1 Introduction

1. Phenology, the timing of seasonal life cycle events such as leafout seed germination. Even (plant) species with similar growth forms, habitat requirements and environmental tolerance can express markedly different phenology. These differences in phenology among species is a strong mediator of species interactions ().

2. In most temperate ecosystems Precocious relative germination phenology, functions as a seasonal priority effect (**??**), allowing early-active species to access limited seasonal resources and modify the growth environment before competitors emerge (**?**).

3. Seasonal priority effects, may play an important role in maintaining species coexistence, serving as a stabilizing (or equalizing?) mechanism between species with different intrinsic competitive abilities (ie weaker competitors germinate first). At an the extreme, precocious germination could also allow weaker competitors to competitively exclude stronger ones— a trait which of often invoked to explain the success of invasive plants, many of which germinate rapidly and early in the growing season (**??**).

4. Phenology is strongly linked to climate. We've seen big changes but responses vary among species. This suggest that SPEs will change too, and their resulting patterns of coexistence too, but can't predict this

5. Why not. Most of our experiments don't factor in climate at all. Plus they are too short.

6. Here, using examples from empirical germination assays, With we then used sexy, awesome models to do stuff, and address our questions.

Seasonal Priorty Effects are dependent on seasonal environmental variation

In most ecological systems, the timing of seed germination is under strong environmental control (). In arid ecosystems water and temperature matters (). In other temperate and boreal systems, chilling matters. Species vary in there sensitivity to the factors (). These factors also vary (). Therefore the phenological differences among species that generate seasonal priority effects are the manifestation of the interaction between sensitivity to the environment (a species-level trait) and the environment itself. This means that interannual variation in environment strongly influences the strength of the seasonal priority effects.

To better understand these dynamics, we performed a series of germination assays with regionally co-occuring herbaceous species under varying chilling and incubation conditions. We used these studies to estimate species level sensitivies to these environmental cues, and forecast phenological differences among species under difference climate conditions (see Supplemental Methods.)

From these trials we see three things. Species have different sensitivities to the same cues (Fig. 1. This was true for species with the same dormancy class, closely related species and those in the same habitat (Make Supplemental figure.)

In general, at higher levels of chilling, the sensitivity differences reduced the realized differenences in germination phenology amoung species and lower levels increased them. (Fig. 2). Incubation temperature were interesting becuase species cross the the optimum (Fig. 1), which also made it that cooler temps standardize phenology (Fig. 2). One thing this means is that species with similar and different sensitives can express different and similar phenology. For example the species in Fig. 3. (I'd potentially like to develop this into a "box" with pretty pictures of the species, some statements about how they might compete—e.g. Dames rocket is an invasive species that can invade meadows where it would compete with milkweed and forest edgeswhere it would compete with jumpseed.).

This also suggests something else. Layout tradeoff theory here. Under a stable environment coexistence could be achieved through a trade off. If that shifts the trade off should shift.

but this is hard to study .Of course the biggest challenge is we cannot observe coexistence. Explain the experiments, most experiments manipulate the SPE directly by sequential planting, that means even in experiments last for multiple seasons, the priority effect is only applied once (decide where to talk about this). Other unrealism of this approach discussed in our previous paper.

The tradeoff between competition and phenology is hard to measure. Models that link all these things can help.

2 Models to the rescue

Models can define sensitivy and competitive ability. Can isolate germination phenology from other germination responses and simulate long term dynamics and environmental change. We modified a model to coexistence to do this.

Paragraoh in the approach

3 Coexistice and competitive exclusion under alternative climate scenario

Under both high and low chill scenarios, coexistence happened due to a tradeoff. The slope got steeper and coexistence less frequencies with lower chilling (Fig. 4). Cases where the stronger competitor (lower Rstar) was extripated due to phenological differences also occured in both scenarion. Slope didn't change, but the frequency did.

Fig. 5 explain both of these phenomena.

4 A path forward

Models are still over simplifications. We can improve experiments and stuff.

