Germination phenology as a seasonal priority effect; competition between native *Cryptotaenia canadensis* and invasive *Hesperis matronalis* seedlings is mediated by their relative timing of germination in pair-wise competition trials.

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1 Introduction

A core task of invasion biology it to identify trait that make a species likely do be invasive

1. Invasive species are characterized by rapid germination and precocious phenology
2. Being so early may function as a seasonal priority effect-niche premption and such
3. This seasonal priority effect might contribute to the competitive dominacne and invasion success of invasives

But it is difficult to infer mechanism from observational studies

1. Because rapid phenology often covaries with other competitive traits. You'd need super high resolution phenolgy and climate data.

Experiments can test role of SPE's in plant competition

1. A common approach is to use sequential planting studies.
2. recent review paper on these experiments by Weidlich:2020aa: 42% of such studies included planting interval treatments of less than 1 month, approximating the time scale of SPEs and all found evidence of priority effects. (How many were invasive vs. native?)

Yet the extent to which these studies are generailizable is questionable

1. Almost all mechanistic tests for SPEs to date have been performed using species from temperate grasslands Weidlich:2020aa, whose germination behavior may differ substantially from taxa in other habitats Tudela-Isanta:2018aa.

2. In many ecosystems, plant communities must re-assemble each year after a period of dormancy. In these communities, priority effects are largely the product of the rate at which dormant plants and seeds respond to their environment and resume growth or germinate when favorable conditions return Rudolf:2019aa, rather than the the timing of the arrival of propagules, which in many cases occurs prior to the dormant season Howe:1982aa,Baskin:1988aa.

3. Therefore, sequential plantings cannot address how important SPE's are in nature because the priority effect is 100% contigent on the choice of the treatment.

In ecological systems where dormancy is common like temperate and boreal forest, say a few other here, environmental conditions such as temperature (cold stratification and incubate), soil moisture, and light control the release of dormancy and germination or growth.

1. Cohabiting species respond with different sensitivites to these elements; and this may be especially true for invasive species which evolved under different climate condition in their home vs. invaded ranges.

2. And climate elements vary over time

3. Together, this suggests that germination or phenological responses between competing species will converge and divirge periodically over time, depending the their specific sensitives and the climate they experience.

4. This variation can be leverage for mechanistic tests of SPEs by a) qunatify how the phenoligical lag between species changes under realistic climate variation , and b) the effect of this variation on competition

Leveraging natural climate variation to test SPEs has major beneifits

1. SPE's are a cornerstone of community assembly theory and modern coexistence theory, and mechansitically qunatifying their contribtion in community interactions is important

2. Anthropogenic climatic change is altering the environments Walck2011 and changing germination and phenology patterns. Such sustained alterations to environmental cues have potential to disrupt SPEs, shifting balances of species' interactions, changing patterns of invasion, and strongly influence biological filtering of communities..

3. So assessing the role of SPE's in species interactions under more realistic germination environments is timely because it can be used to improve spatio-temporal predictions of species interaction under novel climate conditions.

While invasibility, competion, coexistance etc is a property of individual and community interactions, pair-wise comparisons have been a useful tool to identifying and quatify mechanisms of species interactions

1. Why am I saying this? Probably to justify the limited taxonomic scope of my study

Using a combination of germination assays, competition trials and climate projections, we:

1. Quantify gernmination behavior of varying environments to estimate a realistic range of climate driven priority between an widespread invasive and native forb species.

2. Compete them to assess the influences of priority effect on competitive outcome and quantify SPE's contribution vs. other intrinsic competition traits.

3. Use relationship between climate and germination behavior to make first-pass, quick and dirtay and rough prediction about where where interactions between these two species may shift with climate change as a proof-of-concept case study to build on in the future.

Methods

Focal species

Germination Assays

Competition Trials

Data analysis

Some thoughts on Connolleys RGRD models

1. Data at the plot level which makes large assays like the one I did tractable compared with spatially explict ones like heygi index or neighborhood

2. Also is desinged for signle season dynamics unlike Lotke-Volterra and the usual

3. Weakness, isn't designed for monoculture treatments(which we explictely put in out study) since you an't have the log of zero. Maybe I overcome this by converting 0s to 00000.1

Discussion

Germination as a seasonal priority effect

In this study, we found that climate driven differences in the germination timing among species has strong impacts on their competitive dynamics. 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.

