

# Differences in germination responses to environmental variation among species suggests the potential for strong seasonal priority effects in herbaceous forest communities

## 1 Introduction

A core task of community ecology is explain patterns of community assembly across a diversity of ecosystems (Weiher *et al.*, 2011). 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, even driving communities to alternate stable states (Fukami & Nakajima, 2011).

In many ecosystems across the temperate regions of the globe, plant communities must re-assemble each spring after a period of winter 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, 2019), rather than the the timing of the arrival of these propagules, which in many cases occurs in the autumn prior to the dormant season (Howe & Smallwood, 1982; Baskin & Baskin, 1988).

The importance of this subcategory of priority effects, known as seasonal priority effects SPEs (Wainwright *et al.*, 2011) or short-term priority (Young *et al.*, 2017) to seasonal assembly depends on

the magnitude of interspecific differences in germination rate responses to environment. If species have sufficiently different germination rate responses to their environment than the strength of priority effects should vary over time which, can lead to inter-specific coexistence via the storage effect (Towers *et al.*, 2020).

These dynamics have been primarily demonstrated through experiments that stagger the planting time of competing species to evaluate whether SPEs mechanistically effect competitive outcomes among species (Young *et al.*, 2017; Letten *et al.*, 2018). A recent review paper by Weidlich *et al.* (2020) reported that of 42 out of the 43 studies they evaluated found evidence for priority effects, and 18 of those studies (42%) included planting interval treatments of less than 1 month, which can approximate the time scale of SPEs.

While this evidence suggests priority effects may be important in regulating community interactions, it is unclear to what extent these patterns are broadly generalizable. First, almost all mechanistic tests for SPEs to date have been performed using species from temperate grasslands (Weidlich *et al.*, 2020), whose germination behavior may differ substantially from taxa in other habitats (Tudela-Isanta *et al.*, 2018). Second, it is largely unknown if the magnitude temporal lags applied in staggered planting experiments can be generated under nature conditions. In most natural systems, the timing of germination is dictated by environmental cues—temperature (both cool stratification temperatures to break dormancy and warm incubation temperatures to stimulate germination), moisture and light availability (Bewley, 1997; Fenner, 2000). Shared cue use may constrain differences in germination rate responses among species if species utilize cues in the same way. Broadly characterizing the importance of SPEs in community assembly will require quantifying the magnitude of differences in germination rate responses among a diversity of species across a variety of habitats.

This effort is particularly important and timely as anthropogenic climatic change is altering the germination environments of species across the globe (Walck *et al.*, 2011). Such sustained alterations

to environmental cues have potential to disrupt SPEs, shifting balances of species' interactions, and impacting population demography, community composition and ecosystem functions.

In this study, we quantified the differences in germination rate responses to temperature for a suite of herbaceous species found in temperate forests with full-factorial growth-chamber experiment in which we manipulated the duration of stratification duration and incubation temperatures to test whether variation in germination order generated by environmental variability can be on the same magnitude as planting intervals from staggered planting experiments to expect strong priory effects.

## Methods

### Species

1. Mix of field and forest species because seed bank of forest is often old field
2. Mix of dormancy classes

### 1.1 Experimental Methods

### 1.2 Data analysis

I think we're going with the survival model. I'll just mention survival models assume everything germination, which is a bad assumption so we decided anything that the t50 was greater than 30 days (or other) did not germination higher than that.

### 1.3 extension of literature review

1. search terms, how many studies in Young 2017
2. how many we added

## Results

1. table 1: Matrix of species differences under climate change and regular conditions
2. figure 1: mu plots, shape
3. plot of germination ranks under each scenario
4. 3d plots with t50, temperature and stratification for each species?
5. Supp table of lit review with quantification of responses (x out of y studies found priority effects with germination differences of  $\geq 7$  days, 7-21 days etc)

## Discussion

- Yes, it seem like the differences are big enough to alter germination rank
- Next, we have to investigate if these differences drive performance differences (priority effects)
- Our study didn't include risks to early germination–stabilizing selection on germination time.
- Germination may be less important in forest systems But germination may become more important as the need to migrate or disturbance regimes change.
- Population differences, maternal effects etc not accounted for.
- in forest germination compete with tamers not just other seeds.
- These result should fit into larger demography models that include survival, reproductive output etc.

