IN THE NEIGHBORHOOD: PHENOLOGY, SPECIES INTERACTIONS, AND COMMUNITY ENGAGEMENT IN ECOLOGICAL RESEARCH

by
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Primary Thesis Advisor

Phenology, the timing of biological life cycles, is a key indicator of global climatic change and a powerful tool for generating public awareness surrounding environmental issues. Multiple studies have shown that species are shifting their phenology in response to climate change, causing spring events such as leaf-out and flowering onset to arrive earlier and altering the way humans relate to the natural environment. Furthermore, although many studies have suggested that phenological differences influence the way that species within ecological communities interact, there has been minimal empirical consensus surrounding the impact of phenology on species interactions and even more limited research surrounding the reciprocal relationship — how species interactions impact phenology. This presents a significant knowledge gap as unprecedented rates of climate change and land-use change are altering plant community composition, diversity, and dynamics globally. As such, we studied the reciprocal relationship between flowering phenology, fitness, and competitive neighborhoods among annual plant species. We chose to utilize prairie species native to the Willamette Valley, reintroducing them to areas around the city of Eugene, OR and aiming to advance future restoration efforts by contributing to our understanding of their survival and persistence. Recognizing that public awareness and interest are key to the success of restoration and

conservation initiatives, we embedded our experiments within urban natural areas and aimed to generate direct engagement with our research by encouraging community participation in phenological data collection. We found that increased competitor species richness was correlated with the advancement and shortening of flowering periods. We also found that plant fecundity was negatively correlated with competitor density but was unrelated to changes to competitor identity or species richness. Lastly, we observed that the strength of competition tended to vary by competitor identity, but that this variation did not seem to be related to the phenological differences present between species. Our research offers unique evidence that species interactions may impact plant phenology and fitness in complex ways and consequently species' persistence and coexistence conditions in our changing global environment. Reflecting on the public engagement we witnessed, our project also demonstrates how ecological experiments can be used as an implement for both restoration and education.

Acknowledgements

I want to start by thanking my primary advisor, Dr. Jeff Diez, as well as my second reader and graduate mentor, Sarah Erskine, for their guidance throughout this process. Whether it was helping me to discover a passion for ecology, fielding my questions about coding, or taking the time to provide feedback on my drafts, their support was instrumental to my success. Further, I am appreciative of the Diez Lab as a whole, namely our lab manager Katelin Kutella and fellow undergraduates Lindsay Villano and Macy Patel, for help with fieldwork and managing other aspects of the Riverfront and Parks Project. I also want to extend my gratitude to my CHC representative, Dr. Lisa Munger, for her continual advice throughout my undergraduate education and assistance during the thesis process. Beyond the backing I received in Eugene, I am incredibly appreciative of both of my parents, Trina and Albert Callie, for their support of my academics and of Dana Mendoza for the key role she played in my formative environmental education. Finally, this work was supported by NSF grant #2125586 to Dr. Jeff Diez, and we thank the University of Oregon Campus and Facilities Management department for helping to find and prepare a site for the planting experiment.

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Introduction

When someone decides to visit a natural area during peak flowering season or selects which species to seed in their garden, they inadvertently consider phenology, the timing and cyclical patterning of biological life cycles. Phenology may be a term that many people do not recognize, yet it plays a key role in connecting people to the ecosystems that they inhabit (Breckenheimer et al., 2020). Since major phenological cues are often related to climatic variables (e.g., temperature and precipitation), species are experiencing phenological shifts in response to anthropogenic climate change and habitat alteration (Cleland et al., 2007; Parmesan and Rohe, 2003; Root et al., 2003). These shifts can have cascading effects within ecosystems and have altered the timing of key ecological events such as flowering onset and bird migrations (Parmesan and Yohe, 2003; Root et al., 2003). As such, phenology has become a highly visible indicator of environmental change (Bastian and Bayliss Hawitt, 2023; Miller-Rushing et al., 2011; Parmesan and Yohe, 2003; Root et al., 2003). Beyond providing localized examples of the impacts of environmental disruption, considering phenology also exposes people to cross-species conceptions of time and can contribute to combatting anthropocentrism and driving reimagined human-environment relationships (Bastien and Bayliss Hawitt, 2023). Given its ubiquity as well as its ecological and cultural significance, studying phenology presents a unique opportunity to combine scientific research and public engagement in order to uplift the potential of ecology to both restore and educate.

Phenology is ecologically important, and it plays a crucial yet understudied role in structuring ecological communities and driving coexistence and biodiversity patterns within ecosystems (Rudolf, 2019). The phenology of a particular species or population determines its level of development when it interacts with components of its surrounding environment,

including other species as well as its abiotic conditions (Forrest and Miller-Rushing, 2010; Yang and Rudolf, 2010). Although numerous studies have demonstrated that species are shifting their phenology in response to global environmental change (e.g., rising temperatures, nitrogen deposition, elevated CO_2 levels, and altered precipitation patterns), the effects of phenological shifts on species interactions, population dynamics, and community composition are not fully understood (CaraDonna et al., 2014; Cleland et al., 2006; Cleland et al., 2007; Kharouba et al., 2018; Parmesan and Rohe, 2003). In a 39-year study of flowering phenology in the Colorado Rocky Mountains, CaraDonna et al., (2014) underscored how phenological shifts can substantially alter the temporal coordination of an ecological community. Advanced spring flowering is a characteristic indicator of global climate change (Parmesan and Rohe, 2003). However, CaraDonna et al., (2014) observed that climate change is not only contributing to earlier first flower dates within the subalpine plant community but also delayed last flower dates, redistribution of the floral abundance, altered coflowering patterns, and expansion of flowering seasons. Notably, disruptions to the synchronization of species' flowering times could be especially influential within annual plant communities as they undergo complete reassembly each year (Rudolf, 2019).

Phenology is a trait which contributes to both niche differences (i.e., variation in resource use) and fitness differences (i.e., variation in fecundity and the ability to inhabit space) between species (Blackford et al., 2020; Godoy and Levine, 2014; Rudolf, 2019). Therefore, since niche and fitness differences combine to determine coexistence outcomes within ecological communities, phenological shifts could influence community coexistence in complex, non-intuitive ways (i.e., by concurrently impacting both niche and fitness differences between species) (Blackford et al., 2020; Chesson, 2000; Godoy and Levine, 2014; Rudolf, 2019).

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Phenological differences between species are typically associated with temporal niche partitioning; however, they can also promote fitness differences and competitive asymmetries (e.g., through earlier phenology impacting resource access) as well as influence the strength of competition (i.e., per-capita interaction strengths) between species (Alexander and Levine, 2019; Blackford et al., 2020; Godoy and Levine, 2014; Rudolf, 2019). To assess whether phenological differences will limit or promote coexistence requires quantifying the relationship between phenological differences and competition by calculating per-capita interactions strengths (which represent the rate at which a species' fecundity declines as the density of their competitor increases) and using these values to calculate niche and fitness differences between species (Hart et al., 2018; Rudolf, 2019).

Although there has been increasing research demonstrating the pervasiveness of phenological shifts and their influence on ecological community dynamics, we lack a developed understanding of the reciprocal relationship — how species interactions and community composition influence plant phenology. One of the few studies analyzing this relationship experimentally altered plant diversity within a California serpentine grassland and exemplified that shifts in community composition can alter the timing and distribution of flowering events (Wolf et al., 2017). They found that decreased plot diversity was associated with earlier flowering times, and that peak flowering dates were more dispersed among higher diversity plots than in lower diversity plots (Wolf et al., 2017). Another research project, which examined the phenology of woody species in a subtropical forest in China's Jiangxi province, demonstrated a similar trend. They found that there was a relationship between forest diversity and vegetative phenology, with reductions in diversity resulting in the advancement of leaf-out dates (Du et al., 2019). Both studies underscore that declining biodiversity may exacerbate phenological changes

associated with rising global temperatures and highlight the need for further research examining

the relationship between species interactions and phenology (Du et al., 2019; Wolf et al., 2017).

In addition to advancing our understanding of ecological community dynamics, studying

phenology provides a relevant way to increase public engagement with ecological research. One

way to directly engage the community with the study of phenology is by embedding ecological

research in public spaces. Embedded experiments (e.g., transitional ecology and designed

experiments) can augment the impact of ecological research by allowing it to serve a dual

function. Not only do these experiments produce empirical data to guide restoration and

management, but they also engage community members in the scientific process and cultivate

interactions between people and biological phenomena. In turn, this helps to advance

conservation objectives by generating an awareness of the vital services provided by healthy

ecosystems, encouraging a shared drive to protect biodiversity, and working to deconstruct

binary thinking surrounding the separation of humans and nature (Felson et al., 2013; Kay et al.,

2019).

Transitional ecology, the incorporation of ecological field research into temporary public

displays on urban land, is an emerging field of experimental ecology which aids in the

remediation of vacant and degraded areas (Kay et al., 2019). Transitional ecology projects can

take on a myriad of functions. They contribute to urban greening and revitalization efforts, serve

as forms of eco-art, generate a sense of connection between residents and their natural

ecosystems, create places for community interaction, and provide a space for experiential

learning and hypothesis testing (Felson et al., 2013; Kay et al., 2019). In St. Paul, Minnesota,

researchers created the Urban Flower Field (UFF) in order to transform an abandoned downtown

lot into a site for ecological research, environmental education, and community benefit (Fig. 1;

Kay et al., 2019). At the UFF, researchers studied the relationship between phytoremediation and biodiversity (Kay et al., 2019). To create a space that was both functional and aesthetically pleasing, they opted to use perennial and annual wildflowers as their study species, arranged the plots into a spiral pattern, and cooperated with local community members and artists to decorate the area with murals and field stones (Kay et al., 2019). The UFF also incorporated an educational component, featuring signs explaining the biology behind the experiment and hosting events such as art-science discussions and film viewings (Kay et al., 2019).