(a) Germination phenology as a response curve

(b) spaital variability chillnig could go up or down

(c) Experiments with seasonal cary-over

(d) seasonal priort effects and other germinations variation

Figures

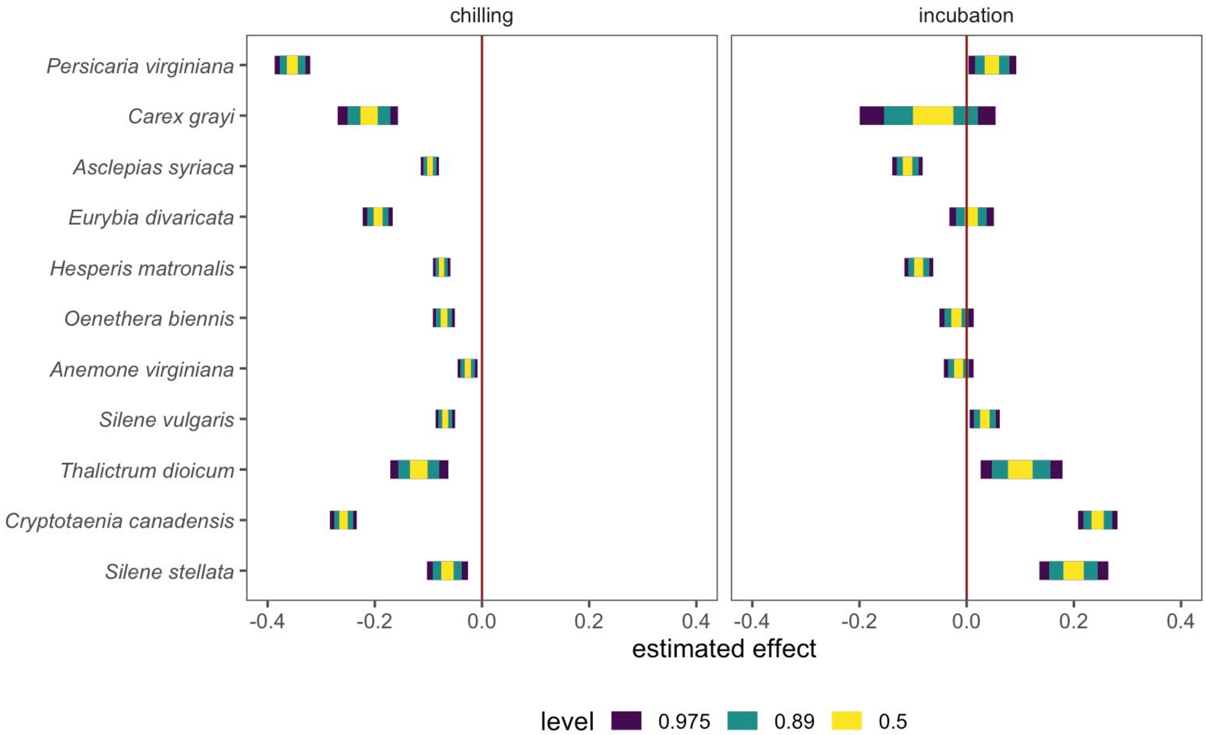

Figure 1: Co-occuring species differ in their sensitivity to environmental variation. Describe plot

