

Competition between native Honewort (*Cryptotaenia canadensis*) and invasive Dame's Rocket (*Hesperis matronalis*) seedlings is mediated by relative germination timing

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To dos:

1. Update results to include niche modification question
2. Update methods to include afore mentioned models
- 3.

Abstract

Introduction

A central tenet of community assembly theory is that the order of arrival of species to a community mediates inter-specific interactions and can dictate the trajectory of community structure in the long term (Fukami, 2015). These historical contingencies, known as priority effects, have been shown to alter the structure and function of communities, driving communities to alternate stable states (Fukami & Nakajima, 2011). In many ecosystems, plant communities must re-assemble each year after a period of dormancy. In these communities, priority effects are the products of phenology, the timing of seasonal life cycle events, and the rate at which dormant plants and seeds respond to their environment and resume growth or germinate when favorable conditions return (Rudolf, 2019).

Invasive plants are often characterized by rapid germination and precocious phenology under a wide variety of environmental condition (Gioria *et al.*, 2018; Gioria & Pyšek, 2017; Wolkovich & Cleland, 2011; Smith, 2013). By contrast, native plants, tend to exhibit more constrained germinations cues (Marushia *et al.*, 2010), producing seed with physiological dormancy that is released by temperature cues such as cold stratification (prolonged exposure to cool temperature) temperatures to break dormancy and stimulate germination (ten Brink *et al.*, 2013; Cavieres & Sierra-Almeida, 2017; Bradford & Nonogaki, 2007) .

These differences in germination physiology can yield strong differences in the relative germination phenology of invasive and native plants, with invaders germination well before their native competitors (hereafter: seasonal advantage). This seasonal advantage can contribute significantly to the competitive abilities, and ultimately invasion success of invasive plants by allowing them to begin drawing down seasonal resources and modifying their environment before their native competitors emerge (Kardol *et al.*, 2013). We refer to this effect of seasonal advantage on competition among species as a seasonal priority effect

Wainwright 2011, Young : 2017aa.

Yet, it is difficult to quantify the contribution of germination seasonal priority effects to the competitive success of invaders. Germination is notorious difficult to monitor in the field, and rapid phenology often co-varies with other competitive traits (Dickson *et al.*, 2012; Milbau *et al.*, 2003; HAO *et al.*, 2009) and the relative importance of seasonal advantage vs. other competitive traits to invasion success and competition dynamics in general is unknown.

Understanding the role that phenological advantage plays in mediating the dynamics inter-specific competition is critical for predicting and managing the structure and function of plant communities in the face of anthropogenic climate change. Due to inter-specific differences in germination response to environmental variation, the sustained alterations to environmental conditions are already shifting-community wide patterns of germination. If the patterns are indeed tightly link the the competitive dynamics of communities than phenological reorganization is likely to shift balances of species' interactions, change patterns of invasion, and strongly influence biological filtering of communities.

Work on this: To address this gap, we leveraged the difference in species germination responses to the environment to quantifying how seasonal advantage among species varies with climate variation. First we performed a series of germination assays in controlled environments temperature regimes to estimate a realistic range of climate-driven variation in germination phenology between widespread invasive and native forbs. With this understanding in hand, we then performed competition trial for these species under contrasting environmental regimes to manipulate the relative germination phenology and quantify the contribution of seasonal priority effect to competitive dynamics among them.

Methods

0.1 Focal species

Dames Rocket (*Hesperis matronalis*) is a herbaceous biennial/perennial species in the *Brassicaceae* originally from Eurasia, and introduced to North America in the 19th century (Francis *et al.*, 2009). It can rapidly invade meadows, forest edges and woodland, forming dense, monotypic stands and excluding native vegetation (Francis *et al.*, 2009). It is currently listed as a noxious or invasive weed is several states and provinces in the United States and Canada (Susko & Hussein, 2008). Honewort (*Cryptotania canadensis*) is a herbaceous perennial in the *Apiaceae* family, native to forests and woodland of North America (Hawkins *et al.*, 2007). The habitat overlap of these two species suggests that they may compete in nature. While their apparent niche may be similar, the two species display a substantial different germination niche, making them a suitable model for our study. *C. canadensis* seeds are classified with deep physiological dormancy and require a substantial

period of cold moist stratification to release dormancy and initiate germination (Baskin & Baskin, 1988). While some reports suggests that cold stratification enhances germination in *H. matronalis* at low incubation temperatures several studies have demonstrated that this fresh and after-ripened (dry-stored) seeds of *H. matronalis* are capable of rapid and complete germination at a wide range of spring temperatures in the temperate zone (Susko & Hussein, 2008). The dynamics suggest that the phenological advantage among the species has potential to be strong mediated by cold stratification and incubation.

0.2 Germination Assays

To investigate the relationship between environmental variation and relative germination timing between competing species, we obtained seeds of 14 spring-germinating herbaceous species common to temperate forest-edges, including our focal species *C. canadensis* and *H. matronalis*, from domestic plant nurseries (see Supporting Information Tab. ?? for details). We performed germination assays in the growth facilities of Arnold Arboretum in Boston MA (42.3074N, 71.1208W). We assigned seeds to a fully crossed set of twenty experimental treatments; 10 levels of cold stratification duration (0,2,4,5,6,7,8,9,11,13 weeks at 4C) , two levels of incubation temperature (warm— 25C:15C (day/night), cool— 20C:10C (day/night)).

