ASSESSING PHENOLOGICAL SENSITIVITY TO CLIMATE CHANGE IN PRAIRIE SPECIES USING CITIZEN SCIENCE DATA

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Phenology, the timing of life cycle events, is a key trait in understanding an organism's response to environmental variables. Shifts in phenology, especially in plant species, have been a key indicator of how climate change is affecting biodiversity and ecosystem dynamics. However, because species often vary in their phenological responses, shifts in phenology also may have profound impacts on species interactions and the dynamics of communities. Despite the understanding of general trends of changing phenology, we lack understanding of why species differ in their responses, and how responses may vary across broad regions. Large-scale citizen science datasets offer new opportunities to explore relationships between the synchrony of life stages, seasonal climate conditions, and spatial variation in plant phenology. Using over 19,000 citizen science observations from the iNaturalist platform, I assess the phenological sensitivity of 28 prairie species within the Willamette Valley-Puget Trough Ecoregion. We used a Bayesian hierarchical model to identify key environmental drivers, such as temperature and latitude, and to evaluate species-specific responses to these changes. Life-history strategies, particularly the distinction between annual and perennial species, were incorporated to

assess how these traits influence phenological shifts. Results revealed that spring temperature, precipitation, and latitude were significant predictors of flowering time, with warmer temperatures generally advancing flowering and higher precipitation and latitude delaying it. Significant interaction between temperature and latitude indicated that temperature effects on phenology vary across geographic space. Species differed in magnitude, but not direction, in their phenological sensitivity, and early flowering species tended to be more responsive to temperature variation. While perennial species flowered earlier on average than annuals, life-history strategy did not significantly explain variation in climate sensitivity. These findings demonstrate the value of citizen science data for capturing phenological patterns across space and taxa. Such approaches will be essential for anticipating shifts in ecological interactions and to improve understanding of the consequences of climate change.

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Introduction

Phenology, the timing of life cycle events, shapes how organisms interact with their environment and with other species by influencing key biological events in response to environmental cues. Changes in seasonality and annual climatic factors, such as temperature and precipitation, influence phenology by impacting an organism's ability to synchronize with environmental conditions (Ramirez-Parada 2024). With increasing vulnerability to climate change, marked by rising temperatures, altered precipitation patterns, and greater climatic extremes, shifts in the climate have continued to alter phenological patterns. Within the Pacific Northwest alone, temperatures have risen over the last century an average of 0.7 °C, summer, average fall precipitation has decreased, and climatic water deficit has increased (Abatzoglou et al., 2013). These climatic changes have significant implications for the region's ecosystems, influencing the timing of critical events such as flowering. The ability to analyze and predict how different plant species with a variety of traits will respond to these changes is essential for managing ecosystems and for protecting native biodiversity (Keller and Shea 2020). Additionally, assessing how plant species' phenological sensitivity varies across space is critical for understanding how regional ecosystems will adapt to ongoing climatic changes (Gerretson et al. 2023).

However, only a few studies have assessed how life history and a species' historical timing of flowering affect phenological sensitivity to climatic changes across space. For instance, a study encompassing 30 functionally diverse species across the eastern United States found that early-flowering plant species showed greater sensitivity to spring temperature changes compared to later-flowering plants (Park et al. 2018). Park et al. noted

that long-lived perennials, unlike annuals, may acclimate to climate change over time resulting in slower phenological shifts. Furthermore, annual herbs have shorter flowering periods and more variance in flowering time compared to perennial herbs (Nagahama and Yahara 2019). This variability allows annual species to be more adaptable to unpredictable habitats relative to perennials, suggesting more fluctuation in their phenology due to climate (Nagahama and Yahara 2019). Identifying key differences in phenological responses between species will help illuminate the underlying mechanisms that govern how plant species may or may not adapt to changing climatic conditions.

Species phenological sensitivity may vary across spatial gradients as well. Recent studies have shown that plant populations from warmer regions have a higher degree of phenological sensitivity compared to populations found in colder regions (Love and Mazer 2021; Park et al. 2019). Similarly, along latitudinal gradients, some studies suggest that northern populations may exhibit increased phenological sensitivity due to greater climatic variability (Prevéy et al. 2017), while others report reduced sensitivity in these regions, highlighting ongoing uncertainty and the potential influence of biome-specific responses (Love and Mazer 2021). Geographic variability in phenological timing could have widespread ecological impacts. Intraspecific variability may alter patterns of gene flow, promoting or inhibiting adaptive evolution (Sexton et al. 2011). Interspecific variability can lead to shifts in community structure, disrupting synchrony of species interactions such as pollination (Rafferty et al. 2020). Few studies have assessed both sources of variability within a specific ecosystem, leaving a gap in understanding how phenological patterns scale from individual- and population-level responses to emergent community-level dynamics. Evaluating the combined effect of geographic variability and species' life history traits on

phenology will provide a more refined understanding of how species in the Pacific Northwest will adapt to current and future climate conditions.

The citizen science platform iNaturalist presents an emerging tool for studying plant phenology at large spatial and taxonomic scales by engaging both scientists and trained volunteers (López-Guillén et al., 2024). Despite its expanding use, few studies have leveraged iNaturalist data to quantify species-specific phenological sensitivity to climate across entire plant communities, highlighting a critical gap this study aims to address. By using iNaturalist, phenological data on many plant species can be collected at a scale that exceeds the potential of a single study. Many studies have demonstrated the potential of citizen science to assess trends in phenological stages and the impacts of climate change on biodiversity. Puchałka et al. (2022) found citizen science to be a reliable tool using a large-scale dataset to find the annual mean temperature and precipitation as the main drivers for *Anemone nemorosa* phenology in Europe. Similarly, Iwanycki et al. (2022) found that iNaturalist data and herbarium data produced comparable results in flowering times. With the recent increase of citizen science platform usage, hopes for more robust large-scale phenological studies are becoming possible by capturing diverse patterns of species' responses to both current and future climate conditions (Puchałka et al. 2022).

iNaturalist data can be leveraged to capture phenological responses within geographically distinct areas. The Willamette Valley-Puget Trough (WVPT) ecoregion is a low-elevation corridor stretching from Oregon’s Willamette Valley through Washington’s Puget Trough. It is characterized by a Warm Mediterranean climate with wet winters and dry summers, and unique plant communities. This region is ecologically significant due to its high biodiversity, large number of endemic and threatened species, and its exposure to

urban fragmentation. Studying phenological sensitivity in the WVPT provides an opportunity to examine plant responses to a fine-scale climatic and spatial gradient within a landscape shaped by both ecological diversity and significant human influence. Insights from this region can be used for development of targeted conservation strategies as climate change intensifies (Prevéy et al. 2020).

In this study, we asked: (i) What are the primary climatic drivers of plant phenology across the region, and how do their effects vary across space and among species? (ii) How do annual and perennial plant species modulate their sensitivity to climatic changes in plant phenology? We hypothesize that spring temperature will be the dominant climatic driver of flowering phenology across the WVPT ecoregion, with increasing temperatures leading to earlier flowering, while higher spring precipitation and latitude will be associated with delayed phenology. Additionally, we predict that phenological responses will vary geographically, with species in more northerly latitudes will exhibit greater phenological sensitivity to temperature compared to southern latitudes. We also expect annuals to be more phenologically sensitive than perennials due to their shorter life cycles and reliance on favorable seasonal conditions.

