VOL. 195, NO. 6 THE AMERICAN NATURALIST JUNE 2020

E-Article

Species Differences in Phenology Shape Coexistence

Christopher Blackford,[1,2] Rachel M. Germain,[1,3] and Benjamin Gilbert[1,*]

1. Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada; 2. Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sault Sainte Marie, Ontario, Canada; 3. Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

Submitted March 6, 2019; Accepted December 9, 2019; Electronically published April 29, 2020

Online enhancements: supplemental PDF. *Dryad data:* https://doi.org/10.5061/dryad.0vt4b8gv9.

ABSTRACT: Ecological theory produces opposing predictions about whether differences in the timing of life-history transitions, or "phenology," promote or limit coexistence. Phenological separation is predicted to create temporal niche differences, increasing coexistence, yet phenological separation could also competitively favor one species, increasing fitness differences and hindering coexistence. We experimentally manipulated relative germination timing, a critical phenological event, of two annual grass species, *Vulpia microstachys* and *V. octoflora*, to test these contrasting predictions. We parameterized a competition model to estimate within-season niche differences, fitness differences, and coexistence and to estimate coexistence when year-to-year fluctuations of germination timing occur. Increasing germination separation caused parallel changes in niche and fitness differences, with the net effect of weakening within-year coexistence. Both species experienced a competitive advantage by germinating earlier, and a 4-day head start allowed the generally inferior competitor to exclude the otherwise superior competitor. The overall consequence of germination separation was to limit coexistence within a given year, although year-to-year variation in the relative timing of germination was sufficient to support long-term coexistence. Our results clarify how phenological differences structure competitive interactions and highlight the need to quantify year-to-year variation in these differences to better understand species coexistence.

Keywords: coexistence theory, competition, germination timing, phenology, priority effects, *Vulpia*.

Introduction

Species in many ecological communities show striking differences in the seasonal phenology of life-history events, but the consequences of phenological differences for species coexistence are widely debated (Rabinowitz et al. 1981). Classic models predict that differences in phenology lead to reduced niche overlap among species, promoting coexistence (Gotelli and Graves 1996; Albrecht and Gotelli 2001). However, earlier phenology may also reduce resources available to later individuals or lead to size-structured competitive asymmetries, reducing the possibility of coexistence (Godoy and Levine 2014; Rudolf 2019). Resolving these conflicting hypotheses is essential in this era of global change—species' phenologies are shifting with climate change at different rates (Edwards and Richardson 2004; Scranton and Amarasekare 2017; Kharouba et al. 2018), and it is unclear how the fitness consequences of those shifts will play out in competitive environments (Yang and Rudolf 2010; Rudolf 2019).

Coexistence theory offers a conceptual framework to understand how competitive interactions change when species differ in phenology. Specifically, Chesson (2000) proposed two types of competitive differences that have opposing effects on coexistence and can be quantified and then associated with specific traits (Kraft et al. 2015), such as phenology (Godoy and Levine 2014): niche differences and fitness differences. Niche differences are present when intraspecific competition exceeds interspecific competition, thus introducing negative frequency dependence that prevents any one species from dominating a community, stabilizing coexistence. By contrast, fitness differences are competitive asymmetries that give one species an advantage over the other and thus limit the potential for coexistence. The combined effects of niche differences and fitness differences determine whether each species in a competitive pair can increase from low density when the other is abundant and thus whether coexistence or exclusion are predicted (fig. 1). Thus, the effects of phenological differences between competing species on coexistence is quantifiable by how they contribute to niche differences, fitness differences, or both.

Research has provided mixed support for predictions of increased and decreased coexistence with phenological differences. Using annual plant communities from California,

* Corresponding author; email: benjamin.gilbert@utoronto.ca.

ORCIDs: Blackford, https://orcid.org/0000-0001-5017-5827; Germain, https://orcid.org/0000-0002-1270-6639; Gilbert, https://orcid.org/0000-0002-4947-6822.

Am. Nat. 2020. Vol. 195, pp. E168–E180. © 2020 by The University of Chicago. 0003-0147/2020/19506-59103$15.00. All rights reserved.
DOI: 10.1086/708719

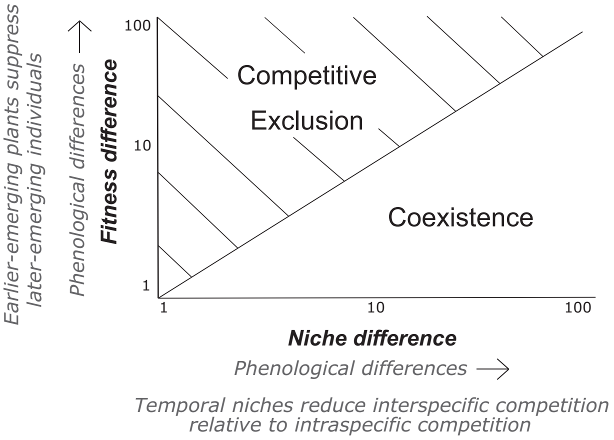


Figure 1: Opposing hypotheses about the effect of phenological differences on coexistence. Conceptual models of the effects of phenological differences (gray) are mapped onto a coexistence framework (Adler et al. 2007). Coexistence occurs below the 1 : 1 line, when niche differences ($1/\rho$) are high and fitness differences (κ) are low. Note that although niche differences are typically presented as $1 - \rho$, causing the coexistence threshold to be nonlinear, our presentation of $1/\rho$ allows a 1 : 1 comparison of these differences to determine coexistence. The formulas relating these differences to coexistence when phenological differences are consistent among years are given in equations (2) and (3).

Godoy and Levine (2014) contrasted niche and fitness differences among plant species that differ in timing of flowering: early, mid, or late in the growing season. They found that although phenological differences did increase niche differences, they contributed most strongly to fitness differences in favor of late-flowering plants (Godoy and Levine 2014). This study provides some of the clearest evidence about how phenological differences among co-occurring species map onto their competitive differences. However, the phenological differences observed were correlated to a suite of competitive traits, and the authors suggest that these correlated traits (rooting depth and biomass) may ultimately be responsible for the observed effect of phenology (Godoy and Levine 2014). Additionally, they considered broad differences in phenology, such as summer versus winter life histories, a magnitude of difference among species that is unlikely to shift with climate change. Recent theory has also highlighted the importance of understanding year-to-year variation in phenological differences for coexistence (Rudolf 2019), suggesting that mean differences between species may not be sufficient for capturing the range of impacts that phenological differences can produce. An experimental approach that manipulates phenology directly is necessary to isolate its effects, especially as shifting climatic regimes alter phenological responses independently of other traits (Kharouba et al. 2018).