Figure 1: Photograph of St. Paul's Urban Flower Field
Source: Lovelee, 2014

Other urban ecological experiments, known as "designed experiments," work to inform the adaptive management of their specific study area by creating a two-way flow of information in which design and science reciprocally inform one another (Ahern, 2009; Felson et al., 2013; Ogden, 2013). For example, in New York City's PlaNYC reforestation initiative, planners and researchers combined tree planting efforts with the creation of experimental plots and the study

of soil characteristics in order to actively improve the urban environment as well as to inform their future planting efforts (Ogden, 2013).

Complementing the public facing nature of embedded experiments, community science initiatives can help to bridge the gap between science and society by involving local community members in the scientific research process (e.g., through helping with data collection or processing) (Bonney et al., 2009; Bonney et al., 2016; Charles et al., 2020; Cooper et al., 2007). This involvement provides opportunities for people to casually interact with experts, helps them learn about the surrounding natural world, and empowers them to become more engaged in scientific research, conservation, and restoration (Bonney et al., 2009; Bonney et al., 2016, Charles et al., 2020; Cooper et al., 2007). In recent years, the expansion of digital technology has led to the creation of online community science platforms which have become a low-cost option for investigating changes in biodiversity across space and time (McDonough MacKenzie et al., 2020). One popular community science platform is iNaturalist. iNaturalist allows users to contribute to ecological research by observing and photographing species using their mobile devices and even contains an explicit function for annotating an observation's phenology. The species occurrence records collected by iNaturalist are shared with scientific data repositories and enhance the taxonomic, temporal, and geographic breadth of data available to scientists (McDonough MacKenzie et al., 2020). Importantly, community science platforms can help address the daunting, resource-intensive task that ecologists face — documenting, interpreting, and predicting how organisms will respond to rapid environmental change (McDonough MacKenzie et al., 2020). For example, Garretson et al., (2023) utilized photodocumented phenology data from iNaturalist in order to study the insect *Oncopeltus fasciatus* and monitor its life history, host plant-insect interactions, and climate responsiveness.

Our project, named the Riverfront and Parks Project, aims to study the relationship between phenology and species interactions while also uplifting the potential of ecological research to concurrently restore and educate. Drawing on concepts of transitional ecology, designed experiments, and community science, the project embeds ecological research within six public natural areas around the city of Eugene, OR (Fig. 2). In doing so, it generates empirical data, reintroduces native prairie plants to urban areas, and engages the public with ideas about phenology, species interactions, and environmental change.
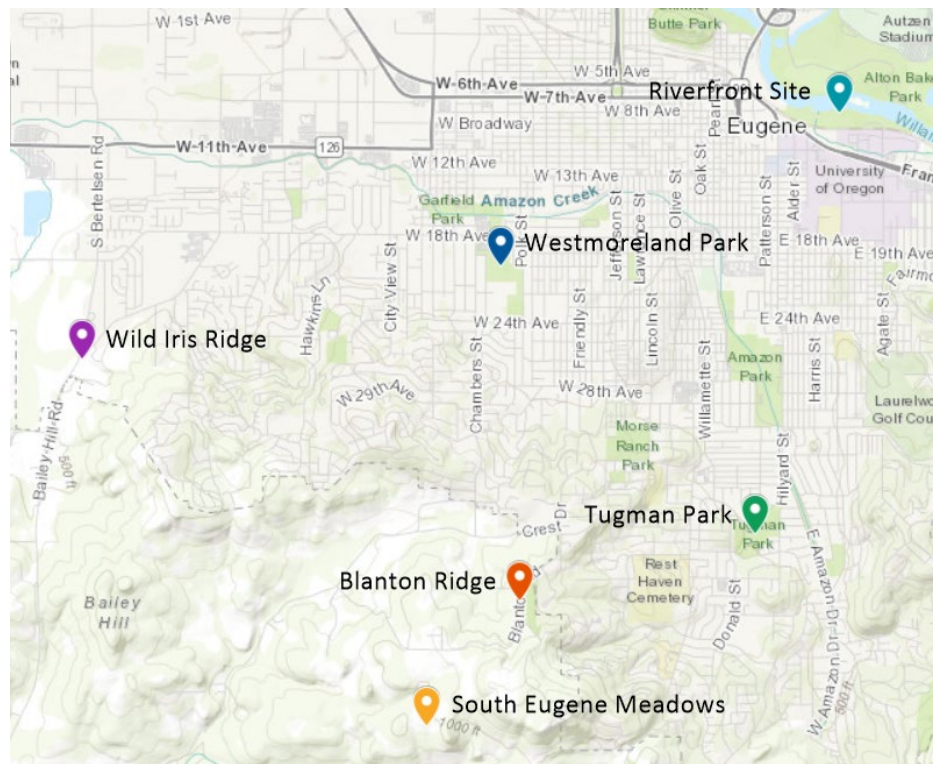
Figure 2: Locations of the Riverfront and Parks Project research sites

At the riverfront site, we studied how plant competitive neighborhoods impact their flowering phenology and fitness. Using an experimental setup which allowed us to quantify the competitive ability of annual plant species, we aimed to advance the understanding of how phenological shifts and differences may impact both short- and long-term plant community dynamics and community composition. As plant diversity mediates characteristics of the abiotic

environment, we hypothesized that increased competitor species richness would be correlated with delayed flowering times and increased fitness. On the other hand, we expected that higher density competitive environments would impose resource stress on plants and therefore be correlated with advanced flowering times and decreased fitness. We also anticipated that the strength of competition experienced by our focal species would vary in conjunction with competitor identity, and that competition from species with similar phenology would be stronger due to increased niche overlap.

Methods

Site Description

We conducted our research along the south bank of the Willamette River in Eugene, OR (44.05 ºN, 123.07 ºS, approximately 130m elevation, 12.06 ºC average annual temperature, 96.11 cm average annual precipitation) (NOAA, 2023). This region has a Mediterranean climate which exhibits a significant seasonal contrast in its temperature and precipitation, featuring warm, dry summers and cool, wet winters. Prior to Euro-American settlement in the 1850s, the site was historically dominated by riparian hardwood forest vegetation; however, over the past 120 years, industrial land uses such as railroad development, gravel mining, fill deposit, and compaction have resulted in habitat loss and degradation (University of Oregon, 2022).

The University of Oregon became involved in the management of our site area in 1989 when they obtained a permit with the City of Eugene to establish the Riverfront Research Park and guide development of the area (University of Oregon, 2022). While this permit lasted until 2012, land use changes were concentrated south of the railroad track, and the land between the railroad track and the Willamette River (the location of our study area) largely remained unrestored (University of Oregon, 2022). This began to change when in 2018, the University was approved for a new 30-year conditional use permit which included a 24-acre area designated as the Willamette River Natural Area (WRNA) (University of Oregon, 2022). The WRNA aims to promote long-term habitat restoration and preservation and enhance the area's potential for education, research, and recreation opportunities (University of Oregon, 2022). Coupled with the completed renovation of the South Bank Path (a segment of local transportation and recreation infrastructure) in 2021, the new conditional use permit marked the beginning of the riverfront's revitalization. The riverfront site also accommodates significant bicycle and foot traffic due to its

proximity to the South Bank Path and the University of Oregon, thereby making it a prime location to engage with the public and showcase our research (Fig. 3).

Figure 3: Riverfront site aerial photograph

Photograph captured May 2023 (Source: University of Oregon Fuller Initiative for Productive Landscapes, 2023). Features zoomed in view of our planting experiment.

Study System

Our study focused on plants native to Willamette Valley prairies. Within the Willamette Valley, prairie habitat is currently found on less than two percent of its pre-settlement area (Willamette Valley Oak and Prairie Cooperative, 2020). Nationally, Pacific Northwest prairies are among the most threatened habitat types (Willamette Valley Oak and Prairie Cooperative, 2020). Our study site lies at the southern extent of this ecosystem.

We used nine species of annual prairie forbs: *Collinsia grandiflora* (COLLIN), *Plectritis congesta* (PLECON), *Plagiobothrys figuratus* (PLAFIG), *Clarkia purpurea* (CLAPUR), *Collomia grandiflora* (COLLOM), *Madia sativa* (MADSAT), *Gilia capitata* (GILCAP), *Epilobium densiflorum* (EPIDEN), and *Navarretia squarrosa* (NAVSQU) (listed from earliest to

latest expected flowering). We selected annual species as they flower each year, and given their short life cycles, are ideal for short-term experiments and asking questions about competitive interactions. We chose these specific forbs due to variation in their respective flowering phenology. We also believed their vibrant flowering periods would draw the attention and interest of community members utilizing the bike path. Finally, we elected to use *C. purpurea* as our focal species due to past germination success and the expectation that its flowering time would be intermediate relative to our other study species.

Experimental Design

Prior to the onset of our experiment, the dominant vegetation within our planting area included non-native shrubs (with significant blackberry cover), grasses, and forbs. To prepare for planting, we mowed to decrease existing vegetation, covered the site with plastic to reduce the seedbank (i.e., solarization), and torched to remove remaining plant material.

