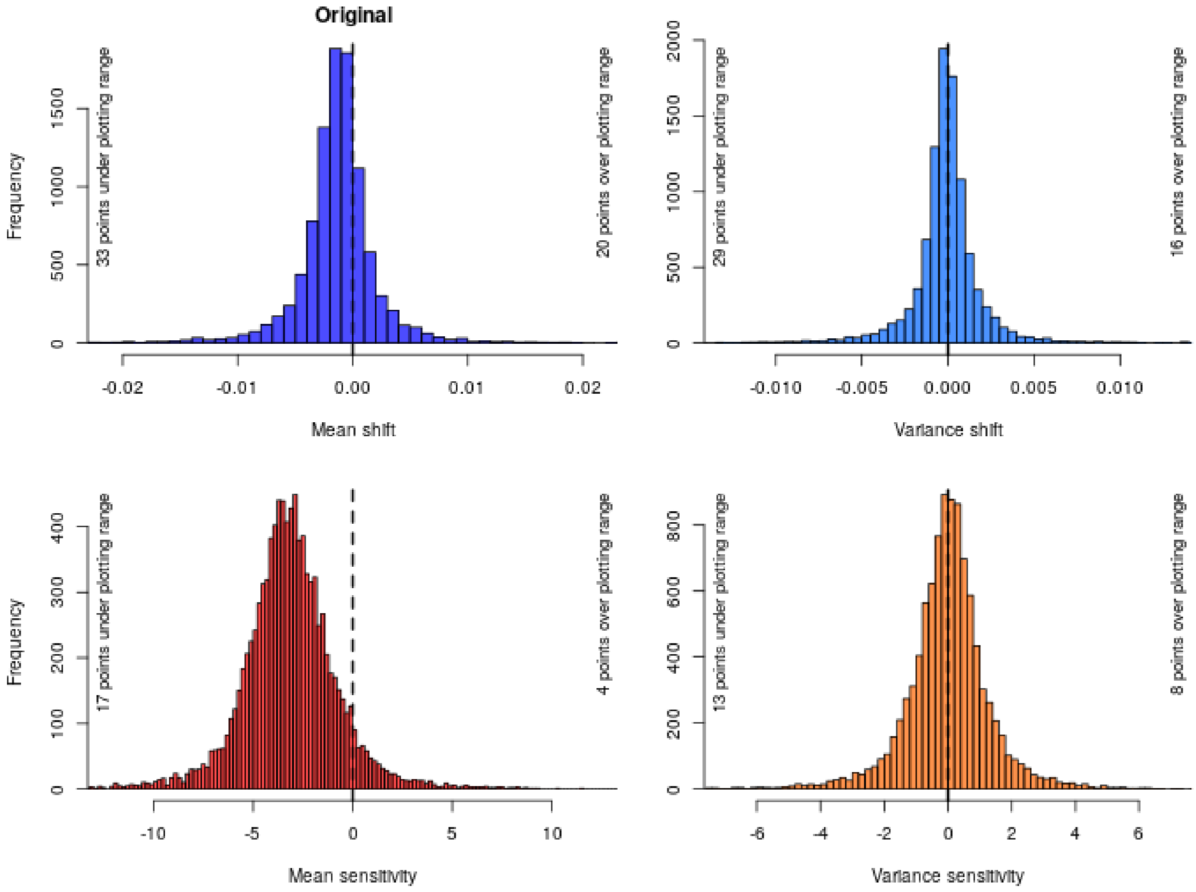


Figure D.4. The drivers of phenology mean shifts over time. Lines are model predictions and points are residuals.

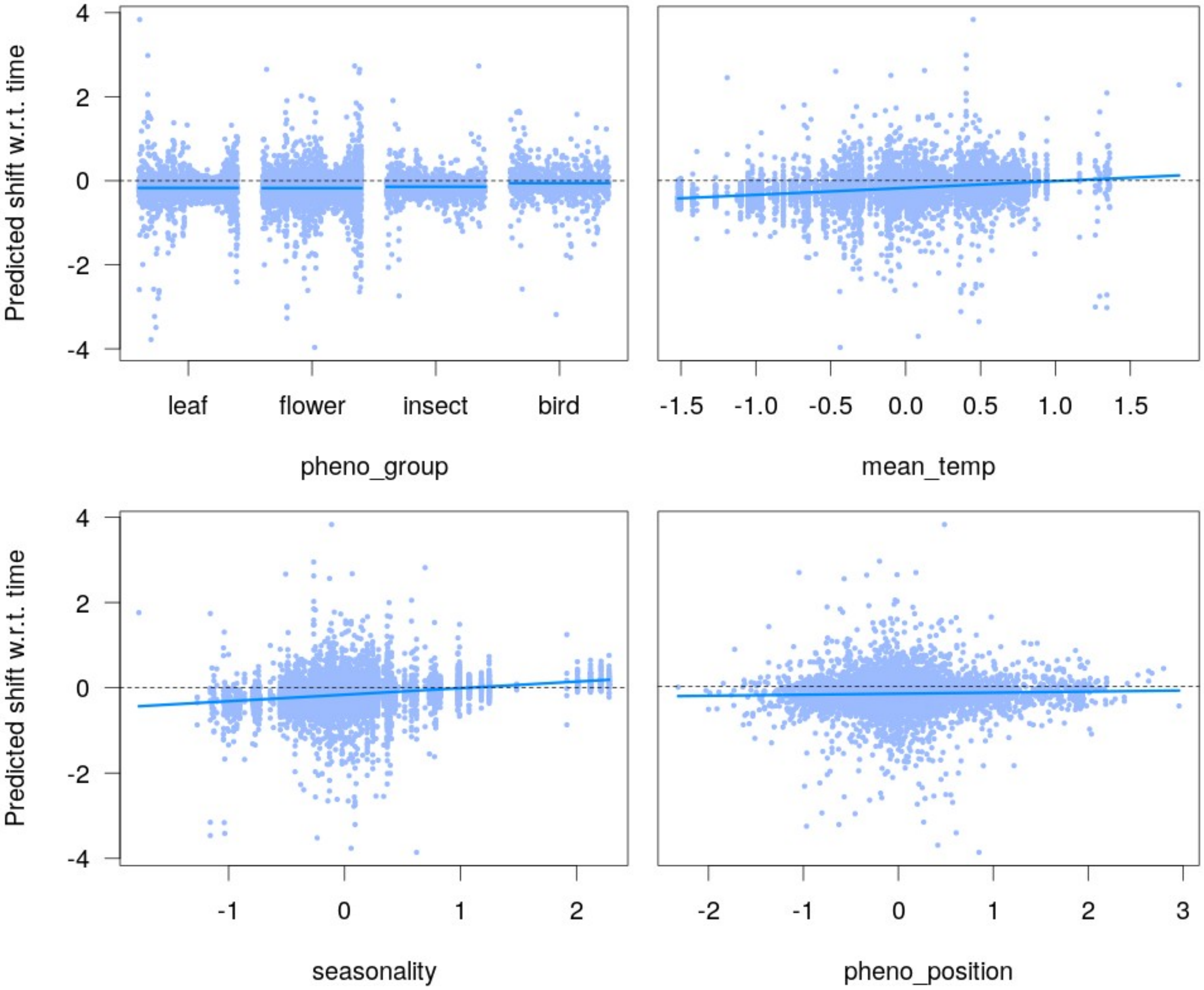


Figure D.5. The drivers of the temperature sensitivity of phenological means. Lines are model predictions and points are residuals.

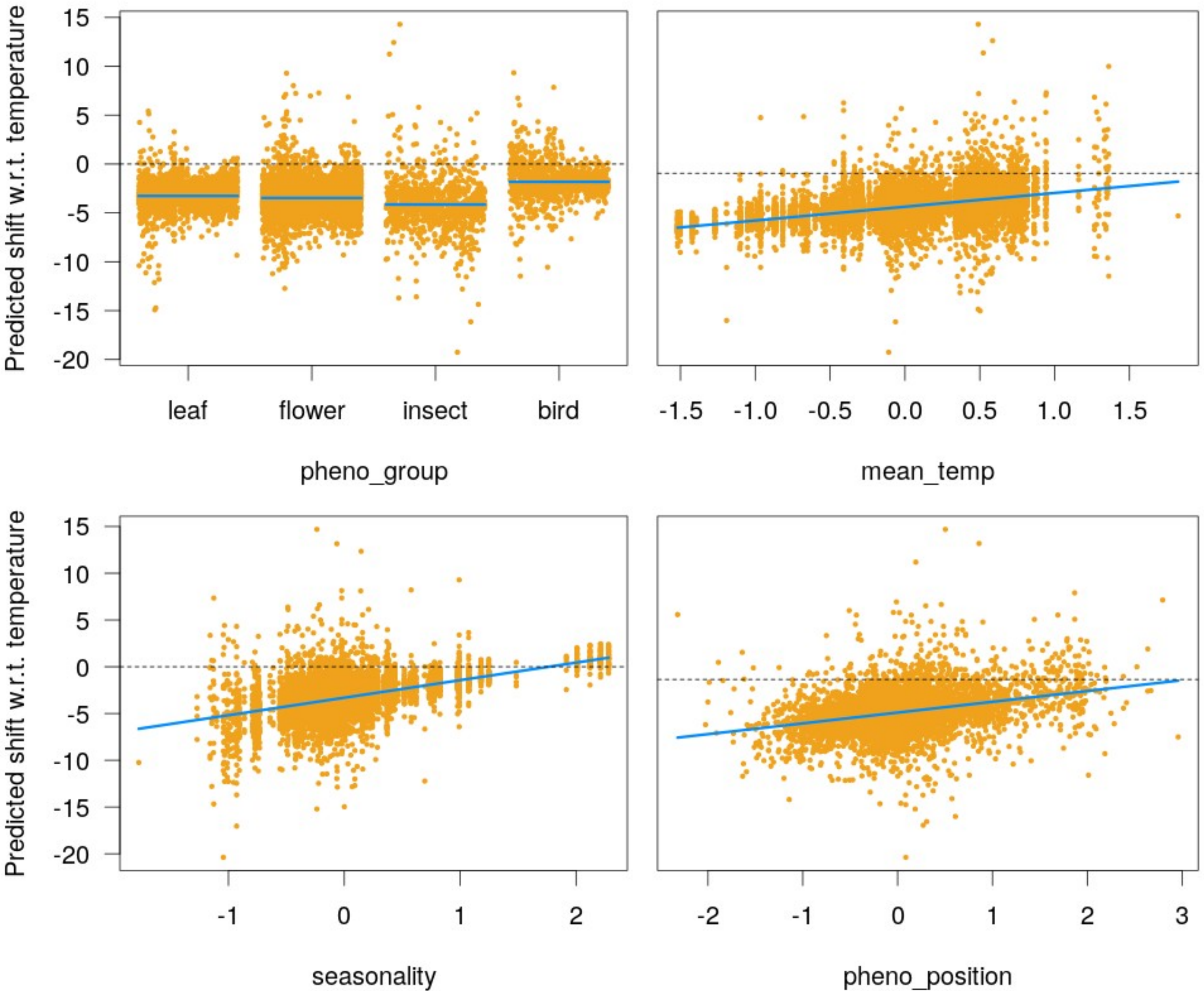


Figure D.6. The drivers of variance shifts over time. Lines are model predictions and points are residuals.