Germination is a key phenological event for plants, as its timing determines whether seedlings will grow in a tolerable climate and sets the competitive arena each plant will face (Donohue 2003), affecting fitness (Akiyama and Ågren 2013). Not surprisingly, germination responds plastically to climate (Young et al. 2001; Levine et al. 2011), such that fluctuating climatic conditions can alter the absolute and relative timing of germination among species (Young et al. 1981). The composition of the neighboring seed community also influences germination timing (Goldberg et al. 2001; Lortie and Turkington 2002). For example, Dyer et al. (2000) observed that a native California bunchgrass, *Nassella pulchra*, altered its timing of germination when seeds of competing species were present, with approximately half of all species causing *N. pulchra* germination to accelerate. This separation of germination timing might be an adaptive response to avoid interspecific competition (Young et al. 2017), especially given that competition tends to be particularly high during the emergence life stage (Goldberg et al. 2001; Chu and Adler 2015). For example, ontogenetic shifts in seedling stoichiometry (Méndez and Karlsson 2005; Zhang et al. 2013) may cause separation in germination timing to increase resource partitioning. If so, species may show greater niche differences and lower fitness differences when their germination is temporally segregated from other species. However, the alternate possibility—that early germination generates competitive differences that benefit earlier species—has also been observed in several studies (Harper et al. 1961; D'Antonio et al. 2001; Abraham et al. 2009; Grman and Suding 2010), although it is unclear whether such advantages of early germination are symmetric or benefit some species more than others, potentially altering coexistence outcomes. Most studies of fine-scale variation in germination phenology do not test their net effects on niche differences, fitness differences, or coexistence, limiting their inferences (e.g., Young et al. 2001).

In this study, we experimentally isolate the effects of differences in germination timing on the coexistence of a congeneric pair of annual grasses, *Vulpia microstachys* ((Nutt.) Munro) and *V. octoflora* ((Walter) Rydb.). Germination phenology offers a unique opportunity for experimental manipulation, as it is straightforward to induce for many species and, in doing so, clearly separates germination phenology from other traits. We manipulated the relative germination timing of these two *Vulpia* species, allowing each to germinate up to 10 days in advance of the other and used an additive competition design to parameterize an annual plant model (Godoy and Levine 2014; Germain et al. 2016). We combined this experiment with information from a previous study to determine (1) the effect of differences in germination timing on niche differences, fitness differences, and coexistence and (2) how these outcomes change if differences in germination timing fluctuate from year to year. We show that early germination generally confers a competitive advantage, and when germination phenology varies from year to year—for example, as a result of climatic variability—the influence of phenology on coexistence differs on short (within-year) and long (year-to-year) timescales.

Methods

Study Species and Competition Experiment

Vulpia microstachys and *V. octoflora* are generalist grasses that are widely distributed in California and commonly co-occur (Brooks 2000; Hoste 2013). As winter annuals, they germinate in late fall under cool, wet conditions and complete their life cycle by midsummer. *Vulpia microstachys* germinates faster than *V. octoflora* under identical environmental conditions (fig. S1; figs. S1–S6 are available online), making it plausible that differences in their germination schedules promote coexistence. *Vulpia microstachys* has been shown to be competitively dominant to *V. octoflora* because of a lower resource requirement (R^*) for several limiting resources (HilleRisLambers et al. 2010) and possibly because of its larger seeds. However, both species frequently persist together in mixed communities (HilleRisLambers et al. 2010).

To begin our competition experiment, seeds of *V. microstachys* and *V. octoflora* were germinated in separate petri dishes over 3 weeks. Each petri dish contained 30 seeds of one species (seed density of 0.47 seeds/cm^2) on filter paper, moistened with a 0.15% (v/v) solution of *Previcur* fungicide to suppress fungal growth that could interfere with germination. There were 130 replicate petri dishes per species, which were sealed and kept under greenhouse conditions that simulated a Californian winter. Daytime temperatures were set to maintain a 20°/15°C day/night temperature schedule with a 10-h day length provided by supplemental high intensity discharge lighting. These conditions were maintained throughout plant growth.

As seeds germinated (i.e., the moment the radicle broke through the seed coat), they were transplanted to 0.65-L cone-shaped pots (diameter of 6.9 cm, depth of 25.4 cm) of sandy-loam soil, with the radicle slightly buried. We manipulated relative germination timing by planting germinants into the same pot on different days. Our pilot studies suggested that *V. octoflora* reaches full germination 5 days after *V. microstachys*, so we experimentally varied the relative order of germination of the two species between -10 and 10 days. Specifically, we constructed five treatments that varied the order of germination for the two species relative to each other, with each species planted 10 and 5 days before the other, and one treatment where both were planted simultaneously (resulting in five treatments). To control for any effect of taking early- or late-germinating individuals and to ensure enough seeds had germinated to conduct our experiment, seedlings were transplanted when total germination of each species reached 50%, which our pilot studies predicted would occur within 1–2 days for *V. microstachys* and 5–6 days for *V. octoflora* (fig. S1). Because of natural variation in the exact time 50% germination was achieved, some of our germinants in this study were not planted precisely at 5-day intervals but instead were planted within a 24-h window of that period. Given that this temporal window is small relative to our treatments, we do not account for this variation in our analysis, and going forward refer to our treatments as -10, -5, 0, 5, and 10 days. There were 20 replicate pots of each treatment (20 pots × 5 treatments $=$ 100 total pots), with pots containing 11 seedlings of each species to produce an overall density of 22 seedlings per pot, or 0.59 seedlings/cm^2, which has previously been shown to be a density at which competitive interactions are apparent (Germain et al. 2016).

We also planted monoculture control treatments (six treatments total) with 11 seedlings per pot. We replicated each monoculture for each species three times for each planting date (0, 5, and 10 days into the experiment), so that they could be paired with the competition experiments, resulting in 60 pots (2 species × 3 planting dates × 10 pots). This additive design allowed us to estimate the effects of adding interspecific competitors and whether this effect differed depending on the absolute date of germination. In combination with estimates of seed production in the absence of any competitors that were taken from a previous experiment (Germain and Gilbert 2014), this also allowed us to parameterize a competition model requiring estimates of intra- and interspecific competition (see below).