We created two main planting areas adjacent to the bike path, a 30m-long planting strip and a 20m-diameter planting circle (Fig. 3; Fig. 4). The planting strip contained 16 $1m^2$ plots of annual prairie plant monocultures as well as four $1m^2$ reduced competition plots and one $10m^2$ density gradient plot containing *C. purpurea* and *C. grandiflora* (Fig. 4b). The planting circle featured three rings (one of monocultures, one of two-species plots, and one of three-species plots) and a center diverse core containing all nine of our study species (Fig. 4a). The multispecies plots contained *C. purpurea* with different combinations of our study species (Fig. 4a). Seed quantities were measured by weight based on the respective areas of plots, and initial sowing occurred in January with some reseeding in March. Throughout the duration of the experiment, we manually removed weeds and plants of the incorrect identity from the plots.
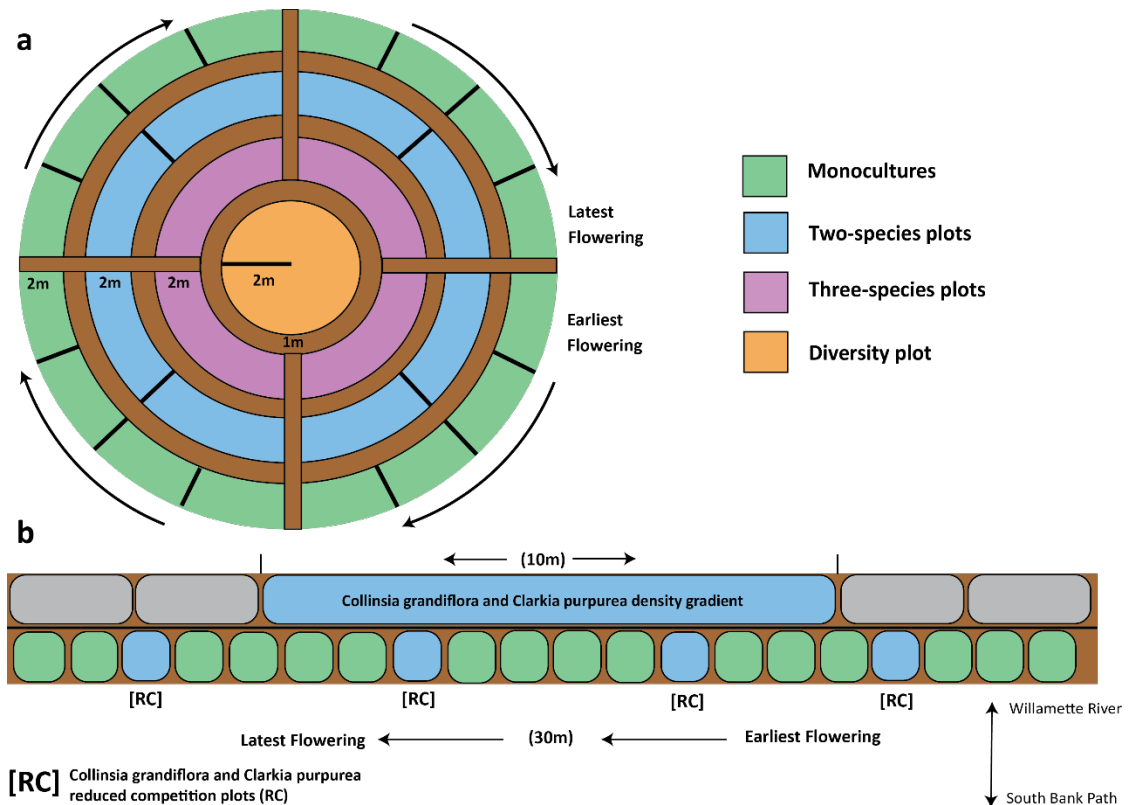
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Figure 4: Planting experiment design

Planting circle (a) and planting strip (b)

We arranged the plots in the planting strip and circle in order of the species' expected flowering times both for aesthetic value and to highlight phenological differences between species (Fig. 4). We mulched the perimeter of the strip and the segments between the circle's rings to create pathways to guide visitors' interactions (Fig. 3; Fig. 4). Alongside the strip, we placed signs for the species which germinated in abundance and included their names, photos of various phenophases (i.e., vegetative, budding, flowering, and fruiting), general phenological timelines, and QR codes to direct community members to aid in the collection of phenological data using the mobile application iNaturalist (Fig. 5). By encouraging community members to document the phenology of our study species, we aimed to generate direct scientific engagement with phenology.
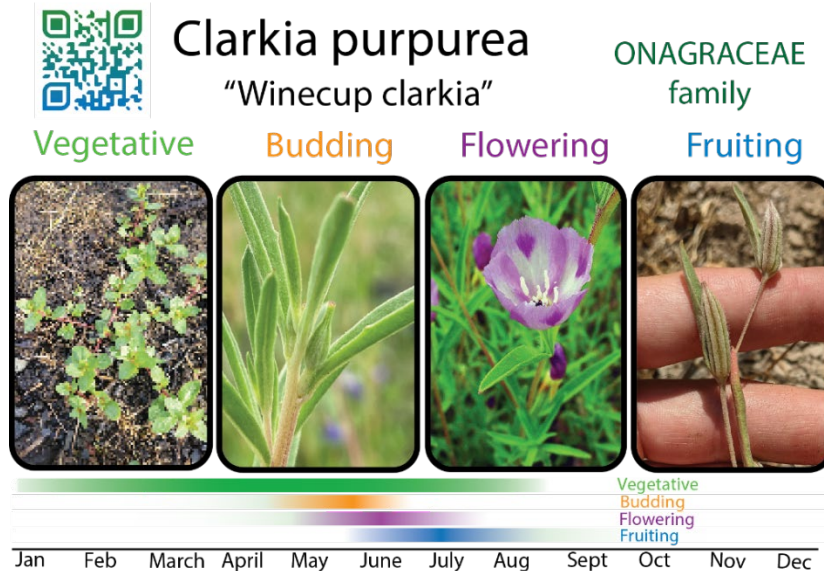
Figure 5: Example photo point sign from the planting strip

To assess how competitive neighborhoods impact the flowering phenology and fitness of *C. purpurea*, we marked multiple focal individuals of *C. purpurea* within plots in the strip and circle, aiming to capture a gradient of competitor density and species richness. We quantified the neighborhood of each focal plant, recording the identity and number of competitors rooted within a 10cm radius, and tagged each plant. We monitored the phenology of these focal plants from May through August with site visitation taking place three times per week prior to the start of *C. purpurea*'s flowering season and daily henceforth. We focused on flowering phenology given the ease of identifying the presence of this phenophase and the general public appeal of colorful flowers. For each *C. purpurea* focal, we recorded the date of the first flower (i.e., first open flower) and last flower (i.e., no open flowers remaining), defining an open flower as one in which all four whorls were visible (Fig. 6). We derived first flower dates for our other eight study species from iNaturalist observations collected from our planting strip. This was done within the iNaturalist "Explore" tab by drawing a custom rectangular boundary around the area of the planting strip, setting the date range to encompass the 2023 growing season, and filtering observations by species. We found that we did not have regular iNaturalist observations for the

last flower dates of these competitor species available from our planting strip; hence, we utilized observations collected within Lane County, OR to estimate their last flower dates. This hybrid estimation combined the first flower dates from our planting strip with flowering lengths from Lane County and allowed us to calculate metrics of phenological overlap and separation between *C. purpurea* and our other species. Once the *C. purpurea* plants matured and reached the end of their flowering periods, we counted the number of fruit present on each plant. We converted these fruit counts to fecundity measurements (i.e., seed counts) by collecting and dissecting fruit from focal plants in backgrounds of varying competitor densities and obtaining average seed-per-fruit counts.

Figure 6: Photograph of a *C. purpurea* with an open flower from August 2023

Statistical Analyses

For translating fruits-per-plant counts into seed counts, we conducted a linear regression to determine whether the mean seed-per-fruit counts varied based on competitor density. Since there was a significant difference between the seed count per fruit within the different competitor

density environments ($p = 8.56 \times 10^{-5}$), we calculated the mean seeds per fruit in three density categories (zero, medium, and high), and then used these values to convert each plant's number of fruits to a seed number based on the density of its competitors.

We aimed to understand the relationships between *C. purpurea*'s flowering phenology and fecundity and the density, species richness, and identity of competitors. Given that competitor density and competitor species richness were positively correlated (Fig. S1, supplement), we used multiple regressions to test for their effects on flowering phenology and fecundity. Four phenological response variables — first flower date, last flower date, flowering length, and peak flowering date — were each regressed against the density and species richness of competitors. Similarly, the response variable of *C. purpurea*'s fecundity was regressed against the density and species richness of competitors. We utilized ANOVAs to test for the effects of competitor identity on *C. purpurea*'s flowering phenology and fecundity.

To quantify how the identity and density of competitors influenced the strength of competition (i.e., the per-capita effects of competition), we modelled individual reproductive output, F_i, using a non-linear Beverton-Holt model as follows:

$$F_i = \frac{\lambda_i}{1 + \alpha_{i,i} N_i + \alpha_{i,j} N_j}$$

where N_i is the number of individuals of species *i*, and λ_i is the intrinsic per-capita seed production (in the absence of competition) and $\alpha_{i,i}$ and $\alpha_{i,j}$ are the per-capita effects of intra- and interspecific competition, respectively, on the seed production of a focal individual. The response variable in these models, F_i, were counts of seed production per plant, and the number of conspecific and heterospecific competitors, N_i and N_j, respectively, were counted in each focal plant's neighborhood. We estimated the parameters of above models using nonlinear Bayesian regression models using Stan (Stan_Development_Team, 2023b), accessed via R

(R_Core_Team, 2022) using the rstan package (Stan_Development_Team, 2023a). We performed pairwise contrasts between the alphas of different competitor species in order to determine whether competitor identity had a significant effect on the per-capita effects of competition ($\alpha_{i,i}$ and $\alpha_{i,j}$).