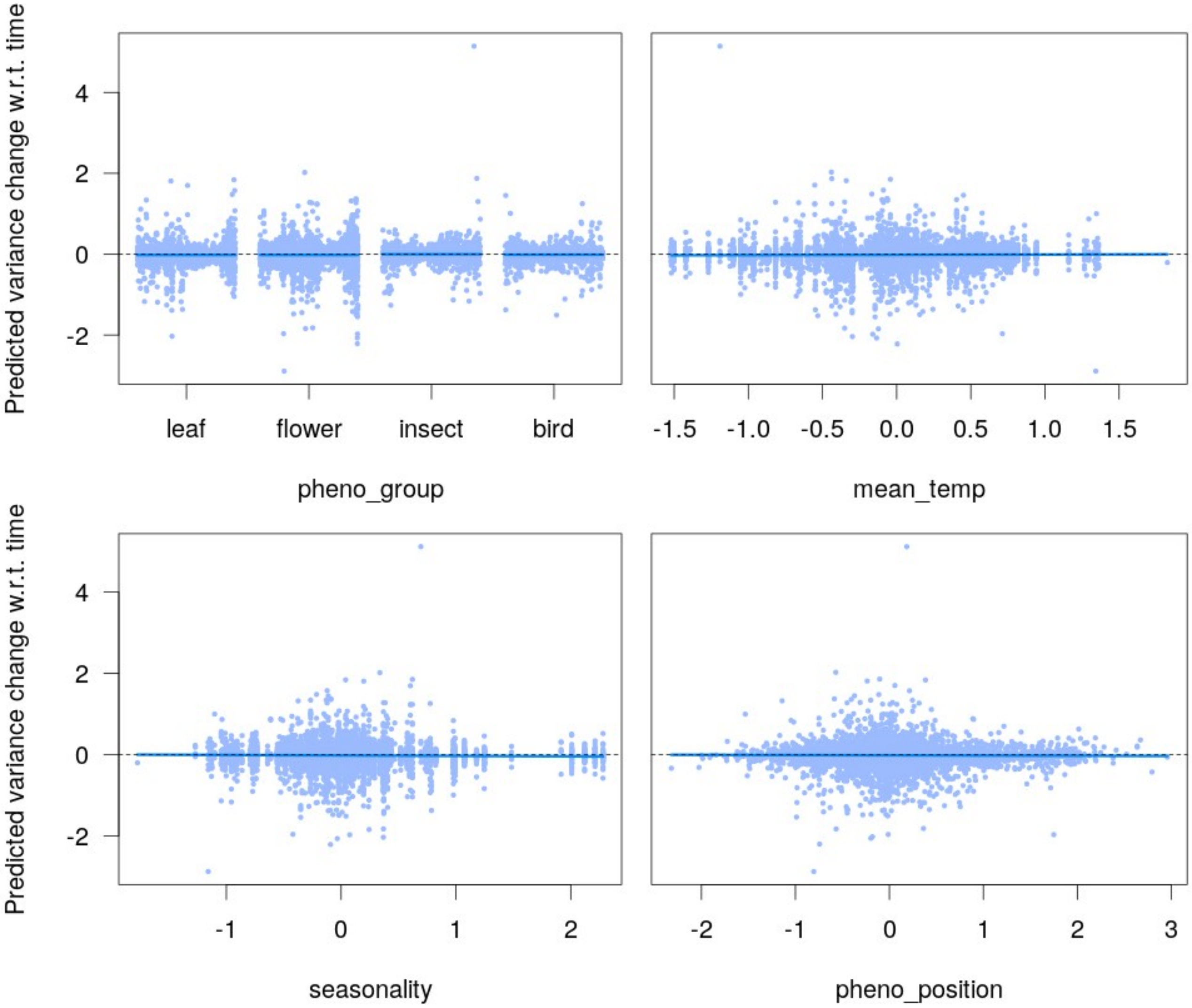
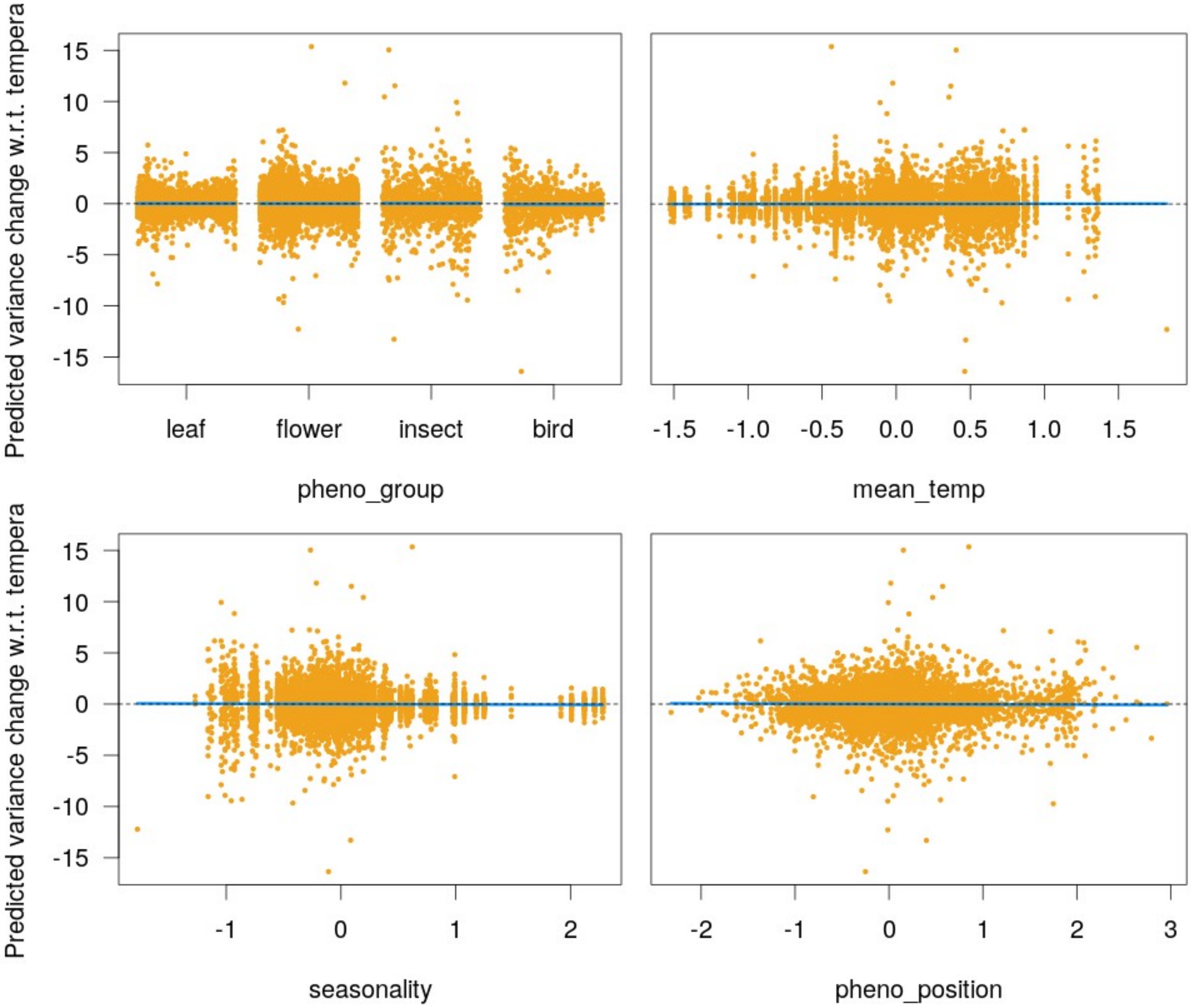


Figure D.7. The drivers of variance temperature sensitivity. Lines are model predictions and points are residuals.



Section D.4: Plant trait analyses

Figure D.8. The drivers of first flowering phenology mean shifts over time. No effects were significant. Lines are model predictions and points are residuals.

