Pacific Northwest Prairie Plant Responses to Warming Among Species, Across Space, and the Implications for Species Interactions and Coexistence

by

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DISSERTATION ABSTRACT

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Title: Pacific Northwest Prairie Plant Responses to Warming Among Species, Across Space, and the Implications for Species Interactions and Coexistence

While plant species are adapted to, and in many cases rely on, temporal fluctuations, the rapid climate warming of the 21st century poses a substantial threat to species and community dynamics. Ecologists use shifting plant phenology, life cycle events such as flowering, as one of the key ways to track how species are being affected by warming. Plant species' responses, phenological and otherwise, often diverge among species and across space, suggesting reshuffled species interactions and uncertain changes in community composition. Modern Coexistence Theory (MCT) has proven a useful framework in recent decades for understanding species interactions and coexistence and investigating how certain environmental variables affect these dynamics.

In this dissertation, I track plant responses to warming, particularly phenological and fecundity responses, to determine how variation in these responses among species and across local environmental gradients can restructure species interactions and coexistence. To do this, I implemented two large field projects using annual forbs native to Pacific Northwest prairies that are commonly used in restoration seed mixes for this ecosystem. The first was a common garden study with seven taxonomically and phenologically diverse species that I used to answer questions about the full phenological life cycle shifts and interspecific differences in species response to warming. In the second, I seeded two forbs in competition plots replicated at eight locations across abiotically variable sites to examine how warming effects vary across small spatial scales. Both studies used open-top chambers to passively create a warming treatment.

In my first chapter, I observed the full life cycle of all seven species, from germination to fruit maturation. These observations provide unique information about early life development stages that are not typically studied and provide greater insight into what drives variation in phenological shifts.

In my second chapter, I use five of the species from chapter one and ask how species - specific responses to warming impact their performance directly and indirectly through changes

in species interactions. I use MCT to examine how these direct and indirect effects cascade to restructure species niche differences and fitness differences and ultimately predict how coexistence outcomes shift with warming.

In my third chapter, I again use MCT to examine how warming affects species interactions and coexistence but focus on how small scale environmental variation has the potential to modify warming effects, leading to unique community -level outcomes across space.

Overall, the results in this dissertation advance our knowledge of how the variation in species responses to warming leads to changes in community dynamics. Using species from Pacific Northwest prairies, a critically imperiled ecosystem, I aim to aid restoration of this system while also providing broad information about how warming impacts species coexistence. *None of the work presented in this dissertation has been submitted for publication. All chapters were co-authored by me and Jeff Diez.*

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CHAPTER 1
INTRODUCTION

Some of the oldest and longest ecological datasets are those tracking plant phenology, going back as early as 16th century (Vitasse et al., 2022). By documenting the timing of phenological events—such as first flowering or leaf emergence—over decades and even centuries, researchers can assess temporal climate variability and the relationship between phenology and climate. These events are among the most easily and consistently observed plant traits and provide clear indicators of climate variation across both space and time (Miller-Rushing & Primack, 2008). In recent decades, phenological studies have become a key metric for detecting rapid climate warming and its ecological impacts, building on these historical foundations to reveal accelerating shifts in nature's timing (Parmesan, 2006; Parmesan & Yohe, 2003). While phenology is not the only plant trait influenced by climate change, it is a critical one: the timing of plant establishment, growth, and reproduction determines temporal overlap with resources, competitors, mutualists, and predators.

Phenology represents just one of many species traits that are shifting with climate change, and these trait changes collectively influence how species interact and coexist in ecological communities (Kraft et al., 2015). As species' traits shift with a changing climate, it follows that species interactions and coexistence will change, but making specific predictions remains challenging. At the turn of the 21st century, Modern Coexistence Theory (MCT) synthesized disparate ideas about coexistence to form a new framework for thinking about and quantifying community dynamics (Chesson, 2000a). This framework, and other theoretical work building off of it, describes two categories of mechanisms that structure species coexistence: stabilizing mechanisms and equalizing mechanisms. Stabilizing and equalizing mechanisms can operate through environmental fluctuations (spatial or temporal) or independently of fluctuations. Fitness differences describe the relative competitive ability between species and represent a fluctuation-independent measure of equalizing effects; mechanisms that reduce fitness differences would be equalizing mechanisms that promote coexistence. Niche differences represent a fluctuation-independent stabilizing mechanism that promotes coexistence by ensuring that species limit themselves through intraspecific density dependence more than they are limited by other species. Importantly, trait differences among species can contribute to both niche differences and fitness

differences simultaneously, even though they have classically been thought of as a form of niche partitioning (Mayfield & Levine, 2010). For example, differences in phenology between species could lead to greater stabilizing niche differences by reducing competitive overlap, while also creating fitness advantages for one species over another. Understanding coexistence therefore requires evaluating the net effect of how trait differences translate into these competing mechanisms. Empirical work stemming from the development of MCT has provided important insights into how traits (Godoy & Levine, 2014), and changes in traits (Van Dyke et al., 2022), impact species interactions and outcomes.

Despite having a strong theoretical framework and empirical studies showing its utility, progress in making community-level predictions of how plant communities will change with climate change remains challenging due to the diversity of plant responses and the complex combination of direct and indirect effects. The ecological literature is full of examples of how co-occurring species respond divergently to warming or drought, and how species responses vary throughout their range. MCT integrates these direct and indirect responses, but more empirical tests are needed to examine the relative important of direct and indirect responses as well as how they jointly alter species' niche and fitness differences. In this dissertation I examine how direct and indirect responses to climate warming vary among different species and across small environmental gradients. I additionally look at whether and how this variation cascades to bring about changes in community-level outcomes.

All three chapters of my dissertation use species native to Pacific Northwest (PNW) prairies, a small and greatly imperiled ecosystem (Noss et al., 1995). Very little remnant prairie remains and so much work in this system is centered around management and restoration (Bachelet et al., 2011). As a central goal of restoration is to increase the diversity of (plant) species, understanding species interactions and coexistence is critical to successful restoration. The PNW region overall is expected to see increasingly warmer temperatures with climate change, and PNW prairies may experience even stronger warming effects as many of the remaining fragments are adjacent to urban areas. Previous work in this ecosystem has found temperature to be a key driver affecting plant population growth rates (Reed, Peterson, et al., 2021a), community composition (Pfeifer-Meister et al., 2016; Reed, Pfeifer-Meister, et al., 2021), and flowering phenology (Reed et al., 2019). Suggested climate-smart management strategies include increasing the number of annual plants on the landscape, and better utilizing

the environmental heterogeneity of prairies, in the hopes that certain places on the landscape may act as refugia from climate change (Bachelet et al., 2011).

In chapter two, I document the response of seven phenophases to experimental warming, capturing the full life cycle of seven annual forbs, from germination to fruit maturation. These observations provide unique information on: 1) early life stages that are not typically studied; 2) how phenological shifts vary across a species' life cycle; and 3) whether variation is driven by differences in organismal sensitivity or environmental conditions.

In chapter three, I explore whether species-specific responses to warming impact species coexistence. Assessments of species-specific responses draw on flowering phenology observations from chapter two, as well as growth and fecundity measurements. Following MCT, I examine how both direct and indirect responses to warming cascade to restructure species' niche and fitness differences and ultimately how coexistence outcomes shift with warming.

In chapter four, I examine how species interactions and coexistence shift with warming across space. Similar to chapter three, I analyze species' direct and indirect responses to warming but additionally replicate my experimental design across multiple locations to capture the environmental heterogeneity typical of PNW prairies. This experimental design allows me to determine how the unique abiotic and biotic conditions of different sies interact with warming and whether these interactions lead to novel effects on species, their interactions, and their ability to coexist.

While none of the questions in these chapters directly test the success of restoration efforts, all questions were devised with restoration challenges in mind. Exploring how phenology, such as germination and flowering times, shift with warming will be important information on how species establishment and reproduction as well as temporal distribution of floral resources for pollinators may change. Examining how species interactions and coexistence may change with warming could inform land managers to what extend they can expect community composition to deviate from previous and current patterns. Many elements of MCT could be incorporated into restoration plans and assessments to improve restoration outcomes (Hallett et al., 2023a). In the discussion of each chapter, I consider how my results could help inform management and restoration decisions.

None of the work presented in this dissertation has been submitted for publication. All chapters were co-authored by me and Jeff Diez

.CHAPTER II

EQUAL VARIATION IN PHENOLOGICAL RESPONSES AMONG PHENOPHASES AND SPECIES

2.1 Contributions

With assistance from Jeff Diez, I developed the research questions. We jointly designed the experiment and performed statistical analysis. I wrote the manuscript and Jeff provided essential suggestions and edits. I led data collection with assistance primarily from Emily Cook, Julia Prange, and Lindsay Villano.

2.2 Introduction

Phenology, the timing of species' life history events, is closely tied to climate, particularly rainfall and temperature (Fitter & Fitter, 2002). As a result, phenology is frequently used as a metric to assess how climate change affects species (Wolkovich & Ettinger, 2014; D. W. Inouye, 2022). Although shifting plant phenology has been widely documented over recent decades, most studies have focused on certain plant growth forms, primarily woody species and herbaceous perennials (Stuble et al., 2021), and certain phenological phases (phenophases), mainly bud burst and flowering (Wolkovich & Ettinger, 2014). Other plant growth forms and phenophases remain relatively unstudied, leaving a gap in our understanding of how entire plant communities may shift with climate change (Stuble et al., 2021). Phenological studies thus far have revealed many general trends in plant responses to climate change but have also document substantial variation in responses among species and phenophases (Fitter & Fitter, 2002; Parmesan, 2007; Stuble et al., 2021). This variation underscores the likelihood that understudied plant groups and phenophases respond in novel ways.

Nearly all studies of herbaceous plant phenological shifts have focused on flowering phenology, while few document pre- or post-flowering phenophases (Stuble et al., 2021). Flowering phenology has received a high level of attention due to its high visibility and public interest, as well as its genuine importance for angiosperm reproduction and the support of pollinator populations. Successful reproduction of angiosperms, however, also depends on the success of other reproductive phenophases, such as fruit development, as well as vegetative phenophases that precede flowering. Recent studies have begun documenting multiple phenophases, specifically leaf emergence, flowering, fruiting, and leaf senescence (Li et al., 2016; Augspurger & Zaya, 2020; Collins et al., 2021). These studies find that most phenophases

advance with warming, but the magnitude of these shifts can vary by phenophase. No clear pattern has yet emerged regarding whether certain phenophases are more responsive than others. In one case, the responsiveness of phenophases varied by the seasonality of species (Augspurger & Zaya), but in another, responsiveness was entirely species-specific (Li et al., 2016). In all these studies, the shift of non-flowering phenophases did not appear to be highly correlated with that of flowering, highlighting the importance of including other phenophases in future studies. So far, our knowledge of how non-flowering phenophases of herbaceous plants respond to a changing climate remains limited to perennial species, and predominantly those in alpine environments.

Even as studies branch out from solely focusing on flowering phenology, early development phenophases such as seedling development and germination remain understudied, likely due to the focus on perennial species. The key phenological events for a plant species can vary by growth form (Denny et al., 2024). For example, leaf emergence is a key phenophase for deciduous trees but not relevant for cacti. Even though perennial and annual plants go through almost identical phenophases, perennial plants go through germination and seedling development less often than annuals which may explain the lack of these early development phenophases in previous studies. Additionally, there is some evidence that annual and perennial flowering times respond differently to a shifting climate (Stuble et al., 2021). Phenological studies of annual plants are needed to provide insight into early development phenophases such as germination and seedling development, as well as to investigate whether the reproductive phenophases of annuals respond differently than those of perennial species. While annuals are globally less common than perennials, they make up a large percentage of species in Mediterranean and arid ecosystems and are predicted to become more prevalent in most of Earth's biomes over the next few decades (Poppenwimer et al., 2023). This shift is driven by hotter temperatures, increasingly irregular precipitation, and human disturbance, as the short life cycle of annual plants and other life-history traits make them better adapted to these conditions (Poppenwimer et al., 2023).

Studying early development phenophases may additionally help explain shifts in flowering phenology or other later phenophases (Wolkovich & Ettinger, 2014; Li et al., 2016; Ettinger et al., 2018). A species' phenology is not made up of independent events, but instead consists of sequential, interrelated phenophases that are part of a continuous lifecycle (B. D. Inouye et al., 2019). When species are observed flowering earlier, this could be driven by the

advancement of previous phenophases in addition to the sensitivity of the flowering phase itself. When tracking leaf-out, flower bud development, and flowering phenology, Li et al. (2018) found that most species that flowered earlier also had earlier flower buds, suggesting that earlier flowering dates may in part be driven by shifts in flower bud timing—a phenomenon we refer to as "partial accumulation" (Figure 1). We illustrate multiple potential scenarios where preceding phenophase shifts could lead to identical shifts in flowering phenology, including a lack of shift in any previous phenophases before flowering ("true sensitivity") and a case where a single early-season shift drives all subsequent phenophases ("full accumulation") (Figure 1). Understanding which phenophases are responsible for shifts in flowering phenology may help improve future predictions of how species' flowering times will shift and help explain the variation in flowering phenology shifts that are often observed.

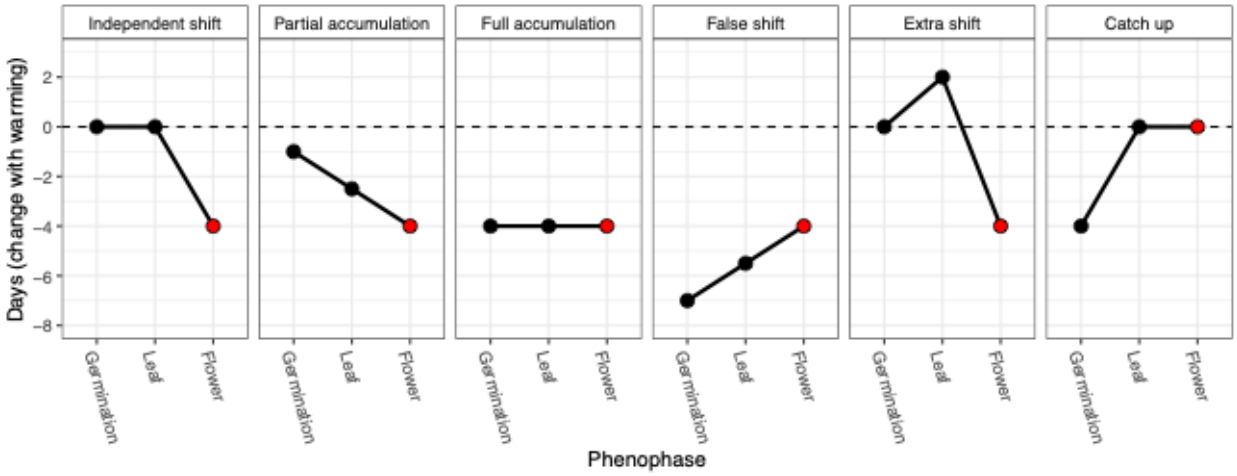


Figure 1. **Conceptual figure illustrating different phenological shift scenarios throughout the plant lifecycle, particularly demonstrating how various scenarios can lead to the same shift in flowering time.** Points show hypothetical phenological shifts of three phenophases- germination, leaf, and open flowers. Lines connect the points to highlight the relation of each shift to the previous and subsequent shift. Points for the flower phenophase are colored in red to ease comparisons across panels. Descriptions of the phenomenon in each panel are as follows. Independent shift: Earlier phenophases remain unchanged, and therefore the observed advance of the flowering phase is entirely due to its own responsiveness. Partial accumulation: Each phenophase advances, and each subsequent phenophase shifts more than the previous, suggesting that all phenophases are responsive, but the magnitude of later shifts may be partially influenced by earlier ones. Full accumulation: The earliest phenophase, germination, advances, and all subsequent phenophases shift by the same amount, suggesting that only germination is directly responsive, and later shifts are fully due to accumulated effects from the earlier shift. False shift: All phenophases advance; however, because each subsequent phenophase shifts less than the previous, these apparent advances may actually reflect relative delays, as later phenophases trend back toward their original timing. Extra shift: The flowering phase is four days earlier, but since the leafing phase was two days later than usual, the flowering shift could be

considered effectively six days earlier relative to the leaf phase, rather than just four. Catch up: This scenario shows a species that advances an early phenophase but then 'catches up' or 'resets' in later stages—demonstrating that a lack of shift in later phenophases does not imply a complete lack of responsiveness.

These varying sensitivities among species and phenophases could be driven by differences in sensitivity to climatic cues and/or differences in the intensity of those cues throughout the year (Chmura et al., 2019). Combinations of temperature, precipitation (and soil moisture), and photoperiod may all drive plant phenology, but their relative importance may vary among co-occurring species and throughout the life cycle of a species (Du et al., 2019; Flynn & Wolkovich, 2018). Because multiple environmental factors interact to influence phenological responses, experimental studies are better suited than observational studies to tease apart these differences, as experiments allow researchers to isolate the effects of individual climatic variables (Wolkovich et al., 2022; Chmura et al., 2019).

In this study, we investigate annual plant phenology in Pacific Northwest (PNW) prairies, a Mediterranean ecosystem that, at least historically, had a high number of annual species. PNW prairies are one of the most critically endangered ecosystems in the United States due to a combination of habitat loss to urbanization and agricultural conversion, invasive species, loss of indigenous fire, and climate change (Dunwiddie & Bakker, 2011). Comparisons of current and historical surveys of these prairies suggest annual forbs have been lost at a much higher rate than other groups of plants (Dunwiddie et al., 2014) and remaining annual forb species comprise high percentages of seed mixes used in restoration. Understanding how annuals forbs respond to climate warming is imperative to the restoration and conservation of this ecosystem, as well as to broaden our understanding of how plant communities will be affected by climate change. We focus on climate warming as previous work in PNW prairies found that the flowering phenology of both annual and perennial herbaceous species responds more to changes in temperature than rainfall (Reed et al., 2019).

Specifically, we conducted an experimental warming study examining phenological responses across the complete life cycle of annual plants. Our study addresses three key questions: 1) Do annual plant phenological responses to warming vary among species, phenological phases, or phenological metrics (e.g. first dates, peak, or lengths of phenophases); 2) What drives variation in responses – the intensity of warming or species' inherent thermal sensitivities; and 3) Do phenological shifts cascade through the life cycle, with early-season

shifts accumulating and driving later reproductive shifts? By examining the full life cycle and multiple metrics of phenological response, this research advances our fundamental understanding of the environmental cues and thermal sensitivities that regulate different life stages in annual plants, which is basic biology that remains poorly understood for most species. These insights into species-specific phenological mechanisms may also help anticipate plant communities shifts under future warming scenarios, identifying which life stages are most vulnerable to climate-driven disruption.

2.3 Methods

2.3.1 Study Site and Species Selection. The experiment was conducted in an outdoor common garden at the University of Oregon's research greenhouses in Eugene, Oregon, USA. Eugene is located at the southern end of the Willamette Valley, which is the southern extent of the Pacific Northwest (PNW) prairie ecosystem. This ecosystem has a Mediterranean climate, with cool, wet winters and hot, dry summers. On average, Eugene receives 108 cm of precipitation annually and has a mean temperature of 11.6°C (PRISM Climate Group, 30-year average). During the 12-month period surrounding the experiment (October 1, 2021, to October 1, 2022), Eugene received 97 cm of precipitation, and the mean temperature was 12.1°C (NOAA). While the study site would have historically been prairie, the soils have been amended and used for research and agriculture for decades.

The PNW prairie ecosystem is bunchgrass-dominated with interspersed perennial and annual forbs. In this system, species typically germinate between September and February and flower between March and July. Only annual forbs were used in this experiment due to both conservation interest in reintroducing annuals to the system and the lack of phenological studies focused on annual plants. We selected species that vary phenologically across the growing season and taxonomically within the pool of annuals commonly used in PNW prairie restoration. Early-flowering species (first flowering date late March-mid-April) included *Plagiobothrys nothofulvus, Plectritis congesta*, and *Collinsia grandiflora,* mid-flowering species (first flowering date mid-May-mid-June) include *Collomia grandiflora, Clarkia purpurea,* and *Gilia capitata*, and the late-flowering species (first flowering date early June-early July) was *Clarkia amoena.* Two Fabaceae species, *Lupinus bicolor* and *Acmispon americanus* were also seeded but did not germinate sufficiently to be used in the study. *Collinsia grandiflora* and *Collomia grandiflora* will be abbreviated as their genus to avoid

confusion. Seed was locally sourced from two native plant nurseries in the southern Willamette Valley, Friends of Buford Park Nursery and Heritage Seedlings & Liners, Inc.

2.3.2 Experimental Design. In late November 2021, species were seeded into 40 $1m^2$ plots, half of which were fitted with open-top warming chambers following a design modified from the International Tundra Experiment (Henry & Molau, 1997; Marion et al., 1997)(Fig S1). Each plot contained approximately three individuals (phytometers) of each of the seven species and a single species growing throughout the plot as the 'background' species at high or low density in both warmed and ambient plots. Additionally, two warmed and two ambient plots were seeded without a background species. This seeding design was used to answer separate research questions related to species interactions. Although the two Fabaceae species were not included as background species due to poor germination, the phytometers of other species growing in those plots were still monitored.

Air temperature was measured every thirty minutes by HOBO Pendant data loggers suspended ~2 cm above the ground in modified radiation shields (Holden et al., 2013). These were placed in six random pairs of warmed and ambient plots. Soil moisture measurements were taken in all plots four times by a Hydrospan Decagon GS3 Sensor in January and February. Three readings were taken throughout each plot and averaged. From March onward, soil moisture and temperature were measured every thirty minutes by four METER TEROS 11 sensors buried ~5cm deep in two paired warm and ambient plots.

2.3.3 Field Measurements Beginning one week after seeding, the phenology of all phytometers was recorded twice per week using seven phenophases: germination (G) — presence of cotyledons; leaf development (l) — growth of the first set of true leaves; leaf (L) — fully developed true leaves with no reproductive structures present; bud (B) — presence of flower buds before any open flowers; flower (FL) — presence of open flowers (i.e., visible anthers and/or stigma); developing fruit (FR) — presence of senesced flowers and/or green fruit; and mature fruit (MT) — presence of brown fruit, and where applicable, dehiscent fruit beginning to split. For most species, multiple reproductive stages (bud, flower, developing fruit, mature fruit) were often simultaneously present. In our analyses, we defined the bud phase as the period when flower buds were observed prior to the appearance of any later reproductive phases. The time periods for other reproductive phases (e.g., flowering or fruiting) however, were not limited in this way. For example, flowering duration was defined as the period when open

flowers were present, which typically overlapped with developing or mature fruits. A phytometer could only be recorded in one of the three vegetative phases at a time. These frequent observations throughout the growing season were used to define species-level first, mean, last, and duration values for phenophases up through flower. As phytometers were removed from plots for measurements related to the species interaction project, only phenological firsts were captured for the two fruit phenophases.

2.3.4 Statistical analysis.

2.3.4.1 Species responses to warming. All statistical analyses were conducted in R (R Core Team, 2025) using the brms package (Bürkner, 2021). We fit separate Bayesian linear models for each phenological metric (first date, mean date, last date, and length of the phenophase) to estimate how the effect of warming varied among species and phenophases. In each case, the dependent variable was the number of days since the experiment was seeded. Each model included a three-way interaction between treatment, phenophase, and species (value ~ treatment × phenophase × species) with a Gaussian error distribution. We used weakly informative default priors and models were run with four Hamiltonian Monte Carlo (HMC) chains of 3,000 iterations each. Convergence was assessed using the Gelman-Rubin statistic (R_hat), with values less than 1.01 indicating successful convergence, and through visual inspection of trace plots to confirm proper mixing and stationarity. We used Pearson's correlation coefficient to determine if different metrics of phenological shifts were correlated, comparing median values from posteriors of our Bayesian models.

2.3.4.2 Phenological sensitivity vs warming intensity. To determine whether species' shifts were driven by their sensitivity to warming or the intensity of the warming effect, we calculated the phenological sensitivity (the number of days shifted per 1°C of warming) for all shifts. To do this, we first selected the time period of each species' phenological firsts, lasts, and entire phenological periods of each phenophase, as well as 30 days previous to each of these phenological time periods. For each of these time periods we calculated the mean increase in daily maximum temperatures with the warming chambers. We used daily maximum temperatures as they were highly seasonally variable, while the warming effect on daily minimum and mean temperatures was only slightly seasonally variable. Finally, we took each median value from the posterior estimates of the number of days phenology shifted with warming and divided it by the degree of warming during its respective time period (using the

month of the species flowering and the preceding month, which has been shown to be a good predictor of the timing of flowering (Fitter & Fitter, 2002; Sparks et al., 2000)). It was not possible to include the full 30 previous days for the germination firsts, means, or lengths as species began germinating 10-13 days after seeding. We used Pearson's correlation coefficient to determine if observed phenological shifts and phenological sensitivity were correlated.

2.3.4.3 Sequential shifts: To assess whether each phenological shift was independent or an accumulation of previous shifts, we calculated the difference between each phenological shift and the previous phenological shift. Specifically, for each metric, we took the difference between 1000 draws from the posterior estimate of each phenological shift and the previous phenological shift. As germination is the first phenophase, there is no previous phase to compare its shift to. Since the duration of a phenophase is less likely to be related to the previous or subsequent phenophase length, or more likely related in the opposite direction, accumulation is only assessed for first, mean, and last dates.