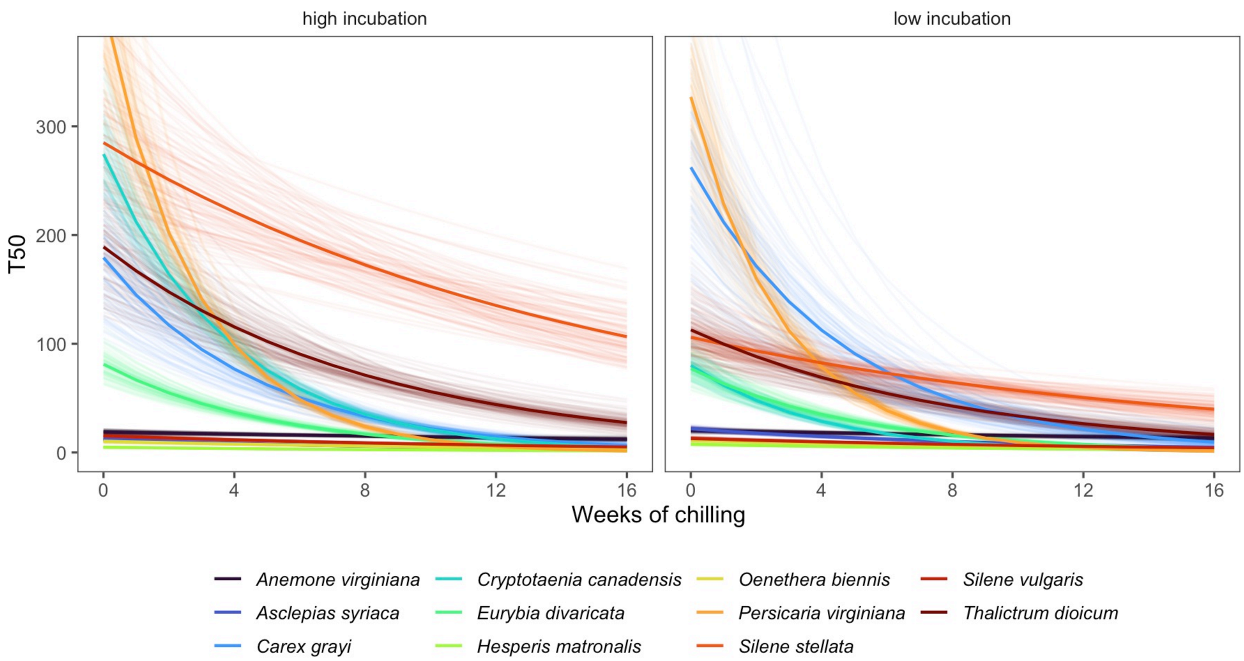

Figure 2: Differences in phenological sensitivity among species are minimized at high chill/low incubations temperatures.