In our germination assays, The germination behavior of H. matronalis was little affected by cold stratification, while germination rate and speed of C. canadensis was strongly enhanced with cold stratification, especially when germianted at cooler temperatures (Fig. 1). These differences are themselves not surprising as *H. matronalis* seeds are considered non-dormant , and seeds of *C. canadensis* are physiologically dormant . , These different responses generated germination dynamics in which under alternative low stratification regimes *H. matronalis* cohorts germinated as much as two weeks before *C. canadensis*, while under high stratification, the species germinated at approximately the same time (Fig. 1).

In our competition trials, we observed that differences in germination on the order of a few days had substantial impacts on both the per capita and plot level relative growth rate differences among species (Fig 2,3). If we consider the range of variability we observed (approximately two weeks lag to simultaneously)

These inter-specific dynamics we observed are comparable to treatments applied in staggered planting experiments , but the fact that we were able to induce these effects through varying the germination environment rather than directly manipulating germination itself is an important phase for translating the estimates from priority effect experiments into natural systems. suggests that the kinds of seasonal priority effects may be important for realz, especially in seasonal environments with high levels of inte-rannual climate variations.

Yet, even with this important step towards biological realism, more research is needed to understand the importance of germination priority effects, especially among perennial plants in seasonal environments.

Our experiment was designed to capture the dynamics on seedling competition, and we cannot assess the longevity of these priority effects on the longer term dynamics of our focal species. Many studies suggest that these short term priority effects many 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. (Mash up below paragraph into this one)

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. Yet, by choosing these more complicated life forms, speculating on the long term impact of germination seasonal priority effects becomes further complicated. *C. canadensis* can rely heavily on vegetative reproduction, clonal plants, competition among ramets may be a strong ecological determinant than competition among seedlings . *C. canadensis* also forms a transient seed bank , suggesting that the within year dynamics of germination and growth captured in our study, could be decoupled from the among year dynamics. It also also invasives invade communities not population, two species studies are limited to predict the invasion dynamics of a species in real tim. No cost do being early.Cite Wainwright.

With these limitations, our study was not designed to predict the the long term dynamics of *C. canadensis* and *H. matronalis* underfield condtions.

.This stage is super critical in general, talk about germination niche. and we cannot assess the longevity of these priority effect, or their ulitmate impacts on fitness. We focused on species with complicated life histories and dynamics, seed banks, vegetative repro etc. With that it suggest our most relevant to the plant establishment, which is relevent both in the context of plant migration, disturbance, and ecological resotoration.

Phenological Diversity as a metric of something low-level jargony

Our pairwise competition study indicates the phenological differences in germination time can strongly influence competitive outcomes. While empirical work with more species will help, if phenology is a mechanism of competitive domianence and invasion, it can also be a mechanisms of invasion resistance or co-existance. Read a bit about the invasability literature and suggest considering phenological diversity as a metri for assessing communities may be critical. COmparing across phases and life forms. Ie germinating seeds also competed with adults. This could be particular important for design ecological restorations.

. Phenolgoical diversity. This will become more imporant with cliamte hcange as new temporal niches are created.

From germination requirements to germnation responses

The first stage to incorperating phenological diversity

So many caveats:

1. These species are perennials, seeds banks. Given our expermental constrait couldn't account for these dynamics. ie competition my happen between raments and seeds. Our simplifed experimental design doesn't

address these important factors, however they add an important piece to the puzzle.

2. Given above, our results may be most relevant in colonization dynamics, especially in super disturbed systems where seed ins important.

3. Limitations of RGRD models from paper

4. We know invasives invade communities not population, two species studies are limited to predict the invasion dynamics of a species in real time

5. What we did do was quantify the contribution of priority effect to invasion success. It's high. This suggest restorations could benefit from consider phenological diversity