2.4 Results

2.4.1 Warming Effects on Air and Soil. Open-top warming chambers increased air temperatures, although the degree of warming varied seasonally (Fig S4). Daily maximum temperatures showed the greatest increase and the highest seasonal variability. In March, daily maximum temperatures rose by 2.45 ± 0.3 °C, whereas in June the increase was only 0.26 ± 0.14 °C. Daily mean and minimum temperatures increased by approximately 0.5 °C throughout the year, with slight seasonal variation following a similar pattern to that of maximum temperatures.

Soil warming followed a similar pattern to air warming, with the strongest effects observed in spring and on daily maximum temperatures. In March, daily maximum soil temperatures increased by 2.6 ± 0.2 °C (Figure S2). Mean daily soil temperatures were 1.5 ± 0.1 °C warmer, and minimum daily soil temperatures were 0.9 ± 0.3 °C warmer. During the summer months, the warming chambers appeared to have a cooling effect on soil temperatures, likely due to increased vegetation cover in the warmed plots, which in turn cooled the soil.

Warming chambers did not reduce soil moisture, measured as volumetric water content (Figure S3). In contrast, soil moisture was occasionally higher in the warmed plots during spring, although this pattern was not consistent. Between June and August, the difference in soil

moisture between the two warmed plots was greater than the difference between the warmed and control plots.

Due to the seasonality of species and the warming effect, species experienced different amounts of warming during different phenophases (Fig S7). In general, the strongest warming effect occurred during leaf development and the early part of the leaf phase, when daily maximum temperatures in the warming chambers were, on average, 1.5–2 °C higher. The degree of warming during reproductive phases varied significantly depending on a species' phenological timing. The greatest variation in warming effect on species occurred during the end of their vegetative phase and the beginning of the bud phase. The earliest flowering species, *P. nothofulvus*, experienced daily high temperatures that were approximately 1.5 °C warmer than those experienced by mid- and late-flowering species during the same phenophase.

2.4.2 Observed Phenology Responses. Four of the seven study species — *Plectritis congesta*, *Collinsia grandiflora*, *Clarkia purpurea*, and *Gilia capitata* — significantly shifted their phenology with the warming treatment (Figures 2 and 3). *Plagiobothrys nothofulvus, Collomia grandiflora* and *Clarkia amoena* showed no phenological response to warming. Phenological shifts were directionally similar with firsts, means, and lasts all advancing with warming, but the number and magnitude of shifts varied among species, phenophases, and metrics. First and mean phenological dates were generally more responsive to warming, while last dates and phenophase durations were less so. Warming had a species-level effect on the duration of phenophases for *G. capitata* even though no individual phenophase showed a significant increase in duration. Otherwise, phenophase durations did not change with warming.

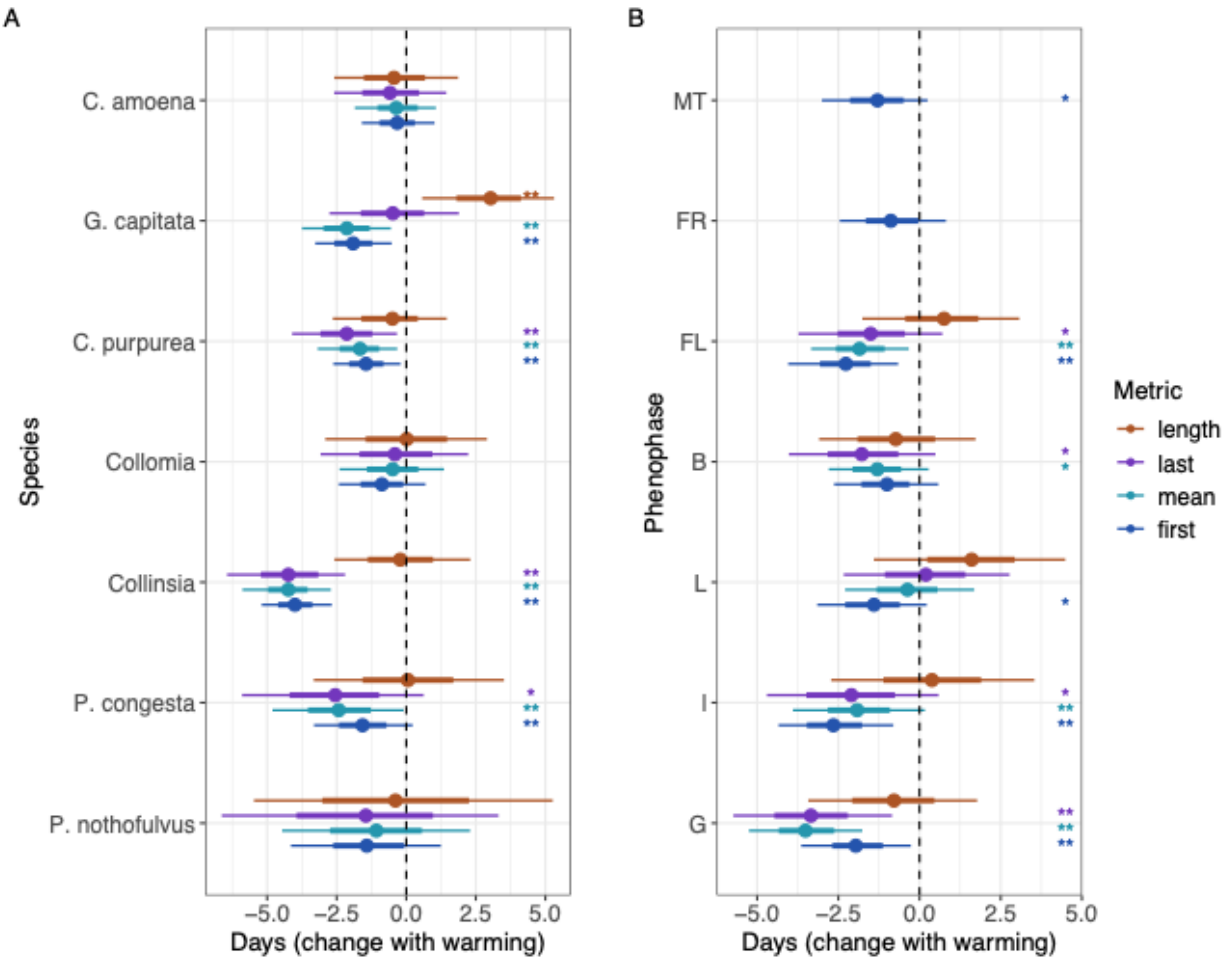


Figure 2. **Overall effects of warming on A) each species and B) each phenophase by metric**. Points are median values from Bayesian posterior estimates; thicker lines show the 66% credible intervals and thin lines show the 95% credible intervals. Each metric is a different color, and asterisks show the probability that each shift with warming was different from zero (** = Pr > 95%; * = Pr > 90%).

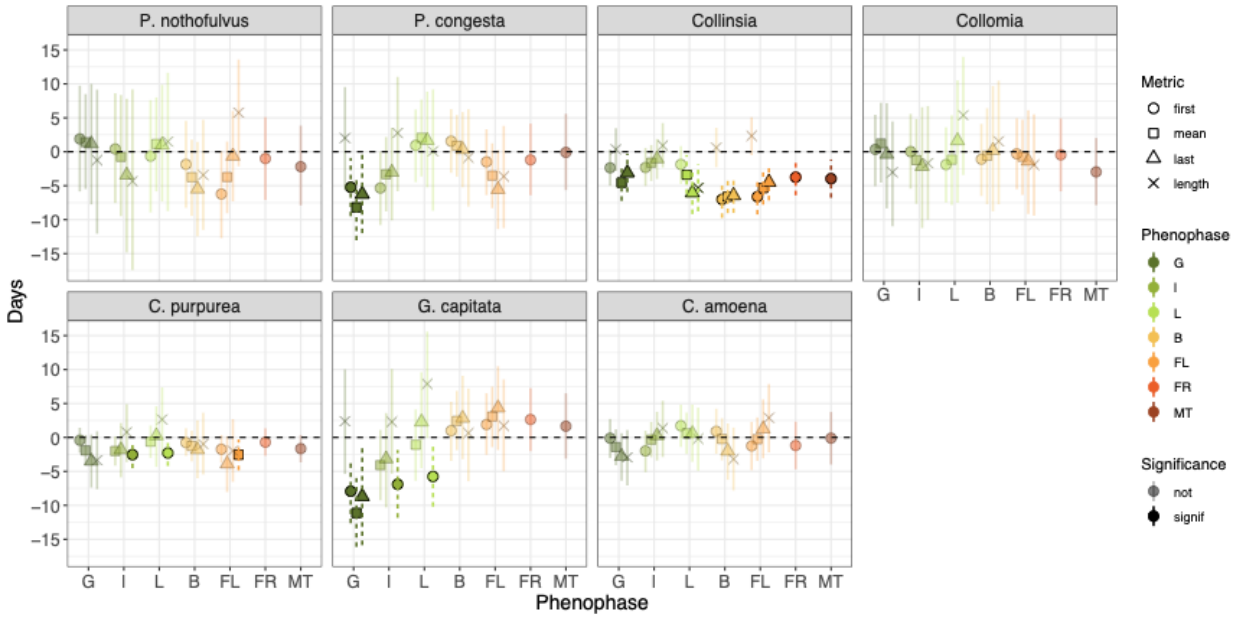


Figure 3. **Phenological shifts across all species, phenophases and metrics.** Points show medians from Bayesian posterior estimates of the number of days of change with warming. Lines show 95% credible intervals. Colors denote phenophase and shapes phenological metric. All non-significant shifts are partial transparent to emphasize significant shifts.

Collinsia was the most phenologically responsive species. All of *Collinsia's* phenophases except leaf development advanced with warming, with multiple metrics or the entire phenophase advancing. The first date of leaf development, first date of fully developed leaves, and mean date of flowering of *C. purpurea* advanced. The entire germination period and the day of first of leaf development and of fully developed leaves of *G. capitata* advanced. The entire germination period of *P. congesta* advanced. Germination phenology shifted with warming more frequently and by a greater number of days than any other phenophase. Leaf development, leaf presence, and flowering times shifted less frequently and fewer days. Other than *C. purpurea* advancing mean flower date, only *Collinsia* shifted its reproductive phases.

Shifts of almost all phenological metrics were highly correlated (Pearson's correlation coefficient, firsts and means: $R = 0.82$, $p > 0.001$; firsts and lengths: $R = -0.54$, $p > 0.001$; firsts and lasts: $R = 0.54$, $p > 0.001$; means and lasts: $R = 0.86$, $p > 0.001$) except for between shifts in means and lengths ($R = -0.13$, $p = 0.47$) (Figure S7).

2.4.3 Phenological Sensitivity. Observed phenological shifts and phenological sensitivities (shifts scaled by the degree of warming) were highly correlated for both significant (Pearson's correlation coefficient, $R = 0.68$, $p < 0.001$) and non-significant shifts ($R = 0.84$, $p <$

0.001)(Figure 4A). However, significant phenological shifts were more similar across phenophases, whereas phenological sensitivity varied more widely among phenophases (Figure 4B). Germination was the most responsive and most phenologically sensitive phenophase. In contrast, the observed shifts of leaf presence and flowering were almost identical, but flowering phenology was almost twice as sensitive to warming as leaf presence.

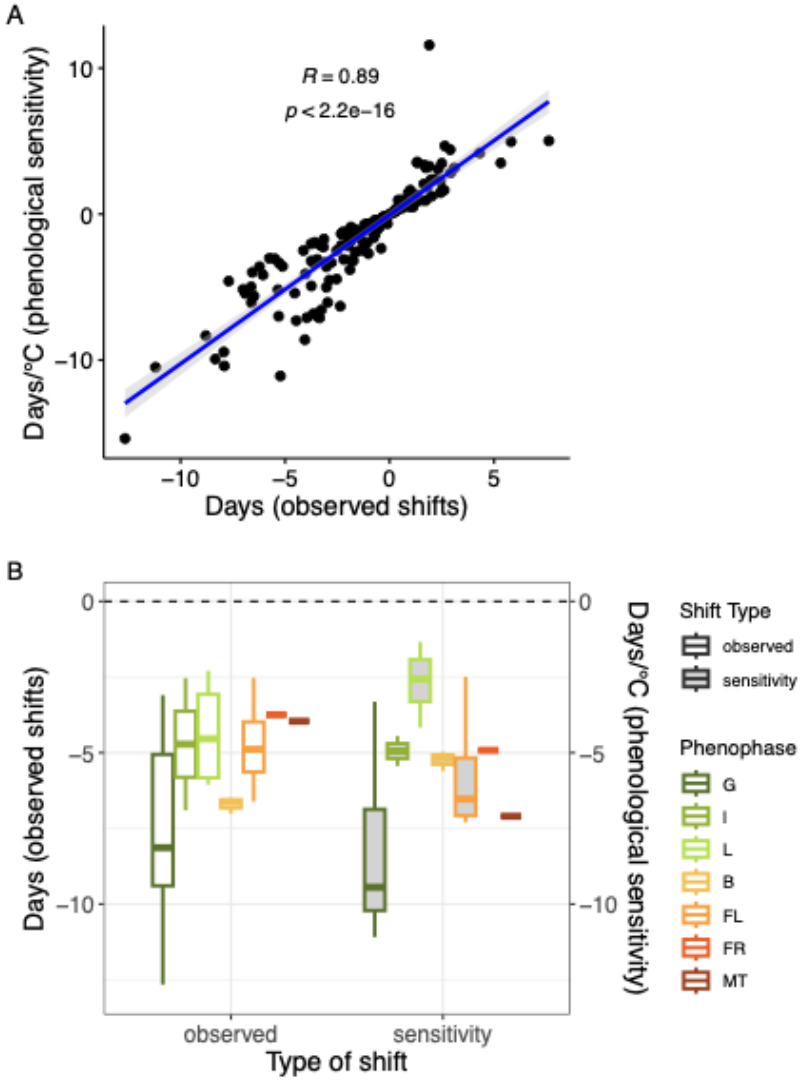


Figure 4. Comparisons between observed phenological shifts and phenological sensitivity. A) The median value from the posterior of each observed shift plotted against the phenological sensitivity of each shift. B) Boxplots on the left show significant observed phenological shifts (white fill) and boxplots on the right show the calculated phenological sensitivity of significant shifts (grey fill), each summarized by phenophase. The outlined color of the boxplot denotes phenophase. Both x-axes are labeled to highlight the slightly different metric of shift, although both shifts are measured in days.

2.4.4 Sequential Shifts. Most phenophase shifts were not significantly different from the preceding phenophase (Figure 5). Of the 98 total phenological shifts (excluding germination), only seven significantly differed from the previous phenophase's shift. Specifically, *Collinsia*'s last leaf, first bud, and mean bud; G. capitata's mean leaf development and first bud; and *P. congesta*'s first leaf shifts differed from the preceding phenophase. Among the 15 significant shifts (again excluding germination), only three were significantly different from the previous shift. *Collinsia*, the most responsive species to warming, had many phenophases that significantly shifted, but most were not significantly distinct from one another. *G. capitata*'s significant leaf-related shifts were not distinct from its germination shifts. None of *C. purpurea*'s significant shifts were distinct from the preceding phenophase. The phenological sequences we observed followed all scenarios illustrated in our conceptual figure except for the "extra shift" scenario.

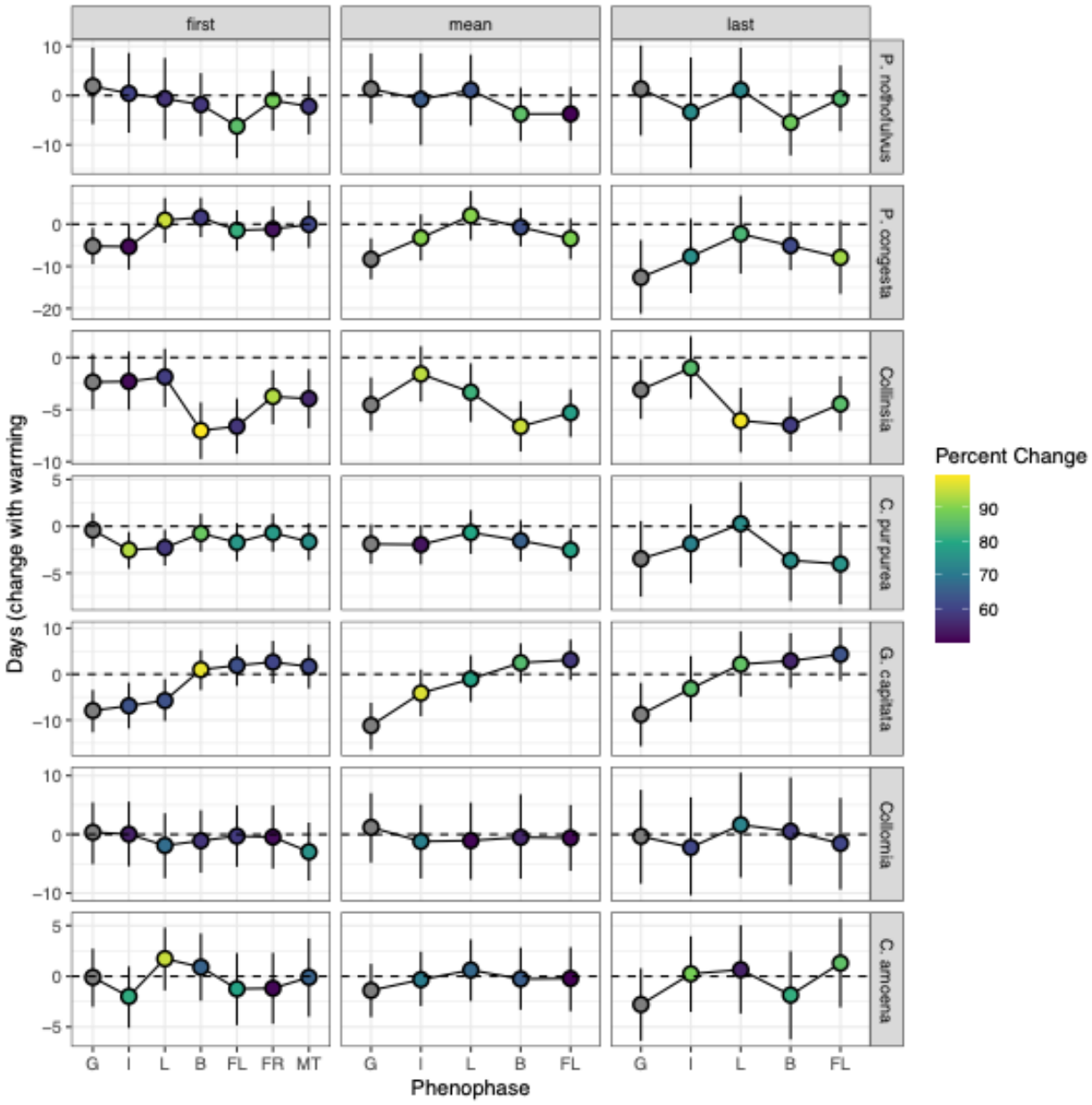


Figure 5. Differences between shifts. Points show medians from Bayesian posterior estimates of the number of days of change with warming and lines around points show 95% credible intervals, the same as in Figure 3. Significant shifts are those where the vertical line, indicating the credible interval, does not cross 0. The color of the points show how different each shift is from the previous one, with yellow and yellow-green colors indicating shifts that are significantly different from the previous one.

2.5 Discussion

Understanding how plant phenology responds to climate has been a central question in ecology for decades, yet substantial gaps remain in our knowledge, particularly regarding annual plants and early developmental stages. Here we address these gaps by examining warming effects on plant phenology across complete life cycles, tracking a diverse group of annual forbs from germination through fruit maturation at fine temporal resolution. We found that while most species and phenophases advanced with warming, the magnitude and consistency of these shifts varied considerably (Figures 2 and 3). This variation was driven by differences in both the strength of warming effects and the sensitivity to warming across species and phenophases (Figure 4). By tracking phenology throughout entire life cycles, we demonstrate that some phenological shifts are partially driven by cascading effects from preceding shifts that accumulate across developmental stages (Figure 5). These findings highlight the importance of understanding phenological change across the full life-cycle of and raise new questions about how cascading effects may influence species interactions, reproductive success, and community dynamics under future climate scenarios.

2.5.1 Species-specific Responses to Warming Across Complete Life Cycles. We observed species-specific responses to warming across all stages of the life cycle (Figures 2 and 3), consistent with earlier studies showing interspecific variation in phenological responses to warming (Fitter & Fitter, 2002; Miller-Rushing & Primack, 2008). However, our findings extend this work by revealing variation across all phenophases, not just first flowering or leaf emergence. The substantial variation we observed, with germination advancing 4.5 to 11.1 days while flowering shifted only 0.3 to 2.9 days across species, suggests that climate change effects could be highly uneven across both species and life stages. Through calculating phenological sensitivity, we demonstrated variation is largely driven by differences in sensitivity to warming across species and phenophases. This differential responsiveness implies that predicting community-level changes requires understanding phenological sensitivity at multiple developmental phases, not just the most conspicuous events traditionally monitored (e.g. flowering).

Interspecific variation in phenological responses is often attributed to factors such as growth form (Panchen et al., 2014), functional traits (Sporbert et al., 2022), phylogeny (Davis et al., 2010; Panchen et al., 2014; Loughnan et al., 2024), and seasonality (Miller-Rushing &

Inouye, 2009; Wolkovich et al., 2012; CaraDonna et al., 2014), yet these factors did not clearly explain the patterns we observed. All of our species were annual forbs, responses of congeners (*Clarkia*) and confamilials (Polemoniaceae) varied, and both early season (*Collinsia*) and late season (*G. capitata*) species were highly responsive. The limited number of species in our study may have prevented many group-level trends from emerging. However, examining functional traits could have provided additional insight, as they have been shown to explain flowering responses in one of the few studies of annuals (Pérez-Ramos et al., 2020). As annuals and early development phenophases are rarely studied, more data are needed to uncover trends and determine if the groupings that explain variation in flowering times are applicable to other phenophases.

2.5.2 Germination as a Keystone Phenological Event. The pronounced sensitivity of germination in frequency and magnitude of response suggests this phenophase could be a particularly important driver of ecological change under warming. Unlike the common focus on flowering phenology, germination timing may be the critical bottleneck determining which species successfully establish and persist in warming climates. Additionally, small, species-specific changes in germination timing, can trigger cascading effects through altered competitive hierarchies and species coexistence patterns (Blackford et al., 2020; Diez et al., 2024). While germination is typically absent from phenological studies of perennials, since they rely on recruitment from seed less often than annuals (Vico et al., 2016), climate change could fundamentally alter this dynamic. As species track suitable climatic conditions by migrating to higher latitudes and elevations, successful range expansion will depend critically on establishment from seed rather than vegetative spread or persistence of existing populations (Kroiss & HilleRisLambers, 2015). This means that germination phenology may become increasingly important to understand for both annual and perennial species. The high sensitivity of germination timing we documented in annuals therefore provides crucial insights into a phenological process that could determine migration success and community reassembly patterns across diverse plant communities in a warming world.

2.5.3 Conservation and Restoration in a Changing Climate. The high sensitivity of germination phenology combined with species-specific variation in responses has direct implications for conservation strategies and restoration practices in threatened ecosystems such as Pacific Northwest prairies. The sensitivity of early life stages suggests that establishment

success may be particularly vulnerable to changing temperature patterns in these ecosystems, requiring fundamental shifts in how restoration is planned and implemented. Restoration seeding schedules could benefit from considering how warming may alter optimal germination timing, potentially requiring shifted seeding dates to maintain synchrony with favorable growing conditions (Wilsey, 2021). The benefits of plastic germination responses have already been observed in non-native species and are considered one of the key mechanisms behind their success in invading new areas (Wainwright et al., 2012; Colautti & Barrett, 2013). Strategically incorporating germination-sensitive species into seed mixes may be a key component of creating plant communities that are competitive and resilient to non-native species now and in the future.

Beyond germination timing, the phenological sensitivity of other life stages must also be considered in restoration planning. Species-specific shifts in flowering can lead to mid-season flowering gaps, affecting the restoration success of other taxa such as pollinators and potentially disrupting the ecosystem services that restoration efforts aim to establish (Aldridge et al., 2011). This suggests that successful restoration under climate change will require a more nuanced understanding of phenological portfolios across entire plant communities, moving beyond traditional approaches that focus primarily on species composition to consider the temporal dynamics that structure ecological communities.

2.5.4 Caveats and Future Research Directions. While our study significantly advances understanding of annual plant phenological responses to warming, it also points to several important questions for future research, particularly regarding the mechanistic basis of differential responses among phenophases and species, and the long-term ecological consequences of such shifts.

A key strength of using open-top warming chambers (OTCs) was our ability to isolate a specific climatic variable and calculate the sensitivity of phenological shifts to the specific degree of warming at different times of the year. However, OTCs do not likely replicate the full complexity of natural warming patterns that longer-term field studies could better address. This is particularly important given that a review of phenological studies found that those using experimental warming tended to underpredict leaf-out and flowering responses (Wolkovich et al., 2012), and another found different effects of warming based on the whether studies were done in the field or in a common garden (Stuble et al., 2021).

Our focus on warming was driven by past evidence that temperature, more so than drought, affects plant phenology in Pacific Northwest prairie forbs (Reed et al., 2019). However, climate change will likely affect rainfall and therefore soil moisture in complex ways, shifting the timing and intensity of precipitation events, even if mean annual rainfall is largely unchanged (Min et al., 2011). During our study period, we observed large deviations from normal rainfall with just 20% of normal rainfall in February and 180% in June, highlighting the potential importance of within-season variation. Further research into how multiple climatic cues shift and interact may be particularly important for germination, since temperature during precipitation events can act as a filter for which species are able to germinate (Kimball et al., 2010).