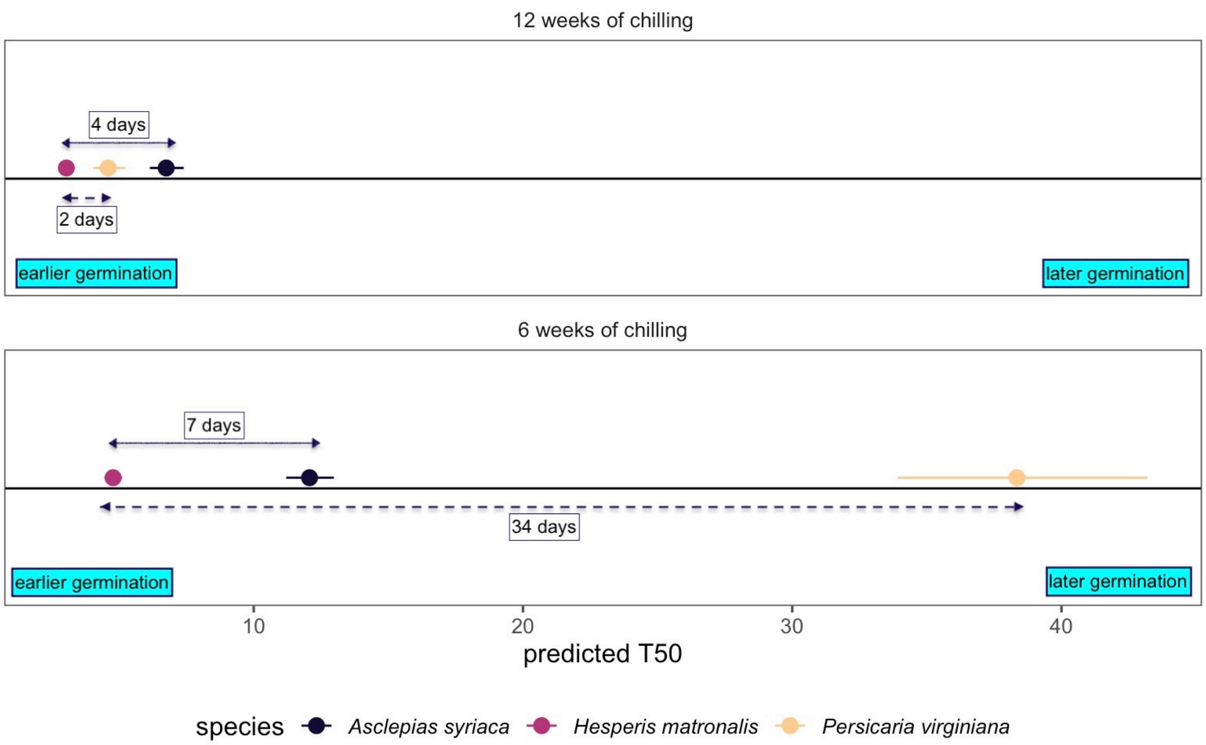

Figure 3: Environmental variation can both increase the difference in germination phenology for species with similar environmental sensitivity (*Hesperis matronalis* vs. *Asclepias syriaca*) and decrease the difference in germination phenology for species with contrasting levels of sensitivity (*Hesperis matronalis* vs. *Persicaria virginiana*). Description of what this plot is. Generally high levels of chilling minimize germination differences amoung species while lower levels of chilling enhance differences.