Growing conditions in the greenhouse were set according to earlier studies that included these same species, facilitating model parameterization (Germain and Gilbert 2014; Germain et al. 2016, 2018*b*). Following planting, 80 mL of water was added to each pot every 3 days via a drip irrigation system, and 75 mL of 1,500 ppm 20-20-20 NPK fertilizer was added after 4 weeks but before flowering. Separately for each species, all mature seed produced in each pot was collected, counted, and weighed. We then used these data to calculate finite rates of increase (number of viable seeds produced per plant) and mean mass per seed (mg/seed). Germination tests were conducted on seeds produced in our experiment to assess the proportion of viable seeds that would germinate (parameter g in eq. [1]; details below). We randomly selected five pots per germination timing treatment, and from those five pots we haphazardly selected 50 seeds per species that were then germinated under the same conditions as the parent seeds (in petri dishes; described above). Although competition models assume the effects of competition manifest through the number of seeds produced, competition might also impact the mass of individual seeds (Germain et al. 2018*a*); we also measured mass per seed to test this possibility. The experiment lasted until all plants had produced seed and senesced.

Effects of Germination Separation on Demography

We first conducted tests to determine which population parameters were influenced by germination separation. To do so, we used the competition treatments to test the effects of germination separation on species' per capita growth rates (log of the number of seeds produced per plant), germination rates of the seeds produced, and seed mass. For these tests, we used generalized linear mixed effects models (lme4 package in R) with species, germination separation, and their interaction included as fixed effects. Experimental "pot" was included as a random factor to account for the lack of independence of measurements performed on both species in a single pot. Germination separation was treated as a continuous variable of the number of days that *V. microstachys* germinated relative to *V. octoflora* (with treatments replicated at −10, −5, 0, 5, and 10 days of separation). Our model testing germination rate used a quasi-binomial distribution, whereas our models for (log) seed number and seed mass used normal distributions. Monoculture control pots were analyzed using generalized linear models that included species and absolute timing of germination as predictors but that lacked random effects, as we had only one response (one species) per pot.

Parameterizing a Two-Species Beverton-Holt Model Using Experimental Data

We combined our experimental data and previously published data (Germain and Gilbert 2014) to parameterize a Beverton-Holt annual plant competition model, which has previously been shown to capture the competitive dynamics of many annual plant species, including our focal species (Levine and HilleRisLambers 2009; Godoy and Levine 2014; Germain et al. 2016). We note that fitting population models requires manipulation of intra- and interspecific densities (e.g., Godoy and Levine 2014; Germain et al. 2016), as we have done here, as well as estimates of each species' population growth rate in the absence of competition (the λ parameters, explained below), for which we have estimates from our previous research under identical conditions. Without estimates of λ, we would be able to test relative differences in the per capita strength of intraspecific and interspecific competition but not the absolute value of each parameter (Broekman et al. 2019). Below, we describe how we incorporated λ estimates from previous research into our Bayesian priors and how we tested how sensitive our main findings were to uncertainty in these estimates.

We parameterized the following Beverton-Holt model with phenological differences:

$$\frac{N_i(t+1)}{N_i(t)} = \frac{g_i\lambda_i}{1 + g_i\alpha_{ii}N_i(t) + g_j\alpha_{ijp}N_j(t)} + (1-g_i)s_i, \tag{1}$$

where the finite rate of increase of species i, $N_i(t+1)/N_i(t)$, depends on the competitive dynamics (fraction on the right-hand side of eq. [1]) of those seeds that germinate (g_i) and the survival rate (s_i) of those seeds that do not germinate (second term on the right-hand side of eq. [1]). Competitive dynamics of germinated seeds are a function of the maximum rate of increase in the absence of competition (λ_i), the per capita intraspecific competitive impact (α_{ii}), and the per capita interspecific competitive effects of species j on species i (α_{ijp}). The subscript p denotes the value of α_{ij} specific to a particular phenology (germination) treatment. Because the Beverton-Holt model is symmetric, the dynamics of species j are represented by switching subscripts i and j in equation (1).

The model in equation (1) makes several assumptions about how phenology influences competitive dynamics. First, it assumes that the maximum rate of increase (λ_i) and intraspecific competition (α_{ii}) do not depend on phenological timing. We made this assumption on the basis of our demographic results; our analyses revealed no effect of planting date on seed production in the monoculture treatments (see "Results" and fig. S2), meaning either that the maximum rate of increase (λ_i) and intraspecific competition (α_{ii} in eq. [1]) did not vary with planting date (a result that is not surprising given that greenhouse conditions were held constant throughout the experiment) or that both varied in a perfectly correlated manner (a biologically unlikely outcome; see the supplemental PDF, available online). These results justify parameterizing our competition model with interspecific competition (α_{ij}, α_{ji}), but not intraspecific competition (α_{ii}, α_{jj}) or maximum rate of increase (λ_i, λ_j), changing as a function of germination separation. We similarly assume that germination and survival of seeds in a generation are not influenced by phenology, although we do measure the effect of phenology on germination rates in the subsequent generation and incorporate these rates into our model for year-to-year variation in germination timing (described below).

Parameters for the Beverton-Holt model were estimated either through Bayesian model fitting (α, λ) or directly from the data (g; table S1; tables S1, S2 are available online). First, the competition (α) and maximum seed production (λ) parameters were estimated through Bayesian model fitting. We opted to use a Bayesian approach because we had biological reason to use informative priors and because it allows a simplified calculation of credible intervals for composite parameters (described below). We fit the first part of equation (1) for seeds that had germinated (the fraction on the right-hand side, excluding the parameter g). For this fitting, we used our experimental data (competition and monoculture pots) as well as data from a previous study that provided λ estimates for our focal species (Germain and Gilbert 2014). In particular, we used informative priors for the λ parameters that were taken from a study designed to estimate maximum rates of increase for these species in growing conditions similar to those used in the current experiment, with mean $\log(\lambda)$ of 5.4 and 7.0 and precision of 4.7 and 4.0 for *V. microstachys* and *V. octoflora*, respectively (table S1; Germain and Gilbert 2014). All α parameters used prior distributions that were constrained to be positive (by assuming each was lognormally distributed) but were otherwise uninformative (for all $\log(\alpha)$, mean $= 0$, precision $= 0.01$). We estimated seven parameters per species (λ, $\alpha_{\text{intraspecific}}$, and five $\alpha_{\text{interspecific}}$ parameters per species, with the five latter parameters being fit for each relative germination timing). Additional details on the Bayesian model fitting are provided in the supplemental PDF (including table S1 and fig. S4).