Prior to applying experimental treatments we performed a “float test” in which all seeds were placed in distilled water, and unfilled seeds (floating) were removed from the experiment (Baskin & Baskin, 2014). We imbibed the remaining seeds in distilled water for 24 hours and then placed 20 seeds per species/ treatment combination in petri dishes on moist pool filter sand. We replicated each treatment combination three times. For the cold stratification treatments, we wrapped petri dishes in aluminum foil to prevent light exposure and placed them in a growth chamber at 4C. After each stratification interval, we transferred the petri dishes to their assigned incubation chamber for 25 days, moistening the germination substrate as necessary to maintain maximum saturation of the medium without flooding the seeds. We check for new germinates every 2 days, defining a seed as germinated when its radical or cotyledon tissue was visible (Baskin & Baskin, 2014). We assessed the viability of any seeds that did not germinate in the 25 day incubation trial by performing a “crush test” in which we applied pressure to the intact seed to evaluate its condition (Baskin & Baskin, 2014). We excluded any seeds deemed unviable from all subsequent analyses. Due to the staggering of our stratification treatments the experiment took place between 27 August- 12 December 2018.

Statistical analysis

To assess inter-specific differences in the relationship between germination rate and temperature variability, we fit a Bayesian mixed-effect accelerated failure time model (AFT) with weeks of stratification and incubation temperature as fixed effects and species as a random effect. Three species, (*Carex grisea*, *Impatiens capensis* and *Phlox cuspidata*), did not germinate at high enough fractions in our assays to analyze, so our final analysis consisted of 11 species.

We chose an AFT model as it allowed for us to account for viable seeds that did not germinate during our incubation window, letting us robustly compare germination timing (t50 or time to 50% germination) even

among treatments with different final germination percentages in the time frame of the experiment (Soltani *et al.*, 2015). One drawback of this approach is that this class of models assume that all viable seeds will eventually germinate, which we would not expect to be true in nature. For this reason, we considered any estimated t50 values greater than 60 days to indicate that seeds would not reach 50% germination under those conditions.

In addition to our full species model described above, to obtain higher resolution estimates for the germination dynamics for our two focal species, we fit an additional AFT model on a subset of data including only *C. canadensis* and *H. matronalis*. In this model we included species as a fixed effect in addition to incubation temperature and stratification duration.

We fit the models using the R package “brms” (Bürkner, 2018) using a weibull distribution for the model’s likelihood function. We ran the model on four chains with 4000 iterations and a 3000 iteration warm up for a total of 4000 posterior draws for each parameter using weakly informative priors. We assessed model performance through ensuring \hat{R} s were between 1 and 1.01 and bulk and tail effective sample sizes were high.

0.3 Competition Trials

To quantify the contribution of seasonal priority effects to inter-specific competition dynamics of our focal species we performed competition trials under controlled condition in a research greenhouse at the Arnold Arboretum in October 2020-February 2021. We planted seeds of *C. canadensis* and *H. matronalis* into 3.5 inch square pots, employing a response surface design where we varied both the overall density of seeds and proportion of each species in each pot (Inouye, 2001). High and low density treatments consisted of 14 and 8 seeds total seeds respectively. Our proportion treatments (100:0%, 25:75%, 50:50%, 75:25%, 0:100% (species A :species B)) Each density by proportion treatment was replicated six times.

We randomly assigned half of the pots low (45 days) and high (72 days) cold stratification treatments at 4C. We staggered the start of the treatments, so that at the conclusion of the pre-treatment, all pots were transferred to a heated greenhouse maintained at 15-25 C with 14 hours of supplemental light. Germination was observed daily from 24 December 2020 - 13 January 2021 and every two days from 15 January 2021 to 1 February 2021. The locations of each pot in the greenhouse were randomly reassigned every 3 days to minimize any blocking effects on germination or growth.

After 35 days, we added 1 tsp per 1 gallon of water of Peter’s 20-10-20 liquid feed fertilizer to all pots. After 62 days, we harvested the above group biomass from all pots, dried them in a oven for 48 hours at 60C, and recorded the dry weight of each species/pot using a Mettler balance.

Statistical analysis

We quantified the phenological advantage between the species by subtracting the mean germination time (MGT) of *H. matronalis* from that of *C. canadensis* in each pot. This allowed us to evaluate the effect phenological advantage with a regression design

For each plot, we calculated the relative growth rate difference among species using the equation below modified from Connolly & Wayne (2005).

$$\text{RGRD} = \ln\left(\frac{Y_{Cc}}{y_{Cc}}\right) - \ln\left(\frac{Y_{Hm}}{y_{Hm}}\right)$$

where Y_{Hm} and Y_{Cc} are the final biomass of the species at the end of the experiment and y_{Hm} and y_{Cc} are the initial biomass of the seeds planted at the outset of the experiment. For this calculation we obtained estimates of seed mass for our focal species from the Kew Gardens Seed Information Database ().

We then modeled the effect of seedling density of *C. canadensis*, *H. matronalis* and phenological advantage time using Bayesian linear regression using the R packages “brms” (Bürkner, 2018). Using weakly informative priors, we ran this model on 4 chains, with 4000 iterations per chain and a warm up of 3000 iterations, for a total of 4,000 posterior samples per parameter. The model is written below:

$$\text{RGRD} = \alpha + \beta_1 y_{Hm} + \beta_2 y_{Cc} + \beta_3 \text{MGT} + \epsilon$$

where β_1 and β_2 are the known as the species influence parameters, or the estimated effect of increasing the seedling density of each species by one individual on the RGRD, and β_3 is the priority effect, or the effect of increasing the difference in MGT between *H. matronalis* and *C. canadensis*. In this formulation α is an un-interpretable intercept (Connolly & Wayne, 2005).