Results

Flowering Times

      C. purpurea's first flower date, last flower date, flowering length, and peak flowering date were negatively correlated with competitor species richness and its last flower date, flowering length, and peak flowering date were negatively correlated with competitor density (simple univariate regressions; $p < 0.05$). However, competitor species richness and competitor density were positively correlated (Fig. S1, supplement; $r_{122} = 0.46, t = 5.71, \ p = 7.96 \ x \ 10^{-8}$), and multiple regressions involving both competitor density and competitor species richness suggest that *C. purpurea*'s flowering times were negatively correlated with competitor species richness (Fig. 7; first flower: $F_{2,119} = 6.58, \ p = 1.82 \ x \ 10^{-3}$; last flower: $F_{2,118} = 12.51, \ p = 3.84 \ x \ 10^{-4}$; flowering length: $F_{2,118} = 7.27, \ p = 0.02$; peak flowering: $F_{2,118} = 12.63 , \ p = 1.61x \ 10^{-4}$) but not competitor density (first flower: $p = 0.94$; last flower: $p = 0.18$; flowering length: $p = 0.12$; peak flowering: $p = 0.30$). *C. purpurea*'s flowering times also varied depending on the identity of the competitor species (Fig. 8; first flower: $F_{8,222} = 4.69, \ p = 2.58 \ x \ 10^{-5}$; last flower: $F_{8,221} = \ 3.9, \ p = 2.31 \ x \ 10^{-4}$; flowering length: $F_{8,221} = 2.12, \ p = 0.04$; peak flowering: $F_{8,221} = 4.76 , \ p = 2.08x \ 10^{-5}$). Furthermore, *C. purpurea*'s first and last flower dates were strongly positively correlated (Fig. S2a, supplement; $r_{119} = \ 0.63, t = 8.80, \ p = 1.26 \ x \ 10^{-14}$) as were its last flower dates and flowering length (Fig. S2c, supplement; $r_{119} = \ 0.86, t = 18.50, \ p = 2.2x \ 10^{-16}$); however, there was no significant correlation between its first flower dates and flowering length (Fig. S2b, supplement; $r_{119} = 0.15, t = 1.61, \ p = 0.11$).
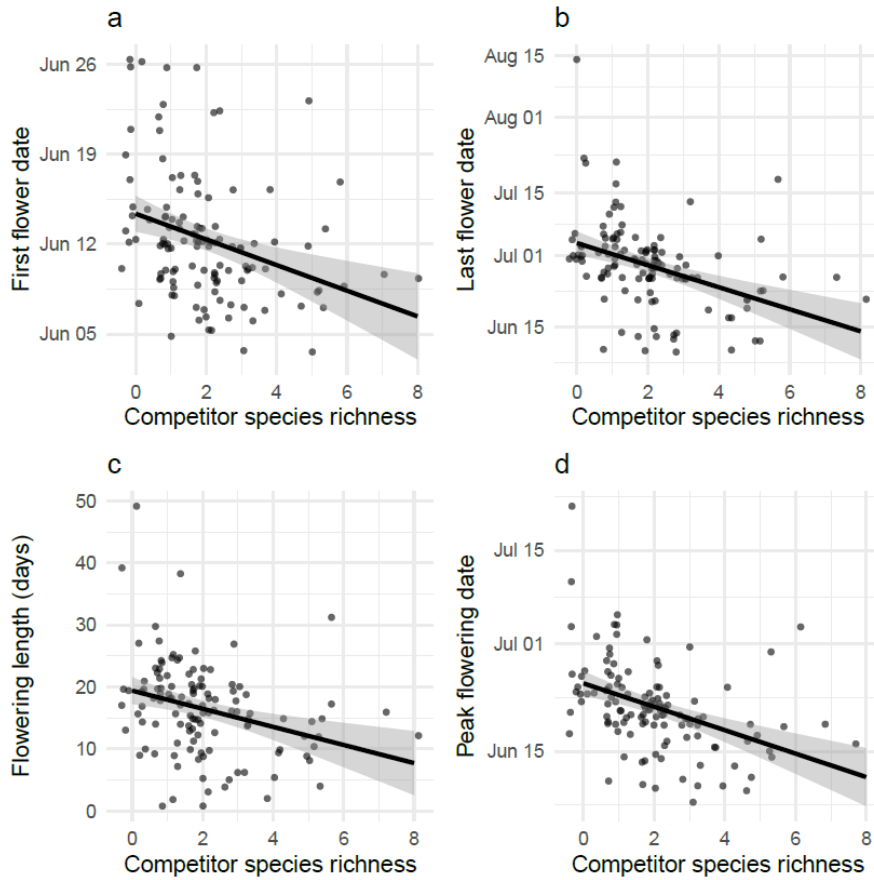
Figure 7: *C. purpurea* flowering phenology versus competitor species richness

Scatter plots fit with linear regressions. Points represent unique focal plants. Shaded areas represent 95% confidence intervals surrounding means of the linear regressions. Accounting for competitor density, *C. purpurea*'s first flower dates, last flower dates, flowering length, and peak flowering dates were each significantly negatively correlated with competitor species richness ($p < 0.05$).

Figure 8: *C. purpurea* flowering phenology by competitor identity

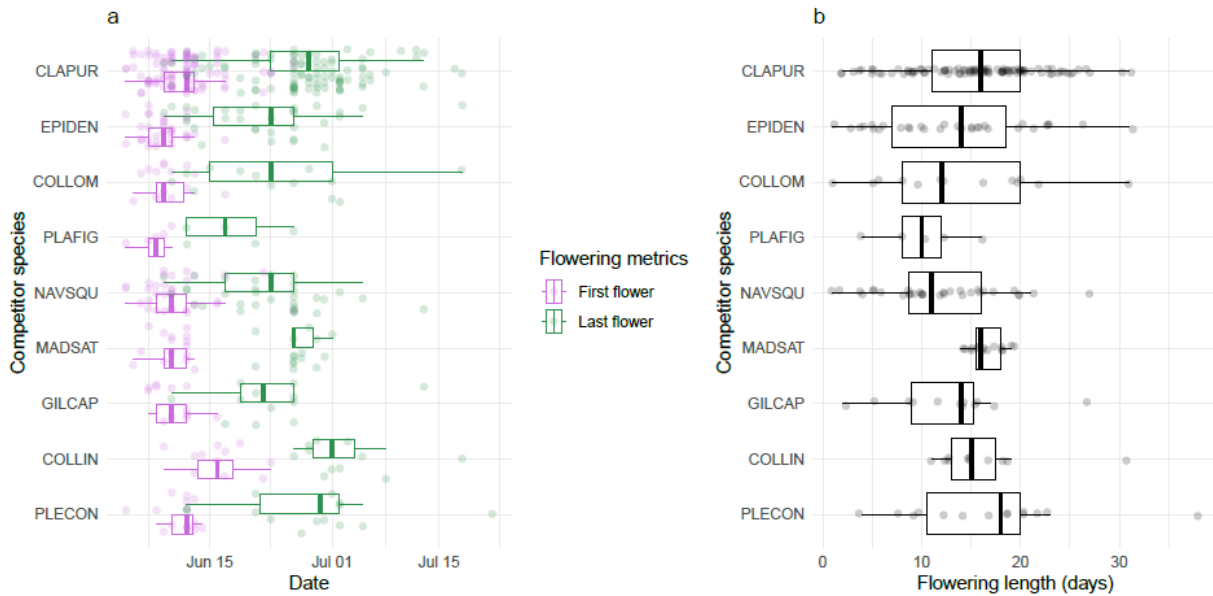Boxplots comparing first flower dates, last flower dates, and flowering length of focal plants against different species of competitors. Points may be repeated within multiple competitor species' boxplots as focal plants were often located in neighborhoods with a competitor species richness greater than one. Outliers are not included within the graphs. Bars represent medians. Boxes represent the interquartile range (IQR). Lines extend out 1.5 times the IQR from the first and third quartiles. *C. purpurea*'s first flower dates, last flower dates, and flowering length were each significantly correlated with competitor identity ($p < 0.05$).

Fecundity

The fecundity of *C. purpurea* was negatively correlated with competitor density (simple univariate regression; $p < 0.05$) but not competitor species richness (simple univariate regression; $p > 0.05$). Multiple regressions including both competitor density and competitor species richness confirm that *C. purpurea*'s fecundity was only negatively correlated with competitor density (Fig. 9; $F_{2,121} = 4.65, p = 0.02$) and not significantly correlated with competitor species richness ($p = 0.47$). Additionally, there was not a significant relationship between *C. purpurea*'s fecundity and competitor identity (Fig. 10; $F_{8,226} = 1.06, p = 0.40$). *C. purpurea*'s fecundity was not significantly correlated with its first flower dates (Fig. 11a; $r_{119} =$

$5.11 x 10^{-3}, t = 0.06, \ p = 0.96$), but it was positively correlated with its last flower dates (Fig.