Methods

Study System

Plant species were selected from the citizen science platform, iNaturalist (https://www.inaturalist.org/), following the select criteria: (i) observation was located within the WVPT ecoregion. (ii) Research grade observations between the years 2018-2024. Observations earlier than 2018 were excluded due to the low frequency and inconsistency. (iii) The presence of flowering had to be easily identifiable to ensure accuracy and reliability of phenological data. (iv) Included at least 50 unique flowering observations across space and time. A total of 28 herbaceous forb species were selected for analysis, representing a range of life history strategies (annual and perennial), native and non-native status, and taxonomic families (Table 1). Only herbaceous forbs were used; large woody species were excluded from the selection to maintain the focus on prairie ecosystems.

Phenological Data

The appearance of flowering was determined by the presence of the reproductive structures within the flower. Volunteers, all who had suitable training or prior experience on flowering structures, contributed to the accuracy and consistency of observation annotations. To ensure coordination, all species were placed on a shared list allowing volunteers to view and verify each species. Volunteers used the "Identify" tab on iNaturalist to scroll through pages of observations, focusing only on annotating images where flowering was not present. This approach was designed to address the inherent bias in citizen science platforms where users are more likely to photograph flowering species. Once all necessary observations were annotated, each species was downloaded following the same pattern: (i) observations annotated with flowers and (ii) observations with no annotations. The data was

downloaded in two different sessions and merged to get presence-only flowering data for each species. The collection date for each observation was converted into day of year (DOY).

Table 1: The number of species and different categorical traits of examined species. Observations refer to the total number of presence-only images.

Family	Species	Observations	Lifespan	Native Status
Fabaceae	Acmispon americanus	97	annual	Native
Boraginaceae	Adelinia grandis	595	perennial	Native
Orobanchaceae	Bellardia viscosa	1035	annual	Introduced
Brassicaceae	Brassica rapa	314	annual	Introduced
Asparagaceae	Camassia leichtlinii	1780	perennial	Native
Gentianaceae	Centaurium erythraea	399	annual	Native
Onagraceae	Clarkia amoena	404	annual	Native
Onagraceae	Clarkia purpurea	205	annual	Native
Plantaginaceae	Collinsia grandiflora	451	annual	Native
Ranunculaceae	Delphinium menziesii	188	perennial	Native
Caryophyllaceae	Dianthus armeria	351	annual	Native
Onagraceae	Epilobium densiflorum	205	annual	Native
Asteraceae	Eriophyllum lanatum	821	perennial	Native
Geraniaceae	Geranium dissectum	339	annual	Introduced
Geraniaceae	Geranium lucidum	2249	annual	Introduced
Iridaceae	Iris tenax	1890	perennial	Native
Apiaceae	Lomatium utriculatum	578	perennial	Native
Fabaceae	Lupinus bicolor	360	annual	Native
Primulaceae	Lysimachia arvensis	401	annual	Invasive
Asteraceae	Madia elegans	506	annual	Native

Boraginaceae	Myosotis discolor	915	annual	Introduced
Boraginaceae	Plagiobothrys figuratus	88	annual	Native
Boraginaceae	Plagiobothrys nothofulvus	51	annual	Native
Valerianaceae	Plectritis congesta	1336	annual	Native
Rosaceae	Potentilla gracilis	197	perennial	Native
Ranunculaceae	Ranunculus occidentalis	568	perennial	Native
Saxifragaceae	Tellima grandiflora	3204	perennial	Native
Asteraceae	Wyethia angustifolia	292	perennial	Native

Climatic and Elevation Data

Average monthly temperature and precipitation data was extracted in 4km resolution from PRISM climate group (http://prism.oregonstate.edu/). This data was applied to each observation to get exact high resolution climate readings for each species *x* year combination. Temperature (spring_temp) and precipitation (spring_precip) predictor variables were created by averaging monthly values from February – May. USGS Elevation data was obtained using the R package, *elevatr* v0.99.0 (Hollister et al. 2023).

Analysis

To model the day of year peak flowering, we parameterized a multiple linear regression model with Markov Chain Monte Carlo sampling from the *brsm R* package v2.22.0 (Bürkner 2021). This model included day of year (DOY) of each observation of flowering as the response variable, with spring temperature, spring precipitation, latitude, elevation, and life history strategy (annual vs. perennial) included as fixed effects. To account for species-specific variation in phenological responses, random slopes and

intercepts were estimated for each species across the four continuous predictors: spring temperature, spring precipitation, latitude, and elevation. To capture the complex relationships between these variables, a five-way interaction was incorporated among the fixed and random effects to assess how predictor variables affect community as a whole and on a more species-specific level. (eq. 1). Including all two-way to higher-order interactions enabled the assessment of how combinations of predictors, such as temperature and latitude, jointly influence phenological timing, reflecting known ecological dependencies.

(eq. 1) $$DOY \sim 1 + elevation \times springtemperature \times springprecipitation \times latitude \times lifehistory + (1 + elevation \times springtemperature \times springprecipitation \times latitude \mid species)$$

Using uninformed priors, the model was fit until convergence. Convergence was assessed both visually and with the Gelman–Rubin statistic (r-hat < 1.1 for all parameters) using four independent chains of 4000 iteration. Model fit was further assessed using visual posterior predictive checks implemented in the *bayesplot* v1.12.0 R package (Gabry & Mahr 2025). All predictor variables were standardized prior to modeling (mean = 0, SD = 1) to facilitate comparison of effect sizes. As a result, model estimates reflect changes in DOY per standard deviation of each predictor. Estimates reported in the results were rescaled to the original units post hoc for ease of interpretation where appropriate. Certainty in the posterior slope estimates were evaluated by reporting the 95% credible interval for each estimate. A secondary analysis was conducted to assess whether earlier-flowering species exhibited greater phenological sensitivity to temperature. A weighted linear regression was

performed using the R package *lme4* v1.1-37 (Bates et al., 2015), where species-specific posterior mean slopes for temperature sensitivity were regressed against each species' mean flowering day of year (DOY), calculated from all flowering observations. Each species was weighted by the inverse of the squared standard error of its posterior estimate, giving greater influence on species with more precise estimates. Standard errors were approximated from the width of the 95% credible interval of each species' posterior slope estimate.

Results

Community-level Phenological Response to Climate and Spatial Gradient

The community of species demonstrated diverse patterns of phenology and significant variation in response to both climate and across space. The response to spring temperature response varied significantly with mean flowering occurring 2.68 ± 1.12 days earlier for each one standard deviation increase in spring temperature. Spring precipitation and latitude both had a negative effect on mean flowering times, with flowering advancing 0.0810 ± 0.0493 days with every additional centimeter in precipitation and 5.29 ± 1.61 days per degree of latitude, respectively (figure 1). Elevation had a weak effect on flowering phenology, with a posterior mean slope of 0.009523 ± 0.0534 days per standard deviation change in elevation. This effect was not considered significant, as the posterior probability of the effect differing from zero was below 95%.

