Title

Phenology in the Anthropocene: Interactions between ecology, climate change, and human society

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PHENOLOGY IN THE ANTHROPOCENE: INTERACTIONS BETWEEN ECOLOGY, CLIMATE CHANGE, AND HUMAN SOCIETY

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Table of Contents

List of Figures and Tables

Figures

Tables

Abstract

Phenology in the Anthropocene: Interactions between ecology, climate change, and human society

Yiluan Song

Phenology, the timing of recurring biological events, is nature's calendar. Changes in phenology are among the most sensitive biological responses to global changes. Anthropogenic climate change has driven widespread phenological shifts, such as the advancement of spring events; human activities also alter phenology more directly in croplands, pastures, and urban landscapes. Phenological change in turn affects human society such as through food security and pollen allergy.

This dissertation offers a multiperspective examination of phenology at the intersection of ecology, climate, and human society. Firstly, I develop a theoretical framework and a novel approach to quantify phenological mismatch, in the broader context of ecological synchrony under climate change. Using this framework and approach, I systematically assess phenological mismatch and investigate the influence of anthropogenic land use. Recognizing the complex responses in phenology and the need for extensive data, I explore an innovative method for inferring pollen phenology, offering potential applications in public health. Lastly, I focus on understanding the human perceptions of pollen phenology, which in turn provides insights for natural science research and climate change communication.

Chapter 1 presents a generalizable theoretical framework for phenological mismatch under climate change. A prediction-based approach can be used to quantify multiple types of phenological mismatch across landscapes, demonstrated by empirical case studies and simulations. Chapter 2 highlights that climate-phenology mismatch is widespread and more pronounced in human-dominated landscapes. Chapter 3 introduces a method for inferring the flowering and pollen phenology of wind-pollinated plants using high-resolution satellite imagery, even at locations without prior observations. Chapter 4 reveals that social media users accurately detect variations in pollen phenology but are ideologically biased in attribution to climate change, underscoring the potential of social sensing and the challenges in climate change communication.

In summary, this dissertation has contributed to our understanding of various forms of socio-ecological coupling related to phenology. Knowledge of such interactions has valuable implications for global change ecology, sustainable management of vegetation, public health, and climate change mitigation. In the Anthropocene, the study of phenology calls for advancements in generalizable theories, the integration of models and data, and an interdisciplinary approach to future research.

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Bae, Edith Gonzales, Whitney Hansen, Clara Qin, Cristina Riani, and Tashina Vavuris, you all have made my time as a PhD student substantially more enjoyable, especially during the tough time of COVID-19. I wish every one of you the best. I also thank Yi Liu, Ruoyu Wu, Shike Zhang, who joined the Zhu Lab later on, for bringing me fresh ideas and energy.

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The text of this dissertation includes reprints of the following previously published material:

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- Song, Y., Zajic, C.J., Hwang, T., Hakkenberg, C.R., & Zhu, K. (2021). Widespread mismatch between phenology and climate in human‐dominated landscapes. *AGU Advances*, *2*, e2021AV000431.

Dr. Kai Zhu directed and supervised the research which forms the basis for the dissertation. All co-authors approve the inclusion of this work in the dissertation.

Introduction

Phenology, often described as nature's calendar, refers to the study of the timing of recurring biological events and its relationship with environmental factors (Lieth, 1974). When we study phenology, we often focus on key phenological events, including the flowering of plants and the breeding behaviors of animals. We also study the continuous changes in seasonal variables such as plant productivity and airborne pollen concentrations. More broadly, we study the phenology of human activities, such as the timing of crop sowing and the seasonal patterns of discussions related to pollen. Phenology exists widely in ecological and social systems.

Climate change induces visible shifts in phenology. Meta-analyses across diverse species and geographic regions documented a consistent trend of advancement in spring phenological events, such as leaf onset and bird migration at an overall rate of 2.3–2.8 days decade^{-1} (Parmesan, 2007; Parmesan & Yohe, 2003). The earlier onset of leaves in spring is accompanied by diverse responses in leaf senescence in fall, resulting in an extended growing season overall (Menzel, 2000). Flowering seasons often have earlier starts and longer durations during climate change (Mo et al., 2017), exacerbating pollen seasons (Anderegg et al., 2021; Ziska et al., 2011, 2019). Phenological shifts are one of the most consistent and sensitive ecological indicators of climate change.

In addition to anthropogenic climate change, human activities modify phenology in various ways, with the prominent examples of agriculture and urbanization. Agricultural practices alter phenology through the sowing and harvesting of crops (Bai et al., 2019; Sacks & Kucharik, 2011), irrigation schemes (de Beurs & Henebry, 2004), and land cover change. For instance, a significant expansion in maize and soybean cultivation in the Midwestern US, coupled with decreases in wheat and oats, delayed the spring green-up of land surface at a rate of 1.8–6.7 day decade^{-1} (X. Zhang et al., 2019). In urban areas, phenology is impacted by multiple factors, including the urban heat island effect, CO_2 fertilization, irrigation, and the introduction of non-native species (Buyantuyev & Wu, 2012; Wang et al., 2019). These anthropogenic factors exacerbate the disruption of natural phenological patterns or facilitate adaptation of managed systems to changing climate conditions.

Phenological changes have profound ecological consequences. One of the most significant impacts is phenological mismatch, where the timing of key events among interacting species becomes misaligned (Cushing, 1969). Phenological mismatch has been examined in various systems, from breeding birds and their food resources and to flowers and their pollinators (Kudo & Ida, 2013; Renner & Zohner, 2018). Meta-analyses showed that the relative timing of key life cycle events in aquatic and terrestrial ecosystems has changed significantly since the early 1980s (Kharouba et al., 2018). Climate-driven phenological change can trigger cascading trophic mismatch in food webs (Ovaskainen et al., 2013). Phenological mismatch have potential effects on ecological processes at multiple scales, including from species interactions (Rafferty et al., 2015; Renner & Zohner, 2018), population persistence (Saino et al., 2011), and ecosystem functioning (Beard et al., 2019).

Phenological changes also impact human societies. Disrupted crop growth and development affects the economic yield of crops and necessitates adaptation measures to ensure food security in the face of climate change (Fatima et al., 2020). Changes in the flowering phenology of wind-pollinated plants are likely to extend and intensify pollen seasons, leading to elevated risks of allergic asthma and allergic rhinitis (hay fever) among susceptible populations (Cecchi et al., 2010; Damialis et al., 2019). In addition, there might also be changes in the experience of cultural and recreational activities, such as the observations of fall foliage and wildflowers (Hille Ris Lambers et al., 2021; Shin et al., 2021). As individuals experience personal impacts related to phenological changes, phenology has the potential to shape human perceptions and actions towards climate change. However, given the complex interplay of physical experience and the influence of political, social, and psychological factors,, it is unclear how humans observe and interpret phenological changes within the context of climate change (Howe & Leiserowitz, 2013).

Phenology is a well-established and dynamic field within ecology that has made significant progress, particularly in the context of climate change (Piao et al., 2019). Substantial advancements have been achieved in understanding the ecological mechanisms underlying changing phenology (Yin et al., 2023), developing process-based and data-driven models to predict phenology (Clark et al., 2014; Qiu et al., 2020), and collecting extensive in-situ and remotely-sensed phenology data (Crimmins et al., 2017; White et al., 2009). While the effects of climate change on phenology have received considerable attention, the understanding of the reciprocal relationship between humans and phenology remains considerably less clear. Moreover, there is a significant gap in incorporating the social science perspective to study humans in the changing ecology and climate (Bastian & Bayliss Hawitt, 2023). Therefore, I adopt fresh perspectives in studying phenology, ones that recognize and address the pivotal role of humans in mediating ecology and climate change.

In this dissertation, I address several emerging questions that lie at the intersection of ecology, climate change, and human society.

1) (Connecting climate change to ecology) How does climate change disrupt the relationship between phenology and its environment?
2) (Connecting humans to ecology) How do human activities influence the mismatch between climate and phenology?
3) (Connecting ecology to humans) Can our knowledge of plant phenology, combined with emerging data sources, be applied to inform public health?
4) (Connecting humans to climate change) Can we leverage human perceptions of pollen phenology to enhance climate change communication?

By answering these questions across four chapters, I aim to provide a multidimensional, though not exhaustive, perspective on phenology in the Anthropocene.

Chapter 1. Prediction-based approach for phenological mismatch across landscapes

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Abstract

Context

Climate change is driving phenological shifts across landscapes, but uncoordinated shifts might cause a potential “phenological mismatch.” There has been little consensus on the existence and magnitude of such a mismatch. The lack of agreement among studies can be attributed to the wide variety of definitions for the term “phenological mismatch,” as well as the methods used to measure it. The lack of comparability among measures of phenological mismatch creates a challenge for conservation.

Objectives

We proposed a novel theoretical framework to generalize existing measures of phenological mismatch and an approach to quantify the decoupling between phenology and the environment using the loss in predictive skill over time. We aimed to estimate the magnitude of phenological mismatch on large spatial scales and test

the proposed predictive approach’s ability to detect multiple types of phenological mismatch.

Methods

We modeled historical climate-phenology coupling and quantified phenological mismatch as the deviation between observed and predicted phenology under climate change. First, we used two large empirical spatiotemporal datasets to estimate phenological mismatch in plant flowering phenology in the eastern United States and bird reproductive phenology in Finland. Historical climate-phenology coupling was modeled with spatial linear regression. Second, we conducted four simulation experiments representing different types of mismatch during climate change. We recovered simulated phenological mismatch by fitting a data-driven nonlinear model (Gaussian Process Empirical Dynamic Modeling) and predicting phenology.

Results

In the eastern US, we found that advancing plant flowering phenology generally matched spring warming from 1895 to 2015, with seven out of the 19 species studied having significant phenological mismatches, with observed flowering time earlier than predictions even considering warming. A similar phenological mismatch was found in birds in Finland from 1975 to 2017, with the bird breeding season advancing more than expected in 21 out of the 36 species studied. In four simulation experiments, we were able to accurately recover the simulated phenological mismatches in the timing of events, pace of development, and intensity of activities, although with greater challenges in quantifying a mismatch in life history.

Conclusions

Overall, these case studies show that our prediction-based measure effectively quantifies multiple types of phenological mismatch, providing a more generalizable and comparable measure of phenological mismatch across study systems and scales. This study will enable the investigation of phenological mismatch at large scales, improving understanding of the patterns and consequences of climate-change-induced phenological changes.

1 Introduction

Since Cushing (1969) proposed the match-mismatch hypothesis, ecologists have been increasingly concerned with whether climate change induces a “phenological mismatch.” Phenological mismatch can lead to negative ecological consequences on multiple scales of ecology: from species interactions (Rafferty et al. 2015; Renner and Zohner 2018) to the persistence of populations (Saino et al. 2011; Visser et al. 2012), and ecosystem functioning (Beard et al. 2019). Meta-analysis shows that the relative timing of key life cycle events in aquatic and terrestrial ecosystems in 1951–2013 has changed significantly since the early 1980s (Kharouba et al. 2018). For example, advancing spring conditions have driven cascading trophic mismatch in the food web from vegetation, insects, birds, to polar bears in the Arctic (Rockwell et al. 2011; Reneerkens et al. 2016). Understanding and mitigating phenological mismatch become particularly crucial given the rapid climate change and human modifications of the landscapes.

Phenological mismatches have been observed either between species and climate or between interacting species. On the one hand, phenological shifts do not always change in concordance with climate change. In a global meta-analysis (Parmesan and Yohe 2003), while 423 out of 484 species changed in their phenology as predicted given the climate change, 61 changed opposite to the prediction. Some phenological mismatches may be the results of anthropogenic activities. For example, in the Midwest US, although warming spring temperatures potentially allowed earlier crop emergence, the remotely-sensed start of season was delayed, due to the replacement of wheat and oat by corn and soybean (Zhang et al. 2019). On the other hand, the widespread phenological mismatch between interacting species under climate change received more attention. For example, the temporal shift in the arriving and hatching of several migratory bird species have been insufficient to match the rapid advancement of spring greenup at their destinations (Visser et al. 1998; Both and Visser 2001; Gaston et al. 2009; Clausen and Clausen 2013; Mayor et al. 2017).

Although phenological mismatch is well studied, our understanding of its magnitude, impacts, and how it changes across scales remains limited. For example, there have been inconsistent findings on whether there are community-level phenological mismatches (Edwards and Richardson 2004; Donnelly et al. 2011; Burthe et al. 2012; Ovaskainen et al. 2013). Part of these inconsistencies arises from the different definitions and methods used to quantify phenological mismatch. Ecologists have realized the difficulty to define a baseline for “matching phenology” (Kharouba and Wolkovich 2020), particularly under global change, as we do not always know how much a species should be shifting to match the change in its environment (Visser and Both 2005). In addition, recent development in phenological mismatch on the community level (Edwards and Richardson 2004; Renner and Zohner 2018) and from a spatial perspective (Post et al. 2008; Vitasse et al. 2018; Aikens et al. 2020) have highlighted the need to expand the concept of phenological mismatch, which traditionally focuses on the population level and a single site. The lack of a coherent and generalizable theoretical framework creates a challenge for understanding and interpreting phenological mismatch across landscapes under climate change.

In this study, we first review the different measures used to quantify phenological mismatch, classifying them into a descriptive approach and a model-comparison approach. After reviewing their advantages and drawbacks, we propose a novel theoretical framework to define a generalized phenological mismatch and measure it with a predictive approach. Last, we conduct three case studies with empirical and simulated data to demonstrate the power and limits of our new predictive approach in detecting and quantifying phenological mismatch.

2 Measures of phenological mismatch

The earliest and most common approach to evaluating phenological mismatch is timing-based, i.e., focusing on the relative timing of phenological events (Fig. 1-1a). One example is the difference in the timing of phytoplankton blooms and fish breeding (Cushing 1969). The main assumption is that there is an optimal time lag between a pair of phenological events (Satterthwaite et al. 2014), and deviations from this time lag indicate a phenological mismatch. These measures can be further divided into two sub-categories. Most studies that use a timing-based approach focus on discrete phenological events, such as peak abundance (Blondel et al. 1993; Reed et al. 2013; Doiron et al. 2015) or emergence (Tikkanen and Julkunen-Tiitto 2003; Satterthwaite et al. 2014) (Fig. 1-1a[1]). Timing-based approaches are often used on the phenologies of species with trophic interactions. In Kudo and Ida (2013), phenological mismatch was measured by the delay in initial bee activity from flowering onset. Reed et al. (2013) defined the phenological mismatch as the difference between the laying date of the first clutch of great tits and the date of peak food abundance, plus 30 days, where both positive or negative mismatch leads to lower fitness. Other timing-based studies treat phenology as a continuous event, such as the continued presence of a species or an environmental condition, and calculate the overlap in timing (McKinnon et al. 2012; Iler et al. 2013) (Fig. 1-1a[2]). Estimation of timing-based mismatch usually requires knowledge of the time lag or overlap that optimizes fitness or population size (Durant et al. 2005). Such knowledge may be gained from empirical data (Reed et al. 2013; Plard et al. 2014; Satterthwaite et al. 2014; Doiron et al. 2015) or models (Jonzén Tikkanen and Julkunen-Tiitto 2003; Niclas et al. 2007). However, more often, there is no visible ecological consequence of varying time lag (Pearce-Higgins et al. 2010; Dunn et al. 2011; Dunn and Møller 2014), and assumptions are used based on expert knowledge.

Impact-based methods focus on the consequences of changes in the relative timing of a focal species and its environment (Fig. 1-1b). The consequences may be on the state of resource availability, environmental conditions, or other variables that affect fitness. A classic example is the quantification of mismatch between the coat color change of snow hares and the presence of snow (Zimova et al. 2014, 2016). The researchers defined a hare to be mismatched when the contrast between its coat color and background exceeded 60%. Another index based on impact is “thermal delay,” which measures the increase in accumulated degree-days when migratory birds arrive at their breeding grounds (Saino et al. 2011). The abundance (Durant et al. 2005; Hipfner 2008; Burger et al. 2012) or diversity (Post and Forchhammer 2008; Post et al. 2008) of a group of prey in predator(s)’ diet has been used as a proxy for temporal overlap. Similarly, Rafferty and Ives (2011) and Petanidou et al. (2014) measured the level of pollination during flowering. The impact-based measures are closely linked to ecological consequences. Nevertheless, similar to timing-based measures, sufficient knowledge has to be obtained to determine the optimal state of environmental conditions for the focal species.

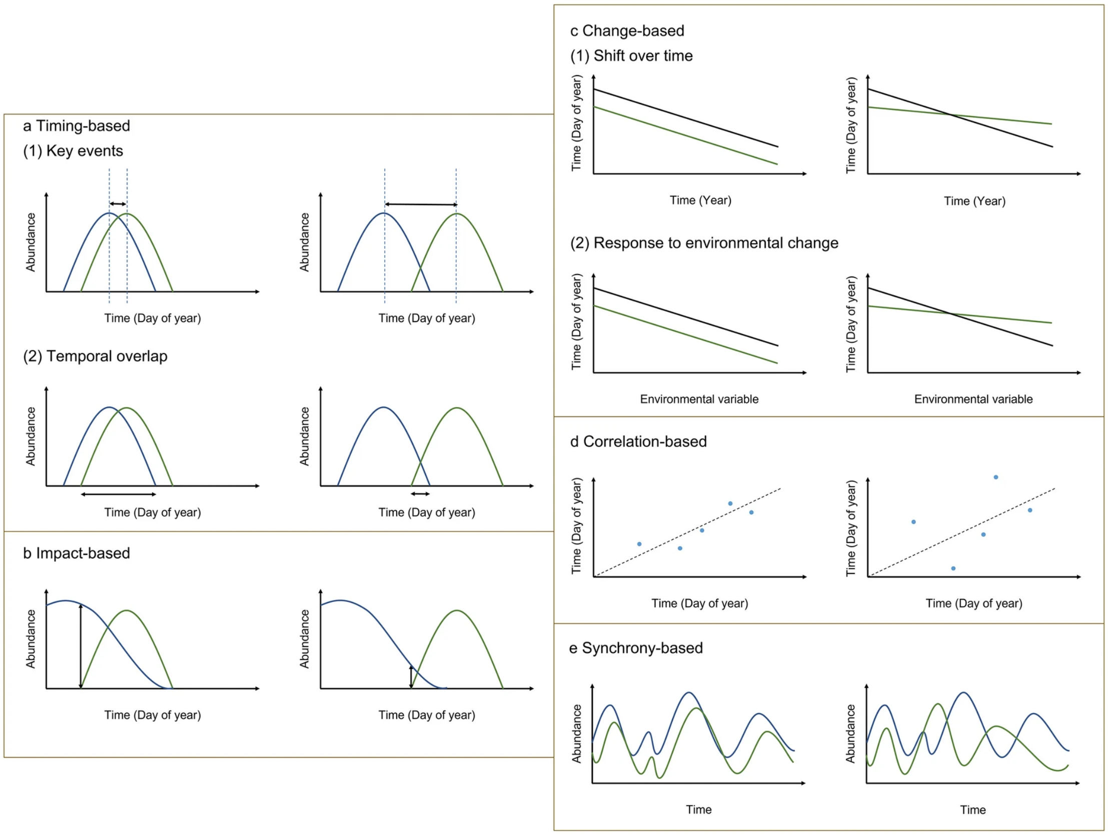

Figure 1-1. Conceptual diagrams of five main methods of measuring phenological mismatch. **(a)** Timing-based methods focus on the relative timing of phenological events or periods. **(b)** Impact-based methods focus on the consequences of changes in the relative timing of a focal species and its environment. **(c)** Change-based methods focus on the change of phenological events over time or in response to environmental change. **(d)** Correlation-based methods focus on the strength of linear coupling between variables. **(e)** Synchrony-based methods focus on the coordination among processes.

Change-based methods de-emphasize the relative timing and instead focus on its change (Fig. 1-1c). Unlike the previous timing-based method that can be used to evaluate phenological mismatch given a pair of timing in a single year and site based on optimal relative timing, the change-based methods detect changes in relative timing with multiple pairs of timing observed over space or time. This approach has been increasingly popular in recent years because of rapid global change and widespread phenological shifts. One method is to compare the rate of change in the timing of phenological events over time, where a non-parallel shift is considered to indicate a mismatch (Fig. 1-1c[1]). This method has been used to suggest several mismatches between the reproductive phenology of animals (often birds and ungulates) and environmental cues such as climatic events (Van Noordwijk et al. 1995; Sanz et al. 2003; Gaston et al. 2009; Jones and Cresswell 2010; Clausen and Clausen 2013) and peak food abundance (Visser et al. 1998; Gaston et al. 2009; Plard et al. 2014). The mismatch is less supported in some tightly coupled relationships, such as between flowering and pollinator activities (Bartomeus et al. 2011; McKinney et al. 2012). Notably, this method allows the comparison of more than two species on the community level. Meta-analyses involving multiple taxa suggested differential phenological change among trophic levels (Edwards and Richardson 2004; Both et al. 2009; Thackeray et al. 2010; Burthe et al. 2012; Ovaskainen et al. 2013). The other change-based method is to compare the response in the timing of phenological events to an environmental change, i.e., comparing the sensitivity or slope of the regression line (Fig. 1-1c[2]). Species that change their phenology differently compared to their interacting species in response to environmental change are considered to face the risk of mismatch (Evans et al. 2013). Observations are often made in experimental settings (Liu et al. 2011; Paull and Johnson 2014) or along environmental gradients (Mjaaseth et al. 2005; Forrest and Thomson 2011; Evans et al. 2013; Iler et al. 2013). Change-based methods have been argued to provide an unbiased measure because it considers species that show little phenological change, which may be under-reported otherwise (Thackeray et al. 2010). However, the result may be sensitive to the time period and area studied. It should also be noted that historical starting points may not benchmark matching phenology due to maladaptation (Blondel et al. 1993) or anthropogenic impacts.

Correlation-based methods are occasionally used, examining the strength of the coupling between the timing of a pair of phenological events or between phenology and environmental conditions (Fig. 1-1d), with a high correlation coefficient representing a greater degree of “matching.” By comparing the timing of shrimp hatching and spring phytoplankton bloom at various latitudes, Koeller et al. (2009) concluded that the shrimp hatching phenology generally matches food availability in the North Atlantic basin. Bloom timing of plankton has been correlated with sea bottom temperature (Koeller et al. 2009) and ice-retreat timing (Ji et al. 2013). In a North Sea pelagic food web, the lack of significant correlations among species phenologies and with sea surface temperature were used as evidence of a trophic mismatch (Burthe et al. 2012). This method requires the assumption of a relatively tight linear coupling between variables.

Very few studies use synchrony-based methods, examining the synchrony of time series of biotic or abiotic variables (Fig. 1-1e). Synchrony usually refers to coordination among processes (Ravignani 2017). Although synchrony can be tested statistically (e.g., with time-lagged correlation), visual inspection is employed more often in practice, limited by the amount of data. For example, the life cycles of fast-growing spring plankton advanced synchronously following earlier spring climatic events, whereas slow-growing summer zooplankton displayed no such synchrony, suggesting a higher risk of phenological mismatch (Adrian et al. 2006). The synchrony between the hatching curves of a pest and the bud burst curve of birch was disrupted in cold years but maintained in warmer years (Jepsen et al. 2011). Synchrony-based methods do not require identifying key phenological events but flexibly consider the continuous changes in processes (Yang and Rudolf 2010). They are also less dependent on knowledge of the underlying mechanism, compared to the other methods, because much information can be learned through past temporal dynamics (Nakazawa and Doi 2012). However, whether asynchrony is indeed an accurate reflection of phenological mismatch deserves further research, as asynchrony may reflect adaptive strategies (Visser et al. 2012) and represent a stable state in the absence of climate change (Singer and Parmesan 2010).

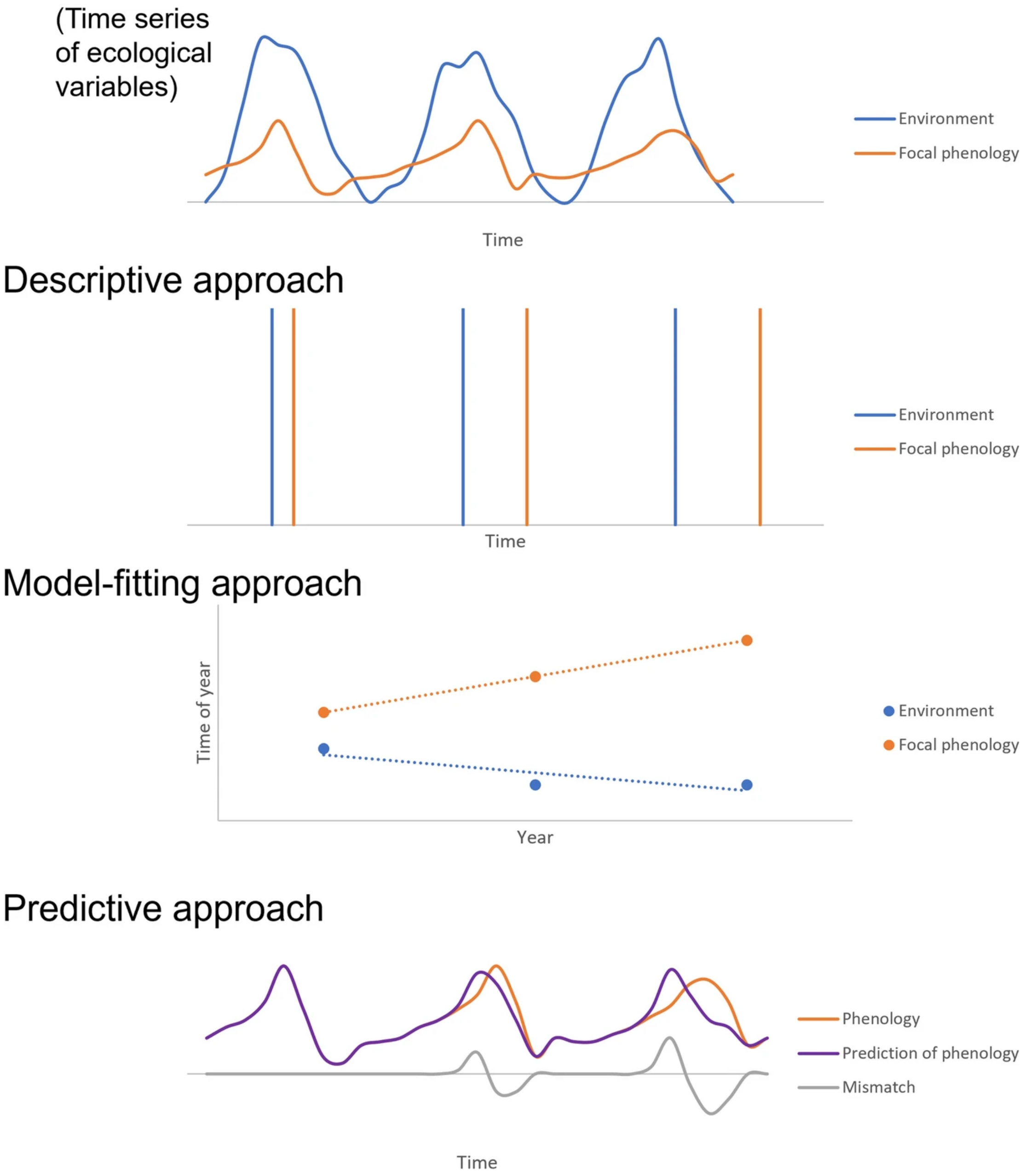

Figure 1-2. Conceptual diagram of two existing approaches (descriptive and model-comparison) approach and our proposed approach (predictive) for quantifying phenological mismatch using time series of ecological variables.

We broadly classified the five methods into two main approaches (Fig. 1-2). The first approach focuses on describing key characteristics of phenological time series (timing of key events, temporal overlap, and impact at a specific time) and comparing the descriptive measure to an optimal measure informed by ecological knowledge (Fig. 1-1a, b). The second approach focuses on fitting models to phenological metrics and compares model parameters (Fig. 1-1c, d, e). In the change-based method, linear models are fitted for the relationship between phenological metrics and time (year) or environmental variables, and the slopes are compared. In the correlation-based method, the error of models is compared. In the synchrony-based method, the phases of wave functions are compared. The common idea of methods with the model comparison is that matching phenology is represented by some optimal model parameters.

These two approaches have their limitations. For the descriptive approach, the key descriptive measure cannot always be specified, especially for activities with weak or irregular seasonality (e.g., tropical forest phenology) (Wu et al. 2017). The optimal descriptive measure that represents matching phenology requires accurate ecological knowledge, which is not always available. For the model-comparison approach, the models used for phenological metrics are often over-simplistic (usually linear) (Keenan et al. 2020) and lack flexibility.

Crucially, using different methods to study the same system can lead to divergent conclusions. For example, despite the differential response of flowering and syrphid phenology, environmental changes resulted in more days of temporal overlap between the flower-syrphid community through early snow melt (Iler et al. 2013). Different interpretations may even arise from similar methods and results, as there is often no clear distinction between “match” and “mismatch,” such as when the shifts in phenology are only partially consistent in a complex community (Burthe et al. 2012; Ovaskainen et al. 2013). Such mixed messages on phenological mismatch arise from the different definitions of phenological mismatch, from the divergence in the research protocol, and from the intrinsic complexity of the climate-phenology system. We argue that a new approach is needed in defining and measuring phenological mismatch that is compatible with the diverse phenological response to climate change and can be similarly applied to all levels of the organization.

3 A new framework based on prediction

We first seek to define a generalizable baseline for "matching phenology" with minimal assumptions on the key feature of phenological time series and the structure of phenology models. To generalize the commonly-used definitions, we consider phenological mismatch to take place when the temporal dynamics of individuals, populations, species, components of the ecosystem, or patches in a landscape do not maintain a stable relationship during climate change. Motivated by complex systems theory, we consider phenological mismatch to be the consequence of a loss of "generalized synchronization" (GS), which describes if a (static) functional relation exists between the states of the systems of interest (Kocarev and Parlitz 1995; Rulkov et al. 1995; Abarbanel et al. 1996; Brown and Kocarev 2000; Boccaletti et al. 2002).

Definition: Generalized synchronization in the phenology-environment coupling system occurs when there is a function, Φ, such that.

$$Y_{s,t} = \Phi\left(\boldsymbol{X}_{\mathrm{s,t}}\right) \qquad [1\text{-}1]$$

where Φ is a nonlinear function describing the relationships between focal phenology (Y) and the environment ($\boldsymbol{X}$), including the phenology of interacting individuals/populations/communities and abiotic conditions. All variables are indexed by space (s) and time (t), which encourages an explicit definition of the spatiotemporal scale of the synchronization. The same functional relationship (Φ) may be found to be consistent on one scale but not another. For example, the relationship may be consistent within a spatial range of d (the distance between s_1 and

s_2) or only at the same location ($d = 0$). The indices are omitted from here onwards for simplicity.

This definition then leads to a natural method for quantifying phenological mismatch, i.e., predicting phenology assuming a static relationship with other phenological and environmental variables, and assessing the discrepancies from observed phenology. This notion of quantifying the extent of GS based on the predictability of time series has been applied in previous studies of simulated chaotic systems and neuroscience (Schiff et al. 1996; Wiesenfeldt et al. 2001). A loss of GS can be detected from a loss in the predictive power of the model (Fig. 1-2).