Another related opportunity for further research would be understanding warming effects across more of the year. We seeded our experiment and installed warming chambers concurrently in mid-November, the typical timing for restoration activities in the Pacific Northwest, but well after some of the species in our experiment naturally reseed. In years following restoration, where species naturally reseed, they will likely experience increased warming during the summer months post seed drop, which may affect dormancy and therefore their ability to germinate in subsequent years. These interseasonal effects provide compelling motivation for multiyear studies that could reveal how climate effects accumulate across seasons and years.

Finally, our focus on seven species, while both taxonomically and phenologically diverse, represents only a fraction of the annual forb community in Pacific Northwest prairies. Other annuals in this region and in other ecosystems may vary in their sensitivity to warming or in what climatic cues govern their phenology, leading to novel response patterns. This limitation points to substantial opportunities for expanding this life-cycle approach across diverse species and ecosystems, particularly given that most phenological research remains concentrated on perennial species in temperate regions, despite evidence that annuals show twice the phenological sensitivity to warming compared to perennials (Stuble et al., 2021).

2.6 Conclusion

Our examination of warming effects across complete annual plant life cycles reveals that climate change impacts on plant communities are complex and variable at all life stages. By demonstrating that phenological sensitivity varies across both species and developmental stages, with early life events like germination showing particularly pronounced responses, this study

suggests new research needs for understanding how plant communities may reorganize under future climate conditions. The cascading effects we documented across life stages, combined with the high sensitivity of germination, suggest that current approaches to predicting and managing climate change impacts may be inadequate without adopting a more holistic, life-cycle perspective. As annual plants remain understudied compared to perennials, expanding this research approach across diverse ecosystems represents both an urgent priority and a significant opportunity to advance our understanding of ecological responses to global change.

2.7 Bridge

This chapter examined plant phenological responses to warming, one of the more commonly documented trait shifts in plants with global climate change. Like most phenological studies, I found that species vary in their responses to warming; however, I documented this trend across seven unique phenological events, whereas most studies typically include only one to few. These results highlight how this common trend of 'species-specific' responses to warming is more complex that previously documented. It has been hypothesized that these species-specific responses will reshuffle species interactions and potentially lead to novel communities. Many studies document community-level shifts yet few demonstrate the link between species-specific responses and these broader outcomes. My third chapter uses Modern Coexistence Theory to assess how the species-specific responses in chapter 2, in addition to shifts in fecundity and height, contribute to community-level changes. In this case, community-level shifts are changes assessed as whether we predict species pairs are predicted to coexist or whether one species will competitively exclude the other.

CHAPTER III

DIFFERENTIAL WARMING RESPONSES AMONG SPECIES YIELD WINNERS AND LOSERS BUT LIMITED COMMUNITY LEVEL EFFECTS

3.1 Contributions

Research question development, experimental design, and manuscript writing was jointly done by me and Jeff Diez. I led data collection with assistance primarily from Emily Cook, Julia Prange, and Lindsay Villano. Jeff Diez led statistical analysis, but both of us contributed. Jeremy Collings provided valuable feedback on analysis.

3.2 Introduction

Climate change is reshaping ecological communities worldwide, yet predicting these changes remains challenging because species often respond to warming in markedly different ways (Valladares et al., 2015). While recent work has documented many individual species' responses to climate change, and there is a long history of experiments that track community-level metrics such diversity and composition (Elmendorf et al., 2012; Reed, Pfeifer-Meister, et al., 2021), there is an interesting gulf between these species- and community-level approaches. Scaling species-level responses to predict community-level outcomes such as composition and diversity in important for understanding mechanisms of change but proves more difficult. A key challenge is that co-occurring species can vary substantially in both the magnitude and direction of their direct responses to warming, likely altering species interactions which could create complex cascading effects that ripple through communities (CaraDonna et al., 2014; Iler et al., 2021; Theobald et al., 2017).

Species-specific responses to climate change have been documented across a wide range of traits and performance measures. Perhaps the most widely studied response involves shifts in phenology, the timing of key lifecycle events such as flowering and reproduction. Although plant species generally advance their phenology with warming, co-occurring species frequently vary greatly in the magnitude of this advance (Stuble et al., 2021), and some species even appear to shift in opposite directions (Sherry et al., 2007; CaraDonna et al., 2014; Chen et al., 2020). Similar interspecific variation has been observed in demographic responses, where species differ in how their fecundity, growth rates, and survival respond to climate change. For example, tree species with contrasting life strategies, such as fast-growing early-successional versus slow-growing late-successional species, can exhibit markedly different growth responses to warming

(Drobyshev et al., 2013). In arctic plant communities, vascular and non-vascular species can also show contrasting responses to warming and nutrient addition, with tall versus low-growing species and grasses versus sedges responding in opposing directions (Klanderud, 2008). This variation can sometimes be explained by differences in species' growth form, seasonality, or functional traits, but the underlying mechanisms remain incompletely understood (Chmura et al., 2019).

When co-occurring species respond differently to climate change, the resulting shifts can fundamentally alter community dynamics through changes in competitive hierarchies and species interactions (Collins et al., 2022). Variation in phenological responses has led to hypotheses of "phenological reshuffling," where the temporal ordering of species within communities changes, with potential consequences for competitive outcomes. For example, Alexander & Levine (2019) found that when a non-native aster advanced its flowering phenology relative to native species, it gained a stronger competitive advantage over many natives in a California grassland. Similarly, when some species increase their performance while others decline under warming, competitive hierarchies may shift. Extreme drought has been shown to reverse competitive dominance between co-occurring tree species (Cavin et al., 2013), illustrating how environmental stress can restructure competitive hierarchies. These indirect effects through altered species interactions have been shown to sometimes exceed the direct effects of climate change (Liancourt et al., 2013; Olsen et al., 2016) and could in some cases even reverse the direction of direct climate effects (Suttle et al., 2007).

To fully understand and predict how warming affects communities, we need experiments and analyses that integrate both direct species responses and their indirect effects through altered interactions. Modern coexistence theory (MCT) provides a framework for combining these effects to scale up and make predictions about community change. MCT quantifies species' abilities to coexist through two key mechanisms: stabilizing niche differences that promote coexistence by reducing competitive overlap, and fitness differences that determine competitive hierarchies when niche differences are insufficient (Godoy & Levine, 2014; Adler et al., 2007; Chesson, 2000a). Applying MCT to climate change scenarios can help determine whether warming alters species coexistence and whether such changes are driven by shifts in competitive effects, niche differences, or fitness differences (Germain et al., 2018; Valladares et al., 2015; Van Dyke et al., 2022). MCT has recently been used to understand how variation in rainfall can

affect coexistence (Hallett et al., 2019; Van Dyke et al., 2022), but the effects of warming on coexistence mechanisms remain unexplored. Since temperature affects plants through different physiological pathways than precipitation, warming may have unique effects on competitive interactions and coexistence outcomes.

Here we report the first study, to our knowledge, to use experimental warming combined with MCT to investigate how plant communities respond to climate warming through both direct species effects and altered competitive interactions. We focus on annual forbs native to Pacific Northwest prairies, one of the most imperiled ecosystems in North America (Noss et al., 1995). The continued warming forecasted for this region, combined with the highly fragmented state of these prairie remnants, makes understanding their responses to warming an important conservation challenge (Bachelet et al., 2011). Using experimental competitive gradients combined with open-top warming chambers, we quantified species' growth, phenology, fecundity, and responses to competitive neighborhoods. We used these data to parameterize population models and calculate coexistence outcomes under both ambient and warmed conditions.

We addressed three primary questions: (1) How does warming affect species directly through changes in growth, phenology, fecundity, and intrinsic growth rates? (2) How does warming alter species interactions and competitive effects? (3) Do these warming-induced changes modify species' ability to coexist through shifts in stabilizing mechanisms and fitness differences?

We hypothesized that warming would produce species-specific direct effects on demographic performance and alter competitive interactions, with these changes integrating in complex ways to influence niche and fitness differences and ultimately coexistence outcomes. Given that species coexistence depends on the interplay between intrinsic growth rates, intraspecific competition, and interspecific competition, we anticipated that warming effects on these underlying processes could shift coexistence dynamics along multiple pathways. We expected that warming could reinforce existing competitive hierarchies in some cases, when dominant species benefit disproportionately from temperature increases. Alternatively, warming could promote greater coexistence potential when sub-dominant species gain competitive advantages or benefit demographically, or when changes in competitive interactions reduce niche overlap between species. However, the inherent complexity of these multi-faceted responses,

whereby direct demographic effects and indirect competitive effects may operate in opposing directions, made specific predictions about coexistence outcomes difficult. We therefore sought to characterize the range of mechanisms through which moderate warming may influence competitive outcomes and to identify the conditions under which these mechanisms translate into meaningful changes in species coexistence.

3.3 Methods

3.3.1 Study Site and Species Selection

The experiment was conducted in an outdoor common garden at the University of Oregon's research greenhouses in Eugene, OR, USA. Eugene is located at the southern end of the Willamette Valley, which is the southern extent of the Pacific Northwest (PNW) prairie ecosystem. This ecosystem has a Mediterranean climate of cool wet winters and hot dry summers. Eugene receives an average of 108 cm of precipitation per year, with high annual variability, and has an average temperature of 11.6°C (PRISM Climate Group, 30-year average). During the 12-month period around the experiment, October 1, 2021-2022, Eugene received 97cm of precipitation and the average temperature was 12.1°C (NOAA). While the study site was likely historically prairie, the soil at the study site has been amended and used for research and agriculture for decades leading to a below ground environment that likely differs from historical field conditions in the region.

PNW prairies are a bunchgrass dominated ecosystem with interspersed perennial and annual forbs. Annual forbs were used in this experiment due to conservation interests of reintroducing annuals to the system. All study species are native to PNW prairies and were selected to be phenologically diverse and important for restoration. We seeded nine forbs but only the following five species germinated at high enough densities to use in this experiment: *Collinsia grandiflora (COLLIN), Collomia grandiflora (COLLOM), Clarkia purpurea (CLAPUR), Clarkia amoena (CLAAMO)*, and *Gilia capitata (GILCAP)* (Table S1). Seed was locally sourced from two native plant nurseries in the southern Willamette Valley, Friends of Buford Park & Mt Pisgah Nursery and Heritage Seedling & Liner, Inc.

3.3.2 Experimental Design

In late November 2021, 40 1m^2 plots were seeded with a single species as the background 'competitor' and three individual 'phytometers' of each of the nine species were planted throughout each plot (Figure S8). Each species was seeded as the background competitor in four

plots and there were four plots where phytometers were planted without any background species ("no competition" plots). Half of the competition plots were seeded for high density competition, with approximately 1000 seeds per plot, and the other half were seeded as low-density competition, with approximately 200 seeds per plot, but actual competitor density varied with germination success. Competition plots where the background species did not germinate well were then fully weeded and treated as "no competition" plots. Phytometers were spaced approximately 20 cm apart within the plot so that competition was predominately with the background species, a distance suggested by previous studies of annual plants in comparable grass-forb systems (Levine & HilleRisLambers, 2009; Mayfield & Stouffer, 2017). Throughout the experiment, plots were hand weeded to remove non-target species. With this design, we were able to measure the performance of each species in the absence of competition and in competition with inter- and intraspecific individuals for all unique pairwise combinations.

To ask how species' performance and interactions changed with warming, we placed open-top warming chambers over two of the four plots of each background and two of the no competition plots on the same day as seeding, using a chamber design modified from the International Tundra Experiment (ITEX) design (Henry & Molau, 1997; Marion et al., 1997). Air temperature was measured in six random pairs of warmed and ambient plots every thirty minutes by HOBO Pendant data loggers suspended approximately 2 cm above the ground under modified radiation shields (Holden et al., 2013). Soil moisture was measured four times throughout January and February in all plots using a Hydrospan Decagon GS3 Sensor, by averaging three readings taken throughout each plot. From March onward, soil moisture and temperature were measured every thirty minutes by four METER TEROS 11 sensors buried approximately 5cm deep in two paired warm and ambient plots.

3.3.3 Field Measurements

To assess the effect of warming on the growth of each species, the height of phytometers in conspecific backgrounds and in no-competition plots was measured every ten days beginning in January. Phenology data for all phytometers were recorded twice weekly. However, only the peak flowering date is analyzed in this study. Peak flowering date was defined as the mean date during the main flowering period. Occasionally, some individual plants produced a few flowers after extended gaps with no flowering; these late flowers were excluded from the main flowering period.

To determine species' intrinsic growth rates and the strength of intra- and inter-specific competition, we quantified competitor density and fecundity (number of seeds) for each phytometer. We counted the number of competitors rooted within a 10cm diameter neighborhood of each phytometer in early April, when all species had germinated and survived the winter. To quantify fecundity, once a phytometer had no buds or open flowers, it was removed from the plot, and the number of fruits was counted. Due to the large size of *G. capitata* plants, we used half of the plants to build a statistical relationship between fruit number and inflorescence number and only counted the number of inflorescences on the other half of the *G. capitata* phytometers. For all species, the number of seeds per fruit was counted for a subset of phytometer fruits and multiplied by fruit counts to calculate fecundity as the total number of seeds produced for each phytometer. The number of fruits per inflorescence and the number of seeds per fruit came from plants in both treatments, but all averages were done at the species level.

3.3.4 Statistical Analysis

3.3.4.1 Species-level Responses. To assess species-level responses to warming we fit linear models with response variables of individual plant fecundities, height, and the peak dates of flowering phenology, as a function of species, warming treatment and a species × treatment interaction. Models assessing the warming effect on fecundity and phenology included all phytometers in the study while the model assessing the effect on height only used the subset of phytometers for which height was measured, as described above. Models were fit in R (R Core Team, 2025).

For the fecundity model, we used the total number of seeds produced per individual plant as the response variable, modeling the data using a linear model with Gaussian error distribution. The height model used maximum plant height (cm) as the response variable, also fit with a Gaussian error distribution. The maximum height of an individual was defined as the mean of the last three height measurements. Only plants that reached reproductive maturity were used. For the flowering phenology model, we used the mean day of year (DOY) when each individual reached peak flowering as the response variable. All models included warming treatment (ambient vs. warmed) and focal species as fixed effects, along with their interaction term to test for species-specific responses to warming.

We conducted post-hoc pairwise comparisons using estimated marginal means (emmeans package; Lenth, 2024) with Tukey adjustments for multiple comparisons. For models with significant species × treatment interactions, we examined treatment contrasts within each species to identify which species showed significant responses to warming. Statistical significance was assessed at alpha = 0.05 for all analyses.

3.3.4.2 Competition Models. We estimated the effects of intra- and inter-specific competition on individual reproductive output, F_i, via a nonlinear Beverton-Holt model:

$$F_i = \frac{\lambda_i}{(1 + \alpha_{ij}N_j + \alpha_{ii}N_i)}$$

where λ is the intrinsic population growth rate, and α_{ii} and α_{ij} quantify the effects of intra-specific and inter-specific competition, respectively, with N_i, and N_j being competitor densities. Parameters were estimated for each species and treatment using a hierarchical structure for the alpha parameters, allowing for pooling of information within focal species and treatments. This is a conservative strategy to limit any influence of extreme data points given the sample size that was logistically possible in a pairwise competition experiment. The lambdas were modeled separately for each focal species x treatment combination. All competition coefficients were constrained to be positive values, reflecting competitive rather than facilitative interactions between species. Although there may in theory be facilitation at very low densities in this study system, for example due to amelioration of stressful abiotic conditions, we almost universally find plants with reduced competition perform better than those under competition. Bayesian models were fit using Stan (Carpenter et al., 2017) accessed through R via the brms package (Bürkner, 2021) using moderately informative priors to facilitate convergence but not influence posterior estimates. Model convergence was assessed using the Gelman-Rubin statistic and by visually examining trace plots from four independent Markov chains.

To assess the significance of warming effects on competition parameters and intrinsic growth rates, we used the posterior probability distributions from fitted models to calculate the probability of difference (PD) between ambient and warmed treatments. These are the proportion of posterior draws where the difference between warming and ambient exceeded zero (for increases) or were below zero (decreases). This approach yields an intuitive measure of the magnitude and certainty of warming effects on all parameters. We used posterior distributions of

all parameters for use in downstream calculations of niche and fitness differences, allowing us to propagate parameter uncertainty throughout the coexistence analysis.

3.3.4.3 Coexistence Analysis. We used estimates of intrinsic growth rates (lambdas) and competition coefficients (alphas) to calculate niche differences and fitness differences following Godoy and Levine (2014) to evaluate the potential for species coexistence under warming conditions. Fitness differences quantify the degree to which one species has an inherent competitive advantage over another in the absence of niche differences, and were calculated as:

$$\frac{\kappa_j}{\kappa_i} = \frac{\eta_j - 1}{\eta_i - 1}\sqrt{\frac{\alpha_{i,j}}{\alpha_{j,i}}\frac{\alpha_{i,i}}{\alpha_{j,j}}},$$

where

$$\eta_i = \frac{\lambda_i g_i}{1 - (1 - g_i)(s_i)}$$

Fitness differences in this formulation can be decomposed into the product of the demographic ratio

$$\frac{\eta_j - 1}{\eta_i - 1}$$

and (ii) competitive response

$$\sqrt{\frac{\alpha_{i,j}}{\alpha_{j,i}}\frac{\alpha_{i,i}}{\alpha_{j,j}}}$$

Niche differences represent the relative strength of intraspecific competition (self-limitation) compared to interspecific competition. The relative strength of stabilizing niche differences compared to destabilizing fitness differences determines the potential for stable coexistence. Niche differences are calculated as 1 - ρ, where ρ is the niche overlap between species, calculated as

$$\rho = \sqrt{\frac{\alpha_{i,j}}{\alpha_{j,j}}\frac{\alpha_{j,i}}{\alpha_{i,i}}}$$

Because we fit models that allow for the possibility of stronger inter-specific competition (numerator) than intra-specific competition (denominator), the value 1 – ρ can be negative, which leads to unintuitive interpretation of negative niche differences. Thus we use the term "stabilization potential" for this quantity (Ke & Letten, 2018). This stabilization potential reflects the relative strength of inter-specific competition (numerator) and intra-specific competition

(denominator), with greater intra-specific competition relative to inter-specific competition leading to greater likelihood of coexistence.

As an additional measure of how treatments affected species, we calculated the competitive ability for each species, *i*, as: $(\lambda_i - 1)/\sqrt{\alpha_{i,i} * \alpha_{i,j}}$), where λ_i is the species' intrinsic growth rate (in the absence of competitors) and the denominator is the geometric mean of the species' intra- and inter-specific competition that it experiences. This measure can thus be understood as species i's average ability to tolerate competition while maintaining offspring production (Hart et al., 2018).

To account for parameter uncertainty, we used 1,000 random draws from the posterior distributions of these parameters, thus yielding posterior distributions of niche and fitness differences. We determined the predicted coexistence outcome by comparing the magnitude of fitness differences to niche differences across all posterior draws, yielding probabilities of each of three possible outcomes: competitive exclusion (when fitness differences exceed niche differences), priority effects (when outcomes depend on initial conditions), and stable coexistence (when niche differences are sufficient to overcome fitness differences). Uncertainty in interaction outcomes was quantified using the 1,000 calculations of niche and fitness differences derived from the posterior parameter distributions. As above for individual parameters, we assessed the significance of warming effects on derived quantities (stabilization potential, fitness differences, demographic ratios, competitive response ratios, and competitive abilities) by calculating the probability of difference (PD) between ambient and warmed treatments.

3.4 Results

3.4.1 Warming Effects on Air and Soil

Warming chambers increased daily maximum (1.27°C ± 1.40 SD), mean (0.42°C ± 0.45), and minimum (0.42°C ± 0.36) air temperatures (Figure S2). With passive warming chambers, the effect of warming varied day to day and seasonally, with the strongest warming effect in the spring and the weakest warming effect in the summer. Soil warming followed a similar pattern with the strongest warming effect in the spring and on daily maximum temperatures (0.83°C ±1.87) (Figure S3). Warming chambers appeared to have a cooling effect on soil temperatures in the summer months, but we suspect this was due to the increased vegetation cover in the warmed plots which in turn cooled the soil. Warming chambers did not reduce soil moisture, measured as

volumetric water content (Figure S4). Conversely, on some days soil moisture was higher in plots with warming chambers and sometimes varied more within than between treatments.

3.4.2 Direct Effects of Warming on Plant Performance

3.4.4.1 Seed Production. Species growing without competitors differed dramatically in their overall fecundity, with CLAPUR by far the most fecund species and COLLOM the least fecund (Figure 6). Warming and species identity had significant overall effects on fecundity ($F_{1,907} = 16.67$, $p < 0.001$, and $F_{4,907} = 307.10$, $p < 0.001$, respectively; Table S2a), but warming effects on fecundity did not vary significantly among species (treatment × species interaction: $F_{4,907} = 1.57$, $p = 0.18$; Table S2a). Nonetheless, post-hoc analysis found that CLAPUR and GILCAP both had significantly lower seed production in the warming treatment (Figure 6; Table S2b).

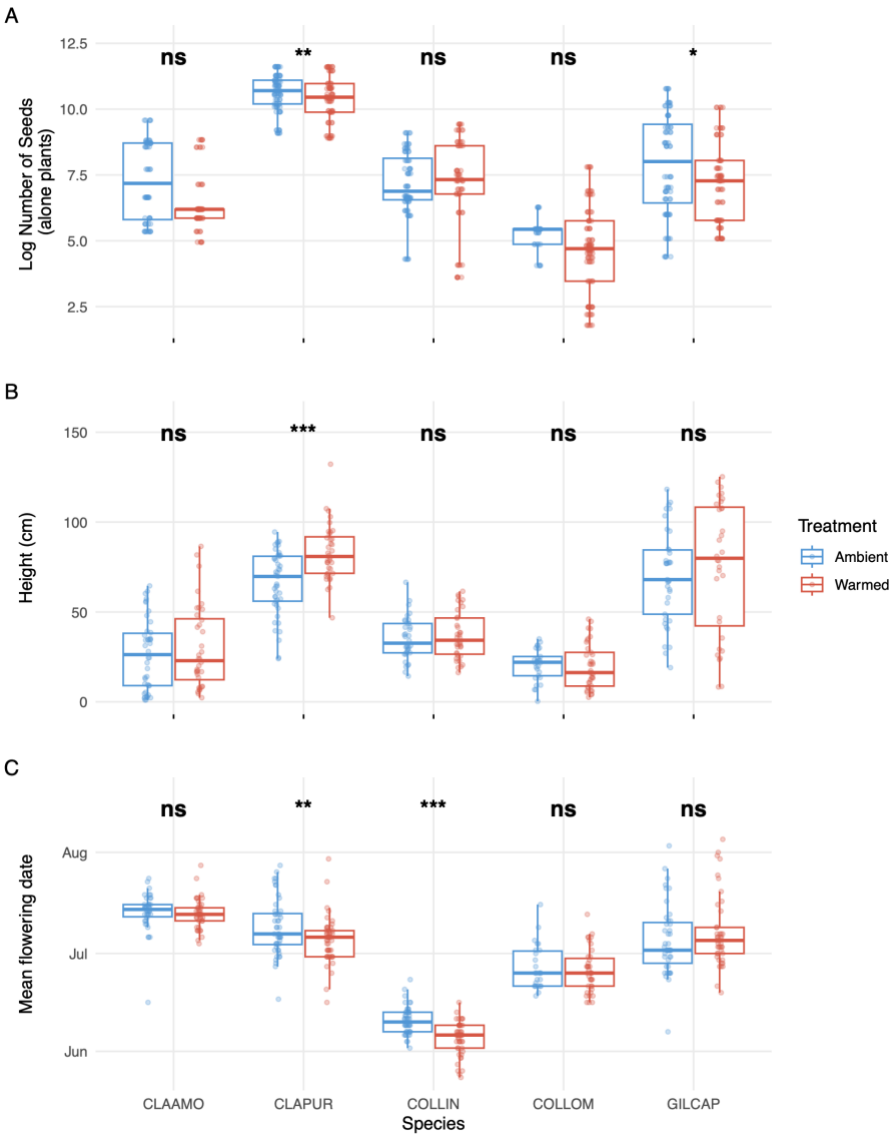


Figure 6. Warming effects on A) fecundity, B) plant height, and C) mean (peak) flowering date. Boxplots show raw data from ambient (blue) and warmed (red) plots. In A), fecundity is the number of seeds each plant produced, only including plants grown without competitors. In B), plant height is the maximum height of species. In C), phenology is represented by the peak flower date. Significance: *** p < 0.001, ** p < 0.01, * p < 0.05, · p < 0.1, ns = not significant").

3.4.4.2 Plant Height. Plant height varied significantly among species ($F_{4,356} = 118.1$, $p < 0.001$; Table S3a), but the warming treatment effect on plant height was not significant ($F_{1,356} = 2.19$, $p = 0.14$; Table S3a), and the treatment × species interaction was only marginally significant ($F_{4,356} = 2.26$, $p = 0.06$; Table S3a). Among individual species, CLAPUR showed the strongest positive response to warming, with plants in warmed conditions averaging 16.93 cm taller than those in ambient plots (CLAPUR: A - W = -16.93 cm, $p < 0.001$; Table S3b). Other

species showed minimal responses to warming treatment (Table S3b). The strong response in CLAPUR was the primary driver of the marginally significant interaction term.