## References

- Baskin, C.C. & Baskin, J.M. (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* **75**, 286–305.

- 85 Bewley, J. (1997) Seed germination and dormancy. *Plant Cell* **9**, 1055–1066.
- 86 Fenner, M. (2000) *Seeds: the ecology of regeneration in plant communities*. CABI Publishing,  
87 Wallingford, UK, 2nd edn.
- 88 Fukami, T. (2015) Historical contingency in community assembly: Integrating niches, species pools,  
89 and priority effects. *Annual Review of Ecology, Evolution, and Systematics* **46**, 1–23.
- 90 Fukami, T. & Nakajima, M. (2011) Community assembly: alternative stable states or alternative  
91 transient states? *Ecology Letters* **14**, 973–984.
- 92 Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal **13**, 201–228.
- 93 Letten, A.D., Dhami, M.K., Ke, P.J. & Fukami, T. (2018) Species coexistence through simultaneous  
94 fluctuation-dependent mechanisms. *Proceedings of the National Academy of Sciences* **115**, 6745.
- 95 Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence.  
96 *Ecology Letters* **22**, 1324–1338.
- 97 Towers, I.R., Bowler, C.H., Mayfield, M.M. & Dwyer, J.M. (2020) Requirements for the spatial  
98 storage effect are weakly evident for common species in natural annual plant assemblages. *Ecology*  
99 **101**, e03185.
- 100 Tudela-Isanta, M., Fernández-Pascual, E., Wijayasinghe, M., Orsenigo, S., Rossi, G., Pritchard,  
101 H.W. & Mondoni, A. (2018) Habitat-related seed germination traits in alpine habitats. *Ecology*  
102 *and Evolution* **8**, 150–161.
- 103 Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2011) Seasonal priority effects: implications  
104 for invasion and restoration in a semi-arid system. *Journal of Applied Ecology* **49**, 234–241.
- 105 Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K. & Poschlod, P. (2011) Climate change  
106 and plant regeneration from seed. *Global Change Biology* **17**, 2145–2161.
- 107 Weidlich, E.W.A., Nelson, C.R., Maron, J.L., Callaway, R.M., Delory, B.M. & Temperton, V.M.  
108 (2020) Priority effects and ecological restoration. *Restoration Ecology* **n/a**, e13317.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. (2011) Advances,  
 challenges and a developing synthesis of ecological community assembly theory. *Philosophical  
 Transactions of the Royal Society B: Biological Sciences* **366**, 2403–2413.

Young, T.P., Stuble, K.L., Balachowski, J.A. & Werner, C.M. (2017) Using priority effects to  
 manipulate competitive relationships in restoration. *Restoration Ecology* **25**, S114–S123.