The evaluation of phenological change and mismatch starts with a baseline of phenology (Y) and phenology-environment coupling (Φ) (Fig. 1-3).

$$Y = \Phi(\boldsymbol{X}) \tag{1-2}$$

If Φ remains the same with changes in the environment ($\boldsymbol{X}_{\mathrm{new}}$), we consider there to be no phenological mismatch. This can be expressed as

$$Y_{\mathrm{pot}} = \Phi\left(X_{\mathbf{new}}\right) = \Phi(X) + \left[\Phi\left(X_{\mathbf{new}}\right) - \Phi(X)\right] = Y + \Delta Y_{\mathrm{pot}} \tag{1-3}$$

where we refer to the model-predicted phenology given $\boldsymbol{X}_{\mathrm{new}}$ as the potential phenology (Y_{pot}), and its difference from Y as potential phenological change (ΔY_{pot}), reflecting the ideal adaptation in focal phenology without any constraint.

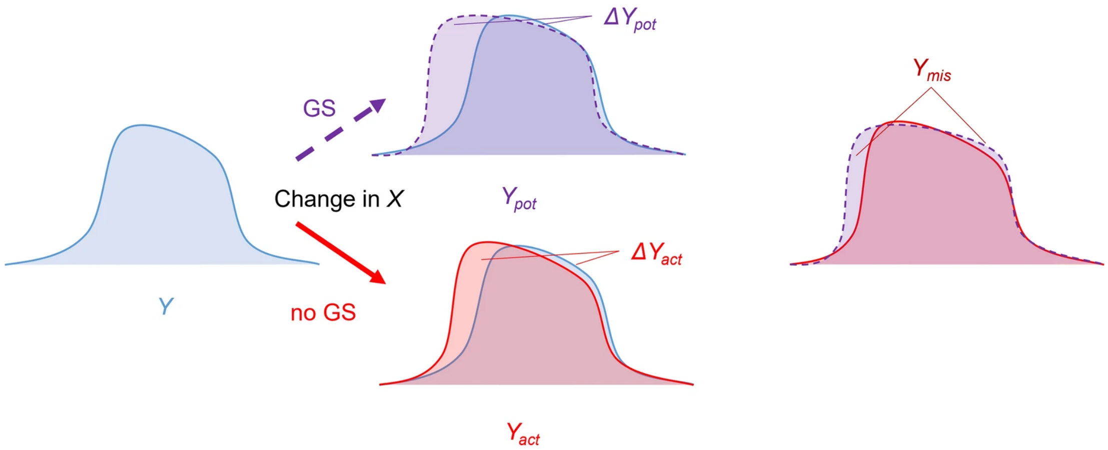

Figure 1-3. With the change in the environmental factors ($\boldsymbol{X}$), the baseline phenology (Y) is expected to change to potential phenology (Y_{pot}) under generalized synchronization (GS) in the ideal case; in reality, however, it is observed to change to actual phenology (Y_{act}). The deviations from Y are referred to as potential and actual phenological change (ΔY_{act} and ΔY_{pot}), respectively. The difference between potential and actual phenology is defined as phenological mismatch (Y_{mis}).

Realistically, there may be changes in the phenology-environment coupling (Φ').

$$Y_{\mathrm{act}} = \Phi'\left(X_{\mathbf{new}}\right) = \Phi(X) + \left[\Phi'\left(X_{\mathbf{new}}\right) - \Phi(X)\right] = Y + \Delta Y_{\mathrm{act}} \qquad [1\text{-}4]$$

Here we refer to the observed phenology given $\boldsymbol{X}_{\mathrm{new}}$ as the actual phenology (Y_{act}), and its difference from Y as the actual phenological change (ΔY_{act}). The phenological mismatch (Y_{mis}) is then defined as the difference between Y_{act} and Y_{pot}. Its magnitude is related to the loss of synchronization, i.e., the extent to which Φ' deviates from Φ.

$$Y_{\mathrm{mis}} = Y_{\mathrm{act}} - Y_{\mathrm{pot}} = \Delta Y_{\mathrm{act}} - \Delta Y_{\mathrm{pot}} \qquad [1\text{-}5]$$

4 Estimating phenological mismatch on large spatial scales with empirical data

4.1 Data

4.1.1 Herbarium and climate data

In order to examine possible mismatch between plant phenology and climate change, we used a published crowdsourced dataset of plant reproductive phenology from herbarium specimens across the eastern continental United States spanning from 1895 to 2015 (Park et al. 2018) (Fig. 1-4a). Park et al. (2018) crowdsourced phenological data online from over 7,000 herbarium specimens representing 30 flowering plant species. Crowdsourcers classified the specimens into flowering and fruiting and each was given a reliability score. For specimens without accurate coordinates, they used county of specimen collection for locality information. Park et al. (2018) also retrieved auxiliary climatic data (monthly temperature and precipitation) from the PRISM dataset at 4 km resolution (PRISM Climate Group 2019). In this case study, we focused on the match between the flowering time (FT) (day of year) and spring mean temperature (SMT) (°C) , defined as the mean of March, April, and May temperatures. We filtered out crowdsourcing records that were unreliable (reliability score = 0) and only kept one record for each specimen. We split the dataset into an early (prior to 1950) and a late (on or after 1950) period, and selected for species with no fewer than 30 records in both periods, leaving 19 species in our analysis.

4.1.2 Bird nestling ringing and climate data

To examine possible mismatch between bird breeding phenology and climate change, we used a published spatiotemporal dataset of over 820,000 nestling ringing records of 73 boreal bird species in Finland spanning from 1975 to 2017 (Hällfors et al. 2020) (Fig. 1-5a). As nestlings can only be ringed at a certain size, ringing dates are highly correlated with egg-laying dates, providing a high-quality indicator for the nestling ringing time (NRT) (day of year). The locations of nests were recorded at 10 × 10 km resolution. For each species, we aggregated nest-level NRT to the regional level by taking the median in 100 km diameter hexagons (Fig. 1-5a) to reduce the noise in data (Freeman et al. 2021). For each nest location, we retrieved auxiliary climatic data, mean annual temperature (MAT) (°C) from the TerraClimate dataset at ~ 4 km (1/24th degree) resolution (Abatzoglou et al. 2018). Similarly, we aggregated MAT by taking the median at all possible nest locations for a species and year in each hexagon. We removed hexagons with fewer than 50 nests with NRT data, leaving 28,017 records (hexagon × year). We split the dataset into an early (prior to 1995) and a late (on or after 1995) period, and selected for species with no fewer than 100 records in both periods, leaving 36 species in our analysis.

4.2 Methods

We preliminarily visualized the relationships between climatic and phenological data in the early and late period (Figs. 1-4b, 1-5b) to inspect the consistency in the climate-phenology functional relationship. We then systematically applied our prediction-based approach for each study system. We fitted a linear regression model between climatic and phenological variables (Eq. 1-6) to data in the early period only. In order to account for spatial autocorrelation among data points, we modeled spatial random effects with an exponential correlation function. We adopted a hierarchical Bayesian approach to build and fit the model, using the *spBayes* package in *R* (Finley et al. 2013).

$$Y(s) = \beta_0 + \beta_1 X(s) + \omega(s) + \varepsilon$$
$$\omega(s) \sim N(0, K) \quad K_{ij} = \sigma^2 \exp\left(-\varphi \left\| s_i - s_j \right\|\right)$$
$$\varepsilon \sim N\left(0, \tau^2\right)$$
$$\begin{pmatrix} \beta_0 \\ \beta_1 \end{pmatrix} \sim MVN\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 100 & 0 \\ 0 & 100 \end{pmatrix}\right]$$
$$\sigma^2 \sim IG(2, 2)$$
$$\varphi \sim U\left(-\frac{\log(0.05)}{100d}, -\frac{\log(0.05)}{0.01d}\right)$$
$$\tau^2 \sim IG(2, 0.1) \qquad [1\text{-}6]$$

where the response variable *Y* is the phenological variable (FS in the plant case study and BS in the bird case study) and the covariates *X* is the climatic variable (SMT in the plant case study and MAT in the bird case study). β_0 and β_1 are the coefficients for intercepts and covariates; *s* is the location of observation (in longitude and latitude for the plant case study and easting and northing in EPSG:3067 projection for the bird case study); ε is the random error. The spatial random effect, ω, is determined by the spatial variance parameter σ^2, the residual error variance τ^2, the spatial decay parameter φ, and the Euclidean distance between locations *i* and *j*. We empirically estimated *d*, the effective range of spatial dependence (Finley et al. 2015), by fitting an exponential function to the semivariograms of the residuals of the corresponding nonspatial linear regression models. We used common choices of diffuse multivariate normal (*MVN*) priors on $\boldsymbol{\beta}$, a diffuse inverse gamma (*IG*) prior on σ^2 , a tight *IG* prior on τ^2, and a diffuse uniform (*U*) priors on φ (Finley et al. 2013). We ran the Markov chain Monte Carlo (MCMC) sampler (10,000 samples for the flowering case study and 1000 samples for the bird breeding case study) (Finley et al. 2013), discarding the first half of the samples as burn-in.

We used the fitted model informed by data in the early period (*X* and *Y*) to predict phenological data in the early and late periods, respectively (Figs. 1-4c, 1-5c). Predictions were compared to observations in the early period to evaluate the model fit using the coefficient of determination (R^2) and root mean square error (RMSE). We similarly compared the predictions in the late period (Y_{pot}) with observations in the late period (Y_{act}) to estimate possible phenological mismatch. Specifically, we calculated and summarized the deviation between observations from predictions (Y_{mis}). We performed one-sample *t*-tests for each individual species to determine if the calculated mismatch was significantly different from zero. All calculations and statistical analyses were conducted in *R* v. 4.2.0 (R Core Team 2021).

4.3 Results

4.3.1 Advancement in flowering matches or outpaces spring warming in eastern US

Temperature niche (median SMT of all specimens) of all 19 species ranged from 6.06 to 16.0 °C. Phenological niche (median FT of all specimens) ranged from 129 to 228 day of year. There were significant correlations between FT and SMT in 17 out of 19 species, with FT being 2–5 days earlier with every 1 °C increase in temperature in these 17 species. When fitting linear models between FT and SMT in the early and late periods, respectively, the intercept changed slightly by −0.815 (95% interval: −36.5, 33.9) days and the slope changed slightly by 0.0684 (−3.39, 5.55) days $°C^{-1}$. Due to spatial bias in sampling and the difficulty of interpreting these parameter changes in linear models, we fitted spatial regression models to each species using data in the early period. For the early period, the fitted data had an R^2 of 0.465 (0.272, 0.819) and an RMSE of 21.0 (6.55, 49.2) days. For the late period, the predicted data had an R^2 of 0.0791 (0.00407, 0.507) and an RMSE of 32.6 (12.0, 65.8) days. The considerable reduction in model fit and increase in error for the late period suggest the loss of predictive skills in the climate-phenology model. The predicted FT in the later period deviated from the observed FT significantly in eight out of 19 species (Fig. 1-4d), with six species having observed FT significantly earlier ($p < 0.05$) than predictions by 5.00 to 14.4 days and two species significantly later by 1.84 to 10.9 days. The observations did not significantly differ from our predictions for most species (11 out of 19). The median of the residuals of all species was significantly lower than zero ($p < 0.05$), suggesting that this loss of predictive skills was not only from the process of extrapolation but also a possible change in the climate-phenology coupling over time.

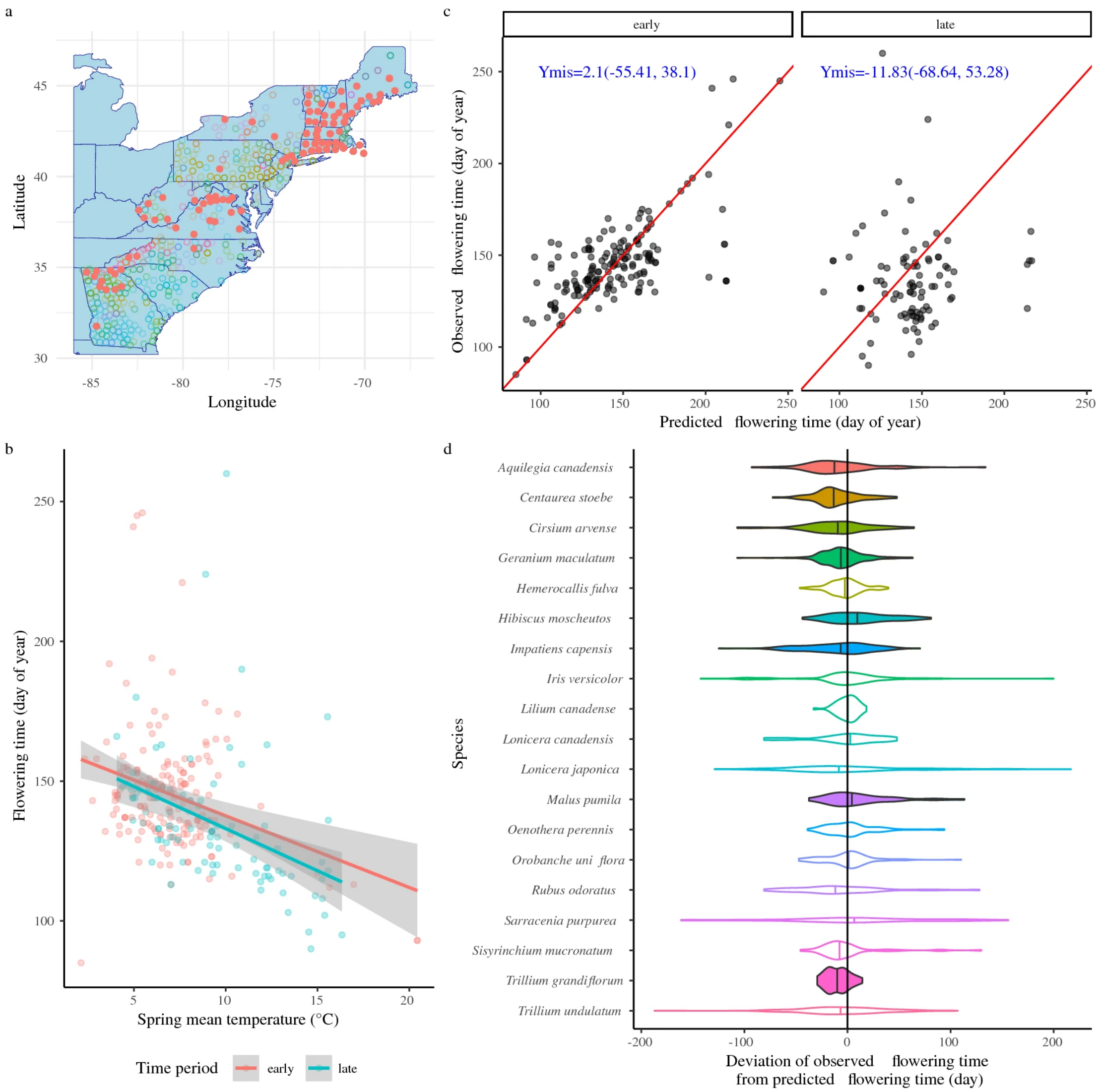

Figure 1-4. (a) Geographical distribution of herbarium specimens from 19 plant species in the eastern United States. Data were originally published in Park et al. (2018). An example species, *Aquilegia canadensis*, is highlighted in solid dots. **(b)** Relationship between the flowering time (FT) and spring mean temperature (SMT) of *Aquilegia canadensis* in the early (before 1950) and late (on or after 1950) periods, respectively. Fitted lines and 95% standard errors are shown for each period. **(c)**

Comparison between observed and predicted FT of *Aquilegia canadensis* in the early and late periods, respectively. 1:1 lines are shown in red. **(d)** Distribution of deviation of observed FT from predicted FT for each species. Species with deviations significantly different from zero are highlighted in solid.

4.3.2 Advancement in bird breeding slightly outpaces warming trends in most species in Finland

On the regional level (after aggregated to 100 km diameter hexagons), temperature niche (median MAT of all nests) of all 36 species ranged from 2.65 to 5.71 °C. Phenological niche (median NRT from all nests) ranged from 128 to 208 day of year. All 38 species experienced significant warming in their habitats from 1975 to 2017, with an increase in MAT ranging from 0.0461 to 0.0496 °C year^{-1}. In response to warming, 34 out of 38 species significantly advanced their NRT at a rate of 0.045–0.258 days year^{-1}. There were significant correlations between NRT and MAT in all 38 species, with NRT being 0.78 to 4.17 days earlier with every 1 °C increase in temperature. When fitting linear models between NRT and MAT in the early and late periods, respectively, the intercept changed very slightly by 0.164 (−8.80, 8.44) days and the slope too by −0.221 (−1.47, 1.69) days °C^{-1}. We fitted spatial regression models to each species using data in the early period. For the early period, the fitted data had an R^2 of 0.188 (0.0601, 0.345) and an RMSE of 7.52 (4.89, 11.4) days. For the late period, the predicted data had an R^2 of 0.100 (0.00375, 0.355) and an RMSE of 7.55 (4.61, 12.9) days. The slight reduction in model fit and increase in error for the late period suggest loss in predictive skills similar to the previous case study, although to a smaller extent. The predicted NRT in the later period deviated from the observed NRT significantly in 26 out of 38 species (Fig. 1-5d), with 20 species having observed NRT significantly earlier than predictions by 0.964–5.80 days and four species significantly later by 0.665–3.20 days. For the remaining 12 species, the observations did not significantly differ from the predictions. The overall significant negative residual among all species ($p < 0.05$) strongly suggests a change in the climate-phenology coupling over time.

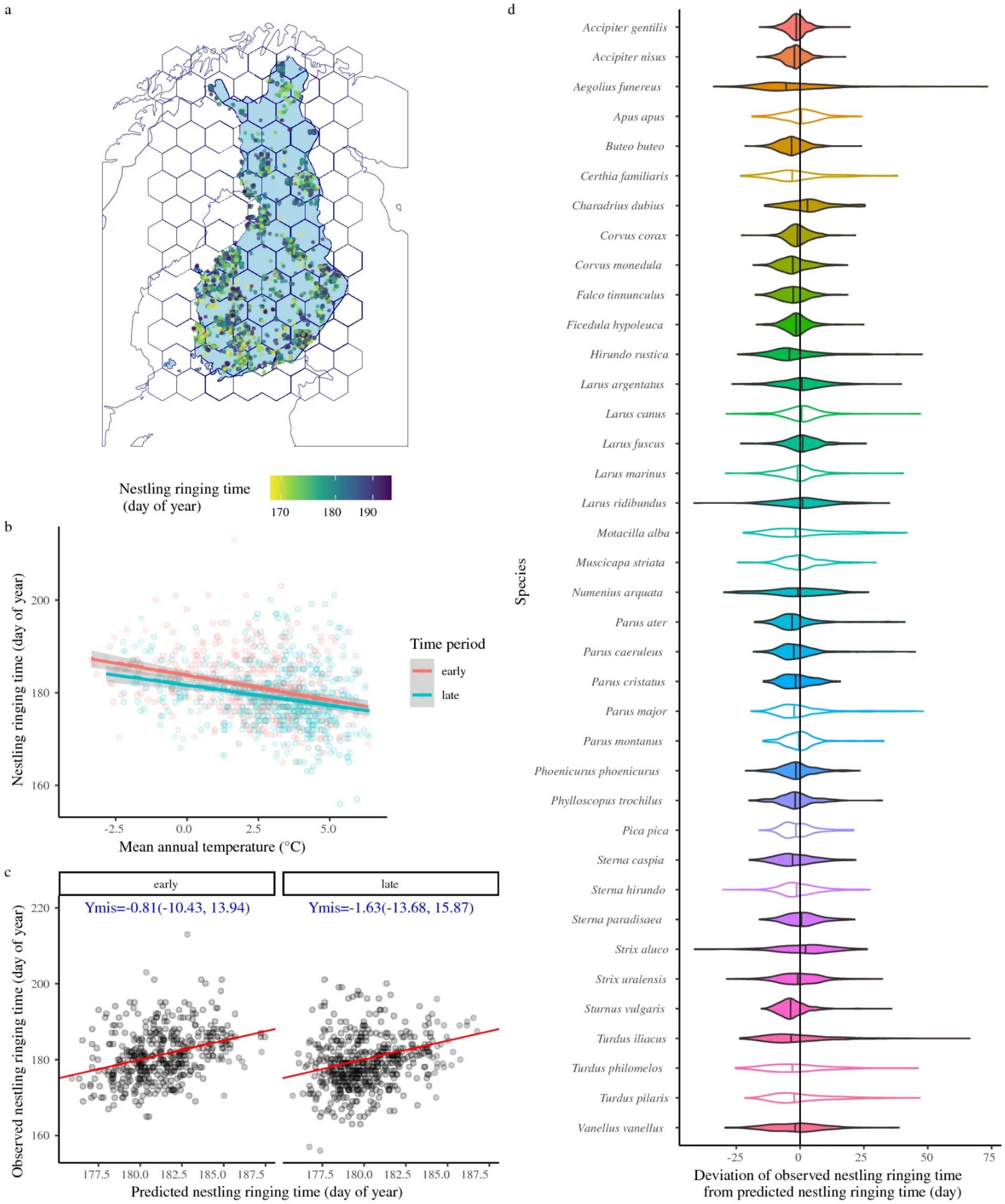

Figure 1-5. (a) Geographical distribution of bird nestling ringing events for an example species, *Phoenicurus phoenicurus*, out of 38 boreal bird species in Finland in this study. Data were originally published in Hällfors et al. (2020). Color of dots

shows the nestling ringing time (NRT) on the nest level. Data were aggregated to 100 km diameter hexagons for further analysis. **(b)** Relationship between NRT of *Phoenicurus phoenicurus* and mean annual temperature (MAT) in the early (before 1995) and late (on or after 1995) periods, respectively. Fitted lines and 95% standard errors are shown for each period. **(c)** Comparison between observed and predicted NRT of *Phoenicurus phoenicurus* in the early and late periods, respectively. 1:1 lines are shown in red. **(d)** Distribution of deviation of observed NRT from predicted NRT for each species. Species with deviations significantly different from zero are highlighted in solid.

5 Recovering phenological mismatch with simulated continuous phenology data

5.1 Methods

5.1.1 Simulate phenology during climate change

The two empirical case studies use empirical data on the annual temporal scale, such as the timing of flowering or hatching. Nevertheless, more characteristics in phenology curves, such as the starting time, peaking time, rate of change, and number of life cycles and their possible mismatch, can be examined using continuous data on finer temporal scales. Due to the difficulty to retrieve long-term continuous phenology data, we conducted four sets of simulation experiments to test the power of the proposed theoretical framework and methods in quantifying more nuanced phenological mismatch.

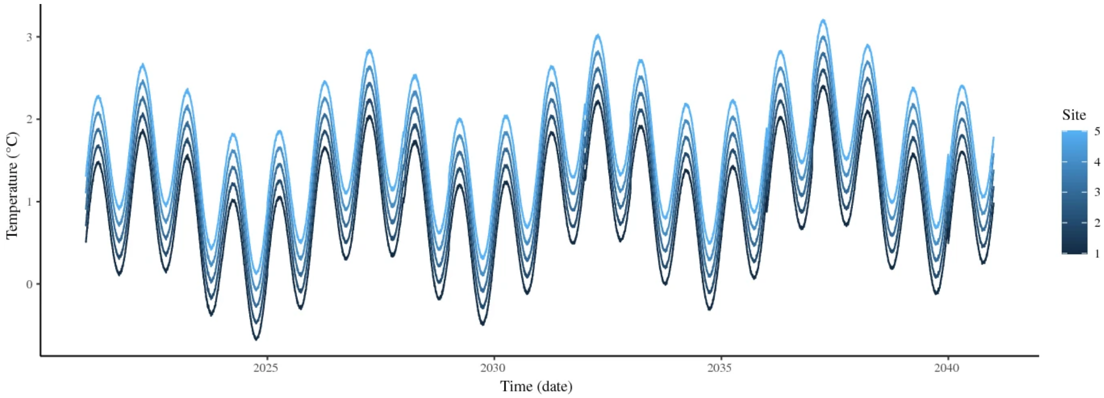

Figure 1-6. Simulated temperature at five sites in a 20-year time period.

We first simulated hypothetical daily temperature curves at five sites in 20 years (January 1, 2021 to December 31, 2040) with an overall increasing linear trend, seasonal cycles, interannual fluctuations (Remsberg and Deaver 2005), and random noise (Eq. 1-7) (Fig. 1-6).

$$
\begin{aligned}
&X_{s,t}=\beta_{0,s}+\beta_1 t+A_1\sin\left(\frac{2\pi}{\lambda_1}\left(t+\phi_1\right)\right)+A_2\sin\left(\frac{2\pi}{\lambda_2}\left(t+\phi_2\right)\right)+\varepsilon_X\\
&\varepsilon_X\sim N\left(0,\sigma_X{}^2\right)\\
&\beta_{0,s}=0.3+0.2s,\ \beta_1=0.0001\\
&A_1=20,\ \lambda_1=365\ or\ 366,\ \phi_1=-\frac{1}{6}\\
&A_2=12,\ \lambda_2=5\times(365\ or\ 366),\ \phi_2=0
\end{aligned}
\qquad [1\text{-}7]
$$

Here $X_{s,t}$ stands for daily temperature, but it can be generalized to represent other environmental variables, t is time (day) since the start of the time period. The five sites are indexed with $s = 1, \ldots, 5$, with increasing temperature from site 1 to 5. β_1 gives an overall increasing trend of 0.0001 °C day^{-1}, which is much faster than the recent observed warming of 0.08 °C decade^{-1} (Huang et al. 2017) in order to demonstrate our approach within a short time period.

We simulated hypothetical daily phenology each year as a double logistic curve, using a parameterization adapted from Elmore et al. (2012) (Eq. 1-8). This curve is commonly used to model ground-based and remotely-sensed leafing phenology (Zhang et al. 2006). A change was made to the original parameterization for this study in order to allow multiple growing seasons in a year (additional parameter m8 for rescaling time depending on the number of life cycles per year).

[1-8]

Here y is a variable that quantifies daily phenology (e.g., vegetation greenness, plankton abundance), d is time in Julian days, and m_1 to m_8 are parameters that determine the shape of the annual development curve (Table 1-1).

$$y = m_1 + \left(m_2 - m_7 d' \right) \left(\frac{1}{1 + \exp\left(\frac{m_3 - d'}{m_4} \right)} - \frac{1}{1 + \exp\left(\frac{m5 - d'}{m_6} \right)} \right) + \varepsilon_y$$

$$d' = \left(d \bmod \frac{365}{m_8} \right) m_8$$

$$\varepsilon_y \sim N\left(0, {\sigma_y}^2 \right)$$

Table 1-1. Meanings of parameters in our adapted double logistic phenology model.

Parameter	Meaning
m_1	Average value in winter
m_2	Difference between summer and winter
m_3	Timing of spring onset
m_4	Slope of curve in spring
m_5	Timing of fall offset
m_6	Slope of curve in fall
m_7	Slope of curve in summer
m_8	Number of life cycles (without rounding)

We extended Eq. 1-7 with hypothetical logistic relationships between the model parameters of year i (m_i) and a certain yearly summary ($X_{\text{summ},i}$) of the environmental variable X (e.g., mean temperature in the first 90 days of a year) (Eq. 1-9).

$$m_i = \frac{L_{\text{upper}} - L_{\text{lower}}}{1 + \exp\left(-k\left(X_{\text{summ},i} - X_0\right)\right)} + L_{\text{lower}} \qquad [1\text{-}9]$$

With Eqs. 1-7 to 1-9, we simulated phenology in 20 years under climate change assuming the same climate-phenology relationship. In order to simulate phenological mismatch, we manually changed the values of m to be different from those generated by Eq. 1-9 in the second half of the time period, representing a change in the climate-phenology relationship. We generated phenology curves using both the unmodified and modified m, representing potential phenology (y_{pot}) and actual phenology (y_{act}), respectively.

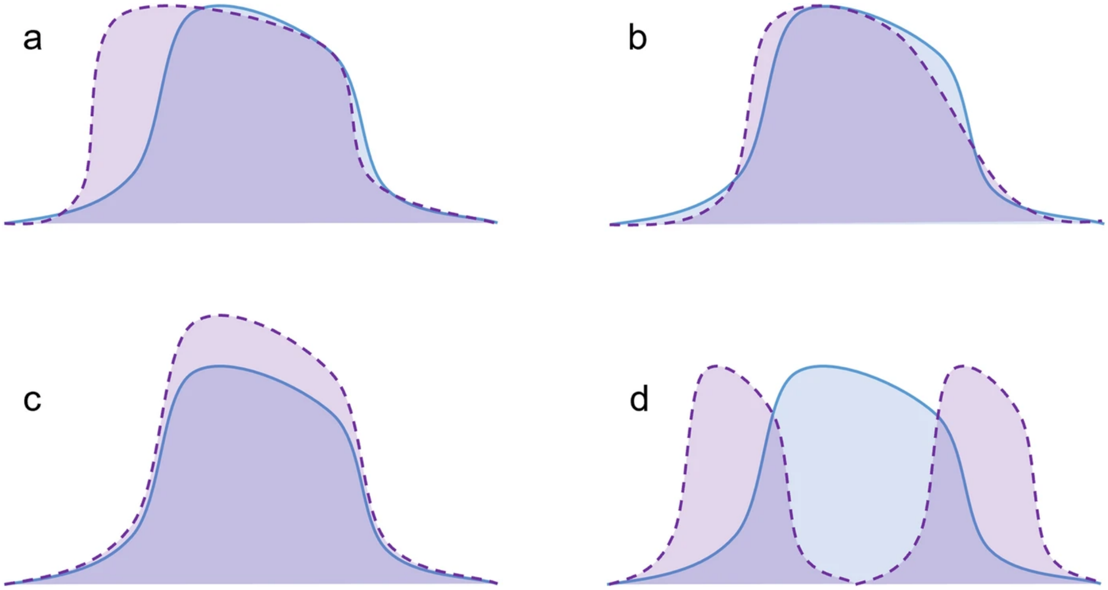

Figure 1-7. Four types of phenological mismatch: **(a)** timing of events, **(b)** pace of development, **(c)** intensity of activities, and **(d)** number of life cycle.

To test the power of our approach in detecting multiple types of phenological mismatch, we manipulated four phenology model parameters: m_3 for mismatch in the timing of events (Fig. 1-7a), m_4 for mismatch in the pace of development (Fig. 1-7b), m_2 for mismatch in the intensity of activities (Fig. 1-7c), and m_8 for mismatch in the number of the life cycle (Fig. 1-7d).

5.1.2 Measure phenological mismatch

We first attempted to model the climate-phenology relationship using data from the first half of the time period. In practice, we do not know the critical environmental cues, the functional relationship between environmental cues and phenology model parameters, and even the correct structure of the phenology model. Commonly used phenology models often assume linear relationships between the timing of events and "critical environmental cues," such as growing degree-days and chilling units (Yun et al. 2017; Hufkens et al. 2018). However, in order to model continuous phenology data and detect mismatch in all parts of the life cycle, a more flexible model is needed.

