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RESEARCH ARTICLE

Germination phenology alters species coexistence outcomes

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Abstract

1. Species-specific phenological responses to changing climate are reshuffling the timing of species interactions, however we do not fully understand the consequences of these changes for species' population dynamics and community composition.
2. In this study, we experimentally manipulated the timing of germination for five annual plant species from southern California and used pairwise competition experiments and coexistence theory to quantify how phenological shifts may impact species interactions and coexistence.
3. We found that phenological shifts may help promote coexistence when they confer an advantage for competitively inferior species, but in other cases promote dominance by competitively superior species. Earlier germination generally increased species' performance relative to competitors, but the relative changes in intra-and inter-specific interactions caused more complex effects on niche and fitness differences. Phenological differences tended to reduce stabilising niche differences for many species pairs and reduced overall coexistence probabilities.
4. *Synthesis*. While phenological differences among species have typically been considered a form of niche partitioning, it seems increasingly likely that phenological offsets could destabilise species coexistence. The net effects of changing phenology on species coexistence will depend on the complex combinations of effects on intra- and inter-specific interactions, which remain challenging to predict.

KEYWORDS
annual plants, competition, germination, phenology, species coexistence

1 | INTRODUCTION

Changes in phenology have been one of the clearest biological indicators of a changing climate, with spring events (such as leaf-out) generally getting earlier and fall events getting later, yielding longer average growing seasons. However, one of the most consistent findings of community-wide phenology studies is the significant variability among species in their phenologies and their phenological sensitivities to climate. This variability is interesting because it suggests the potential 'reshuffling' of species' relative phenologies—that is changes in the relative phenology of different species—as climate conditions change. However, we still know very little about how the relative timing of phenological events among species impact species interactions, population dynamics and community composition. Most studies of phenological impacts on species interactions have investigated trophic 'mismatches', such as the potential offset in timing between predators and prey (Renner & Zohner, 2018; Visser & Gienapp, 2019). There have been fewer studies of how variation

in phenological offsets within a trophic level affect species interactions and the fitness of competing species (Blackford et al., 2020; Carter & Rudolf, 2019).

There are a variety of ways that shifting phenologies may impact species interactions within a trophic level. Generally, the timing of activity could affect access to resources and the ability of species to compete for limited resources (Rudolf, 2019; Rudolf & McCrory, 2018; Yang & Rudolf, 2010). However, the specifics of how phenological timing affects interactions may vary among the different establishment, growth and reproductive phenophases. In many organisms, establishment or emergence is a critical early phenophase that sets life in motion in a given year and may structure species interactions. Priority effects are one well-known version of this, in which the arrival times of species have important consequences for which species can outcompete another (Fukami et al., 2016; Grainger et al., 2019). However, being first or early may not always be an advantage, if it comes with abiotic or resource trade-offs, such as susceptibility to suboptimal climate conditions or access to resources, mutualists and so forth. Thus, even though flowering phenology is the most commonly studied phenophase of plants, understanding the consequences of germination phenology of plants may be critical for predicting coexistence outcomes.

Modern coexistence theory (MCT) has emerged as a useful framework for exploring how species interactions may influence population dynamics and persistence (Chesson, 2000, 2018). MCT suggests that species differences, including phenological differences, could affect species interactions in nonintuitive ways. For instance, phenological differences among species have typically been thought to represent temporal niche partitioning, implying for example that introduced species with different phenologies may be more likely to succeed (Wolkovich & Cleland, 2011). However, MCT describes how species' population dynamics and coexistence of species depends on the relative strength of stabilising niche differences and destabilising fitness differences, and any species dissimilarities, including phenological differences, could affect both niche and fitness differences (Mayfield & Levine, 2010). Niche and fitness differences are functions of intra- and inter-specific interactions and species' relative performance in the absence of competition. Thus, to evaluate how phenological differences affect coexistence, the relationships between phenological differences and competition need to be quantified (Rudolf, 2019), but there have been few empirical studies thus far.

Perhaps the first empirical study of phenological effects on coexistence used natural differences among species to show that later-growing grass and forb species in California had greater fitness advantages over earlier-season species, and these fitness advantages surpassed the greater niche differences (Godoy & Levine, 2014). In contrast, a recent study utilising the phenological local adaptation of a globally distributed introduced species showed that earlier-flowering genotypes were more likely to outcompete native species (Alexander & Levine, 2019). However, because phenology is likely correlated with other life history traits, it is difficult to isolate the effect of phenology per se on species interactions, so experimentally altering species' relative phenology may help isolate the effects of phenology per se. For example, experimental manipulations of hatching phenologies of two amphibian species (Carter & Rudolf, 2019) demonstrated the potential for phenology to provide enough of an advantage to inferior competitors to promote coexistence. In the only experimental manipulation of plant phenology to date, in order to quantify effects on coexistence, Blackford et al. (2020) used a greenhouse experiment to show that earlier relative germination timing of two congeneric grass species (*Vulpia* spp.) could determine which species was competitively dominant, and through simulations showed that variation in germination timing across years could promote coexistence. These studies together suggest the promise of experimental approaches for teasing apart the specific effects of phenological differences on species interactions and therefore coexistence.

Here, we conducted a manipulative experiment in a common garden to test whether germination phenology of five plant species can have a strong enough effect on species interactions to influence species coexistence. To affect coexistence, phenological differences would need to have relatively greater impacts on either stabilising niche or destabilising fitness differences. Based on prior research, we hypothesised that (i) shifted relative germination timing may lead to competitive exclusion of otherwise coexisting species, and (ii) earlier germination could provide an advantage to inferior competitors to allow coexistence with otherwise competitively dominant species. We further hypothesised that all else being equal, phenological differences should increase niche differences by reducing inter-specific resource overlap and thereby promote species coexistence. With a study design allowing calculation of relative phenological effects on species interactions and coexistence outcomes for five species (10 unique pairs of competing species), this study offers a unique look at the patterns of how phenological offsets may affect coexistence within communities.