To assess whether the rapid germination phenology of *H. matronalis* modified the germination niche of *C. canadensis* we performed two additional Bayesian multiple regressions. We assessed the influence of competition type (single species vs. mixed competition) on the the likelihood of *C. canadensis* germination using a bernoulli distribution and the MGT of *C. canadensis* using a Gaussian distribution. In both models we included stratification treatment as a fixed-effect covariate. As above, we ran these models using the R packages “brms” (Bürkner, 2018), with weakly informative priors.

Results

Germination advantage

In our germination assays, cold stratification duration has a significant effect on germination phenology, advancing the time to 50% germination across species (mean: -0.14, $CI_{95}(-0.23, -0.067)$), though the strength

of this effect varied significantly among species (Fig. 1a., Fig. ??). The overall estimated effect of incubation temperature on germination phenology was weak (mean: 0.03, $CI_{95}(-0.06, 0.12)$) but this was due to strong inter-specific differences in the directional response to increasing incubation temperatures. The germination phenology of 5 species advanced with increasing incubation temperature, and was delayed for 6 species (Fig. 1b.).

Considering our focal species, *H. matronalis* reached 50% germination in under five days for all environmental treatments, always exceeded 75% germination regardless of environmental conditions (Fig. 2, Tab. ??). Increasing cold stratification duration and incubation temperature only marginally enhanced the germination rate of this species (Fig. 2). By contrast, increasing incubation temperature had a delaying effect of the germination rate of *C. canadensis*, suggesting that the mean 20C temperatures of our warm incubation treatment are supra-optimal for the species (Fig. 2). Without sufficient cold stratification (>5 weeks for low incubation and > 7 weeks for high incubation temperatures), seeds of *C. canadensis* did not reach 50% germination during the duration of our experiment (Fig. 2, Tab. ??). However, under high levels of cold stratification, (>7 weeks with cool incubation) germination rates of *C. canadensis* began to converge on those of *H. matronialis*, and at levels of stratification greater than 10-12 weeks and low incubation temperatures, the germination rate and fraction of *C. canadensis* was well matched to that of *H. matronialis* (Fig. 2, Tab. ??).

Given the strong inter-specific differences in phenological sensitivity to stratification and incubation, our results indicate that climate strongly shapes patterns of phenological assembly, and patterns of phenological advantage can highly variable due to climate variation.

Germination priority effects

In our competition trials, both competitor influence parameters and phenological priority effects had a substantial impact on the competitive interactions between *C. canadensis* and *H. matronalis*. The species influence parameters for *H. matronalis* and *C. canadensis* were 0.126 ($CI_{95}: 0.0767, 0.174$) and -0.40 ($CI_{95}: -0.474, -0.341$) respectively, indicated that with no phenological advantage, the influence of adding one individual of *H. matronalis* is almost 4x less than adding one individual of *C. canadensis* to the plot level RGRD. The estimated effect of phenological advantage (ie the priority effect) was 0.146 ($CI_{95}: 0.082, 0.209$) indicating that an increase of just one day of *H. matronalis* advantage has approximately the same influence on shifting the community biomass composition towards *H. matronalis* as adding an individual of that species to the community and weakens the species influence parameter of *C. canadensis* by 35% (Fig. 3, Tab. ??). Together, these result suggest that *H. matronalis* will come to dominate the community biomass composition unless *C. canadensis* is as high relative abundance or the phenological advantage of *H. matronalis* is small (Fig. 4).

Priority effects and germination niche modification

We found no significant differences in the final germination fraction or mean germination time of *C. canadensis* between monoculture and competition plots at both low or high levels of stratification (Fig. 5). These results

do not provide evidence that the rapid germination of *H. matronalis* modified the germination environment of *C. canadensis*.

Discussion

Germination advantage as a seasonal priority effect

In this study, we found that climate driven differences in the germination advantage among species has strong impacts on their competitive dynamics. Our model predicts that the invasive species *H. matronalis* is under the majority of species' abundance levels the competitive dominant at the seedling stage (Fig. 4). Yet at reasonably high relative abundance level, environmental conditions that reduce the phenological advantage of *H. matronalis*, can facilitate the competitive success *C. canadensis* by mitigating *H. matronalis*'s germination priority effect (Fig. 4). We found that seasonal priority effects *H. matronalis* we proportionate to its abundance influence parameter (Define this earlier in the paper) (Fig. 3), suggesting that precocious germination is an important mechanism for its competitive dominance, and potentially invasion success.

While we found priority effects impacted within-year dynamics of seedlings, our experiment was not designed to the longevity of these priority effects on the longer term, among year dynamics of our focal species. Many studies suggest that these short term priority effects may be transient, though several studies that used staggered planting methods at similar scale to the phenological lags we observed in our trials saw the influence of these initial priority effect on community composition several seasons later (). In perennial communities, these long terms dynamics are even more difficult to assess as many perennial herbs, *C. canadensis* included, rely heavily on vegetative reproduction (). Because of this, the kind of seedling to seedling competition we observed in our experiment, may be less common, and therefore less important to overall community demography than competition among vegetative ramets, or between ramets and seeds (). Understanding how phenological differences across life stages of of long-lived perennial plants affects within season inter-specific competition and

Additionally, in our experiment, there was no cost to germinating too early. it is generally accepted that optimum germination phenology is driven by a tradeoff between maximizing the growing season and the risk of exposure to damaging environmental episodes when germinating too early (). In dry grassland ecosystem, it has been demonstrated that the precocious germination of invasive has a substantial cost in water availability is too low (). In temperate forest ecosystems, the primary risk of early phenology is damage from late season frost (). Future work could further clarify the contribution of seasonal priority effects to forest community interactions by experimentally manipulating this trade-off as well.