Therefore, we used a state-of-the-art data-driven approach, empirical dynamic modeling (EDM), to model the nonlinear climate-phenology relationship (Sugihara and May 1990; Sugihara et al. 1994; Munch et al. 2017). According to Takens' theorem (Takens 1981), the time series of each variable contains information about all other variables in the same system. This theorem allows us to reconstruct the behavior of dynamical systems by taking the time-lag coordinates of the single variable as proxies for the other variables. In this study, we build on the Gaussian Process EDM (GP-EDM) algorithm initially applied to forecasting fish population dynamics

(Munch et al. 2017). Operating with minimal assumptions, this approach holds the promise of revealing complex causal relationships from time series and outperforms parametric alternatives in prediction.

The model was set up as follows.

$$
\begin{aligned}
&p(y \mid g, \boldsymbol{X}, \varepsilon) \sim N(g(\boldsymbol{X}'), \varepsilon) \\
&p(g \mid \gamma) \sim GP\left(f, \Sigma_s\right) \\
&p(f \mid \omega) \sim GP\left(h, \Sigma_d\right) \\
&p\left(h \mid \phi, \tau^2\right) \sim GP\left(0, \Sigma_X\right) \\
&\Sigma_{s,ij} = \exp\left(-\frac{\gamma}{2}\left\|s_i - s_j\right\|^2\right)\Sigma_d \\
&\Sigma_{d,ij} = \exp\left(-\frac{\omega}{2}\left\|d_i - d_j\right\|^2\right)\Sigma_X \\
&\Sigma_{X,ij} = \tau^2 \exp\left(-\frac{\phi}{2}\left|\boldsymbol{X}'_i - \boldsymbol{X}'_j\right|^2\right) \\
&\boldsymbol{X}' = \left(\overline{\boldsymbol{X}_{i,-1:14}}, \overline{\boldsymbol{X}_{i,-15:28}}, \ldots, \overline{\boldsymbol{X}_{i,-337:364}}\right) \\
&\\
&\operatorname{logit}\left(\frac{\phi_k - 10^{-50}}{2\pi^2 - 10^{-50}}\right) \sim N\left(0, 0.1\exp\left(-\frac{\left({}^{\delta_k}\!/_{365}\right)^2}{5}\right)\right) \\
&\operatorname{logit}\left(\frac{\varepsilon - 0.001}{0.0615 - 0.001}\right) \sim N(0, 0.5) \\
&\operatorname{logit}\left(\frac{\tau^2 - 0.001}{0.0615 - 0.001}\right) \sim N(0.0625, 50) \\
&\operatorname{logit}\left(\frac{\omega - \left({}^{1}\!/_{30}\right)^2}{1 - \left({}^{1}\!/_{30}\right)^2}\right) \sim N(0, 0.5) \\
&\operatorname{logit}\left(\frac{\gamma - \left({}^{1}\!/_{100}\right)^2}{\left({}^{1}\!/_{0.01}\right)^2 - \left({}^{1}\!/_{100}\right)^2}\right) \sim N(0, 0.5)
\end{aligned}
\tag{1-10}
$$

For each *GP* distribution, we assume that the predicted function values and observed data points (also called basis) have a jointly multivariate normal distribution with a covariance matrix determined by the similarity in predictors. The environmental predictor $\boldsymbol{X}'$ for a specific site and time is a vector of time-lagged $\boldsymbol{X}$, consisting of 26 of 14-day averages in the past 364 days. A baseline functional relationship h between y and $\boldsymbol{X}'$ is a *GP* parameterized by pointwise-prior variance in the function τ^2 and lag-specific length-scale parameters $\phi_{1:26}$. The functional relationship is more similar at closer day of year (the degree of similarity controlled by ω) and at closer sites (the degree of similarity controlled by γ). The process variance is ε. Informed priors were imposed on transformed parameters, with δ_k indicating the temporal distance of the k-th predictor to the data point.

We initialized five sets of random EDM parameters with the prior distribution. With training data in the first ten years, we optimized these five sets of EDM parameters with stochastic backpropagation (Riedmiller and Braun 1993), giving rise to a model ensemble with five members. Using this model ensemble, we predict the phenology in the whole time period, including the potential phenology under climate change in the late period (y'_{pot}). The estimated phenological mismatch (y'_{mis}) was calculated as the difference between observed mismatched phenology and predicted potential phenology in the late period.

$$y'_{\mathrm{mis}} = y_{act} - y'_{\mathrm{pot}} \qquad [1\text{-}11]$$

This estimate was compared to the simulated phenological mismatch (y_{mis}), which was the difference between observed mismatched phenology and simulated potential phenology.

$$y_{\mathrm{mis}} = y_{act} - y_{\mathrm{pot}} \qquad [1\text{-}12]$$

We used normalized RMSE to summarize the overall phenological mismatch. Here we normalized the RMSE to a percentage of the range of training phenology data (i.e., y in the first 10 years). This metric describes how much the observed mismatched phenology deviates from the potential phenology expected with the same climate-phenology relationship.

$$\Delta'_{\text{mis}} = \frac{\sqrt{\frac{1}{N}\sum_{i=1}^{n}\left(y_{\text{act}} - y'_{\text{pot}}\right)^2}}{\max(y) - \min(y)}$$

$$\Delta_{\text{mis}} = \frac{\sqrt{\frac{1}{N}\sum_{i=1}^{n}\left(y_{\text{act}} - y_{\text{pot}}\right)^2}}{\max(y) - \min(y)} \qquad [1\text{-}13]$$

To evaluate the goodness-of-fit of our GP-EDM, we calculated the normalized RMSE between predicted phenology (y'_{pot}) and simulated phenology (y_{pot}). This metric is also the difference between estimated and simulated phenological mismatch.

$$\Delta_{\text{error}} = \frac{\sqrt{\frac{1}{N}\sum_{i=1}^{n}\left(y - y'\right)^2}}{\max(y) - \min(y)} \qquad [1\text{-}14]$$

5.2 Results

5.2.1 Experiment 1: Timing of events

Shifts in the timing of spring phenological events, such as migration and breeding, are widespread in animals. A meta-analysis has shown an overall significant advancement by 2.88 days per decade in the timing of spring events since 1950 (Cohen et al. 2018), although delays have also been found in individual studies

(Cohen et al. 2018). It has been a concern whether these phenological shifts in the timing of events can cause phenological mismatches among interacting species and between the species and the environment (Cohen et al. 2018). In this experiment, we simulated breeding activities, with the timing of spring onset increasing with the mean daily temperature of the last 90 days in the previous year ($T_{-90:-1}$) (Fig. 1-8a). We further assumed that the mismatched phenology has later spring onset compared to the expected timing (Fig. 1-8b).

Our data-driven model accurately characterized how temperature cue controls the timing of spring onset of breeding activities (Fig. 1-8c, d). The estimated mismatch was close to the simulated mismatch and was larger in magnitude compared to the model predictive error (Fig. 1-8e). In the late period, the overall phenological mismatch was estimated to be $\Delta'_{\mathrm{mis}} = 0.108$, comparable to the simulated value $\Delta_{\mathrm{mis}} = 0.130$, and larger than the model predictive error $\Delta_{\mathrm{error}} = 0.0500$.

5.1.2 Experiment 2: Pace of development

In plant phenology literature, there has been a trend to focus on not only discrete events but the continuous development, such as the speed of vegetation leaf development (Clark et al. 2011). Studies using remote sensing have found that spring green-up is accelerated in years with higher temperature (Seyednasrollah et al. 2018) or with faster spring warming (Qiu et al. 2020). The sensitivity of the speed of spring green-up to temperature anomaly appeared to differ among cold, normal, and hot years (Seyednasrollah et al. 2018), but it has not been assessed whether there exists any phenological mismatch. In this experiment, we simulated leaf development characterized by enhanced vegetation index (EVI), with the speed of spring green-up increasing with the mean daily temperature of the first 14 days in the same year ($T_{1:14}$) (Fig. 1-9a). We further assumed that the mismatched phenology has slower spring green-up compared to the expected speed (Fig. 1-9b).

The model accurately characterized how temperature cue controls the pace of spring greenup (Fig. 1-9c, d). The estimated mismatch was close to the simulated mismatch and was larger in magnitude compared to the model predictive error (Fig. 1-9e). In the late period, the overall phenological mismatch was estimated to be $\Delta'_{\mathrm{mis}} = 0.104$, comparable to the simulated value $\Delta_{\mathrm{mis}} = 0.101$, and larger than the model predictive error $\Delta_{\mathrm{error}} = 0.0370$.

5.1.3 Experiment 3: Intensity of activities

On the ecosystem level, it has been shown that there is a trade-off between length of the growing season and peak net primary productivity (NPP) (Duveneck and Thompson 2017). In warmer years, there are often longer growing seasons but lower summer NPP. This trade-off has been well documented but only described with simple statistical models. It is, therefore, hard to determine if changes in productivity track climate change. Using our approach, we consider the continuous change of NPP as phenology on the ecosystem level and quantify the mismatch with temperature. In this experiment, we simulated NPP, with the peak NPP increasing with the mean daily temperature of the first 90 days in the same year ($T_{1:90}$) (Fig. 1-10a). We further assumed that the mismatched phenology has a lower peak NPP compared to the expected intensity (Fig. 1-10b).

The model accurately characterized how temperature cue controls the peak NPP (Fig. 1-10c, d). The estimated mismatch was close to the simulated mismatch and was larger in magnitude compared to the model predictive error (Fig. 1-10e). In the late period, the overall phenological mismatch was estimated to be $\Delta'_{\text{mis}} = 0.0857$, comparable to the simulated value $\Delta_{\text{mis}} = 0.0740$, and larger than the model predictive error $\Delta_{\text{error}} = 0.0409$.

5.1.4 Experiment 4: Life history

Climate change can cause more complex changes in phenology, such as a change in life history. Several insect taxa, such as Lepidoptera species and bark beetles, have been found to complete more generations per year over time (from univoltine to bivoltine or multivoltine life cycles). These changes have been attributed to longer and warmer growing seasons (Forrest 2016). Many of these changes are economically important, especially when the insects are pests or parasites (Jönsson et al. 2009). Previous studies have taken a phenological perspective to study the synchrony between plants, pests, and parasites, leading to diverse findings on phenological mismatch (Senior et al. 2020). Nevertheless, it has rarely been assessed how changes in life history induce phenological mismatch. In this experiment, we simulated insect abundance, with the number of life cycles (without rounding) increasing with the mean daily temperature of all days in the same year ($T_{1:365}$) (Fig. 1-11a). We further assumed that the mismatched phenology has a lower number of life cycles compared to the expected intensity (Fig. 1-11b).

The data-driven nonlinear model relatively accurately characterized how increasing temperature accelerates the pace of development thus increasing the number of life cycles (Fig. 1-11c, d). The estimated mismatch was close to the simulated mismatch, and was larger in magnitude compared to the model predictive error (Fig. 1-11e). In the late period, the overall phenological mismatch was estimated to be $\Delta'_{mis} = 0.136$, comparable to the simulated value $\Delta_{mis} = 0.172$, and larger than the model predictive error $\Delta_{error} = 0.0831$.

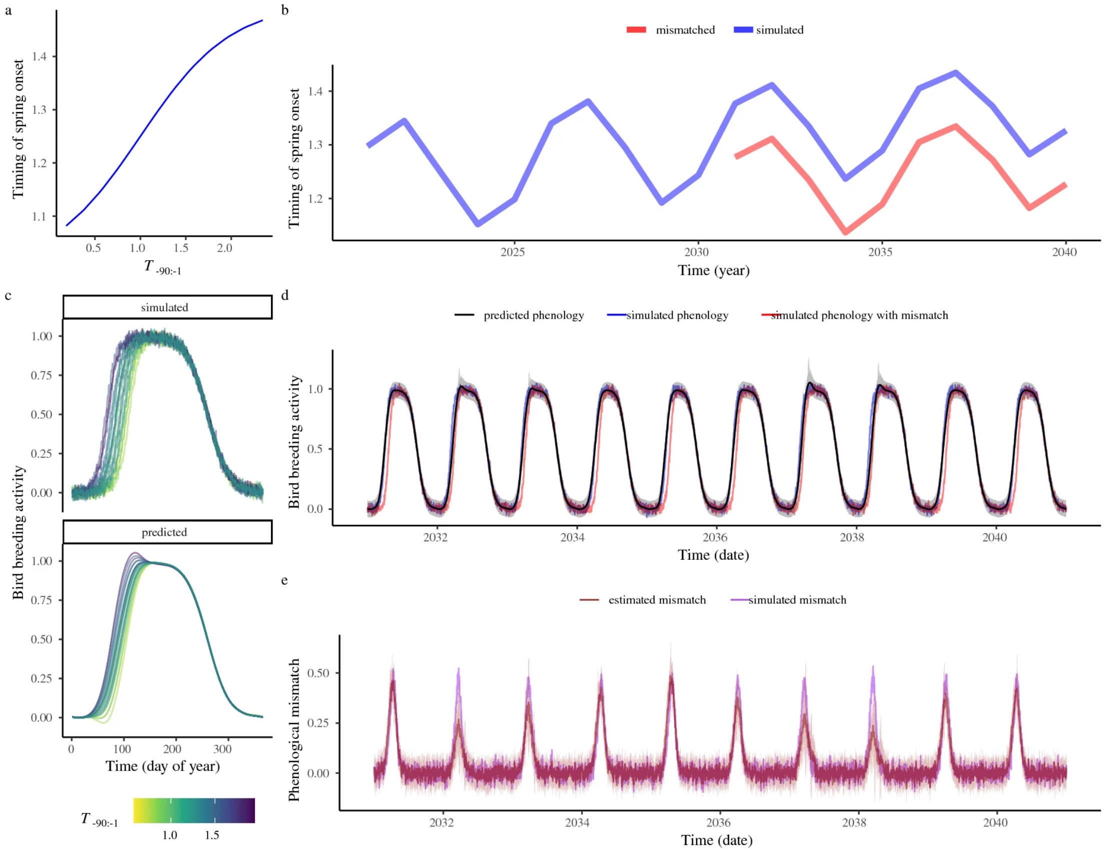

Figure 1-8. Measuring phenological mismatch in the timing of events. **(a)** Functional relationship between the timing of spring onset (m_3) and the mean daily temperature of the last 90 days in the previous year ($T_{-90:-1}$). **(b)** Simulated and mismatched timing of spring onset (m_3). **(c)** The influence of mean daily temperature of the last 90 days in the previous year ($T_{-90:-1}$) on the simulated and model-predicted breeding activity in a year. **(d)** Time series of simulated breeding activity (blue), mismatched breeding activity (red), and predicted breeding activity (black). **(e)** Simulated phenological mismatch (purple) and estimated phenological mismatch (dark red). The ribbons around predicted phenology in (d) and estimated mismatch in (e) indicate estimated 95% confidence intervals.

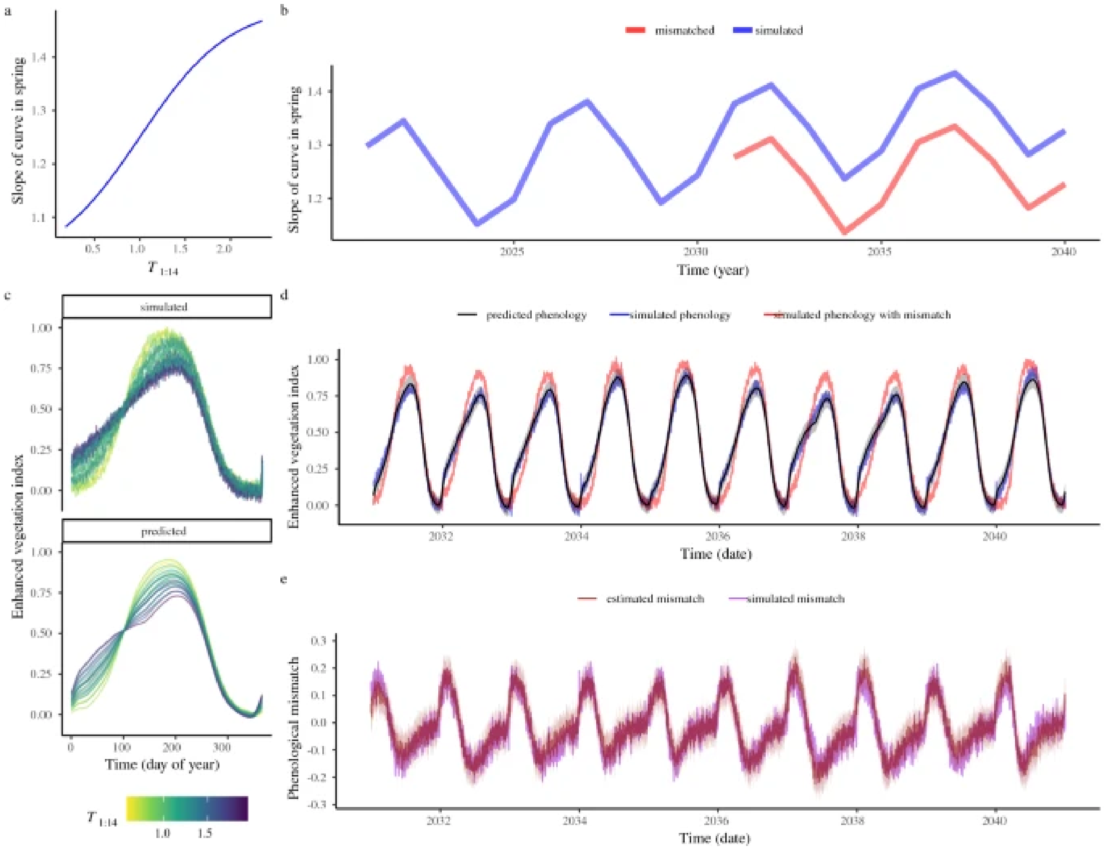

Figure 1-9. Measuring phenological mismatch in the pace of development. **(a)** Functional relationship between the slope of curve in spring (m_4) and the mean daily temperature of the first 14 days in the same year ($T_{1:14}$). **(b)** Simulated and mismatched slope of curve in spring (m_4). **(c)** The influence of mean daily temperature of the first 14 days in the same year ($T_{1:14}$) on the simulated and model-predicted EVI in a year. **(d)** Time series of simulated EVI (blue), mismatched EVI (red), and predicted EVI (black). **(e)** Simulated phenological mismatch (purple) and estimated phenological mismatch (dark red). The ribbons around predicted phenology in (d) and estimated mismatch in (e) indicate estimated 95% confidence intervals.

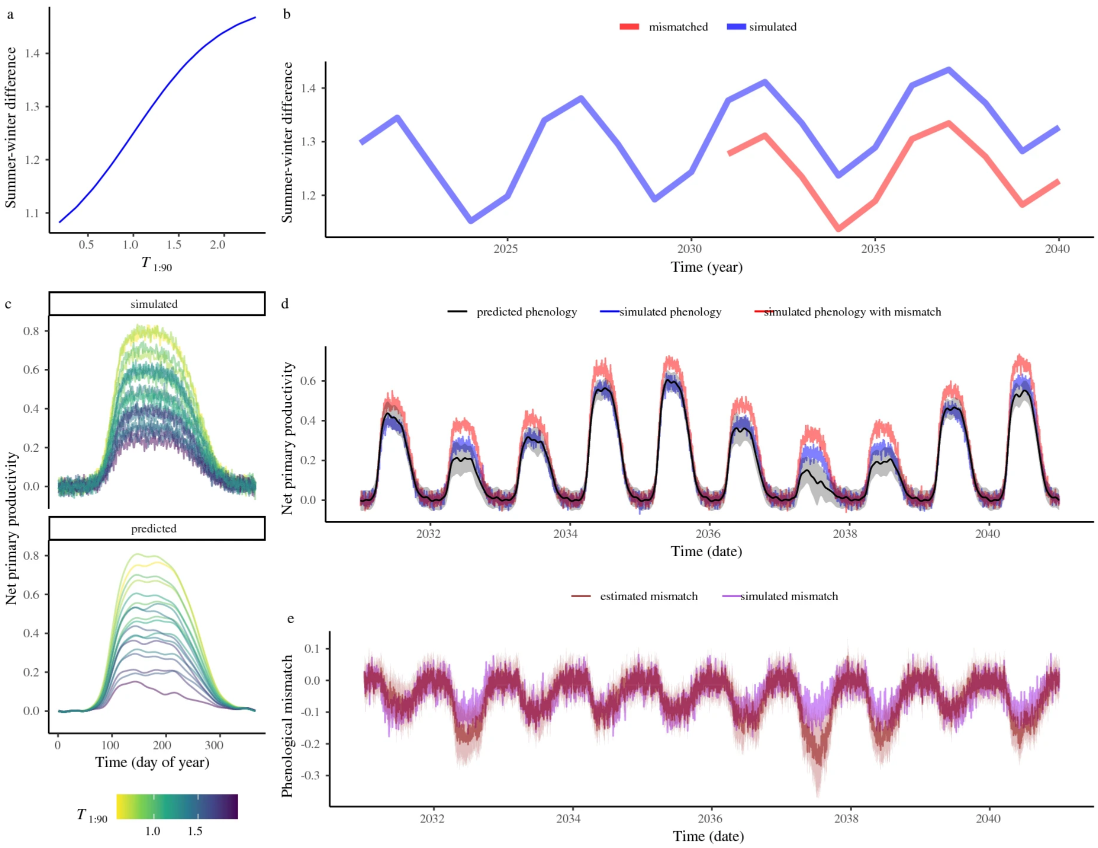

Figure 1-10. Measuring phenological mismatch in the intensity of activities. **(a)** Functional relationship between the difference between summer and winter (m_2) and the mean daily temperature of the first 90 days in the same year ($T_{1:90}$). **(b)** Simulated and mismatched difference between summer and winter (m_2). **(c)** The influence of mean daily temperature of the first 90 days in the same year ($T_{1:90}$) on the simulated and model-predicted NPP in a year. **(d)** Time series of simulated NPP (blue), mismatched NPP (red), and predicted NPP (black). **(e)** Simulated phenological mismatch (purple) and estimated phenological mismatch (dark red). The ribbons around predicted phenology in (d) and estimated mismatch in (e) indicate estimated 95% confidence intervals.

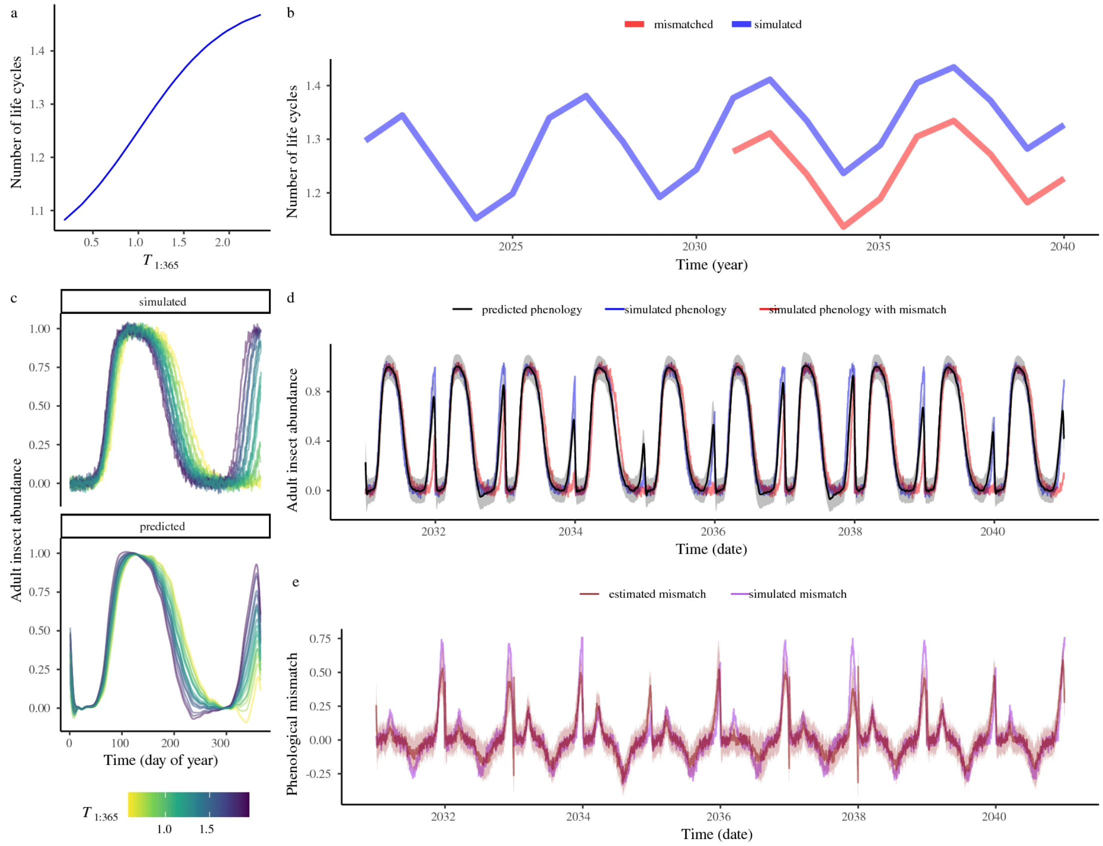

Figure 1-11. Measuring phenological mismatch in life history. **(a)** Functional relationship between the number of life cycles (without rounding) (m_8) and the mean daily temperature of all days in the same year ($T_{1:365}$). **(b)** Simulated and mismatched number of life cycles (without rounding) (m_8). **(c)** The influence of mean daily temperature of all days in the same year ($T_{1:365}$) on the simulated and model-predicted insect abundance in a year. **(d)** Time series of simulated insect abundance (blue), mismatched insect abundance (red), and predicted insect abundance (black). **(e)** Simulated phenological mismatch (purple) and estimated phenological mismatch (dark red). The ribbons around predicted phenology in (d) and estimated mismatch in (e) indicate estimated 95% confidence intervals.

6 Discussion

In this work, we sought to improve our understanding of phenological mismatch by (1) reviewing and classifying existing methods used to quantify phenological mismatch, (2) proposing a generalizable definition of synchrony and a predictive approach for quantification, and (3) quantifying phenological mismatch on large spatial scales under climate change using empirical and simulated data.

Despite the increasing research on phenological research on large scales, we have not yet seen a study that links phenological mismatch across multiple scales. This may be because the concept of phenological mismatch has been applied differently on different levels of the organization. For example, the population-level definition in the Cushing match-mismatch hypothesis, i.e., any change to the relative timing between the peak of the most energetically demanding period of the consumer and the peak of resource availability (Cushing 1969), can hardly be applied to another level of the organization. Our more general framework and approach may enable future studies that compare or even scale phenological mismatch across scales.

Compared to existing descriptive and model-comparison approaches, our predictive approach has the following advantages. First, we allow very flexible modeling of the baseline phenology-environment coupling, such as linear relationship in the empirical case studies and nonlinear relationship in the simulated case studies. Multivariate models can be used when phenology studied is controlled by complex mechanisms (e.g., grasslands) (Shen et al. 2011). In cases when asynchrony is a historical baseline prior to climate change (Singer and Parmesan 2010; Visser et al.

2012), models can be designed accordingly to represent increased synchrony as a type of phenological mismatch. Second, the resulting measure of phenological mismatch has the same unit as the phenological data, and can be normalized to a percentage, enabling easy interpretation and comparison across scales. The magnitude of phenological mismatch can therefore be quantitatively compared across scales. Third, we allow the analysis of continuous phenological curves without identifying critical features of phenological time series, making the approach generalizable to diverse study systems. This is particularly useful in systems with weak or cryptic seasonality (e.g., evergreen forests) (Wu et al. 2017; Abernethy et al. 2018), irregular periodicity (e.g., drought-controlled forests) (Killmann and Thong 1995; Borchert 1996), or more than one cycle per year (e.g. crops and insects) (Meza et al. 2008; Seifert and Lobell 2015; Forrest 2016).

Two empirical case studies showcased how the predictive approach can be applied to large spatiotemporal datasets to systematically quantify phenological mismatch. In the eastern US, we found plant flowering phenology to generally match or even outpace the increase in spring temperature from 1895 to 2015. This finding is consistent with a previous finding on the rapid advancement of plant spring phenology outpacing the shift in the spring timing, defined as the timing when temperature increases most rapidly in a year (Ovaskainen et al. 2013). In a continental-scale study using remote sensing data, land surface phenology also outpaced changes in mean annual temperature in natural landscapes in the eastern US (Song et al. 2021). These results suggest that plant flowering phenology in many species responds sensitively to warming and may even be mismatched in an unexpected direction. Advancing of spring phenology beyond the extent of warming might expose plants to extreme weather conditions such as frost (Richardson et al. 2018). There are several possible reasons for such outpacing phenological mismatch. First, the late period we defined in this case study (1950–2015) has much overlap with the "global warming hiatus" (Medhaug et al. 2017), such that the advancement in plant phenology may appear to be overcompensating. Second, although plant phenology responds to climate change through both phenotypic plasticity and adaptive evolution, directional selection may be more dominant (Anderson et al. 2012), such that advanced phenology may not respond rapidly to the slowdown of warming. Third, although our case study spanned around 120 years, it is still a limitation that climate change has taken place during the early period that we defined (1895–2014) (Masson-Delmotte 2018). The baseline climate-phenology coupling we inferred from this period may still not represent a status without phenological mismatch. Last, phenology may be more strongly controlled by extreme weather conditions rather than mean temperatures (Crabbe et al. 2016). It is common that phenology shifts to match some climatic conditions but not the others. For example, tree swallows that advanced their egg laying in response to warming expose their offspring to more harsh weather events which reduced food availability (Shipley et al. 2020). Therefore, better mechanistic understanding is needed to identify the most ecologically relevant climate-phenology coupling for the quantification of phenological mismatch.

We focused on phenological mismatch on higher trophic levels in the bird breeding case study. We found a very similar pattern to the plant flowering case study in Finland, where the advancement of bird breeding season slightly but significantly outpaced warming. Although there have been many examples of bird reproductive phenology changing insufficiently in response to changes in climate or plant phenology (Visser et al. 1998; Both and Visser 2001; Gaston et al. 2009; Burger et al. 2012; Clausen and Clausen 2013; Mayor et al. 2017; Descamps et al. 2019; MacKenzie et al. 2019; Merkel et al. 2019), there are considerable variation among species (Dunn and Møller 2014) and study area. In this case study, it is not completely surprising that bird breeding phenology advanced more than expected given climate change, given that bird breeding phenology is often strongly coupled with spring vegetation greenness (La Sorte and Graham 2020), and that Finland land surface phenology seem to be outpacing warming in the last three decades (Song et al. 2021). This finding may be region-specific and therefore does not support the general opinion that lagging phenological mismatch is greater on higher trophic levels. A meta-analysis involving various terrestrial, freshwater, and marine taxa suggests differential phenological change among trophic levels, with secondary consumers having the slowest advancement in timing (Thackeray et al. 2010). The constraint of the phenological shift in higher-level consumers, and thus growing phenological mismatch with their resources, has also been suggested in terrestrial food webs (Both et al. 2009). More long-term datasets on the phenological relationship across trophic levels will help to examine these claims more systematically.