2 | MATERIALS AND METHODS

2.1 | Study system

Southern California exhibits significant annual and spatial climate variability that can influence phenology of plant species, and different species are adapted to germinating under different temperature and precipitation conditions. We studied five species of annual forbs and grasses common within the coastal sage scrub (CSS) community in southern California, a semi-arid shrub-dominated community that has been invaded extensively by exotic grasses. CSS is characterised by drought-deciduous shrubs such as *Encelia farinosa*, *Artemisia californica and Eriogonum fasiculatum*, and a diverse understory of herbaceous annuals and non-native grasses (Cleland et al., 2016). CSS is one of the most endangered vegetation types in North America due to habitat loss and fragmentation, as well as the widespread invasion by Mediterranean annual grasses. They appear to be dominant competitors against native annual forbs and shrubs and may alter both

above and below-ground resource availability for native species. It is an excellent system to study coexistence questions because of the predominately annual life histories, and the need to better understand the processes leading to progressive dominance by non-native species.

Both the amount of rain and the timing of first rains have strong impacts on these ecosystems and interactions within them. Late fall/winter rain events of approximately 0.5 inches (12.7 mm) instigate germination of native species, whereas invasive species are able to germinate earlier, with less rain and warmer temperatures. These differences may in part be driving the fluctuations in community composition in response to climate. There is also significant spatial variability in the region, with precipitation and soil water holding capacity depending strongly on topography, soil type and texture.

We focused on five study species: two non-native grasses, *Bromus diandrus* (BRDI) and *Bromus rubens* (BRRU), and three native forbs, *Lasthenia gracilis* (LAGR), *Nemophila menziesii* (NEME) and *Plantago erecta* (PLER). The native species are common members of the herbaceous community, and the two non-native grasses are both species that are well-known to become abundant at the expense of local native species diversity and abundance. The non-native grasses tend to be able to germinate more quickly with the first rains (Cleland et al., 2016; Cox & Allen, 2007; Goldstein & Suding, 2014).

2.2 | Experimental design

We conducted a common garden competition experiment at the University of California, Riverside's Agricultural Operations facilities, in Riverside, CA (approximately 300 m elev.; 33°58′16″ N, 117°20′17″ W) in spring 2020. The experiment was designed to calculate pairwise interaction coefficients (including intra-specific interactions) for all combinations of the five species, yielding 10 unique species pairs. Each study species was sown into three plots (1 m^2) at low, medium and high densities, to form a competitive density gradient for each species. Into each plot, we sowed focal individuals of each species, establishing all pairwise combinations of competitive interactions. The relative timing of germination between the focal species and competitors was manipulated by offsetting the introduction of seeds by 3 weeks in both directions. These species of annual plants all have fast germination rates when they are exposed to enough water (within 3–4 days), as they are adapted to germinate with the beginning of seasonal rains during the cool wet winters of southern California. Thus, we watered them after sowing seeds, causing 3-week differences in germination dates. In 'focal first' plots, the focal seeds were sown and then 3 weeks later the competitor species were sown (Figure S1). Similarly, 'background first' plots were established by waiting 3 weeks after sowing competitor species to introduce the focal species. Finally, a 'same time' treatment was established by sowing focal plants and competitors at the same time, mid-way between the first and last dates. Each species was also sown into plots without competitors to help estimate the performance of each species in the absence of competition. This design resulted in a total of 2850 focal individuals in 114 plots (5 species × 3 background densities × 2 replicates × 3 phenology treatments + 24 'no competition' plots). The garden was irrigated and weeded regularly to maintain suitable growing conditions and as 'weed-free' pairwise competition plots as possible.

Reproductive output of focal individuals was measured at the end of the growing season, along with the number and identity of competitors within a 20 cm diameter neighbourhood. As seed counts were logistically impossible, we counted flowers of all focals and obtained estimates of number of seeds per flower for each species. Prior to counting total of flowers, 10 flowers per species had seeds extracted and counted to determine an average seed count per flower. These quantities were used to convert flower counts to seed estimates for each focal plant. Seed germination rates were estimated from a combination of buried seeds in nylon mesh bags, and germination trials in a greenhouse. We tried a variety of seed survival rates to mirror the typical pattern that the native species in this ecosystem have longer-lived seed banks than the non-native grasses, however all results were quantitatively and qualitatively robust to very different seed survival values.

2.3 | Analyses

Our analyses consisted of the following three general steps, each described further below: (i) we used the seed production and competition data to estimate pairwise interaction coefficients (α) and intrinsic growth rates in the absence of competition (λ) as a function of the relative phenology treatment; (ii) we used these parameters to fit population models for each species and estimate their pairwise invasion growth rates (IGR), a measure of mutual invasibility and species' ability to coexist; (iii) for each species pair and each phenology treatment we used the fitted population models to calculate niche and fitness differences to better understand the mechanisms of how phenology affects species interactions and thus coexistence (Spaak et al., 2021; Spaak & De Laender, 2020).

2.3.1 | Estimating interaction coefficients

As is common for annual species, the effects of competition (intra- and inter-specific) were estimated as their influence on individual reproductive output, F_i, via a nonlinear Ricker model:

$$F_i = \lambda_i \exp^{(\alpha_{i,j} N_j + \alpha_{i,i} N_i)}, \quad (1)$$

where the data are as follows: F_i is the number of seeds of a focal individual i, N_i is the number of individuals of species i, 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 inter-specific competition, respectively, on the seed production of a focal individual. The response variables in these models were estimated seed production per plant, and alpha and lambda parameters were allowed to vary among phenology treatments. 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 did not constrain the alphas to be less than zero (denoting competition), allowing the data to determine whether interactions were competitive or facilitative. A Bayesian measure of *R*-squared was calculated for each model according to Gelman et al. (2019). To further test model performance, a full model including species interactions was compared to a null model without species interactions using the difference in expected log pointwise predictive density (elpd) calculated using the loo package (Vehtari et al., 2017, 2024).