3.4.4.3 Flowering Phenology. The warming treatment significantly affected peak flowering timing across species ($F_{1,412} = 9.20$, $p = 0.003$; Table S4a), with significant species-specific responses to warming (treatment × species interaction: $F_{4,412} = 3.70$, $p = 0.006$; Table 4). Among the species, COLLIN showed the strongest phenological response, with peak flowering significantly advanced by 5.31 days in warming compared to ambient conditions (COLLIN: A - W = 5.31 days, $p < 0.001$; Table S4b). CLAPUR also exhibited significantly advanced flowering under warming conditions (CLAPUR: A - W = 4.06 days, $p = 0.008$; Table S4b), while all other species were not statistically significant. GILCAP was the only species with a mean trend toward later flowering in the warming treatment.

3.4.3 Competition Coefficients and Intrinsic Growth Rates. The Beverton-Holt competition models revealed that warming significantly altered both intra- and interspecific competition coefficients, although responses varied considerably among species pairs (Figure 7A). Several specific interactions showed significant changes with warming: COLLIN's competitive effect on CLAAMO increased under warmed conditions (PD = 97%), while CLAPUR's competitive effects on both COLLIN and GILCAP decreased(PD = 95%, 98%). Conversely, CLAPUR's competitive impact on COLLOM increased with warming (PD = 97%). Notably, GILCAP exhibited reduced intraspecific competition under warming conditions, suggesting weaker self-regulation under warmer temperatures.

Intrinsic growth rates (λ) also responded differently among species to the warming treatment (Figure 7B). CLAAMO and GILCAP both showed decreased intrinsic growth rates under warming (PD = > 99%), indicating reduced per-capita reproductive potential at elevated temperatures. In contrast, COLLIN demonstrated increased intrinsic growth rates with warming (PD = 95%), suggesting this species may benefit from the temperature increases projected under climate change scenarios.

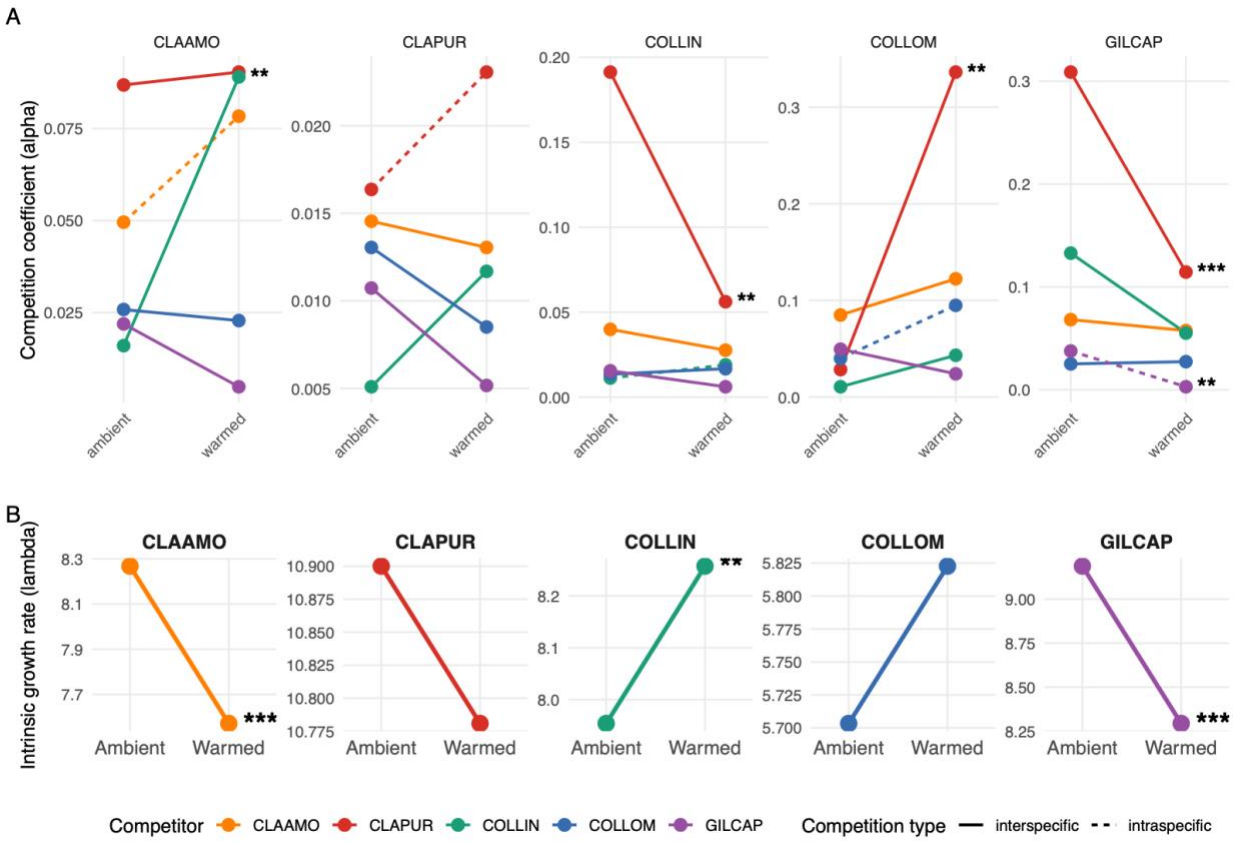


Figure 7. Species-specific responses of competition coefficients and intrinsic growth rates to experimental warming. Points show median estimates from Beverton-Holt models fit to each species in ambient and warmed treatments. Lines connect treatment pairs to illustrate warming effects. (A) Competition coefficients (alphas): dashed lines indicate intraspecific competition (self-limitation), while solid lines show interspecific competition between the focal species (rows) and each competitor species (colors). Higher values indicate stronger competitive effects. (B) Intrinsic growth rates (lambdas) representing population growth potential in the absence of competition. Asterisks indicate statistical significance based on Bayesian posterior distributions: *** = probability of difference (PD) > 97.5%, ** = PD > 95%, * = PD > 90%. Species codes: CLAAMO = *Clarkia amoena*, CLAPUR = *Clarkia purpurea*, COLLIN = *Collinsia grandiflora*, COLLOM = *Collomia grandiflora*, GILCAP = *Gilia capitata*.

3.4.4 Stabilization and Fitness Differences (FD). The two components yielding coexistence, niche and fitness differences, showed relatively modest and species-specific changes with warming (Figure 8). The magnitude and direction of these changes varied considerably across species pairs, with some interactions showing increased stabilization of coexistence while others showed decreased potential. For example, the probability of increased stabilization potential with warming was relatively high (PD >70%) for the COLLIN-CLAPUR and COLLOM-CLAAMO pairs, while the COLLOM-GILCAP pair showed a 64% probability of

decreased stabilization potential. Fitness differences between species pairs also showed relatively weak net changes with warming but exhibited consistent directional trends for individual species (Figure 8). COLLOM consistently decreased in relative fitness against all other species under warming conditions. Conversely, GILCAP increased in relative fitness compared to all competitors. COLLIN showed improved relative fitness against three of four species, while CLAAMO experienced decreased relative fitness against three of four competitors. CLAPUR experienced decreased relative fitness against two competitors and increased relative fitness against the two other competitors.

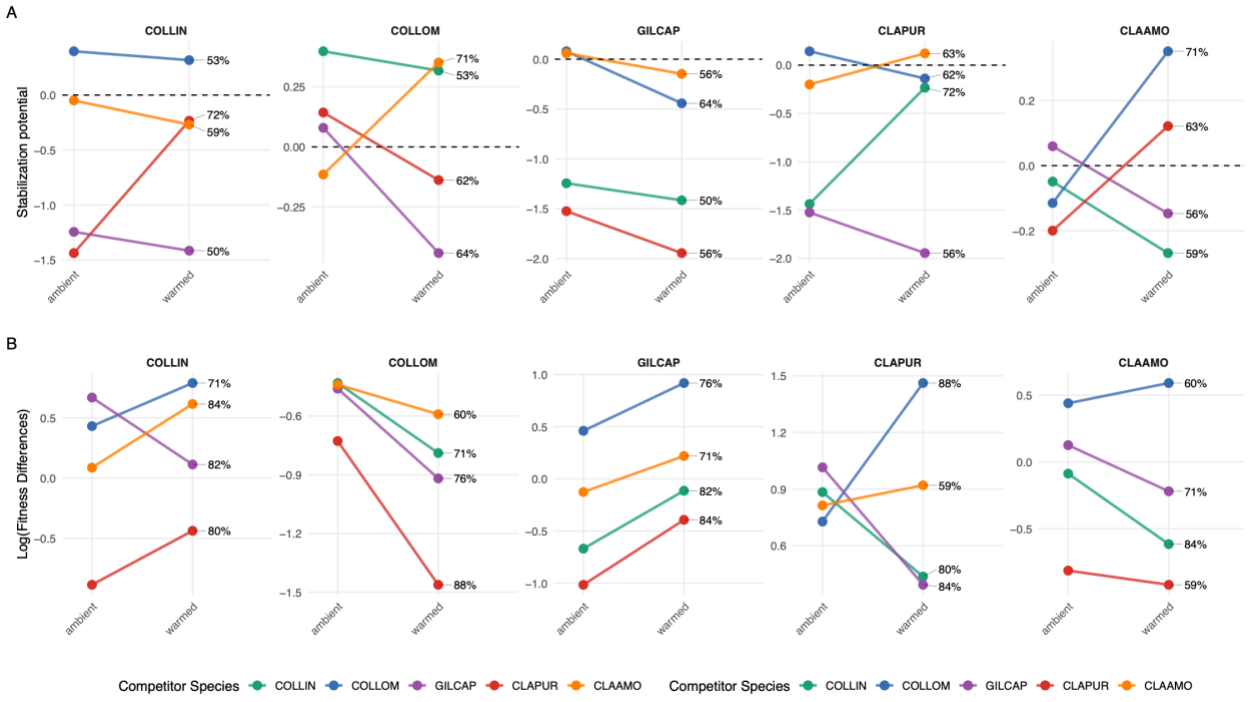


Figure 8. Species-specific responses of coexistence mechanisms to experimental warming. (A) Stabilization potential and (B) log fitness differences between species pairs in ambient and warmed treatments. Points show median estimates from posterior predictive distributions, with lines connecting treatment pairs to illustrate warming effects. Colors indicate the focal species in each comparison. Numbers show the probability of difference (PD) from Bayesian posterior distributions, indicating the certainty that warming changed each metric. (A) Stabilization potential measures the strength of negative frequency dependence that promotes coexistence; values are symmetric for each species pair regardless of which species serves as the focal species. (B) Log fitness differences measure competitive asymmetries between species pairs; positive values indicate the focal species has higher fitness than its competitor. Unlike stabilization potential, fitness differences are asymmetric and depend on which species is designated as the focal species versus the competitor. Species codes: CLAAMO = *Clarkia amoena*, CLAPUR = *Clarkia purpurea*, COLLIN = *Collinsia grandiflora*, COLLOM = *Collomia grandiflora*, GILCAP = *Gilia capitata*.

3.4.5 Demographic ratios and Competitive Responses (FD Components).

Demographic ratios showed stronger responses to warming compared to other coexistence metrics (Figure 9C). Several species exhibited consistent patterns of demographic decline or enhancement across multiple competitive interactions. GILCAP showed demographic declines against three of four competitors under warming (PD = > 99%), as did CLAAMO (PD = > 99%). Conversely, COLLOM demonstrated demographic increases against two of four competitors, and COLLIN showed positive demographic responses against three of four competitors. CLAPUR exhibited mixed responses, with demographic increases against CLAAMO and GILCAP but decreases when competing with COLLIN.

Competitive response ratios, measuring species' susceptibility to competition from others, showed modest but species-specific changes (Figure 9B). GILCAP demonstrated trends toward increased competitive responses against all other species under warming (but all PD ≤ 86%), suggesting this species may become more tolerant of competitive pressure under elevated temperatures. Warming effects on competitive abilities were also generally modest, with some notable exceptions (Figure 9A). GILCAP showed increased competitive ability against all other species under warming conditions. In contrast, COLLOM exhibited significant decreases in competitive ability against CLAPUR (PD = 93%) and COLLIN (PD = 85%), while CLAAMO showed reduced competitive ability against COLLIN (PD = 92%).

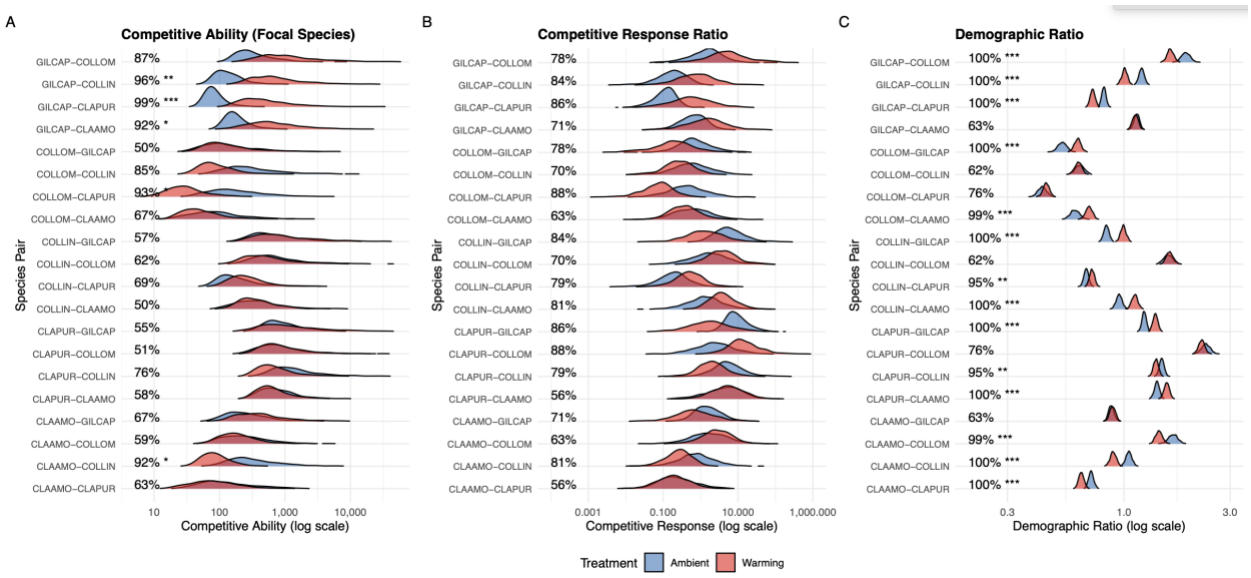


Figure 9. Posterior distributions of invasion analysis metrics showing warming effects on competitive dynamics. Ridge plots display full Bayesian posterior distributions for (A) competitive ability of focal species, (B) competitive response ratio, and (C) demographic ratio between species pairs in ambient (blue) and warmed (red) treatments. Each ridge represents the probability density of parameter estimates on log scales, with wider distributions indicating greater uncertainty. Species pairs are labeled as focal-competitor. Numbers show the probability of difference (PD) between treatments, with asterisks marking statistically significant changes: *** = PD ≥ 97.5% or ≤ 2.5%, ** = PD ≥ 95% or ≤ 5%, * = PD ≥ 90% or ≤ 10%. Species codes: CLAAMO = Clarkia amoena, CLAPUR = Clarkia purpurea, COLLIN = Collinsia grandiflora, COLLOM = Collomia grandiflora, GILCAP = Gilia capitata.

3.4.6 Coexistence Outcomes and Community Assembly. The predicted coexistence outcomes revealed that warming differentially affected species pair interactions, with some pairs remaining largely unaffected while others experienced substantial shifts in the probabilities of different coexistence outcomes (Figure 10). Multiple types of changes were observed, including shifts towards coexistence, shifts toward competitive exclusion, and increased probability of priority effects where initial conditions determine competitive outcomes. However, competitive exclusion by one species was the most commonly predicted outcome in both conditions. Overall, coexistence was unlikely in ambient conditions (0-29%) and less likely with warming (0-21%).

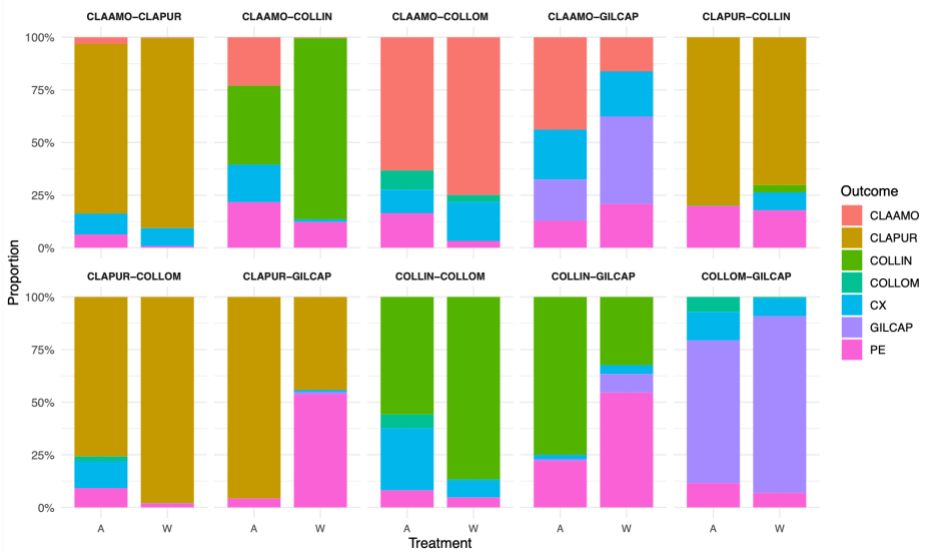


Figure 10. Coexistence outcomes in ambient and warmed plots. Bars show the probability of each possible outcome of species interactions and which species would exclude the other if competitive exclusion is the most likely outcome. Each outcome is shown with a different color, including different colors for each species. CX = coexistence; PE = priority effects. Species codes: CLAAMO = Clarkia amoena, CLAPUR = Clarkia purpurea, COLLIN = Collinsia grandiflora, COLLOM = Collomia grandiflora, GILCAP = Gilia capitata.

3.5 Discussion

Understanding how climate change affects species directly and indirectly through species interactions is critical for predicting community responses to global warming, yet the mechanisms linking individual species' responses to community-level outcomes remain poorly understood. Modern coexistence theory (MCT) provides a framework for dissecting these mechanisms by quantifying how environmental change influences niche differences that stabilize coexistence and fitness differences that drive competitive exclusion. Although previous studies have applied MCT to examine responses to experimental drought (Hallett et al., 2019; Van Dyke et al., 2022), this is the first study to our knowledge to evaluate how experimental warming impacts species interactions and coexistence outcomes in plant communities. Our results demonstrate that even moderate warming can cause species-specific effects on demographic performance and alter the niche and fitness differences governing coexistence. However, these changes translated into moderate shifts in community outcomes for only a subset of species pairs. The limited overall changes in predicted coexistence appear partially due to strong competitive asymmetries that persisted under both ambient and warmed conditions. Overall, these results illustrate both the potential for warming to reshape species performance and

competitive dynamics and the capacity for complex ecological interactions to potentially buffer community-level responses to climate change.

3.5.1 Direct Effects. In this study, experimental warming caused species-specific effects on multiple measures of plant performance, with effect sizes and directions varying substantially among co-occurring species. This differential sensitivity to warming, even under modest temperature increases, aligns with growing evidence that climate change impacts on plant communities will be highly species-specific, potentially leading to significant ecological reshuffling (Cleland et al., 2007; Theobald et al., 2017; Stuble et al., 2021). The magnitude of phenological shifts we observed, with flowering advancing approximately five days in some species, falls within the lower range of responses documented in previous Pacific Northwest prairie research (Reed et al., 2019), likely reflecting the more moderate passive warming approach used in our study compared to consistent experimental heating.

The relationships between phenological sensitivity and overall performance were more complex than past predictions of straightforward correlated phenology and performance (Cleland et al., 2012; Zhang et al., 2025). CLAPUR demonstrated responses across all measured traits, including earlier phenology and increased height under warming, but also reduced seed production, illustrating how warming can create mixed effects within individual species. This pattern suggests potential physiological trade-offs where accelerated growth comes at the cost of reproductive output, possibly due to resource allocation or shortened reproductive periods. Similarly, COLLIN showed significant phenological advancement but maintained stable growth and reproductive patterns, indicating that species may buffer warming effects on some measures of performance while responding via others. The reduced fecundity of the two highest-performing species (CLAPUR and GILCAP) under warming conditions suggests that even species that appear to benefit from warming in terms of vegetative growth (height) may experience reproductive costs. These results underscore that a species' sensitivity to warming can vary significantly across different metrics, even among those typically considered closely linked, such as growth and phenology.

3.5.2 Warming Effects on Coexistence. Because species coexistence is determined by a combination of intrinsic growth rates, intra-specific competition, and inter-specific competition, there are numerous pathways by which warming effects on these underlying processes yield changes in coexistence outcomes. We can broadly categorize the diverse set of responses in this

study into a few primary groups of mechanisms. First, several species pairs exhibited enhanced competitive dominance under warming through multiple mechanisms that strengthened existing competitive asymmetries. The most pronounced example was increased dominance of COLLIN over CLAAMO, driven by a combination of increased fitness differences (84% probability) and decreased competitive ability of CLAAMO (92%). These shifts resulted from stronger competitive effects of COLLIN on CLAAMO, increased intrinsic growth rates of COLLIN, and decreased intrinsic growth rates of CLAAMO. The demographic ratio component of fitness differences increased substantially (>99% probability), reinforced by increased competitive response ratios (81% probability), creating multiple pathways for enhanced COLLIN dominance. COLLIN also increased its dominance over COLLOM under warmer conditions, which appeared to also be driven mostly by increased FD, but competitive response ratios appeared to be more important than the relative demographic ratio.

Similarly, GILCAP gained competitive advantages over CLAAMO through a switch in relative fitness differences advantage with warming. This reversal was driven primarily by increased competitive response ratios for GILCAP (71% probability) and significantly decreased intraspecific competition in GILCAP, which reduced self-limitation and enhanced competitive ability (92% probability). While both species experienced decreased intrinsic growth rates under warming, the reduction in GILCAP's self-regulation more than compensated for this demographic decline, illustrating how changes in competitive interactions can override direct effects on performance.

A second category of observed warming responses was the maintenance of competitive superiority despite warming induced shifts. For example, CLAPUR maintained its competitive dominance across all species pairs under warming despite some constraining factors. This species exhibited consistently strong competitive effects on other species and maintained large fitness advantages, even while experiencing increased self-limitation under warming conditions. The persistence of CLAPUR dominance was particularly evident in its interactions with COLLIN, where multiple shifts favored COLLIN or coexistence, yet not enough to shift the dominant predicted outcome of species interactions. Specifically, an increase in COLLIN's intrinsic growth rate lead to a shift in the demographic ratio favoring COLLIN which, in combination with CLAPUR's increase in self-limitation, reduced fitness differences (80% probability). Additionally, the stabilization potential increased (72% probability) yet CLAPUR

was still predicted to competitive exclude COLLIN with warming. This pattern demonstrates how competitively superior species may maintain their dominance even when warming imposes some demographic costs.

A third category of shifts involved coexistence outcomes changing from competitive exclusion to priority effects under warming, meaning that initial colonization patterns may determine competitive outcomes more so than inherent species differences. This occurred most notably for CLAPUR-GILCAP and COLLIN-GILCAP pairs, which transitioned from clear competitive dominance under ambient conditions to scenarios where establishment order becomes critical. For CLAPUR-GILCAP, this shift resulted from weaker competitive effects of CLAPUR on GILCAP combined with increased competitive ability of GILCAP, and despite GILCAP's decreased intrinsic growth rate. The emergence of priority effects suggests that warming may reduce competitive asymmetries in some interactions, making initial colonization and establishment timing increasingly important determinants of community composition. In other systems, warming has been shown to increase the importance of initial colonization by increasing the effect the first species to arrive had on depleting finite resources (Grainger et al., 2018).

A final category of responses is that shifts in underlying species interactions and demographic rates in response to warming may yield minimal net changes in coexistence outcomes due to opposing forces that partially offset each other. For example, there was very little change in expected coexistence outcomes between CLAAMO and CLAPUR despite a number of underlying shifts in their interactions and demography. Both species tended to have stronger self-limitation (intra-specific competition) with warming, and the decrease in intrinsic growth rate of CLAAMO was offset by a decrease for CLAPUR as well. We hypothesize this phenomenon of offsetting or partially-offsetting responses yielding only modest net consequences could be more common than previously recognized due to the complexity of how processes scale up to community interactions. There is a complex interplay between different mechanisms governing species interactions and no a priori reason to believe warming will affect different underlying processes consistently. For instance, when warming simultaneously affects multiple components of competitive interactions in opposing directions, such as decreasing intrinsic growth rates while reducing self-limitation, or increasing competitive response ratios

while decreasing demographic ratios, the net effect on coexistence may appear modest despite significant underlying changes.

3.5.3 Implications for Community Responses to Climate Change. Within this five-species subset of a prairie community, the diversity of warming responses and the persistence of strong competitive asymmetries suggest that climate warming may lead to compositional shifts that amplify existing dominance patterns, rather than trigger a complete community reorganization. The consistent patterns of winners and losers, with GILCAP and COLLIN generally gaining competitive advantages while CLAAMO and COLLOM became more vulnerable to exclusion, indicate that warming may primarily alter the relative abundances of existing dominant and subordinate species rather than fundamentally restructuring competitive hierarchies.