The accuracy of the proposed measure requires reasonable predictive power of the phenology model and is, therefore, sensitive to model structure. The better we can predict potential phenology during climate change, the better we can estimate phenological mismatch. Our experiments with simulated data demonstrated the accuracy of predicting phenological response under climate change and quantifying varying types of phenological mismatch. Nevertheless, the estimated phenological mismatch might be confounded by the loss of predictive skill that is expected during extrapolation, due to the variance in data and imperfect model fitting rather than a true phenological mismatch. Although phenological mismatch was shown to be a lot greater than model predictive error to estimated mismatch in the simulated studies, it is often not possible to assess the true predictive errors in the hypothetical scenario without phenological mismatch in empirical data. It is then helpful to conduct out-of-sample tests with a random subset of the data to understand model performance. It is necessary to interpret the estimated phenological mismatch with care, considering the following caveats.

(1) When high-quality continuous phenology data are not available, there will not be sufficient information to determine the environment-phenology relationship, making it difficult to estimate phenological mismatch based on model predictions.

(2) Without a reasonable model structure for the environment-phenology relationship, the estimate of phenological mismatch can be incorrect and misleading. We here demonstrate that even using a nonlinear data-driven model, the performance when recovering highly complex climate-phenology coupling could still be limited, as shown in the simulation experiment 4 on life history. The GPEDM we used also suffers from limitations of modeling threshold effects or extrapolating to extreme conditions. Therefore, we suggest continuous searching and improvement of predictive models, such as through integrating mechanistic knowledge into data-driven models (Read et al. 2019).

(3) If climate change has driven the environmental conditions out of the historical range, it is difficult to define what phenological response is tracking and what is mismatched with the environment. In our simulation experiments, we apply a space-for-time substitution, using data from sites with temperature differences to inform phenology in a wide range of environmental conditions in history. Alternatively, manipulative experiments might inform the expected behavior under unprecedented conditions.

(4) The estimated phenological mismatch is subjective to the choice of time periods compared. Although it would be ideal to set a baseline for climate-phenology coupling using data prior to anthropogenic climate change (Abram et al. 2016), such data are usually not available. Here we demonstrated our approach in the empirical studies by splitting a long-term dataset into an early and a late period. We need to interpret the estimated

phenological mismatch relative to the time scale of the dataset, acknowledging that a comparison to the pre-industrial conditions may not be fully achieved.

(5) At the current stage, it has not been experimentally or empirically validated if our measure of phenological mismatch is linked to fitness or demographic consequences. Nevertheless, as it can detect several individual types of phenological mismatch that have verified consequences (e.g., in timing of events), we are optimistic that our proposed measure is ecologically meaningful.

Chapter 2. Climate-phenology mismatch in human-dominated landscapes

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Abstract

Plants track changing climate partly by shifting their phenology, the timing of recurring biological events. It is unknown whether these observed phenological shifts are sufficient to keep pace with rapid climate changes. Phenological mismatch, or the desynchronization between the timing of critical phenological events, has long been hypothesized but rarely quantified on a large scale. It is even less clear how human activities have contributed to this emergent phenological mismatch. In this study, we used remote sensing observations to systematically evaluate how plant phenological shifts have kept pace with warming trends at the continental scale. In particular, we developed a metric of spatial mismatch that connects empirical spatiotemporal data to ecological theory using the "velocity of change" approach. In northern mid-to high-latitude regions (between 30–70°N) over the last three decades (1981–2014), we found evidence of a widespread mismatch between land surface phenology and climate where isolines of phenology lag behind or move in the opposite direction to

the isolines of climate. These mismatches were more pronounced in human-dominated landscapes, suggesting a relationship between human activities and the desynchronization of phenology dynamics with climate variations. Results were corroborated with independent ground observations that indicate the mismatch of spring phenology increases with human population density for several plant species. This study reveals the possibility that not even some of the foremost responses in vegetation activity match the pace of recent warming. This systematic analysis of climate-phenology mismatch has important implications for the sustainable management of vegetation in human-dominated landscapes under climate change.

1 Introduction

Phenology, the timing of recurring biological events, is nature's calendar, and changes in vegetation phenology are known to be among the most sensitive responses to ongoing climate change (Parmesan & Yohe, 2003). Evidence clearly shows warming-driven shifts in vegetation phenology at the global scale, such as earlier greenup and later senescence (Laskin et al., 2019; Menzel et al., 2020; W. Zhu et al., 2012). However, changes in phenology may fail to keep pace with warming trends (Duputié et al., 2015), possibly due to limited plasticity (B. A. Richardson et al., 2017), constraints due to photoperiod (Fu, Piao, et al., 2019; Fu, Zhang, et al., 2019), moisture (Peng et al., 2019; Wheeler et al., 2015), and unfulfillment of chilling requirements (Fu et al., 2015). Such climate-phenology seasonal mismatches can reduce individual fitness (A. D. Richardson et al., 2018), constrain species distributions (Morin et al., 2008), and drive biological invasions (Fridley, 2012). There is, however, little consensus on the existence and magnitude of climate-phenology mismatches.

Phenological mismatch, or the desynchronization in the timing of critical biotic and abiotic events, has long been discussed. The Cushing match-mismatch hypothesis (Cushing, 1969), for example, postulates that any change to the relative timing between consumers' activity and resource availability will lead to a "mismatch." Though this concept has mainly been applied to interacting species, we use it here in a broader sense to describe plant activity under favorable climatic conditions (Ovaskainen et al., 2013; Soolanayakanahally et al., 2013). Despite abundant evidence of shifting phenology and the sensitivity of phenology to climate change, the quantification of phenological mismatch remains challenging, partly due to the lack of a baseline from before the onset of anthropogenically driven climate change (Kharouba & Wolkovich, 2020). Such disconnects between ecological data and theory hinder our ability to understand the mechanisms and consequences of climate change at a large scale.

Human activities, particularly active management of croplands, pastures, and timberlands, have drastically changed land surface phenology. Possible pathways include modifying environmental conditions such as moisture and temperature (Kariyeva & van Leeuwen, 2012; Roetzer et al., 2000), changing vegetation cover and species composition (Buyantuyev & Wu, 2012), or altering natural disturbance regimes (Andela et al., 2017). However, it is unclear how these factors have been influencing emergent climate-phenology mismatches. On the one hand, in urban heat islands (Li et al., 2017) and adaptively managed agricultural systems (Bai et al., 2019), earlier greenup and subsequent longer growing seasons with time might promote synchrony between phenological shifts and warming. On the other hand, political or economic factors might lead to a decoupling between phenology and climate, such as the de-intensification of agricultural irrigation during wars (de Beurs & Henebry, 2008) and the change in crop types in response to policies and markets

(Zhang et al., 2019). Despite the contributions of these local studies, we do not yet know how these results can be generalized to larger extents.

To systematically quantify long-term climate-phenology mismatch in both human-dominated (possessing human residence and intense land use) and natural landscapes at global scales, we first seek to establish a generalizable definition of the concept. We define phenological mismatch as the deviation between actual phenological response and expected phenological response based on historical phenology-environment relationships. This definition is deeply rooted in ecology. For example, Reed et al. (2013) defined the optimal egg-laying date of great tits to be 30 days before the date of peak food abundance. Their breeding phenology is expected to shift at the same pace as the timing of food abundance, but the actual breeding may be earlier or later, therefore potentially lowering the fitness of these birds. There can be multiple ways to quantify phenological response under this general definition. In this study, we develop a specific metric of spatial mismatch: the deviance between actual and expected movement in phenological isolines, where the expected movement corresponds to the movement of climatic isolines. The pace of geographic movement along the isoline over time (Loarie et al., 2009) is established as the velocity of change (Burrows et al., 2011) (Fig. 2-1). Numerous studies have used this approach, to assess the pace of climate change (Burrows et al., 2011; Loarie et al., 2009), and to compare climate change with changes in species distribution (Burrows et al., 2011; Hamann et al., 2015; Lenoir et al., 2020) and productivity (Huang et al., 2017). This approach has also been used to compare changes in phenological and meteorological variables at an annual scale (O'Leary, 2020).

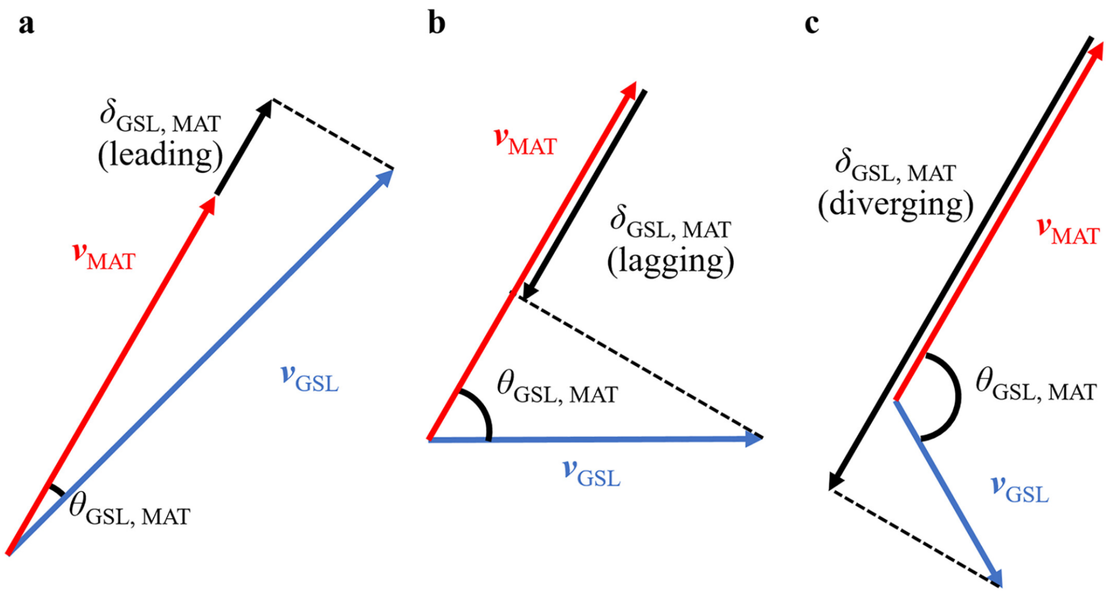

Figure 2-1. Schematic diagram showing three scenarios of climate tracking and the corresponding climate-phenology metrics. The velocity of mean annual temperature change, $\boldsymbol{v}_{\text{MAT}}$ (km yr^{-1}) and the velocity of growing season length change, $\boldsymbol{v}_{\text{GSL}}$ (km yr^{-1}) at a location were compared using the difference in two velocity directions, $\theta_{\text{GSL, MAT}}$ (°) and the spatial mismatch, $\delta_{\text{GSL,MAT}}$ (km yr^{-1}). **(a)** A positive $\delta_{\text{GSL,MAT}}$ and a positive $\theta_{\text{GSL, MAT}}$ characterizes a leading mismatch; **(b)** A negative $\delta_{\text{GSL,MAT}}$ and a positive $\theta_{\text{GSL, MAT}}$ characterizes a lagging mismatch; **(c)** A negative $\delta_{\text{GSL,MAT}}$ and a negative $\theta_{\text{GSL, MAT}}$ characterizes a diverging mismatch.

Our generalized definition and quantification method enable large-scale measurement of phenological mismatch using remote sensing data. Remote sensing data offers an excellent opportunity to examine the climate-phenology mismatch due to the extensive temporal and spatial coverage. We used a temporally and spatially contiguous remotely sensed land surface phenology (LSP) data set (VIPPHEN EVI2 Phenology data product v. 4.1) (Didan & Barreto, 2016) in this study. We first tested the hypothesis that shifts in vegetation phenology, characterized by remotely sensed LSP, have not been keeping pace with warming trends in mid-to high-latitudes in the Northern Hemisphere (between 30–70°N) over the past three decades (1981–2014). We further tested the hypothesis that climate-phenology mismatch is more pronounced in anthropogenically impacted regions than in natural landscapes. We acknowledge that remote sensing data are limited in their spatial resolution and the ability to reflect ground-observed phenological events. Therefore, in addition, we employed independent ground observations to analyze the possible anthropogenic influence on the mismatch of spring phenology in several plant species. We aim to provide insights on the effect of anthropogenic activity on climate-phenology mismatch at a global scale under ongoing unprecedented rates of climate and land use change. Resolving these questions hold the potential to inform future sustainable management of croplands, pastures, and timberlands.

2 Materials and methods

2.1 Remote sensing analyses

2.1.1 Land surface phenology, climate, land use, and human population density data

For latitudes between 30–70°N, we quantified the velocities of mean annual temperature (MAT) and growing season length (GSL), defined by the period between greenup and senescence, from 1981 to 2014. We chose to focus on the mid-to high-latitude Northern Hemisphere because of its high vegetation coverage and strong seasonality (X. Wang et al., 2019). In this area, GSL is highly correlated to MAT, suggesting a strong temperature control on phenology. We retrieved near-surface temperature data from 1981 to 2014 using the Climate Research Unit (CRU) time-series (TS) data set v. 4.03 (Harris et al., 2014). This data set reports monthly climatic variables from 1901 to 2018 at a 0.5-degree resolution, interpolated from meteorological station observations. We calculated the mean annual temperature (MAT) by taking the mean of near-surface temperatures of all months each year. We employed the VIPPHEN EVI2 Phenology data product v. 4.1 (Didan & Barreto, 2016) to obtain the satellite-observed LSP, represented by growing season length (GSL) in the present study. This data product provides reliable phenological metrics at a 0.05-degree resolution, derived from modified Enhanced Vegetation Index 2 (EVI2) using an adapted Half-Maximum Vegetation Index algorithm (White et al., 2009). EVI2 was calculated using surface reflectance data from the Advanced Very High Resolution Radiometer (AVHRR) (1981–1999) and Moderate Resolution

Imaging Spectroradiometer (MODIS)/Terra MOD09 (2000–2014). Phenological data were subjected to two rounds of filtering in order to focus on areas with a single growing season and good data quality. Specifically, areas with multiple growing seasons (information provided in the phenology data product) were excluded as its phenology is often controlled by precipitation, rather than temperature, patterns (Ralhan et al., 1985). To eliminate the effects of data uncertainty, for each year only pixels with a single growing season and “excellent,” “good,” or “acceptable” data reliability were used, determined by the “number of seasons” and “data quality” fields in the data product. The raw LSP data were aggregated to a 0.5-degree resolution to match the spatial scale of the movement of temperature and phenology isolines over 34 years.

To understand the relationship between anthropogenic factors and phenological responses, we used two datasets to qualitatively and quantitatively characterize anthropogenic land use. Qualitatively, the Anthromes v. 2 data set (Ellis et al., 2010) classifies land use for the year 2000. Quantitatively, we retrieved human population density for the year 2000 at a 0.5-degree resolution from the Gridded Population of the World data set v. 4 (Center For International Earth Science Information Network-CIESIN-Columbia University, 2018) as a proxy for anthropogenic activities. Since we focus on the Northern Hemisphere, we cropped all global datasets to the latitudes between 30°N and 70°N.

2.1.2 Climate and phenology velocities

We quantified the velocity of MAT change, $\boldsymbol{v}_{\mathrm{MAT}}$ (km yr^{-1}), and the velocity of GSL change, $\boldsymbol{v}_{\mathrm{GSL}}$ (km yr^{-1}) by estimating the speed and direction of isoline movement, which implicitly makes use of a space-for-time substitution. Based on these assumptions, we calculated instantaneous local velocities from the ratio of temporal (°C yr^{-1} or day yr^{-1}) gradients in the 34 years, and spatial gradients (°C km^{-1} or day km^{-1}) in grids of 0.5 for each variable (Burrows et al., 2011) using the *VoCC* package in *R* (Molinos et al., 2019):

$$\boldsymbol{v}_{\mathrm{MAT}} = \frac{\mathrm{d}y}{\mathrm{d}t} = \frac{\frac{\mathrm{d}MAT}{\mathrm{d}t}}{\frac{\mathrm{d}MAT}{\mathrm{d}y}}$$

$$\boldsymbol{v}_{\mathrm{GSL}} = \frac{\mathrm{d}y}{\mathrm{d}t} = \frac{\frac{\mathrm{d}GSL}{\mathrm{d}t}}{\frac{\mathrm{d}GSL}{\mathrm{d}y}} \qquad [2\text{-}1]$$

where t is time and y is space (distance with direction). The temporal gradient ($\mathrm{d}MAT/\mathrm{d}t$ or $\mathrm{d}GSL/\mathrm{d}t$) is the slope coefficient in the linear regression of the variable of interest with time. Pixels with fewer than 10 out of the 34 years of valid observations in either the MAT or GSL products were removed from analyses. The spatial gradient ($\mathrm{d}MAT/\mathrm{d}y$ or $\mathrm{d}GSL/\mathrm{d}y$) is the vector sum of the N–S and E–W gradients in a 3 × 3 pixel neighborhood, pointing in the direction of the decreasing variable of interest. When the temporal gradient is positive, the direction of the velocity (θ_{GSL} or θ_{MAT}) is in the same direction as that of the spatial gradient. When the temporal gradient is negative, the direction of velocity is the opposite of that of the spatial gradient. As velocity metrics are sensitive to spatial gradients, we acknowledge that high spatial heterogeneity in phenology may lead to slightly under-estimated $\boldsymbol{v}_{\mathrm{GSL}}$ values, especially in human-dominated landscapes.

To quantify how well the velocity of phenology change keeps pace with the velocity of temperature change, we took the directions of both vectors into account (Ordonez et al., 2016) and calculated two scalar metrics: the directional difference and relative pacing from two vector measures, $\boldsymbol{v}_{\mathrm{GSL}}$ and $\boldsymbol{v}_{\mathrm{MAT}}$ (Fig. 2-1). First, we calculated the absolute difference in the directions of velocities, $\theta_{\mathrm{GSL,MAT}}$, using

$$\theta_{\mathrm{GSL,MAT}} = \min\left\{ \left|\theta_{GSL} - \theta_{MAT}\right|, 360 - \left|\theta_{GSL} - \theta_{\mathrm{MAT}}\right| \right\} \qquad [2\text{-}2]$$

where θ_{GSL} and θ_{MAT} are the directions of $\boldsymbol{v}_{\mathrm{MAT}}$ and $\boldsymbol{v}_{\mathrm{GSL}}$, respectively, measured in degrees starting from the north. $\theta_{\mathrm{GSL,\,MAT}}$ ranged from 0° to 180°, with smaller $\theta_{\mathrm{GSL,MAT}}$ implying that GSL and MAT isolines move in more closely aligned directions. This metric describes how GSL and MAT are coupled in space, such that a $\theta_{\mathrm{GSL,MAT}}$ smaller than 90° represents a positive alignment and a $\theta_{\mathrm{GSL,MAT}}$ larger than 90° represents a negative alignment.

Second, we evaluated the pacing of phenology relative to climate, $\delta_{\mathrm{GSL,MAT}}$ by projecting $\boldsymbol{v}_{\mathrm{GSL}}$ onto $\boldsymbol{v}_{\mathrm{MAT}}$ and subtracting by $\boldsymbol{v}_{\mathrm{MAT}}$ (Fig. 2-1), using

$$\delta_{\mathrm{GSL,MAT}} = \left|\boldsymbol{v}_{\mathrm{GSL}}\right| \times \cos\theta_{\mathrm{GSL,MAT}} - \left|\boldsymbol{v}_{\mathrm{MAT}}\right| \qquad [2\text{-}3]$$

In addition to GSL, we also quantified the velocity of phenology change using the start of season (SOS) and end of season (EOS). Instead of MAT, we compared these velocities to the velocities of change in mean spring temperature (MST) (March to May) and mean fall temperature (MFT) (September to November), respectively.

2.1.3 Effects of Anthropogenic Land Use

We assessed the effects of anthropogenic activities on climate-phenology mismatch using two approaches. First, we compared four climate-phenology metrics ($\boldsymbol{v}_{\mathrm{MAT}}$, $\boldsymbol{v}_{\mathrm{GSL}}$, $\theta_{\mathrm{GSL,MAT}}$, and $\delta_{\mathrm{GSL,MAT}}$) between different land-use types based on the Anthromes data set (Ellis et al., 2010). The data set broadly classifies our study area into “dense settlements,” “villages,” “croplands,” “rangelands,” “semi-natural,” and “wildlands,” with the first five types modified by anthropogenic activities to different extents. The “villages” and “dense settlements” categories were then consolidated into a larger land-use type that we call “settlements” and subsequently removed from the analysis (only 5% of all pixels analyzed) as these patches are usually on a smaller scale than the spatial resolution of this analysis (0.5 degree). We ranked the other four land-use types according to the median value of the climate-phenology metrics in each area. We compared the climate-phenology metrics in areas with anthropogenic land use to those in “wildlands” using one-way ANOVA with post-hoc Tukey HSD tests.

Second, we modeled how four climate-phenology metrics are correlated to both population density and latitude, in order to detect the underlying anthropogenic gradient in these metrics, while controlling for the latitudinal gradient. We log-transformed the velocities of change and logit-transformed the difference in directions, as an angle, to better account for their distributions and meet the normality assumption of linear regression:

$$v'_{\mathrm{MAT}} = \log(v_{\mathrm{MAT}})$$
$$v'_{\mathrm{GSL}} = \log(v_{\mathrm{GSL}})$$
$$\theta'_{\mathrm{GSL,\,MAT}} = \log\left(\frac{\theta_{\mathrm{GSL,\,MAT}}}{180 - \theta_{\mathrm{GSL,\,MAT}}}\right) \qquad [2\text{-}4]$$

All datasets were upscaled to a 5-degree resolution by taking the median value of all pixels, in order to reduce noise at the finer scale and focus on large-scale patterns in the regression analyses. The upscaled raster was then reprojected to an azimuthal equidistant projection centering at the north pole, so that the Euclidean distances between pixels could be calculated more accurately.

We adopted a Bayesian approach because of its flexibility in incorporating information on spatial structures empirically determined from the data to infer the effects of population density and latitude. Latitude (related to photoperiod) is a potential confounding factor as it may be correlated to the rate of warming, rate of phenological shift, and population density. Although phenological shift is strongly dependent on topography (Cornelius et al., 2013; Delpierre et al., 2009; Elmore et al., 2012; Hwang et al., 2011, 2014; A. D. Richardson et al., 2006; Vitasse et al., 2011), we do not include topographical variables like elevation as predictors, as they are implicitly accounted for in temperature. The elevational shift in phenological variables is expected to track that of temperature variables, as is predicted by Hopkin's law (Hopkins, 1918). Therefore elevational shifts are reflected in our calculation of horizontal velocities of change, such as environmental lapse rates. We fitted Bayesian spatial linear regression models with exponential spatial correlation using the spBayes package in R (Finley et al., 2013):

$$
\begin{aligned}
& y(s) = \beta_0 + \beta_1 X_1(s) + \beta_2 X_2(s) + \omega(s) + \varepsilon \\
& \omega(s) \sim N(0, K) \quad K_{ij} = \sigma^2 \exp\left(-\varphi \left\| s_i - s_j \right\|\right) \\
& \varepsilon \sim N\left(0, \tau^2\right) \\
& \begin{pmatrix} \beta_0 \\ \beta_1 \\ \beta_3 \end{pmatrix} \sim MVN\left[\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} 100 & 0 & 0 \\ 0 & 100 & 0 \\ 0 & 0 & 100 \end{pmatrix}\right] \\
& \sigma^2 \sim IG(2, 2) \\
& \varphi \sim U\left(-\frac{\log(0.05)}{100d}, -\frac{\log(0.05)}{0.01d}\right) \\
& \tau^2 \sim IG(2, 0.1)
\end{aligned}
\qquad [2\text{-}5]
$$

where the response variable y is $\boldsymbol{v}'_{\mathrm{MAT}}$, $\boldsymbol{v}'_{\mathrm{GSL}}$, $\theta'_{\mathrm{GSL,MAT}}$, or $\delta_{\mathrm{GSL,MAT}}$, the covariates X_1 and X_2 are human population density (on a logarithmic scale) and latitude, β_0, β_1, and β_2 are the coefficients for intercepts and covariates, $\boldsymbol{s}$ is the location of observation, and ε is the random error. The spatial random effect, ω, is determined by the spatial variance parameter σ^2, the residual error variance τ^2, the spatial decay parameter φ, and the Euclidean distance between locations i and j. We empirically determined the general form of the spatial correlation structure from the semivariograms of the residuals of the corresponding nonspatial linear regression models. We empirically estimated the effective range of spatial dependence, d (i.e., the distance at which the correlation drops to 0.05), by fitting an exponential function to the semivariograms (Finley et al., 2015). We set the interval of φ that corresponds to a wide interval of possible d. For all models, we used common choices of diffuse multivariate normal

(*MVN*) priors on $\boldsymbol{\beta}$, diffuse inverse gamma (*IG*) priors on τ^2 and σ^2, and diffuse uniform (*U*) priors on φ (Finley et al., 2013).

We ran the Markov chain Monte Carlo (MCMC) sampler for 10,000 samples (Finley et al., 2013), discarding the first 5,000 samples as burn-in. We verified convergence and stability of estimates by visual inspection of the MCMC chains, their autocorrelation and partial autocorrelation functions, and summarized the medians and 95% credible intervals (CI) of $\boldsymbol{\beta}$. For the three models with transformed response variables, the $\boldsymbol{v}_{\mathrm{MAT}}$, $\boldsymbol{v}_{\mathrm{GSL}}$, or $\theta_{\mathrm{GSL,MAT}}/(180-\theta_{\mathrm{GSL,MAT}})$ change by β_1 percent for every percent increase in population density. We back-transformed and then interpreted the coefficients.

2.2 Ground observation analyses

2.2.1 Ground-observed phenology data

In addition to the remote sensing analyses, we used the USA National Phenology Network (USA-NPN) database (Elmendorf et al., 2016) to inform the climate-phenology mismatch on the ground level. In particular, we retrieved the site-specific onset of leaf-out activities, described as “breaking leaf buds,” “breaking needle buds,” “budburst,” “emergence above ground,” “emerging leaves,” “emerging needles,” “first leaf,” or “initial growth,” in the database. We also retrieved the growing degree days, maximum spring temperature, and minimum spring temperature associated with these phenometrics from the USA-NPN database. To control the data quality and to limit the scope of our analysis, we focused on the “calibration” species labeled in the database, which are monitored to provide patterns of plant phenophase responses across the US. We also filtered for species with more than 100 records.

2.2.2 Calculating mismatch and inferring anthropogenic effect

Due to the limited spatiotemporal coverage of ground observations, we were unable to calculate their velocity of change in phenology, and therefore the spatial climate-phenology mismatch. As an alternative, we fitted a climate-phenology model for each species, with the leaf-out day of year as the response, and three temperature variables (growing degree days, maximum spring temperature, and minimum spring temperature) as predictors. The absolute model predictive errors were taken as a measure of climate-phenology mismatch. This alternative method is conceptually consistent with our general definition of climate-phenology mismatch (the deviation between actual and expected phenological response) and hence consistent with the previous velocity method for the remote sensing analyses. Here, the assumption is that with close climate-phenology coupling, there should be a stable functional relationship between climate and phenology, and deviations from this relationship are signs of decoupling. Due to the limited sample size, we adopted a linear model structure and recognized the nonlinear relationships as a potential future research direction.

We strived to make the ground-based and remote sensing analyses as comparable as possible. For the ground observations, we tested the relationship between the prediction error (climate-phenology mismatch) and human population density (on a logarithmic scale) for each species. Latitude was included as a predictor to account for its potential confounding effect. Both designs are similar to Eq. 2-5 in the remote sensing analyses. All calculations and statistical analyses were conducted in *R* v. 3.6.0 (R Core Team., 2019).

3 Results

3.1 Mismatches between velocities of climate and phenology

The isolines of climate and phenology show rapid movement in the study region (Fig. 2-2a, b), with a median velocity of mean annual temperature change ($\boldsymbol{v}_{\mathrm{MAT}}$) of 2.2 km yr^{-1} (95% CI: 0.2, 15.1 km yr^{-1}). There is considerable spatial heterogeneity in $\boldsymbol{v}_{\mathrm{MAT}}$, with higher $\boldsymbol{v}_{\mathrm{MAT}}$ in high-latitude North America and Siberia and low $\boldsymbol{v}_{\mathrm{MAT}}$ in western N. America and E. Asia. The direction of vMAT is northward in the majority (78.3%) of the area, especially at high latitudes. The median velocity of growing season length change ($\boldsymbol{v}_{\mathrm{GSL}}$) is 5.4 km yr^{-1} (95% CI: 0.2, 37.5 km yr^{-1}), which is more than twice that of $\boldsymbol{v}_{\mathrm{MAT}}$. Similar to the spatial pattern observed for $\boldsymbol{v}_{\mathrm{MAT}}$, $\boldsymbol{v}_{\mathrm{GSL}}$ is higher in high-latitude N. America and Siberia, but lower in eastern N. America and E. Asia. The directions of $\boldsymbol{v}_{\mathrm{GSL}}$ are less consistent than those of $\boldsymbol{v}_{\mathrm{MAT}}$, with 61.4% of pixels indicating a northward direction, mainly at high latitudes.

There are wide discrepancies between the directions of $\boldsymbol{v}_{\mathrm{MAT}}$ and $\boldsymbol{v}_{\mathrm{GSL}}$, as measured by $\theta_{\mathrm{GSL,MAT}}$ (Fig. 2-2c), with 34.1% of pixels having a $\theta_{\mathrm{GSL,MAT}}$ greater than 90° and a median $\theta_{\mathrm{GSL,MAT}}$ of 54.9° (95% CI: 1.9, 174.1°). We find smaller $\theta_{\mathrm{GSL,MAT}}$ values at high-latitudes (50°–70°N) than those of mid-latitudes (30°–50°N), with the largest $\theta_{\mathrm{GSL,MAT}}$ values in eastern N. America, Europe, central Asia, and E. Asia. To quantify how well $\boldsymbol{v}_{\mathrm{GSL}}$ kept pace with $\boldsymbol{v}_{\mathrm{MAT}}$, we calculated their spatial mismatch, $\delta_{\mathrm{GSL,MAT}}$ (Fig. 2-2d). A positive $\delta_{\mathrm{GSL,MAT}}$ corresponds to $\boldsymbol{v}_{\mathrm{GSL}}$ leading ahead of $\boldsymbol{v}_{\mathrm{MAT}}$ (a leading mismatch), while a negative value corresponds to $\boldsymbol{v}_{\mathrm{GSL}}$ lagging behind (a lagging mismatch) or being in the opposite direction (a diverging mismatch) (Fig. 2-1). Overall, the combination of high $\boldsymbol{v}_{\mathrm{MAT}}$, low $\boldsymbol{v}_{\mathrm{GSL}}$, and large $\theta_{\mathrm{GSL,MAT}}$ leads to a $\delta_{\mathrm{GSL,MAT}}$ of −0.7 km yr^{-1} (95% CI: −24.2, 18.1 km yr^{-1}), with negative $\delta_{\mathrm{GSL,MAT}}$ values in 55.4% of the study area. The two velocities are similar between 50°–70°N, but $\delta_{\mathrm{GSL,MAT}}$ is highly negative between 30°–50°N. Highly negative $\delta_{\mathrm{GSL,MAT}}$ is observed in Europe and part of N. America, but $\delta_{\mathrm{GSL,MAT}}$ is near-zero in E. Asia. Finally, some areas of Siberia and high-latitude N. America possess a positive $\delta_{\mathrm{GSL,MAT}}$. The velocities of change and spatial mismatches calculated with remotely sensed phenology data are comparable to those calculated with field data in the order of magnitude.