11b; $r_{119} = 0.42, t = 5.11, \ p = 1.25 \ x \ 10^{-16}$) and flowering length (Fig. 11c; $r_{119} = 0.54, t = 6.92, \ p = 2.41 \ x \ 10^{-10}$).
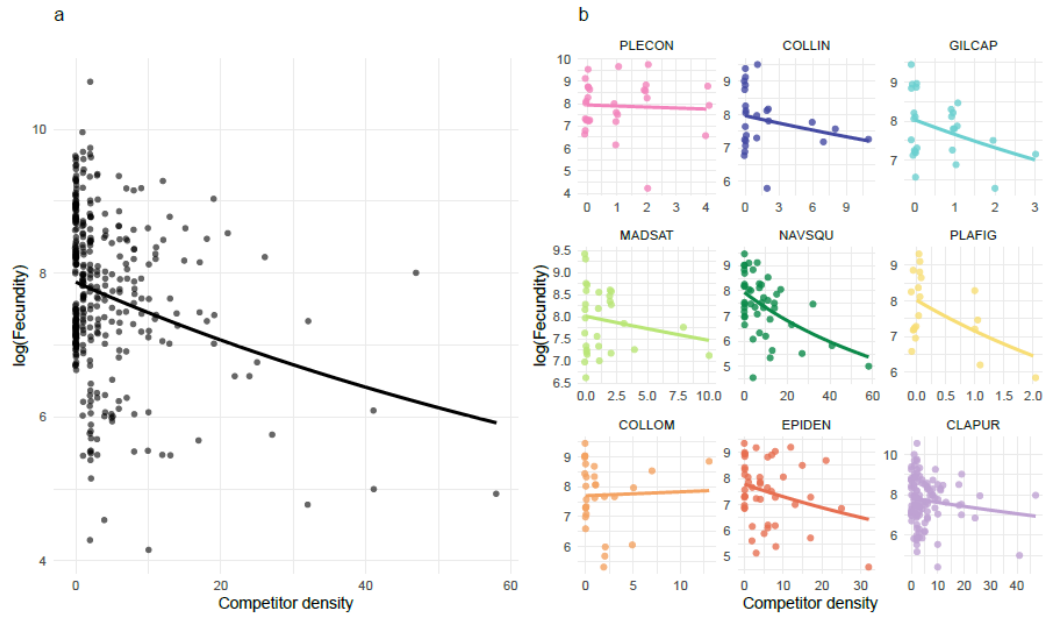
Figure 9: *C. purpurea* fecundity versus competitor density

Points in graph (a) represent unique focal plants. Points in graph (b) may be repeated across multiple competitor species' plots as focal plants were often located in neighborhoods with a competitor species richness greater than one. Curves are non-linear, Beverton-Holt regressions. Fecundity is displayed using a logarithmic scale. The slope of the curve represents the strength of competition (alpha) experienced by *C. purpurea*. Y-intercepts represent *C. purpurea*'s fecundity in the absence of competition (lambda). Accounting for competitor species richness, there was a significant negative correlation between *C. purpurea*'s fecundity and competitor density ($p < 0.05$).
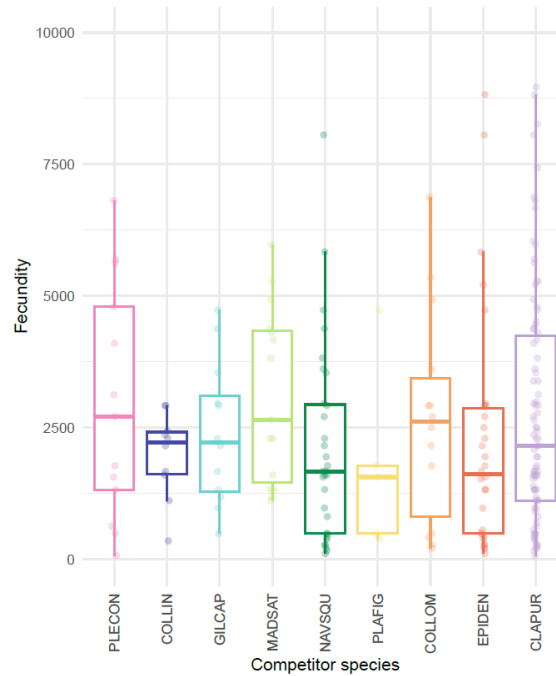
Figure 10: *C. purpurea* fecundity by competitor identity

Boxplots comparing the fecundity of focal plants against different species of competitors. Points represent focal plants and may be repeated across multiple competitor species as focal plants were often located in neighborhoods with a competitor species richness greater than one. Outliers are not included in the graph, and focals with a fecundity above 10,000 are also not included as the y-axis is truncated to preserve graph clarity. Bars represent medians. Boxes represent the interquartile range (IQR). Lines extend out 1.5 times the IQR from the first and third quartiles. *C. purpurea*'s fecundity was not significantly correlated with competitor species identity ($p > 0.05$).

Figure 11: *C. purpurea* flowering phenology versus fecundity

Scatter plots fit with linear regressions. Points represent unique focal plants. Shaded areas represent 95% confidence intervals surrounding the means of the regressions. *C. purpure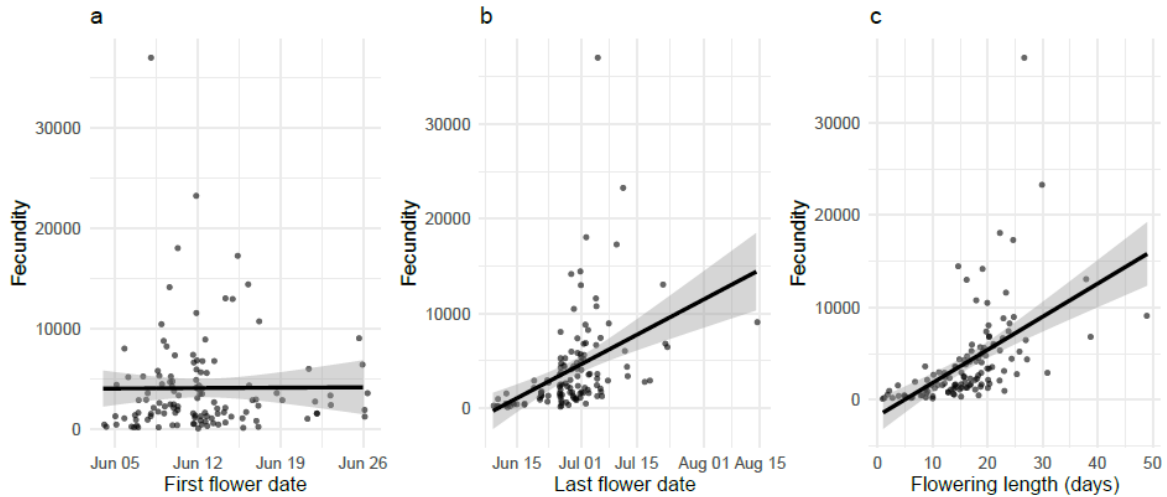a*'s first flower dates were not significantly correlated with its fecundity ($r_{119} = 5.11x10^{-3}, p > 0.05$). *C. purpurea*'s last flower dates were moderately positively correlated with its fecundity ($r_{119} = 0.42, p < 0.05$). *C. purpurea*'s flowering lengths were strongly positively correlated with its fecundity ($r_{119} = 0.54, p < 0.05$).

Strength of Competition

For two of the pairwise contrasts between alpha values, we found a > 90% probability that the alphas were significantly different; hence, we can conclude that there is a significant overall effect of competitor identity on the strength of competition (alpha) experienced by *C. purpurea* (Fig. 12; Table S1, supplement). Furthermore, the strength of competition experienced by *C. purpurea* was not significantly related to phenological differences (e.g., difference in first flower dates, difference in last flower dates, flowering length, days of flowering overlap, and difference in peak flowering dates) between *C. purpurea* and our other study species (Fig. 13; Table S2, supplement; $p > 0.05$). However, a linear regression of *C. purpurea*'s first flower dates versus the strength of competition highlights a trend towards a positive relationship between these two variables (Table S2, supplement; Fig. 13a).
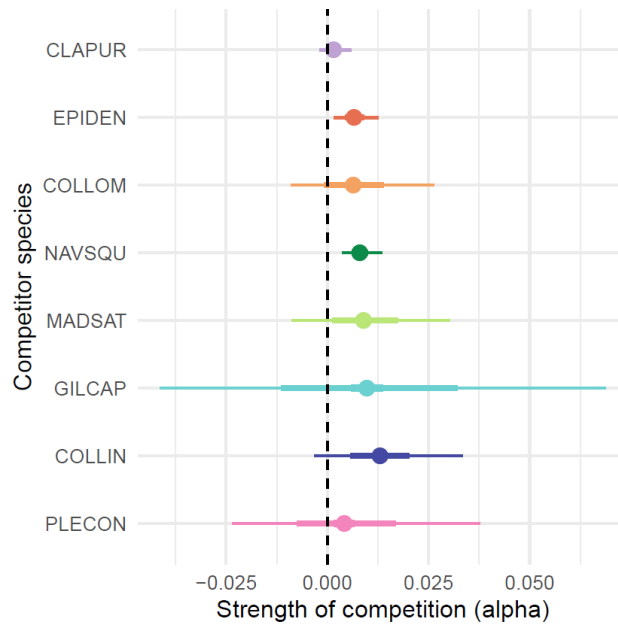
Figure 12: Strength of competition (alpha) experienced by *C. purpurea* by competitor identity