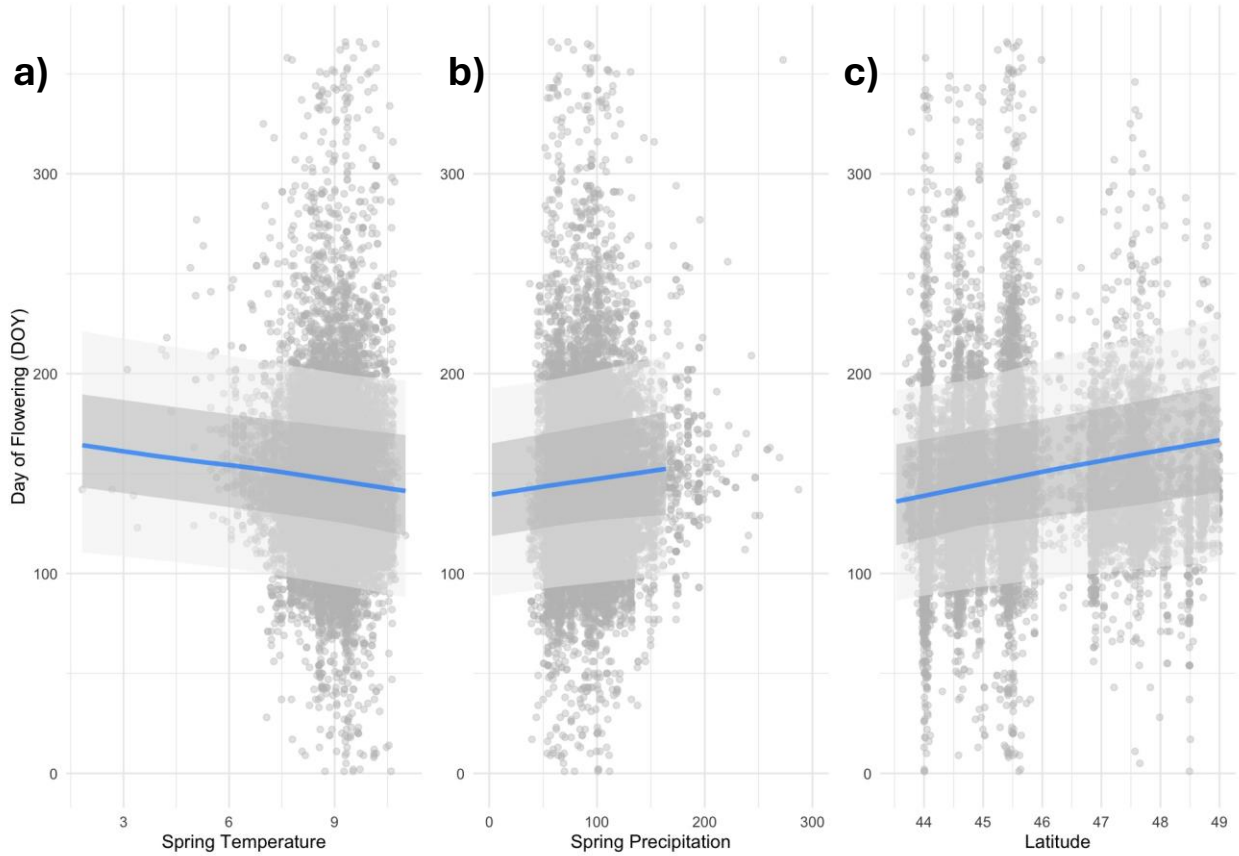

Figure 1. Community-level phenological responses to climatic and spatial predictors. A) Interaction between spring temperature and day of flower (DOY), B) interaction between spring precipitation and DOY, C) interaction between latitude and DOY. Grey data points indicate observed flowering observations. Solid blue lines indicate posterior mean estimates from the Bayesian model; shaded ribbons represent 95% credible intervals.

A significant interaction between spring temperature and latitude was observed at the community level ($\beta = 0.0630 \pm 0.0393$), indicating that a phenological response to temperature varies across the latitudinal gradient (figure 3a). Specifically, the negative effect of temperature on flowering time became weaker at higher latitudes, compared to lower latitudes that had a much stronger negative relationship. In contrast, the interaction between temperature and precipitation was not significant ($\beta = 0.00983 \pm 0.00106$), indicating no evidence that precipitation modified the temperature response at the community level.

Species-level Phenological Sensitivity

Species-level slopes for each variable showed substantial variation, with species differing phenological sensitivity to climatic and spatial drivers. While the direction of response to spring temperature, precipitation, and latitude was generally consistent across species, the magnitude of these responses varied (figure 2). Posterior estimates of species-level slopes revealed a wide range of sensitivities, with some species exhibiting steeper phenological shifts than others under equivalent climatic conditions. These effects were credibly different from zero for 18 of 28 species for spring temperature, 20 of 28 for spring precipitation, and 27 of 28 for latitude. The variance in posterior distributions for these effects was greatest for latitude, followed by temperature and precipitation, suggesting differential contributions of spatial versus climatic drivers at the species level. Of the 28 species, 11 species consistently exhibited strong and credible responses to all three predictors.

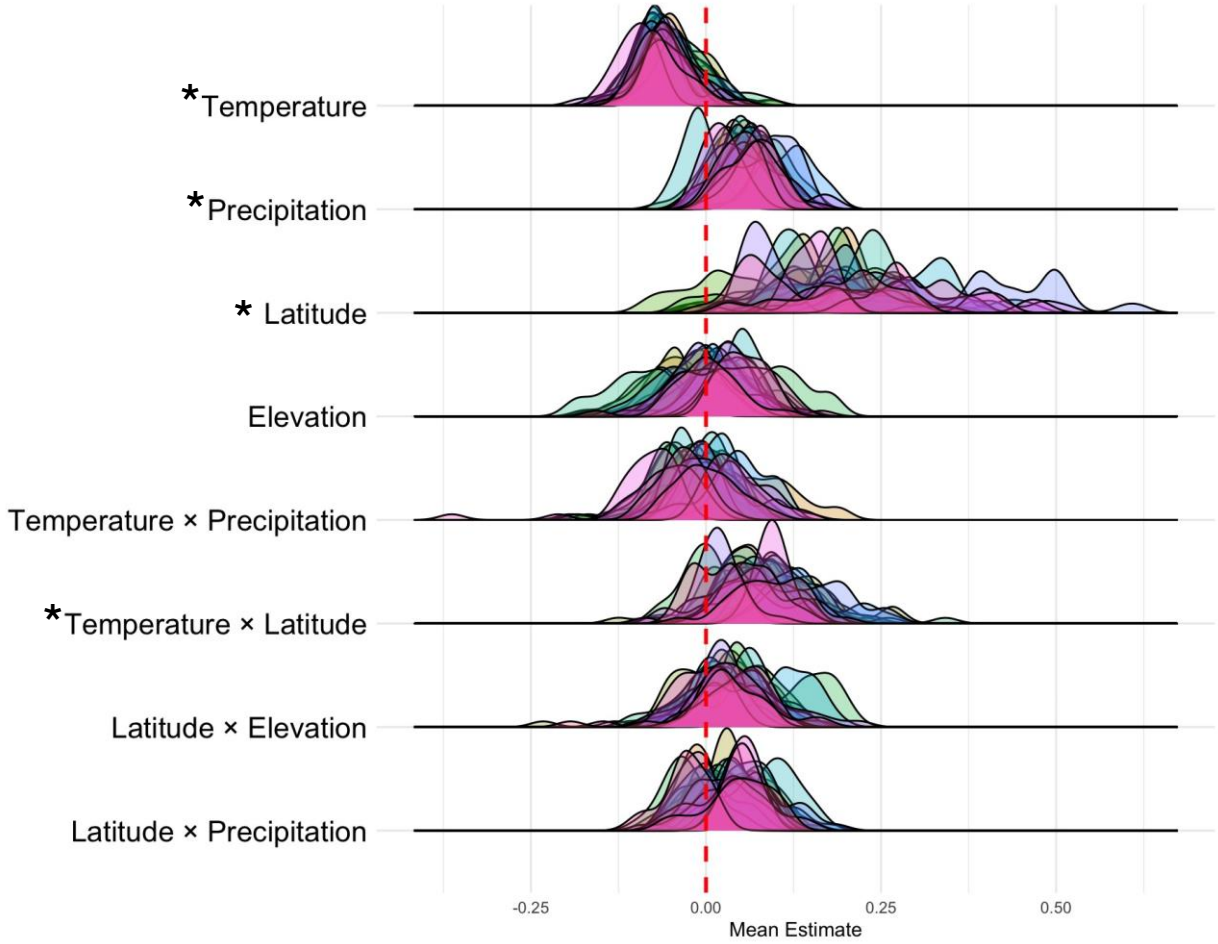

Figure 2. Species-specific posterior slope distributions for climate and spatial predictors. Each density plot represents the mean posterior estimate for an individual species' response to a given predictor. Asterisks (*) indicate predictors with a credible community-level effect, where the 95% credible interval of the community mean does not overlap with zero. The red dashed line indicates a slope of zero.