The emergence of priority effects in formerly asymmetric interactions may have particularly interesting consequences for community assembly under climate change. As competitive dominance weakens for some species pairs, the timing and sequence of species establishment may become increasingly critical. This shift toward historical contingency in community assembly suggests that warming may increase the importance of dispersal timing, disturbance regimes, and other factors that influence colonization patterns (Grainger et al., 2018). Among the phenological stages, the timing of germination (a seasonal "arrival" for annual plants) has been shown to be consequential for coexistence among species (Blackford et al., 2020; Diez et al., 2024).

Overall, the relatively weak effects of warming on competitive interactions, despite clearer direct effects on species performance, may reflect several important ecological realities. The modest magnitude of shifts observed in our study may not have been sufficient to substantially alter competitive dynamics. Evidence that species-specific phenological shifts can influence competitive interactions comes from a study involving shifts on the scale of weeks, whereas we observed shifts of only a few days (Alexander & Levine, 2019). However, the short experimental timeframe may mask longer-term changes in that emerge over time as competitive outcomes accumulate across generations. Nonetheless, as more studies document the mechanisms by which warming can impact species interactions, we may build capacity to understand and predict likely changes over longer time frames and across systems.

3.5.4 Limitations and Future Directions. While our results provide valuable insights into how moderate warming affects plant community dynamics, several study constraints suggest important avenues for future research and consideration when extrapolating these findings to natural systems.

First, multi-year experiments would help disentangle year-specific climate effects and life cycle complexities that may have dampened the observed warming effects. The relatively wet conditions during our study year likely reduced both competitive intensity and warming effectiveness, as Eugene received 150% of average rainfall during the critical April-June period when Pacific Northwest prairie plants typically experience their most intense competition for water. This higher than normal precipitation coincided with increased cloud cover that may have reduced the intensity of the warming treatments and alleviated some resource limitation that normally intensifies competitive interactions. Additionally, our modest 0.5°C mean temperature increase represents a conservative warming scenario compared to regional projections of 1-1.5°C increases over the next two decades (Mote & Salathé, 2010). While this study therefore may reflect the important transition period in coming years, stronger community effects may emerge over longer, stronger warming conditions.

Second, as with most controlled experiments examining coexistence mechanisms, our study necessarily focused on pairwise plant competitive interactions while excluding other factors that may mediate warming effects on community structure in the full complexity of natural systems. Plant-pollinator phenological mismatches (Kudo & Ida, 2013; Xie et al., 2022), soil microbial communities (Collings et al., 2025), and higher-order multispecies interactions (Mayfield & Stouffer, 2017) all represent potentially important pathways through which climate could influence species coexistence that warrant future investigation. Similarly, our experimental approach could not incorporate the temporal and spatial coexistence mechanisms that operate across broader landscape scales and longer time horizons in natural communities (Chesson, 2000a).

These constraints also highlight opportunities for future research that integrate controlled experimental studies with broader observational work across multiple spatial and temporal scales. The mechanistic insights from our study provide a foundation for predicting how the individual components of coexistence respond to warming, which can inform larger-scale studies examining how these mechanisms interact with landscape heterogeneity, disturbance regimes,

and other community assembly processes to determine climate change effects on natural plant communities.

3.6 Conclusion

This study demonstrates that even moderate experimental warming can produce species-specific effects that alter the niche and fitness differences governing species coexistence, extending our mechanistic understanding of how climate change may affect plant communities. However, these results also highlight the complexity by which warming effects may (or may not) cascade up through communities. Changes in underlying species performance and interactions may not translate to shifts in predicted coexistence outcomes, due to strong competitive asymmetries and conflicting or compensating effects. Nonetheless, shifts from competitive exclusion to priority effects in several species pairs reveal how warming could reduce community predictability, replacing relatively clear competitive dominance with outcomes dependent on colonization timing and historical contingency. These findings are particularly significant given that our study employed a relatively mild warming scenario of just 0.5°C above ambient temperatures, while regional climate projections anticipate 1-1.5°C increases within the coming decades. This work highlights the critical need for continued experimental research examining climate effects on competitive interactions, particularly studies that integrate multiple environmental drivers, longer temporal scales, and broader taxonomic diversity to fully capture the complex pathways through which global warming will reshape plant community dynamics.

3.7 Bridge

In my third chapter, I observed species-specific responses to warming of species' phenology, growth, and reproduction. Using Modern Coexistence Theory, I assess how species interactions and ability to coexist were relatively unchanged with warming, despite these species-specific responses. Like many studies, we record a species-level response, averaged across many plants grown in one location and in one year. In reality, species exist across spatial and temporal scales and therefore their responses to warming may vary greatly across these spatial and temporal scales. In my fourth chapter, I used an almost identical experimental set up to test similar questions as in chapter three, but I replicated the experiment across a local spatial scale to investigate how environmental gradients interact with warming and whether this produced unique warming effects across space.

CHAPTER IV.

DIRECT AND INDIRECT RESPONSES TO WARMING ACROSS A SMALL SPATIAL SCALE BUT COMMUNITY OUTCOMES REMAIN UNCHANGED

4.1 Contributions

With assistance from Jeff Diez, I came up with the research question. We jointly designed the experiment and wrote the manuscript. I led data collection assisted by Katelin Kutella and Julia Prange. Jeff Diez led statistical analysis, but both of us contributed. Jeremy Collings and Peter Ralph provided valuable feedback on analysis.

4.2 Introduction

Ecologists have made substantial progress on the mechanisms that allow species to coexist, particularly the balance between stabilizing niche differences and average fitness differences (Chesson, 2000b; HilleRisLambers et al., 2012). Climate warming can reshape this balance through direct effects on species' vital rates and traits as well as indirect effects that alter biotic interactions, so that community change reflects the net of these pathways rather than either in isolation (Alexander et al., 2015, 2016; Chu et al., 2016). Predicting outcomes is further complicated by spatial environmental heterogeneity; microclimates vary strongly across landscapes and even within meters, modulating exposure to warming and the intensity of interactions across multiple spatial scales (Potter et al., 2013; Suggitt et al., 2011). Although many studies document unequal, spatially variable direct responses of species to climate, we still know relatively little about how this spatial variation propagates to community-level processes (such as composition and coexistence) across landscapes where interaction strengths themselves vary in space. This general gap motivates this study, a landscape-scale test of how warming influences intrinsic performance, competitive interactions, and their combined consequences for coexistence.

Spatial environmental variation is commonly thought to promote species coexistence (and thereby species diversity) for the intuitive reason that different species are adapted to different conditions which vary spatially. More technically, according to coexistence theory, space can alter the balance between stabilizing niche differences and average fitness differences across locations (Chesson 2000; Barabás et al. 2018). Two broad classes of mechanisms can contribute to spatial coexistence: fluctuation-independent processes (e.g., spatial niche partitioning along persistent edaphic or light gradients) and fluctuation-dependent processes that

arise from environmental variability interacting with life-history buffering and nonlinear competition (Barabás et al., 2018; Snyder & Chesson, 2004). In real landscapes in nature, multiple gradients co-occur and operate at different spatial scales, so the same environmental mosaic might simultaneously strengthen stabilization in some places while amplifying fitness inequalities in others. This spatially structured view of modern coexistence theory motivates asking *where* climate warming will most greatly alter the two coexistence axes (niche differences and fitness differences) rather than assuming a single, uniform community response.

Recent empirical work underscores how multiple drivers act through different pathways and scales to shape coexistence. For example, in Mediterranean annual grasslands, Lanuza et al. (2018) showed that above-ground floral visitors and below-ground soil salinity modified population dynamics both directly (seed production) and indirectly (competitive responses), with opposing effects on coexistence determinants. Floral visitors tended to promote coexistence at neighborhood scales, whereas soil salinity promoted coexistence over larger spatial scales by altering which species was competitively dominant (Lanuza et al. 2018). Their study illustrates how different drivers can pull niche and fitness differences in opposite directions, perhaps sometimes yielding compensatory outcomes. Extending that logic to climate change, warming may shift intrinsic performance and interaction strengths via distinct pathways (e.g. physiology, phenology, resource supply, soil processes), potentially in countervailing ways across a landscape.

Building on this framework, we consider three non-exclusive ways warming could reconfigure spatial environmental variation: (1) intensification, which steepens gradients and makes patches more distinct; (2) homogenization, which erodes gradients and makes patches more similar; and (3) parallel shift, which moves conditions in all patches by a similar amount without changing their relative differences. Each scenario has potential implications for coexistence, as intensification could strengthen spatial niche partitioning (boosting stabilization) or magnify fitness inequalities; homogenization might remove refuges and reduce stabilization; and parallel shifts may alter average relative fitness but not change spatial structure. Recent research on microclimates suggests that local conditions often buffer or reshape macroclimate warming, decoupling experienced temperatures from regional trends (De Frenne et al., 2019; Lembrechts et al., 2019; Suggitt et al., 2011). At the same time, multi-site and gradient studies show that warming responses of traits and demography are non-uniform across space, with

species' population growth, phenology, and interaction opportunities diverging among nearby sites and across elevations or latitudes (DeMarche et al., 2021; Rafferty et al., 2020; Reed, Peterson, et al., 2021b). Together, these insights imply that even for the same community composition, warming could shift the relative strength of stabilizing niche differences and destabilizing fitness differences from place to place.

In this study we aimed to test these prediction of shifting species interactions and niche and fitness differences using a landscape-scale experiment that quantifies warming effects on intrinsic performance, competition, and their combined consequences for coexistence. We conducted a replicated, pairwise competition experiment with passive warming across multiple sites within a heterogeneous prairie landscape in the Pacific Northwest. By using sites across a mild elevation gradient and with variation in shade, exposure, and soils within a relatively small spatial extent, we were able to isolate how local context modulates warming effects (De Frenne et al., 2019; Lembrechts et al., 2019; Suggitt et al., 2011). We asked several overall questions: (1) How does warming change intrinsic performance and competition for each species? (2) Do those changes consistently shift niche/fitness differences and predicted coexistence outcomes? and (3) Are warming effects related to variation in local microclimate and site conditions, as expected if microclimate buffering is reshaping warming effects across the landscape? By exploring climate warming's effects on species performance, intra- and inter-specific interactions, and following them through to effects on niche and fitness differences across microclimates, we present a novel test of whether landscape heterogeneity buffers or amplifies climate impacts on coexistence.

4.3 Methods

4.3.1 Study Site and Species. Our experiment was conducted at a preserve that contains one of the largest remaining intact prairie-oak woodland systems in the Willamette Valley, The preserve is located at the base of the Coburg Hills east of Springfield, OR, USA (44°05'34.9"N 123°00'48.0"W), approximately south of the Willamette Valley and Pacific Northwest Prairie (PNW) ecosystem which is characterized by a mosaic of open prairie interspersed with oak and riparian woodlands. Pacific Northwest prairies have a large amount of topographic and edaphic variability within a geographically restricted range, making them an ideal system for studying fine-scale environmental variation in climate responses.

The climate is Mediterranean with cool, wet winters and hot, dry summers. This area receives an average of 108 cm of precipitation annually and has a mean temperature of 11.6°C (PRISM Climate Group, 30-year average). During the 12-month period spanning our experiment (September 2022-2023), the site received 79 cm of precipitation with an average temperature of 12.1°C (NOAA). The native vegetation consists of perennial bunch grasses with perennial and annual forbs occupying the interspaces. However, numerous non-native perennial and annual grasses and forbs are now present and often dominant. Most species in this ecosystem germinate with fall rains and flower between early April and early July.

We focused on two native annual forb species: *Collinsia grandiflora* (Plantaginaceae) and *Clarkia purpurea* (Onagraceae), referred to subsequently with four-letter codes, COLLIN and CLAPUR respectively. Both species are distributed throughout the Willamette Valley in prairie and oak woodland habitats and are commonly used in restoration projects. The species exhibit somewhat different phenologies, with *C. grandiflora* flowering early in the season (first flower: late March to early April) while *C. purpurea* flowers in mid- to late season (first flower: late May to early June).

4.3.2 Experimental Design. Within the preserve, we established eight experimental sites across four distinct prairie units to capture the environmental heterogeneity typical of Pacific Northwest prairies (Figure S10). Prairie units ranged from 0.1-0.4 km² in area and were generally separated by 500-800 m of oak woodland and mixed broadleaf-conifer woodland. All sites were located within a 2 km² area, with distances to the nearest neighboring site ranging from 50 m to 1 km. Sites were located on five distinct soil types, varied in proximity to oak woodland, and spanned gradients of elevation (282-495 m), aspect (138-268°), and slope (3-18%).
From May through October 2022, we prepared eight approximately 5×8 m experimental areas using standard restoration methods to remove existing biomass and reduce the seed bank. Site preparation included mowing, apply glyphosate herbicide, covering the ground with thick clear plastic (solarization, to reduce soil seed bank), and burning with handheld propane torches to eliminate residual vegetation, mimicking the effects of prescribed burns commonly used in this region.

Each site contained eight experimental plots that were seeded in mid-November 2022. Heavy herbivory at three of the sites prevented us from robustly estimating parameters, so we present analyses for five sites. Each site had eight plots which included four distinct competition

treatments. Four of these plots were competition plots' with ~1500 seeds of Clarkia purpurea in two plots and Collinsia grandiflora in the other two as the 'competitor species'. The other four plots had no competitor species seeded. Two of these plots were weeded throughout the project to be 'no competition' plots and the other two were not weeded, allowing the species in the seed bank to grow back in these 'natural competition' plots. Into each of these different competitive backgrounds, exactly 80 seeds of each species were seeded as the 'phytometers'. Experimental warming chambers were installed on four of the eight plots at each site on the same day plots were seeded, creating ambient and warmed versions of each competition treatment. This design allowed both species to experience intraspecific competition, interspecific competition, no competition, and natural competition under both ambient and experimentally warmed conditions. While only a single replicate plot existed for each treatment combination per site, substantial competition gradients occurred naturally within each plot due to the randomness of hand seeding and variable germination success.

Four TOMST TMS4 data loggers were installed at each site (two in warmed plots, two in ambient plots) to record soil moisture and temperature at approximately 5 cm depth, air temperature at 1 cm above ground, and air temperature at 10 cm above ground at 15-minute intervals throughout the experiment. In late December 2022, herbivores (likely slugs) consumed nearly 100% of seedlings in the four lowest-elevation sites. Remaining seedlings were removed, and these plots were reseeded in mid-January 2023.

4.3.3 Field Measurements. Immediately following seeding, plots were monitored every ten days to document germination patterns. New germinants were counted in both ambient and warmed no-competition and natural-competition plots, where only 80 seeds of each species had been planted per plot, allowing for accurate germination assessment. A second round of germination monitoring was conducted following the January reseeding of the lower-elevation plots. Data from natural competition plots are reported only for germination analyses and are not included in competition parameter estimates.

Once germination ceased, plots were visited biweekly to remove non-target species and measure heights of four randomly selected phytometer plants per species per plot. Beginning in mid-May when flower buds appeared, monitoring frequency increased to twice weekly to track flowering phenology. We recorded the date of first flower and date of last flower for every

phytometer individual. Plants were considered flowering when stigma and anthers were visible and finished flowering when all petals had senesced.

Following flower senescence, we counted the total number of fruits produced by each phytometer plant and recorded the number of competitor plants within a 10 cm radius to quantify local competition. To convert fruit counts to seed production (fecundity), we collected approximately 50 fruits of each species from each site under both ambient and warmed conditions. Fruits were collected on multiple dates throughout the fruiting season and from plants experiencing both intraspecific competition and no-competition conditions to capture temporal and competitive variation in seeds per fruit. Final fecundity estimates for each phytometer were calculated as the product of fruit number and mean seeds per fruit, providing our primary measure of individual reproductive success for competition modeling analyses.

4.3.4 Statistical Analysis.

3.3.4.1 Competition Models. We estimated the effects of experimental warming on intra- and inter-specific competition and individual reproductive output using a nonlinear Beverton-Holt competition model:

$$F_i = \frac{\lambda_i}{(1 + \alpha_{ij}N_j + \alpha_{ii}N_i)}$$

where F_i is the reproductive output (fecundity) of focal species i, λ_i is the intrinsic population growth rate of species i, α_{ii} and α_{ij} quantify the per-capita intra- and inter-specific competitive effects, respectively, and N represents the density of competitors of each species. We fit this model for each focal species, allowing alphas and lambdas to vary with site and treatment. The model was structured as a hierarchical Bayesian framework that allowed for pooling of information across sites within species and treatments, while estimating site-specific variation. Intrinsic growth rates were modeled with treatment-specific effects and random site-level variation. This hierarchical structure enabled us to estimate landscape-wide treatment effects while quantifying spatial heterogeneity in warming responses across the five sites.

All parameters (lambdas and alphas) were constrained to be positive values, with intrinsic growth rates reflecting population growth potential and competition coefficients representing competitive rather than facilitative interactions. Models were fit using Bayesian methods

implemented in Stan (Carpenter et al., 2017) accessed through R via the brms package (Bürkner, 2021). We employed moderately informative priors that facilitated model convergence while avoiding undue influence on posterior parameter estimates. Model convergence was assessed using the Gelman-Rubin statistic ($\hat{R} < 1.01$) and by visually examining trace plots from four independent Markov chains, each run for 5,000 iterations with 2,500 warm-up iterations discarded.

To assess warming effects on competition parameters and intrinsic growth rates, we extracted posterior distributions from fitted models and calculated the probability that parameter values differed between ambient and warmed treatments. We report these as posterior probability differences (PD), representing the proportion of posterior draws where treatment effects exceeded zero (for increases) or were below zero (for decreases). This approach allows us to propagate parameter uncertainty through all downstream coexistence analyses while providing intuitive measures of effect magnitude and certainty.

3.3.4.2 Coexistence Analysis. We used site- and treatment-specific estimates of intrinsic growth rates (λ) and competition coefficients (alphas) to calculate niche differences and fitness differences following the theoretical framework of Godoy and Levine (2014). This analysis evaluates the potential for species coexistence under ambient and experimentally warmed conditions at different sites across the landscape.

Fitness differences quantify the degree to which one species has an inherent competitive advantage over another and were calculated as:

$$\frac{\kappa_j}{\kappa_i} = \frac{\eta_j - 1}{\eta_i - 1}\sqrt{\frac{\alpha_{i,j}}{\alpha_{j,i}}\frac{\alpha_{i,i}}{\alpha_{j,j}}}$$

The first term represents the demographic ratio (relative intrinsic fitness), where

$$\eta_i = \frac{\lambda_i g_i}{1 - (1 - g_i)(s_i)}$$

and the second term represents the competitive response ratio (relative competitive tolerance):

$$\sqrt{\frac{\alpha_{i,j}}{\alpha_{j,i}}\frac{\alpha_{i,i}}{\alpha_{j,j}}}$$

This formulation allows fitness differences to be decomposed into these two biologically meaningful components, enabling us to identify the demographic versus competitive mechanisms underlying warming effects on species interactions.

We quantified niche differences as the stabilization potential: 1 - ρ, where ρ represents niche overlap calculated as:

$$\rho = \sqrt{\frac{\alpha_{i,j}}{\alpha_{j,j}} \frac{\alpha_{j,i}}{\alpha_{i,i}}}$$

This metric reflects the relative strength of intraspecific competition (promoting coexistence through stabilizing mechanisms) compared to interspecific competition (destabilizing coexistence). We use the term "stabilization potential" rather than "niche differences" because our modeling approach allows for the possibility that interspecific competition may exceed intraspecific competition, yielding negative values that complicate interpretation of traditional "niche difference" terminology (Ke & Letten, 2018). Nonetheless, higher stabilization potential indicates greater likelihood of coexistence.

As an additional metric of species responses to warming, we calculated competitive ability for each species *i*, as: $(\lambda_i - 1)/\sqrt{\alpha_{i,i} * \alpha_{i,j}})$, where λ_i is the species' intrinsic growth rate (in the absence of competitors) and the denominator is the geometric mean of the species' intra- and inter-specific competition that it experiences. This measure integrates both intrinsic growth capacity and tolerance to both intra- and interspecific competition, representing species i's overall ability to maintain reproductive output under competitive pressure (Hart et al., 2018).

4.3.4.3 Treatment Effects and Spatial Analysis. To quantify warming effects while accounting for parameter uncertainty, we performed all coexistence calculations using 1,000 random draws from the posterior distributions of competition parameters and intrinsic growth rates. This approach yielded posterior distributions for niche differences, fitness differences, and competitive abilities, enabling probabilistic assessment of treatment effects at each site and across the landscape.

We determined predicted coexistence outcomes by comparing the magnitude of fitness differences to stabilization potential for each posterior draws. Four outcomes were possible: (1&2) competitive exclusion by either CLAPUR or COLLIN, occurring when fitness differences exceed stabilization potential and the superior competitor excludes the inferior one; (3) priority effects, occurring when both fitness differences and stabilization potential are low; and (3) stable coexistence, occurring when stabilization potential exceeds fitness differences and both species can persist regardless of initial conditions. We calculated the probability of each outcome based on the proportion of posterior draws meeting each criterion.

To explore potential environmental drivers of the observed spatial variation in warming effects, we conducted Spearman rank correlation analyses between site-specific changes in coexistence parameters (under warming relative to ambient conditions) and site environmental characteristics including aspect, elevation, slope, and shade conditions. Given our limited sample size (n = 5 sites), these analyses should be considered exploratory rather than definitive tests of environmental relationships.

All results based on the Bayesian posteriors are reported as posterior probability differences (PD) representing the proportion of posterior samples supporting a given directional effect, with PD > 0.80, PD > 0.90, and PD > 0.95 serving as our criteria for weak, moderate, and strong evidence of treatment effects, respectively. Site-specific results are presented alongside landscape-wide summaries obtained by averaging posterior distributions across all sites, providing both local and regional perspectives on warming effects on species interactions and coexistence potential. For correlation analyses, we report traditional p-values with significance thresholds of $p < 0.05$, $p < 0.01$, and $p < 0.001$.

4.4 Results

4.4.1 Abiotic Warming Effects. Ambient temperatures varied across the five sites throughout the year (Figure S11). The experimental warming treatment successfully elevated temperatures across all five study sites, though the magnitude and patterns of warming varied considerably among sites and between air and soil measurements (Figure S12). Daily maximum air temperatures showed the greatest increase under warming, followed by daily means and daily minimums. The warming effect on air temperatures intensified progressively throughout the experiment, while soil temperature responses were more heterogeneous across sites.

Air temperature increases ranged from approximately 1°C in winter to 6°C in summer, with spring showing intermediate warming of around 3°C. Soil temperatures generally increased by 0.25-1°C across most sites, with notable exceptions at sites 5, 7, and 8, where summertime daily maximum soil temperatures increased by approximately 2.5°C. Surprisingly, at sites 1 and 3, soil temperatures in warmed plots were cooler than in ambient plots, with this cooling effect intensifying throughout the experimental period. Mean seasonal warming effects showed substantial spatial variation, ranging from 0.5-5°C among sites for soil temperatures and 0.5-3°C for air temperatures, with this variation increasing over the course of the experiment.

Soil moisture responses to warming were site-specific and variable (Figure S13). Volumetric water content decreased in warmed plots at site 8, increased at site 3, and remained unchanged at the other three sites, indicating that warming effects on soil hydrology varied considerably across the landscape.

4.4.2 Direct Effects of Warming on Species Performance. Experimental warming had different effects on the reproductive output of the two study species under low competition conditions (Figure 11). CLAPUR showed significantly enhanced fecundity under warming at all five sites (PD > 0.95), with some variation in the magnitude of increase, but generally showed a relatively consistent positive response to elevated temperatures across the entire landscape. In contrast, COLLIN exhibited a significant increase in fecundity under warming at only one site (PD > 0.95), suggesting more limited or site-specific benefits from experimental warming.

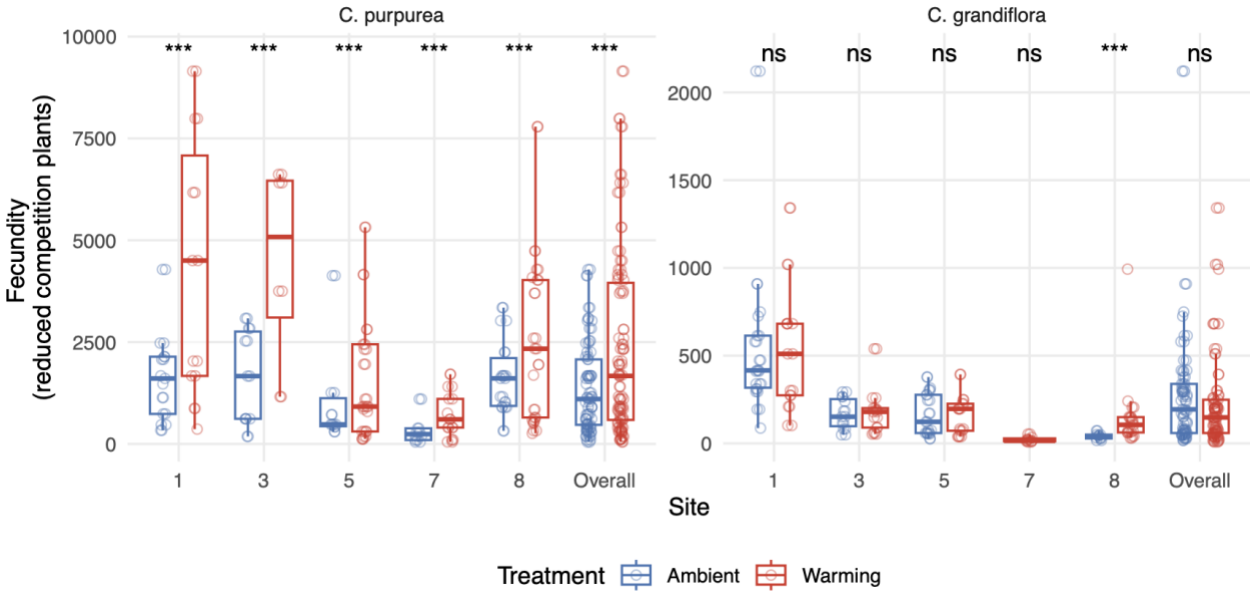


Figure 11. Effects of experimental warming on reproductive output (fecundity) under low competition conditions for CLAPUR and COLLIN across five sites. Boxplots show raw seed production data, with individual site results and landscape-wide averages. Significance levels indicate the probability that the difference in ambient and warming posterior distributions differs from zero: * PD > 0.80, ** PD > 0.90, *** PD > 0.95; ns = not significant = PD < 0.80.