Given these caveats, we cannot assert our study could accurately predict the long term outcomes of competition in plant communities, even between our focal species. However, our findings are likely to be most critical use conditions where seedling competition may be most important, including colonizing new habitats through range shifts, recovering from large scale disturbances, and perhaps most importantly ecological restorations.

Environmental drivers of seasonal priority effect

Our results join a growing body of experiments demonstrating that relative germination phenology can function as a seasonal or short term priority effect, enhancing the performance of the earliest germinating species at the expense of later germinants (). While this effect has been primarily commonly demonstrated in experiments in which the planting of competing seeds is staggered at increasing intervals (), we were able to generate substantial variation in relative germination timing among our competing species though by opporationalizing their differential sensitivity to environmental cues.

While we observed similar effects of stratification duration on germination phenology for *H. matronalis* between our germination assays and competition trials, the effect of cold stratification on the germination phenology of *C. canadensis* was distinctly less pronounced in the germination trials(approximately 20 day advance in germination assays between 6 and 10 weeks of stratification Fig. 2 a) vs. approximately 4 day advance at the same stratification difference in in the germination trials Fig. ??). There are several differences among these experiments that may explain these differences.

1. MGT vs. T50

2. Greenhouse temperatures

3. Medium

0.4 Seasonal priority effects and climate change

Our results join a growing body of experiments demonstrating that relative germination phenology can function as a seasonal or short term priority effect, enhancing the performance of the earliest germinating species at the expense of later germinants (). While this effect has been primarily commonly demonstrated in experiments in which the planting of competing seeds is staggered at increasing intervals (), we were able to generate substantial variation in relative germination timing among our competing species though by opporationalizing their differential sensitivity to environmental cues.

While experiments have done this before a major uncertainty has been the fact the germination phenology is depends on the abiotic environment. We show how the germination advantage shifts in association with changes in the abiotic envrioment. This is useful for cliamte change.

0.5 Germination Priority Effects and Climate Change

This link between environmental conditions, relative germination phenology and competitive dynamics suggest that shifts in environment due to anthropogenic climate change has potentially to strongly alter early stage competition among species with deeper dormancy like *C. candensis* and consistent rapid germinating species like *H. matronalis*. Because stratification conditions occur at intermiately low temperature (usually 0-10 ()), global warming is likely to increase the extent of stratification conditions in some locations, while decreasing it in others (). In regions with decreasing stratification, the rapid phenology of many invasives may allow them to exploit an unoccupied phenological niche, exerting stronger seasonal priority effects on

the native community and increase the relative abundance. By contrast, in regions where stratification conditions are being maintained or increasing, native communities may be more likely to fill the early season phenological niche, more effectively resisting invasion from species with rapid germination phenology.

This bears out for our focal species but in communities as large (Fig. 6, Fig. ??)

Considering the impacts of seasonal priority effects in forest communities

While most studies on seasonal priority effects focus on grassland environments with annual taxa () we explicitly conducted our experiment with forest perennials to better understand the generality of these effects to other ecological systems.

There has been an increasing call to increase phenological diversity in restoration planning (Hess *et al.*, 2019). Studies in have found that including early active species in plantings can suppress the abundance of invaders in both grassland (Cleland *et al.*, 2013) and forest ecosystems (Schuster *et al.*, 2020). At the same time, restoration mixes tend to lack species which fill the early season phenological niche (Havens & Vitt, 2016). The results of our study suggestion the minimizing the priority effect advantage conferred to invasive species to due rapid germination and early phenology by including species with similar, early phenological traits, could be a powerful too for managing plant invasions and restoring native ecosystems.

Things to note: Germination was poorer in competition. Medium matters. Green house temperatures were perhaps too high. More about cliamte change implicatins