As stated above, we could not have parameterized the Beverton-Holt model without λ estimates from a previous experiment conducted in similar conditions (Germain and Gilbert 2014). An important assumption of the approach taken is that those estimates are accurate for our experiment. Although we cannot test this assumption with our data (we lack a low-density treatment necessary to independently estimate λ), we can test the sensitivity of our results to this assumption by varying λ priors to see whether differences in these priors caused our conclusions to change. To do this, we used all combinations of λ priors that ranged from one-half the estimate to the actual estimate to twice the estimate reported (supplemental PDF). This sensitivity analysis confirmed that the qualitative trends we report are robust to a range of λ estimates (figs. S5, S6).

Unlike the α and λ parameters, we estimated g directly by conducting germination tests on the viable seeds produced in our experiment. Because measuring the survival rate of ungerminated seeds (s) in a greenhouse setting is not meaningful (e.g., no seed predators), we repeated all analyses with two extreme values, $s = 0$ and $s = 1$, to determine the sensitivity of our results to this parameter. For within-year calculations (eqq. [2]–[4]), this parameter did not qualitatively change our results, so we report only $s = 0$ using mean germination rates for each species (table S2).

Estimating Within-Year Niche and Fitness Differences

Once we had estimates of germination, seed survival, and competitive interactions as a function of our manipulations of germination timing, we used these parameters to calculate niche differences, fitness differences, and their net effect on coexistence. When all viable seeds germinate, a stabilizing niche difference ($1/\rho$) in the Beverton-Holt model is

$$\frac{1}{\rho} = \sqrt{\frac{\alpha_{jj}}{\alpha_{ijp}} \cdot \frac{\alpha_{ii}}{\alpha_{jip}}}. \tag{2}$$

And the pairwise fitness difference (κ) is given as

$$\kappa = \max\left(\frac{\kappa_j}{\kappa_i}, \frac{\kappa_i}{\kappa_j}\right),$$

where

$$\frac{\kappa_j}{\kappa_i} = \frac{\lambda_j - 1}{\lambda_i - 1} \cdot \sqrt{\frac{\alpha_{ijp}}{\alpha_{jj}} \cdot \frac{\alpha_{ii}}{\alpha_{jip}}}. \tag{3}$$

Coexistence is predicted to occur when $\kappa < 1/\rho$ (Godoy and Levine 2014; Germain et al. 2016), meaning that fitness differences are less than niche differences. When this condition ($\kappa < 1/\rho$) is met, populations of each species are expected to increase when at low density and the other is at its equilibrium abundance. The subscript p denotes the phenological separation for a year (affecting interspecific competition), and the niche and fitness differences calculated here assume that this separation is constant through time. We note that niche differences are often presented as $1 - \rho$, but we use the definition in equation (2) because it allows for a clearer graphical interpretation of coexistence outcomes by putting niche and fitness differences on the same scale (i.e., a linear coexistence threshold in fig. 1); whenever the point defined by equation (2) exceeds that defined by equation (3), both species are expected to increase when initially at low densities. When some viable seeds fail to germinate, equation (3) changes such that the first fraction becomes

$$\frac{\eta_j - 1}{\eta_i - 1},$$

where

$$\eta_j = \frac{\lambda_j g_j}{1 - s_j + s_j g_j}$$

(Godoy and Levine 2014). High levels of germination in our study (97% and 86% mean germination rates for *V. microstachys* and *V. octoflora*, respectively) caused $\eta \approx \lambda$.

The coexistence criteria $\kappa < 1/\rho$ specifies the conditions necessary for both species to have positive population growth rates when at low density. Population growth rates under these conditions are referred to as "invader growth rates" (Siepielski and McPeek 2010), which we can also solve directly using the equation

$$\log(\lambda_{\text{inv}}) = \log(\lambda_i) - \log\left(1 + \alpha_{ij}\left(\frac{\lambda_j - 1}{\alpha_{jj}}\right)\right). \quad (4)$$

When both species have positive invader growth rates (eq. [4] > 0), meaning that both competitors can invade when their competitor is at its equilibrium abundance, coexistence is predicted because both are buffered from extinction when at low abundances (Chesson 2000). We note that equation (4) can be modified to include a seed bank, as in equation (1). Examining invader growth rates allows a simple examination of the net effect of niche differences and fitness differences on the relative success of each species as well as a straightforward test of coexistence outcomes on longer timescales (described in the next section).

Simulating Year-to-Year Variation in Germination Phenology

To explore how year-to-year variation in germination phenology alters coexistence outcomes, it is necessary to know the distribution of phenological differences that species experience through time. Because this distribution is not known for any system that we are aware of, we simulated a simple scenario for which each species germinated in advance of the other by *n* days half of the time. For example, *V. microstachys* would germinate 5 days in advance of *V. octoflora* half of the time and 5 days behind half of the time, 10 days in advance and 10 days behind, and so on. We then solved the mean of the invader growth rate for each species or, equally, the long-term invader growth rate when the focal species is rare and the competing species is at its long-term equilibrium. This analysis is greatly simplified because the resident carrying capacity was unchanged by fluctuating germination dates, so that only interspecific competition varied in equation (4) (see "Results"; app. S1 in the supplemental PDF). However, germination rate and seed survival also influence temporal coexistence (e.g., Chesson and Huntly 1989; Abrams et al. 2013), and we found that germination varied slightly among treatments for *V. microstachys* (see "Results"). As a result, we used the germination rate recorded for each treatment in our temporal simulations and supplemented this analysis by exploring how sensitive the outcome was to seed survival rate by testing the extreme cases of no survival or perfect (100%) survival.

Results

Each species produced a greater number of seeds per individual when it germinated earlier than the other species (fig. 2; significant species × germination time [$F_{1,196} = 617.3$, $P < .001$]). *Vulpia microstachys* showed a twofold increase in seed production when it germinated 10 days earlier versus 10 days later than *V. octoflora*, whereas this difference was tenfold for *V. octoflora* (fig. 2). We found no effect of planting time on the number of seeds produced when each species was grown alone in monoculture (fig. S2; nonsignificant time and time × species interaction [$P > .2$]), meaning that intraspecific competition was independent of planting date.