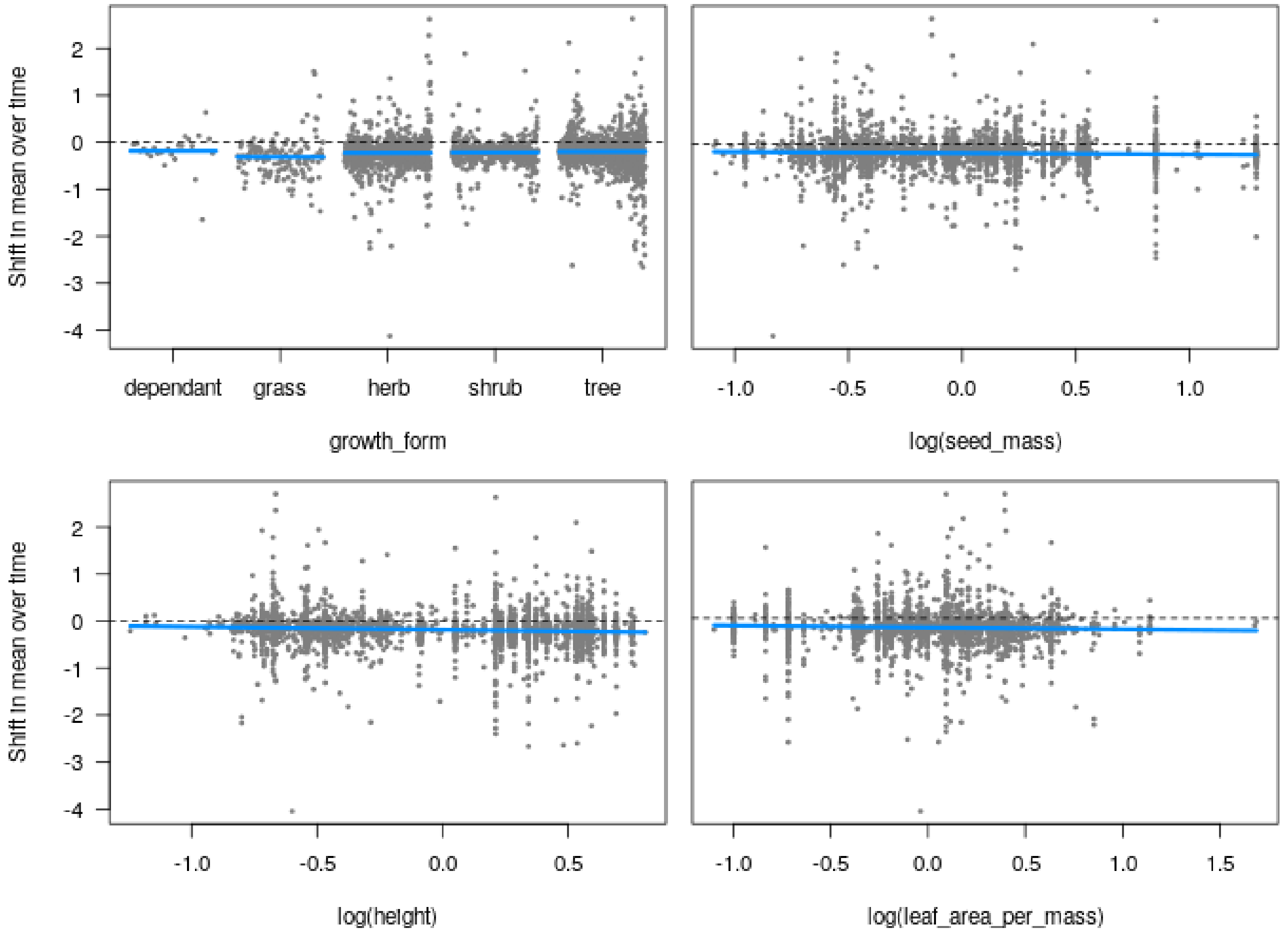


Figure D.9.The drivers of first flowering mean temperature sensitivity. Dependents were significantly less sensitive than the other growth forms. Lines are model predictions and points are residuals.

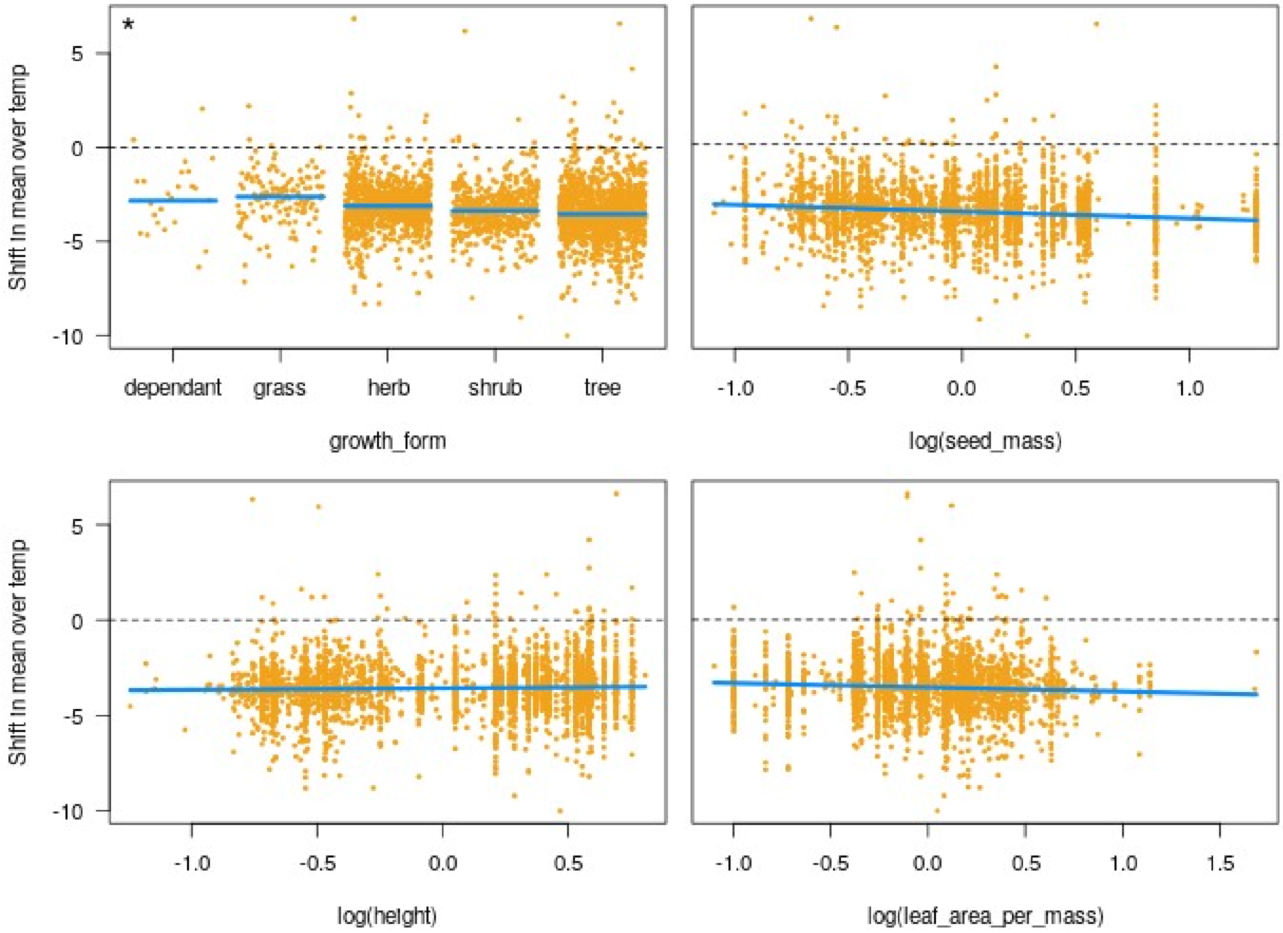


Figure D.10. The drivers of variance changes in first flowering over time. No effects were significant. Lines are model predictions and points are residuals.

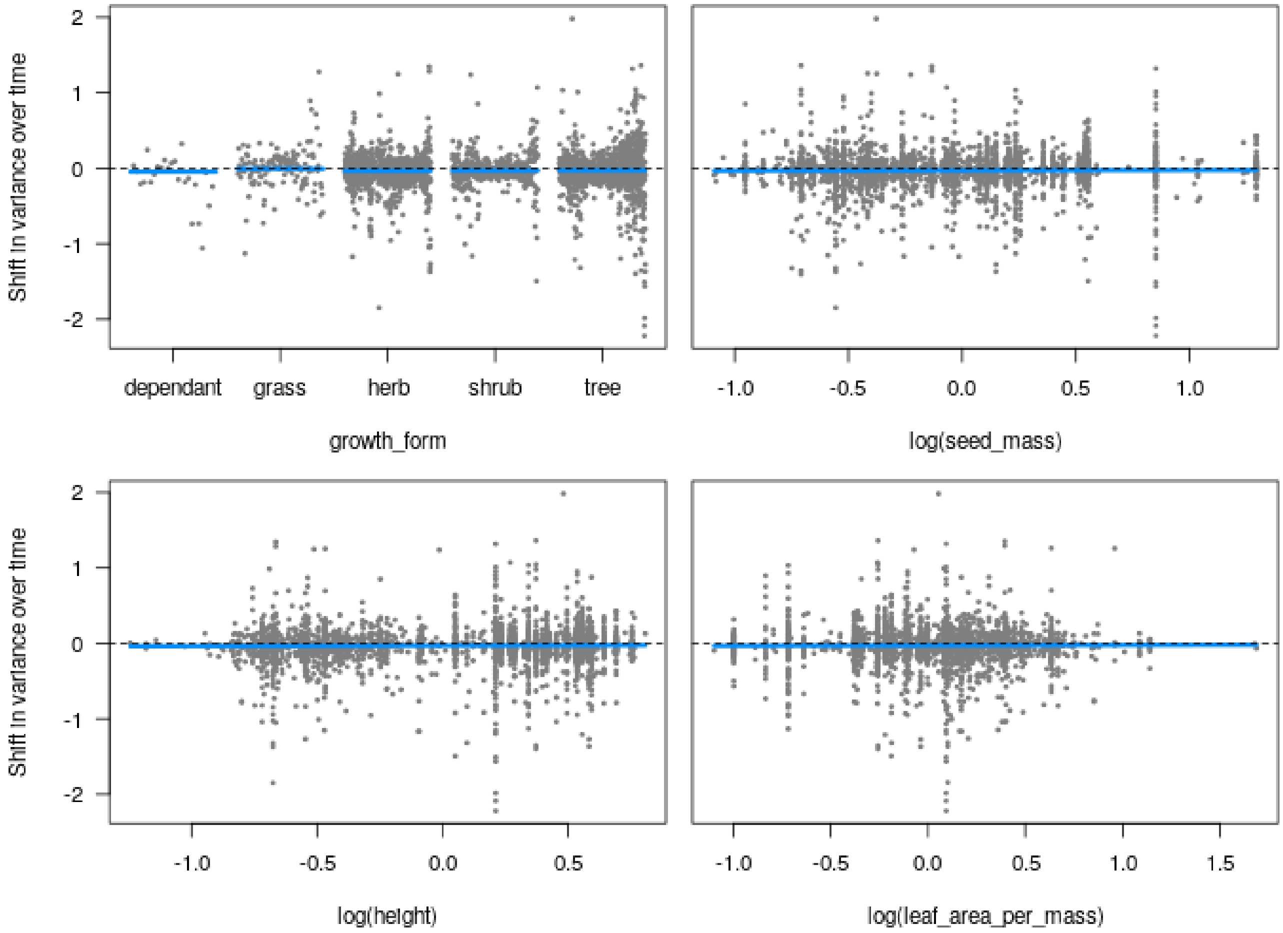


Figure D.11. The drivers of the temperature sensitivity of variance changes in first flowering. No effects were significant. Lines are model predictions and points are residuals.