2.3.2 | Population models, invasion growth rates and coexistence outcomes

To examine the effects of germination phenology on coexistence, we parameterised an annual plant population model for each species and then simulated their invasion growth rate (IGR) when facing each pairwise competitor. This IGR is one way to assess the ability of species to coexist. Specifically, coexistence is predicted if each species can increase from low numbers when competing with an equilibrium number of the other species, whereas an inability to increase from rarity suggests competitive exclusion. The posterior distributions of alpha and lambda parameters were used to simulate population models and calculate subsequent measures of competition and coexistence, thereby propagating uncertainty.

The population model for these annual plant species describes how seed numbers change year to year due to both survival in the seed bank and new production of seeds by adult plants, as follows:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1-g_i)s_i + g_i F_i, \tag{2}$$

where g_i is the germination rate of species i, s_i is its survival rate of seeds in the soil, and F_i is the density-dependent fecundity term described above. To simulate IGR, we simulated the introduction of one individual of a species in the presence of an equilibrium number of competitors. We calculated the probability of coexistence for each species pair, in each treatment, by propagating the uncertainty in the posterior distributions of alphas and lambdas. For each draw of the posterior, we calculated the coexistence outcome as a 1 if both species had positive GRWR and as a 0 if one or more species had negative GRWR. And therefore, probabilities of coexistence were estimated as the proportion of outcomes that yielded coexistence.

2.3.3 | Niche and fitness differences

To further understand the mechanisms by which shifting germination phenology affected coexistence, we also used the estimated parameters and population models to calculate the niche and fitness differences between each pair of species, which together determine coexistence outcomes. We used the measures of niche and fitness differences described by Spaak and De Laender (2020) that allows there to be facilitative inter-specific interactions. In this approach, niche differences (ND) and fitness differences (FD) are calculated as properties of species, not communities. Here, we were explicitly interested in how these species-level measures of coexistence may change as a function of that species' relative germination timing, so we calculated ND and FD for each species, competing against each of the other species, and under each phenology treatment. In this framework, ND are defined as

$$\mathrm{ND}_i = \frac{r_i - \eta_i}{\mu_i - \eta_i}, \tag{3}$$

where r_i is species i's invasion growth rate, η_i is its intrinsic growth rate, and μ_i is the 'no-niche' growth rate. The no-niche growth rate, estimated via simulations, is the growth rate of a species competing against the density of conspecific individuals that would use equivalent resources to an equilibrium density of the competitor species (Spaak & De Laender, 2020). In pairwise communities (2 species), the ND are the same for the two species in the absence of facilitation. Like other definitions of niche differences, ND reflects the relative strength of intra-and inter-specific competition, with greater coexistence stabilisation as intra-specific competition increases relative to inter-specific competition.

Fitness differences were calculated as

$$\mathrm{FD}_i = 1 - \frac{\eta_i}{\mu_i - \eta_i}, \tag{4}$$

where again, η_i is species' i's intrinsic growth rate, and μ_i is the 'no-niche' growth rate (Spaak et al., 2021). Fitness differences measure differences in competitive ability between the focal species and its competitors, and is determined by a combination of their inherent ability to grow in the absence of competition and their sensitivity to competition. A highly competitive species will have a high intrinsic growth rate, low sensitivity to competition or a combination of both (Godoy & Levine, 2014; Hart et al., 2018). The relative balance of stabilising niche differences between species and the de-stabilising, inherent fitness differences between species together determine coexistence. To calculate ND and FD we used the python code provided by Spaak on github (https://github.com/juergspaak/NFD_definitions).

3 | RESULTS

The three-week delayed seed sowing treatment achieved the desired effect of experimentally lagged germination timings. Although these species all have relatively fast germination rates when exposed to water (within 3–4 days), they have different early growth rates, which are likely to create competitive asymmetries within the first few weeks post-germination (Figure S2). In particular, the two non-native grasses, BRDI and BRRU, had faster growth rates over the first 3 weeks than the native forbs, LAGR, PLER and NEME.

Species generally had higher seed production when they arrived first (Figure 1; Figure S3), and in all cases, species performed worst