Points represent mean alpha values. Thick lines represent 50% of the Bayesian posterior distribution used to discern credible intervals. Thin lines represent 90% of the Bayesian posterior distribution used to discern credible intervals. *P. figuratus* is not included due to low sample size. Pairwise contrasts between the alpha values of some species demonstrate that there is a > 90% probability of alpha values being significantly different; therefore, competitor identity had a significant overall effect on the strength of competition experienced by *C. purpurea*.
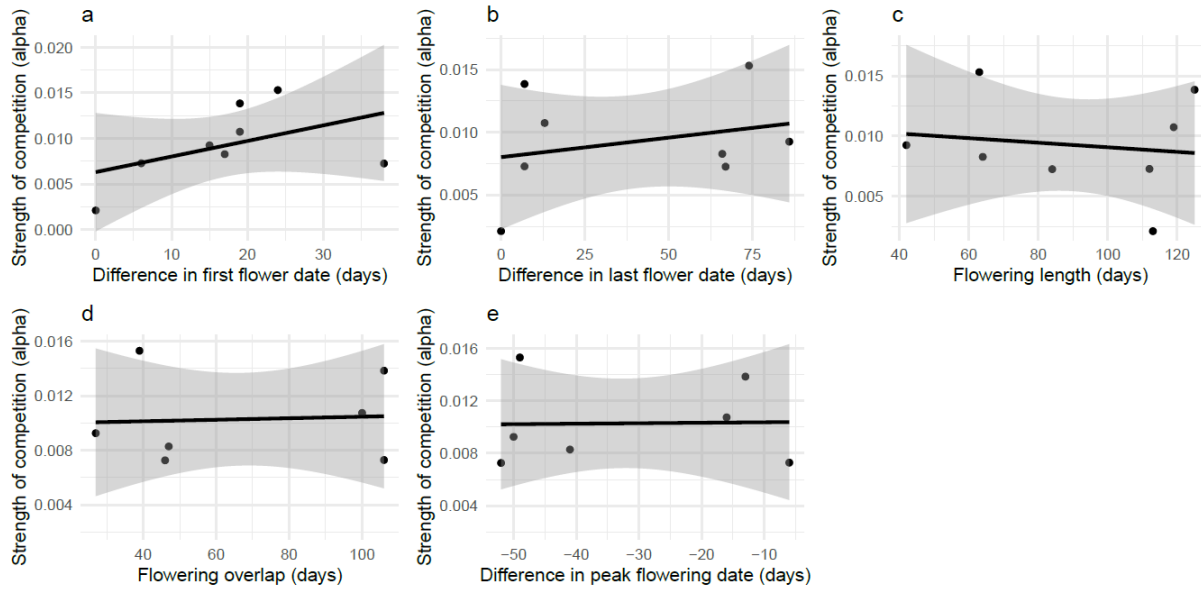
Figure 13: Strength of competition (alpha) experienced by *C. purpurea* versus phenological separation between other study species and *C. purpurea*

Each point represents a unique competitor species. *P. figuratus* is not included due to low sample size. Flowering phenology data is sourced from iNaturalist using a hybrid estimation of dates based on observations from the planting strip and Lane County, OR. Days of flowering overlap represents the number of days a given study species was flowering concurrently with *C. purpurea*. Peak flowering date is defined as the median date of a species' flowering period. Difference in peak flowering date subtracts the peak flowering date of a given competitor from the peak flowering date of *C. purpurea*. There was not a significant relationship between any of the measures of phenological separation and the strength of competition experienced by *C. purpurea* ($p < 0.05$).

iNaturalist Phenology Observations

Estimates of phenological comparisons between species varied based on the geographic bounds used to filter iNaturalist observations (Fig. 14). Estimates sourced only from our planting strip tended to have shorter overall flowering lengths, with all nine study species exhibiting shorter flowering lengths when using planting strip observations versus Lane County observations (Fig. 14a; Fig. 14b). The order of species' first flower dates was fairly similar between the two data sources; however, there was some variation in the order (by a magnitude of

days) of the intermediate flowering species (*P. figuratus, N. squarrosa, M. sativa, and G. capitata*) (Fig. 14a; Fig. 14b). *C. purpurea* and *E. densiflorum* had the latest flowering periods based on all three data sources (Fig. 14). Based on planting strip and Lane County observations, *C. purpurea* had the latest first flower date and *E. densiflorum* had the second latest first flower date (Fig. 14a; Fig. 14b). Moreover, according to hybrid and Lane County estimates, *C. purpurea* had the latest last flower date, but using planting strip observations, *E. densiflorum* had the latest last flower date (Fig. 14).
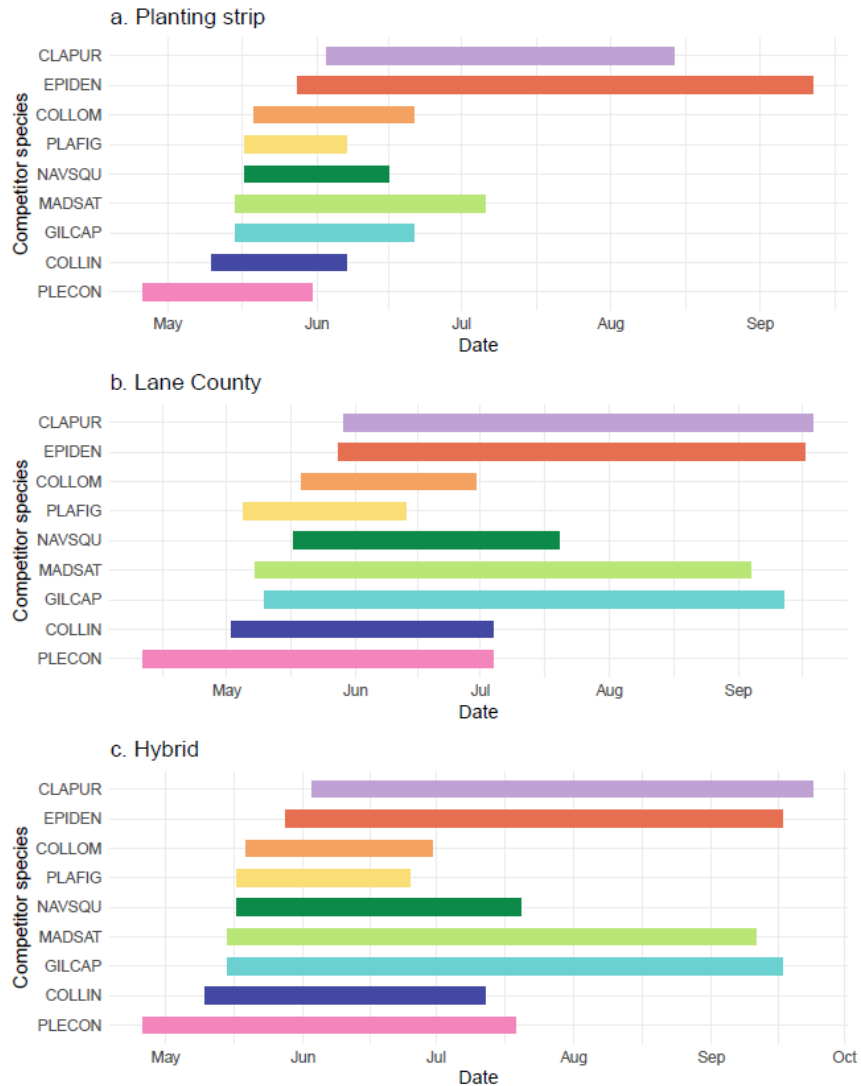
Figure 14: Comparison of study species' first flower dates, last flower dates, and flowering lengths using different data sources

Species are arranged along the y-axis in order of earliest to latest first flower dates in the planting strip. Starts of lines represent first flower dates, ends of lines represent last flower dates, and lengths of lines represent the flowering lengths. All data is sourced from iNaturalist during the 2023 growing season using different geographic bounds to filter observations of the study species. Graph (a) uses observations from the planting strip. Graph (b) uses observations from Lane County, OR. Graph (c) uses observations from the planting strip for its first flower dates, observations from Lane County for its flowering length, and the Lane County flowering length to estimate its last flower dates.

Discussion

Despite the fact that biodiversity loss, habitat alteration, and climatic change are occurring at an unprecedented global scale and altering the composition and diversity of plant communities, we know surprisingly little about the relationship between plant phenology, species interactions, and community dynamics. In this study, we examined the relationship between competitive neighborhoods and the flowering phenology and fitness of annual native prairie plants. We found that of the three neighborhood characteristics studied (i.e., competitor density, species richness, and identity), species richness and identity were correlated with flowering times, density was related to fitness, and identity influenced the strength of competition between species, with differences being seemingly unrelated to phenological differences between species. With these results, we suggest that there is not a single predictor variable for how plants will respond to changes in their competitive environments and that the relationship between phenology and fitness is multifaceted and could influence coexistence in complex, nonintuitive ways. Further, we conducted our research along a local riverfront bike path, integrating principles of transitional ecology, designed experiments, and community science into our experiment in order to generate direct public engagement with ideas of phenology, species interactions, and environmental change. Overall, we underscore how ecological research and embedded experiments can be conducted in a way which allows them to concurrently educate and engage the community about topics such as biodiversity and suggest that this may play a key role in helping to further restoration and conservation objectives.