4.4.3 Competition Coefficients and Intrinsic Growth Rates. Experimental warming altered both the strength of competitive interactions and species' intrinsic growth rates, with effects varying substantially across sites and between species (Figure 12). At least one pairwise

competitive interaction changed significantly at every site except site 7, indicating widespread but spatially heterogeneous effects of warming on species interactions.

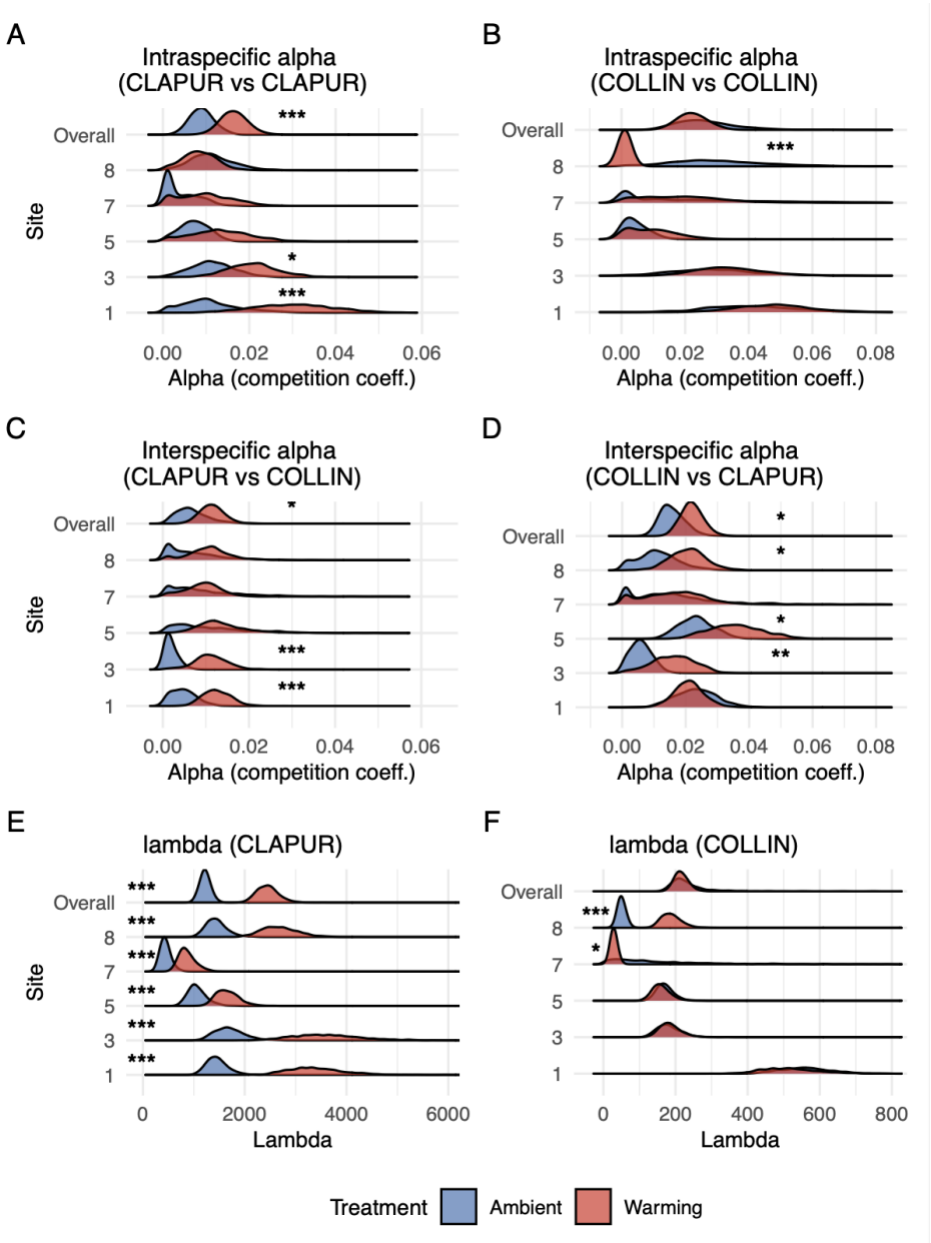


Figure 12. Effects of experimental warming on species competition parameters and intrinsic growth rates. **A-B**: Intraspecific competition coefficients (α_ii) showing the strength of within-species competitive effects for CLAPUR and COLLIN respectively. **C-D**: Interspecific competition coefficients (α_ij) quantifying between-species competitive interactions, with CLAPUR competing against COLLIN (C) and COLLIN competing against CLAPUR (D). **E-F**: Intrinsic growth rates (λ) representing species performance in the absence of competition for CLAPUR and COLLIN respectively. All panels show posterior distributions under ambient (blue) and warming (red) treatments for individual sites and landscape-wide averages (Overall). Higher α values indicate stronger competitive effects, while higher λ values indicate greater intrinsic growth potential. Significance levels: * PD > 0.80, ** PD > 0.90, *** PD > 0.95.

For CLAPUR, warming significantly intensified both intraspecific competition (PD > 0.95 overall and at sites 1 and 3) and interspecific competition (PD > 0.95 overall and at the same two sites where intraspecific effects were significant). COLLIN showed significantly stronger intraspecific competition under warming overall (PD > 0.95) and at three of the five sites (PD > 0.95), but interspecific competitive effects were significant only at site 8 (PD > 0.95), with no significant change when averaged across sites.

Intrinsic growth rates (lambda) responded positively to warming for CLAPUR, with significant increases at all five sites to varying degrees (PD > 0.95) and overall (PD > 0.95). COLLIN showed more variable responses, with significantly higher lambda under warming at one site, significantly lower lambda at another site, and no significant difference when averaged across all sites.

4.4.4 Coexistence Outcomes. Experimental warming had modest but significant effects on the mechanisms governing species coexistence (Figure 13). Fitness inequalities decreased significantly under warming at two sites (PD > 0.95) but showed no significant change when averaged across all sites. Niche differences increased significantly at one site under warming (PD > 0.95) – notably the same site that showed the strongest decrease in fitness inequalities – but again showed no significant overall effect across sites.

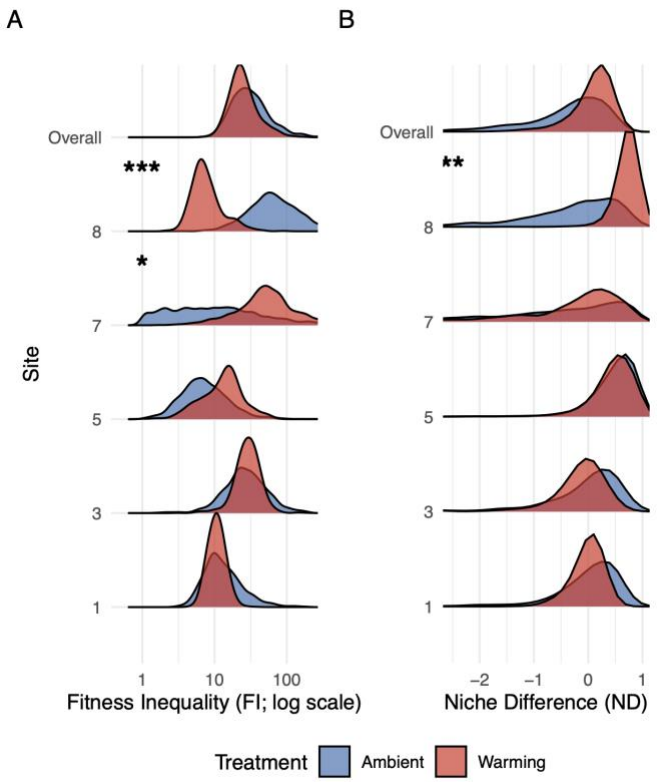


Figure 13. Effects of experimental warming on (A) fitness inequalities and (B) niche differences across sites. Fitness inequalities represent competitive asymmetries between species, while niche differences quantify the degree of ecological differentiation that promotes coexistence. Lower fitness inequalities and higher niche differences both promote species coexistence. Significance levels: * PD > 0.80, ** PD > 0.90, *** PD > 0.95.

Overall, CLAPUR dominated COLLIN across the landscape under both ambient and warmed conditions (Figure 14). Experimental warming produced only modest changes in predicted coexistence outcomes when averaged across sites, with a shift from priority effects toward more consistent competitive dominance patterns. The spatial variability in warming effects on underlying competitive parameters translated into site-specific changes in coexistence predictions, though these did not result in strong overall shifts in species interaction outcomes.

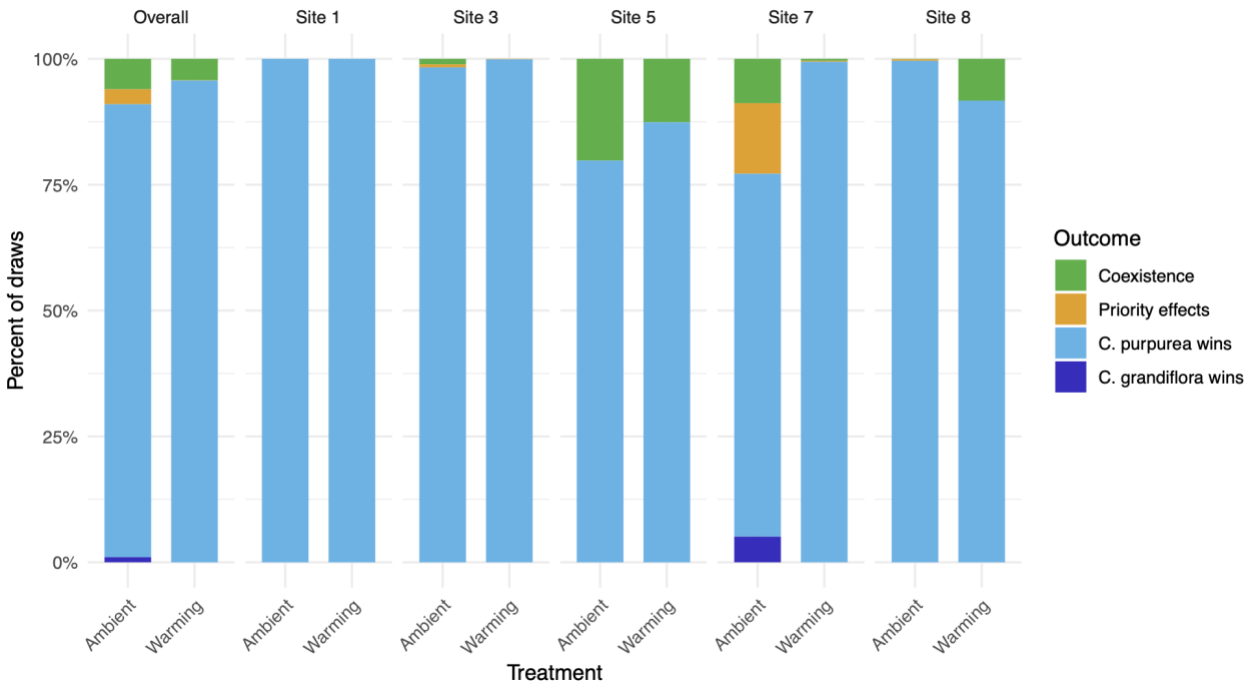


Figure 14. Predicted species interaction outcomes under ambient and warmed conditions at (A) individual sites and (B) landscape-wide average. Categories represent different coexistence scenarios: competitive exclusion where one species dominates, priority effects where initial abundance determines outcomes, and stable coexistence where both species can persist. Results show the probability distribution of these outcomes based on estimated competition parameters.

4.4.5 Components of Fitness Inequalities.

4.4.4.1 Competitive Response Ratios. Competitive response ratios, calculated as the proportional effect of heterospecific versus conspecific competition, showed site-specific responses to warming (Figure 15c-d). Only sites 1 and 8 exhibited significant changes in competitive response ratios under warming (PD > 0.95). At both sites, CLAPUR showed decreased competitive response under warming while COLLIN showed increased competitive response. When averaged across all sites, this pattern held, with CLAPUR showing significantly decreased competitive response (PD > 0.95) and COLLIN showing significantly increased competitive response (PD > 0.95) under experimental warming.

4.4.4.2 Demographic Ratios. Demographic ratios, representing the relative fitness of species in the absence of interspecific competition, showed stronger and more consistent responses to warming than competitive response ratios (Figure 15a-b). Overall, both CLAPUR and COLLIN exhibited significantly increased demographic ratios under warming (PD > 0.95). However, substantial site-level variability was evident: CLAPUR showed decreased

demographic ratios at site 8 but increases elsewhere, while COLLIN showed the opposite pattern with increased ratios at site 8 but decreases at other sites.

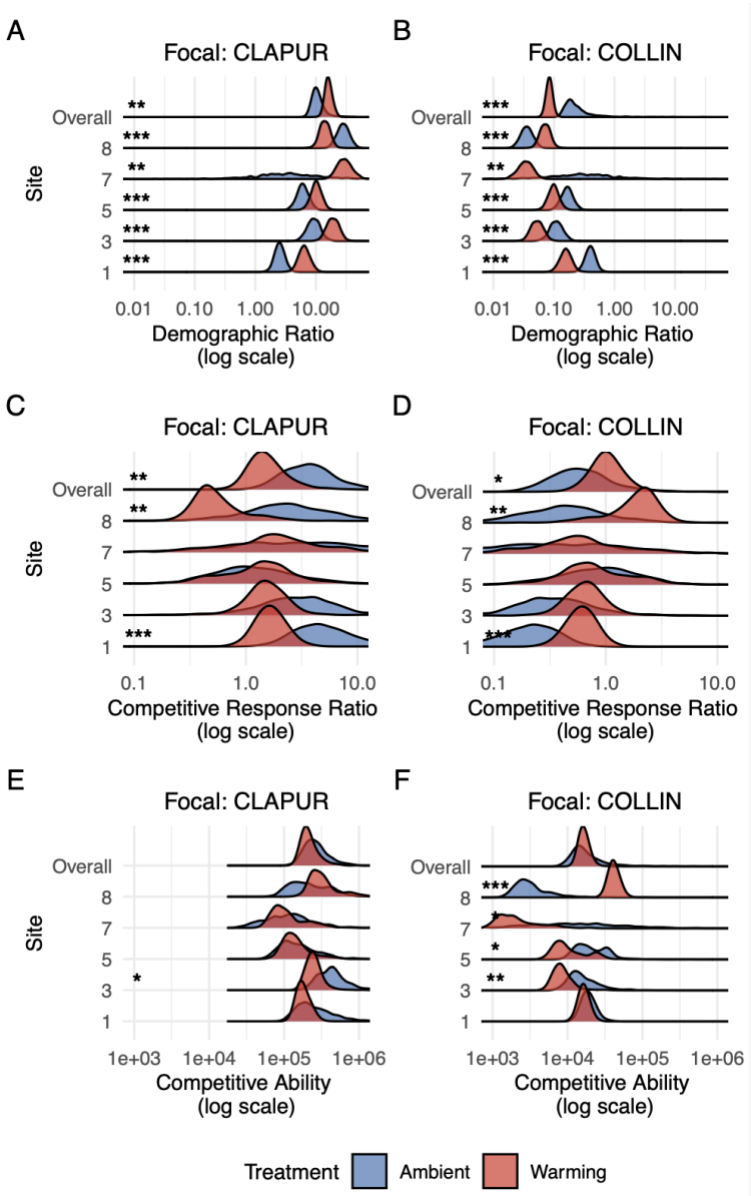


Figure 15. Effects of experimental warming on derived competition metrics integrating species interactions and fitness differences. **A-B**: Demographic ratios representing relative fitness of each species in the absence of interspecific competition (fitness_i/fitness_j), capturing intrinsic performance differences between CLAPUR and COLLIN independent of competitive interactions. **C-D**: Competitive response ratios quantifying how species' responses differ between intra- and interspecific competition, calculated as the proportional effect of heterospecific versus conspecific competition for CLAPUR and COLLIN respectively. **E-F**: Competitive ability integrating both intrinsic growth rate and competitive interactions for CLAPUR and COLLIN, with higher values indicating greater competitive ability. All panels display posterior distributions under ambient (blue) and warming (red) treatments for individual sites and landscape-wide averages (Overall). Significance levels: * PD > 0.80, ** PD > 0.90, *** PD > 0.95.

4.4.6 Species' Competitive Abilities. Integrating both intrinsic growth rates and competitive interactions, overall competitive ability responses varied between species (Figure 15e-f). CLAPUR showed no significant change in competitive ability under experimental warming across sites. In contrast, COLLIN exhibited significant changes in competitive ability at four of the five sites (PD > 0.95), though these changes varied in direction among sites, resulting in no significant net change when averaged across the landscape.

4.4.7 Site-level Correlations with Environmental Variables. Given the limited number of study sites (n=5), robust statistical analysis of environmental drivers of warming effects was not feasible. However, exploratory Spearman correlation analyses revealed several notable patterns (Figure 16, Figure S14). Site aspect emerged as the environmental variable most strongly correlated with warming effects on fitness inequalities and niche differences in coexistence outcomes. Under ambient conditions, niche differences were positively correlated with aspect, but this relationship disappeared under experimental warming. Similarly, shadier sites showed decreased fitness inequalities and increased niche differences under ambient conditions, but these correlations were eliminated in the warming treatment.

The two study species showed contrasting responses to site topography, with CLAPUR and COLLIN exhibiting opposite fecundity responses relative to site slope. Competition intensity also varied with elevation in a species-specific manner: under ambient conditions, competitive effects on COLLIN (both intra- and interspecific) were stronger at higher elevation sites, while competitive effects on CLAPUR were stronger at lower elevations. Warming altered these elevation-dependent patterns, particularly eliminating the association between elevation and CLAPUR's competitive effect on COLLIN.

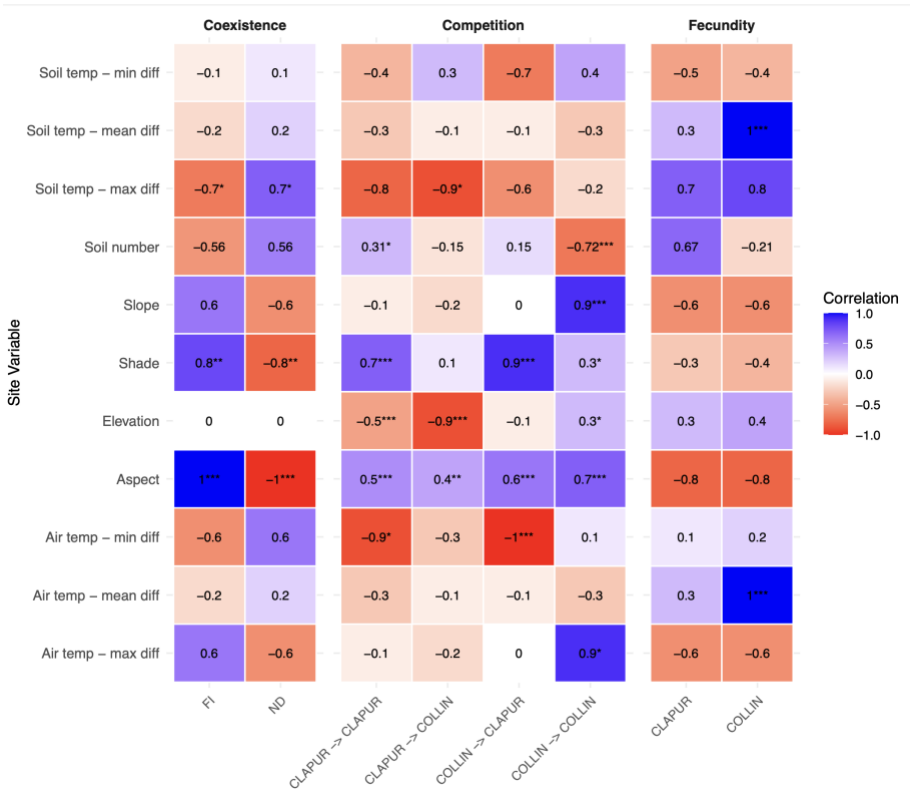


Figure 16. Correlations between warming-induced changes in species performance and coexistence metrics with site environmental variables. Box colors indicate the direction and strength of Spearman's correlation coefficients: blue represents positive correlations and red represents negative correlations, with darker shades indicating stronger correlations. Significance levels for correlations: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Environmental variables include site aspect, elevation, slope, and shade conditions. Temperature metrics on the y-axis are all temperatures differences between warmed and ambient plots.

4.5 Discussion

This study provides unique experimental evidence that climate warming effects on species coexistence mechanisms can vary spatially, even at local landscape scales. Our experimental warming study reveals that climate change effects on species coexistence are mediated through complex, spatially variable changes in both individual species performance and competitive interactions. We found significant changes in either species' performance and/or competitive interactions at every site except one, yet coexistence outcomes remained relatively stable due to counter-balancing effects on underlying demographic rates. This finding challenges the common assumption that climate effects on communities can be predicted from single-site studies or regional averages, as recent research also emphasizes the importance of understanding biotic interactions in shaping climate change impacts. To our knowledge, this is the first study to

experimentally demonstrate that a species pair can have different interaction outcomes under warming depending on local environmental context. While results suggest that warming may not simply shift competitive balance uniformly, but rather reorganize species interactions spatially across heterogeneous landscapes (Grainger et al., 2019; Terry, 2025), this case study also demonstrates how counteracting responses of intrinsic performance and species interactions to warming may in effect moderate changes at the community level.

4.5.1 Species- and Site-specific Warming Effects. Theoretical expectations for how warmer and drier conditions impact competition strength are somewhat mixed. The stress gradient hypothesis predicts that competition should decrease under environmental stress (including drought and heat), with negative interactions becoming less important while positive interactions like facilitation become more prominent (Maestre et al., 2006). However, when both interacting species have similar competitive life histories and stress is driven by resource limitation (e.g., water), competitive effects can remain negative across the entire stress gradient (Maestre et al., 2006). Alternatively, when warming increases metabolic rates and resource demands while simultaneously reducing resource availability through drought, it's logical that competition may actually intensify rather than decrease. This complexity is particularly interesting in mediterranean climates where warming may alleviate stress when moisture is available but increase stress later in the growing season as conditions become dry.

In our study, experimental warming had contrasting effects on the two focal species' performance and competitive interactions, with these responses varying across sites. CLAPUR generally benefited from warming through increased fecundity and intrinsic growth (lambda), showing significantly higher performance under warming at all sites. However, CLAPUR simultaneously experienced stronger competition under warming, with both its intra- and interspecific competition coefficients increasing significantly overall and at the warmer, south-facing sites. COLLIN's responses were more mixed, with warming leading to slight increases in lambda at one cooler site and decreases at another hotter site, with no significant overall effect on intrinsic growth. For COLLIN, intraspecific competition tended to strengthen under warming at three sites, whereas interspecific competition increased at only one site.

These contrasting effects on intrinsic growth rates versus competitive interactions suggest a potential compensation occurring within individual species' responses to warming. Such compensatory dynamics can stabilize aggregate community properties in response to

perturbations (Brown et al., 2016), and align with theoretical expectations that when environmental changes relax growth constraints, competitors may respond by depleting resources more rapidly, intensifying competition. The intensification of both intra- and interspecific competition under warming suggests that moderate warming acted to heighten competition rather than ameliorate it, contradicting stress gradient hypothesis predictions but supporting resource competition theory.

4.5.2 Higher-Level Compensatory Buffering and Coexistence Stability. The compensation observed at the species level, between individual performance and competitive intensification, propagated to higher-level compensatory dynamics that ultimately mediated coexistence outcomes. Modern coexistence theory predicts that species persistence depends on the balance between niche differences (which promote coexistence) and fitness differences (which favor competitive exclusion), with coexistence occurring when stabilizing niche differences overcome destabilizing fitness inequalities (Barabás et al., 2018; Chesson, 2000b). In this study, despite the shifts in underlying growth rate and competitive parameters, coexistence outcomes remained surprisingly stable across sites, with CLAPUR maintaining dominance under both ambient and warmed conditions. This stability arose in part from compensatory shifts between the two components of fitness differences: warming increased CLAPUR's demographic ratios (reflecting higher intrinsic performance) but decreased its competitive response ratios (reflecting stronger competition effects), while COLLIN experienced the opposite pattern. This compensation is analogous to demographic compensation, where different responses among demographic rates can stabilize a species' population growth rate (Yang et al., 2022), but is operating at the community level between relative demographic performance and relative competitive experiences.

Such compensatory dynamics are predicted to be a long-term feature of community dynamics across models and can have strong stabilizing effects at the community level (Gonzalez & Loreau, 2009). This buffering effect occurs because warming can simultaneously impact processes that have a stabilizing effects on coexistence, and destabilizing, with the net effect depending on their relative magnitudes. Together, these results demonstrate how multiple levels of compensation, from individual species responses to community-level coexistence mechanisms, may buffer ecological communities against environmental perturbations, even when underlying competitive processes are altered.