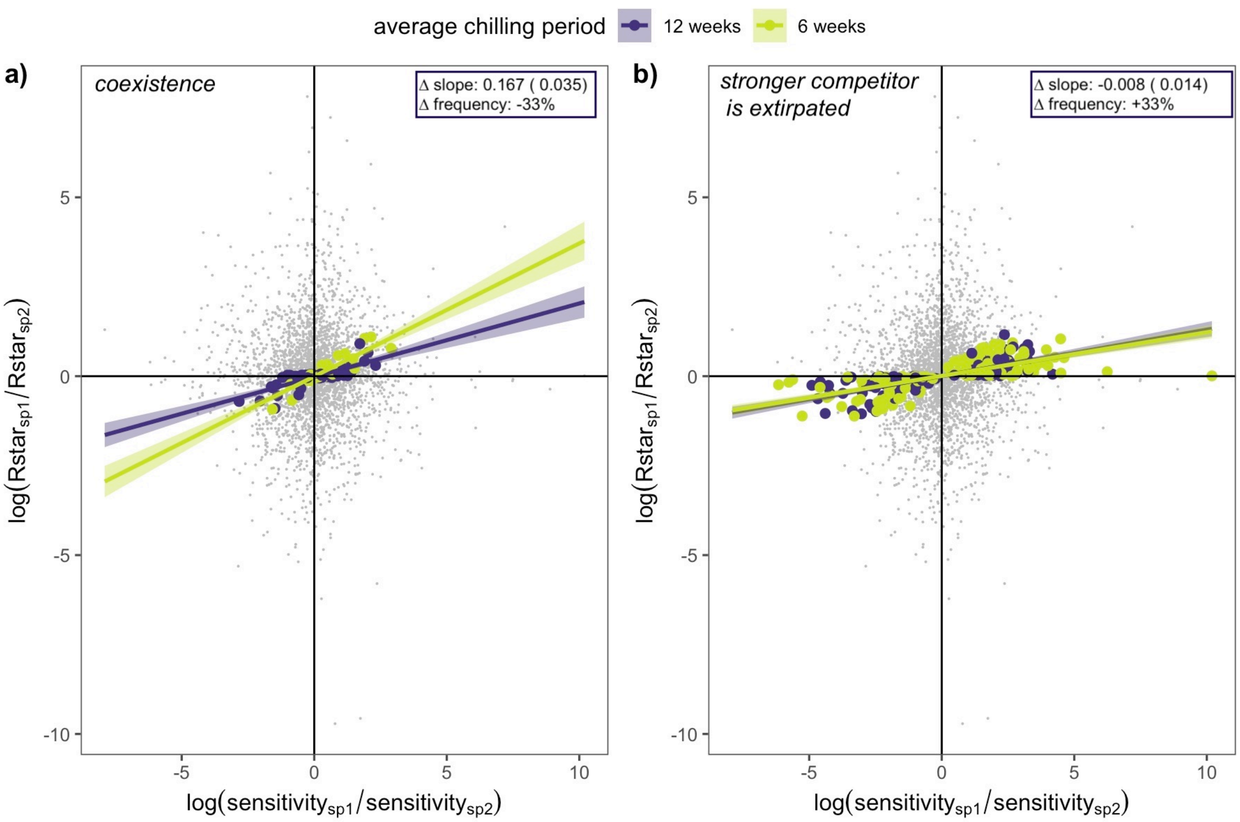

Figure 4: Reduced chilling shifts the slope of the coexistence tradeoff between priority effects and competitive ability, reduces frequency that coexistence occurs and increase the frequencey that stronger competitor are exptripated due to phenological differences.

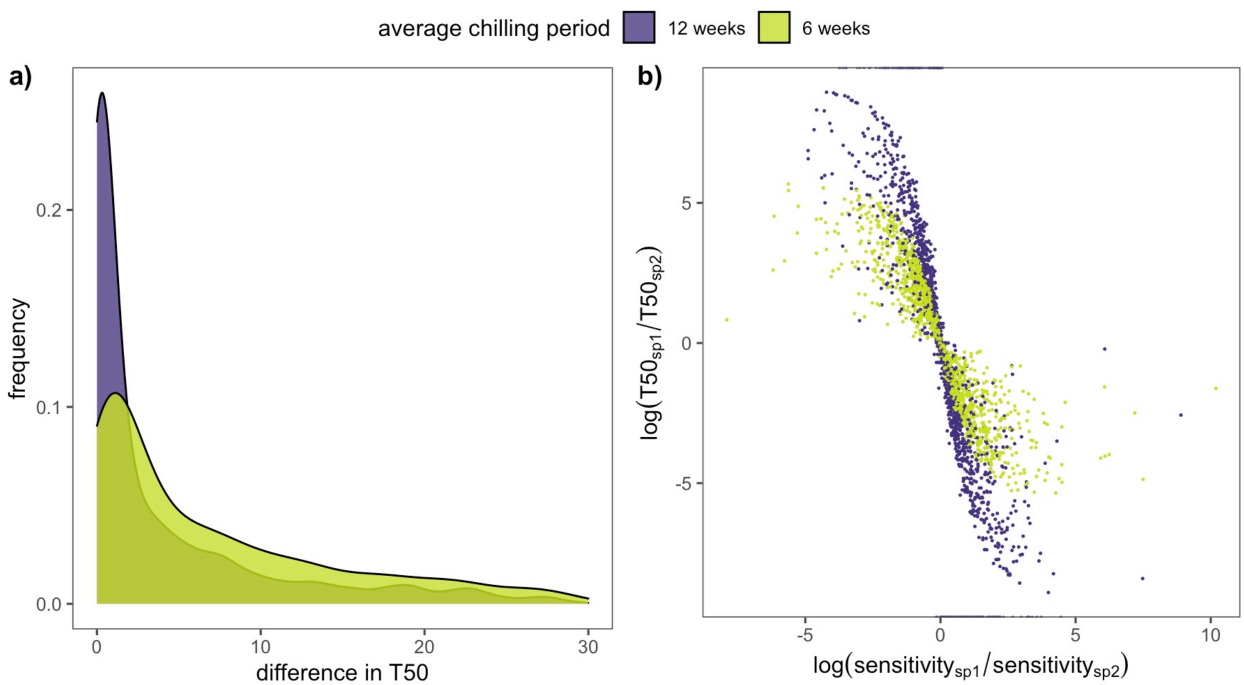

Figure 5: Under high chilling, species frequently germination closer together than under lower chilling conditions (a). This environmental variation also alters the relationship between inherent sensitivity differences amoung species and realized differences in germination phenology (b). This explains patterns in Fig. 4.