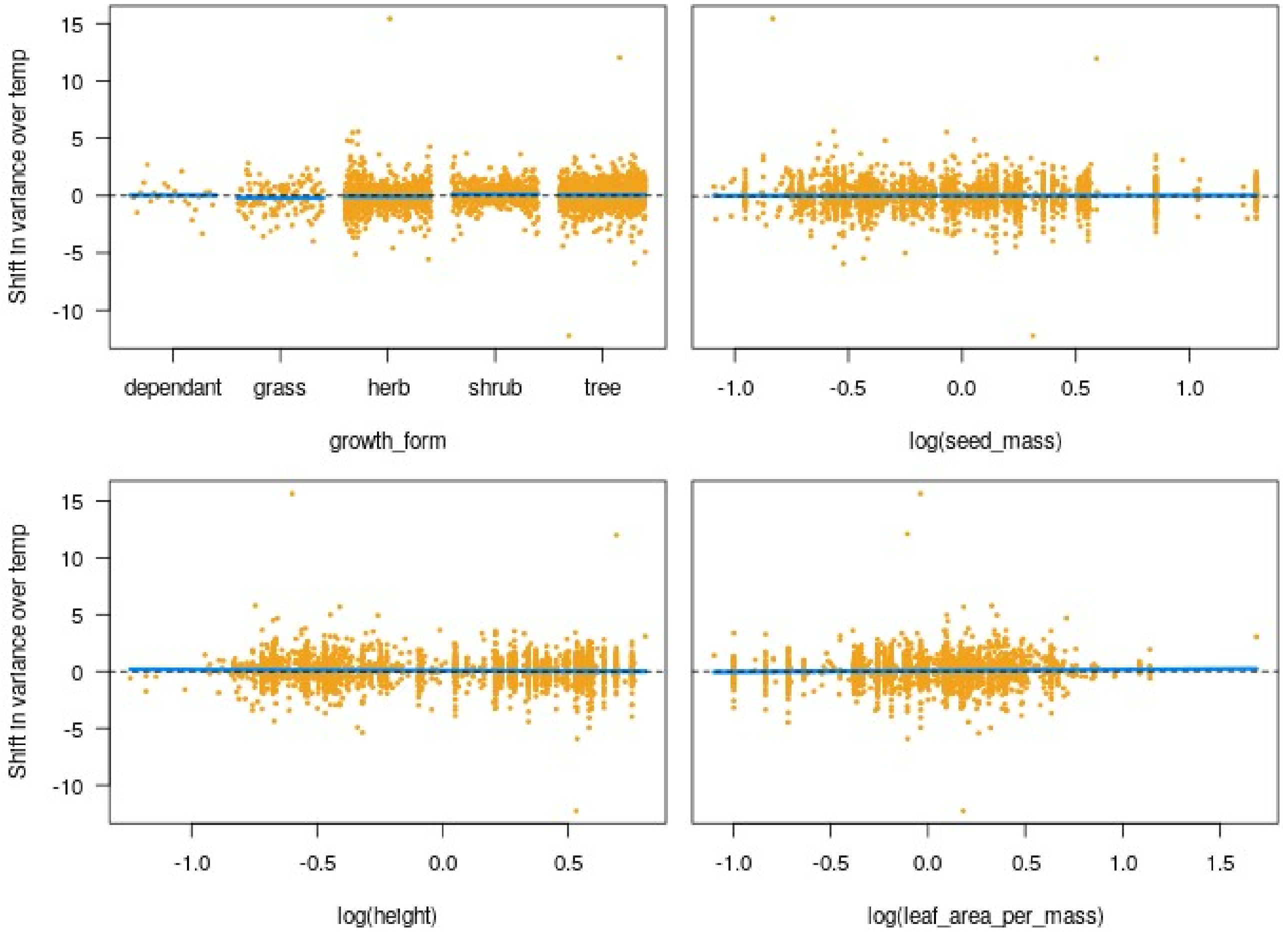
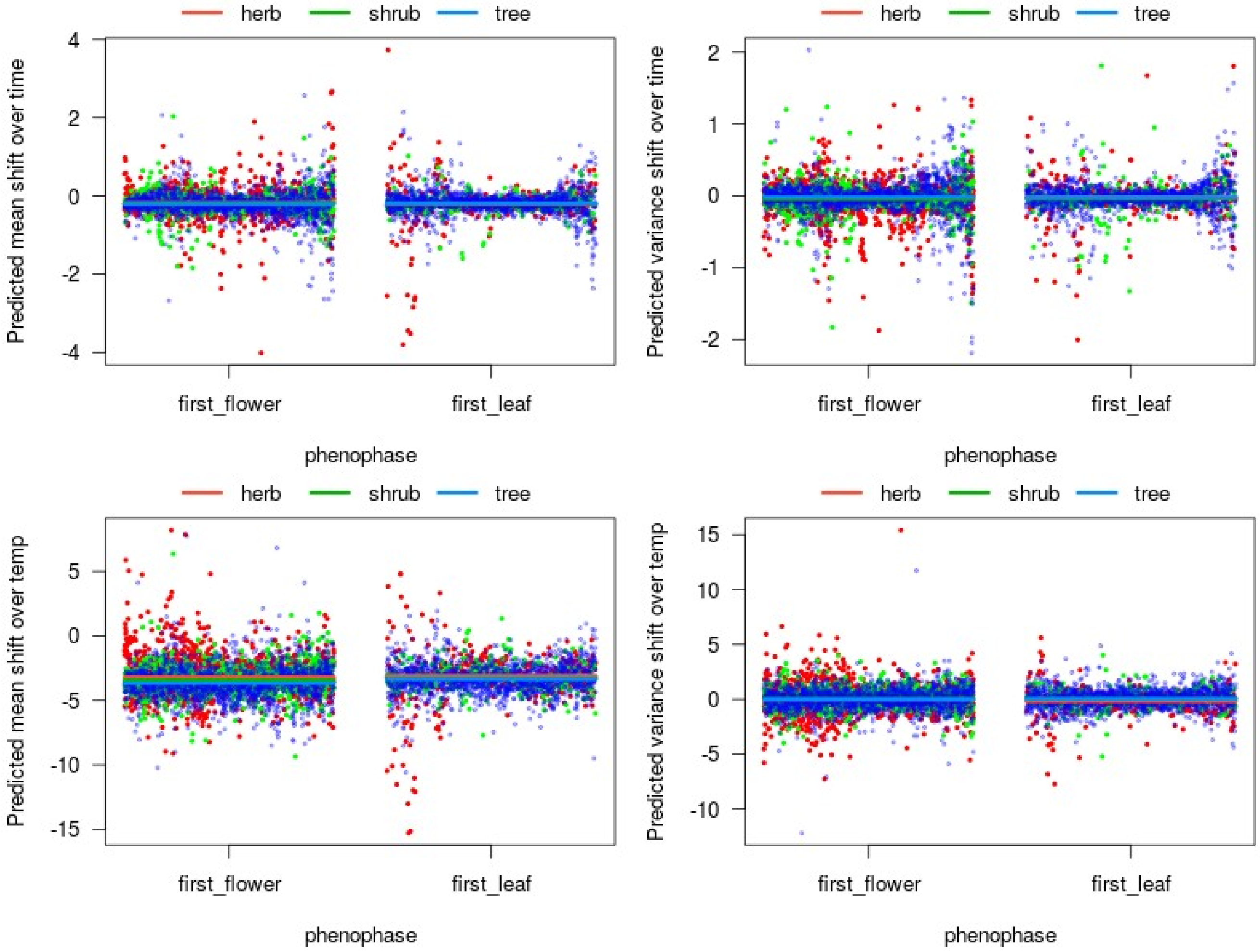
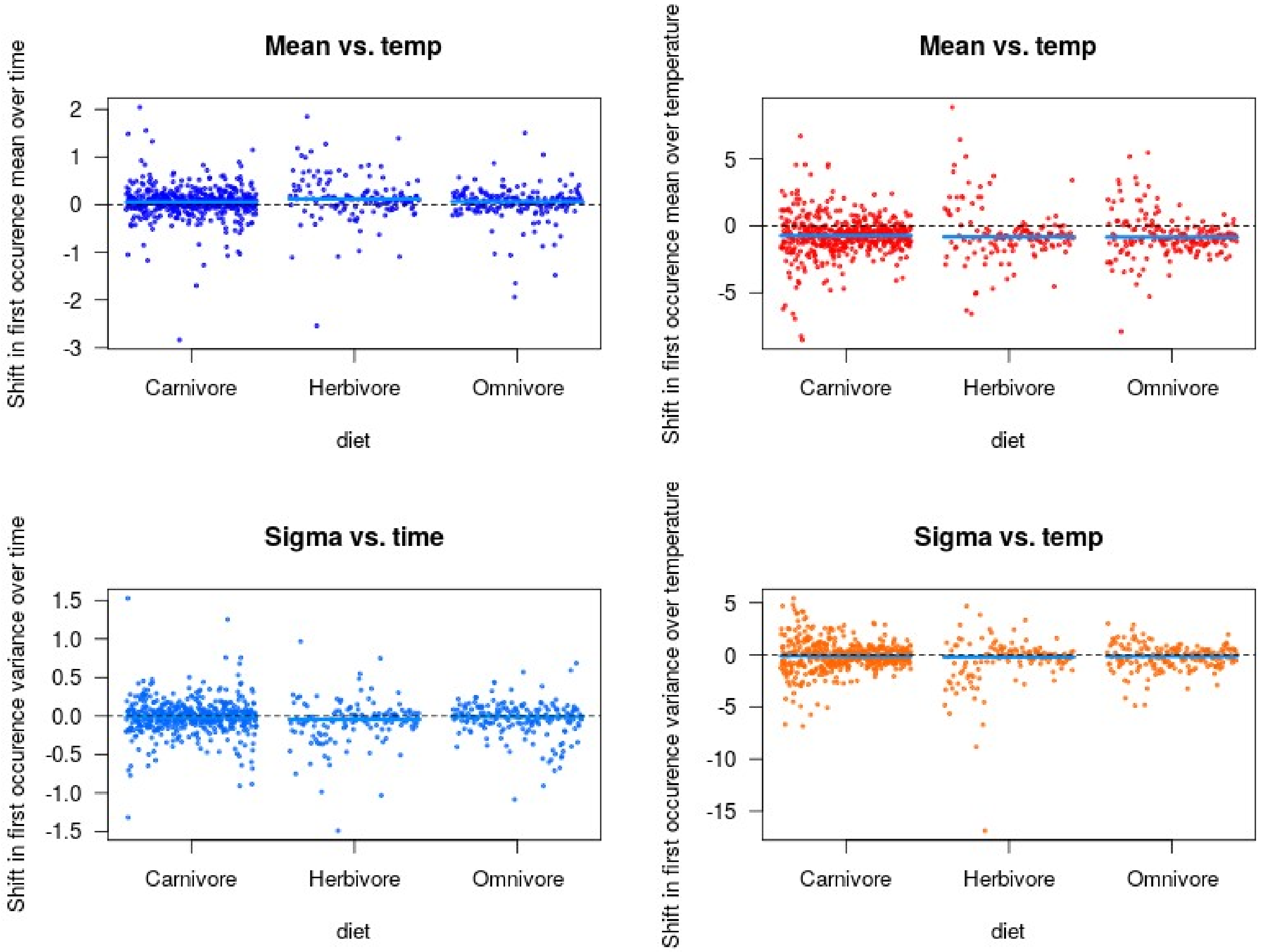