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337 **Figures**

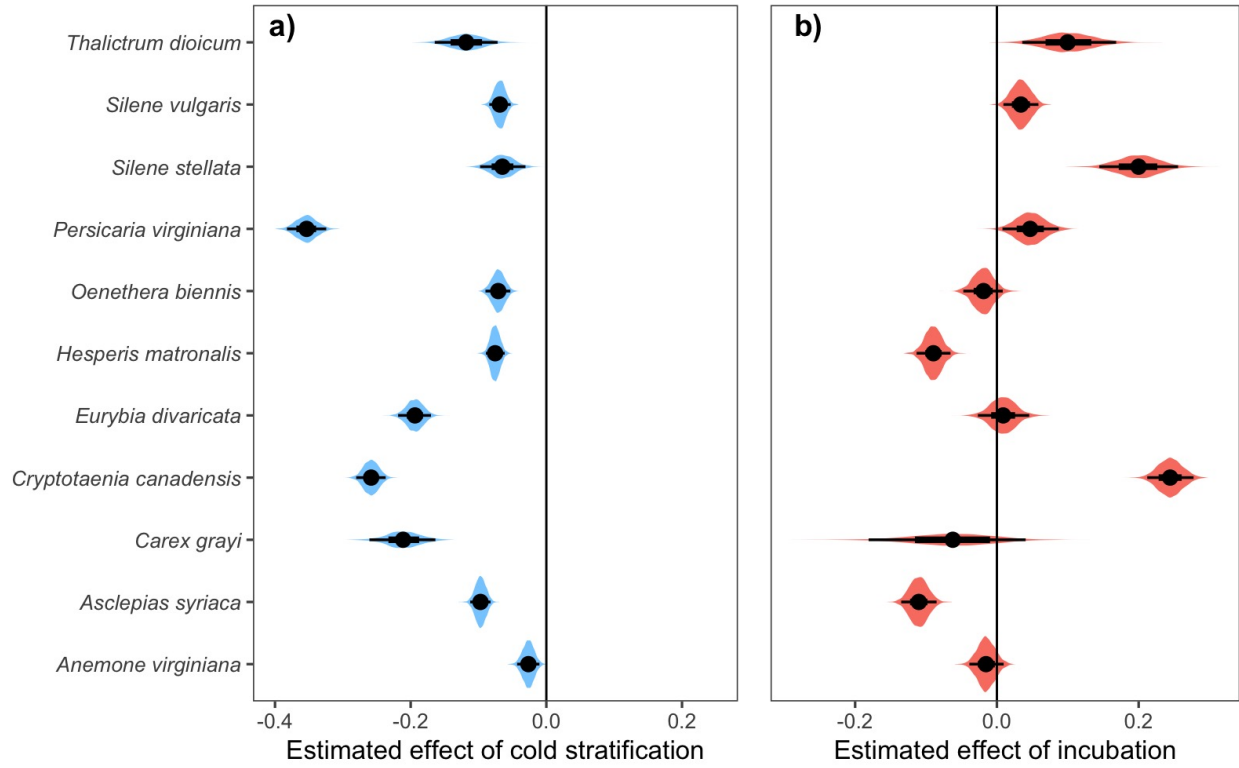


Figure 1: Estimated effects of weeks of cold stratification (a)) and incubation temperature (b) on the time to 50% germination (T50) for a suite of temperate herbaceous species. Negative estimates describe an advance in T50 and positive values a delay, estimates are on the log scale. The points indicate the mean estimated effect of each parameter, thicker and thinner bars the 50% and 95% credible intervals respectively. The full posterior distribution for each parameter is also depicted

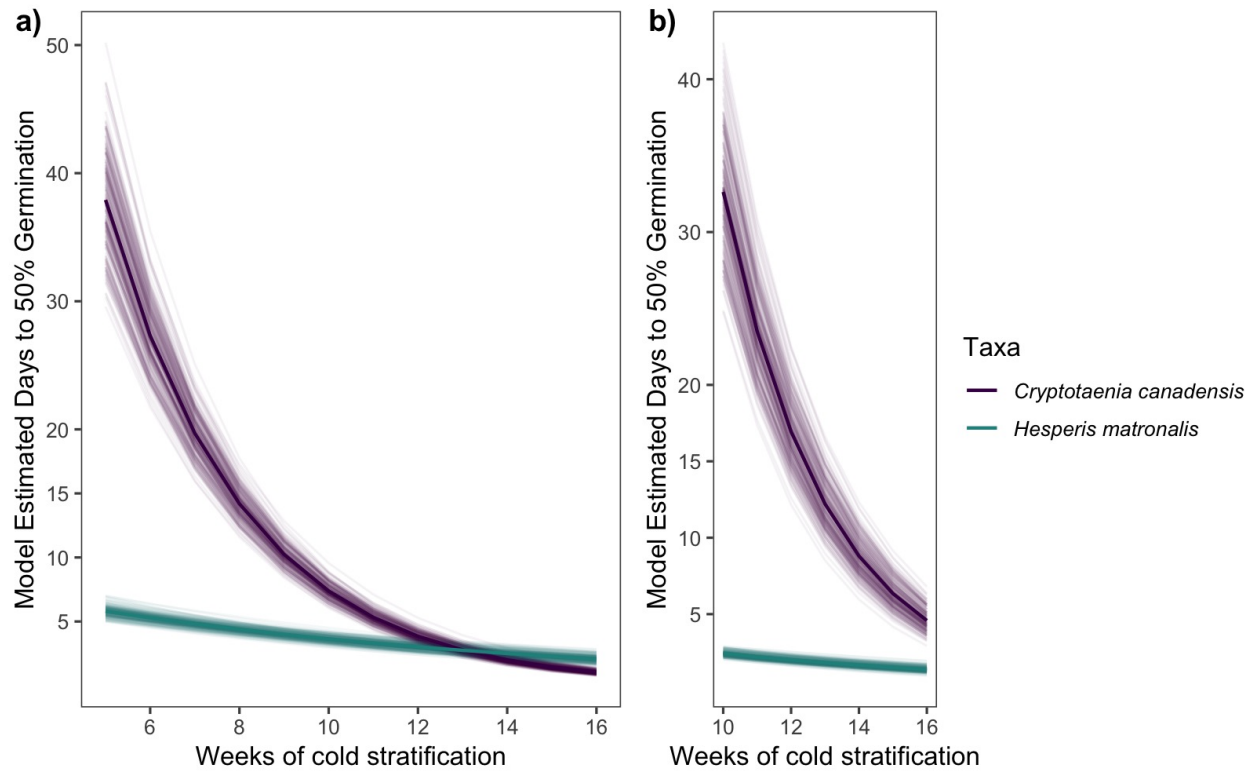


Figure 2: The effects of weeks of cold stratification at 4C on the time to 50% germination of *Cryptotaenia canadensis* and *Hesperis matronalis* under a) cool and b) warm (20/10C vs. 25/15C day/night) incubation conditions, estimated with accelerated failure time model. Only stratification treatment levels which allowed both species to reach 50% germination in less than 50 days are depicted here. The solid lines indicated the mean estimate, while lighter lines depict uncertainty with 100 random draws from the posterior distribution.