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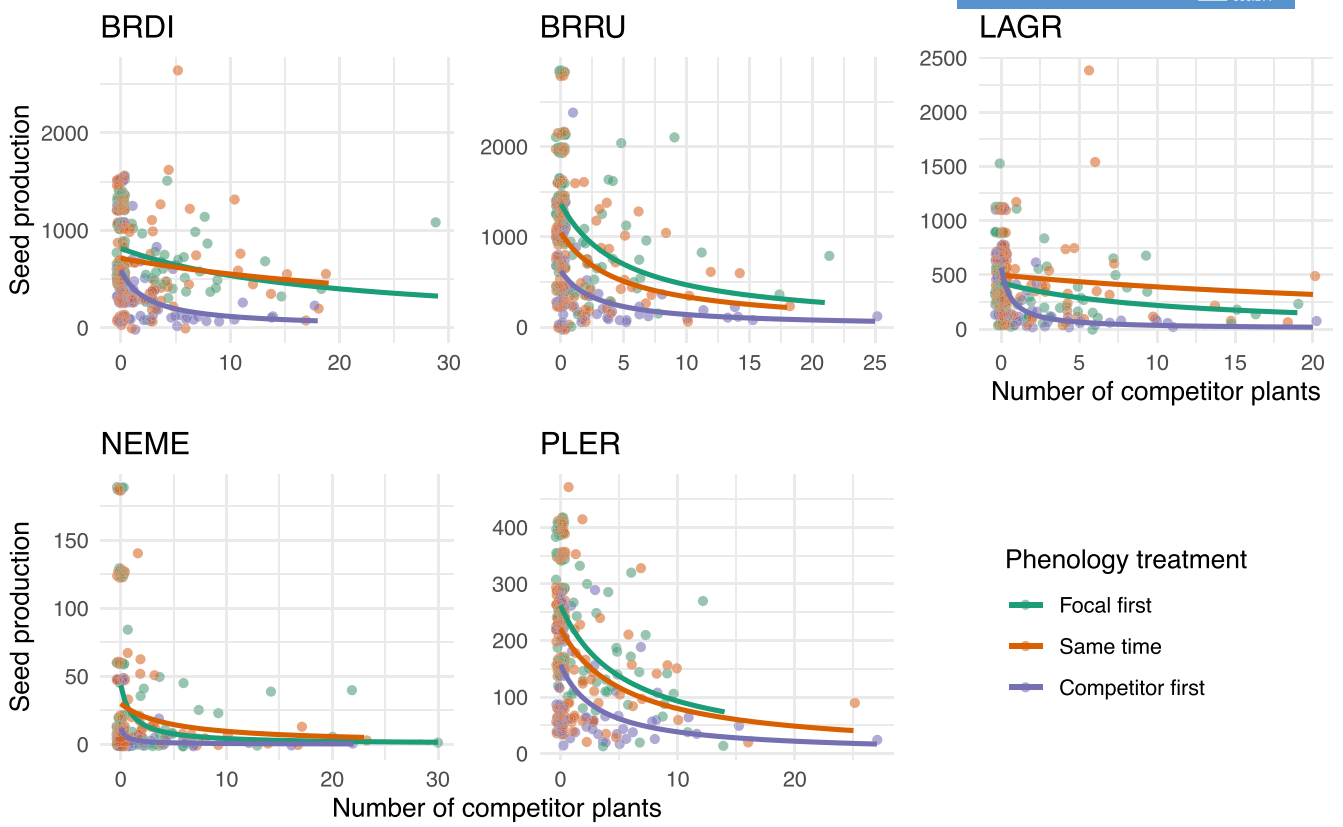

FIGURE 1 Raw relationships between species' seed production and the number of competitors in the three treatments. For each species, 'focal_first' is the treatment in which that species' seeds were sown 3 weeks prior to the background competitor species, 'background_first' is the reverse, and in the 'same_time' treatment, the focal and background seeds were sown at the same time. Analyses were performed on pairwise species interactions; these curves just show best-fit least-squares, nonlinear Beverton–Holt functions with all the background competitors pooled together for each focal species. BRDI, *Bromus diandrus*; BRRU, *Bromus rubens*; LAGR, *Lasthenia gracilis*; NEME, *Nemophila menziesii*; PLER, *Plantago erecta*.

when their seeds arrived second ('background first'). For four of the species (BRDI, BRRU, LAGR and PLER), competition became stronger with delayed germination timing relative to all of their competitors (alphas became more negative; Figure 2). *Nemophila menzezii* (NEME), the weakest overall competitor, also experienced stronger competitive effects when it germinated later than all its competitors except for when competing against the non-native grass, *Bromus diandrus* (Figure 2). Most competition coefficients were positive, indicating competition in the Ricker model (52 out of 60 pair-treatments estimates). The model with interactions was supported via model selection (Vehtari et al., 2017) over the null model without species interactions (elpd_diff = −81.4; se_diff = 7.7). Nonetheless, models estimating alpha and lambda values had R^2 values ranging from 0.07 to 0.2, reinforcing the importance of propagating parameter uncertainty.

These effects of different germination phenology on species interactions yielded altered coexistence outcomes (Figure 3). There were two categories of how the probability of coexistence changed: (i) in five out of ten cases the probability of coexistence was largest when species germinated at the same time; (ii) in the other five cases, coexistence was more probable when the inferior competitor germinated first. (Figure 3). Overall, pairwise probabilities of coexistence were low, ranging from close to zero to approximately 55%. Finally, changes in relative germination timing often caused a reversal in predicted outcome from competitive dominance by one species to that of the other; and in the case of clearly inferior competitors (e.g. NEME), earlier germination relative to the competitors moved the outcome closer to coexistence but still was not enough to avoid competitive dominance.

Both niche differences and fitness differences between species were also significantly affected by relative germination timing (Figure 4). Using the methods of Spaak and De Laender (2020) and Spaak et al. (2021) niche differences are a species-specific value within a given community, so here we report 20 pairwise ND values. For a given pair of species i and j, $ND_i = ND_j$ under competitive circumstances, but not necessarily when there is inter-specific facilitation. In this study, niche differences peaked when species germinated at the same time in 15 of 20 pairwise comparisons (Figure 4). Moreover, relative germination timing often shifted niche differences between areas indicating positive frequency dependence ($ND < 0$) to areas of negative frequency-dependence ($0 < ND < 1$). In several cases, $ND > 1$ suggested positive interspecific interactions, corresponding to cases of positive α_{ij} values in the Ricker model.