Figure D.12. Neither mean phenological shifts over time, temperature sensitivity, nor changes in variance varied significantly between leaf and flower phenology. The patterns also did not significantly differ between trees, shrubs, and herbs, and there were no significant interactions between growth form and phenophase. Red lines and points are model predictions and residuals for shrubs, and blue ones are those for trees.



Section D.5: Bird trait analyses

Figure D.13. Bird diet did not significantly predict mean phenological shifts over years, temperature sensitivity, or variance changes. Lines are model predictions and points are residuals.



Section D.6: Additional analyses

Figure D.14. Sites within datasets were regionally clustered and spanned different segments of the seasonality gradient.

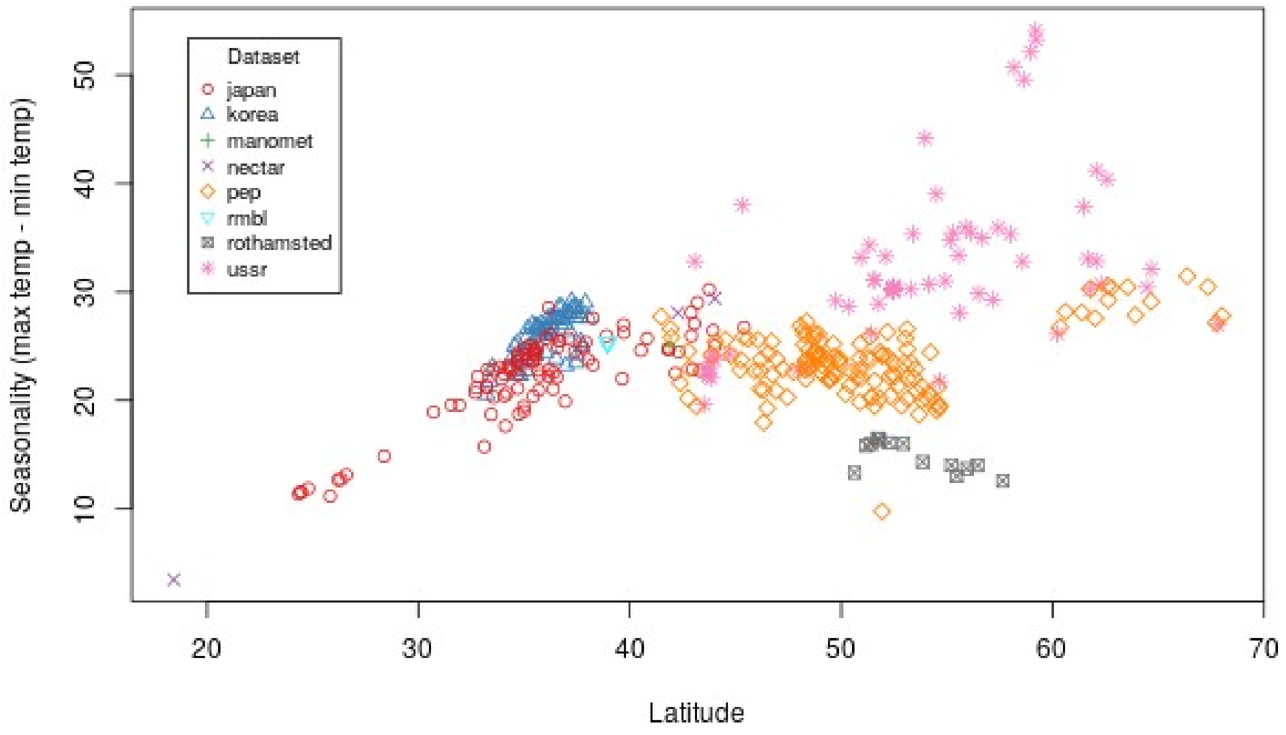


Figure D.15. No one dataset was responsible for the positive relationship of seasonality and mean sensitivity. Each point represents a time-series, colored by the dataset from which it was taken. Lines represent a linear model of mean sensitivity predicted by seasonality with each dataset sequentially withheld. The color of the line corresponds to the dataset that was withheld from the model. Excluding the Rothamsted dataset results in the smallest slope (gray line), and excluding the Chronicles of Nature Calendar dataset (ussr) results in the greatest slope (pink line).

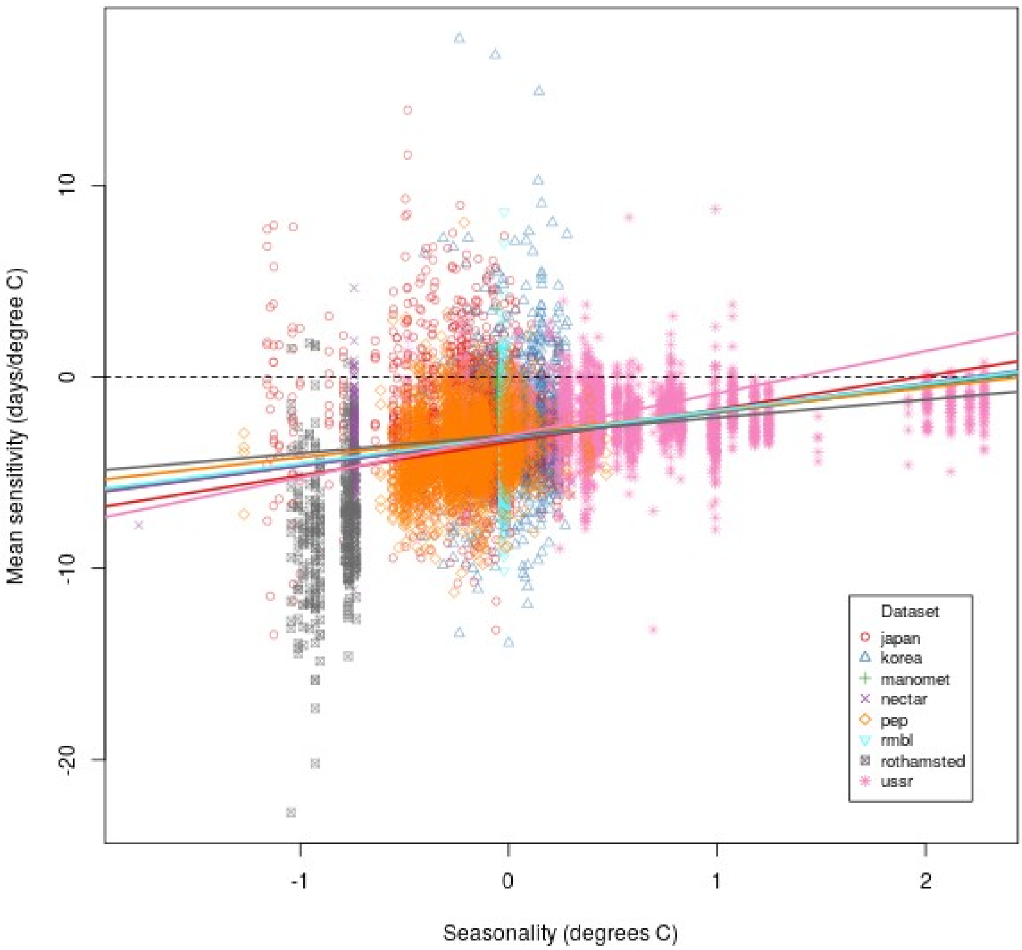


Figure D.16. Changes in population size can artificially shift phenology mean and variance estimates when first-occurrence data is used. As population size increases, the observed first-occurrence advances and variance decreases. For each population size level (n=10, n=1000, n=100000), n draws were made from normal distributions with mean 100 and standard deviation 10, the minimum observation was recorded (points shown) and the procedure was performed 1000 times.