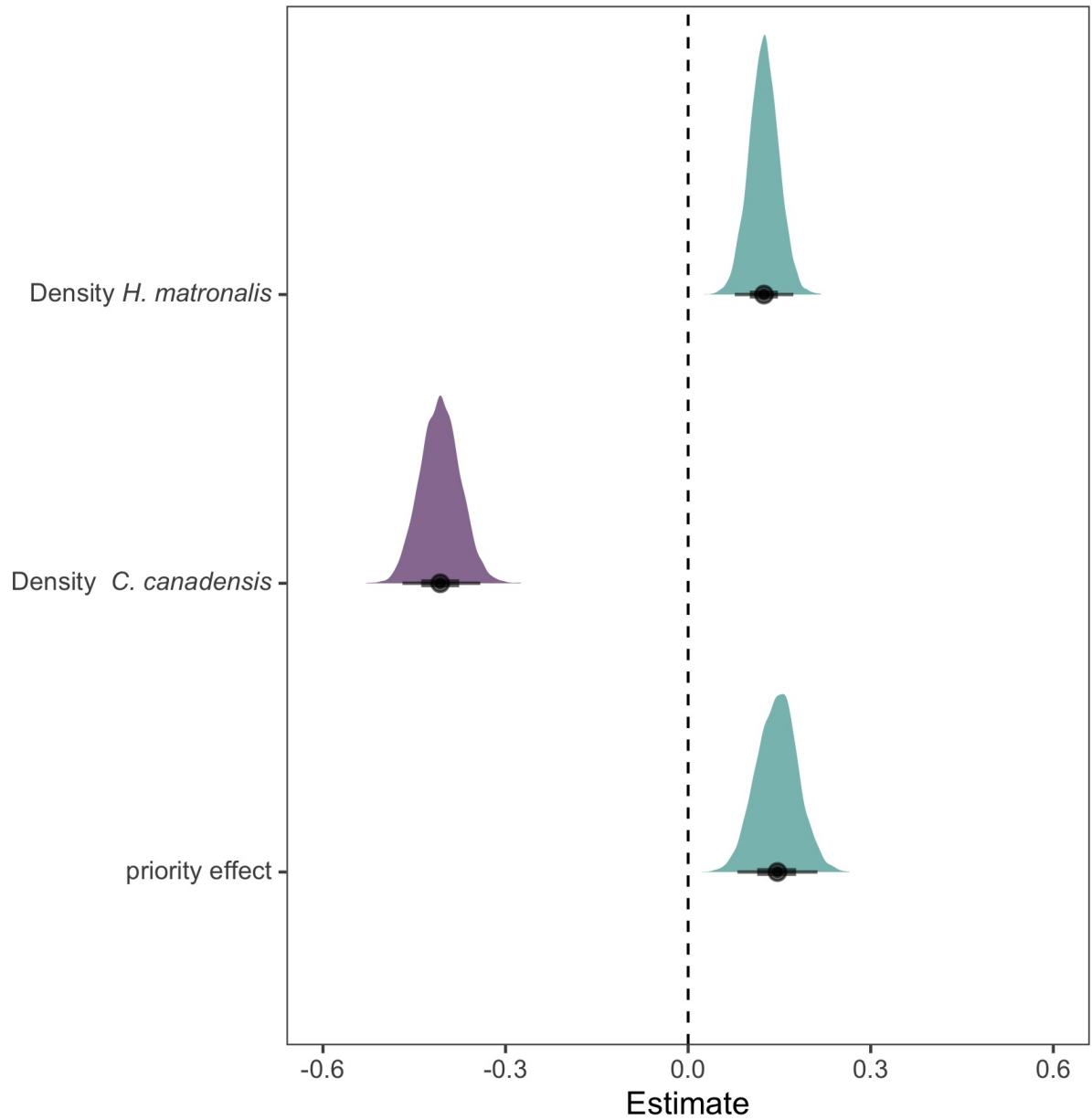


Figure 3: Estimated effects of species' abundance and phenological advantage on the relative growth rate difference between *H. matronalis* and *C. canadensis*. Negative parameter estimates indicate the community biomass composition shifts to favor *C. canadensis* while positive estimate towards dominance by *H. matronalis*. The points indicate the mean estimated effect of each parameter, thicker and thinner bars the 50% and 95% credible intervals respectively. The full posterior distribution for each parameter is also depicted.