Further examination of species-specific responses to the spring temperature × latitude interaction revealed consistent directional sensitivity across species (Figure 3b). Several species exhibited credible interaction terms, indicating that latitude modulated their temperature sensitivity. These patterns indicate that while a community-level interaction was detected, species-specific responses to this interaction were more variable. 7 of the 28

species had credible interaction terms for all four of the predictors discussed (spring temperature, spring precipitation, latitude, and temperature x latitude).

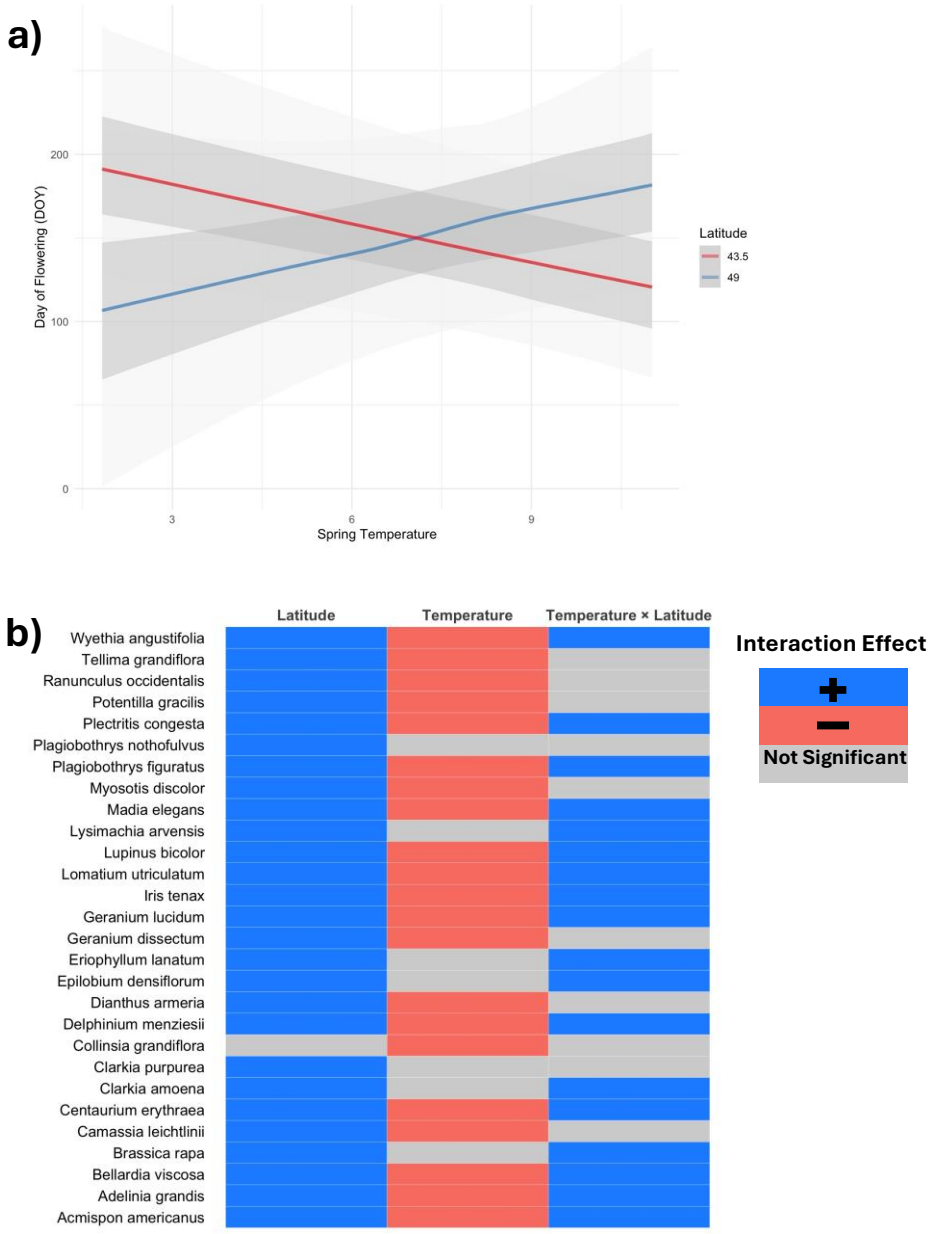

Figure 3. (a) Community-level interaction effect showing how the relationship between spring temperature and day of flowering (DOY) varies across the latitudinal gradient. (b)

Species-specific significance of effects for latitude, temperature, and the latitude × temperature interaction. Each colored cell represents a significant posterior slope estimate for the corresponding species and predictor: blue for positive effects, red for negative effects, and gray for non-significant effects (posterior distributions overlapping zero).

Mean flowering time for all species ranged from April 9th (99th DOY, *Adelinia grandis)* to August 1st (213th DOY, *Epilobium densiflorum).* A significant positive correlation was observed between the day of flowering and mean temperature sensitivity (*p-value* = 0.000637) (Figure 4), with earlier-flowering species tending to exhibit more negative slope estimates. The linear regression explained 37% of the variation in temperature sensitivity across species (R^2 = 0.37).