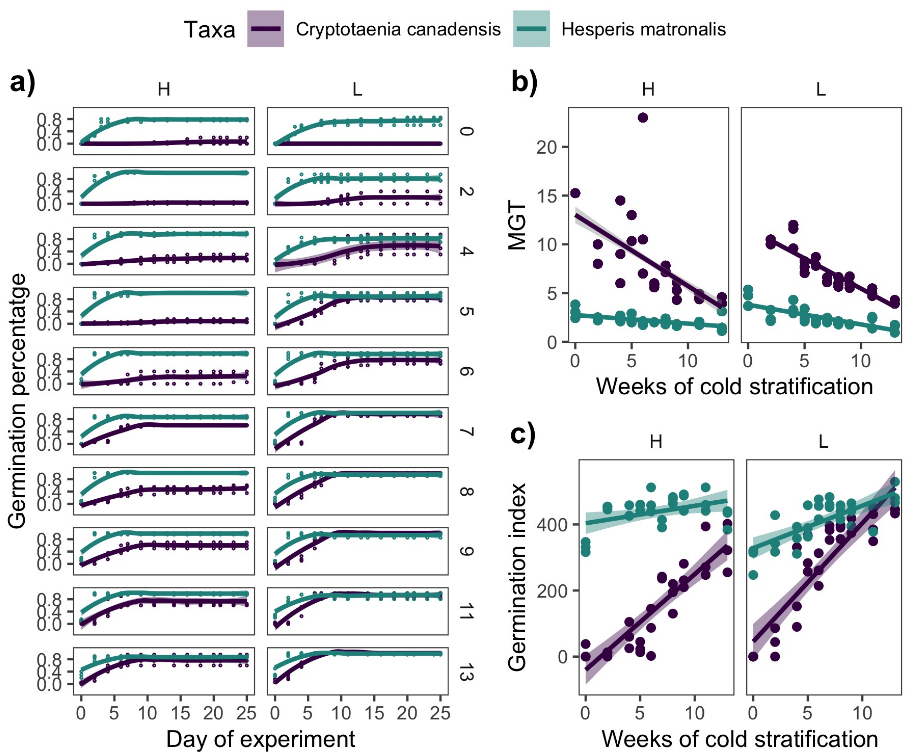

Figure 1: Germination behavior of *H. matronalis* and C. canadensis indicate that the rate of C. canadensis approaches that of *H. matronalis* under cool temperatures and high levels of stratification. a) Shows germination time courses for both species at each level of incubation (H,L) and stratitification (0-13, y-axis). b) Dipicts Mean germination time for each species as a function of weeks of stratifcation and both high (H) and low (L) incubation temperature. c) Show a composite germination index for each species that account for the speed and percentage of germination for each species as a function of weeks of stratifcation and both high (H) and low (L) incubation temperature.

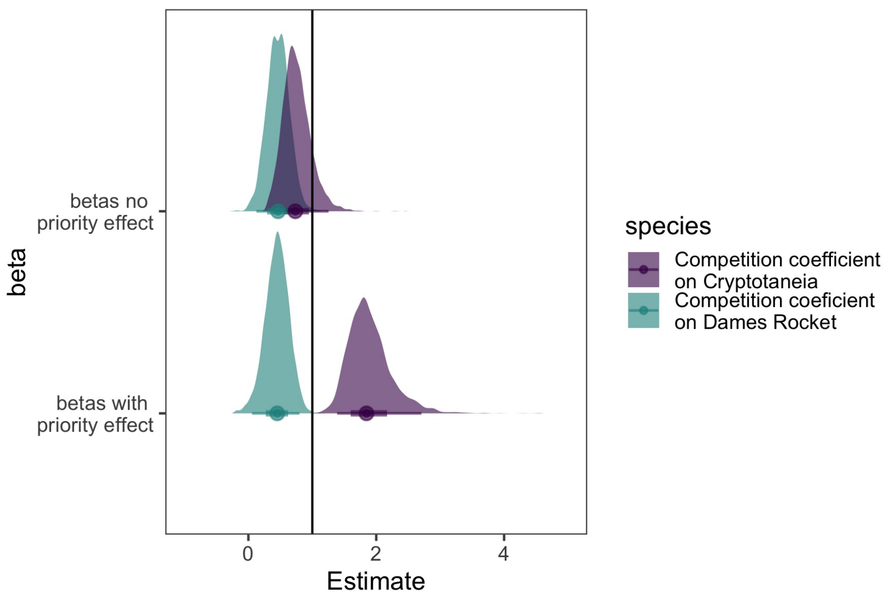

Figure 2: Estimated of competition coefficients with and without priority effect. Without priority effect, species would be expected to coexist (for both species, intra-specific competition is highe than interspecific i.e. coefficients are less than one). When just one day of priority effects are included in the calculation Dames rocket's interspecific competition increases realtive to its intraspecific competition strength, suggesting with will ultimately competitively exclude Honewort.