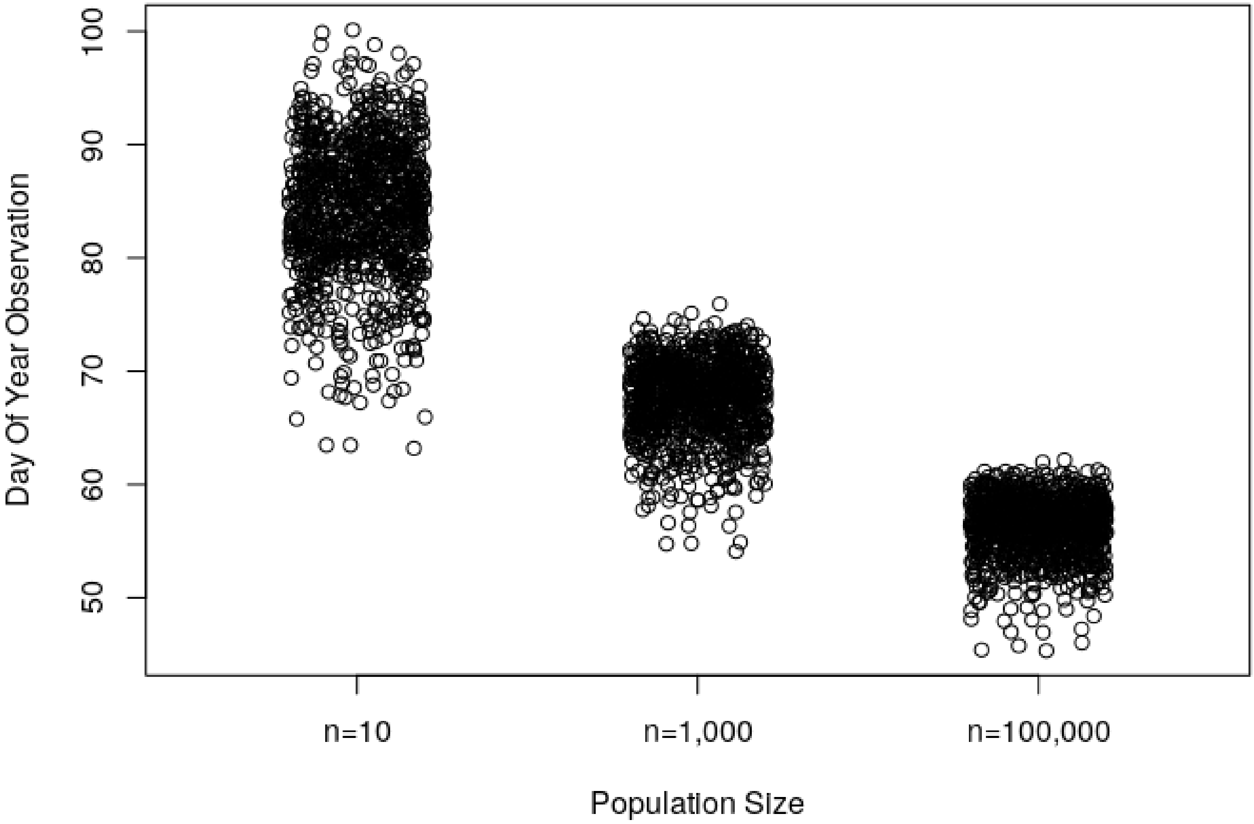


Figure D.17. Seasonal environmental filters may change the skewness of phenological distributions and therefore the inter-annual variance of first-observation dates. In this hypothetical example, there is an environmental filter (red line) in the early season that interacts with the underlying phenological distribution (light blue solid line) to produce a filtered, realized distribution (light blue dashed line). The influence of the environmental filter only comes out when the phenological distribution shifts into its time window; historic, unadvanced phenology (dark blue line) is effectively not influenced by the environmental filter.

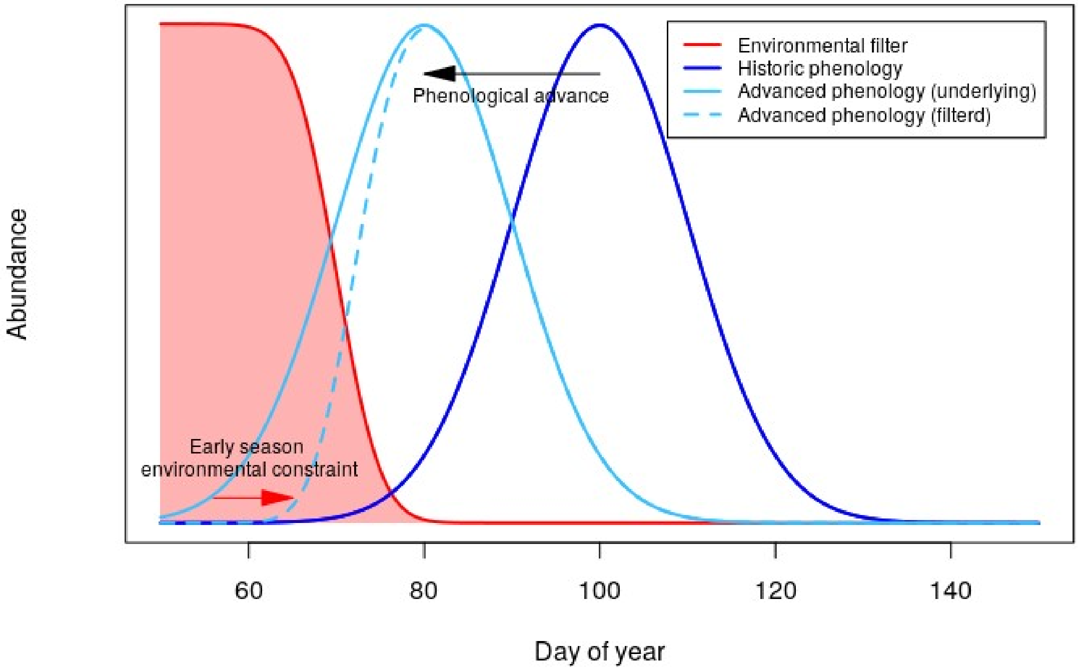


Figure D.18. Spring temperatures have increased markedly at the site locations of this study (left panel), but inter-annual variance has decreased slightly on average (right panel).

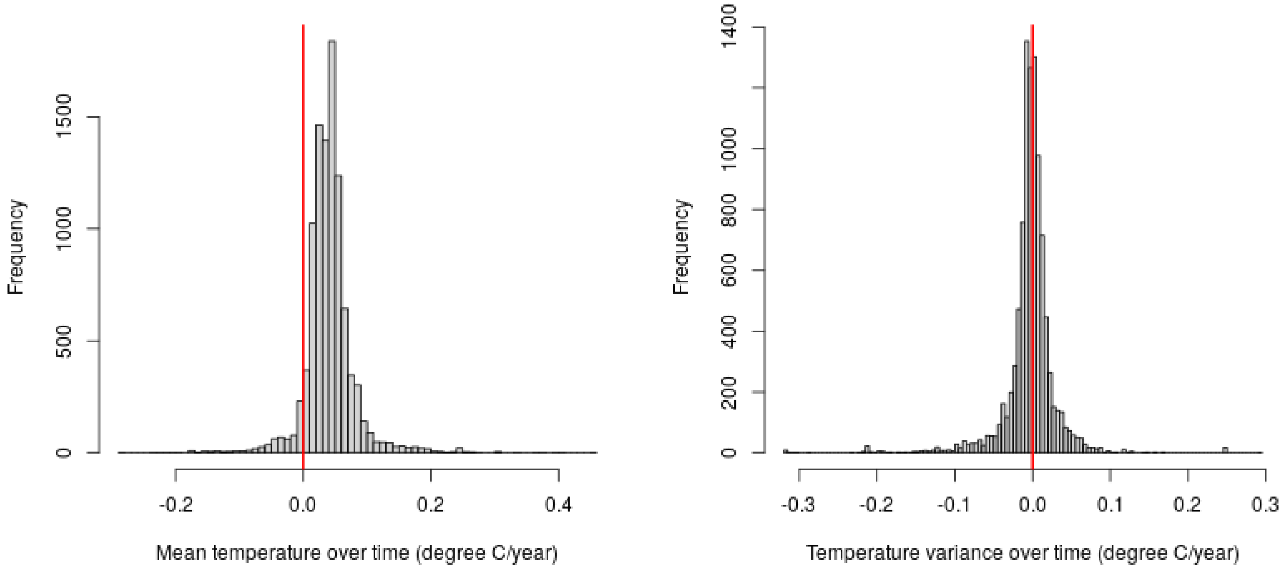


Figure D.19. Histograms showing mean (a) and variance (b) shifts. Color and shading are the same as in Figure 3 in the main text.

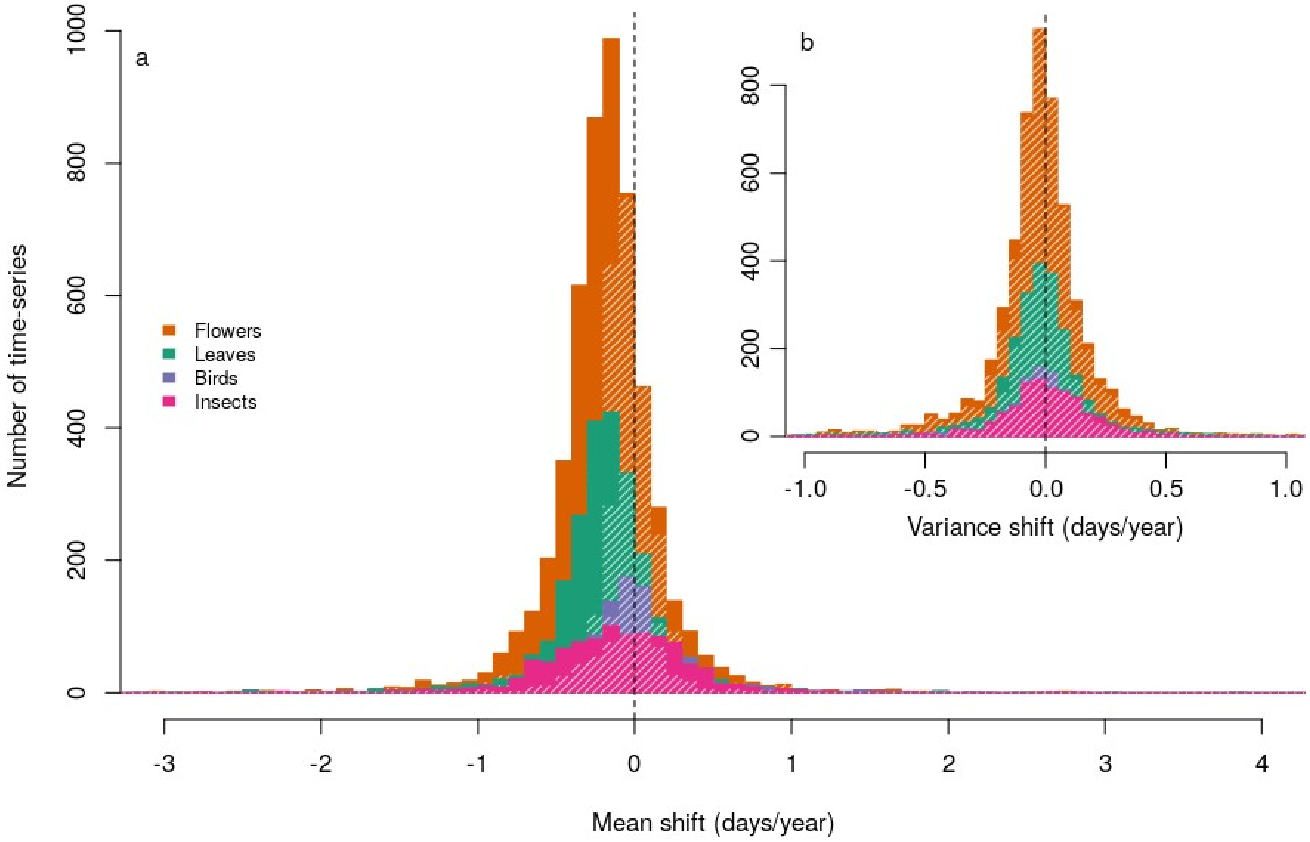
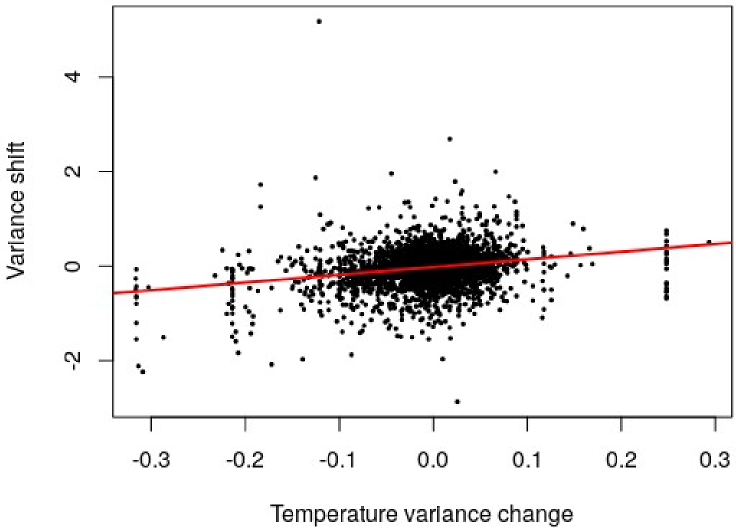