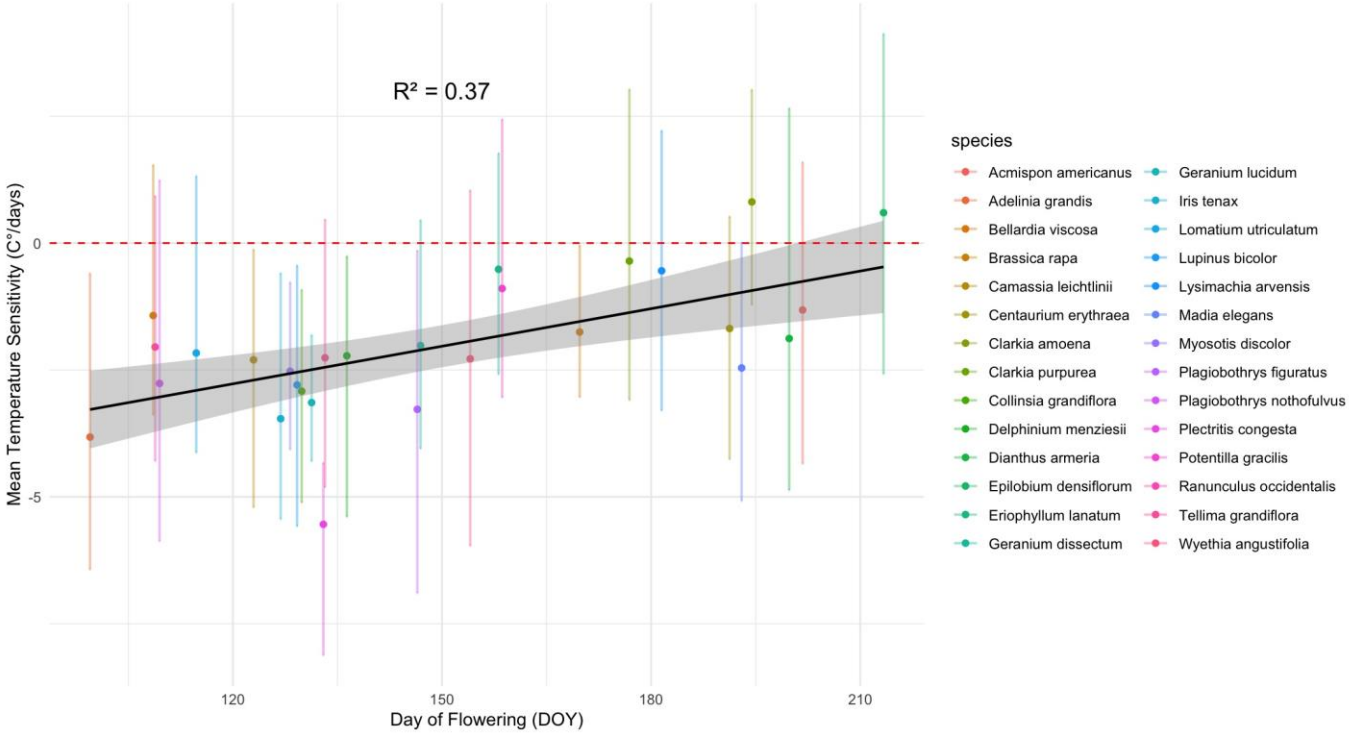

Figure 4. Relationship between mean day of flowering (DOY) and species-specific sensitivity to spring temperature. Each point represents a species-level posterior mean for temperature sensitivity, with vertical lines indicating 95% credible intervals. The black line shows the fitted regression trend (R^2 = 0.38), with the shaded band representing the 95% confidence interval. The red dashed line indicates a slope of zero.

Variation in Phenological Responses between Annual and Perennial Species

Life history strategy (annuals vs. perennials) was significantly associated with mean flowering time. Perennial species flowered earlier on average than annual species, as indicated by a credible negative effect of lifespan on day of year (DOY, $\beta = -0.716 \pm 0.736$). However, no significant interactions were detected between life history strategy and any of the climatic predictors, spring temperature, precipitation, latitude, or any combined interactions. Posterior slope estimates for climate sensitivity overlapped considerably between annuals and perennials across all predictors, indicating that life history strategy did not explain variation in phenological sensitivity to climate.

Discussion

As climate change continues to impact plant communities' phenological timing globally, it is important to understand what this looks like at a more species-specific scope and across a spatial scale. In this study, 19,000 iNaturalist observations covering 28 species throughout the Willamette Valley-Puget Trough ecoregion were used to better understand the effects of climate and geographic variation on plant phenological sensitivity. The results showed that spring temperature, spring precipitation, and latitude were all significant drivers of flowering phenology. A more complex relationship between latitude and temperature was presented as latitude modified the effects of temperature, and no effects of life history strategy (annual vs. perennial) were present on phenological sensitivity to temperature or any other predictor variable.

Climate and Spatial Drivers of Phenology

Consistent with previous citizen science and field observation of community phenology, we found that the phenology of flowering plants accelerated with warming spring temperatures (Puchałka et al. 2022; Willis et al. 2017; Park et al. 2019). In addition, we observed delayed flowering with increasing spring precipitation and latitude, indicating that both hydrological and spatial climatic gradients play important roles in shaping phenological timing. The average number of days of phenological advancement per degree increase of temperature (-2.68 ± 1.12 C°/days) aligned similarly with prior research (Park et al. 2019; Willis et al. 2017), reinforcing the robustness of the climate-phenology relationships across methods and regions. The positive slope with spring precipitation (0.081 ± 0.049 days per

mm) may reflect moisture-driven delay, suggesting that higher amounts of precipitation could allow plant species to invest more in growth and belowground storage before reproducing (Munson & Long 2017). With a similar positive relationship found along a latitudinal gradient, this result follows patterns seen among temperate systems, where higher-latitudinal populations often face cooler overall temperatures resulting in delayed flowering across the community.

A significant effect was observed for the interaction between spring temperature and latitude on phenological response at the community level. Specifically, the direction of flowering response to warming temperatures changed across the gradient with populations at lower latitudes exhibiting the expected advancement in flowering with higher spring temperatures, whereas more northerly populations showed a reduction in sensitivity and, in some cases, delayed flowering under warming conditions. These findings align in part with previous studies that have found that warmer, lower latitude populations tended to be more phenological sensitive to temperature as compared to colder, higher latitude populations (Park et al 2018; Love & Mazer 2021). However, the observation of delayed flowering in northern populations under warming temperatures departs from the patterns reported in many prior studies, which typically find a muted but still negative phenological response at higher latitudes. Prevéy et al. (2017) found in a broad assessment of 47 species that phenological sensitivity to temperature of tundra plants at colder, higher latitudes was greater than at warmer, lower latitudes. These contrasting findings across ecosystems suggest that spatial variation in temperature sensitivity may depend heavily on regional climatic context and biome-specific adaptation. This divergence may reflect local climate adaptation, highlighting the continued need for future region-specific studies.

The lack of interaction found between spring temperature and spring precipitation could be explained by the underlying complexity of their relationship that was not fully captured in a Bayesian linear regression model. These interactions likely vary across spatial and temporal scales and may be better resolved through models that incorporate nonlinear or threshold responses (Madden & Williams 1978). Additionally, the lack of an elevation effect may be attributed to limited elevation range within the study region, as most observations were concentrated at relatively low altitudes (range of altitudes). Previous studies have noted the influence of elevation on phenological timing, providing context for how the reduced topographic heterogeneity may have constrained detection of elevational effects (Rafferty et al. 2020).

Species-Specific and Interaction-Level Variation

In addition to community-level trends, species-level analyses revealed heterogeneity in phenological sensitivity to climatic and spatial drivers. While the direction of response to spring temperature, precipitation, and latitude was broadly consistent across the majority of species, the magnitude of response varied. Posterior estimates for species-specific slopes showed that some species exhibited steep phenological shifts under changing conditions, while others remained relatively insensitive.

In addition to variation across species, a moderate relationship was observed in which early flowering species exhibited greater sensitivity to temperature. This aligns with previous findings suggesting that mechanisms causing advancements in the flowering date of late-flowering species caused by spring warming would be smaller than those of early-flowering species, resulting in a weaker phenological response to temperature in late-flowering species (Moore & Lauenroth 2017; Park et al. 2018). This trend reflects the

dissimilarity of phenological shifts of plant species along a temporal scale in which other factors could affect or modify reproductive timing, such as higher sensitivity to precipitation in late-flowering species.

Furthermore, species-level variation of the interaction between spring temperature and latitude was observed. Among the species for which this interaction effect was statistically credible, the direction and nature of their phenological responses aligned with the overall trend identified at the community level, phenological sensitivity to warming diminished or reversed at higher latitudes. As climate change progresses, these interactions suggest that phenological responses may not only differ in magnitude among species but may also shift direction across geographic space. Such spatially contingent sensitivity implies that even within a single species, populations may exhibit opposing phenological trends depending on their latitudinal position. Assessing both interspecific and intraspecific phenological patterns is therefore essential to accurately forecast phenological responses and to identify species or populations at greater risk to climate change (Love & Mazer 2021).