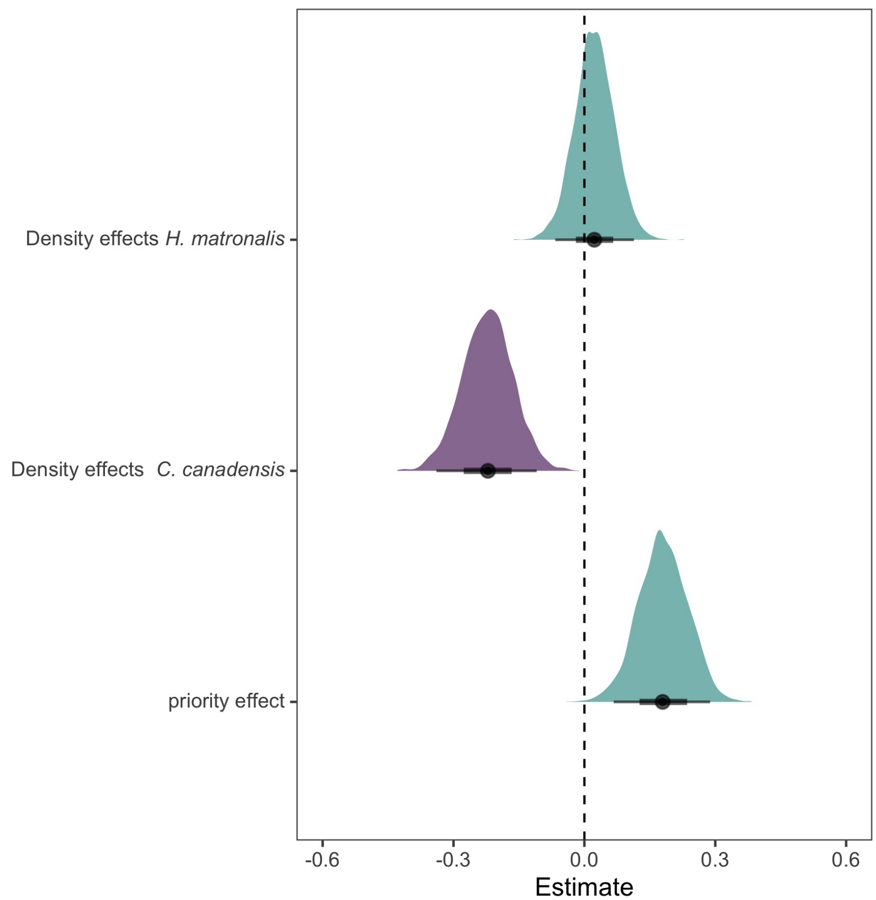

Figure 3: Estimated effects of density influence parameters and temporal priority effect on the relative growth rate difference between *H. matronalis* and C. canadensis. As per Connonly and Wayne 2005, The positive estimate of priorty and density of Hesperis matronalis tip competitive balance towards it, while the negative estimate of density of C. canadensis favor that species. Like Fig. 2, this suggests that priorty effects are a key mediator of competitive sucess in H. matronalis.

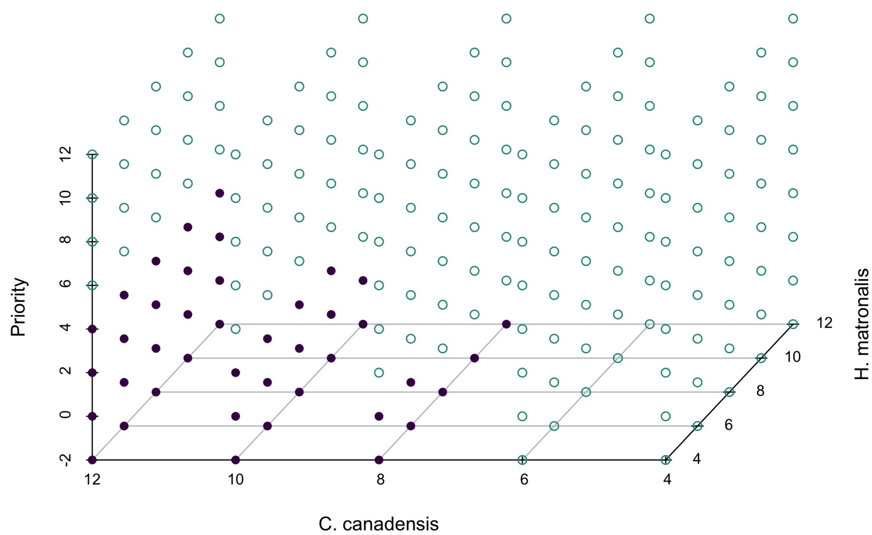

Figure 4: Predicted outcome of competition under vary inter-specific densities and temporal priority. Purple is C. canadensis and green *H. matronalis*. Need to add legend here. As can been seen C. canadensis is predicted to compete with H matronalis only at low priority effects or high densities.