Increases in seed production due to early germination were not counteracted by shifting seed mass. Although seed mass varied with differences in germination time, each species produced larger seeds on average when they germinated earlier (fig. S3; significant germination time × species interaction [$F_{1,100} = 25.8$, $P < .001$]), reinforcing the seed number trends. Although present, seed mass changes were small relative to seed number trends, increasing 1.06- and 1.11-fold for *V. microstachys* and *V. octoflora*, respectively, between the earliest and latest germination times (fig. S3). Because of this relatively small change in seed mass and the unknown consequences for seed mass on competition, we did not incorporate seed mass into calculations of coexistence. Rates of offspring seed germination for *V. microstachys* also showed a significant but small shift from a mean of 99.6% (10 days in advance) to 97.2% (10 days behind), but they did not change significantly for *V. octoflora* (quasi-binomial regression $P = .029$ for *V. microstachys*, $P = .145$ for *V. octoflora*; table S2). Although the effect of differences in *V. microstachys* germination rate was small, we used germination at each treatment level for *V. microstachys* when calculating the consequences of fluctuating phenological timing (detailed below).

The effect of germination separation on niche differences and fitness differences was asymmetric (fig. 3*A*); both differences increased with germination separation when *V. microstachys* germinated first, but these differences first decreased and then increased when *V. octoflora* germinated first. This asymmetric effect can be understood by examining invader growth rates (fig. 3*B*). Fitness differences were smallest when invader growth rates intersected, at ~4–5 days germination separation, and niche differences largely paralleled these fitness differences.

The overall effect of differences in germination timing was that each species could invade and exclude the other when its germination was sufficiently in advance of the other (fig. 3*B*). There was a narrow window where coexistence was predicted to occur—when *V. octoflora* germinates

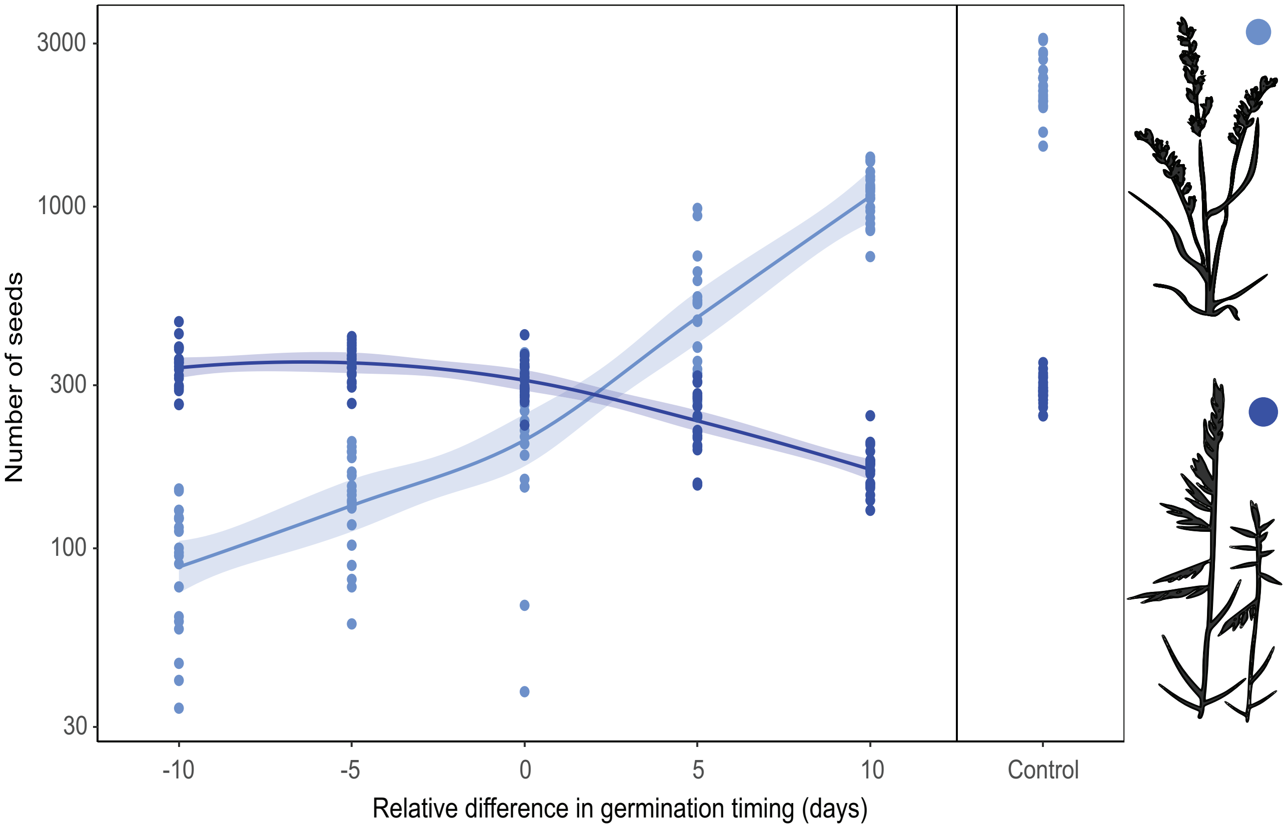


Figure 2: Differences in germination timing increase seed production for the earlier species. Plants produce two (*Vulpia microstachys*; dark blue) to 10 (*V. octoflora*; light blue) times the number of seeds when they germinate 10 days in advance of the other species relative to when they germinate 10 days after the other. Relative germination timing is negative when *V. microstachys* germinates earlier. Each data point shows the number of seeds produced per experimental pot with 11 individuals of the focal species and its competitor. Control plots are monospecific with 11 individuals.

~4 days ahead of *V. microstachys*—but we note that this narrow window was interpolated from data at different phenological separations (we tested 0- and 5-day separations but not a 4-day separation). Interestingly, invader growth rate responses to germination timing were also qualitatively different for these species. *Vulpia octoflora* rates increased linearly as germination advanced, whereas for *V. microstachys* invader growth rates were constant up until *V. microstachys* had a 5-day head start and showed only small changes up until equal germination (0-day difference), after which it decreased sharply (fig. 3*B*). This nonlinear response was caused by the invasion growth rate of *V. microstachys* being limited by its maximum finite rate of increase, rather than by competition, when it germinated earlier than *V. octoflora*. Data underlying figures 2 and 3 have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.0vt4b8gv9; Blackford et al. 2019).