As climate and phenology begin to shift with climate change, communities are expected to undergo a “reshuffling” of species, altering their ecology (Rafferty 2020). Changes in phenological overlap across ranges will have direct consequences on key mechanisms such as competition or pollination, potentially leading to disruptions in community structure and function. This reshuffling of communities, reducing overlap, can also have effects on adaptive evolution as gene flow may increase among previously (temporally) isolated populations of some species and decrease among others (Rushing et al. 2021; Park et al. 2018). Additionally, populations at lower latitudes may be particularly

vulnerable to these effects due to heightened climatic variability and increased risk of phenological mismatches with key mutualists, such as pollinators or seed dispersers. (Thomson 2010).

Annual and Perennial Life History Strategy

Although life history strategy, specifically whether a plant is annual or perennial, had a significant effect on overall flowering time, it did not significantly predict phenological sensitivity to climate drivers such as spring temperature or precipitation. The perennials present in this study might flower earlier due to an overwintering advantage, where they can develop earlier in the season due to their pre-established root systems. This result could also be established due to the higher frequency of early-flowering perennials included in this study. Despite these differences in timing, the lack of differential sensitivity to climatic variables suggests that their lifespans alone do not capture the full scope of phenological response. The addition of other species traits, such as plant height or leaf area, might play a more centralized role in mediating a plants phenological responsiveness (Sporbert et al. 2022). Categorizing species into binary life history strategies may obscure this variation that could be better captured by a multi-trait approach.

We must also consider the temporal scope of the dataset. The six-year period (2018-2024) that the data was collected from may have had long-lived perennial species that may not have fully acclimated their phenological sensitivity to changing climatic conditions, requiring a longer timeframe (Park et al. 2018). Future work with extended temporal datasets and finer-resolution trait data may yield clearer insight into the ecological strategies that govern phenological responses to climate change.

Limitations and Future Directions

While our study provides valuable insights into phenological sensitivity across species and space using citizen science data, several limitations must be acknowledged. Although citizen science provides broad geographic coverage and high-resolution species-level data, it is not without bias. Flowering individuals are more likely to be photographed and submitted than non-reproductive individuals, potentially inflating flowering-time estimates. Though only presence-only images were utilized to avoid this bias, it must still be considered. Furthermore, variation in observer expertise across space and time may contribute to inconsistencies in annotation and data quality, despite quality controls and filtering protocols (López-Guillén et al. 2024). Additionally, observations maybe clustered more heavily around paved roads or more dense urban settings, impacting the true depth of a species range (Geurts et al. 2023).

Another limitation stems from the relatively short temporal scale of the dataset, which spans only six years (2018–2024). This period may not be sufficient to capture long-term trends or detect gradual acclimation processes, particularly for long-lived perennial species. Phenological sensitivity to climate may change over time requiring longer datasets in order to evaluate whether these relationships persist or shift with continued climate change. Past research has addressed this limitation by coupling citizen science records with longer, more extensive herbarium databases, thereby expanding temporal coverage and improving sensitivity to long-term trends (Iwanycki et al. 2022). Similarly, the integration of other climate scenario projections, an approach utilized by other phenological studies, could offer a valuable assessment of how patterns could change over future climate conditions, projecting the more gradual acclimation processes (Puchałka et al. 2022; Prevéy et al. 2020).

To expand the study further, the addition of other phenological stages such as fruiting or budding would provide a more comprehensive understanding of plant reproductive timing and its sensitivity to climate variables. While flowering is a critical phenophase, it represents only one component of the reproductive cycle. Including other stages would allow for the evaluation of potential mismatches between flowering and adjacent processes. Additionally, extending the geographic scope of the research region to include full species range would allow for a more complete assessment of spatial variation in phenological sensitivity. Many species included in this study have ranges that extend well beyond the Willamette Valley-Puget Trough ecoregion, into more southern or northern latitudes. Including populations from a broader latitudinal and elevational extent could reveal important intraspecific variation within each species. This broader spatial coverage would also help unravel local climate effects from broader biogeographic patterns, enhancing the generalizability and ecological relevance of the findings.

Conclusion

Building on previous phenological research by utilizing over 19,000 iNaturalist prairie plant observations across the Willamette Valley-Puget Trough ecoregion, we have demonstrated that climate and spatial gradients significantly influence flowering phenology. We show that spring temperature, precipitation, and latitude are all important predictors of phenological timing, with species generally flowering earlier in warmer, drier, and more southerly conditions. An interaction between temperature and latitude further emphasizes the complexity of phenological responses, revealing that the influence of climate on flowering is not uniform across space. While flowering time differed between annual and perennial species, phenological sensitivity to climate did not vary significantly between annual and perennial plant species, suggesting that other traits may be more predictive of climate responsiveness. Heterogeneity was observed at the species level, with some species exhibiting high sensitivity to climate variables, highlighting the need for species-specific approaches in predicting and managing phenological change. Our findings also reinforce the value of citizen science data for ecological research, especially in tracking phenological shifts across large spatial scales and taxonomic groups. Despite certain limitations, such as observational bias and short temporal coverage, platforms like iNaturalist offer powerful tools for understanding how species are responding to ongoing climate change. As climate change accelerates, shifts in phenology will likely lead to community-level reshuffling, with potential consequences for ecological interactions and evolutionary dynamics. The differences in both magnitude and direction of responses highlight how climate change will result in community reshuffling throughout time.

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Tables and Figures

Table 1: The number of species and different categorical traits of examined species. Observations refer to the total number of presence-only images.

Family	Species	Observations	Lifespan	Native Status
Fabaceae	Acmispon americanus	97	annual	Native
Boraginaceae	Adelinia grandis	595	perennial	Native
Orobanchaceae	Bellardia viscosa	1035	annual	Introduced
Brassicaceae	Brassica rapa	314	annual	Introduced
Asparagaceae	Camassia leichtlinii	1780	perennial	Native
Gentianaceae	Centaurium erythraea	399	annual	Native
Onagraceae	Clarkia amoena	404	annual	Native
Onagraceae	Clarkia purpurea	205	annual	Native
Plantaginaceae	Collinsia grandiflora	451	annual	Native
Ranunculaceae	Delphinium menziesii	188	perennial	Native
Caryophyllaceae	Dianthus armeria	351	annual	Native
Onagraceae	Epilobium densiflorum	205	annual	Native
Asteraceae	Eriophyllum lanatum	821	perennial	Native
Geraniaceae	Geranium dissectum	339	annual	Introduced
Geraniaceae	Geranium lucidum	2249	annual	Introduced
Iridaceae	Iris tenax	1890	perennial	Native
Apiaceae	Lomatium utriculatum	578	perennial	Native
Fabaceae	Lupinus bicolor	360	annual	Native

Primulaceae	Lysimachia arvensis	401	annual	Invasive
Asteraceae	Madia elegans	506	annual	Native
Boraginaceae	Myosotis discolor	915	annual	Introduced
Boraginaceae	Plagiobothrys figuratus	88	annual	Native
Boraginaceae	Plagiobothrys nothofulvus	51	annual	Native
Valerianaceae	Plectritis congesta	1336	annual	Native
Rosaceae	Potentilla gracilis	197	perennial	Native
Ranunculaceae	Ranunculus occidentalis	568	perennial	Native
Saxifragaceae	Tellima grandiflora	3204	perennial	Native
Asteraceae	Wyethia angustifolia	292	perennial	Native