Analyses of the climate tracking of spring and fall phenology offer similar, yet more nuanced understandings of climate-phenology coupling (Fig. 2-2). The velocity of start of season (SOS), $\boldsymbol{v}_{\mathrm{SOS}}$ (median 4.1 km yr^{-1}, 95% CI: 0.2, 29.7 km yr^{-1}) greatly exceeded the velocity of MST, $\boldsymbol{v}_{\mathrm{MST}}$ (median 2.7 km yr^{-1}, 95% CI: 0.2, 19.5 km yr^{-1}), but there were large $\theta_{\mathrm{SOS,MST}}$ (median 65.4°, 95% CI: 2.3°, 176.0°) and $\delta_{\mathrm{SOS,MST}}$ (median −2.1 km yr^{-1}, 95% CI: −25.1, 12.4 km yr^{-1}). Similarly, the velocity of end of season (EOS), $\boldsymbol{v}_{\mathrm{EOS}}$ (median 6.0 km yr^{-1}, 95% CI: 0.2, 48.7 km yr^{-1}) greatly exceeded the velocity of mean fall temperature (MFT), $\boldsymbol{v}_{\mathrm{MFT}}$ (median 3.6 km yr^{-1}, 95% CI: 0.4, 21.4 km yr^{-1}), but there were large $\theta_{\mathrm{EOS,MFT}}$ (median 59.1°, 95% CI: 2.0°, 174.4°) and $\delta_{\mathrm{EOS,MFT}}$ (median −1.8 km yr^{-1}, 95% CI: −33.6, 20.6 km yr^{-1}).

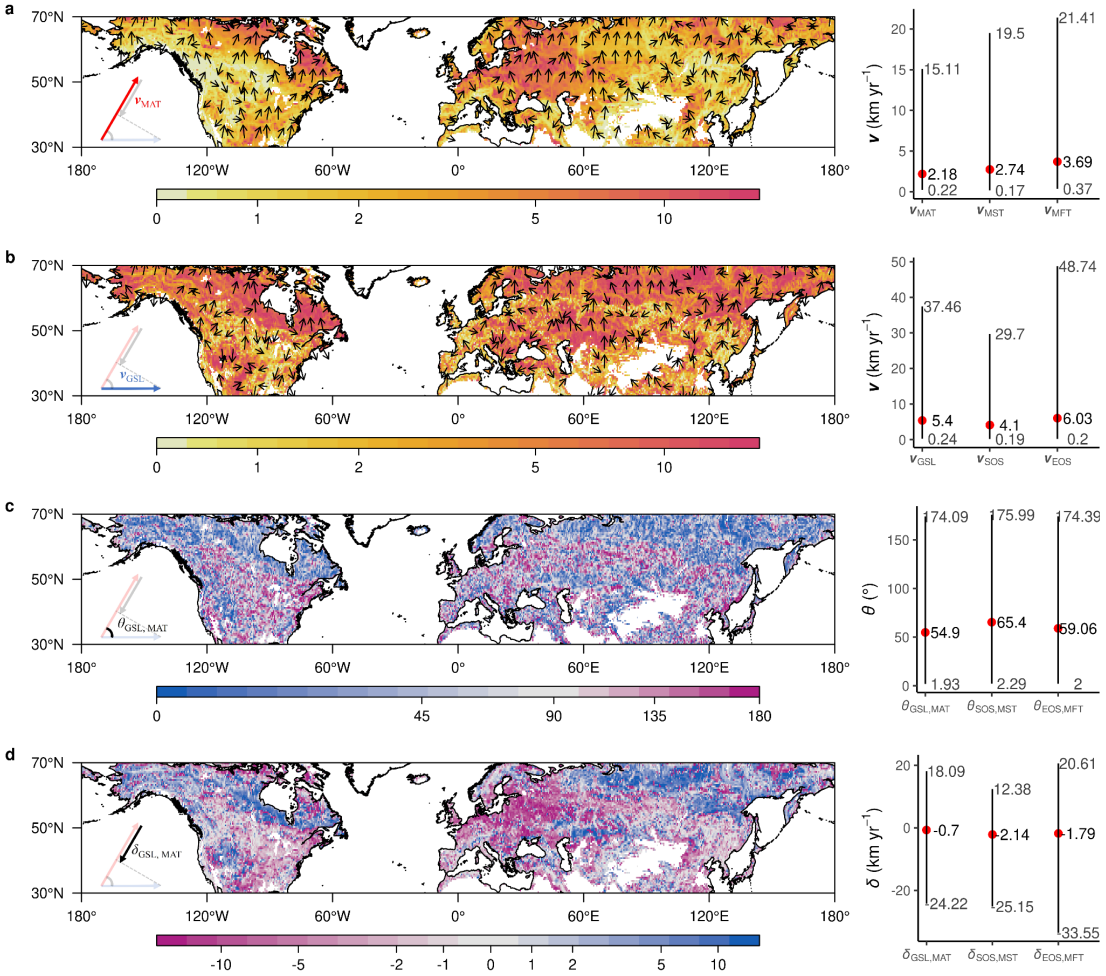

Figure 2-2. Spatial patterns of four climate-phenology metrics. **(a)** Velocity of mean annual temperature change, $\boldsymbol{v}_{\mathrm{MAT}}$ (km yr^{-1}). **(b)** Velocity of growing season length change, $\boldsymbol{v}_{\mathrm{GSL}}$ (km yr^{-1}). **(c)** Difference in direction, $\theta_{\mathrm{GSL,MAT}}$ (°). **(d)** Pace of phenology change relative to climate, $\delta_{\mathrm{GSL,MAT}}$ (km yr^{-1}). Color bars show the magnitude of each metric, with cutpoints chosen to divide the data into quantiles. For (a) and (b), the cutpoints were chosen based on pooled $\boldsymbol{v}_{\mathrm{MAT}}$ and v_{GSL}, so that they are directly comparable. Arrows show the direction of the velocities of change in selected pixels. Inset figures depict how metrics were calculated (see more details in Fig. 2-1). Panels

on the right show the median and 95% intervals of climate-phenology metrics calculated using growing season length (GSL), start of season (SOS), end of season (EOS) as proxies for phenology, and using mean annual temperature (MAT), mean spring temperature (MST) and using mean fall temperature (MFT) as proxies for climate, respectively.

3.2 Climate-phenology mismatches in anthropogenic landscapes

To examine possible anthropogenic influences on the climate-phenology mismatch, we compared four climate-phenology metrics ($\boldsymbol{v}_{\mathrm{MAT}}$, $\boldsymbol{v}_{\mathrm{GSL}}$, $\theta_{\mathrm{GSL,MAT}}$, $\delta_{\mathrm{GSL,MAT}}$) based on the five land-use types from the global anthropogenic biomes Anthromes 2 data (Ellis et al., 2010) (Fig. 2-3). Croplands had the highest $\boldsymbol{v}_{\mathrm{MAT}}$, followed by wildlands, semi-natural, and rangelands. Croplands had the lowest $\boldsymbol{v}_{\mathrm{GSL}}$, greatest $\theta_{\mathrm{GSL,MAT}}$, and lowest $\delta_{\mathrm{GSL,MAT}}$. Semi-natural and rangelands were similar in these three metrics, while wildlands had the highest $\boldsymbol{v}_{\mathrm{GSL}}$, smallest $\theta_{\mathrm{GSL,MAT}}$, and highest $\delta_{\mathrm{GSL,MAT}}$. Notably, $\boldsymbol{v}_{\mathrm{GSL}}$ outpaced $\boldsymbol{v}_{\mathrm{MAT}}$ only in wildlands (positive $\delta_{\mathrm{GSL,MAT}}$), but it lagged behind or moved in opposite directions in all anthropogenic land uses (negative $\delta_{\mathrm{GSL,MAT}}$). Kolmogorov-Smirnov tests showed that statistical distributions of the four climate-phenology metrics in all anthropogenic land-use types were significantly different from those in the wildlands ($p < 0.001$). Nevertheless, the comparison across land use types might be confounded by the correlation between land use and latitude, which is addressed by a subsequent model to account for both.

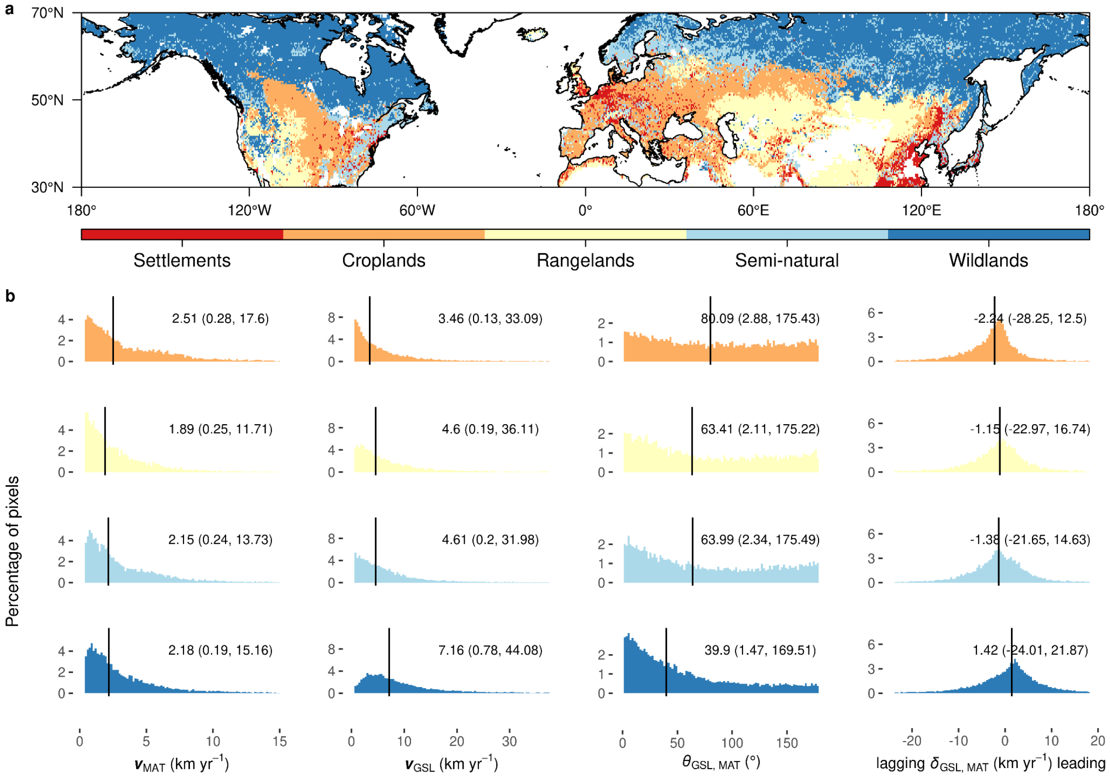

Figure 2-3. Climate-phenology metrics by land-use types. **(a)** Map of land-use types in 2000, based on the Anthromes 2 data (Ellis et al., 2010). Land uses were classified into five different types: settlements, croplands, rangelands, semi-natural, and wildlands. Settlements were excluded from the following comparisons as their small spatial scales might lead to inaccurate calculation of climate-phenology metrics. **(b)** Distributions of the velocity of mean annual temperature change, $\boldsymbol{v}_{\mathrm{MAT}}$ (km yr^{-1}), the velocity of growing season length change, $\boldsymbol{v}_{\mathrm{GSL}}$ (km yr^{-1}), the difference in direction, $\theta_{\mathrm{GSL,MAT}}$ (°), and the pacing of phenology relative to climate, $\delta_{\mathrm{GSL,MAT}}$ (km yr^{-1}) in five land-use types. Histograms are ranked based on the medians of the distributions in the land-use type (vertical lines). For $\boldsymbol{v}_{\mathrm{MAT}}$, $\boldsymbol{v}_{\mathrm{GSL}}$, and $\delta_{\mathrm{GSL,MAT}}$, only values between 2.5% and 97.5% quantiles are presented in the histograms.

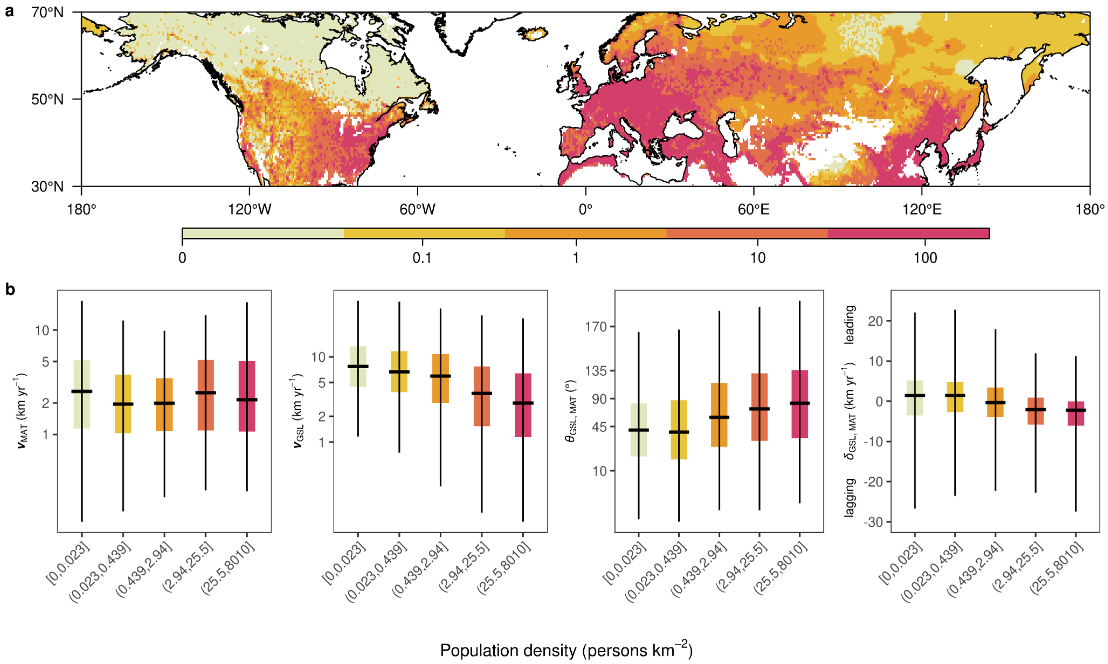

Figure 2-4. Relationship between population density and climate-phenology metrics. **(a)** Map of population density (persons km^{-2}) in the study area in 2000 (Center For International Earth Science Information Network-CIESIN-Columbia University, 2018). Color shows the population density, with cutpoints chosen to divide the data into quantiles. **(b)** Velocity of mean annual temperature change, $\boldsymbol{v}_{\text{MAT}}$ (km yr^{-1}), velocity of growing season length change, $\boldsymbol{v}_{\text{GSL}}$ (km yr^{-1}), the difference in direction, $\theta_{\text{GSL,MAT}}$ (°), and the pacing of phenology relative to climate, $\delta_{\text{GSL,MAT}}$ (km yr^{-1}) in five quantiles of population density. The lower end of the whiskers, lower boundary of the boxes, middle of the boxes, higher boundary of the boxes, and the higher end of the whiskers are 0.025, 0.25, 0.5, 0.75, and 0.975 quantiles of the distributions, respectively. For visualization, the y-axis scales have been log-transformed for $\boldsymbol{v}_{\text{MAT}}$ and $\boldsymbol{v}_{\text{GSL}}$, and logit-transformed for $\theta_{\text{GSL,MAT}}$.

We tested for a natural-anthropogenic gradient underlying climate-phenology mismatches by modeling the relationship between the four climate-phenology metrics and human population density (Center For International Earth Science Information Network-CIESIN-Columbia University, 2018) (Fig. 2-4). One might argue that these relationships could be confounded by latitude, as population density, agricultural intensity, and agricultural practices might covary with the climate-phenology metrics along the latitudinal gradient. We used a Bayesian spatial model to explicitly account for a latitudinal trend and possible spatial autocorrelation in the response variables. After accounting for these factors, we found that population density is significantly correlated with $\boldsymbol{v}_{\mathrm{GSL}}$ and $\delta_{\mathrm{GSL,MAT}}$. A 1% increase in human population density corresponds to a 0.15% reduction in $\boldsymbol{v}_{\mathrm{GSL}}$ and a 0.69 km yr^{-1} increase in the lagging or diverging mismatch between $\boldsymbol{v}_{\mathrm{GSL}}$ and $\boldsymbol{v}_{\mathrm{MAT}}$. Despite the possible latitude-population correlation, latitude was not a significant predictor of $\delta_{\mathrm{GSL,MAT}}$, highlighting the role of anthropogenic influence.

3.3 Ground-observed climate-phenology mismatches along population gradients

In order to understand the natural-human gradient at finer spatial scales, we analyzed the ground-observed leaf-out dates of seven selected plant species. The median absolute predictive error, representing climate-phenology mismatch on the ground level, was 6.4 days (95% interval: 0.3, 26.7 day). We again tested for the relationship between the absolute predictive error and the log-transformed human population density (Center For International Earth Science Information Network-CIESIN-Columbia University, 2018) (Fig. 2-5). We found that human population density (on a logarithmic scale) was positively associated with the absolute predictive error in six out of seven species (coefficient 0.005–0.76) and negatively associated in only red maple (coefficient −0.02). The relationship was significant ($p < 0.05$) for common lilacs, which has the largest sample size. Overall, a 1% increase in human population density corresponds to a 0.28 day increase in the absolute predictive error ($p < 0.05$).

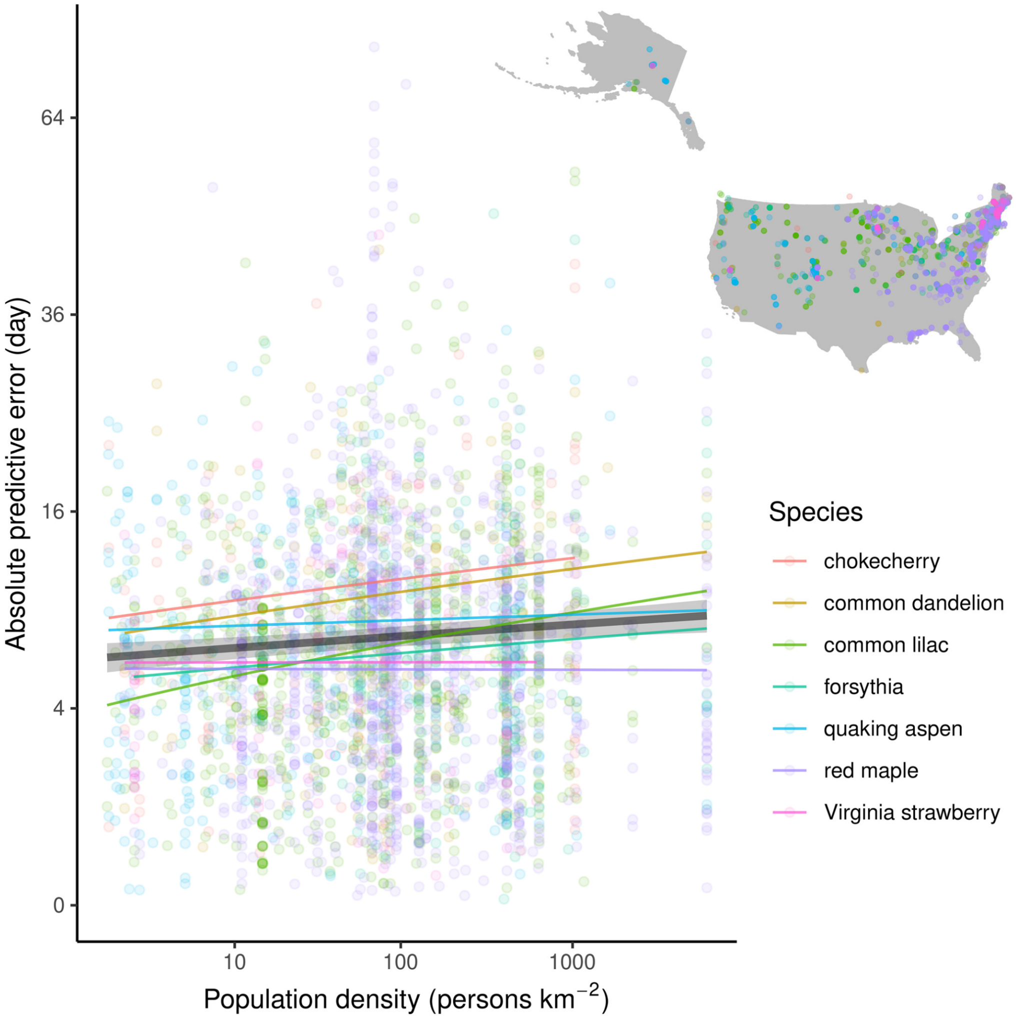

Figure 2-5. Anthropogenic influence on the ground-level climate-phenology mismatch calculated from the leaf-out dates of seven selected plant species in the USA-NPN database. Scatterplot shows the relationships between log-transformed human population density and absolute predictive error (day) between observed and model-predicted leaf-out dates. Black line and gray ribbon show the overall linear trend and 95% interval, respectively. Colored lines show the species-specific linear trends. Inset map shows the locations of observational sites with phenometrics on the leaf-out dates of the studied species.

4 Discussion

From our global analyses of remote sensing and ground-based data, we found that plant phenology does not perfectly track climate change, and that the mismatch is greater in human-dominated landscapes. Previous studies have found that the rapid advancement of spring phenology outpaces the shift in the seasonal timing of spring temperatures (Ovaskainen et al., 2013). Those results are partly supported by our finding of a leading mismatch between phenological shifts and temperature changes in natural landscapes (Fig. 2-3). However, across the entire study area, there is an overall lagging or diverging spatial mismatch in mixed natural and anthropogenic landscapes. Several possible mechanisms explain why the movement of phenology isolines lags behind or is oriented in the opposite direction compared with those of temperature isolines, including insufficient phenotypic plasticity (Duputié et al., 2015), photoperiod limitations (Bauerle et al., 2012; Fu, Piao, et al., 2019; Fu, Zhang, et al., 2019; Körner & Basler, 2010; Zohner et al., 2016), and the interaction between warming and chilling requirements (Fu et al., 2015). These lags might also be explained by phenological response to factors other than temperature, such as drought stress (Peng et al., 2019) and CO_2 concentration (S. Wang et al., 2019). In the remote sensing analysis, the landscape-level lag may be additionally attributed to insufficient species compositional change (Helman, 2018). A possible explanation for the decoupling of phenology and climate is the decreasing sensitivity of vegetation phenology to temperature (Fu et al., 2015), but this mechanism is open to discussion because of known issues in the calculation of temperature sensitivity (Keenan et al., 2020). Plant functional types can be another factor that explains the outpacing phenology patterns in wildlands, especially in high-latitude regions dominated by shrublands, evergreen needleleaf forests, and grasslands.

Phenology responds to multiple climatic factors in complex ways. We used MAT as a proxy for climate in this study and focused on temperate areas with distinct seasonality, where temperature is the main driver of phenology. However, we acknowledge that there are many ecosystems where phenology is driven by precipitation instead of temperature, particularly in grasslands (Miao et al., 2017). For example, warming-induced drought stress could delay greenup onset and advance senescence in temperate grasslands (Tao et al., 2008), whereas an increase in preseason precipitation often causes the opposite (Ren et al., 2018). Note that climate-phenology tracking is stronger in spring compared to the fall ($\delta_{\mathrm{SOS,MST}}$ are generally closer to zero compared to $\delta_{\mathrm{EOS,MFT}}$ in Fig. 2-2d), which can be interpreted as higher sensitivity of senescence to water stress or photoperiod than greenup. We therefore suggest future studies use multivariate vectors when calculating the velocity of change in climate and high-dimensional nonlinear models when calculating model predictive errors.

Our findings on phenological shifts can be situated in a broader context of ecological responses to climate change, including phenological, distributional, and physiological responses (Hällfors et al., 2021). Apart from plant phenology, recent studies on plant migration and productivity have also shown lags in biotic responses to climate change. For example, the velocity of climate change has been suggested to exceed optimistic estimates for plant migration rates (~1 km yr^{-1}) in 28.8% of the globe (Loarie et al., 2009). This estimation was confirmed by a systematic analysis of forest inventory data, which revealed that the minimal northward expansion of tree ranges in the eastern US has failed to keep pace with climate change (K. Zhu et al., 2012). An analysis of changes in plant productivity suggests that the velocity of productivity change lags behind that of temperature change in 80% of the northern high latitudes (Huang et al., 2017). Altogether, these studies corroborate results from this analysis to reveal the possibility that not even some of the most rapid responses in vegetation activity match the pace of recent climate change.

Our study suggests that anthropogenic effects are closely associated with the desynchronization of land surface phenology and temperature. Despite intensive land management, croplands had one of the highest climate-phenology mismatches among all land uses, with strong warming trends often accompanied by shortened growing seasons (Figs. 2-2b, 2-3b). The accuracy of remote sensing in detecting the phenology of crops has been validated with ground observations, such as the crop progress stages reported by the U.S. Department of Agriculture (USDA) National Agricultural Statistics Service (NASS) (Duncan et al., 2015; Gao et al., 2017; Peng et al., 2019; Sakamoto et al., 2005). Crop phenologies have complex responses to climate change. On the one hand, the established climate-phenology coupling may be disrupted. Warming can accelerate crop development and cause early flowering, maturity, and harvesting, therefore shortening the growing season in croplands (Bai et al., 2019; Liang et al., 2021). Instead of tracking temperature change, farmers may respond to changing precipitation regimes, such as that maize is usually planted when average precipitation and potential evapotranspiration fall within suitable ranges (Sacks et al., 2010). Complex adaptations such as crop rotations (Marini et al., 2020) and hybrid varietal selection for fast growth, high yield, and stress tolerance (Atlin et al., 2017) may lead to climate-phenology decoupling. For example, in the Midwestern US, a significant expansion in maize and soybean cultivation, coupled with decreases in wheat and oats, delayed greenup at a rate of 1.8–6.7 day decade^{-1} during 1982–2014 (Zhang et al., 2019). Failure to take advantage of the warming-induced extension of the potential growing season may give rise to a novel yield gap (Lobell et al., 2009) under climate change, leading to a missed opportunity to enhance productivity and pose challenges to achieving food security. On the other hand, active management of the agricultural landscape can help maintain the relationship between phenology and changing climate. For instance, maize and soybeans in the US advanced in planting dates and lengthened growing seasons from 1981 to 2005 due to increased growing degree day accumulation (Sacks & Kucharik, 2011). In northeastern China, the negative impact of a warming-induced shortened rice growth period was partly offset by earlier sowing dates and the adoption of cultivars with a longer growth period (Bai et al., 2019). With further studies on the crop yield and economic consequences of the climate-phenology mismatch, agricultural managers can better optimize sowing dates and crop varieties. In the long term, assessments of climate-phenology mismatch can help design crop ideotypes and guide crop breeding to further expand the toolbox for agro-adaptation.

The relationship between phenological shifts and climate change in semi-natural lands varies greatly over space (Fig. 2-3b). For example, although forests in New England in the Northeastern United States have been reported to have lengthened their growing season as a result of warming (Janowiak et al., 2018) our analysis suggests otherwise, with most of the area having experienced a decrease in growing season length (arrows in New England point to the south in Fig. 2-2b). It should be noted that previous studies have mostly focused on mono-specific forests at a local scale, but satellite-observed phenology also captures phenological change induced by species compositional changes, such as the dramatic reduction in evergreen hemlock caused by introduced pathogens (Knighton et al., 2019) and the replacement of spruce-fir forests with maple-beech-birch and oak-hickory forests (Alig & Butler, 2004) in the northeastern US. Large-scale afforestation and reforestation programs, such as the Three-North Shelter Forest Program in Northeastern China (Lu et al., 2018), can significantly alter land surface phenology, possibly extending the growing season and mitigating climate-phenology mismatch. The influence of timberland management on phenology and corresponding adaptive strategies under climate change has rarely been examined and deserves further investigation.

Given the small number of pixels with human settlements as the dominant land use in the study area, we could not test the net effect of land use changes like urbanization, on climate-phenology mismatch. Nevertheless, phenological shifts in urban areas may be desynchronized from regional climate patterns due to urban heat island effects (S. Wang et al., 2019), CO_2 fertilization (S. Wang et al., 2019), irrigation (Buyantuyev & Wu, 2012), and the introduction of non-native species (Buyantuyev & Wu, 2012). Larger-scale changes in plant phenology might be observed in the future, given the rapid expansion of urban areas.

This study provides one of the first quantifications of continental-scale widespread phenological mismatch, especially in human-dominated landscapes. Looking forward, a concerted effort will be needed to further establish the mechanisms and consequences of phenological mismatch. First, the scaling of phenological mismatch at finer resolutions should be investigated, as phenology is highly heterogeneous and mediated by local microclimate variables in complex terrain (Villegas et al., 2010; Ward et al., 2018). Second, insights from land surface phenology in this study can be enhanced by the inclusion of individual-to species-level phenology data that are free of confounding factors such as species composition, disturbance, and snow (C. Wang et al., 2017). Last, the relationship between measurements of phenological mismatch and fitness measurements, such as productivity and stress, needs to be tested systematically, extending beyond several classic examples of interacting species (Visser & Both, 2005). Although these efforts are currently limited by the lack of long-term phenology observations and fitness measurements, future data collection may enable us to more rigorously test well-known ecological theories about phenological mismatch, to more sustainably manage plant species and mitigate the pernicious impacts of climate change.

5 Conclusions

Plant phenology is expected to closely track the changing climate, but this phenology-climate coupling might be disrupted by human activities during rapid climate change. While studies have revealed the possibility of climate-phenology decoupling, until now we lack a systematic quantification of this mismatch and its correlation with anthropogenic activities. Our findings confirm that land surface phenology changed rapidly over the past three decades in northern mid-to high-latitudes. Our results show that, however, the movement of phenology isolines outpaced that of temperature isolines in wildlands but lagged behind those in anthropogenic landscapes. Anthropogenic activities are not only associated with the slower movement of phenology isolines, but also an increased climate-phenology mismatch. A stable relationship between land surface phenology and climate in human-dominated landscapes is critical to maintaining biodiversity and increasing ecosystem productivity. Our study demonstrates a coherent approach to quantify climate-phenology mismatches and understand their spatial pattern. Insights from these findings help guide sustainable management strategy through the optimized selection of species and planting practices in the human-dominated Earth.