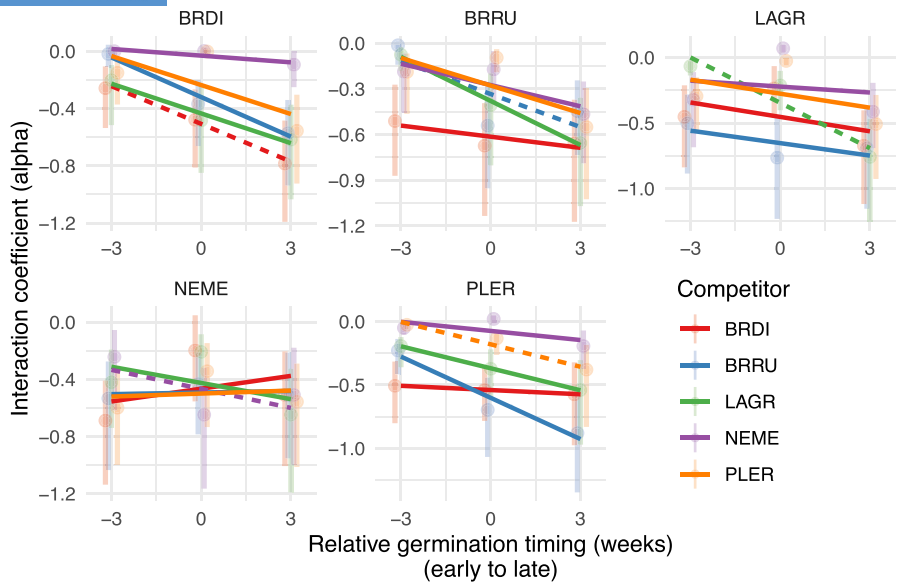

FIGURE 2 Estimated relationships between phenology treatment and pairwise competition coefficients (alpha). Generally, species experienced weaker competition when they germinated earlier than the competitor (left side of graphs) compared to when they germinated later than the competitor (right), for both intra- (dashed lines) and inter-specific (solid lines) competition. There were some exceptions to this pattern, most notably for *Nemophila menzezii*, the weakest overall competitor. The vertical bars around points represent parameter uncertainty (central 50% of the posterior distributions). BRDI, *Bromus diandrus*; BRRU, *Bromus rubens*; LAGR, *Lasthenia gracilis*; NEME, *Nemophila menziesii*; PLER, *Plantago erecta*.

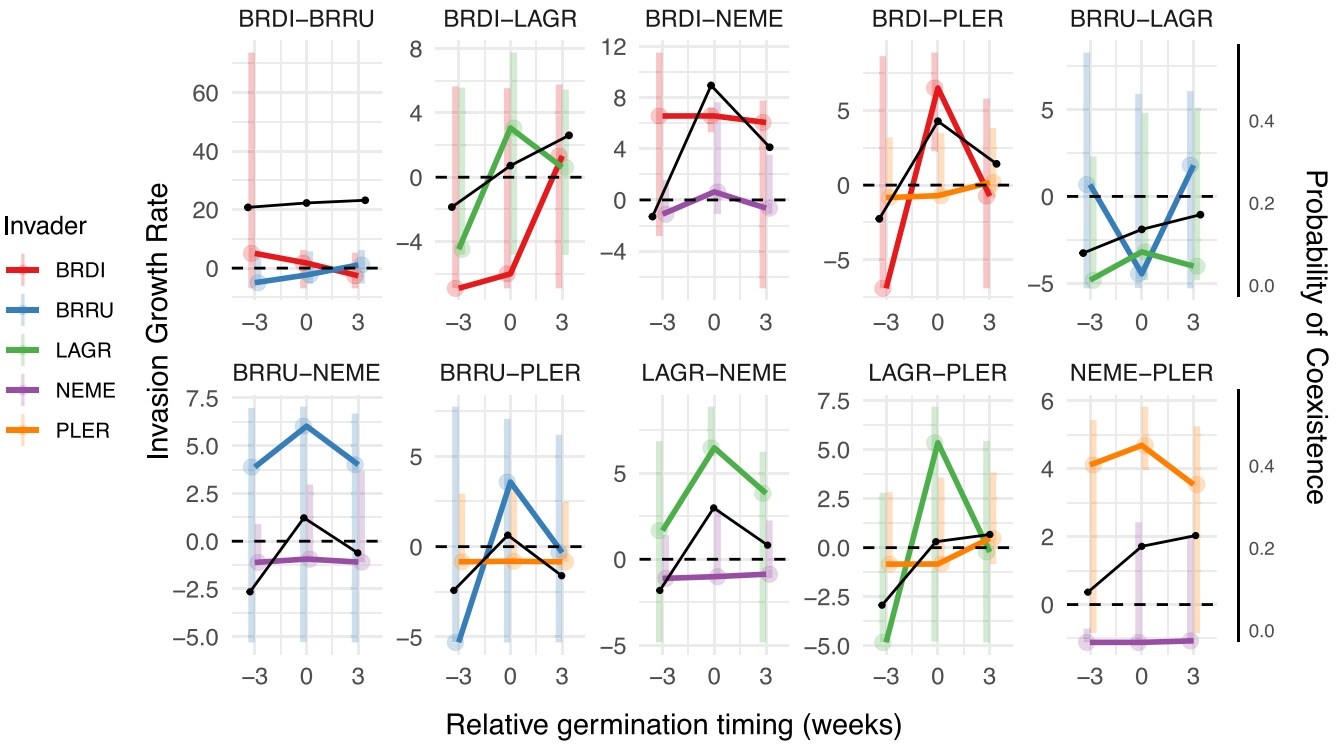

FIGURE 3 Invasion growth rates and resulting probabilities of coexistence of competing species pairs, as a function of relative germination timing. The *x*-axis shows relative germination time (in weeks) of the first species listed in the species pair (e.g. BRDI in left-most panel) relative to the second species (e.g. −3 weeks means that BRDI germinated 3 weeks before BRRU, 0 means they germinated at the same time and 3 means BRRU germinated 3 weeks earlier than BRDI). The vertical shaded bars show the 90% posterior probability distributions for each estimated growth rate. The probabilities of coexistence for each species pair (black lines) were calculated as the proportion of draws from posterior distributions in which both species had a predicted positive invasion growth rate. BRDI, *Bromus diandrus*; BRRU, *Bromus rubens*; LAGR, *Lasthenia gracilis*; NEME, *Nemophila menziesii*; PLER, *Plantago erecta*.