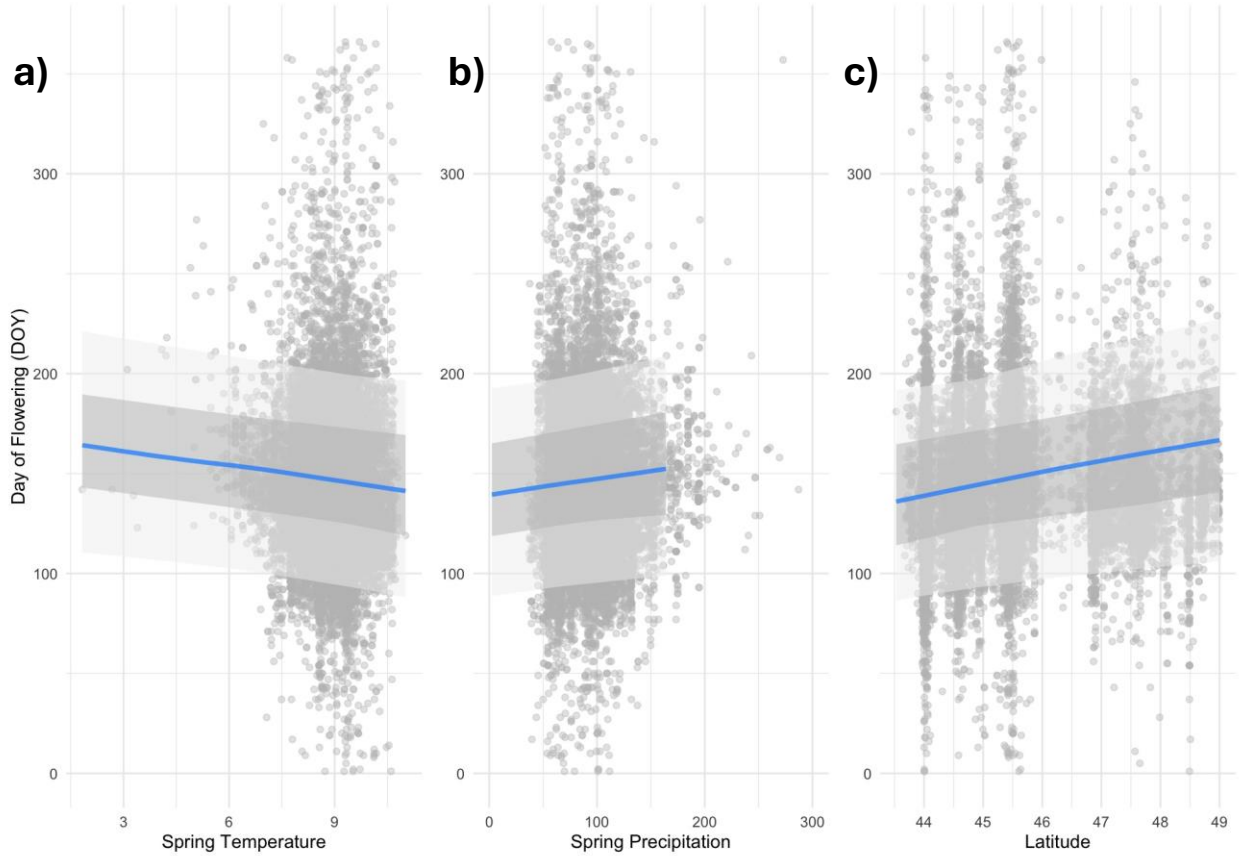

Figure 1. Community-level phenological responses to climatic and spatial predictors. A) Interaction between spring temperature and day of flower (DOY), B) interaction between spring precipitation and DOY, C) interaction between latitude and DOY. Grey data points indicate observed flowering observations. Solid blue lines indicate posterior mean estimates from the Bayesian model; shaded ribbons represent 95% credible intervals.

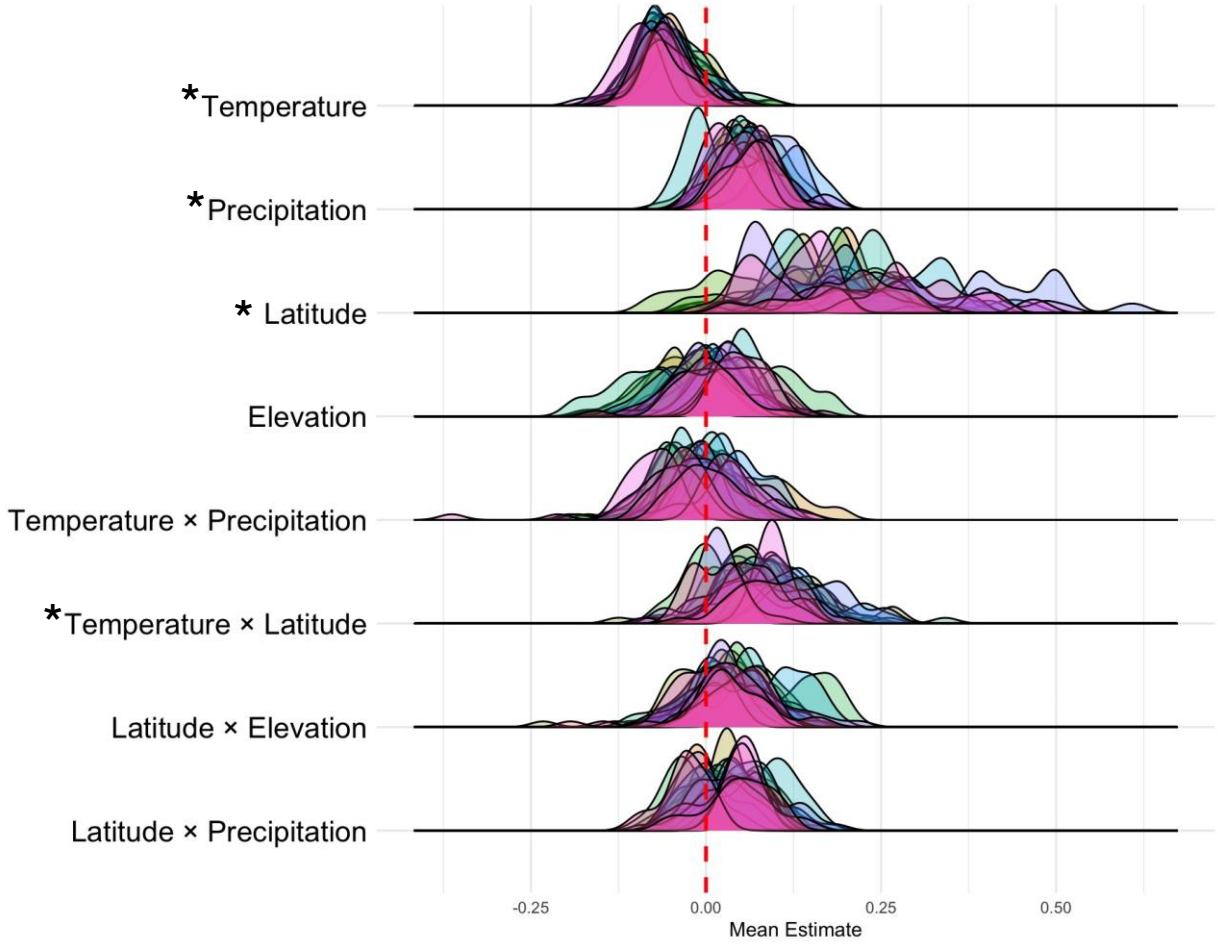

Figure 2. Species-specific posterior slope distributions for climate and spatial predictors. Each density plot represents the mean posterior estimate for an individual species' response to a given predictor. Asterisks (*) indicate predictors with a credible community-level effect, where the 95% credible interval of the community mean does not overlap with zero. The red dashed line indicates a slope of zero.