Flowering Times

We found that *C. purpurea'*s flowering times were correlated with competitor species richness (i.e., diversity) and identity but not density. *C. purpurea* exhibited earlier first and last

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flower dates and shorter flowering lengths with increasing competitor species richness (Fig. 7).

C. purpurea also showed some variation in its first flower dates, last flower dates, and flowering

lengths depending on the identity of the competitor species (Fig. 8). The variation in flowering

dates we observed could be related to the stress imposed by different competitive environments.

The higher species richness of a more diverse community could increase the likelihood of

functional trait redundancy and niche overlap occurring between species and therefore increase

the amount of competition present (Wagg et al., 2017). In response to these competitive

stressors, plants may experience physiological changes which alter their flowering times, thereby

reducing niche overlap between competing species and fostering complementary resource use

(Jensen et al., 2019). We did not find that first flower dates were related to plant fecundity (i.e.,

earlier first flower dates did not provide a fitness benefit); however, we suggest that earlier first

flower dates may confer other advantages such as decreasing competition for pollinators and

allowing plants to avoid harsher, late-summer abiotic conditions during fruit maturation (Fig.

11a; Elzinga et al., 2007; Galloway and Burgess, 2012; Rafferty and Ives, 2011). In contrast to

these potential benefits of earlier first flower dates, we observed that earlier last flower dates and

shorter flowering lengths were negatively correlated with fecundity, thereby highlighting how

phenological shifts may not always be advantageous to plant species (Fig. 11b; Fig. 11c). Lastly,

given the observational nature of the study, it is difficult to exclude the possibility that another

unmeasured factor may have been responsible for contributing to plant stress and resulting in

earlier flowering phenology and decreased plant fecundity.

In response to changes in competitor diversity, we observed that *C. purpurea*'s peak

flowering dates were delayed 1.56 days per species lost (Fig. 7d). This contrasts with the

findings of Wolf et al., (2017) who examined the impact of biodiversity loss on flowering

phenology and found that for each species lost, peak flowering advanced by 0.6 days. We suggest that the differences in our results may be partially attributable to differences between our two study systems. Our research was conducted was conducted in a former riparian hardwood forest whereas Wolf et al., (2017) conducted their research in a serpentine grassland, and these two ecosystems may have different cues which impact flowering onset. Whereas our site tends to be temperature and moisture limited, serpentine grasslands are often nutrient limited; our site also had compact, clay soil resulting from its industrial land use history. Moreover, there has been a lack of research on how plant species diversity may influence phenology, and beyond study system differences contributing to our divergent results, we propose that the relationship between biodiversity and phenology is more variable than previously considered. Altering diversity impacts an ecosystem's abiotic and biotic character, making it difficult to disentangle which specific processes are driving phenological shifts. Changes to plant communities (e.g., diversity) can alter local scale abiotic processes such as soil surface temperature, nutrient availability, and water availability, and since flowering cues are related to the abiotic environment, these abiotic differences could in turn affect flowering times (Cleland et al., 2006; Elzinga et al., 2007; Tooke and Battey, 2010; Wolf et al., 2017). A further complicating factor is that plant density and diversity are often positively correlated; therefore, higher diversity environments could be resource constrained, consequently affecting the onset and length of flowering. Highlighting the variability in the relationship between phenology and biodiversity, Wolf et al. (2017) even had one annual species within their study which exhibited delayed rather than advanced flowering in response to reduced biodiversity. As such, future studies should continue to explore the relationship between diversity and phenology as well as how biotic interactions couple with abiotic factors to shape community dynamics. Namely, it would be

valuable to conduct this research in additional ecosystem types and with species of varied

functional traits as this would allow researchers to understand the degree to which shifts in

flowering phenology are system and species specific.

Fecundity

Our result that *C. purpurea*'s fecundity was correlated with competitor density but not

competitor species richness or identity was consistent with the large body of literature that finds

fecundity to be density dependent (Fig. 9; Beverton and Holt, 1957; Hart et al., 2018). To

expand, although we found that fecundity and flowering phenology are related to different

neighborhood characteristics (with fecundity being related to competitor density and flowering

phenology being related to competitor species richness and identity), we observed a correlation

between fecundity and flowering phenology, highlighting how these responses do not operate

independently of one another (Fig. 11). Among annual plants, flowering has a strong influence

on subsequent activities of the vegetative body, with flower initiation decreasing the rate of

biomass production, inducing leaf senescence, and ultimately causing "self-destruction" once

fruits contain mature seeds (Hirose et al., 2005). Altering the flowering phenology of an annual

plant species, Shitaka and Hirose (1998) observed that there is an optimal time for flowering in

order to maximize reproductive yield (i.e., fitness) which is related to the proportion of growth

dedicated to vegetative versus reproductive bodies. They found that earlier flowering reduced the

length of the growth period, contributing to smaller vegetative body size, increased reproductive

growth rates, and shortened reproductive periods (Hirose et al., 2005; Shitaka and Hirose, 1998).

On the other hand, later flowering extended the length of the growth period, leading to larger

vegetative body size, reduced rates of reproductive growth, and later senescence (Hirose et al.,

2005; Shitaka and Hirose, 1998). Finally, we wish to exercise caution in generalizing about the

relationship between flowering phenology, fecundity, and biotic interactions. Abiotic factors also influence both of these response variables, and the correlation we witnessed could be due to environmental variability alone (e.g., as a result of microsite differences).

We observed that average fecundity values did not vary by competitor species, yet we do not believe this result reflects the full picture of how competitor identity influences plant fitness (Fig. 10). We did not control competitor density within our experiment, and this may have caused our mean fecundity values (subdivided by competitor identity) to not appear statistically different due to high variability in competitor density between our different competitive neighborhoods. Nonetheless, we observed some significant differences in our pairwise contrasts of the strength of competition (i.e., alpha values) based on competitor identity (Table S1, supplement). Since the strength of competition expresses the rate of fecundity decline as competitor density increases, the presence of significant pairwise contrasts suggests that competitor identity did in fact impact *C. purpurea*'s fecundity. Moreover, we expect that if we had a larger sample size, we would have had smaller credible intervals surrounding our alphas and yielded more significant results.

Strength of Competition

Although the strength of competition experienced by *C. purpurea* was related to competitor identity, we did not find a significant relationship between the strength of competition and phenological differences between our study species (Fig. 13; Table S2, supplement). In contrast to our findings, Alexander and Levine (2019) demonstrated that phenological differences impact the strength of competition between species, observing that native California annuals experienced stronger competitive effects from earlier flowering invasive competitor species than from later flowering species. We intended for *C. purpurea* to have intermediate

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phenology relative to its competitor species. However, all of our study species ended up having earlier first flower dates than *C. purpurea*, ultimately preventing us from studying how earlier, same, and later phenology within species pairings impacts competitive dynamics. Another factor influencing our results was that our regressions for the strength of competition versus phenological differences only utilized one data point to represent each competitor species (for a total of eight points being used within the model), and this limited dataset may have obscured any salient results.

Comparing the strength of competition experienced by *C. purpurea* against intra- and interspecific competitors, we found that *C. purpurea* experienced weaker intraspecific than interspecific competition within all of our species pairings (Fig. 12). This result is interesting as within coexisting communities, intraspecific competition is expected to be stronger than interspecific competition given the high degree of niche overlap and limited complementary resource use present between intraspecific competitors (Adler et al., 2018; Chesson, 2000). Additionally, strong intraspecific competition is thought to promote coexistence by limiting the growth rates of a particular species at high frequencies whereas strong interspecific competition is thought to limit coexistence as it can lead to competitive exclusion (Chesson, 2000). Given that we did not collect fecundity data for *C. purpurea*'s competitors, we were unable to calculate niche and fitness differences between our study species and empirically determine the outcome of competition. Nonetheless, we suggest that the lack of strong intraspecific competition experienced by *C. purpurea* could potentially limit coexistence within our system.

Public Engagement

In addition to its aim of generating empirical ecological data, our experiment was designed with the intention of engaging the public. In order to achieve this goal, we integrated

principles of landscape design into the planting experiment and encouraged the public to participate in data collection using the mobile application iNaturalist. We positioned signage adjacent to the bike path with QR codes to make accessing iNaturalist facile, yet we did not receive many observations from individuals who were not associated with our lab. Since community science initiatives tend to be more successful when data collectors are recruited and trained for a specific project, we propose that by enlisting specific community groups and University of Oregon classes as volunteer data collectors, we could increase public participation in our data collection in subsequent years of the project (Bonney et al., 2009).

Although participation in data collection was limited, we were nonetheless excited by the informal public engagement we witnessed at the riverfront experiment. This included a tendency of individuals using the South Bank Path to stop by the planting strip, look at the species, and initiate conversations with our researchers, highlighting their curiosity about our research and the scientific process. These conversations also included expressions of gratitude for the reintroduction of native species and satisfaction with the planting design, including its arrangement in order of flowering time. We also noticed that individuals utilizing the bike path tended not to walk over and engage with the planting circle as much as the planting strip. This may have been related to the fact that we never mulched a pathway between the two planting areas. Likewise, the growth of large blackberry and sweet pea plants obscured the view of the planting circle from the strip and pathway, and it is possible that people did not know that the planting circle was there. Mowing the region between the two planting areas more frequently could help to increase the visibility of the circle and increase visitation, and adding a bench offset from the pathway could also increase the usability of the space and encourage individuals who may not normally stop by the experiment to do so (Kay et al., 2019). We could also work on

improving how we promote our research (e.g., framing the planting circle as a "phenology garden") and enhancing the project's overall aesthetics. Successful transitional ecology projects tend to be interdisciplinary, and we believe collaborations with other University of Oregon research groups, such as the Fuller Initiative for Productive Landscapes and The Land Lab, could be uplifted in order to extend the reach of our research (Kay et al., 2019). Lastly, within our experiment, we did not have any infrastructure in place to quantify public engagement or assess how the project was impacting people's perceptions of phenology, species interactions, biodiversity, or environmental change and believe it could be interesting to incorporate an online survey (e.g., accessed via QR codes on the signage adjacent to our experiment) or interview component in the future.