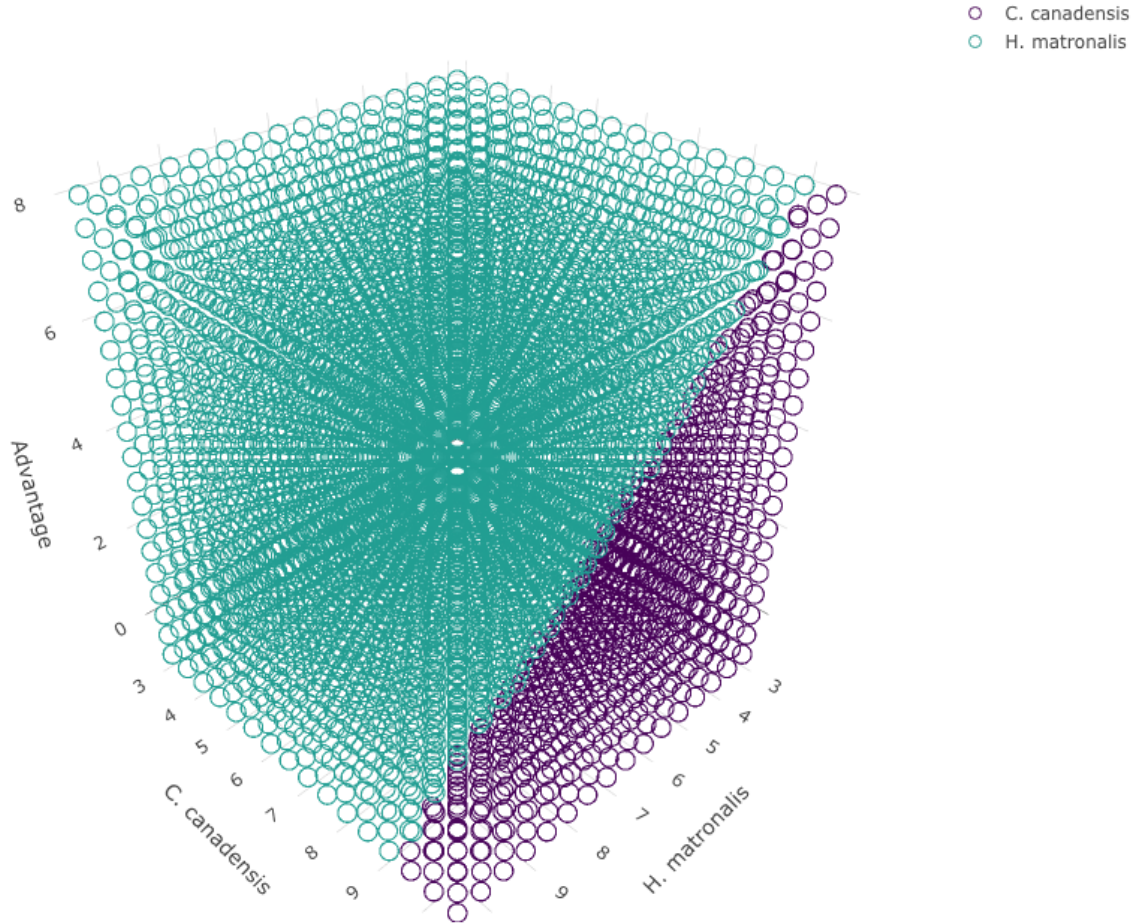


Figure 4: Predicted outcome of competition under differing combinations of *C. canadensis* and *H. matronalis* abundance and phenological advantage of *H. matronalis*. Purple dots indicate conditions that favor *C. canadensis* in community biomass composition while green dot conditions favor *H. matronalis*. Estimates are based on multiple regression models estimating the effect of each variable on the relative growth rate difference among species.