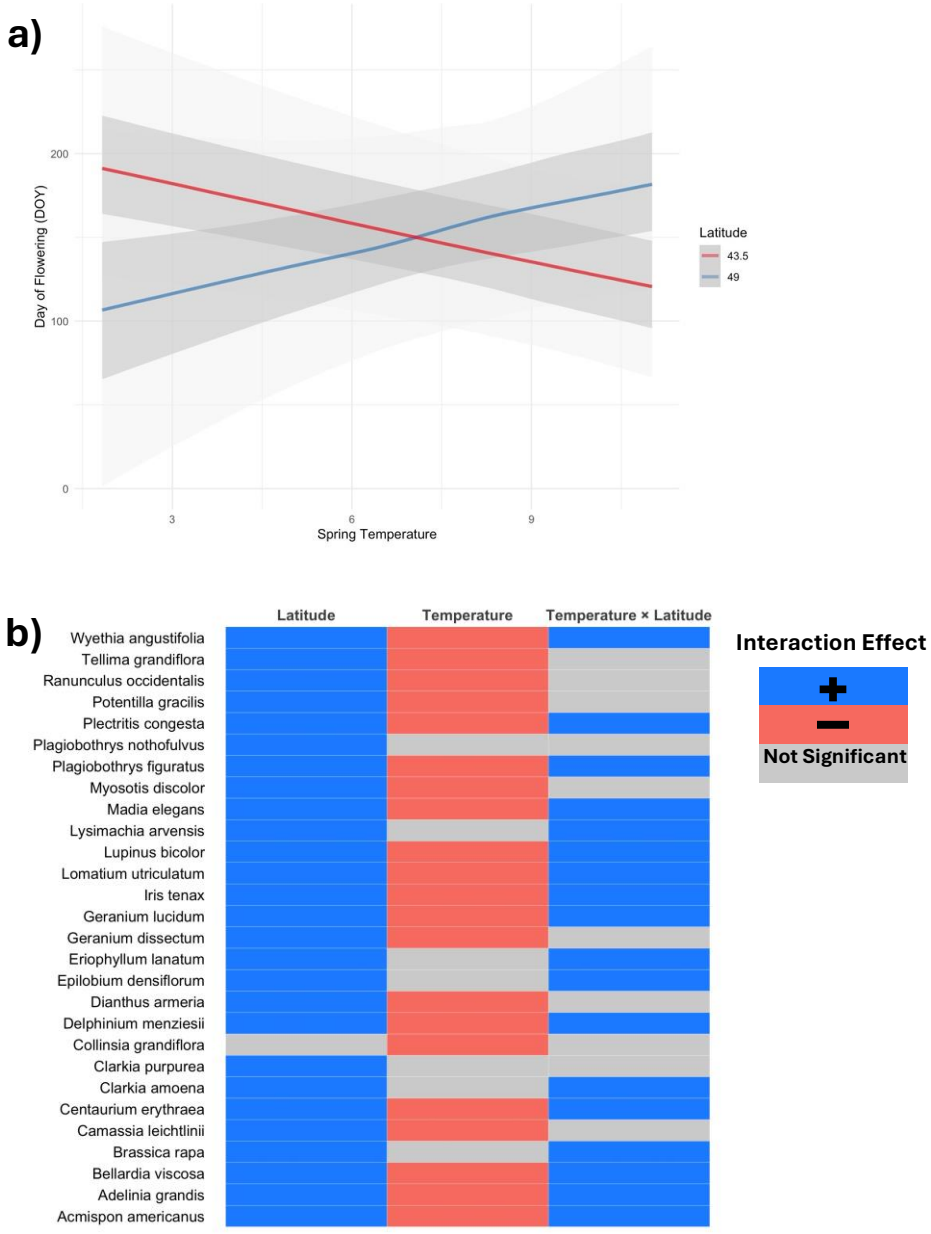

Figure 3. (a) Community-level interaction effect showing how the relationship between spring temperature and day of flowering (DOY) varies across the latitudinal gradient. (b) Species-specific significance of effects for latitude, temperature, and the latitude × temperature interaction. Each colored cell represents a significant posterior slope estimate for the corresponding species and predictor: blue for positive effects, red for negative effects, and gray for non-significant effects (posterior distributions overlapping zero).

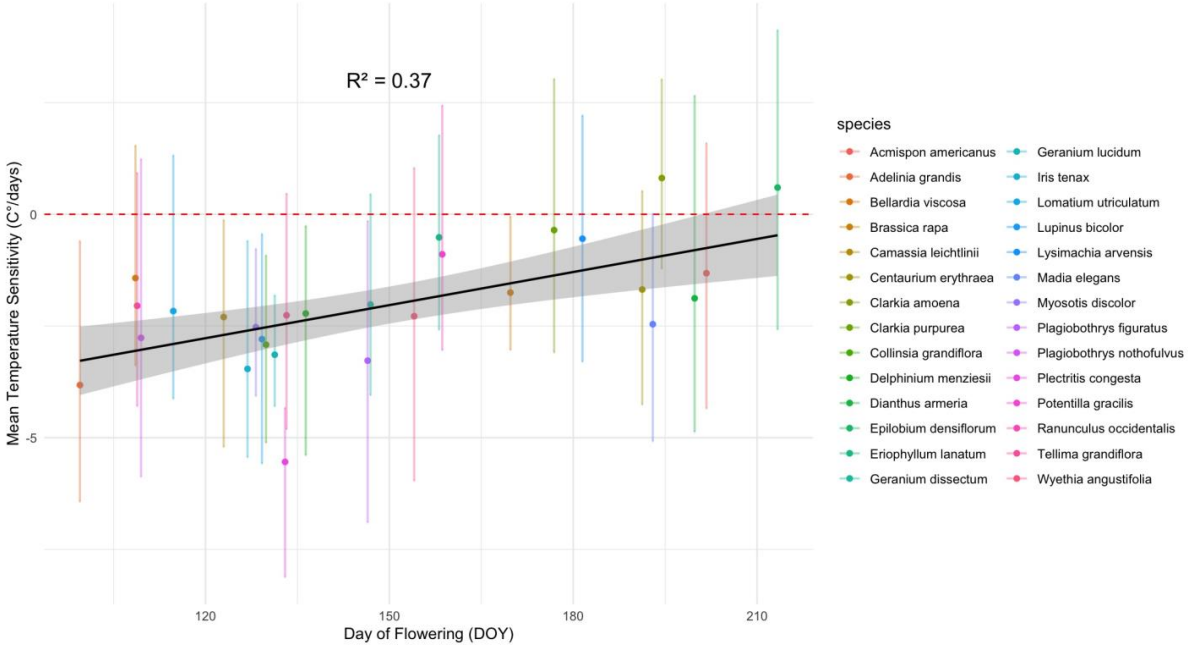

Figure 4. Relationship between mean day of flowering (DOY) and species-specific sensitivity to spring temperature. Each point represents a species-level posterior mean for temperature sensitivity, with vertical lines indicating 95% credible intervals. The black line shows the fitted regression trend ($R^2 = 0.38$), with the shaded band representing the 95% confidence interval. The red dashed line indicates a slope of zero.