Our analysis of invader growth rates (eq. [S5]) indicates that year-to-year variation in interspecific competition via germination timing could promote long-term coexistence. Since differences in per capita interspecific competition (the only parameter in eq. [1] to vary with germination separation) favored different species in different scenarios, fluctuations through time might prevent exclusion of one species by the other from being realized. Mathematically, this occurs even in the absence of other fluctuations for two reasons. First, the curvature of competitive impact with germination separation can cause the mean effect of competition to differ from competition at the mean separation simply as a result of Jensen's inequality (Rudolf 2019). Second, fluctuations in interspecific competition reduce its geometric mean (the second half of eq. [4]) and thereby increases the long-term invader growth rate for both species (app. S1 in the supplemental PDF). To test the hypothesis that germination timing alters coexistence, we simulated invasion potential of each species when germination timing fluctuated from year to year, giving one species an advantage only half of the time. We found that *V. octoflora*, the weaker competitor on average, could persist when germination

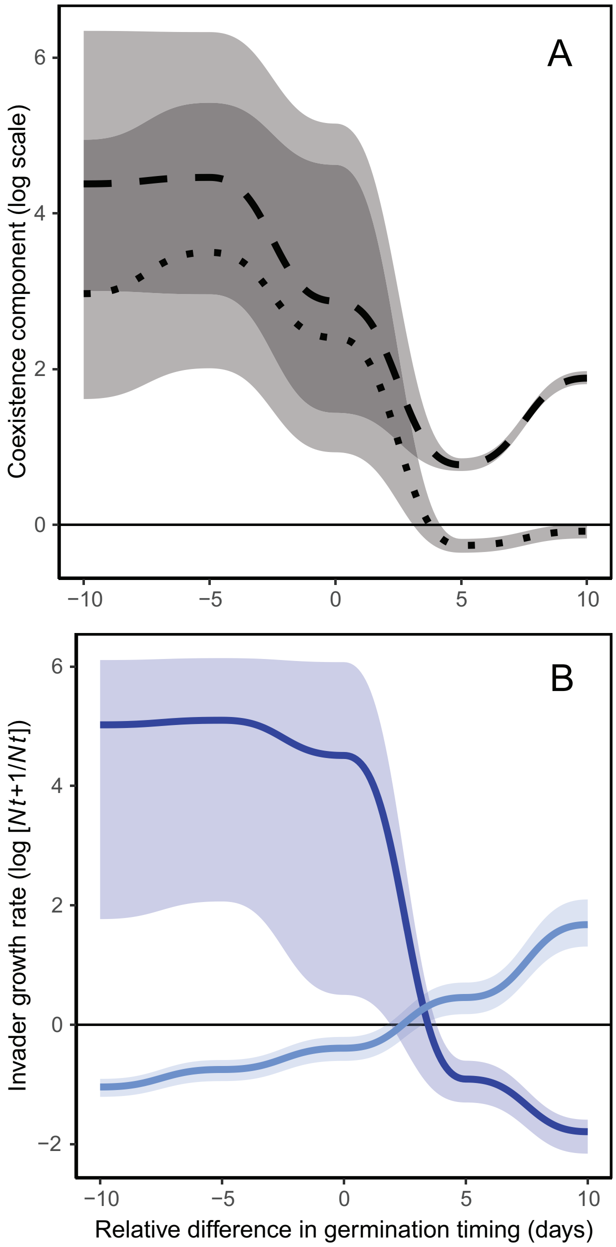


Figure 3: Differences in germination timing structure fitness differences and niche differences. *A*, Fitness differences (dashed line; eq. [3]) and niche differences (dotted line; $1/\rho$ from eq. [2]) are greatest when phenological differences are large and cause *Vulpia microstachys* to germinate first (left side of *A*). These components have the property that niche differences must exceed fitness differences for stable coexistence in a given environment. Minimum fitness differences coincide with minimum niche differences (i.e., maximum niche overlap), meaning that the components that limit coexistence are each favored by different phenological pairings. *B*, Greater phenological differences in germination increase low-density growth rates of the earlier germinating species. *Vulpia microstachys* is shown in dark blue, and *V. octoflora* is shown in light blue. Coexistence appeared to be possible when shifts in germination timing caused a change in the superior competitor (~4-day difference). We note that the crossover in higher fitness between species (~4 days, where log fitness differences have to equal zero) was not captured by the interpolation in *A*. In general, consistent differences in relative germination timing causes larger fitness differences than niche differences. Lines in both panels represent medians of data, and envelopes delineate the 50% credible intervals (25th to 75th percentile). Phenology effects were measured at 5-day intervals (−10, −5, 0, etc.), and lines between points were extrapolated using a weighted function.

timing shifted between ±7 or more days per year (fig. 4). In contrast, *V. microstachys* persisted regardless of the amount of year-to-year variation. Thus, stable long-term coexistence was predicted only under scenarios of larger fluctuations in relative germination timing.

Discussion

Phenological differences between species have the potential to promote coexistence through increasing niche differences or drive competitive exclusion through increasing fitness differences. Thus, predicting how species' phenological differences affect species coexistence is not clear, especially when those phenological differences fluctuate through time (Carter et al. 2018; Rudolf 2019; Satyanti et al. 2019). Our experiment shows that although phenological differences in germination timing between two *Vulpia* species contribute to both niche and fitness differences, increases in fitness differences outweigh any increases in niche differences. Thus, the net effect is limited coexistence in almost all circumstances (with the exception of a very narrow difference in germination timing), so long as phenological differences are consistent among years. However, long-term coexistence is possible through fluctuations in phenological timing among years that effectively alternate the identity of the dominant competitor from year to year. Together, these results suggest that apparently contrasting research concluding that phenological differences limit coexistence (e.g., Godoy and Levine 2014) or promote coexistence (e.g., McKane et al. 1990) may be due in part to the temporal scales considered.