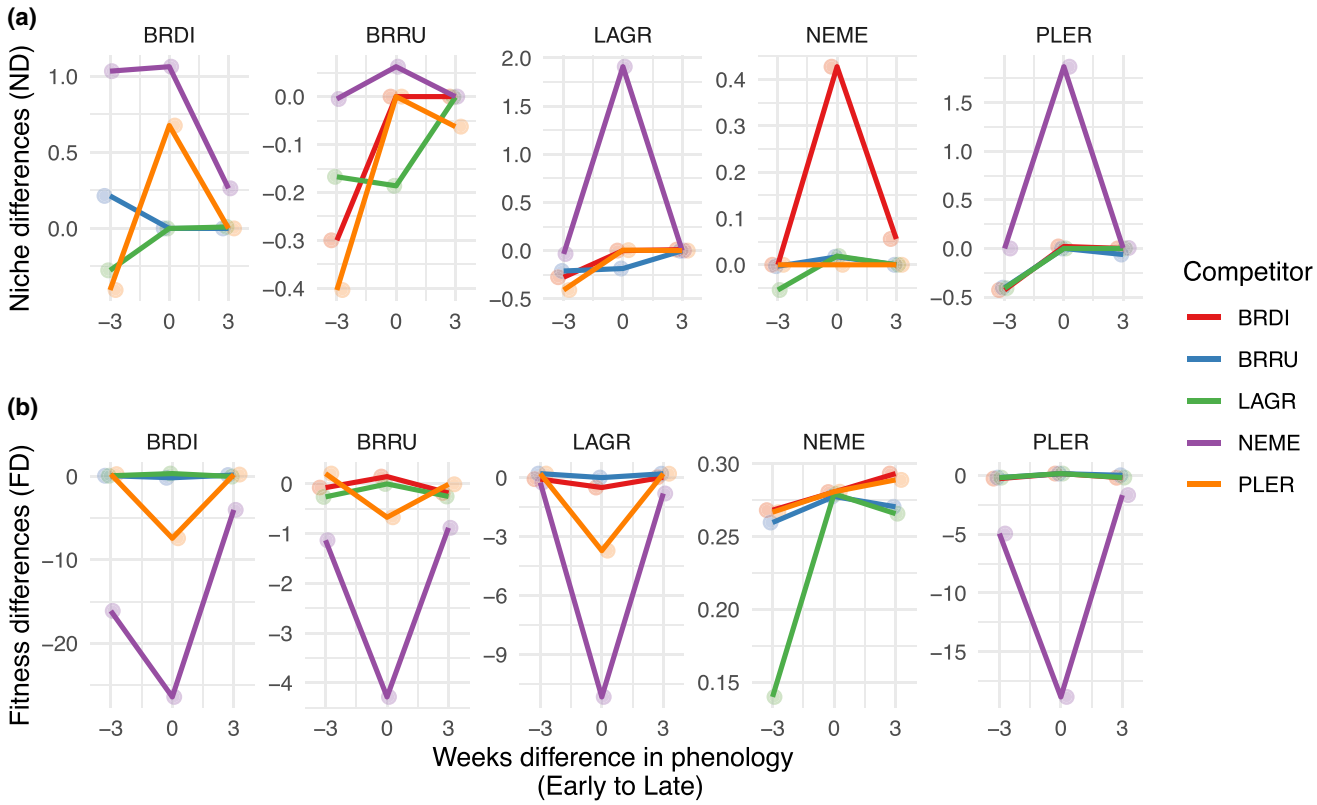

FIGURE 4 Effects of relative germination timing on niche differences (a) and fitness differences (b) for all pairwise species combinations. In each graph, the *x*-axis shows relative timing from the 'focal' species' perspective, with the focal species germinating 3 weeks early on the left and 3 weeks late on the right. For clarity, this version does not show uncertainty surrounding point estimates, but a version showing posterior uncertainty is in Supporting Information (Figure S6). BRDI, *Bromus diandrus*; BRRU, *Bromus rubens*; LAGR, *Lasthenia gracilis*; NEME, *Nemophila menziesii*; PLER, *Plantago erecta*.

Fitness differences between species also changed with relative germination timing, in some cases leading to decreased FD when species germinated at the same time (Figure 4). As a reminder, in the framework of Spaak et al. (2021), species with lower FD values are predicted to be competitively superior to the other species in the absence of niche differences. The shifts toward lower FDi values (relatively more competitive for species *i*) corresponded to cases in which there were either weaker inter-specific competition or even facilitation (correlation of α_{ij} with r_i in Figure S10).

4 | DISCUSSION

Despite widespread documentation of changing phenology as a result of climate change, we know surprisingly little about what these phenological shifts mean for population dynamics and community composition in ecological communities. Although the predominate hypothesis has been that phenological differences should represent niche differences that help promote coexistence (Wolkovich & Cleland, 2011), modern coexistence theory has highlighted how any trait differences among species, including phenology, may either promote coexistence via stabilising niche differences or lead to competitive exclusion through increased fitness differences (HilleRisLambers et al., 2012; Mayfield & Levine, 2010). Therefore, empirical studies are needed to test how differences among species impact both mechanisms. In this study, we experimentally show how differences in germination phenology can impact species' competitive interactions and coexistence outcomes via shifts in both niche and fitness differences. We specifically found that earlier germination timing by inferior competitors has the potential to offset their competitive inferiority, leading to increased probabilities of coexistence. Further, we show that counter to conventional wisdom, phenological differences in any direction decrease the probability of coexistence in half of the species pairs.

The key empirical challenge for linking phenological differences to coexistence outcomes is to quantify competition-phenology relationships; that is, how the strength of intra- and inter-specific competition changes with phenological differences (Rudolf, 2019). Our study provides a unique example of doing this for all the pairwise interactions between five species of plants. Twenty-two of the twenty-five competition coefficients (both intra- and inter-specific alphas) became more negative (stronger competition) with more delayed phenology relative to the competitor (Figure 2). Consequently, the 'winner' of competition often flipped depending on relative phenological timing, as seen in the changes in species' pairwise invasion growth rates (Figure 3). The increasing strength of competition as species germinate relatively later is consistent with the idea that early establishment in this ecosystem yields a competitive advantage

for soil water and nutrients, which is critical because of the relatively short winter/spring growing season. The exception to this pattern was *Nemophila menziesii* (NEME), the weakest competitor overall, for which earlier germination timing did not always decrease competition (Figure 2).