4.5.3 Environmental Drivers of Spatial Variation. Site topographic characteristics, particularly aspect and shade conditions, were correlated with how warming altered competitive dynamics, suggesting that local environmental context mediates climate change effects on species interactions. Site aspect was the strongest predictor of warming effects on coexistence parameters, likely because south-facing slopes experience more intense warming and altered moisture regimes compared to north-facing slopes (Dobrowski, 2011). Under ambient conditions, more shaded sites showed higher stabilization and reduced fitness inequalities. Warming tended to reverse this relationship, however, with decreased niche differences and increased fitness inequalities in the shadier sites, such that these correlations disappeared. This suggests that experimental temperature increases may have homogenized microclimatic variation that normally drives spatial patterns in species interactions.

These findings align with growing evidence that climate change effects are highly context-dependent and vary with local environmental conditions (Lenoir et al., 2013). Previous research has demonstrated that microclimatic variation can buffer species responses to climate change by providing thermal refugia and maintaining cooler conditions in topographically complex landscapes (Graae et al., 2012; Suggitt et al., 2018). Our study extends this concept, showing that even modest topographic variation within a single landscape can create differential warming responses in competitive interactions. The elimination of ambient-condition correlations under experimental warming suggests that climate change may erode the buffering capacity of environmental heterogeneity (Lembrechts et al., 2019), potentially reducing the spatial portfolio effects that currently stabilize regional coexistence patterns.

However, given our limited number of study sites (n=5), these correlations should be interpreted cautiously as exploratory analyses that generate hypotheses rather than definitive conclusions about environmental drivers. The patterns we observed, particularly the role of aspect and shading in mediating warming effects, warrant further investigation through replicated experiments across larger numbers of sites spanning broader environmental gradients. Such studies could test whether the homogenization of competitive environments under warming is a general phenomenon or specific to particular landscape contexts.

4.5.4 Implications for Climate-Change Ecology, Conservation & Restoration. This study demonstrates that fine-scale spatial heterogeneity can mediate climate responses, creating a "climate response mosaic" even within a single landscape. The magnitude of warming effects on

competition across our sites matched differences often observed across much larger geographic scales, challenging climate-envelope models that assume uniform species responses and underscoring the importance of incorporating spatially explicit biotic interactions into predictions (Lembrechts et al., 2019; Urban et al., 2016). These results highlight that competitive landscapes, not just climatic envelopes, determine species persistence under climate change. Conservation approaches that focused solely on projected temperature and precipitation changes (Keppel et al., 2012) may fail if warming simultaneously alters competitive dynamics unfavorably. Instead, conservation and restoration planning should prioritize protecting environmental heterogeneity that preserves diverse competitive contexts (Dobrowski, 2011; Morelli et al., 2016). The compensatory dynamics we observed, with changes in competitive parameters buffered coexistence outcomes, support calls for conservation strategies that focus on maintaining the ecological processes and heterogeneity rather than simply preserving current species composition (Hobbs et al., 2014). For restoration, the spatial variation in warming effects suggests practitioners could strategically target locations where competitive outcomes favor desired species assemblages (Hallett et al., 2023b). Rather than uniform treatments, managers could tailor approaches based on microclimatic conditions—for example, establishing competitively inferior native species on north-facing slopes where warming effects on competition are reduced.

4.5.5 Limitations and Future Directions. While our study provides novel insights into spatial variation in climate change effects on species interactions, several limitations suggest important directions for future research. First, our experimental approach focused specifically on fluctuation-independent coexistence mechanisms, examining how niche and fitness differences respond to warming at fixed locations across the landscape. However, we did not address fluctuation-dependent mechanisms such as the spatial storage effect, where species benefit from spatial variation in environmental conditions and dispersal among sites with different competitive outcomes (Sears & Chesson, 2007). Although there is still very limited evidence suggesting the prevalence of spatial storage effect in natural communities (Towers et al., 2020), future research should investigate how warming affects these spatial coexistence mechanisms. Particularly because the spatial storage effect depends on covariance between intrinsic growth rates and competitive effects, the divergent effects of warming observed here could have interesting effects on this spatial mechanism. Ultimately, understanding the interplay between

fluctuation-independent and fluctuation-dependent mechanisms under climate change will be critical for comprehensive coexistence predictions.

Second, our one-year experiment captures short-term responses but obviously may miss longer-term evolutionary or demographic changes that could alter competitive outcomes over multiple generations. The debate about the relative importance of density-dependence versus abiotic influences in population regulation extends to community-level dynamics (Houlahan et al., 2007), and longer experiments are needed to assess whether compensatory buffering persists across generations or represents a transient response to environmental perturbation.

Third, the two-species focus of our study was pragmatic, allowing a unique, distributed warming experiment to investigate the mechanistic understanding species interactions and coexistence. One reason there are no other such distributed coexistence experiments, to our knowledge, is that it is quite laborious and the scale of such controlled studies increases exponentially with the number of study species. However, the restriction to two species obviously limits our ability to predict responses in more diverse plant communities where indirect effects and higher-order interactions may be important (Levine et al., 2017). Real plant communities involve complex interaction networks where changes in pairwise interactions can cascade through the community in unpredictable ways. Additionally, we manipulated only temperature, whereas real climate change involves multiple interacting drivers, including precipitation and CO_2 that could interact with temperature effects in non-additive ways (Dieleman et al., 2012).

Fourth, as previously mentioned, our limited number of study sites (n=5) restricted statistical power for identifying environmental drivers of spatial variation, allowing only exploratory correlations that generate hypotheses for future testing. Larger-scale experiments across broader environmental gradients and longer time periods are needed to determine the generality of our findings and to develop predictive frameworks for how local environmental conditions mediate climate change effects on species interactions. A possible solution to this conundrum of recognizing the laborious nature of controlled competition experiments *and* needing experiments with more species and larger numbers of sites, would be to monitor plants in existing multi-species communities (Bimler et al., 2024; Lanuza et al., 2018), but the trade-off is less confidence that estimates of species interactions are real.

An additional interesting future research direction would be to integrate physiological mechanisms underlying the competitive responses we observed. Understanding whether changes in competition result from increased metabolic demands or altered resource depletion rates, for example, would improve our ability to predict these effects in other systems and under different climate scenarios.

4.6 Conclusion

Our findings highlight that climate warming effects on coexistence operate through spatially variable shifts in both intrinsic performance and intra- and inter-specific competition. Given this complexity, compensatory dynamics may prove more common than anticipated, leading to greater inertia for community dynamics. In this case study, the strength of the dominant species' advantage varied with local context and was buffered by compensatory mechanisms between demographic performance and competitive effects. This buffering produced unexpected stability in coexistence outcomes, suggesting potential resilience of community structure under moderate warming, at least in the short term. The consequences of global change for maintaining species diversity clearly depend on a complex integration of each species' responses to the environment and on the interactions among them. This highlights a key challenge for forecasting climate impacts on biodiversity, of how to account for spatial heterogeneity in biotic interactions and the potential compensatory dynamics that may buffer communities against environmental change.

CHAPTER V.

CONCLUSION

Studying the effects of climate change on species and communities is not a new topic in ecology, yet additional work still remains. Quantifying the response of every species and community may be impractical, but it remains important to identify broad patterns in the extent and type of variation in responses, as well as the mechanisms through which inter- and intraspecific variation affects communities. The work in this dissertation both highlights additional variation in how species respond to climate warming and answers questions about the consequences of variable responses for species interactions and community level outcomes.

In my second chapter, I tracked phenological events across the entire life cycle of seven annual forbs. To my knowledge, no other studies provide such a full, beginning-to-end, comprehensive assessment across so many phenophases. By doing so, I was able to compare the relative sensitivity of each phenophase and found that certain phenophases, such as germination and flowering, were more responsive to warming than other phenophases, such as true leaf presence or fruit development in these species. I attributed the variation in responses to organismal differences by calculating the sensitivity of each phenophase shift to the specific degree of warming it experienced. An additional advantage of this full life cycle approach was that it provided further evidence of how phenological shifts are non-independent events, and that for some species, phenological shifts may accumulate across the life cycle. These results suggest the need for further research that includes early life phenophases and improve our understanding of what drives variation in phenological shifts.

In my third and fourth chapters, I documented species' direct and indirect responses to warming to look at how species-specific responses to warming reshuffle species interactions and alter coexistence. My third chapter used five species to look at a wider diversity of species-specific responses while my fourth chapter used two species at multiple locations to include both inter- and intraspecific variation in response to warming. In both chapters there were species-specific responses to warming, but only moderate changes in species interactions and responses rarely translated to changes in coexistence outcomes. In both chapters, the lack of change in coexistence outcomes was largely due to the fact that *Clarkia purpurea* was much more competitively dominant than all other species. In my third chapter, warming increased the

importance of priority effects for determining the outcome between some species-pairs, highlighting how warming could lead to less certainty in community assembly patterns. Despite coexistence predictions not changing at any of my sites in the fourth chapter, there was interesting variation in species-interactions across the sites, despite minimal variation in species' direct responses to warming across sites.

While year-to-year (temporal) variation was not a component of this research, using the same species, with the same treatment, across two years with highly different precipitation patterns gave interesting insight into another type of intraspecific variation. For example, the intrinsic growth rate of *C. purpurea* in 2022 did not significantly shift but trended negative with warming, while in 2023, it increased significantly at all sites.

It remains to be seen if and how land managers can incorporate the findings presented here into on the ground management decisions. As mentioned above, it is improbable to test the phenological responses and coexistence dynamics of the hundreds of plant species that exist in Pacific Northwest prairies. However, the results showing the high sensitivity of germination phenology and the degree of species- and community-level variation across multiple prairie units will hopefully be useful.

SUPPLEMENTAL FIGURES

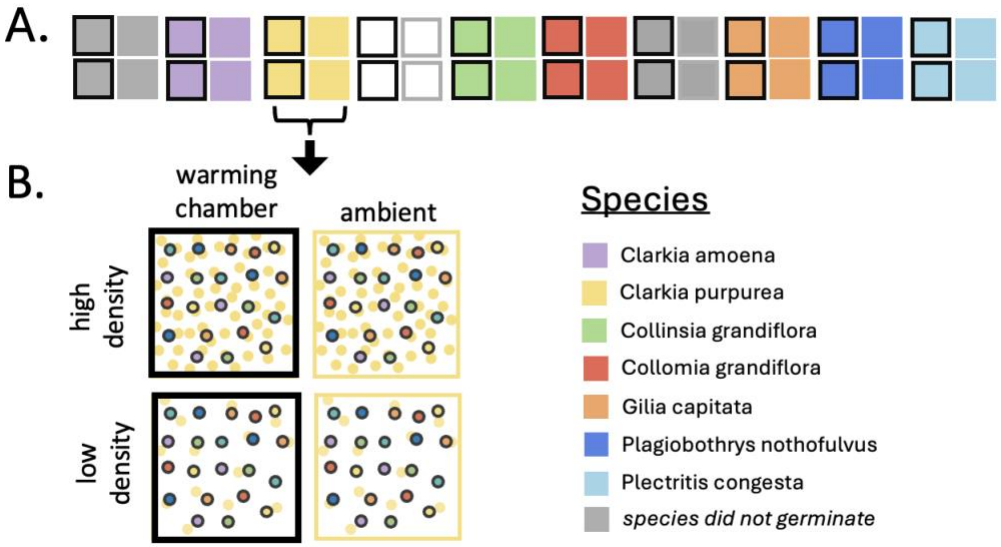


Figure S1. Experimental design. A) Plot layout: Each square shows a 1m^2 plot with the background competitor species shown by color and warming chambers indicated with thick black outlines. B) Seeding design: Points with no border represent competitor individuals and points with borders represent focal plants. Species identity is show with color. The top two plots for each competitor species had a higher density of competitors seeded in and the bottom two plots a lower density of competitors.

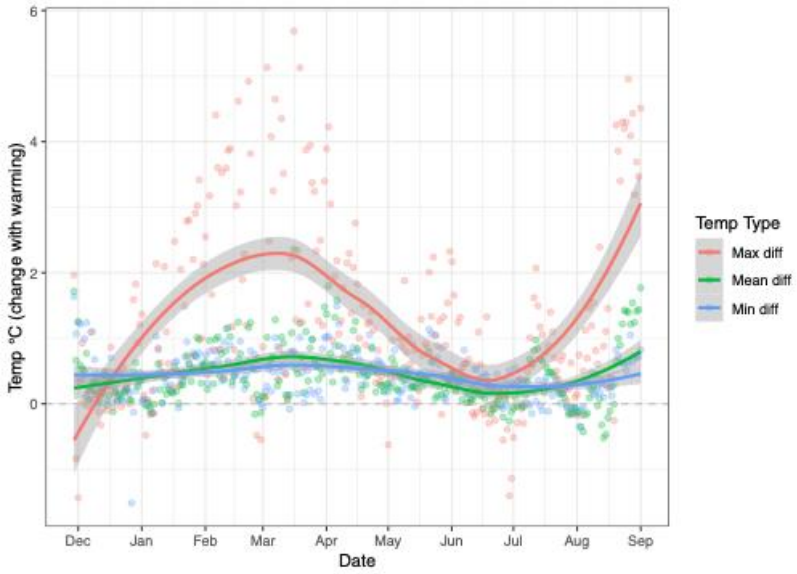


Figure S2. Warming chamber effect on air temperature, specifically change in daily maximum temperatures (red), mean temperatures (green), and minimum temperatures (blue). Each point is the change in temperature for one day and lines are smoothed means with standard error around the lines shown in grey.

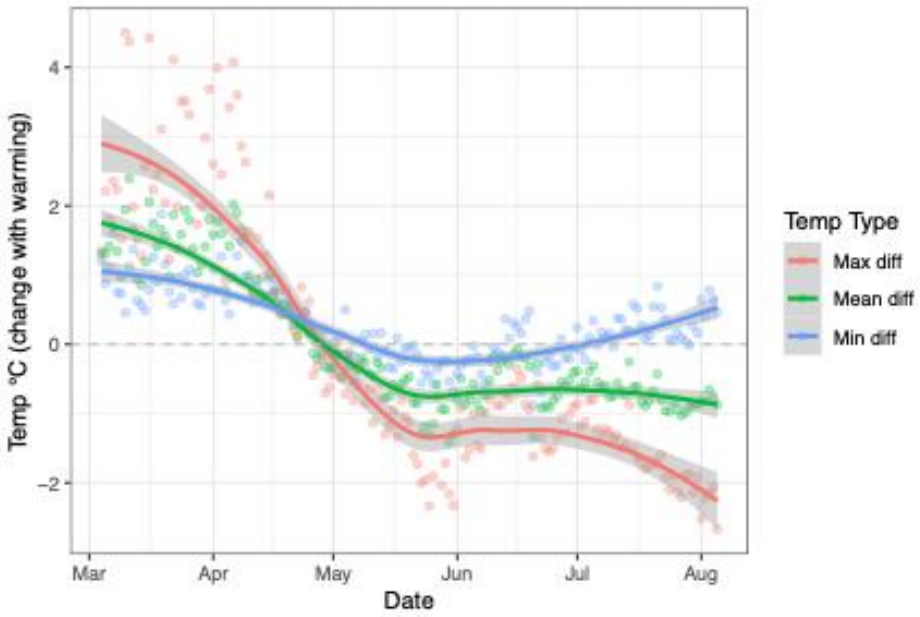


Figure S3. Warming chamber effect on soil temperature, specifically change in daily maximum temperatures (red), mean temperatures (green), and minimum temperatures (blue). Each point is the change in temperature for one day and lines are smoothed means with standard error around lines shown in grey.

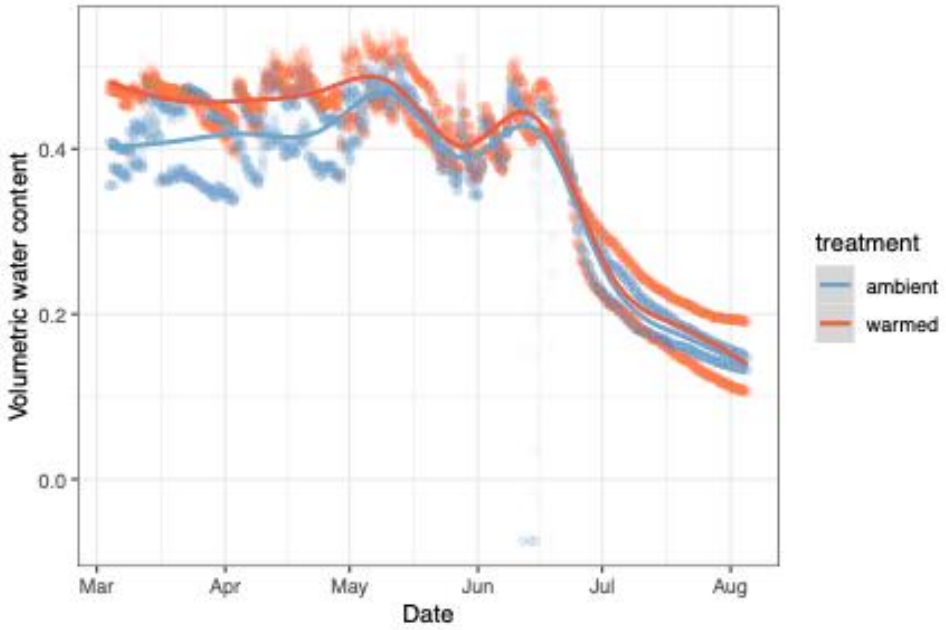


Figure S4. Warming chamber effect on soil moisture. Volumetric water content was measured in two plots with warming chambers and two plots without warming chambers. Points are raw data and lines are smoothed means of the two plots per treatment.

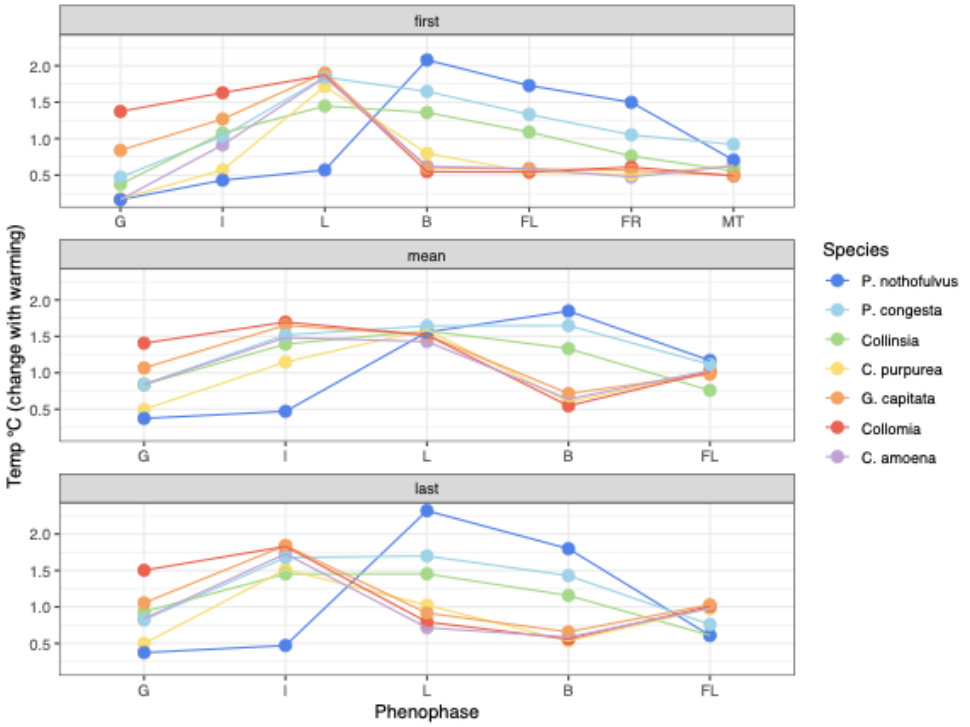


Figure S5. Average increase in daily maximum temperatures during the firsts, means, and lasts of each phenophase for each species. Each point shows a mean value of the difference in maximum daily temperature. Lines connect points to help visualize how the warming effect varies among phenophases.

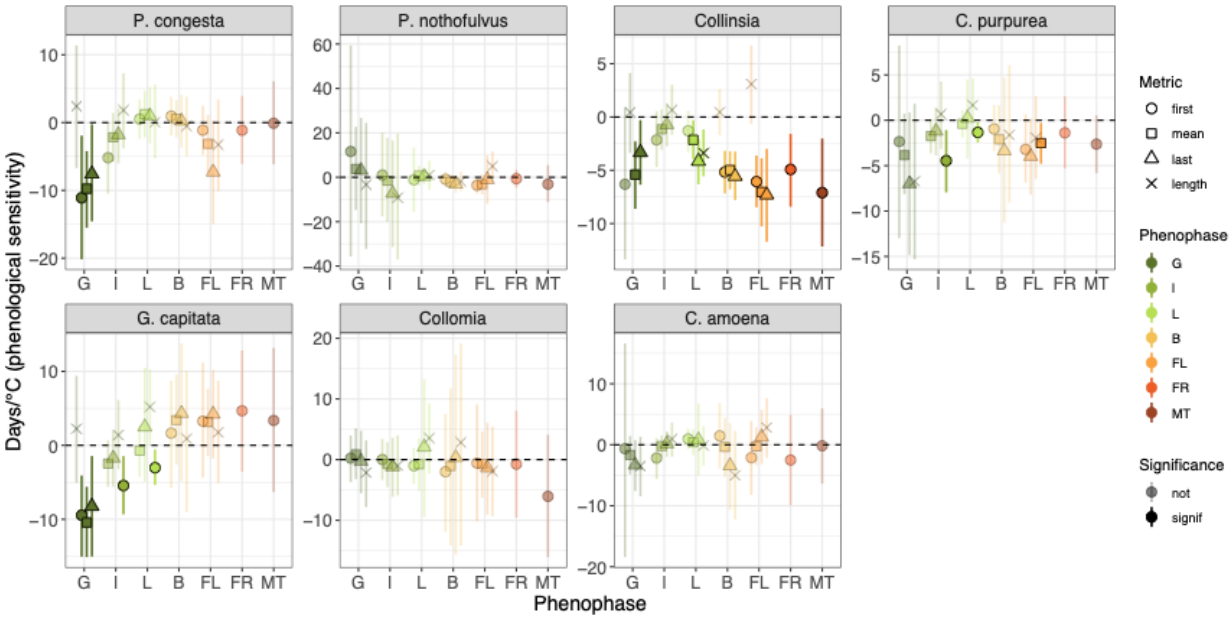


Figure S6. Phenological sensitivity of all shifts. Points are scaled median values from Bayesian posterior estimates of the number of days of change with warming. Lines show 95% credible intervals from posteriors also scaled. Colors denote phenophase and shapes phenological metric. All non-significant shifts are partial transparent to emphasize significant shifts.

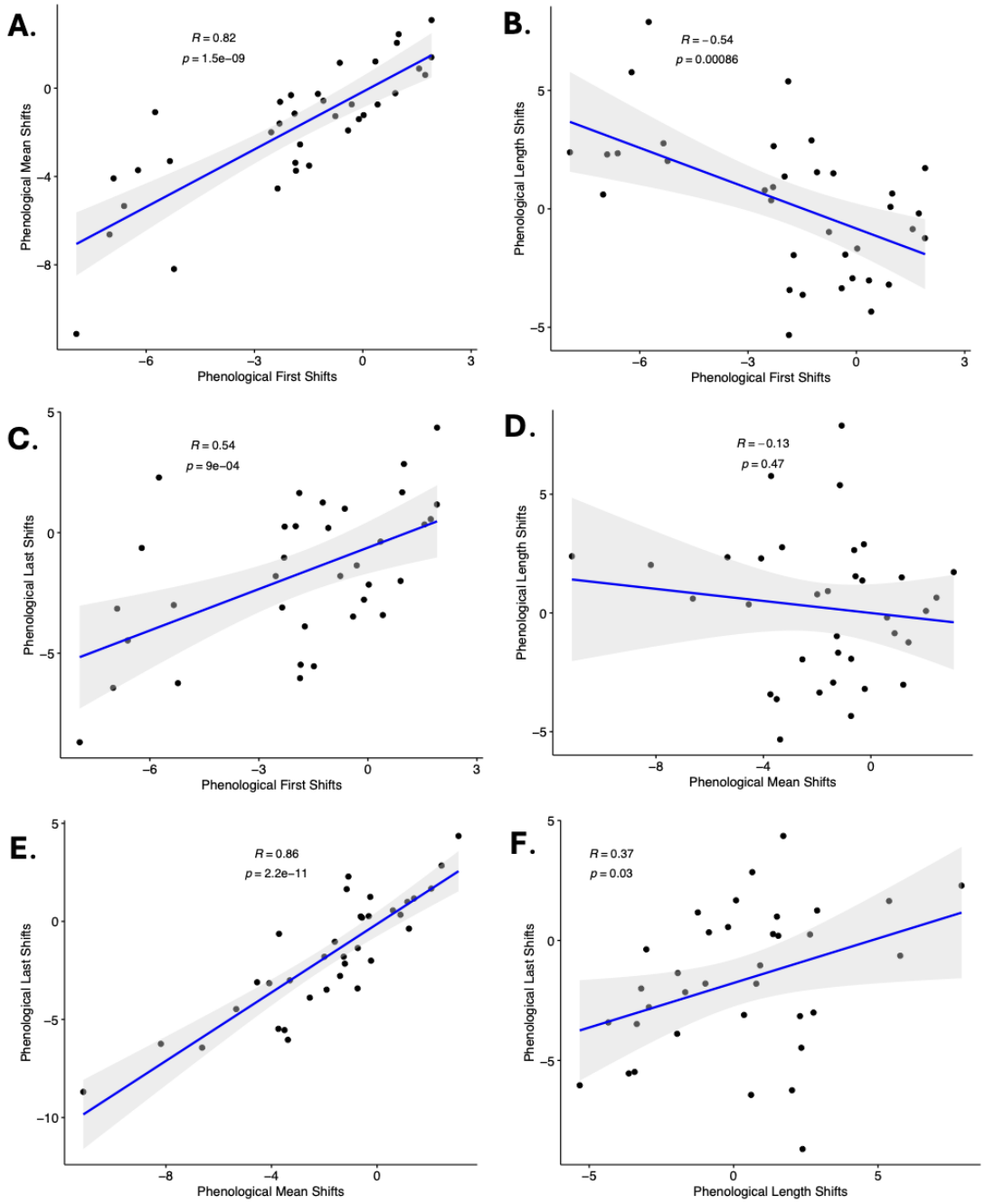


Figure S7. Correlations between phenological metrics. Phenological shifts of all phenophases and species are plotted to assess the correlation between shifts in A) firsts and means, B) firsts and lengths, C) firsts and lasts, D) means and lengths, E) means and lasts, and F) lengths and lasts. Points are median values from Bayesian posteriors estimating the number of days a species at a specific phenophase shifted with warming. Shifts are in number of days. Lines are linear regressions, and grey areas are 95% confidence intervals. Pearson's correlation coefficient was used to calculate the R value.