Chapter 3. Inferring pollen phenology with remote sensing for public health

Abstract

Pollen exposure is likely to intensify in the future given ongoing and projected changes under climate change, imposing increasing costs on public health. A better understanding of flowering and pollen phenology could improve airborne pollen predictions and reduce pollen exposure. Previous efforts have been constrained by the limited amount of observational data of plant reproductive phenology. Here, we infer the reproductive phenology of wind-pollinated plants with high spatial resolution satellite imagery from PlanetScope, complemented by *in-situ* flower and pollen observations. Due to the challenge of detecting wind-pollinated flowers from space, we leveraged the correlation between vegetative and reproductive phenology. On the individual tree level, we extracted remotely-sensed green-up time and validated its correlation to flowering time using flower observations in a high-quality local dataset and a continental-scale observatory network. Scaling up to the city level, we developed a novel approach to characterize pollen phenology from remotely-sensed vegetative phenology, by optimizing two tuning parameters: the threshold of green-up or green-down and the time lag between green-up/down and flowering. We applied this method to seven cities in the US and eight key wind-pollinated tree taxa, calibrated by measurements of airborne pollen concentrations. Our method

characterized pollen phenology accurately both in-sample and out-of-sample, benchmarked with an existing statistical method. Leveraging high-resolution remote sensing, our approach enables us to infer the flowering and pollen phenology of wind-pollinated plant taxa on a large scale, including areas with limited prior in-situ flower and pollen observations.

1 Introduction

Phenology, the timing of recurring biological events, is widely recognized as nature's calendar. Changes in phenology are among the most sensitive biological responses to global changes. Across the Northern Hemisphere, meta-analyses documented an overall 2.3–2.8 days decade^{-1} of spring advancement (Parmesan, 2007; Parmesan & Yohe, 2003). Flowering seasons, in particular, have earlier starts and often longer durations over time (Mo et al., 2017). Changes in flowering phenology are closely related to the onset, duration, and intensity of pollen seasons. Indeed, climate change has led to extended pollen seasons and increased pollen abundance (Anderegg et al., 2021; Ziska et al., 2011, 2019). In addition, pollen production is also increased by rising atmospheric carbon dioxide concentration (Ziska & Caulfield, 2000). Exposure to pollen is a trigger of allergic asthma and allergic rhinitis (hay fever). Increased pollen exposure imposes significant costs on public health and is likely to exacerbate under future global change. The elevated risk calls for major improvements in the mechanistic understanding and prediction of plant reproductive phenology.

Previous research on plant reproductive phenology for public health has been limited by insufficient observational data. In the field of aerobiology, pollen phenology is studied with airborne pollen concentration data from aerial sampling, accelerated by the expansion of national pollen monitoring networks (Scheifinger et al., 2013). These pollen concentration data are collected with systematic protocols at a near daily temporal resolution, thus serving as a high-quality source for pollen modeling. However, aerial sampling of pollen is expensive and the stations are still spatially sparse (Anderegg et al., 2021). Aggregated over a large area and identified to the family or genus level, pollen from aerial samples often does not allow us to study fine-scale spatial variations and intra-genus variations. In the field of ecology, observations of flowering phenology , from observatory networks and crowd-sourcing, has been correlated with pollen phenology (Crimmins et al., 2017; Elmendorf et al., 2016; Templ et al., 2018). These phenological observations have a larger spatial coverage and a finer taxonomic resolution compared to aerial sampling data, but are limited by their discrete format (Donnelly et al., 2022) and sampling bias (Pearse et al., 2017). Although both aerial samples and phenological observations have been used to advance pollen modeling, these models are still limited in spatial robustness (Scheifinger et al., 2013). Data-driven pollen models are largely confined in a local scale; process-based pollen models extrapolate better but the accuracy varies greatly by taxa (Chuine & Belmonte, 2004). To achieve large-scale and locally-accurate pollen modeling, there is a need for plant reproductive phenology data with a large spatial coverage and fine spatial resolution.

To overcome the data challenge, remote sensing has been explored to inform pollen and flower phenology, building on the correlation between reproductive phenology and vegetative phenology. The onset of bud burst detected from Moderate Resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index (NDVI) and Global Inventory Monitoring and Modeling System (GIMMS) NDVI were found correlated with the onset of birch flowering (Karlsen et al., 2008) and birch pollen season (Hogda et al., 2002), respectively, on continental and decadal scales. Remotely-sensed green-up time was able to explain interannual variations in flowering time of multiple plant functional types (Delbart et al., 2015). Moving beyond correlation, data-driven predictive pollen models have also benefited from incorporating MODIS Enhanced Vegetation Index (EVI) as a predictor (Huete et al., 2019; F. A. Lo, 2020; Yang et al., 2022). These studies show the feasibility of using satellite remote sensing to greatly expand the spatial coverage of reproductive phenology data and to improve pollen models.

Despite their broad spatial coverage, satellite remote sensing data products previously used to study flowering and pollen phenology have a limited spatial resolution, specifically 250 m (MODIS), 500 m (MODIS), or 8 km (GIMMS). Land surface phenology detected on this resolution suffers from the mixed pixel problem (X. Chen et al., 2018). This is particularly problematic for urban landscapes that are highly heterogeneous in land cover and plant species. Given that pollen exposure and plant reproductive phenology are highly spatially heterogeneous within a city (Katz et al., 2019; Katz & Carey, 2014), land surface phenology at a coarse spatial resolution does not satisfy the need for spatially-explicit pollen modeling for public health.

PlanetScope imagery on 3 m resolution provides an excellent opportunity to gather plant reproductive phenology data on an individual tree level. We identified the untapped potential of PlanetScope imagery for public health from two streams of research. On the one hand, PlanetScope imagery has been used to successfully detect large and brightly-colored flowers within a stand, with indices designed to capture spectral signatures of flowers, such as enhanced bloom index (EBI) (Campbell &

Fearns, 2018; B. Chen et al., 2019; Dixon et al., 2021). Although supporting the use of PlanetScope to detect canopy-level phenological variations, PlanetScope-derived bloom index can hardly be applied to wind-pollinated flowers that are small and inconspicuous (Kim et al., 2020). Reproductive phenology of wind-pollinated flowers will therefore largely rely on the inference from vegetative phenology. On the other hand, PlanetScope-derived EVI has been shown to be a reliable data source for individual-level vegetative phenology, validated by other remote sensing data products (Moon et al., 2021) and ground observations (Moon et al., 2022; Zhao et al., 2022). Nevertheless, PlanetScope data were shown to capture the across-site variations in phenology driven by climate, but nor within-site variations (Zhao et al., 2022). Despite promising applications of PlanetScope imagery to detect spatial variations among individual canopies and to derive vegetative phenology, it has not yet been used to infer individual-level flowering phenology from vegetative phenology. Further, there has not been research linking PlanetScope directly to pollen phenology to our knowledge, which is central to modeling pollen exposure.

In this study, we assessed the potential of using vegetative phenology data extracted from PlanetScope to infer the flowering and pollen phenology of wind-pollinated trees. Specifically, the study focused on answering the following research questions. 1) On the individual tree level, does Planetscope-derived vegetative phenology correlate with flowering phenology monitored by field observations? How does this correlation vary depending on the type of field observations? 2) Upscaled from the individual tree level to the city level, can

Planetscope-derived vegetative phenology be used to accurately infer pollen phenology characterized by airborne pollen concentrations? To what extent does this inference extrapolate to locations where airborne pollen concentration data are unavailable? In answering these two questions, we developed a novel workflow of obtaining cross-scale reproductive phenology data from PlanetScope imagery.

2 Materials and methods

2.1 Field data and processing

2.1.1 Individual-level flowering observations

To test whether PlanetScope can capture individual-level variations in flowering phenology, we gathered two field datasets. We first used a high-quality field census for 115 oak (*Quercus* spp.) trees in nine neighborhoods in Detroit during the spring of 2017 (Katz et al., 2019). Oak trees are distributed widely and contribute greatly to allergenic airborne pollen. Methods of sampling are discussed in detail in Katz et al. (2019) and briefly introduced here. The percent of flowers in each developmental stage (immature, mature, or senesced) was visually estimated for each tree twice a week. The percent measurements ranged from 0% to 100%, with a precision of approximately 5%. The percent of mature flowers was interpolated linearly to obtain a continuous time series of flowering phenology. We took the first day of the interpolated percentage of mature flowers equal to or above 95% as the peak day of flowering, later used for comparison with remotely-sensed green-up time. Trees that did not reach 95% mature flowers were removed from the analysis.

On a large spatial extent, we retrieved plant phenology observations from the National Ecological Observatory Network (NEON) (DP1.10055.001) that were integrated into the USA National Phenology Network (USA-NPN) (National Ecological Observatory Network, 2020). We focused on 36 primary sampling sites within the continental United States (CONUS) (excluding five sites in the Mediterranean climate) that have available coordinates of tagged individual plants. We included data from 2018 to 2022, as fully operational PlanetScope data collection started in 2018. At each site and in every year, 90–100 tagged individual plants were observed for their reproductive phenophase status with varying sampling frequencies up to three times per week, following the sampling protocol of NPN. We downloaded individual phenometrics from the NEON data submitted to NPN, which are the estimates of the dates of phenophase onsets and ends, measured from a series of consecutive "yes" phenophase status records. We focused on three selected wind-pollinated tree taxa that were widely represented in the NEON data (≥ 100 records): *Acer* spp. (maple) and *Quercus* spp. (oak).

2.1.2 City-level pollen observations

To examine the potential of using PlanetScope for city-level pollen phenology and to inform public health, we obtained consistent and accurate pollen concentration data from stations associated with the American Academy of Allergy, Asthma & Immunology (AAAAI) and the National Allergy Bureau (NAB) (AAAAI, 2022). At around 80 stations located throughout the continental US, airborne pollen was sampled daily using volumetric impactor samplers including either Rotorod or Burkard samplers (Frenz, 1999) and then classified to the genus or family level and counted by NAB-certified operators. The NAB dataset serves as one of the most commonly used data sources for the description and prediction of pollen phenology in public health and ecological research in North America.

We focused on seven deciduous wind-pollinated tree taxa with considerable public health impacts in the Continental USA and Southern Canada region (F. Lo et al., 2019): *Quercus* spp. (oak), *Morus* spp. (mulberry), *Ulmus* spp. (elm), *Fraxinus* spp. (ash), *Betula* spp. (birch), *Acer* spp. (maple), and *Populus* spp. (poplar, aspen, cottonwood). *Ulmus* spp. were considered to have an early- and a late-flowering group, whose phenology was analyzed separately. We focused on seven US cities with an available street tree inventory and a nearby pollen counting station (Fig. 3-1): Austin (AT), Detroit (DT), Denver (DV), Houston (HT), New York (NY), Seattle (ST), and Tampa (TP). Most focal cities have a pollen counting station within the city, with a mean distance from the pollen counting station to all trees ranging from 9.5 km to 38.8 km. Two exceptions were that Denver's pollen concentration data were from Colorado Springs (mean distance 96.4 km), and that Detroit's pollen concentration data were from Sylvania (mean distance 92.2 km). We obtained pollen concentration data collected until late 2021.

We processed pollen concentration data to characterize pollen phenology in several steps.

1) We extended data in each year to day-of-year (DOY) 274 (Oct 1) in the previous calendar year to day 151 (May 31) in the following year in order to include at least one full pollen peak. Data on day 366 in leap years were ignored.

2) We transformed all pollen concentration values to their square root to compress extreme values and stabilize the variance (Bastl et al., 2018; Bonini et al., 2022).
3) We filled data gaps no longer than 14 days with linear interpolation and filled longer data gaps with zero.
4) We smoothed the time series with the Whittaker method ($\lambda = 10$) (Kong et al., 2019).
5) In order to focus on single pollen peaks for plant taxa that have both early- and late-flowering variations, as well as to reduce the confounding effect of outliers outside the reproductive season, we constrained the pollen seasons for each taxon, setting the pollen concentration outside the season to zero. Taxa-specific pollen seasons were determined by summing the total pollen concentration over all cities and years, fitting a Gaussian distribution, calculating a window of mean±1.96×standard deviation, and extending the window by 50 days on both ends. An exception was that the early and late pollen windows of *Ulmus* spp. were detected by fitting a Gaussian mixture model.
6) We normalized the processed pollen concentration for each taxa, city, and year, to obtain the daily probability of observing pollen, which sums to one over all days. This step extracts pollen phenology from concentration measurements, which removes the spatiotemporal differences from sampling methods and vegetation cover.

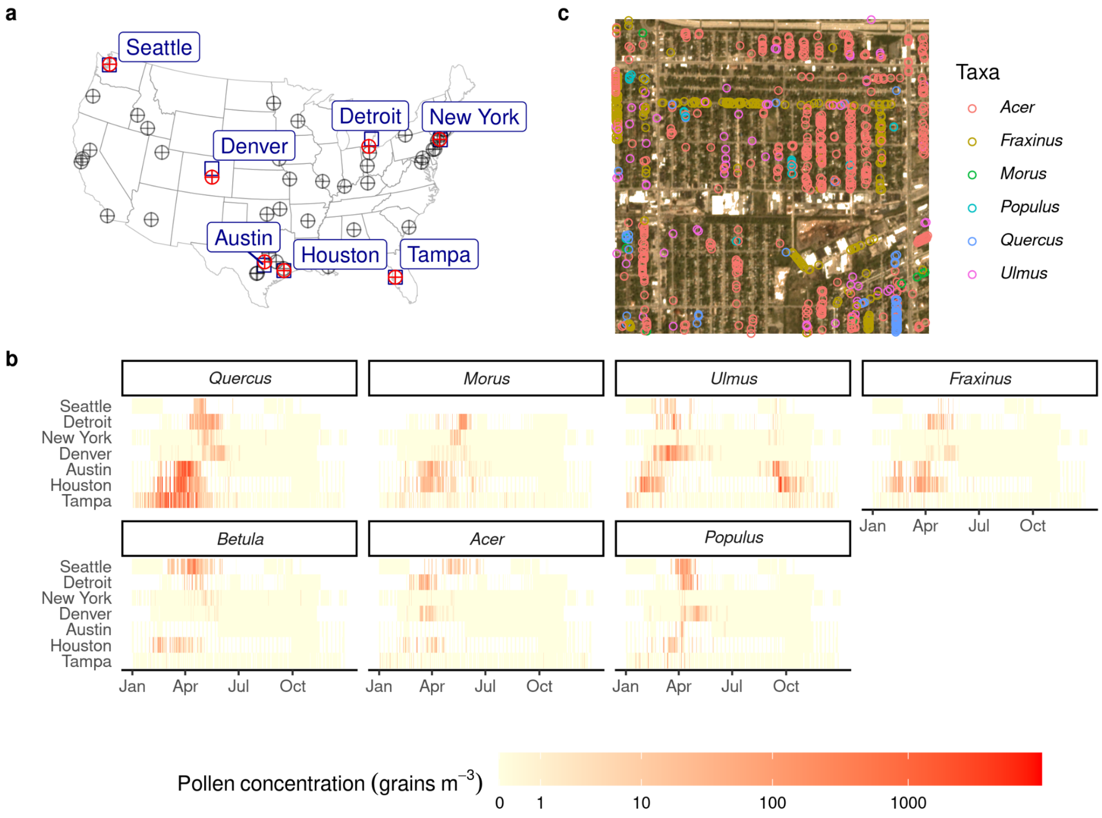

Figure 3-1. Data for inferring pollen phenology from PlanetScope imagery on the city-level. **(a)** Map of studied cities with street tree inventory (blue squares) and pollen counting stations associated with the National Allergy Bureau (NAB) (red crossed circles). Pollen counting stations were located within 100 km of the centroid of the city's street trees. Other NAB pollen counting stations not used in this analysis are marked in gray crossed circles. **(b)** Multi-year average daily pollen concentration (grains m^{-3}) of seven key pollen-producing taxa in studied cities. Cities are ordered according to their latitude. **(c)** A subset of street trees in Detroit overlayed on a true color PlanetScope image. Colors of points indicate different taxa.

2.2 PlanetScope data and processing

2.2.1 Retrieving phenological time series

We retrieved PlanetScope imagery from 2017 to 2022 for all trees involved in the analyses, including 1) sampled trees in Detroit, 2) sampled trees at NEON sites, and 3) street trees from seven wind-pollinated tree taxa in seven selected US cities. The extent of PlanetScope imagery and pixels used for phenological analyses were determined by the coordinates of the trees of interest. For the individual-level flowering phenology analysis, we used the recorded coordinates of the Detroit oak trees, and retrieved the accurate coordinates of tagged NEON trees using the *geoNEON* package in *R* (National Ecological Observatory Network, 2023). For the city-level pollen phenology analysis, we obtained street tree inventories in selected cities (Fig. 3-1c; Table 3-1). Necessary reprojections were performed to convert all coordinates in street tree inventories to longitude and latitude. The taxonomy of street trees was resolved with the *taxize* package in *R* (Chamberlain & Szöcs, 2013) for selecting trees in the taxa of interest. When there were more than 2,000 trees of a taxon at a city, we randomly selected 2,000 trees.

Table 3-1. Source of street tree inventories for seven cities used to analyze the inference of pollen phenology from PlanetScope-derived vegetative phenology.

City	Inventory source	URL
Austin	OpenTrees.org	https://opentrees.org/#pos=11/30.2623/-97.7426
Detroit	Private request from City of Detroit, Michigan	
Denver	OpenTrees.org	https://opentrees.org/#pos=11/39.7273/-104.9455
Houston	koordinates.com, mirrored from a previous dataset on mycity.houstontx.gov	https://koordinates.com/layer/25245-houston-texas-street-tree-inventory/
New York	OpenTrees.org	https://opentrees.org/#pos=11/40.7056/-73.9764
Seattle	OpenTrees.org	https://opentrees.org/#pos=11/47.6154/-122.33
Tampa	TampaTreeMap	https://www.opentreemap.org/tampa/map/

At coordinates of the trees of interest, we obtained the reflectances in the red, green, blue, and near-infrared bands from the PlanetScope atmospherically corrected surface reflectance product (ortho_analytic_4b_sr) (Planet Team, 2017). For quality control, we applied Usable Data Masks (UDM2) (Planet Team, 2023) to include only pixels that were clear, had no snow, ice, shadow, haze, or cloud, and had algorithmic confidence in classification ≥ 80%. For each date, pixel, and band, we took the mean reflectance if there were multiple visits in a day. We calculated the enhanced vegetation index (EVI) (Liu & Huete, 1995) (Eq. 3-1) to characterize vegetative phenology, as PlanetScope EVI has been shown to accurately extract leaf phenology metrics validated by local PhenoCams, robust to different atmospheric conditions and less likely to saturate in dense vegetated areas compared to PlanetScope normalized difference vegetation index (NDVI) (Wu et al., 2021).

$$EVI = \frac{2.5(NIR - Red)}{NIR + 6 \times Red - 7.5 \times Blue + 1} \qquad [3\text{-}1]$$

We used the following three criteria to filter out possibly contaminated data points:

1) Reflectances in all visible bands were positive values.
2) EVI was between zero and one.
3) EVI did not deviate more than 0.2 from the climatology of EVI for the corresponding taxon and city.

The taxa- and city-specific climatology was calculated by taking the median of EVI, filling all gaps with linear interpolation, and smoothing with the Whittaker method (λ = 50).

We processed PlanetScope data to characterize individual-level vegetative phenology in the following steps.

1) We extended the time series in each year to day 274 (Oct 1) in the previous calendar year to day 151 (May 31) in the following year in order to include at least one full growing season with green-up and green-down. This step was necessary for the detection of green-up day when EVI increases from the minimum before the New Year, and the detection of green-down day when EVI decreases to the minimum after the New Year.
2) We removed extended time series with fewer than 50 data points.

3) We filled gaps in all extended time series with linear interpolation.

4) We smoothed all extended time series with Whittaker smoothing ($\lambda = 50$).

2.2.2 Extracting phenological metrics

We extracted phenological metrics, specifically green-up or green-down time, for each individual tree of interest. We first detected significant seasonality in the time series of EVI. In particular, we fitted a simple linear regression model and then three piecewise regression models with one, two, and three changepoints, respectively. We ranked the four models according to the Akaike information criterion (AIC). If a simple linear regression was the best model, we discarded the pixel as it may lack the typical seasonal change in greenness.

Once seasonality has been established, we used the EVI time series to identify the green-up/down phases empirically (Fig. 3-2). The end of a green-up phase was determined as the day of year when EVI reaches the maximum in the growing season. The start of a green-up phase was then determined as the day of year when EVI is at the minimum, prior to the end of the green-up phase. Similarly, the start of a green-down phase was determined as the day of year when EVI reaches the maximum in the growing season; the end of a green-down phase was then determined as the day of year when EVI is at the minimum, after the start of the green-down phase. We then determined the timing of green-up/down at multiple thresholds, including 0%, 10%, 20%, …, 100% green-up for taxa that flower in the spring (all except late-flowering *Ulmus* spp.), and 100%, 90%, 80%, …, 0% green-down for taxa that flower in the fall (late-flowering *Ulmus* spp.). This empirical method of defining green-up/down time has been widely applied to remote-sensing data in order to be compatible with different plant functional types with various seasonality (Moon et al., 2021).

2.3 Inferring flowering phenology on the individual tree level

For all Detroit oak trees sampled for flowering phenology in 2017, we tested the linear correlation between the green-up time measured at various thresholds and the flowering time measured by peak flowering day. As the field sampling was done in 2017, we first compared green-up and flowering time in 2017, even though PlanetScope data were sparse at the start of 2017. We then compared the green-up time from 2018 to 2021, when we had dense EVI time series, to the flowering time in 2017. We tested these correlations despite the mismatch in the year of data collection, based on the premise that there is a relatively stable rank in phenology among individuals, i.e., early flowering individuals always flower earlier relative to the others despite some interannual variations (Crawley & Akhteruzzaman, 1988). We assessed the Pearson correlation coefficients and the significance of the correlations between green-up and flowering time.

For trees at NEON sites monitored for phenology, we tested the correlation between the 50% green-up time and the flowering time measured by day of flower onset in the corresponding year from 2018 to 2022. We assessed the Pearson correlation coefficients and the significance of the correlations both across all sites and within each site.

2.4 Inferring pollen phenology on the city level

2.4.1 Upscaling and parameter optimization

To infer city-level pollen phenology from individual-level vegetative phenology monitored by PlanetScope, we developed the following nonparametric model with two tuning parameters (Eq. 3-2).

$$t_{\text{green-up/down}} = \Phi(EVI, \theta)$$
$$t_{\text{flower}} = t_{\text{green-up/down}} + \delta$$
$$f\left(t_{\text{pollen}}\right) = f\left(t_{\text{flower}}\right)$$
$$c_{\text{pollen}} \propto f\left(t_{\text{pollen}}\right) \quad [3\text{-}2]$$

Here, θ is the green-up or green-down threshold in growing season EVI time series that is used to obtain green-up/down time; δ is the time lag between the timing of green-up/down and flowering. Here Φ extracts the day of year when growing season EVI crosses the green-up/down threshold, and $f(t_{\text{green-up/down}})$, $f(t_{\text{flower}})$, and $f(t_{\text{pollen}})$ represent the probability density function of green-up/down time, flowering time, and pollen emission time. We assumed that the pollen concentration (c_{pollen}) of a taxa, city, and year is proportional to the probability density function of flowering time. We allowed the threshold to vary by taxa and the lag to vary by both taxa and city, but neither of the parameters varied by year.

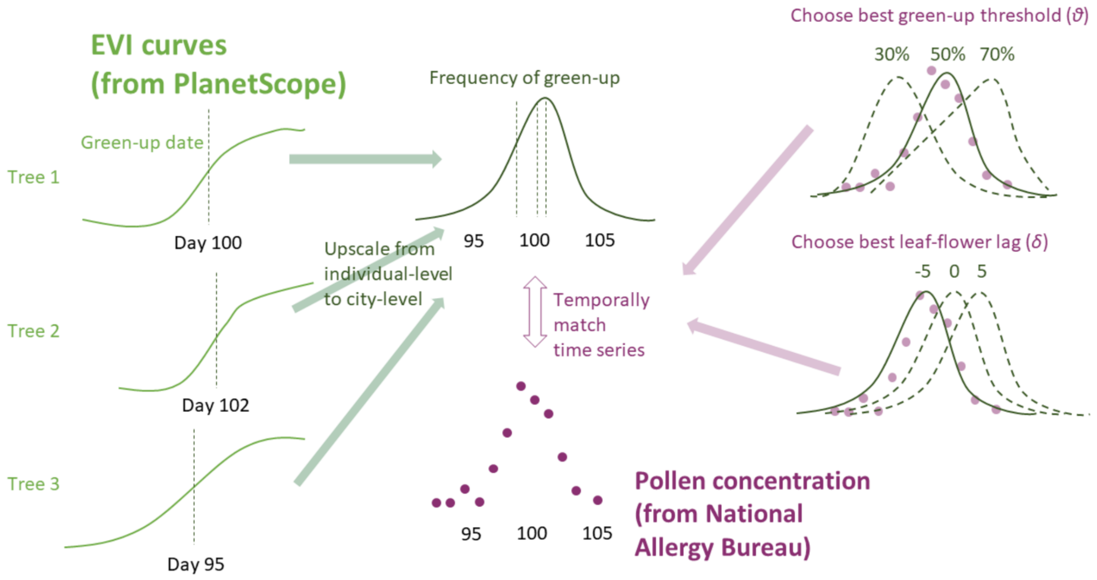

Figure 3-2. Workflow for inferring flowering phenology from remotely-sensed vegetative phenology. Enhanced vegetation index (EVI) time series of individual trees are used to determine green-up/down days at various green-up/down thresholds. The green-up/down days were then summarized to the city level as green-up/down frequencies. The green-up/down frequencies were compared with the time series of pollen concentration. For all taxa and across all cities, the green-up/down threshold that led to the best match in the shapes of vegetative and pollen phenology curves was chosen. For each city specifically, the best lag between vegetative and pollen phenology curves was chosen.

To fit the designed model, we first summarized the timing of green-up/down in all pixels to give the frequency of green-up/down on each day in a year, normalized to probability density that sums up to one. We then optimized the two tuning parameters (threshold and lag) to match the vegetative and pollen phenology measured by their probability density functions (Fig. 3-2). Specifically, we calculated the lagged correlation between vegetative and pollen phenology for each threshold with the lags ranging from –100 to 100. For each threshold and lag, we calculated the weighted mean square error (MSE) between vegetative and pollen phenology, with weights proportional to pollen probability density values. We selected for each plant taxa the threshold giving the smallest mean weighted MSE, and further for each city, the lag giving the smallest weighted MSE. The vegetative phenology modified by the optimized threshold and lags was considered remotely-sensed pollen phenology. We assessed the accuracy of remotely-sensed pollen phenology with the root mean square error (RMSE) with observed pollen phenology without gap filling and smoothing. We removed combinations of taxa and city when 1) there were no more than 20 trees of interest or 2) there were no more than 20 pollen concentration records greater than or equal to 5 grains m^{-3}.

2.4.2 Accuracy assessment

To benchmark the performance of our method, we applied an existing statistical method to characterize pollen phenology for each taxa and city, by fitting a Gaussian distribution to the total pollen concentration (Zhang & Steiner, 2022). The start and end of pollen season derived from mean and standard deviations of the Gaussian distribution were tuning parameters that differed by taxa and city. This method represented a statistical approach to infer pollen phenology, whereas our proposed approach represented an empirical approach. We similarly assessed the accuracy of

Gaussian pollen phenology with the RMSE with observed pollen phenology without gap filling and smoothing.

We compared the RMSE from the two methods for inferring pollen phenology both in-sample and out-of-sample. In-sample tests assessed the ability of the PlanetScope method to characterize variations in pollen phenology, whereas out-of-sample tests assessed the effectiveness of the PlanetScope method to infer pollen phenology for cities with no prior pollen concentration observations. For in-sample tests, all cities were used in the optimization of parameters in the PlanetScope method and the Gaussian method. For out-of-sample tests, we conducted leave-one-out cross-validation. Specifically, we removed a random city from the training dataset at a time and optimized threshold and lags in the remaining cities. To predict the lag for the city held for validation, we assumed a linear relationship between the lag and climate. The climate of each city was represented with the mean annual temperature in the Climatologies at high resolution for the earth's land surface areas (CHELSA) climatology dataset (30 arc sec resolution) (Brun et al., 2022). With an optimized threshold and a predicted lag, we subsequently inferred pollen phenology from vegetative phenology at the city held for validation. We performed a similar leave-one-out cross-validation for the Gaussian method. We removed a random city at a time, and predicted the start and end of pollen season assuming a linear relationship with climate (Zhang & Steiner, 2022) for the city held for validation, and predicted its pollen phenology. This method may give unreasonable predictions, with the start of season being later than the end of season, in which case we assumed the standard deviation of the Gaussian distribution to be five days. As the out-of-sample tests rely on extrapolation over a climatic gradient, we could only implement them for taxa that were present in six or more cities.

All calculations and statistical analyses were conducted in *R* v. 4.2.0 (R Core Team 2021).

3 Results

3.1 Correlation with flowering phenology

We found significant positive correlations between the timing of remotely-sensed green-up and ground-observed flowering for oak trees in Detroit in 2017 (Fig. 3-3a). Among eleven green-up thresholds tested ranging (0%, 10%, 20%, …, 100%), four thresholds (40%, 50%, 60%, and 70%) led to significantly positive correlation ($p \leq 0.05$). The correlation coefficient was the greatest when the time of green-up was determined based on a 60% threshold (Fig. 3-3b). When focusing on years with more complete PlanetScope data (i.e., 2018–2021), the correlation between 50% green-up and flowering timing was statistically significant for 2019–2021 (Fig. 3-3c).

Compared to flowering phenology data collected across CONUS from NEON sites, we again found individual-level correlations between remotely-sensed vegetative phenology measured by 50% green-up day and flowering phenology measured by flower onset day (Fig. 3-4). The positive correlations were significant in both *Acer* spp. and *Quercus* spp. However, when examined within each site instead of across all sites, the significant positive individual-level correlation only held in 6 of 19 combinations of taxa and sites that had no fewer than 10 samples.