These effects of relative germination timing on the strength of competition scaled-up to create changes in invasion growth rates and the overall probability of coexistence (Figure 3). Two general patterns were discernable. First, the most common pattern among species-pairs was for the probability of coexistence to peak when the species germinated at the same time, and decrease with earlier germination by either species. Changes in niche and fitness differences are driven by the underlying changes in intra- and inter-specific competition coefficients, which suggests that differences in phenology increased the relative strength of inter-specific competition compared to intra-specific competition. Higher coexistence probabilities were associated with a combination of stronger intra-specific limitation (α_{ii} and α_{ij}, Figure S11), as expected by theory.

In a second type of response, earlier germination by one of the species yielded the highest probability of coexistence for some species pairs (Figure 3). This result occurred due to different shifts in underlying species interactions. For example, the probability of coexistence of BRRU and LAGR increased monotonically the earlier LAGR germinated relative to BRRU because BRRU is a superior competitor. With earlier germination, the competitive effect of LAGR on BRRU became stronger more quickly than the effect of BRRU on LAGR (Figure 2). In contrast, coexistence of PLER with the slightly weaker competitor, NEME, increased as PLER germinated earlier because its competitive effect on PLER did not strengthen as much as the reciprocal effects of PLER on NEME. These different patterns of change illustrate how the effects of relative phenology on coexistence outcomes will depend on the specific underlying responses of all relevant intra- and inter-specific interactions. Although the general pattern emerges that earlier germination of weaker competitors tends to promote coexistence, the specific outcomes will depend on the combination of these underlying density-dependent processes.

These results support and extend the finding of Blackford et al. (2020), the only other experimental test, to our knowledge, of how germination phenology affects plant species coexistence. They manipulated the relative timing of germination of two annual grass species in a greenhouse pot experiment and found that increasing separation of germination timing between species altered both niche and fitness differences, with a net effect of weakening coexistence. Both species gained competitive advantages from germinating earlier, and a four-day advantage was enough to allow the inferior competitor to exclude the superior competitor. Clearly, the amount of phenological difference that will alter competitive interactions may vary among ecosystems depending on species traits and the climatic drivers of phenology. In a Mediterranean climate such as our study system, with most precipitation falling during the cool winters, it is not unexpected that individuals could germinate several weeks apart, either due to bet hedging strategies or differences among species in the combination of environmental cues.

The estimated probabilities of coexistence are conditional on the data collected and all estimates of alphas and lambdas contained uncertainty that contributed to uncertainty in the coexistence outcomes. The coexistence probabilities are lower than expected given that these species are often observed together in nature, although we have no data on their interactions in nature. Thus, it is difficult to evaluate how our experimentally measured coexistence probabilities relate to those in nature. However, it is clear that this kind of controlled experiment, like others, necessarily under-estimates coexistence probabilities. These types of experimental arrays lack other forms of variability (spatial, temporal) that may be crucial mechanisms of coexistence in natural systems. Nonetheless, comparisons of how treatments change the probabilities of coexistence in an experiment are critical for dissecting the mechanisms contributing to coexistence.

Coexistence theory describes how coexistence outcomes are ultimately driven by stabilising niche differences and fitness differences. Using the alphas and lambdas to build population models and estimate stabilising effects and fitness differences, we found that phenological differences have important effects on these determinants of coexistence outcomes (Figure 4). Overall, niche differences were maximised in all but a few cases when species germinated at the same time and decreased when there were phenological differences (Figure 4). In contrast, species' fitness differences were often reduced when germinating at the same time, suggesting significant effects of germination timing on a species' overall performance.

The value of the Spaak and De Laender (2020) formulation of species-specific niche and fitness differences is the potential to relate outcomes to several general processes that determine species coexistence: frequency dependence, positive species interactions, and whether persistence is possible without the presence of other species (Spaak et al., 2021). In this study, we observed some species' niche differences to change between positive frequency dependence ($ND < 0$) to negative frequency-dependence ($0 < ND < 1$) depending on relative germination timing. The observed ND also often peaked when species germinated at the same time, suggesting that the likelihood of negative frequency-dependence increased when species had similar germination times. Furthermore, in several cases ND exceeded one when species germinated at the same time, pointing to inter-specific facilitation (Spaak et al., 2021). Similarly, the peaks and troughs in fitness differences when species germinated at the same time suggests that the relative advantages for species ($FD < 0$) and relative advantages ($FD > 0$) were often maximised when species overlapped the most (Figure 4).

4.1 | Generalising across taxa and phenophases

The observed effects of phenological differences on coexistence are also consistent with recent results from different taxa. Carter and Rudolf (2019) experimentally manipulated hatching phenologies

and population synchrony of two competing amphibians, showing that phenological synchrony influences intraspecific competition by changing the density of individuals and relative strength of competition for early versus late-arriving individuals. A recent study of two species of spider mites showed that the order of arrival of mites on plants can affect species competition and change the coexistence outcomes (Fragata et al., 2022). In that study system, the early arrival of the inferior competitor was needed to promote coexistence, and this was thought to be the result of spatial variation in niches. Arrival times may or may not be considered phenological events, as they often are with bird migration, for example, but are analogous to germination times in plants if they are related to developmental processes rather than random dispersal events.

The influence of arrival time on processes of community assembly is typically referred to as 'priority effects', but confusingly this is also one of the coexistence outcomes from modern coexistence theory (Grainger et al., 2019). Indeed by manipulating relative germination times in our study we altered the within-season 'arrival times' of these annual species. In modern coexistence theory, priority effects refer to positive frequency-dependent growth rates, which can create conditions under which neither species can invade an established population of its competitor. Recent theoretical work has begun integrating these two different, but related, types of priority effects (Zou & Rudolf, 2023). In our study, we are focused on the within-season effects of earlier gemination phenology, rather than the multigenerational positive frequency-dependence that could arise.