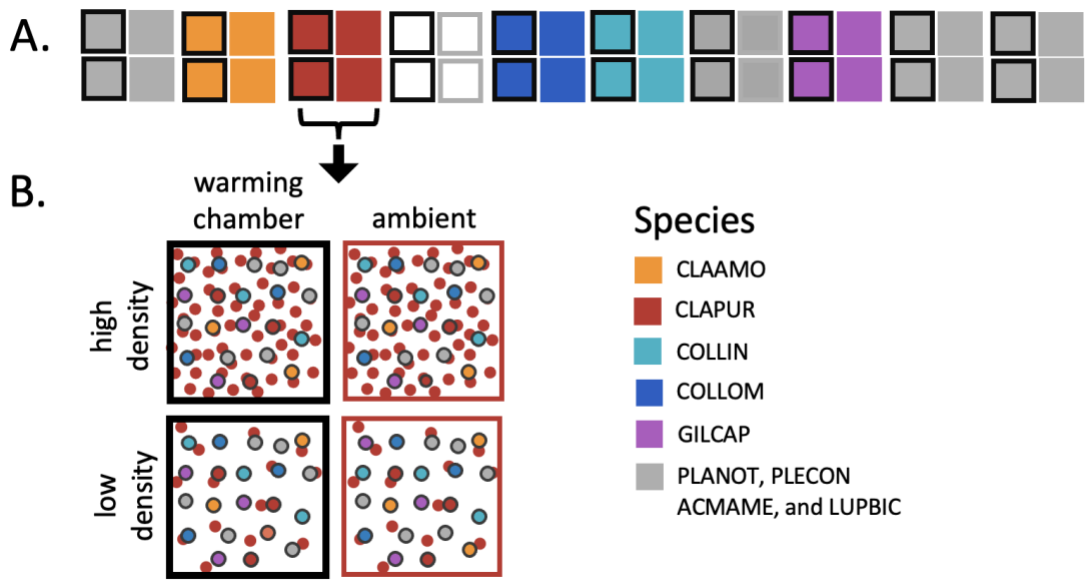


Figure S8. **Experimental design**. A) Plot layout: color denotes competitor species with grey representing species that did not germinate at high enough rates to use, empty boxes have no background competitor, and black borders represents warming chambers. B) Plot design: phytometers are points with black outlines and competitors are points without black outlines.

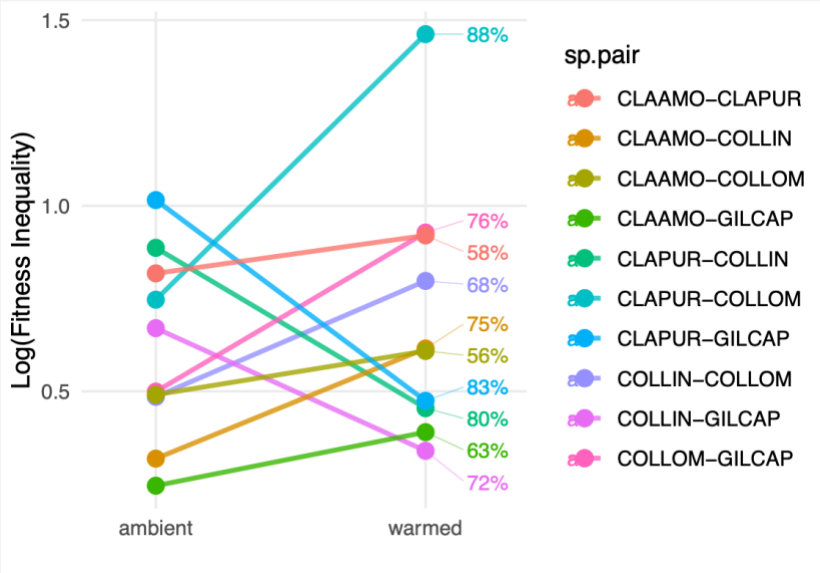
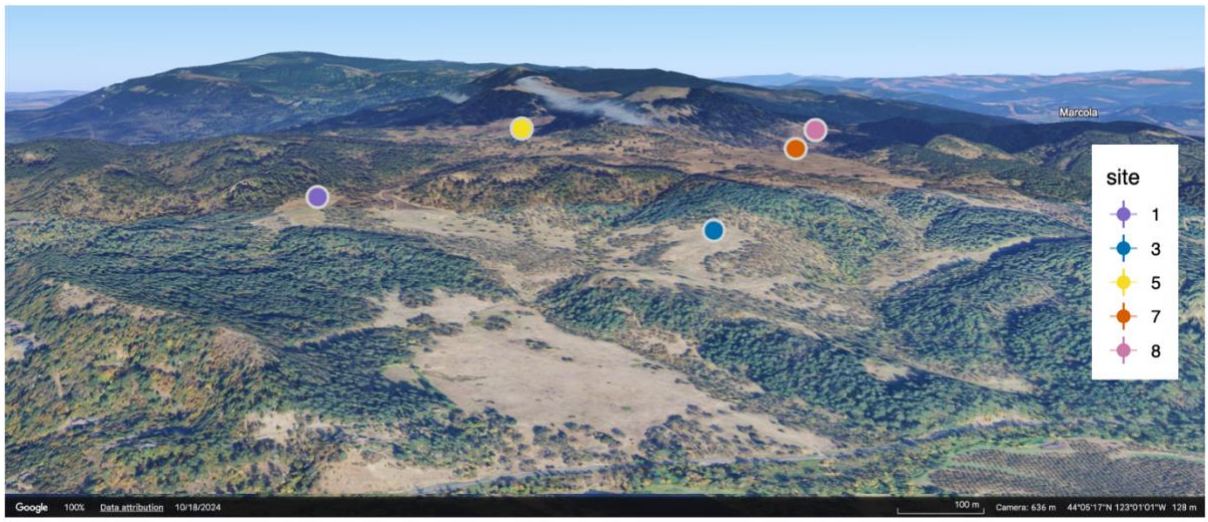


Figure S9. Fitness inequalities between species pairs in ambient and warmed treatments. Points show the median log fitness inequality (the larger of the two fitness differences) for each species pair, with lines connecting treatments to illustrate warming effects. Colors distinguish different species pairs as indicated in the legend. Numbers show the probability of difference (PD) between treatments from Bayesian posterior estimates. Species codes: CLAAMO = *Clarkia amoena*, CLAPUR = *Clarkia purpurea*, COLLIN = *Collinsia grandiflora*, COLLOM = *Collomia grandiflora*, GILCAP = *Gilia capitata*.

A



B

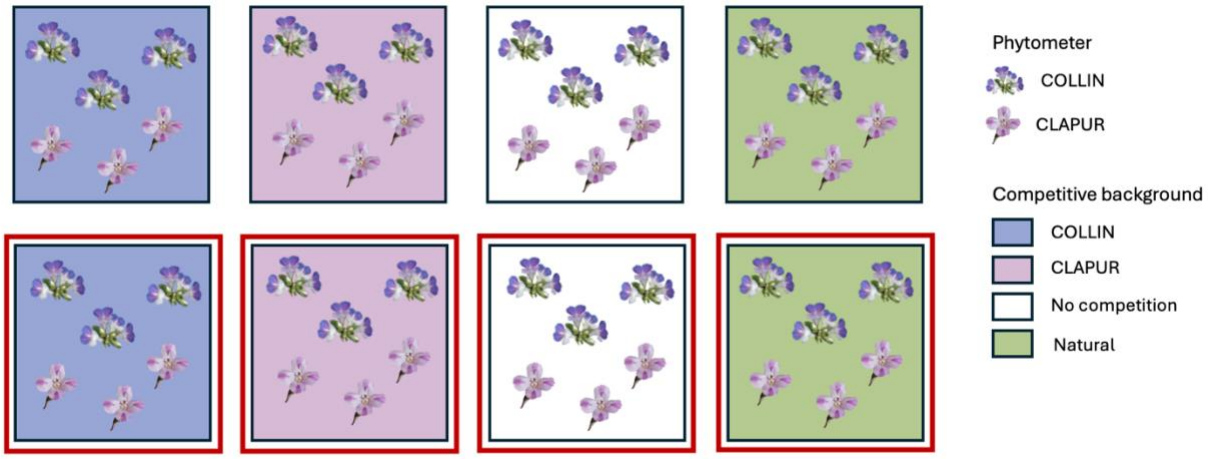


Fig S10. Plot A) locations and B) layout. A) Map show the relative locations of each of the five sites. B) The plot layout here was replicated at each site. Each square shows a single $1m^2$ plot and the color of the square (plot) denotes the competitor species or group. Photos of plants within plots represent phytometers but do not accurately show the number of phytometers per plot. Red borders represents warming chambers.

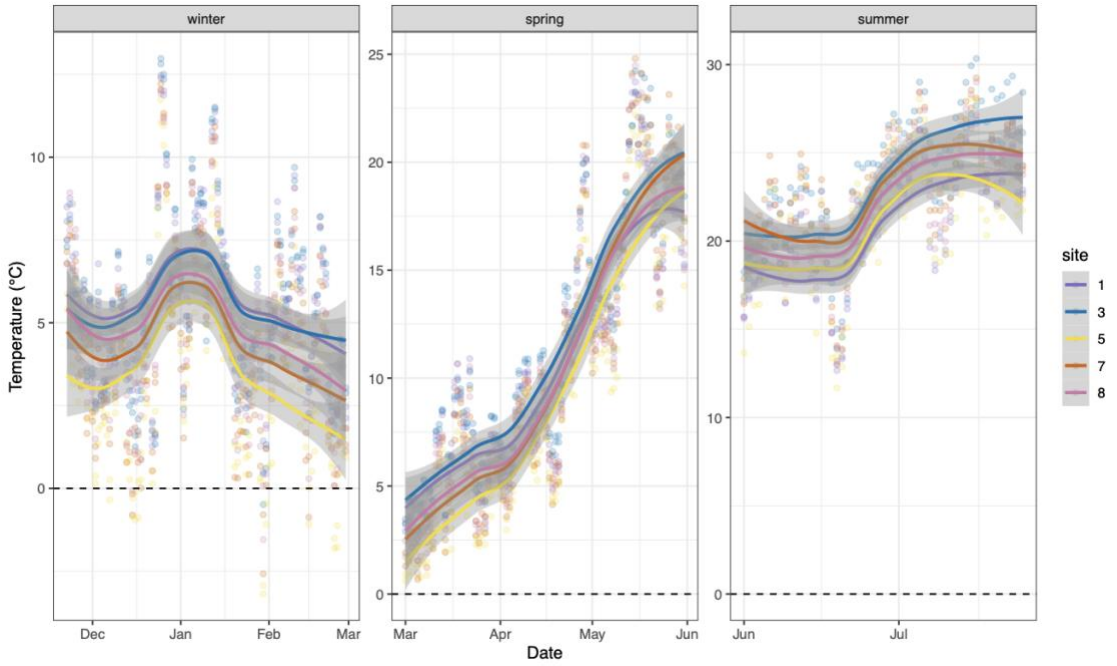


Figure S11. Ambient temperature at all sites. Points show daily mean air temperatures in ambient plots and lines show smoothed means across time, and grey shading shows error.

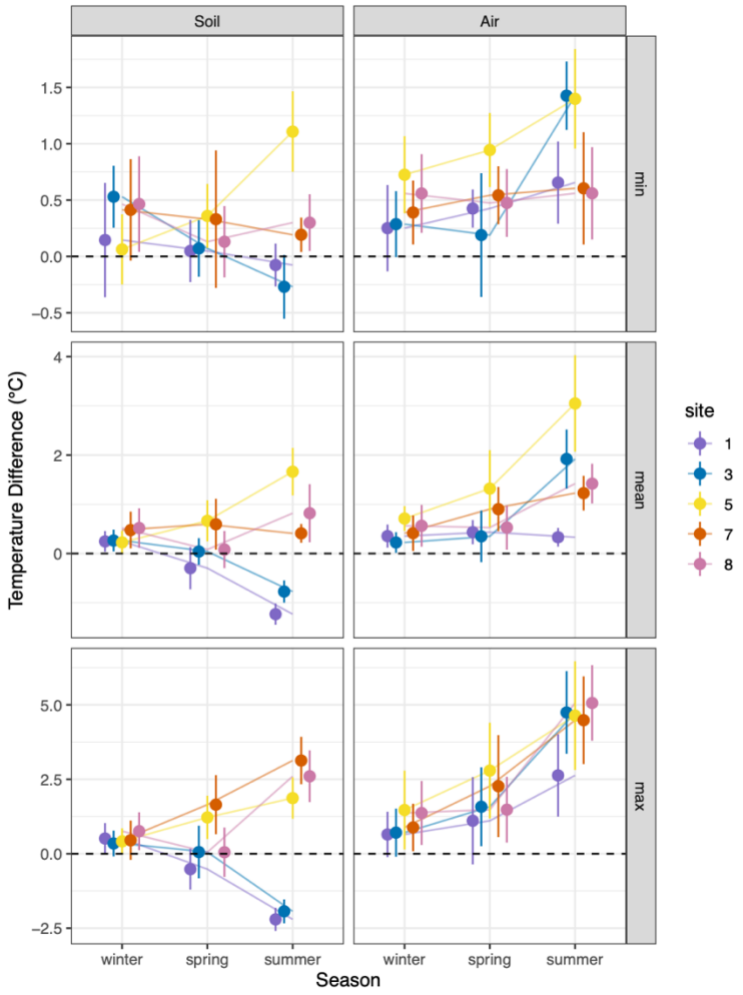


Figure S12. Change in air and soil temperatures. All panels show the change in temperature in the winter, spring, and summer at all five sites. Points show the mean/median change, vertical lines show standard error, and horizontal lines connect points by site to help visualize the change in warming effect throughout the year. Panels on the left show values from ~5cm below ground and panels on the right show values that are an average from sensors at ground level and ~15cm above ground level.

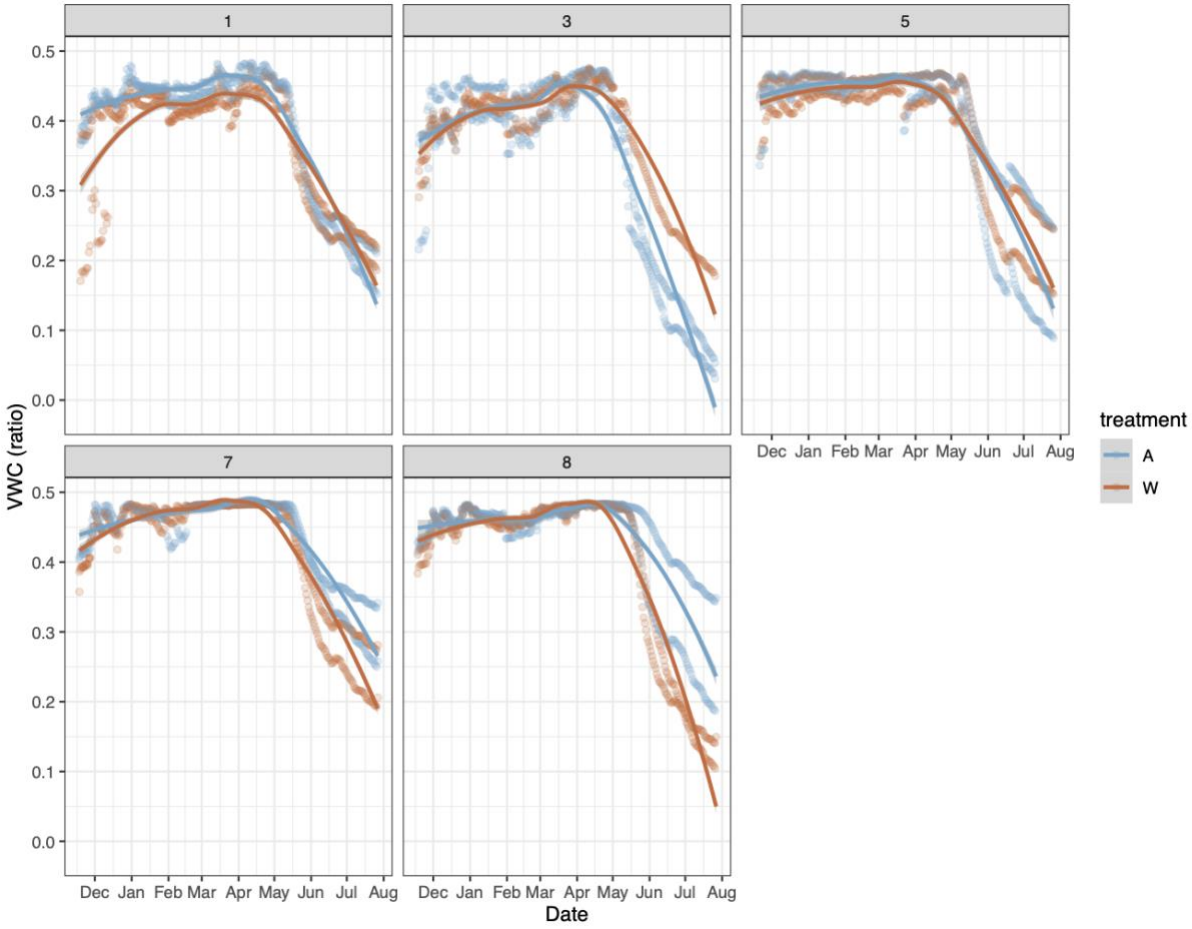


Figure S13. Volumetric water content in ambient and warmed plots. Points show raw data of mean volumetric water content in ambient (blue) and warmed (red) plots. Lines are smoothed means between the two plots per treatment.

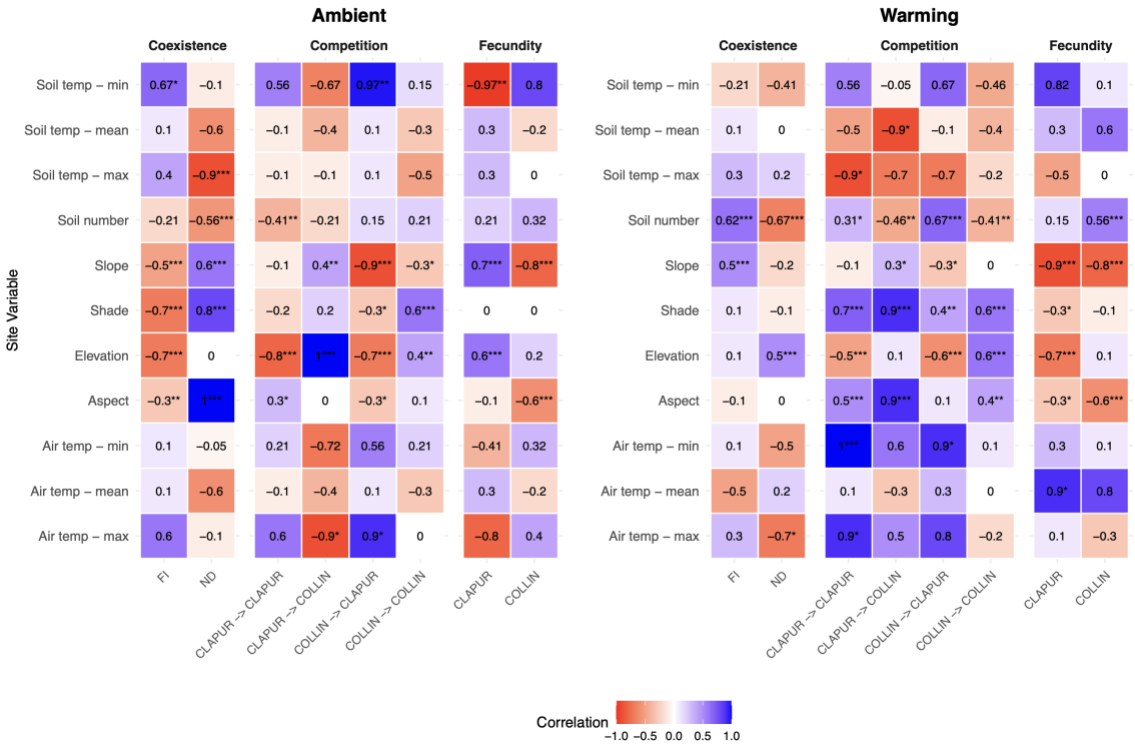


Figure S14. Correlations between changes in species performance and coexistence metrics with site environmental variables. NOTE: unlike Figure 5, the variables on the x-axis are not differences between warming and ambient, but rather raw values in ambient conditions (left) and warming (right). Similarly on the y-axis, temperature metrics are all temperatures, not differences between warmed and ambient plots. Box colors indicate the direction and strength of Spearman's correlation coefficients: blue represents positive correlations and red represents negative correlations, with darker shades indicating stronger correlations. Significance levels for correlations: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Environmental variables include site aspect, elevation, slope, and shade conditions.

Table S1. Species used in the experiment with taxonomic and phenological information. Other seeded species that did not germinate at high enough densities to use include *Acmispon americanus*, *Lupinus bicolor*, *Plagiobothyrus nothofulvus*, and *Plectritis congesta*.

Scientific name	Family	Germination	Flowering
Collinsia grandiflora	Plantaginaceae	Sept	April-June
Collomia grandiflora	Polemoniaceae	Nov-Jan	May-June
Clarkia purpurea	Onagraceae	Sept	June-July
Gilia capitata	Polemoniaceae	Oct-Nov	June-July
Clarkia amoena	Onagraceae	Sept	July-August

Table S2 a-b. Fecundity model

Table S2a. ANOVA (Fecundity; alone plants)

Term	Df	Sum Sq	Mean Sq	F value	p-value	Signif.
Treatment	1	3996714390	3996714390	16.67	4.85e-05	***
focal_spp	4	294573528289	73643382072	307.10	5.95e-167	***
treatment:focal_spp	4	1504212126	376053031	1.57	0.18	
Residuals	907	217501291964	239802968			

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table 2b. Fecundity Model: Species Contrasts by Treatment

Term	Estimate	Std. Error	t value	p-value	Signif.
CLAAMO: A - W	2304.48	2851.43	0.81	0.42	
CLAPUR: A - W	5382.49	2523.25	2.13	0.03	*
COLLIN: A - W	-1019.54	2659.64	-0.38	0.70	
COLLOM: A - W	-96.87	3149.32	-0.03	0.98	
GILCAP: A - W	5996.74	2559.94	2.34	0.02	*

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table S3 a-b. Plant height model

Table 3a. ANOVA (Plant height)

Term	Df	Sum Sq	Mean Sq	F value	p-value	Signif.
treatment	1	877	877	2.19	0.14	
focal_spp	4	189007	47252	118.10	5.29e-64	***
treatment:focal_spp	4	3615	904	2.26	0.06	.
Residuals	356	142441	400			

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table 3b. Height Model: Treatment Contrasts by Focal Species

Term	Estimate	Std. Error	t value	p-value	Signif.
CLAAMO: A - W	-3.63	4.54	-0.80	0.43	
CLAPUR: A - W	-16.93	4.47	-3.78	1.81e-04	***
COLLIN: A - W	-1.69	4.71	-0.36	0.72	
COLLOM: A - W	0.97	4.96	0.20	0.85	
GILCAP: A - W	-5.61	4.83	-1.16	0.25	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table S4 a-b. Flowering phenology model

Table S4a. ANOVA (Flowering DOY)

Term	Df	Sum Sq	Mean Sq	F value	p-value	Signif.
Trt	1	515	515	9.20	0.003	**
f.spp	4	70286	17572	313.89	1.30e-123	***
trt:f.spp	4	830	207	3.70	0.006	**
Residuals	412	23064	56			

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

Table S4b. Phenology Model: Treatment Contrasts by Focal Species

Term	Estimate	Std. Error	t value	p-value	Signif.
CLAAMO: A - W	0.61	1.68	0.36	0.72	
CLAPUR: A - W	4.06	1.52	2.67	0.008	**
COLLIN: A - W	5.31	1.54	3.46	5.98e-04	***
COLLOM: A - W	0.94	1.89	0.49	0.62	
GILCAP: A - W	-2.37	1.61	-1.47	0.14	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1

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