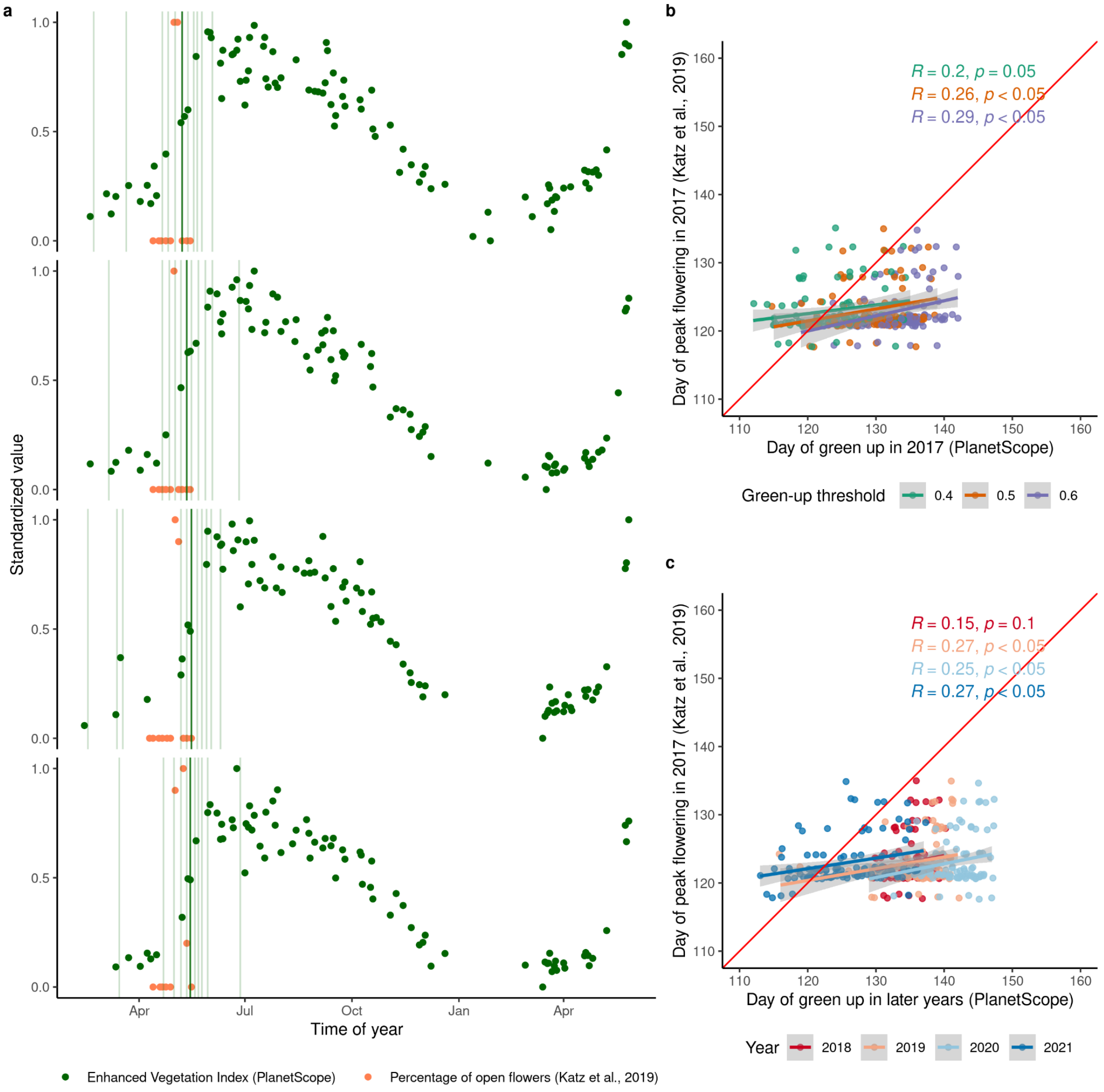

Figure 3-3. Correlation between vegetative and flowering phenology of oak trees in Detroit on the individual tree level. **(a)** Enhanced vegetation index (EVI) (green points) from PlanetScope data are used to calculate the green-up time at different thresholds of green up (vertical green lines) (50% green-up highlighted), compared with flower percentage (orange points) for four random trees in Detroit. **(b)** Correlation between green-up days in 2017 and observed flowering days (the first day

exceeding 95% flowering) in 2017 for different green-up thresholds. **(c)** Correlation between 50% green-up days in four different years (2018–2021) and observed flowering days (the first day exceeding 95% flowering) in 2017.

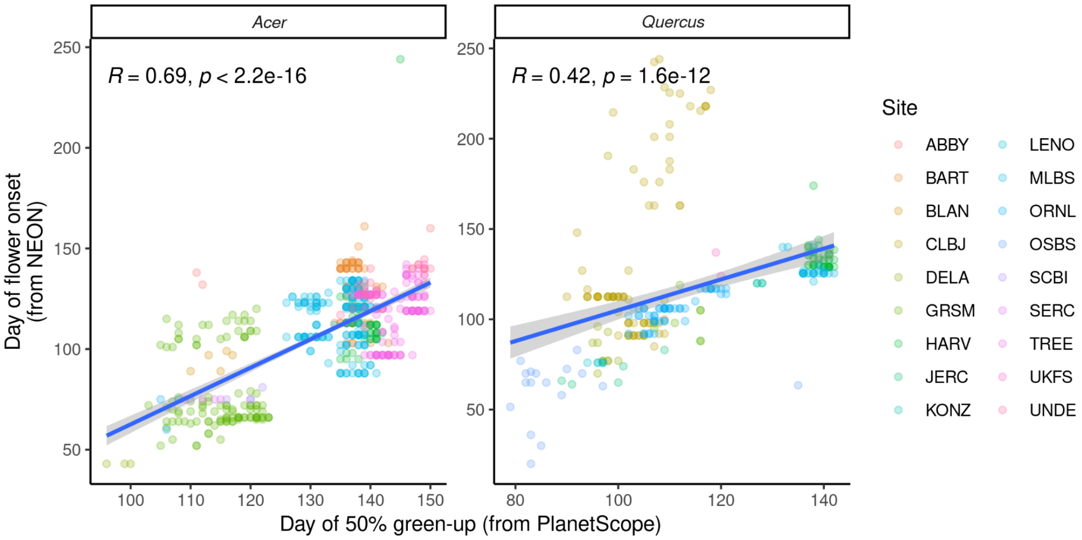

Figure 3-4. Correlation between 50% green-up time from PlanetScope and flowering time from the National Ecological Observatory Network (NEON). Different colors indicate NEON sites.

3.2 Accuracy of pollen phenology inference

We were able to infer city-level pollen phenology from remotely-sensed vegetative phenology at a reasonable accuracy with optimized green-up/down thresholds for each taxa and further the leaf-flower lag for each city (Fig. 3-5). Among all 33 combinations of taxa and cities, the in-sample accuracy of the PlanetScope method (RMSE 0.0281, 0.00843–0.107; median, 95% interval) were generally better than that of the Gaussian method (RMSE 0.0291, 0.0101–0.102). We were able to conduct out-of-sample tests for oaks that were present at seven cities, but not for other taxa that were less widespread. Among seven cities, the out-of-sample accuracy of the PlanetScope method (RMSE 0.0172, 0.00774–0.0399) was also generally better than that of the Gaussian method (RMSE 0.0200, 0.0118–0.0378). For *Quercus* spp., the accuracy improved compared to the Gaussian method both in-sample and out-of-sample.

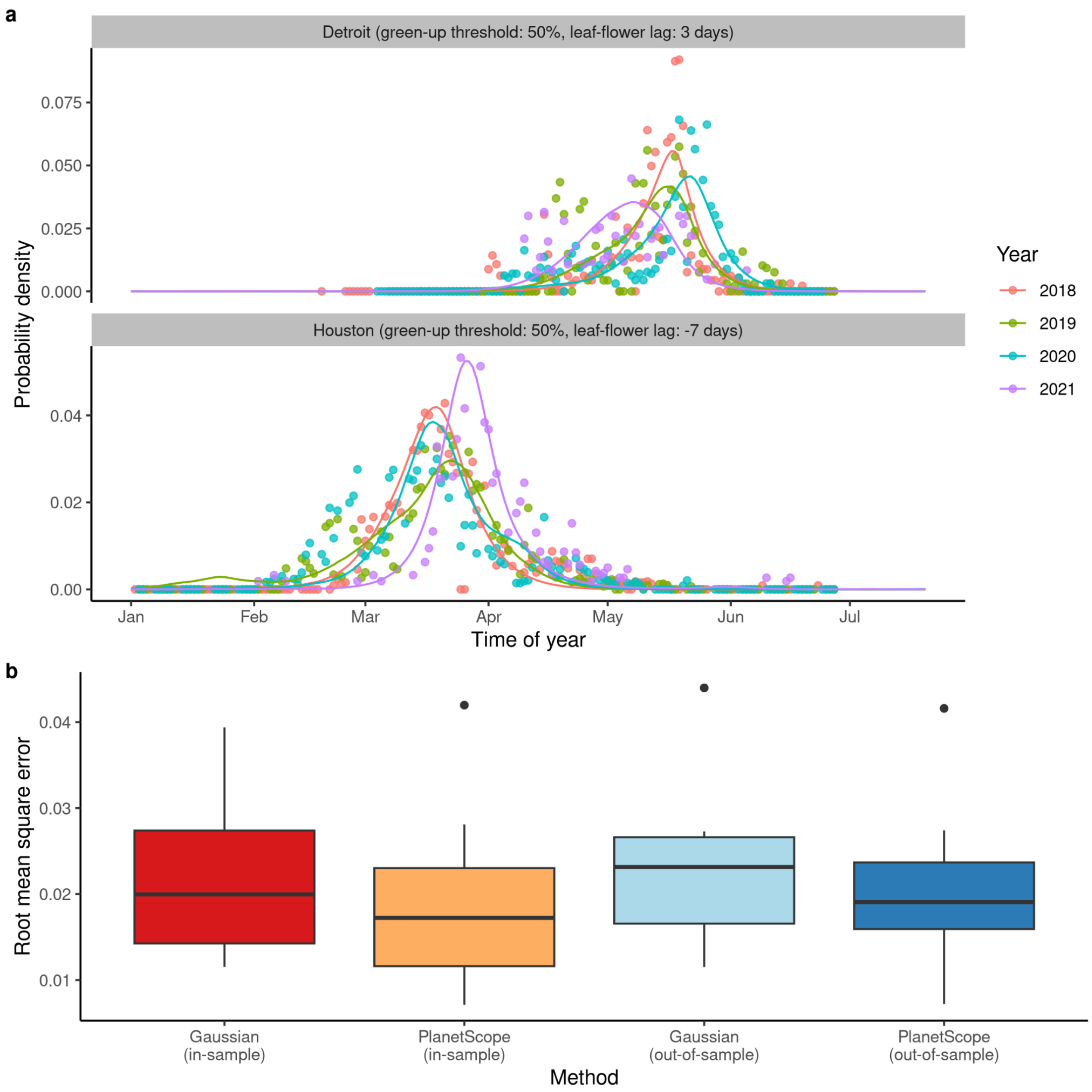

Figure 3-5. Comparing remotely-sensed pollen phenology from PlanetScope and city-level pollen phenology from aerial sampling. **(a)** Pollen phenology inferred from remotely-sensed vegetative phenology tuned to the optimal green-up/down thresholds and leaf-flower lags (lines) compared to pollen phenology inferred from airborne pollen concentration (points). Pollen phenology from both data sources was converted to probability density within each city year for comparison. Here we show

examples of oak pollen phenology at two cities on the south (Houston) and north (Detroit) of CONUS. **(b)** Accuracy of inferring oak pollen phenology with the Gaussian method and the PlanetScope method, both in-sample (fitting model with data from all cities) and out-of-sample (leave-one-out cross-validation), measured by root mean square error of probability density of pollen emission.

4 Discussion

In this study, we developed a workflow to infer flowering and pollen phenology from PlanetScope-derived vegetative phenology, calibrated by in-situ phenological observations and measurements of airborne pollen concentrations. On the individual tree level, PlanetScope-derived green-up time was correlated with flowering time, giving the potential of mapping flowering phenology within a city in great spatial details. On the city level, PlanetScope-derived green-up/down time at a specific threshold and shifted by a time lag can be used to characterize pollen phenology, with the possibility to predict out-of-sample in cities without pollen concentration observations. This study reveals the potential of high-resolution remote sensing imagery for understanding the reproductive phenology of wind pollinated plants and predicting allergenic pollen exposures.

4.1 Relationship between vegetative and reproductive phenology

In all three analyses, we showed the link between vegetative and reproductive phenology, either flowering or pollen emission. Similar relationships have been widely supported in previous studies, but on large spatial and taxonomic scales. Across locations within the geographical range of species distribution, remotely-sensed land surface phenology explained variations in flowering and pollen season onset (Hogda et al., 2002; Karlsen et al., 2008). The regional-level leaf-flower correlation can be explained mechanistically that spring flowering and green-up times are both functions of accumulated temperature for many species (Cook et al., 2012).

Across species, there was a significant positive correlation between the timing of the first flower and the timing of the first leaf, after controlling for phylogeny (Davies et al., 2013; Du et al., 2017). The phylogenetic conservatism of this leaf-flower correlation suggests deep evolutionary linkages between phenological responses to a common set of environmental cues (Davies et al., 2013; Delbart et al., 2015; Du et al., 2017). Despite established leaf-flower correlation across space and species, this relationship has not been previously examined on the individual tree level.

Here we showed that individuals that green-up earlier also tend to flower early, which may be attributed to the shared response of both phenology to spatial variations in microclimates (Katz et al., 2019), or genetic differences in plant development among individuals (Primack, 1985). By revealing leaf-flower correlation that holds on a scale smaller than previously known, we suggest the presence of fine-scale mechanisms for this correlation in addition to climatic and phylogenetic control. With growing knowledge on phenology on the community and population levels, PlanetScope can provide valuable data to understand phenological patterns on the relatively understudied individual tree level (Primack, 1985).

4.2 Detecting individual tree-level phenology with PlanetScope

With two individual-level analyses, we closely examined the often-assumed potential of PlanetScope to detect individual-level phenology (Cheng et al., 2020; Wu et al., 2021; Zhao et al., 2022), both across sites and within sites. Across NEON sites, PlanetScope-derived phenometrics captured individual-level variations in the onset of maple and oak flowers. This result is consistent with the finding that PlanetScope-derived phenometrics explained variations in the individual-level leaf onset of deciduous trees across NEON sites (Zhao et al., 2022). Within sites, we had seemingly contradicting findings, with PlanetScope-derived phenometrics being correlated with the peak flowering time of oak in Detroit, but significant positive correlations with flower onset time were not found within most NEON sites. The weak within-site correlations also observed in Zhao et al. (2022) were explained with both the uncertainty of extracting phenometrics from PlanetScope imagery and inconsistencies in field phenological observations.

While both explanations are still valid for our study (Donnelly et al., 2022), we provided additional insights for this individual-level discrepancy by comparing the data type and summary statistics of our two analyses. In the Detroit sampling, flowering phenology was measured as a continuous variable, and we focused on the peak of flowering. In comparison, NEON phenometrics were derived from discrete status data and focused on the start of flowering. It is possible that within-site individual-level variations in phenology can indeed be captured by PlanetScope-derived phenometrics, but less so by discrete and onset-focused field observations. This speculation on the robustness of PlanetScope-derived phenometrics was supported by that the flowering time of oak in Detroit in 2017 was correlated with the green-up time not only in 2017 but in most following years, suggesting that PlanetScope-derived phenometrics preserved the rank of phenology among individuals (Fig. 3-3b, c).

Our interpretation of the difference in detecting individual-level phenology within-site has two implications. On the one hand, we might have to be cautious about the accuracy of traditional phenological sampling protocol when used to study fine-scale phenological variations. Our comparison supported the idea that data for transition dates are ordinal and interval-censored, with unclear error structure, thus misrepresenting the continuous nature of phenology development (Clark et al., 2014). Our comparison also helped to answer the remaining question of which of the statistics that describe slightly different properties might be the most appropriate for representing the flowering phenology of an individual (CaraDonna et al., 2014; Primack, 1985). On the other hand, it remains promising to use PlanetScope imagery to reduce the need to simulate fine-scale phenological variations from individual phenotype, microclimate, and local nutrient availability.

4.3 Connecting in-situ and remotely-sensed phenology data

In the city-level analysis using pollen concentration data, we proposed a novel workflow to predict pollen phenology from PlanetScope imagery, linking multiple data sources. There were two core ideas in this workflow. First, we made use of the established individual-level relationship between green-up and flowering to infer individual-level flowering time. Second, individual-level flowering time was upscaled to the city level as a probability density function, which can be approximated with pollen concentration. This was a simplified model, overlooking details such as differential responses of vegetative and reproductive phenology to the environment

(Geng et al., 2022) and non-phenological factors that influence pollen concentration, such as pollen dispersal (Latorre, 1999). Nevertheless, this is one of the first models that can integrate three key data sources, remote sensing, field phenological observations, and airborne pollen concentration data, to collectively inform pollen modeling (Katz et al., 2023; Scheifinger et al., 2013).

The significant correlation between pollen phenology derived from airborne pollen concentration data and PlanetScope imagery suggested that PlanetScope-derived vegetative phenology explained intra-annual variations in pollen concentration. By empirically inferring the continuous change in pollen phenology, we moved beyond traditional pollen phenology modeling that rely on annual phenometrics (Clark et al., 2014). By comparing the empirical PlanetScope method to the statistical Gaussian method, both driven by long-term climate of the site, we showed that the PlanetScope method further improves the accuracy of oak pollen phenology prediction by providing the model with vegetative phenology data (Fig. 3-5a). Even without explicitly accounting for inter-annual variations in temperature, the PlanetScope method was able to explain some inter-annual variations in pollen phenology with vegetative phenology. This finding has previously been shown on a coarser resolution, with remotely-sensed green-up date explaining inter-annual variations in ground-observed flowering dates (Delbart et al., 2015).

4.4 Pathway to informing public health

The out-of-sample accuracy of PlanetScope-derived pollen phenology of oak trees (Fig. 3-5b) suggested the possibility of predicting pollen concentration even at locations with limited prior observations. We suggest four enhancements before operationalizing the proposed workflow to inform decision-making in public health. First, in addition to the individual-level validation of flowering phenology we presented, more fine-scale ground truths for pollen phenology are needed. Examples are newly initiated crowd-sourcing of pollen phenology (Katz et al., 2023) and within-city pollen concentration data (Weinberger et al., 2018). Second, our study was partly limited by the number of cities used for model tuning, which will benefit from obtaining street tree inventories from more cities. Apart from direct requests from cities, operationalized identification of trees with remote sensing data, such as the Auto Arborist dataset (Beery et al., 2022), may be particularly efficient. Third, by focusing on phenology, our method addressed the relative change of pollen concentration but not the absolute magnitude of pollen peaks, which can be achieved by accounting for the total pollen production per tree and abundance of the taxa of interest (Zhang & Steiner, 2022). Last, although this study retrospectively demonstrates the inference of pollen phenology, this method can be combined with accurate forecasting of vegetative phenology (Song et al., 2023; Taylor & White, 2020) to achieve near-term predictions for the early warning of pollen season. With widespread public health concerns on pollen allergy, this study provides the possibility of more spatially equitable access to pollen level forecasting.

5 Conclusions

We showed that high spatial resolution remote sensing imagery from PlanetScope is highly promising in inferring flowering and pollen phenology from vegetative phenology. On the individual tree level, remotely-sensed green-up time correlated with field-observed flowering time. The correlation depends on the method used for field observation. When flowering phenology was observed as a continuous variable, such correlation held within a city; when observed as a discrete variable, such correlation could only be detected across sites but not within sites. We upscaled individual-level remotely-sensed vegetative phenology to the city level and accurately inferred pollen phenology, calibrated by pollen phenology monitored by aerial sampling. This empirical method of inference outperformed an existing statistical method in model fit. With our proposed workflow, it is feasible to describe and predict pollen phenology at locations without prior pollen concentration data.

Chapter 4. Perceptions of pollen phenology revealed by social media discussions

Abstract

Climate change drives changes in pollen season, directly influencing individual human experiences, such as allergies. This connection presents an opportunity to harness observations of pollen phenology by the general public for scientific data collection and climate change impact communication. However, there is limited understanding of human perceptions of phenology, including detection accuracy and attribution patterns. Here, we reveal that discussions on pollen on social media aligned with natural pollen phenology both temporally and spatially. Nevertheless, social media users' understanding of the drivers of pollen phenology varied based on ideology. Our findings suggest social media users accurately detect variations in pollen phenology but are likely biased in attributing these variations. Our study highlights the value of social media as a data resource for monitoring pollen phenology and emphasizes the need to address ideologically biased perceptions in climate change communication.

1 Introduction

Phenology, the timing of recurring biological events, is widely recognized as nature's calendar. Changes in phenology are among the most sensitive biological responses to global changes (Parmesan & Yohe, 2003). In particular, climate change has shifted pollen phenology, leading to generally earlier starts (at a rate of up to 7 days decade-1) and longer durations (up to 11 days decade^{-1}) of spring pollen seasons (Anderegg et al., 2021; van Vliet et al., 2002; Y. Zhang et al., 2015; Y. Zhang & Steiner, 2022; Ziska et al., 2011). Such changes in pollen phenology were compounded by the climate-driven increases in pollen concentration during pollen seasons (Anderegg et al., 2021; Ziska et al., 2019). As exposure to pollen is a trigger of allergic asthma and allergic rhinitis (hay fever), climate change is anticipated to worsen seasonal allergies, imposing increasing costs on human well-being (D'Amato et al., 2014; Lake et al., 2017; Traidl-Hoffmann et al., 2003). Despite potentially profound climate change impacts on humans through the changing pollen seasons, the connection between pollen phenology and human perceptions has rarely been systematically studied. It is important to understand this connection for two motivations.

First, personal observations of pollen by the general public may provide a valuable untapped data source for pollen models. Current pollen models mainly use data from aerial sampling at pollen counting stations (Scheifinger et al., 2013), which are expensive and spatially sparse (Lo et al., 2019). There have been recent incentives to integrate crowdsourced natural observations of flower and pollen to improve process-based models of pollen phenology (Katz et al., 2023). Nevertheless, pollen data can be further expanded to a large scale through “social sensing,” where humans or devices on their behalf collectively gather data of the physical world, such as through discussions on social media (Wang et al., 2015a). Nevertheless, given great uncertainty in social sensing (Wang et al., 2015b), the accuracy of unintentional detection of pollen by the general public needs to be validated with pollen concentration data.

Second, changing pollen seasons framed as a potentially effective message to communicate the impacts of climate change. There have been inconsistent findings on if framing around public health can enhance climate change communication (Li & Su, 2018; Maibach et al., 2010). Nevertheless, the framing around changing pollen seasons, unlike other aspects of public health, has the unique advantages of strong scientific consensus (Corner et al., 2015) and strong ties to personal experiences (Ballew et al., 2019; Broomell et al., 2015; Jones et al., 2017; McDonald et al., 2015; Rudman et al., 2013; Scannell & Gifford, 2013). Nevertheless, personal experiences may not necessarily be associated with climate change, as this attribution process is influenced by psychological, demographic, cultural, and political factors (Akerlof et al., 2013; Hulme, 2014; Lahsen & Ribot, 2022; Myers et al., 2013; Reser & Bradley, 2020; van der Linden, 2015). In particular, there is a persistent ideological divide in perceptions (Dunlap et al., 2016), with individuals with more liberal values more likely to perceive the impacts of extreme weathers and associate them with climate change (Cutler, 2015; Howe & Leiserowitz, 2013). It is yet to be explored how the general public attribute changes in pollen phenology and if messages revolving pollen phenology can help bridge the ideological divide in climate change communication.

These two motivations prompted us to systematically study human perceptions of pollen phenology, both in terms of the accuracy of detection and patterns in attribution. These two questions may be answered using social media data. On the one hand, social media discussions is a promising method for social sensing of phenology. A one-year study showed that Twitter trends on allergy symptoms and antihistamine drugs correlated with pollen concentration in the United States (US) (Gesualdo et al., 2015). In addition, text and images posted to Twitter have been used to detect vegetation phenology (Shin et al., 2021; Silva et al., 2018). Nevertheless, it has also been suggested that the flowering at a National Park may be temporally mismatched with tourists' posts on Flickr (Breckheimer et al., 2020). Therefore, it is not completely clear if discussion on social media accurately reflects natural pollen phenology. On the other hand, social media data also contain rich textual information that can provide in-depth insight on public discourse. For example, the public attribution of the COVID-19 crisis on Twitter was shown to be driven by users' political orientation (W. Zhang et al., 2023). The attribution of pollen phenology by social media users is largely understudied.

This study aims to understand how social media users perceive pollen phenology under climate change from two perspectives. First, we test the hypothesis that social media users accurately detect variations in pollen phenology, such that the discussion of pollen on social media reflects temporal and spatial variations in natural pollen phenology. Second, we test the hypothesis that social media users' attribution of pollen phenology does not depend on ideology, specifically addressing the attribution to weather change and climate change.

2 Materials and methods

2.1 Processing and summarizing pollen discussions on Twitter

We retrieved social media discussions on pollen from the Twitter Decahose dataset, 10% sample of tweets, hosted at the University of Michigan (UM). During Dec 2–7, 2022, we queried the Twitter Decahose dataset using a PySpark tool “decahose-filter” (Meyer, 2022/2022) with the keyword “pollen” in the Great Lakes High-Performance Computing environment at UM. Queried data covered the time period of 2012 to 2022, with gaps in 2017 and a few other months that had missing or invalid data files. Queried data contained variables including unique tweet id, date (in the local time zone), user name, user description, user location, language, and text.

We applied reverse geocoding to geolocate Twitter users for two purposes: to filter for tweets that likely originated in the US and to further analyze spatial patterns across states within the US (Velardi et al., 2014). User location, self-described by users, often represents the location of tweeting, although not always. Note that many Twitter users choose not to describe their user location, and not all user location information can be identified to a known place (Dredze et al., 2013; Hecht et al., 2011). For users with location information, we took three steps in reverse geocoding. First, we located users to the US by searching for US-related keywords ("us", "u.s.", "u.s", "u.s.a.", "u.s.a", "usa", "united states", "united states of america", "america") in user location, ignoring case differences. Second, we attempted to locate users to states, based on the proximity of their coordinates to a known US postal code or direct mentioning of the name of a US place (county, city, or state) in a geoname database. Last, we attempted to locate users to large cities (with over 100,000 population) within the US, based on the proximity of their coordinates to a known large city or direct mentioning of the name of a large city. For the last two steps, we used a python package "twitter-user-geoencoder" (Bian, 2015/2023). Geonames and postal codes used were retrieved from https://download.geonames.org/ on Dec 23, 2022. If a user could be located in any of the three steps, we considered them to be within the US. We located users to states within the US whenever possible with the last two steps.

In order to focus on Twitter discussion on pollen, we applied the following filters. We removed all tweets with duplicated unique id. We kept only tweets posted in English. We removed tweets that only contain "pollen" in a tag, in a url, or as a part of a longer word, in order to keep tweets that contain the exact complete word "pollen". We kept only tweets posted by a user within the US identified from reverse geocoding.

We summarized the general patterns of the Twitter discussion on pollen in three aspects. First, we calculated the number of tweets (referred to as tweet count) within the US on each day to study the temporal trend of pollen phenology detected by Twitter users. Second, we calculated the average tweet count per day for each state to compare the intensity of discussion over space. Whenever analyzing tweet count, we adjusted for the expansion in US Twitter use base over time (Eq. 4-1), making values in early years comparable to the current ones from approximately 68 million US Twitter users.

$$\text{tweet count} = \text{raw tweet count} \times \frac{\text{estimated current number of US Twitter users}}{\text{estimated current number of US Twitter users of the year}} \quad [4\text{-}1]$$

Last, after text cleaning, we calculated the frequency of words in tweet text (including text that was retweeted and replied to) and generated a word cloud. The keyword “pollen” was removed from this analysis as it was present in all tweets collected. The authors also sampled 1000 random tweets to qualitatively summarize the common topics of discussion.

2.2 Validating with pollen concentration from aerial sampling

To validate if trends in pollen discussion on Twitter reflect natural pollen phenology, we obtained consistent and accurate pollen concentration data dating back to 2012 from 98 stations in the continental US associated with the American Academy of Allergy, Asthma & Immunology (AAAAI) and the National Allergy Bureau (NAB) (AAAAI, 2022). At stations located throughout the continental US, airborne pollen was sampled near daily using volumetric impactor samplers including either Rotorod or Burkard samplers (Frenz, 1999) and then classified to the genus or family level and counted by NAB-certified operators. The NAB dataset serves as one of the most commonly used data sources for the description and prediction of pollen phenology in public health and ecological research in North America. We cleaned the pollen concentration data to obtain pollen concentration (grains m^{-3}) summed over all plant taxa for each day and station.

We compared Twitter pollen phenology characterized with daily tweet count and natural pollen phenology characterized with daily pollen concentration. We assessed the correlation between Twitter and natural pollen phenology on the US level. We performed the following data processing steps.

1) We removed combinations of station and year with lower than a total pollen concentration of 100 grains m^{-3} to remove possibly erroneous data.
2) We transformed all tweet count and pollen concentration to their square root to compress extreme values and stabilize the variance (Bastl et al., 2018; Bonini et al., 2022).
3) We standardized each time series, either US-level tweet count or station-specific pollen concentration, to approximately between zero and one, by dividing all values by the resective 95th percentile. This step allowed comparability of natural pollen phenology across sites and between Twitter and natural pollen phenology.
4) We upscaled natural pollen phenology from the station level to the US level, by averaging the transformed pollen concentration over all stations for each day, removing average values generated by fewer than five data points.
5) We filled gaps in both US-level Twitter and natural pollen phenology time series (Katz et al., 2023) that were no longer than 14 days with linear interpolation.

6) We smoothed both US-level Twitter and natural pollen phenology time series with the Whittaker method (Kong et al., 2019).

We then tested the linear correlation between Twitter and natural pollen phenology, both over all dates with available data and during the spring pollen window from day-of-year (DOY) 41 to 180. To assess the detection of long-term trends in pollen phenology by Twitter discussions, we tested the linear correlation between the peak of Twitter and natural pollen phenology curves within the spring pollen window.

Spatially, we assessed the correlation between Twitter and natural pollen phenology on the state level. We performed the following data processing steps.

1) We removed combinations of station and year with lower than a total pollen concentration of 100 grains m^{-3} and combinations of state and year with lower than a total tweet count of 100.
2) We upscaled natural pollen phenology from the station level to the state level, by taking the average of pollen concentration over all stations in a state for each day.
3) We estimated long-term Twitter and natural pollen phenology on the state level, using tweet count and pollen concentration on each DOY from 1 to 365 averaged over all years for each state. As pollen concentration data collection had various starting dates, we removed average pollen concentration values generated by fewer than three data points.
4) We transformed all tweet count and pollen concentration to their square root.
5) We filled all data gaps no longer than 14 days with linear interpolation.

6) We smoothed all time series with the Whittaker method.

7) We identified for each state the start of Twitter pollen seasons ($\mathrm{SOS}_{\mathrm{Twitter}}$) as the first DOY that reaches 25% of the cumulative sum of tweet count in the spring pollen window (DOY 41–180) and identified the end of Twitter pollen season ($\mathrm{EOS}_{\mathrm{Twitter}}$) as the last DOY that reaches 75% of the cumulative sum of tweet count in the spring pollen window (Nilsson & Persson, 1981; Rasmussen, 2002). We similarly identified for each state the start and end of natural pollen seasons ($\mathrm{SOS}_{\mathrm{natural}}$, $\mathrm{EOS}_{\mathrm{natural}}$) using the cumulative sum of pollen concentration instead.

Using time series after data processing step 6), we generated animations for “pollen wave” from Twitter and natural pollen phenology, analogous to the idea of “green wave” that describes the flush of green over the course of the spring season across the country. We quantitatively tested the linear correlations between phenological metrics (start and end of pollen season) derived from Twitter and natural pollen phenology.

2.3 Identifying ideological patterns in attribution

We examined patterns in US Twitter users’ attribution of variations in pollen phenology specifically to weather change and climate change. We identified three groups of Twitter users in the US: a group of users that discuss the phenology of airborne pollen (“pollen group”), a subgroup of users that attributes changes in airborne pollen level to changes in weather related to temperature (“pollen-weather group”), and a subgroup of users that attributes changes in airborne pollen level to climate change (“pollen-climate group”).