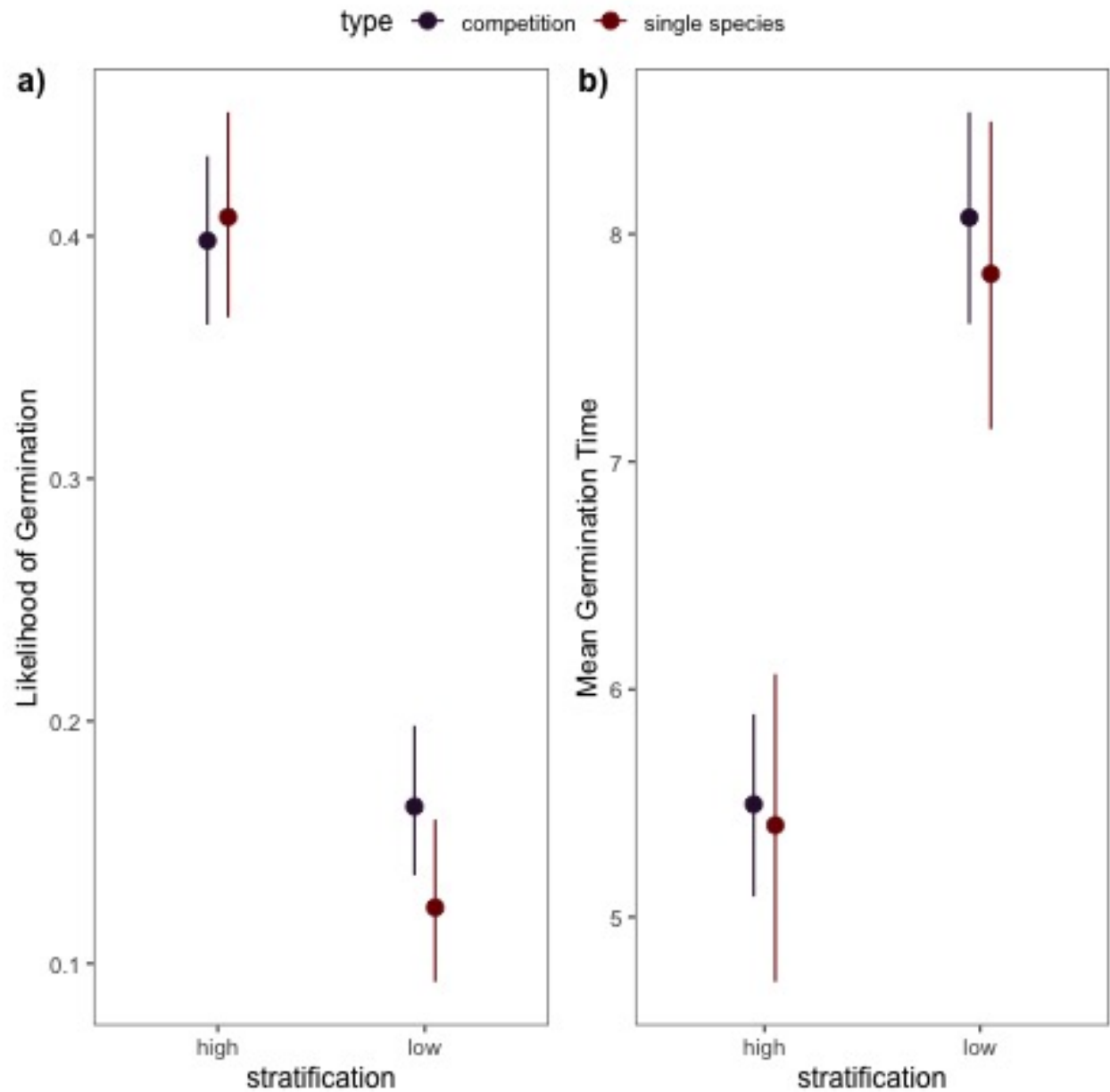


Figure 5: Estimated effects of intra-vs. inter-specific competition on the germination dynamics of *Cryptotania canadensis* under 6 (low) and 10 weeks (high) of cold stratification at 4C. Panel **a)** depicts differences germination likelihood and **b)** shows the estimated mean germination time in single species mono-cultures vs. competition plot. Colored dots represent the mean estimate under each planting type and bars represent 80% credible intervals.

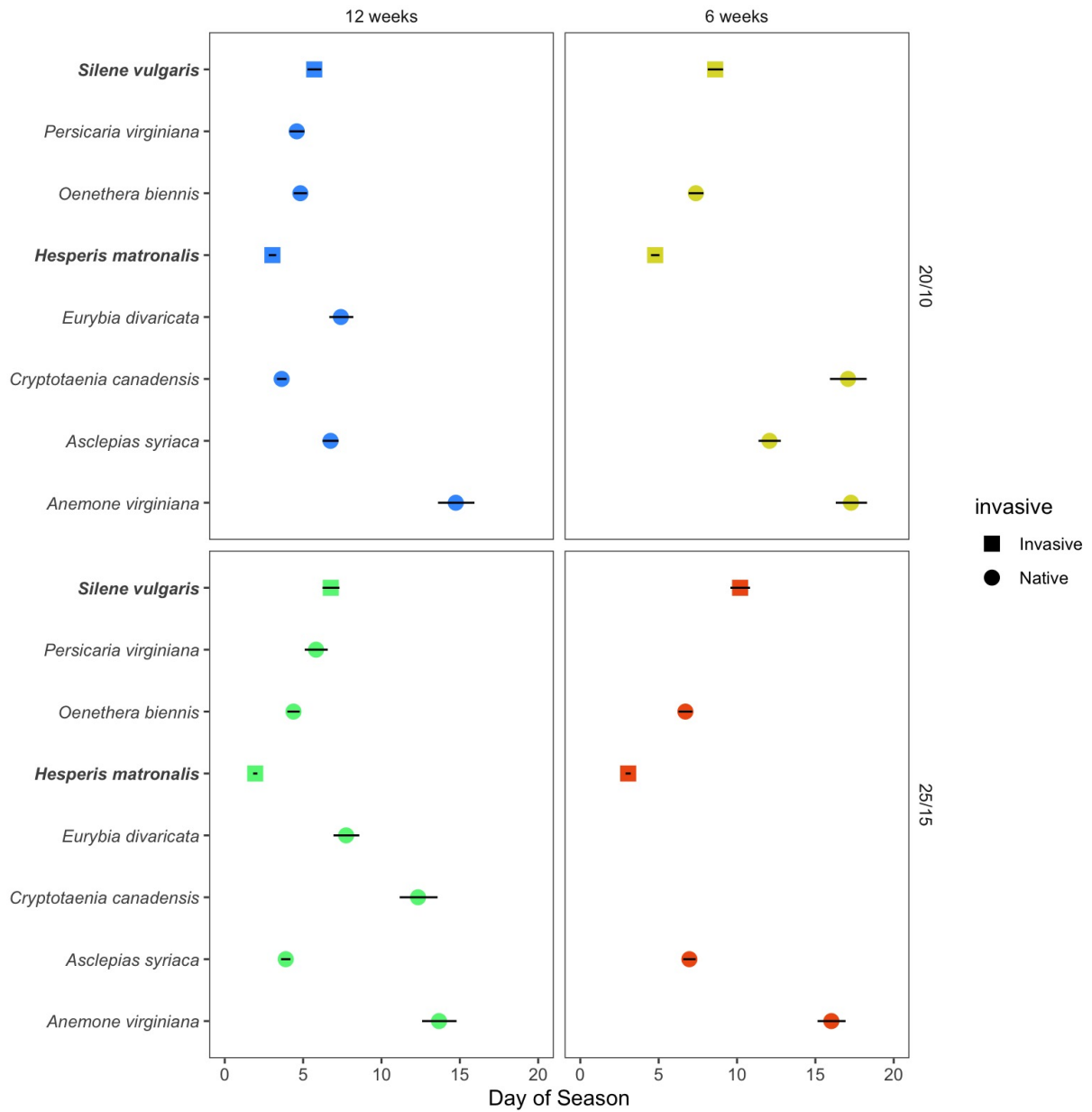


Figure 6: Predicted germination phenology of a suite of temperate herbs under varying cold stratification (6 vs. 10 weeks at 4C) and incubation (20/10C vs. 25/15C day/night) levels within the first 20 days of the growing period. Longer stratification periods increased the ratio of native to invasive species (circles vs. squares) that germinate within 20 days of the growing period, and reduced the phenological advantage of the invasive species in this study