Earlier Phenology Increases Fitness Differences More Than Niche Differences

Our research clarifies how consistent phenological differences reduce coexistence by primarily affecting fitness asymmetries, with more dramatic phenological differences leading to larger fitness differences. This result echoes the conclusion of a recent field-based study of phenology that is, to our knowledge, the only other phenological research to disentangle coexistence mechanisms (Godoy and Levine 2014). Despite these apparent similarities between studies, phenological differences conferred fitness

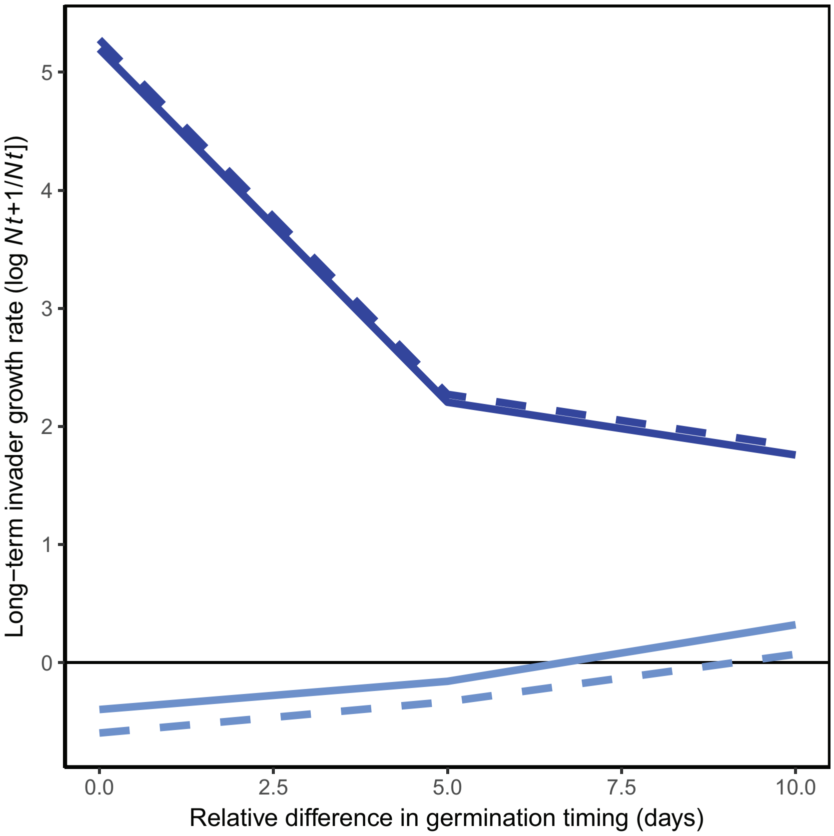


Figure 4: Large changes in the relative timing of germination from year to year favors coexistence. Shown is the invasion potential of both species when conditions cause one species to germinate earlier half the time and the other species to germinate earlier the rest of the time. The more extreme the differences in germination timing, the more coexistence is favored; both species are predicted to persist if the annual differences in germination timing are 7 days or more and all dormant seeds survive (solid lines) or greater than 9 days even with no dormant seed survival (dashed lines). Colors are light blue for *Vulpia octoflora* and dark blue for *V. microstachys*. See "Methods" for details.

advantages in opposite scenarios—we found that earlier phenological timing caused species to be more competitive, whereas Godoy and Levine (2014) found the opposite. These opposing findings may be explained by two differences in how phenology was examined. First, in our study we examined differences in phenology through separation of germination timing, whereas Godoy and Levine (2014) contrasted species that flower and reproduce at different times of the year (early spring vs. summer) despite germinating concurrently. In other words, our experiment provided plants with constant light and water throughout the experiment, which provided the earlier-to-germinate species with a "head start" on resource uptake and competitive ability (Ross and Harper 1972). By contrast, in Godoy and Levine (2014) species with later phenology had a demographic advantage due to an extended growing season, which allowed for resource uptake after the early species had senesced. Second, our experimental approach isolated the impacts of germination timing, whereas their approach captured phenological differences that correspond with suites of traits that influence reproductive rates (e.g., rooting depth and stem height; Godoy and Levine 2014). As a result of these differences between studies, it is unclear if our common response of fitness differences to phenology reflects a broad pattern or was simply coincidental, warranting future manipulative experiments in other species.

We additionally found that the two *Vulpia* species differed in their sensitivity to separation of germination timing, illustrating that even closely related species respond differently to small changes in germination phenology by accruing different absolute advantages with early germination. The competitively dominant species *V. microstachys* had large impacts on *V. octoflora* in all treatments, reducing seed production compared with the monoculture control treatment even when germinating 10 days after *V. octoflora* (fig. 2). By contrast, *V. octoflora* showed minimal impact on *V. microstachys* seed production compared with the monoculture control treatment when *V. microstachys* germinated first (figs. 2, 3). These differences suggest that greater phenological separation would disproportionately benefit the weaker competitor, as only *V. octoflora* has the potential to further increase its low density growth rate when phenological separation increases beyond the range manipulated in our experiment. These differences in competitive effect and maximum seed production reflect differences in seed size and number; *V. octoflora* produces almost ten times as much seed as *V. microstachys* in the absence of competition (fig. 2), but *V. microstachys* seeds are approximately five times heavier. Overall, the asymmetry in the importance of phenological timing for our *Vulpia* species suggests that differences in species' traits that determine coexistence outcomes, such as seed size and fecundity (Coomes and Grubb 2003), are likely to also influence how phenology alters competitive interactions.

A fitness advantage conferred to a species by arriving in advance of others is commonly referred to as a "priority effect" (Fukami 2015). Priority effects are well studied but tend to be measured over timescales that span generations, such as when a second species arrives after an earlier-arriving species has reached its equilibrium density (Peay et al. 2012). Measuring priority effects over shorter timescales—within the timescale of a generation—is less common (but see Black and Wilkinson 1963; Cleland et al. 2015) despite this being a relevant timescale for priority in life-history transitions to alter competitive outcomes. We show how differences in germination timing cause strong priority effects, reversing which species is competitively excluded with as little as a 5-day separation. While previous work has shown that competition may be altered by germination timing (e.g., Aarssen 1989; Bergelson and Perry 1989; Cleland et al. 2015), it is surprising that the effects we document are large enough to be comparable to those caused by separation over generations (Fukami 2015).

Unlike priority effects that are produced over longer timescales from positive density-dependent population growth and never promote local coexistence (Ke and Letten 2018), we show that within-season priority through germination differences could actually promote long-term coexistence if germination hierarchies vary from year to year. Specifically, we found that fluctuating conditions that lead to each species germinating in advance of the other in different years can promote coexistence through competitive fluctuations alone, even though coexistence is not possible if germination timing is consistent among years. This finding supports recent theoretical predictions (Rudolf 2019) and suggests that manipulating germination phenology could alter coexistence outcomes of native and exotic plant species (Wainwright et al. 2011). Interestingly, our analysis suggests that species alternating germination timing from year to year has the potential to benefit both species when at low density (eq. [S5]), suggesting a larger role for fluctuations in phenological timing on coexistence. While this hypothesis has not been tested explicitly, the results of our empirically parameterized simulations and widespread differences in germination timing commonly found in nature indicate that it may be important for species coexistence in systems with periodic recruitment, such as annual grasslands.