Caveats

Beyond improving community engagement with our research and enhancing the aesthetics of our experiment, we think it would be valuable to modify our experimental design and data collection so that our project is able to answer coexistence questions. We also believe it could be useful to quantify interannual environmental variation within our system as the relationship between phenological differences and species interactions is influenced by environmental context (Wolkovich and Donahue, 2021). Another caveat of our experimental design was that we chose to reseed our planting area two months after the initial seeding took place due to low germination success, potentially creating differences in germination timing among our focal plants. Further, we seeded the planting strip and circle at different dates; however, given that the majority of our focal plants were from the planting circle, we do not think this would have had a notable influence on our results. Our sample size was also relatively small, and ideally, we would have marked a greater number of focal plants and represented a

wider range of competitive environments. Lastly, in early August following an unseasonal bout of precipitation, a small number of focal plants which had already reached their last flower dates experienced new vegetative growth, budding, and resurgent flowering. Given that this flowering episode seemed to be independent from the first episode and that we had already performed fruit counts for the focal plants, we opted not to use these isolated last flower dates in our analyses.

Conclusion

Among the many impacts of global environmental and climatic change, biodiversity is being lost at an unprecedented rate and plant species are experiencing phenological shifts which are reshaping the temporal composition of ecological communities (CaraDonna et al., 2014). Moreover, these changes to community diversity and phenology are having cascading effects, influencing not only plant population dynamics but also broader relationships such as those between plants and pollinators and humans and natural icons (Breckenheimer et al., 2020; Hille Ris Lambers et al., 2021; Kharouba et al., 2018). Ecological and human communities are inextricably linked, and environmental changes which influence the health, longevity, and stability of our ecosystems inherently influence that of our cities and societies. Drawing on this intersection, it is critical that we find ways to transform our current urban and socioecological systems, prioritize conservation initiatives, and address the impact of anthropogenic activities on the environment. The Riverfront and Parks Project,, as well as transitional ecology, designed experiments, and community science initiatives more broadly, mark an important first step towards catalyzing these shifts. By bringing us closer to biological phenomena, educating the public about conservation science, encouraging reimagined human-environment relationships, and generating a shared drive to protect biodiversity, they are key implements for ensuring our collective wellbeing and future.
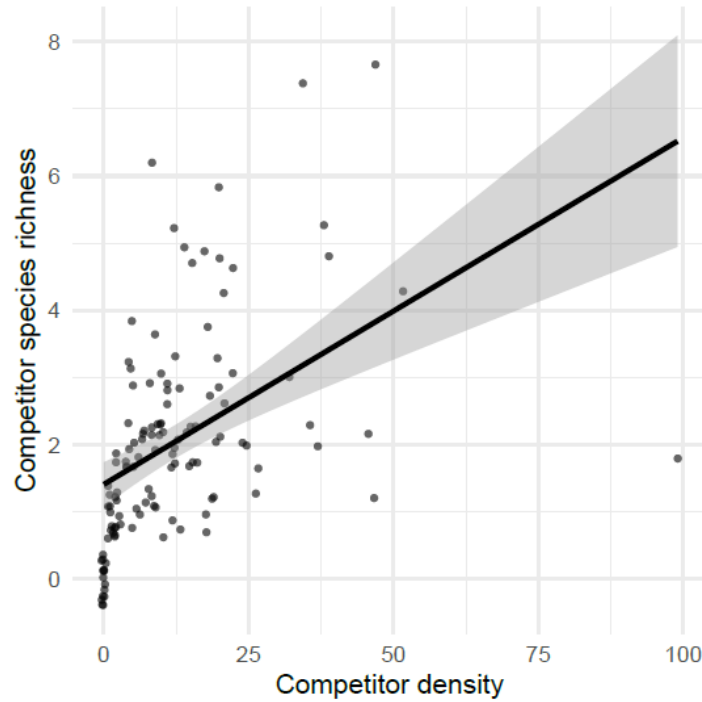
Supplements

Figure S1: Competitor species richness versus competitor density

Scatter plot fit with a linear regression. Points represent unique focal plants. Shaded area represents 95% confidence interval surrounding the mean of the regression. Competitor species richness and competitor density are moderately positively correlated ($r_{122} = 0.460, p < 0.05$).
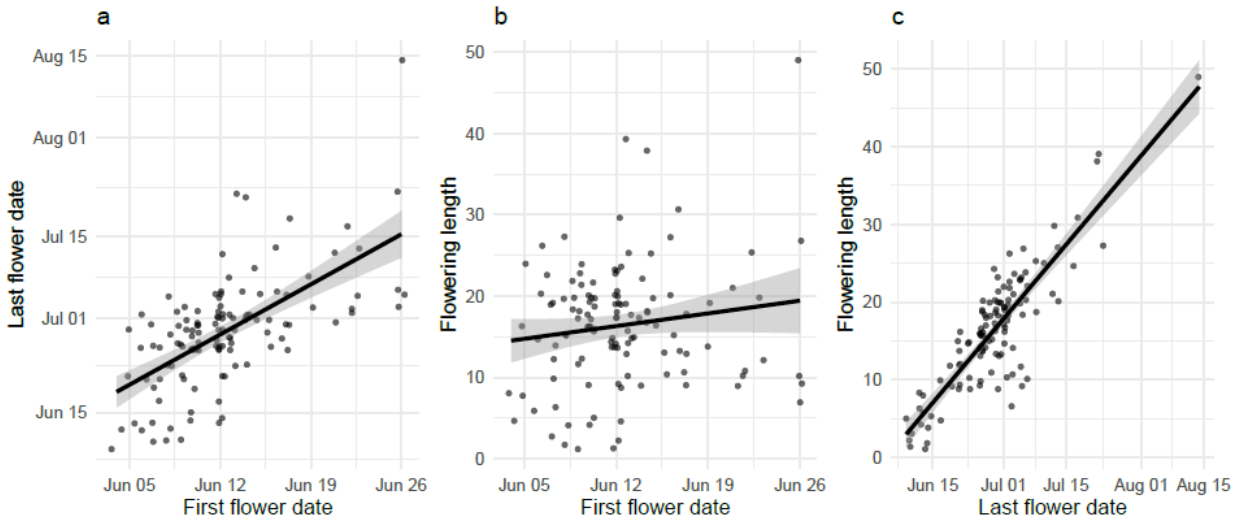
Figure S2: Relationships between different flowering metrics of *C. purpurea*

Scatter plots fit with linear regressions. Points represent unique focal plants. Shaded areas represent 95% confidence intervals surrounding the means of the regressions. *C. purpurea*'s first flower dates and last flower dates were strongly positively correlated ($r_{119} = 0.628, p < 0.05$). There was no significant correlation between *C. purpurea*'s first flower dates and flowering length ($r_{119} = 0.146, p > 0.05$). *C. purpurea*'s last flower dates and flowering length were strongly positively correlated ($r_{119} = 0.861, p < 0.05$).

Competitor species pairing	Probability of statistical difference
COLLIN - CLAPUR	0.86
COLLOM - CLAPUR	0.66
COLLOM - COLLIN	0.66
EPIDEN - CLAPUR	0.92
EPIDEN - COLLIN	0.71
EPIDEN - COLLOM	0.51
GILCAP - CLAPUR	0.6
GILCAP - COLLIN	0.52
GILCAP - COLLOM	0.55
GILCAP - EPIDEN	0.54
MADSAT - CLAPUR	0.73
MADSAT - COLLIN	0.58
MADSAT - COLLOM	0.57
MADSAT - EPIDEN	0.58
MADSAT - GILCAP	0.51
NAVSQU - CLAPUR	0.94
NAVSQU - COLLIN	0.65
NAVSQU - COLLOM	0.57

NAVSQU - EPIDEN	0.62
NAVSQU - GILCAP	0.52
NAVSQU - MADSAT	0.54
PLECON - CLAPUR	0.56
PLECON - COLLIN	0.66
PLECON - COLLOM	0.54
PLECON - EPIDEN	0.56
PLECON - GILCAP	0.56
PLECON - MADSAT	0.6
PLECON - NAVSQU	0.58

Table S1: Results of pairwise contrasts between alpha values of different competitor species

Comparisons highlight whether the strength of competition *C. purpurea* experienced from a particular competitor species were significantly different. EPIDEN-CLAPUR and NAVSQU-CLAPUR pairings are significantly different at a probability > 90%.

	Difference in first flower dates	Difference in last flower dates	Flowering length	Flowering overlap	Difference in peak flowering date
p-value	0.24	0.51	0.73	0.9	0.96
F-statistic	1.71	0.48	0.13	0.02	2.59×10^{-3}
df (with and between groups)	1, 6	1, 6	1, 6	1, 5	1, 5

Table S2: Results of linear regressions for strength of competition (alphas) experienced by *C. purpurea* versus metrics of phenological separation between *C. purpurea* and other study species

There were no significant relationships between alpha values and phenological differences ($p < 0.05$).

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