Users in all groups tweet with the keyword “pollen,” which was already ensured for all tweets in the dataset. In addition, we filtered for users in the “pollen-weather group” by searching for keywords related to short-term temperature change (i.e., “warm”, “warmer”, “warming”, “hot”, and “hotter”); we filtered for users in the “pollen-climate group” by searching for keywords related to climate change (i.e., “climate” and “warming”). We identified all tweets that contained corresponding keywords for the three groups and took a random sample of 1,000 when more tweets were found.

As the keyword searching approach was coarse and often did not accurately classify users’ to our defined groups, we read and interpreted the full text in samples from the three groups. We imposed the following criteria to identify users in these three groups.

A) “pollen group” (e.g., “*this pollen is killing me*”)
    1) The tweet was about airborne pollen, i.e., pollen grains dispersed through the air. Discussions about pollen in fossils, pollen as human food, or pollen carried by pollinators, for example, did not qualify.
    2) The tweet was time-sensitive. General statements about pollen allergies (e.g., “*I am allergic to dust and pollen*”) and air filter commercials did not qualify.

B) "pollen-weather group" (e.g., "*pollen level is high and warm weather will make it worse*")

   1) The tweet satisfied all criteria in the "pollen group."
   2) Temperature-related keywords were used in a context of weather. Keywords when used in other contexts (e.g., "*my throat feels warm and itchy because of pollen allergy*", "*I am a hot mess in this pollen season*") did not qualify.
   3) The tweet implied a short-term change in temperature (within a year or a few years). In particular, discussions on climate change did not qualify for this group.
   4) The tweet implied correlation between weather and pollen. Simply having both ideas in the same sentence without correlation (e.g., "*I can't go out because it is too hot and there is too much pollen*") did not qualify. Implications that warm temperatures and high pollen level usually co-occur (e.g., "*I wish I could have this warm weather all year minus the pollen*", "*spring brings warm weather but also pollen*") did qualify.

C) "pollen-climate group" (e.g., "*global warming could make your pollen allergies a lot worse*")

   1) The tweet satisfied all criteria in the "pollen group."

2) The tweet implied a long-term change in temperature (on a decadal scale or longer). In particular, discussions on weather change did not qualify for this group.
3) The tweet implied causal impacts of climate change on pollen. Simply having both ideas in the same sentence without causation (i.e., "*there is global warming, wars, and a very high pollen count*"). We did not include tweets that discussed the effects of pollen on climate (i.e., "*find out about how pollen affects cloud formation and maybe climate*"), the effects of extreme heat reducing pollen activity (e.g., "*climate change = no pollen = good*"), or the understanding of pollen directly causing climate change (e.g., "*tree pollen causing climate change*").
4) The user did not disagree with the climate change impact on pollen phenology. We excluded tweets that explicitly expressed disagreement or skepticism (e.g, "*increase in pollen season caused by global warming???????*") or sarcasm (e.g., "*guess WaPo is going to recycle their old story about climate change making pollen season worse*").

Among all US Twitter users in the dataset, we summarized the conditional probability of a user attributing pollen phenology to weather or climate drivers, given the general interest in pollen phenology (Eq. 4-2).

$$P(\text{ weather} \mid \text{pollen}) = \frac{n_{\text{pollen-weather}} / \rho_{\text{pollen-weather}}}{n_{\text{pollen}} / \rho_{\text{pollen}}}$$

$$P(\text{ climate} \mid \text{pollen}) = \frac{n_{\text{pollen-climate}} / \rho_{\text{pollen-climate}}}{n_{\text{pollen}} / \rho_{\text{pollen}}} \qquad [4\text{-}2]$$

Here, *n* refers to the number of distinct users in each group after manual labeling; *ρ* refers to the sampling rate for a group when we took a random sample for manual labeling, calculated as the ratio between the number of distinct users in the sample of tweets containing respective keywords and the number of distinct users in all tweets containing respective keywords.

We further estimated the ideology of identified users in these three groups using an established method of correspondence analysis (Barberá et al., 2015). This method uses commonly followed Twitter accounts, not necessarily political, to project users to a latent ideological space, assuming that users who follow a similar set of accounts are more likely to have similar ideology. A more positive ideology score corresponds to relatively conservative ideology, and a more negative ideology score corresponds to relatively liberal ideology. We retrieved users' followed accounts using Twitter's API between Mar 29 and 31, 2023. Our ideology scoring was implemented with functions adapted from the *R* package *tweetscores* (Barberá, 2021). Note that not we could not estimate the ideology of all users, because many have deleted their accounts, did not give permission to access friends list, or did not follow any popular accounts.

We examined the effects of ideology on attribution in two ways. First, we qualitatively compared the probability density distribution of user ideology in three groups, after smoothing histograms with Gaussian kernels of 0.2 bandwidth. Second, we quantitatively tested for the correlation between conditional probability of attribution and ideology. We calculated both conditional probability (weather given pollen and climate given pollen) for each bin of ideology (Eq. 4-3). We chose to bin ideology scores from –2 to 2, at intervals of 0.5, leading to eight bins in total.

$$P_i(\text{ weather} \mid \text{pollen}) = \frac{n_{i,\text{pollen-weather}} / \gamma_{\text{pollen-weather}} / \rho_{\text{pollen-weather}}}{n_{i,\text{pollen}} / \gamma_{\text{pollen}} / \rho_{\text{pollen}}}$$

$$P_i(\text{ climate} \mid \text{pollen}) = \frac{n_{i,\text{pollen-climate}} / \gamma_{\text{pollen-climate}} / \rho_{\text{pollen-climate}}}{n_{i,\text{pollen}} / \gamma_{\text{pollen}} / \rho_{\text{pollen}}} \qquad [4\text{-}3]$$

Here, *i* refers to the bin of ideology score, ranging from 1 to 8; *γ* refers to the retrieval rate for a group when we only successfully retrieved ideology for a subset of identified users, calculated as the ratio between the number of distinct users with estimated ideology and the number of distinct users identified to be in the group; we also similarly adjusted for sampling rate *ρ*. We tested if the conditional probability was linearly correlated to the bin of ideology score.

All linear correlations mentioned above were quantified with the Pearson correlation coefficient (*r*) and tested for statistical significance with *t*-tests. All data analyses were performed in *R* v. 4.2.0 (R Core Team, 2023).

3 Results

3.1 Patterns of pollen discussions on Twitter

We queried the Twitter Decahose dataset, 10% of all tweets, with the keyword "pollen" and obtained 1,465,675 tweets from 2012 to 2022. We selected 190,473 unique English tweets with the exact word "pollen" generated within the US for further analyses. Given that only 66% users in our dataset described their location, our filtered dataset was a subset of all pollen discussion on Twitter in the US, and numerical results should be interpreted in relative terms.

We found strong seasonality in the trends of pollen discussions (Fig. 4-1a), with the daily tweet count sharply increasing in March, peaking in early April, and gradually decreasing until late June. In our dataset, 71% of the tweets were posted in the spring pollen window from DOY 41 (around Feb 10) to DOY 180 (around June 29), with an average of 120 tweets per day. The highest daily tweet count every year ranged from 323 to 2903, with the highest peak of 2903 tweets (1665 before adjustment for Twitter user increase) observed on Mar 20, 2012.

With 177,722 tweets that could be located at the state level, we found that the intensity of pollen discussion varied by state (Fig. 4-1b). The average tweet count per day in the spring pollen window was the highest in Georgia (20 tweets day^{-1} in our dataset), followed by Texas (11 tweets day^{-1}) and North Carolina (11 tweets day^{-1}), California (9 tweets day^{-1}), and New York (7 tweets day^{-1}). Pollen discussions were generally more intense in coastal states compared to inland states and in southern states compared to northern states.

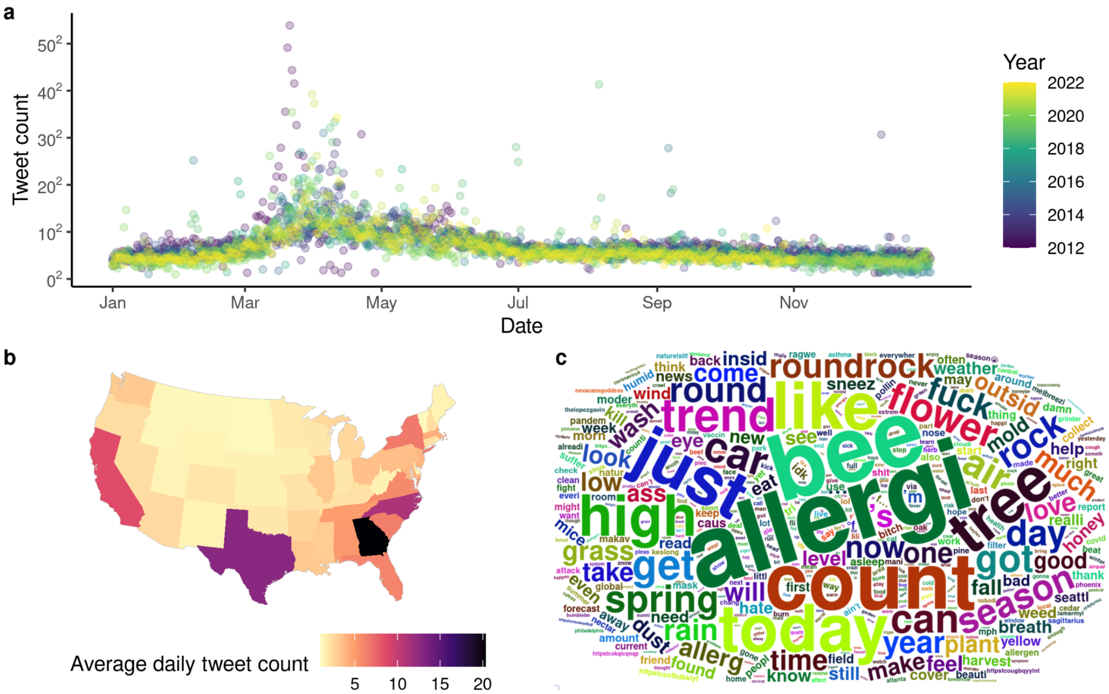

Figure 4-1. Temporal, spatial, and topical patterns of discussions on pollen on Twitter in the US. **(a)** Estimated tweet count on each day of the year. Colors indicate different years. **(b)** Average daily tweet count posted from DOY 41 to 180 in each state. Colors indicate intensity of discussion on pollen. **(c)** Word cloud of frequent words in tweets. All data were derived from 190,473 tweets that were a subset of all pollen discussion on Twitter within the US.

We identified frequent word stems in pollen discussion on Twitter in the US (Fig. 4-1c), with the top 15 being "allergi", "bee", "count", "just", "like", "today", "tree", "high", "trend", "car", "get", "can", "flower", "air", and "got". The keyword "allerg*" was present in 12% of tweets collected within the US. These frequent words reflect several common topics in pollen discussion, including pollen allergy, pollen level forecasting, bee pollen as food, nature observations, car wash, sentiments about spring, and air filter commercials.

3.2 Alignment with natural pollen phenology

Comparing Twitter pollen phenology characterized with tweet count and natural pollen phenology characterized with pollen concentration, we examined how accurately pollen discussions on Twitter reflect temporal and spatial variations in pollen phenology. We found generally similar temporal trends between Twitter and natural pollen phenology on the US level (Fig. 4-2a). The most dominant pollen peaks in spring were evident in both Twitter and natural pollen phenology, while the minor pollen peaks in fall and around New Year were not captured in Twitter pollen phenology. There was a significant correlation between pollen phenology derived from two sources (Pearson correlation coefficient $r = 0.691$, $p \leq 0.001$, *t*-test), which was slightly weaker when focusing on the spring pollen window ($r = 0.602$, $p \leq 0.001$).

Both Twitter and natural phenology exhibit a latitudinal gradient over space, with southern states experiencing earlier pollen seasons compared to northern states (Fig. 4-2b). Across 29 states, we found a significant correlation between the start of Twitter and natural pollen seasons ($\mathrm{SOS}_{\mathrm{Twitter}}$ and $\mathrm{SOS}_{\mathrm{natural}}$), defined as DOYs crossing the 25% of cumulative sum of tweet count or pollen concentration in the spring pollen window ($r = 0.180$, $p \leq 0.05$). Similarly, there was a significant correlation between the end of Twitter and natural pollen seasons ($EOS_{Twitter}$ and $EOS_{natural}$) defined as DOYs crossing the 75% of cumulative sum ($r = 0.360$, $p \leq 0.001$). These results together supported the hypothesis that the discussion of pollen on social media reflects in natural pollen phenology, both over time and over space.

3.3 Ideological bias in attribution to climate change

We identified three groups among all US Twitter users in our dataset, including a "pollen group" that discussed pollen phenology, a "pollen-weather group" that attributed pollen phenology to weather, specifically temperature changes, and a "pollen-climate group" that attributed pollen phenology to climate change (Fig. 4-3a). After manually screening samples of tweets with selected keywords, we identified 143,577 distinct users in the "pollen group", 1,871 in the "pollen-weather group, " and another 790 in the "pollen-climate group." In a random sample of our dataset, we estimated 641, 413, and 421 users falling into the "pollen group," "pollen-weather group," and "pollen-climate group," respectively. Given the general interest in pollen phenology. the conditional probability of a user attributing pollen phenology to weather change ($P(\text{weather}|\text{pollen}) = 0.00838$) was higher than that of attributing pollen phenology to climate change ($P(\text{climate}|\text{pollen}) = 0.00430$).

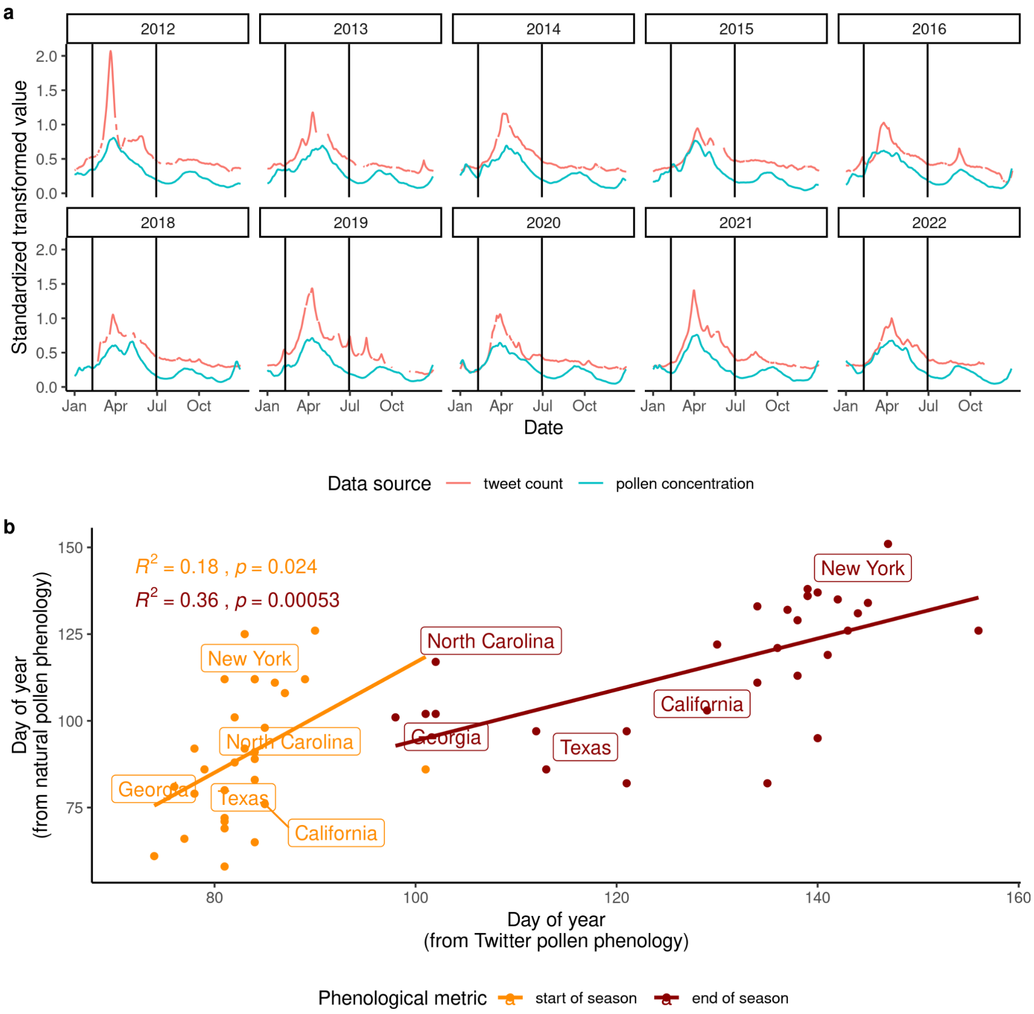

Figure 4-2. Twitter pollen phenology aligns with natural pollen phenology over time and space. **(a)** Trends in Twitter pollen phenology and natural pollen phenology in the US, calculated from the standardized transformed tweet count and pollen concentration, respectively. Vertical lines delineated a defined spring pollen window (from day-of-year 41 to 180). **(b)** Correlation between state-level phenological metrics (*t*-test), including the start of season (SOS) and the end of season (EOS), derived from Twitter and natural pollen phenology, respectively. Data points corresponding to selected states are labeled.

We further explored the ideology of users in these three groups and how user ideology affected attribution of pollen phenology to weather and climate change. Qualitatively, the probability density distribution of user ideology in all three groups showed bimodal distributions, with two peaks corresponding to relatively conservative (positive ideology score) and relatively liberal users (negative ideology score) (Fig. 4-3b). Nevertheless, the relative weight of the two peaks varied among groups. In the "pollen group," there were more conservative than liberal users. We closely read the descriptions and tweets of some users with positive ideology scores and found a large proportion located in conservative states such as Georgia and Texas. However, in the "pollen-climate group," there were considerably more liberal than conservative users. Note that we noticed a considerable portion of users in the "pollen-climate group" to be media and scientists, with 535 out of 596 tweets from this group generated based on news or scientific articles.

Quantitatively, we found that the conditional probability of attributing pollen phenology to climate change was significantly correlated to the bin of ideology a user was in ($r = -0.246$, $p > 0.05$), with more liberal users being more likely to make the attribution to climate change (Fig. 4-3c). In contrast, we did not find significant correlation between attribution to weather change and user ideology ($r = -0.846$, $p \leq 0.01$). These results partly rejected the hypothesis that social media users' attribution of pollen phenology does not depend on ideology, by revealing that users were likely to be biased when attributing pollen phenology to climate change, but not when attributing to weather change.

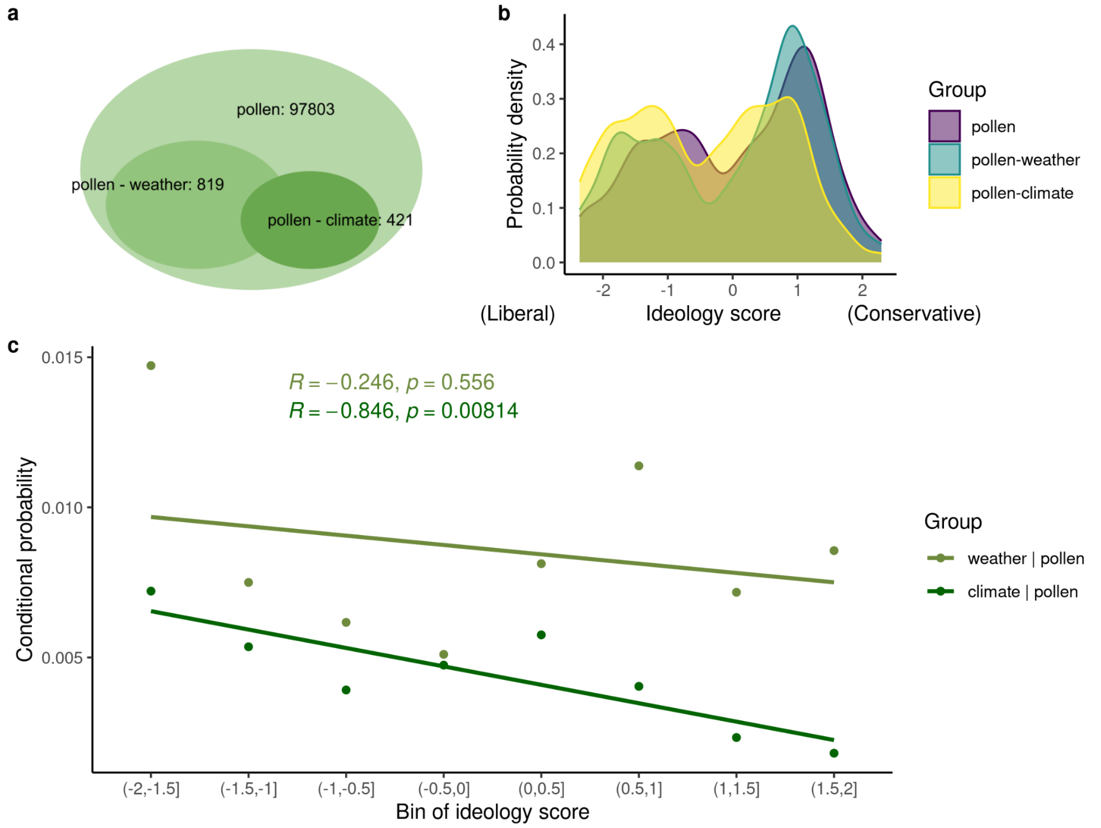

Figure 4-3. Twitter users' attribution of pollen phenology were likely ideologically biased. **(a)** Venn diagram showing the relationship between three groups of US Twitter users identified in this study, showing the estimated number of US Twitter users in each group identified from a dataset containing 190,473 tweets. **(b)** Probability density functions showing the distribution of ideology score in three groups of users. **(c)** Correlation between conditional probability of a user attributing pollen phenology to a specific driver, either weather or climate change, and the bin of ideology the user was in (*t*-test).

4 Discussion

In this study, we focused on the human dimension of climate change by examining social media users' perceptions of changing pollen phenology. Pollen discussions on Twitter in the US showed strong seasonality, spatial heterogeneity, and topical diversity. Twitter-derived and natural pollen phenology aligned over time and space, suggesting that social media users are likely to be accurate social sensors to variations in pollen phenology. Analyzing a subset of text and users, we revealed an ideological bias in attributing variations in pollen phenology to climate change but not to weather change, with liberal users more likely to agree with climate change impacts on pollen phenology. Our study contributed to our understanding of human perceptions to one of the most visible climate change impacts, with implications for scientific data collection from public discourse and message framing for climate change communication.

Social sensing provides promising avenues for expanding data collection beyond traditional methods to advance scientific understandings on climate change impacts. Our findings validate that social media users respond predictably to variations in pollen phenology, including rises and falls of pollen concentration in the US, and the sequence of pollen season across US states. Our results were supported by previous findings that Twitter discussion on allergy symptoms and antihistamine drugs aligned with natural pollen phenology in 2017 on the US and state levels (Gesualdo et al., 2015). The accurate detection of pollen phenology by Twitter users gives confidence to harness social media data to enhance pollen phenology models.

The efficiency and quality of data collected from human behaviors will benefit from advancements in natural language processing (Ghanem & Erbay, 2023; Hodorog et al., 2022; Nistor & Zadobrischi, 2022; Zhou et al., 2022). Pollen phenology might present a relatively special case with high accuracy of social sensing. In comparison, there were greater uncertainties in detecting vegetation greenness (Silva et al., 2018) and fall phenology (Shin et al., 2021). There was even greater complexity in linking Twitter discussion with temperature, with users generally not sensitive to absolute temperature or extreme weather events, but rather local temperature anomalies (Hamilton & Stampone, 2013; Kirilenko et al., 2015). In addition to social media, pollen phenology has been inferred from internet search (Hall et al., 2020), medication sales (Sheffield et al., 2011), and hospital visits (Lappe et al., 2023; Wakamiya et al., 2019), suggesting diverse ways of using individuals as sensors to lower the cost and increase the coverage of data collection under climate change.

Our study revealed both challenges and opportunities for leveraging pollen phenology as a message to communicate the personal impacts of climate change. While the general public is sensitive to changes in pollen seasons, connecting these personal experiences to climate change can be challenging (Kirilenko et al., 2015). Indeed, our findings suggested that agreement to the message of climate-driven pollen season changes depended on ideology, consistent with the ideological bias in other climate change perceptions (Dunlap et al., 2016; Falkenberg et al., 2022; Jang & Hart, 2015; McCright et al., 2016; McCright & Dunlap, 2011; Weber, 2010). Previous research has suggested various factors that contribute to such ideological bias, including the influence of media and opinion leaders (Brulle et al., 2012; Carmichael et al., 2017), the politicization of climate-related issues (Bolsen & Druckman, 2018), underlying ideological worldviews (Kahan et al., 2012), trust in scientific institutions (Hmielowski et al., 2014), and the role of social networks (Hart et al., 2015; Williams et al., 2015). These factors often interact and reinforce each other, perpetuating biased perceptions. In our study, we also observed the influence of media and opinion leaders, including scientists, in shaping the discourse on climate change impacts on pollen phenology. Biases in the media and opinion leaders (Boykoff & Boykoff, 2004), reflected in the lack of representation of extreme right users in this discourse, may further perpetuate ideological bias, even on such a topic with strong scientific consensus.

Despite these challenges, we identified encouraging signs that discussions on pollen phenology have the potential to reduce the ideological divide on climate change perceptions. We observed a high level of interest among relatively conservative users in pollen discussions, which was consistent with the high pollen concentration in conservative states. The association between pollen and weather resonated with users across different ideologies, offering an opportunity to establish common ground in climate change communication (Bloodhart et al., 2015; Shao, 2016). In addition, the impacts of pollen on individuals' daily lives went beyond allergies, seen from the complaints about car washing after pollen deposition. Despite the foreseeable challenges (Egan & Mullin, 2012), messages revolving pollen phenology holds promise in strategically bridging the ideological divide in public perceptions about climate change.

We identified several caveats in our study. First, not all tweets in our dataset were generated by individuals from the general public, as they also originated from weather stations, news media, and scientists. Consequently, the findings regarding social media users' perceptions cannot be directly interpreted as personal perceptions. To mitigate this issue, we expanded our analysis to include both organic tweets, replies, and retweets when assessing detection accuracy, and we focused on distinct users when examining attribution patterns, in order to enhance the representation of individual users within the datasets. Second, discussions on pollen on social media may not solely reflect personal experiences related to pollen but are likely influenced by exposure to media (Egan & Mullin, 2017), which may exhibit its own seasonality in news coverage. Similarly, the attribution of pollen phenology in our dataset may be influenced by ideas propagated by the media at the time, rather than solely stemming from users' inherent long-term understanding (Carvalho, 2010). Third, our data collection through social media represents a passive form of observation, and numerous relevant factors could not be directly or accurately measured, including user location, user identity, contextual information of tweets, and ideology. Despite our efforts to estimate user ideology using a method suitable for the general public (Barberá et al., 2015), missing data and considerable uncertainties remain. Therefore, further investigations with systematically designed data collection are necessary. Despite these limitations, our study represents a significant step towards achieving a more comprehensive understanding of the intricate relationship between climate change, pollen phenology, and human perceptions.

Conclusion

Situated at the intersection of ecology, climate change, and human society, the field of phenology faces new challenges in the era of global changes. Climate change and human modifications have resulted in shifting relationships between phenology and the environment, impacting both ecological and social systems. In this dissertation, I investigate several emerging interactions in phenology in the Anthropocene. I demonstrate that anthropogenic climate change has the potential to disrupt the coupling between phenology and other environmental cues, leading to phenological mismatches (Chapter 1). Moreover, in human-dominated landscapes, the management of vegetation may further exacerbate the mismatch between climate and land surface phenology (Chapter 2). New data on vegetative phenology from high-resolution remote sensing can be used to characterize and predict pollen phenology, with potential applications to public health (Chapter 3). Observations of pollen by the general public provide another promising data source for phenological studies, as well as an opportunity for climate change communication, although it is crucial to address potential ideological biases in perceiving the impact of climate change on pollen season (Chapter 4). I identify several recurring themes in these studies.

Firstly, the four studies highlight the importance of synthesizing our scientific understanding of phenology. Previous meta-analyses have presented a qualitative consensus that phenology is a clear fingerprint of climate change (Parmesan & Yohe, 2003). Nevertheless, substantial variances exist in how phenology responds to climate change and human modification across space, time, and study systems (Ovaskainen et al., 2013; Park et al., 2019; Wang et al., 2019). I seek to advance our systematic understanding by developing a generalizable theoretical framework and a widely applicable quantitative approach (Chapter 1), as well as conducting long-term studies spanning continental to global scales (Chapters 2–4). Such systematic studies enable the validation of findings on large scales (Chapter 4), identification of patterns and drivers (Chapter 2), extrapolation of our understanding (Chapter 3), and comparison among various study systems (Chapter 1). Further theoretical advancements may be made through linking phenological mismatch to fitness (Kharouba & Wolkovich, 2020, 2023), explicitly considering the role of human modifications in phenology (Ruas et al., 2022), and formalizing the scaling of phenology and phenological responses (Cleland et al., 2007).

Secondly, the studies have shed light on the convoluted mechanisms underlying phenology in ecological and social systems. While the coupling between phenology and the environment might be disrupted during climate change and land use change, accurate predictions of such disruptions have not been achieved (Chapters 1 and 2). Flowering phenology displays large unexplained variations on the species and individual plant levels, possibly attributed to factors including plasticity, genetic makeup, or microclimate (Chapter 3). Social media discussions exhibit phenological patterns that are generally synchronized with natural phenology, but the underlying mechanisms that drive this synchronization are not clear (Chapter 4). Emerging data sources such as herbarium specimens (Jones & Daehler, 2018), high-resolution remote sensing (Zhao et al., 2022), and social media (Gesualdo et al., 2015) provide opportunities for improving phenology models. Although these big data significantly benefit data-driven phenology models, it is vital to gain mechanistic understanding from process-based models (Clark et al., 2014), both to constrain the prediction of phenology under unprecedented climate change and to identify potential intervention strategies. A promising pathway forward is to integrate process-based and data-driven models (Read et al., 2019) to understand and predict the complex mechanisms of phenology.

Lastly, these studies collectively explore an interdisciplinary approach in the investigation of phenology as a socio-ecological system (Armatas et al., 2016; Breckheimer et al., 2020). The framework and methods developed for phenological mismatch, motivated by theory in dynamical systems, can be applied to the mismatch between human activity and natural events (Chapter 1). The potential climate-phenology mismatch prompts the consideration of sustainable management practices in croplands, rangelands, and timberlands (Chapter 2). Development in the modeling of pollen phenology requires the integration of data and knowledge from ecology and public health (Chapter 3). Moreover, interpreting and addressing ideologically biased human perceptions of pollen phenology in a changing climate requires insight from various social science disciplines, including politics, sociology, and psychology (Chapter 4). The intricate reciprocal relationship between ecology and human society determines that the field of phenology is transforming into an interdisciplinary field (Bastian & Bayliss Hawitt, 2023).

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Introduction

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Chapter 1

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Chapter 2

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