# Figures

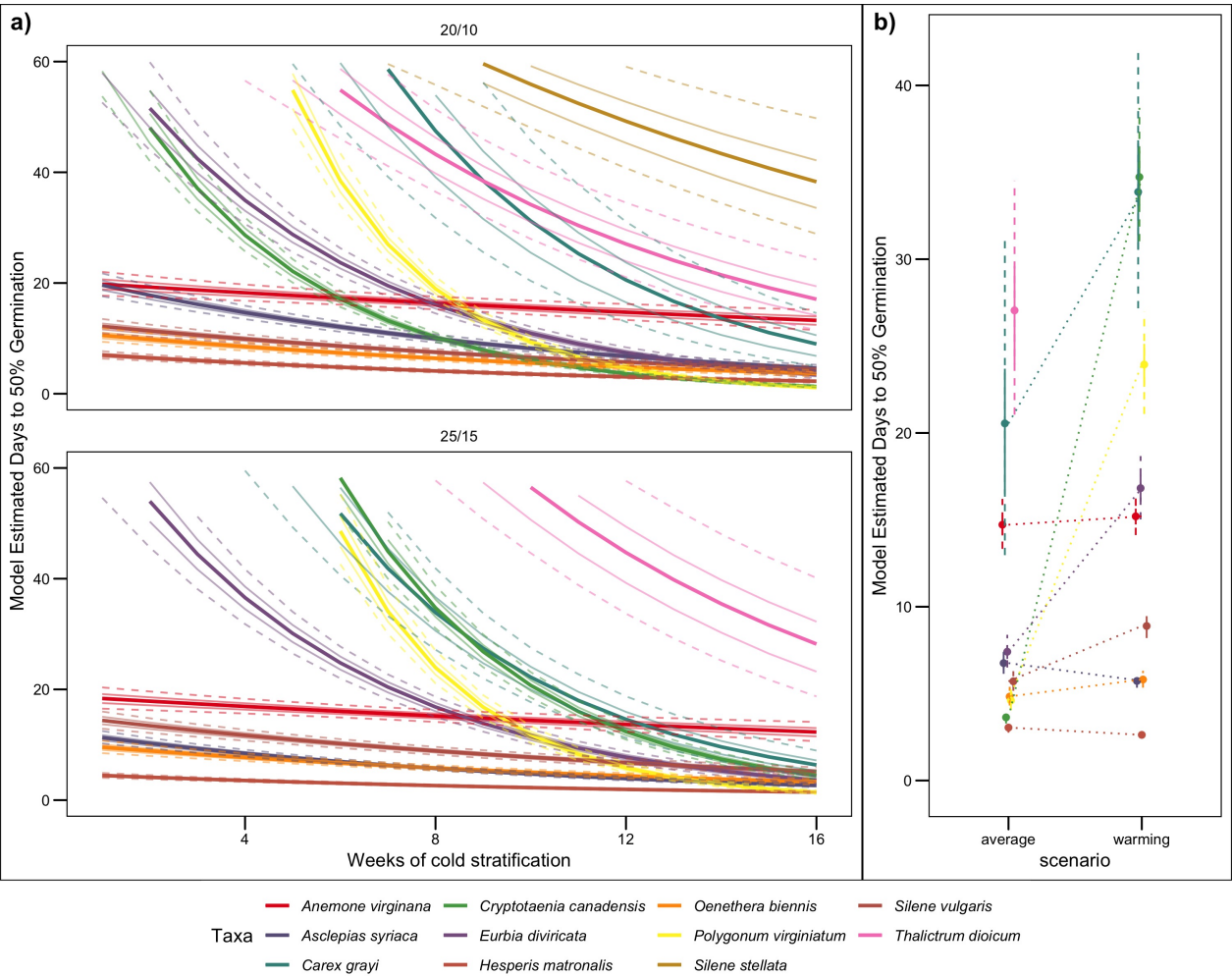


Figure 1



```
## Registered S3 method overridden by 'xts':
## method from
## as.zoo.xts zoo
```

	Taxa	Hesperis matronalis	Silene vulgaris	Oenothera biennis	Asclepias syriaca	Silene stellata	Eurbia divir
1	Hesperis matronalis						
2	Silene vulgaris	3.6					
3	Oenothera biennis	1.4	-2.2				
4	Asclepias syriaca	-0.6	-4.2	-2			
5	Silene stellata	124.6	121	123.2	125.2		
6	Eurbia diviricata	9.8	6.2	8.4	10.4	-114.7	
7	Anemone virginana	0.9	-2.7	-0.5	1.5	-123.7	-8.9
8	Cryptotaenia canadensis	31.5	27.9	30.1	32.1	-93.1	21.7
9	Carex grayi	13.7	10.1	12.3	14.3	-110.8	3.9
10	Thalictrum dioicum	44.9	41.3	43.5	45.5	-79.7	35.1
11	Polygonum virginiatum	19.8	16.1	18.3	20.4	-104.8	9.9