Figure D.20. Changes in the variance of temperatures at sites significantly predicted observed phenology variance shifts, explaining around 5% of the variance in phenology variance shifts.



Section D.7: Data summary and model coefficient tables

Table D.1. Data summary table

dataset	n time-series	sites	species	n obs.	mean time-series length	mean lat.	mean lon.	mean annual max. temp.	mean seaslty	data range	pheno. groups
PEP	3,188	134	38	129,278	41	50.3	12.6	13.0	22.9	1958-2018	leaves, flowers
CNC	2,278	76	586	69,817	31	55.5	57.8	6.8	33.7	1958-2017	all
Japan	1,674	97	39	73,824	44	35.7	136.4	18.5	22.9	1958-2011	all
Korea	1,391	68	15	44,150	32	36.1	127.8	17.5	26.0	1958-2006	all
RMBL	521	30	91	11,706	22	39.0	-107.0	8.9	25.3	1973-2017	flowers
Rothamsted	317	13	49	10,893	34	53.3	-1.4	13.2	15.0	1976-2016	insects
NECTAR	283	4	257	8,441	30	49.7	-14.3	13.8	18.8	1958-2009	leaves, flowers
Manomet	53	1	53	1,860	35	41.9	-70.5	14.7	25.0	1970-2018	birds

Table D.2. Main model coefficients. Estimates are standardized effect sizes.

Metric	Coefficient	Estimate	Std. Error	df	t-value	p-value
μ shift	leaf	-0.163	0.011	1,027.100	-14.938	< 0.001
	flower	-0.166	0.010	680.524	-17.140	< 0.001
	insect	-0.135	0.021	647.651	-6.329	< 0.001
	bird	-0.050	0.017	1,019.960	-2.919	0.004
	seasonality	0.153	0.019	324.071	7.874	< 0.001
	mean_temp	0.167	0.019	435.558	8.918	< 0.001
	pheno_position	0.025	0.009	1,537.239	2.732	0.006
μ sensitivity	leaf	-3.109	0.070	1,214.518	-44.155	< 0.001
	flower	-3.318	0.065	903.497	-51.064	< 0.001
	insect	-3.991	0.150	773.493	-26.560	< 0.001
	bird	-1.666	0.109	1,025.837	-15.232	< 0.001
	seasonality	1.875	0.126	366.330	14.852	< 0.001
	mean_temp	1.446	0.123	533.333	11.752	< 0.001
	pheno_position	1.119	0.060	2,632.439	18.758	< 0.001
σ shift	leaf	-0.022	0.005	458.632	-4.588	< 0.001
	flower	-0.022	0.004	284.810	-5.673	< 0.001
	insect	-0.004	0.008	234.678	-0.501	0.617
	bird	-0.015	0.007	390.310	-2.049	0.041
	seasonality	-0.012	0.008	223.339	-1.374	0.171
	mean_temp	0.007	0.008	265.393	0.914	0.362
	pheno_position	-0.006	0.004	260.399	-1.364	0.174
σ sensitivity	leaf	0.010	0.031	666.876	0.321	0.748
	flower	0.001	0.025	396.720	0.060	0.952
	insect	0.031	0.060	497.831	0.520	0.604
	bird	-0.051	0.048	650.527	-1.059	0.29
	seasonality	-0.032	0.049	340.975	-0.658	0.511
	mean_temp	0.011	0.050	504.088	0.228	0.82
	pheno_position	-0.028	0.032	567.712	-0.885	0.377

Table D.3. Plant traits model coefficients. Estimates are standardized effect sizes.

Metric	Coefficient	Estimate	Std. Error	df	t-value	p-value
μ shift	(Intercept)	-0.528	0.195	2,899.778	-2.707	0.007
	dependant	0.357	0.204	2,631.835	1.750	0.08
	grass	0.230	0.198	2,817.303	1.163	0.245
	herb	0.316	0.195	2,877.204	1.617	0.106
	shrub	0.325	0.196	2,864.746	1.661	0.097
	tree	0.342	0.196	2,845.628	1.740	0.082
	height	-0.063	0.031	300.914	-2.006	0.046
	seed_mass	-0.028	0.018	140.573	-1.543	0.125
μ shift	SLA	-0.039	0.021	245.590	-1.881	0.061
	(Intercept)	-1.636	1.175	2,325.933	-1.393	0.164
	dependant	-1.232	1.260	1,793.902	-0.978	0.328
	grass	-1.026	1.198	2,142.623	-0.857	0.392
	herb	-1.517	1.174	2,298.541	-1.292	0.196
	shrub	-1.771	1.179	2,250.150	-1.502	0.133
	tree	-1.950	1.187	2,192.715	-1.642	0.101
	height	0.093	0.230	355.208	0.404	0.686
μ sensitivity	seed_mass	-0.365	0.148	276.098	-2.459	0.015
	SLA	-0.219	0.152	345.495	-1.439	0.151
	(Intercept)	0.172	0.127	2,904.826	1.354	0.176
	dependant	-0.217	0.132	2,569.310	-1.643	0.1
	grass	-0.181	0.128	2,804.939	-1.410	0.159
	herb	-0.205	0.127	2,880.956	-1.620	0.105
	shrub	-0.202	0.127	2,868.089	-1.587	0.113
	tree	-0.201	0.128	2,847.273	-1.572	0.116
σ shift	height	0.006	0.020	240.151	0.281	0.779
	seed_mass	0.004	0.012	112.835	0.373	0.71
	SLA	0.004	0.014	195.586	0.327	0.744
	(Intercept)	0.915	0.711	3,115.869	1.286	0.198
	dependant	-0.851	0.741	2,981.127	-1.149	0.251
	grass	-1.079	0.718	3,056.521	-1.502	0.133
	herb	-0.956	0.712	3,101.397	-1.344	0.179
	shrub	-0.776	0.712	3,103.907	-1.089	0.276
σ sensitivity	tree	-0.828	0.714	3,094.650	-1.159	0.247
	height	-0.097	0.093	125.268	-1.047	0.297
	seed_mass	0.023	0.049	47.709	0.458	0.649
	SLA	0.104	0.060	104.195	1.728	0.087

Table D.4. Plant phenophase model coefficients. Estimates are standardized effect sizes.

Metric	Coefficient	Estimate	Std. Error	df	t-value	p-value
μ shift	(Intercept)	-0.170	0.012	448.328	-14.042	< 0.001
	shrub	-0.019	0.014	393.017	-1.386	0.167
	tree	-0.041	0.013	293.610	-3.073	0.002
	first_leaf	-0.033	0.016	2,226.633	-2.037	0.042
μ shift	shrub:first_leaf	0.028	0.023	3,756.175	1.259	0.208
	tree:first_leaf	0.056	0.018	2,574.400	3.112	0.002
	(Intercept)	-3.200	0.083	794.642	-38.369	< 0.001
	shrub	-0.236	0.106	508.994	-2.221	0.027
μ sensitivity	tree	-0.457	0.110	433.528	-4.141	< 0.001
	first_leaf	0.106	0.086	5,904.757	1.232	0.218
	shrub:first_leaf	0.022	0.120	5,908.542	0.185	0.853
	tree:first_leaf	0.205	0.098	5,938.300	2.099	0.036
σ shift	(Intercept)	-0.037	0.007	310.355	-5.599	< 0.001
	shrub	-0.001	0.008	276.135	-0.145	0.885
	tree	0.021	0.008	214.137	2.619	0.009
	first_leaf	0.018	0.010	1,251.689	1.755	0.08
σ shift	shrub:first_leaf	-0.017	0.014	2,565.694	-1.153	0.249
σ shift	tree:first_leaf	-0.025	0.012	1,468.193	-2.149	0.032
σ sensitivity	(Intercept)	-0.005	0.035	483.361	-0.151	0.88
σ sensitivity	shrub	0.070	0.047	299.705	1.485	0.139
σ sensitivity	tree	-0.002	0.045	225.870	-0.038	0.969
σ sensitivity	first_leaf	-0.176	0.055	2,221.437	-3.197	0.001
σ sensitivity	shrub:first_leaf	0.147	0.080	3,710.289	1.839	0.066
σ sensitivity	tree:first_leaf	0.239	0.064	2,527.327	3.728	< 0.001

Table D.5. Bird traits model coefficients. Estimates are standardized effect sizes.