Together, these results are beginning to detail how early phenological stages may shape species interactions, but to generalise these findings to phenological differences broadly, it is worth considering how the relative advantages and disadvantages of being early or late may vary among phenophases. Plants have many potentially consequential phenophases, the timing of which could impact performance in important ways (Iler et al., 2021). In perhaps the first empirical study of how phenological differences influence coexistence, Godoy and Levine (2014) used competition experiments with species having naturally distinct phenological patterns to investigate how timing affects competition and coexistence. They found that species with later growth phenology (timing of peak biomass accumulation) had increased competitive abilities, allowing the later species (typically the non-native invaders) to outcompete earlier native competitors. Results suggested that fitness differences outweighed the stabilising niche differences created from phenological differences. Although it is difficult to infer the role of phenology per se because phenology covaries with other life history traits, this study was the first to demonstrate how quantifying niche and fitness differences can help understand how phenology may affect the outcomes of species interactions and invasion success. The advantage for late-phenology species contrasts with our findings of relative advantages for early germinating species, highlighting the important ecological differences of timing offsets among phenophases.

Reproductive (a)synchronies among species has also been of great interest for ecologists. In theory, if flowering phenology is related to intra-specific and/or inter-specific competition for pollinators, then it could impact species coexistence (Pauw, 2013), although the predictions for the relative effects on stabilising and equalising mechanisms remain unclear. It seems likely that the effects of relative timing of flowering could be quite context-dependent, including the specificity and redundancy of the plant-pollinator networks. Nonetheless, frequency-dependent pollinator visitation could affect coexistence (Benadi & Pauw, 2018), and an observational study found that pollinator visitation promoted coexistence (Lanuza et al., 2018). Using variation among populations of a plant introduced around the world, Alexander and Levine (2019) showed that evolved variation in reproductive phenology was correlated with coexistence outcomes. Although clever experimental approaches to manipulating relative flowering phenology are possible (Rafferty & Ives, 2011; Waters et al., 2020), it is challenging and may prove difficult to scale up to the design necessary for estimating pairwise interaction coefficients. Ultimately, if different phenophases are responding uniquely to climate change (Buonaiuto & Wolkovich, 2021), it may also be necessary to integrate the effects on coexistence across multiple phenophases, particularly because the nature of species interactions may change over ontogeny (Yang & Rudolf, 2010).

4.2 | Caveats

One factor complicating how we scale up inference from experimental results is that the effects of phenological differences may depend on the interaction between species traits and specific environmental context of a given year. The specific abiotic and biotic conditions of a given year may influence the costs and benefits of different phenological timing (Wolkovich & Donahue, 2021), as well as the relative effects on stabilising and equalising mechanisms. And these costs and benefits may be different for species with different traits and life history strategies. For example, the demographic implications of germination timing, which is often triggered by rainfall and temperature cues, may depend on the specific conditions post-germination in a given year. In our study, phenological timing had strong effects on competitive responses, but in some years germination timing could affect intrinsic fitness more strongly if species encounter less suitable conditions (e.g. poorly timed drought or frost events). It may be helpful for generalising these results to link species traits to the sensitivity of their competitive responses. Rudolf and McCrory (2018) also showed that while arrival times of tadpoles could reverse competitive dominance, the strength of the early arrival advantage was dependent on resource availability. Other plant phenophases, such as duration of flowering, have been shown to depend on annual climatic conditions, with resulting consequences for pollinator visitation (Endres et al., 2021) and may interact with co-flowering patterns to affect plant fitness (Faust & Iler, 2022). Future studies crossing a phenological manipulation with an environmental treatment could explore how climate and timing may interact to affect coexistence.

5 | CONCLUSIONS

In summary, although there is an exciting proliferation of large phenological datasets documenting spatial and temporal change in the timing of life cycle events in nature, it remains unclear what the implications of these changes are for shaping the composition and diversity of ecological communities. In particular, the ubiquitous species-specific phenological responses may reshuffle species interactions and cause complex changes in species interactions. More experimental tests, coupled to population models and coexistence theory, may help to understand what changing phenology may mean for population dynamics, species interactions and coexistence.

AUTHOR CONTRIBUTIONS

Jeff Diez conceived the study ideas, and Jeff Diez and Jen Schlauch designed methodology; Jen Schlauch, Elysa DuCharme, Jeff Diez, and Sarah Erskine collected the data; Jeff Diez analysed the data; Jeremy Collings and Sarah Erskine provided discussion of ideas and interpretation of results; Jeff Diez wrote the manuscript. All authors contributed to subsequent drafts. Statement on Inclusion: Data collection was conducted on the property of UC Riverside. While intentions were to include undergraduate researchers in this process, the COVID-19 pandemic restrictions in spring 2020 made this not possible.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available on the Dryad Digital Repository https://doi.org/10.5061/dryad.7pvmcvf2c (Diez, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Experimental design.

Figure S2: Growth curves of the study species, highlighting variation among species in growth rates within first month, which is likely to influence competitive abilities.

Figure S3: Raw (A) seed production data of all plants ('Raw fitness'), (B) estimated lambdas (fitness in the absence of competition), and (C) scaled lambdas (to better see the variation within species).

Figure S4: Estimated competitive abilities A species' competitive ability can be calculated as (Hart 2018): $\frac{\lambda_i - 1}{\alpha_{i,i} \times \alpha_{i,j}}$.

Figure S5: Effects of relative germination timing on the fitness differences (FD) and niche differences (ND) map.

Figure S6: Effects of relative germination timing on niche and fitness differences for all pairwise species combinations.

Figure S7: Experimental Garden photos: (top) before, (bottom) peak growing season.

Figure S8: Raw data and fitted competition curves.

Figure S9: Posterior distributions of estimated R^2 values for each species' model, using the method from Gelman et al. (2019).

Figure S10: Raw seeds per flower data used to convert the number of flowers to the number of seeds produced.

Figure S11: Correlations among estimated parameters.

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