Metric	Coefficient	Estimate	Std. Error	df	t-value	p-value
μ shift	(Intercept)	0.048	0.027	100.555	1.784	0.077
	Herbivore	0.064	0.035	111.821	1.833	0.069
	Omnivore	0.010	0.030	93.272	0.330	0.742
	log(mass)	-0.055	0.026	124.441	-2.086	0.039
μ sensitivity	(Intercept)	-0.756	0.168	122.018	-4.497	< 0.001
	Herbivore	-0.096	0.206	158.507	-0.466	0.642
	Omnivore	-0.111	0.183	145.824	-0.607	0.545
	log(mass)	-0.196	0.150	159.318	-1.304	0.194
σ shift	(Intercept)	-0.012	0.007	64.201	-1.753	0.084
	Herbivore	-0.034	0.016	823.627	-2.081	0.038
	Omnivore	0.002	0.013	819.642	0.125	0.901
	log(mass)	-0.003	0.011	284.518	-0.290	0.772
σ sensitivity	(Intercept)	-0.061	0.045	825.000	-1.363	0.173
	Herbivore	-0.096	0.102	825.000	-0.948	0.344
	Omnivore	-0.028	0.085	825.000	-0.334	0.738
	log(mass)	0.239	0.069	825.000	3.484	0.001

CURRICULUM VITAE

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Education

Utah State University	Ph.D.	Ecology	2023

Adviser: William D. Pearse
"The effects of recent climate change on spring phenology, with a special focus on patterns of bee foraging"
GPA: 3.8

North Carolina State University	B.S.	Biology	2015

Concentration: Ecology, Evolution, Conservation Biology
Minor: Mathematics
Valedictorian, GPA: 4.0
University Scholars Program

Professional Experience

Research Technician 2016 – 2018

North Carolina State University, Department of Applied Ecology

Identified bee collection specimens and conducted field work on a long term pollinator phenology project at the Rocky Mountain Biological Lab.

Environmental Education Intern 2016

North Carolina Invasive Plant Council

Created educational materials and presented at professional meetings, public events, and outreach programs.

Research Assistant 2014 – 2016

North Carolina State University, Center for Research in Scientific Computation

Designed and executed laboratory microcosm experiments on *Daphnia magna*, developed population models using inverse problem techniques in MatLAB, and compiled literature reviews.

Undergraduate Research Intern 2015

Sierra Nevada Research Institute

Studied the climate response of conifers in and around Yosemite National Park by analyzing long term population data in R and conducting seedling surveys.

Publications

Stemkovski, M., Dickson, R. G., Griffin, S. R., Inouye, B. D., Inouye, D. W., Pardee, G. L., Underwood, N., & Irwin, R. E. (2023). Skewness in bee and flower phenological distributions. *Ecology*, 104(1), 1–9.

Stemkovski, M., Bell, J. R., Ellwood, E. R., Inouye, B. D., Kobori, H., Lee, S. D., Lloyd-Evans, T., Bricmack, R. B., Templ, B., & Pearse, W. D. (2022). Disorder or a new order : How climate change affects phenological variability. *Ecology*, 103(1), 1–14.

Felton, A. J., Shriver, R. K., **Stemkovski, M.**, Bradford, J. B., Suding, K. N., & Adler, P. B. (2022). Climate disequilibrium dominates uncertainty in long-term projections of primary productivity. *Ecology Letters*, 25(12), 2688-2698.

Smith, T. P., **Stemkovski, M.**, Koontz, A., & Pearse, W. D. (2022). AREAdata: A worldwide climate dataset averaged across spatial units at different scales through time. *Data in Brief*, 43, 108438.

Pardee, G. L., Griffin, S. R., **Stemkovski, M.**, Harrison, T., Portman, Z. M., Kazenel, M. R., ... & Irwin, R. E. (2022). Life-history traits predict responses of wild bees to climate variation. *Proceedings of the Royal Society B*, 289(1973), 20212697.

Lembrechts, J. J., van den Hoogen, J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kemppinen, J., **...** & Hik, D. S. (2022). Global maps of soil temperature. *Global Change Biology*, 28(9), 3110-3144.

Smith, T. P., Flaxman, S., Gallinat, A. S., Kinosian, S. P., **Stemkovski, M.**, Unwin, H. J. T., ... & Pearse, W. D. (2021). Temperature and population density influence SARS-CoV-2 transmission in the absence of nonpharmaceutical interventions. *Proceedings of the National Academy of Sciences*, 118(25), e2019284118.

Stemkovski, M., Pearse, W. D., Griffin, S. R., Pardee, G. L., Gibbs, J., Griswold, T., Neff, J. L., Oram, R., Rightmyer, M. G., Sheffield, C. S., Wright, K., Inouye, B. D., Inouye, D. W., & Irwin, R. E. (2020). Bee phenology is predicted by climatic variation and functional traits. *Ecology Letters*, 23(11), 1589–1598.

Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., **...** & Rocha, A. (2020). SoilTemp: A global database of near-surface temperature. *Global Change Biology*, 26(11), 6616-6629.

Banks, H. T., Collins, E., Flores, K., Pershad, P., **Stemkovski, M.**, & Stephenson, L. (2017). Statistical error model comparison for logistic growth of green algae (Raphidocelis subcapitata). *Applied Mathematics Letters*, 64, 213-222.

Stemkovski, M., Baraldi, R., Flores, K. B., & Banks, H. T. (2016). Validation of a mathematical model for green algae (*Raphidocelis subcapitata*) growth and implications for a coupled dynamical system with *Daphnia magna*. *Applied Sciences*, 6(5), 155.

Adoteye K., Banks H., Cross K., Eytcheson S., Flores K., LeBlanc G., Nguyen T., Ross C., Smith E., **Stemkovski M.**, Stokely S. (2015) Statistical validation of structured population models for *Daphnia magna*. *Mathematical Biosciences*, 266, 73-84.

Presentations

Stemkovski, M., Bell, J. R., Ellwood, E. R., Inouye, B. D., Kobori, H., Lee, S. D., Lloyd-Evans, T., Bricmack, R. B., Templ, B., & Pearse, W. D. (2022) Disorder or a new order : How climate change affects phenological variability. Oral Session, *MacArthur Academy Conference*, Logan, Utah.

Stemkovski, M., Bell, J. R., Ellwood, E. R., Inouye, B. D., Kobori, H., Lee, S. D., Lloyd-Evans, T., Bricmack, R. B., Templ, B., & Pearse, W. D. (2022) Disorder or a new order : How climate change affects phenological variability. Oral Session, *Ecological Society of America*, Montreal, Canada.

Stemkovski M., Pearse W.D. (2019) Modeling the seasonal abundance curve of solitary bees.

Oral Session, *Entomological Society of America*, St. Louis, Missouri.

Stemkovski M. (2015) Climate Response of Sierra Nevada Conifers. Oral Session, *Yosemite REU Student Symposium*, El Portal NPS Headquarters, California.

Stemkovski M. (2014) Multi-scale modeling of *Daphnia magna* population dynamics. Oral Session, *State of North Carolina Undergraduate Research and Creativity Symposium*, Raleigh, North Carolina.

Press

Gilbert, L. (2022, December 6). Catching Up to Climate Change By Tracking Big-Picture Patterns. *Utah State Magazine*. Retrieved from https://utahstatemagazine.usu.edu/environment/catching-up-to-climate-change-researchers-track-big-picture-patterns-in-plant-transformations/

Muffoletto, M. (2020, August 25). Out of sync: Ecologists report that climate change is affecting bee, plant life cycles. *NSF*. Retrieved from https://beta.nsf.gov/news/out-sync-ecologists-report-climate-change

Rott, N. (2018, July 23). Spring Is Springing Sooner, Throwing Nature's Rhythms Out Of Whack. *NPR*. Retrieved from https://www.npr.org/2018/07/23/630181622/spring-is-springing-sooner-throwing-natures-rhythms-out-of-whack

Awards

Graduate Research Fellowship	2021-2022
National Science Foundation	$138,000
Graduate Research Award	2021
USU Ecology Center	$5,000
Matt Del Grosso Endowed Graduate Research Award	2021
USU Department of Biology	$2,000
Joseph E. Greaves Endowed Scholarship	2019
USU Department of Biology	$4,500

Graduate Fellowship	2019
Rocky Mountain Biological Laboratory	$870

Teaching

Workshop instructor – R for Ecologists 2021-2022

Utah State University, Ecology Center

Led workshops on data management, data visualization, and basic programming in R for graduate students through the USU Ecology Center.

Teaching Assistant – Introductory Biology laboratory 2022

Utah State University, Department of Biology

Taught weekly lab classes for two sections of ~25 students each, graded materials, and worked individually with students on class material.

Tutor – Programming in R 2022

Utah State University, Ecology Center

Delivered specific guidance on R programming projects and statistical analyses for graduate students by individual appointment and office hours.

Teaching Assistant – Ecological Forecasting and Dynamics 2021

Utah State University, Department of Wildland Resources

Taught guest lectures, assisted with class projects, and held office hours for graduate students in Ecological Forecasting and Dynamics.

Teaching Assistant – Principles of Genetics 2014-2015

North Carolina State University, Department of Plant and Microbial Biology

Led weekly recitation sessions for students in Principles of Genetics, held semiweekly office hours, and graded class materials.

Tutor – Organic Chemistry 2013-2014

North Carolina State University, Undergraduate Tutorial Center

Led tutorial sessions in Organic Chemistry for individuals and groups.

Mentorship

Li Wang – MSc student 2022

Imperial College London

“Chaos in ecological population time-series”

Bailee Rasmussen – undergraduate researcher 2020

Utah State University

“What landscape factors determine the community assembly of wild bees?”

Laura Naslund – REU student 2018

Rocky Mountain Biological Laboratory

“Evaluating Critical Thermal Tolerances of Solitary Bees”

Matthew Turnley – REU student 2018

Rocky Mountain Biological Laboratory

“The effect of surrounding bloom color on pan trap success in Rocky Mountain bees”

Hildreth Rocha – REU student 2017

Rocky Mountain Biological Laboratory

“Effects of Climate Changes on Ecologically Important Bees and Flowers”

Service

Mentor – USU Writing Center GRFP workshop series 2020-2022

President – USU Biology Graduate Student Association 2019

Committee chair – BGSA Graduate Student Travel Award 2019