Relevance to Natural Systems

In this study, manipulating the germination timing of two competing *Vulpia* congeners altered their competitive interactions (figs. 2, 3). Although we do not have data on how sensitive the germination timing of each *Vulpia* species is in natural conditions, our goal was not to predict the actual coexistence of these species in the real world. Rather, we aimed to reveal the ecological consequences of germination timing. Our study suggests that even when germination timing is independent of environmental conditions, early germination can provide a sufficient advantage to overturn competitive outcomes. In the field, the timing of additional ecological factors might tip the balance of pros and cons of early germination in ways that may not be consistent among years (fig. 4), for example, if germinating too early makes individuals susceptible to frost (Inouye 2008), predation (Waterton and Cleland 2016), or a fluctuating (a)biotic environment (Thomson et al. 2017). However, we predict that although such an effect would either increase or decrease fitness asymmetries, within-season niche differences are probably affected only rarely. For an ecological factor to affect within-season niche differences, it must reinforce or counteract negative frequency-dependent population dynamics. For example, if herbivores preferentially consume the most abundant plant species only when plants germinate at similar times, an increase in germination differences would decrease niche differences. Variation in additional ecological factors among years could also facilitate coexistence in conjunction with germination differences (fig. 4) by creating fluctuations in species performances from year to year (e.g., Chesson et al. 2004). We highlight a research opportunity for similar manipulative experiments, potentially involving multiple aspects of phenology (e.g., adding plant hormones to induce flowering), that additionally alter the ecological conditions within which competition is playing out (e.g., constant vs. depleting resources, seasonal changes in environmental stress). Doing so would allow a rich understanding of when and why phenology and competition interact under scenarios of global change.

In other species, fine-scale phenological differences in germination can vary from year to year, even among closely related species (Milbau et al. 2009; Mondoni et al. 2012). In a study of 23 subarctic plant species exposed to treatments of varying snow cover and temperature, Milbau et al. (2009) found that responses to these germination cues varied among species in both direction and strength. More data like these are needed as most researchers tend to record relative differences in species' germination fractions and not differences in germination timing. Beyond germination timing, other life-history traits show variation in relative phenology across years; for example, Laube et al. (2014) show that photoperiod and temperature interact to rearrange the relative phenological timing of budburst. Similar to budburst, germination responds to multiple environmental cues, some of which are very specific (e.g., timing of rains or fires; Donohue et al. 2010). Given that different species are primed to different environmental cues and that the timing of those cues can vary across years, relative germination timing likely varies to a significant degree in the field. These differences have likely been ignored or gone unnoticed in many field systems because they may shift phenological timing by only days (e.g., 11 days in the case of *Vaccinium* species studied in Milbau et al. 2009)—a key conclusion that emerges from our study is that even shifts in relative phenology of just a few days can change competitive and coexistence outcomes.

Implications of Phenological Shifts under Climate Change

Climate change is expected to shift the relative timing of species' life-history events, which viewed through the lens of our experimental results could impact patterns of species coexistence and, as a corollary, species composition of ecological communities (Kimball et al. 2010; Levine et al. 2011). For example, Kimball et al. (2010) found that although the Sonoran Desert is becoming warmer and drier through time, species composition is shifting in favor of species that germinate and grow under colder conditions. The timing of winter rains that initiate germination has shifted to later in the year (December vs. October), causing plants to germinate under colder conditions even if average annual temperatures are on the rise. Our results imply that in the absence of interannual variability in the timing of germination, increased differences in germination phenology are unlikely to confer sufficient niche differences to increase coexistence and diversity, instead increasing the likelihood of competitive exclusion by early species. This finding offers a critical link to help predict the ecological consequences of observed phenological shifts among competitors that might arise due to climate change. At the same time, we show how year-to-year variability in germination phenology could facilitate coexistence in the long term, a plausible outcome of climate change for some species given predicted increases in interannual climate variability (IPCC 2014). Our research highlights the need to distinguish between chronic shifts in the relative timing of phenological events and fluctuations in relative timing that may produce qualitatively different outcomes for competing species (Rudolf 2019). Greater resolution on how shifts in phenological traits alter coexistence across ecological communities and the temporal scales over which these shifts are likely to have an impact is an important next step for predicting local consequences of climate change.

Acknowledgments

We thank B. Hall, A. Petri, and A. Rego for assistance in the greenhouse. Research funding was provided to B.G. by the Natural Sciences and Engineering Research Council of Canada (NSERC; DG 2016-05621) and personal funding to R.M.G. by NSERC Canada Graduate Scholarships–Doctoral Program (CGS-D), the Biodiversity Research Centre, and the Killam Trust.

Statement of Authorship

C.B. and B.G. developed the research question. C.B., R.M.G., and B.G. developed the experimental design. C.B. performed the greenhouse experiment and recorded seed data. B.G. performed model parameterization in R, and all authors contributed to figure formatting and presentation. C.B., R.M.G., and B.G. all contributed significant text to the manuscript.

Literature Cited

Aarssen, L. W. 1989. Competitive ability and species coexistence: a "plant's-eye" view. Oikos 56:386–401.

Abraham, J. K., J. D. Corbin, and C. M. D'Antonio. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. Pages 81–92 *in* A. G. Van der Valk, ed. Herbaceous plant ecology: recent advances in plant ecology. Springer Netherlands, Dordrecht.

Abrams, P. A., C. M. Tucker, and B. Gilbert. 2013. Evolution of the storage effect. Evolution 67:315–327.

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Akiyama, R., and J. Ågren. 2013. Conflicting selection on the timing of germination in a natural population of *Arabidopsis thaliana*. Journal of Evolutionary Biology 27:193–199.

Albrecht, M., and N. J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134–141.

Bergelson, J., and R. Perry. 1989. Interspecific competition between seeds: relative planting date and density affect seedling emergence. Ecology 70:1639–1644.

Black, J. N., and G. N. Wilkinson. 1963. The role of time of emergence in determining the growth of individual plants in swards of subterranean clover (*Trifolium subterraneum* L.). Australian Journal of Agricultural Research 14:628–638.

Blackford, C., R. M. Germain, and B. Gilbert. 2019. Data from: Species differences in phenology shape coexistence. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.0vt4b8gv9.

Broekman, M. J. E., H. C. Muller-Landau, M. D. Visser, E. Jongejans, S. J. Wright, and H. de Kroon. 2019. Signs of stabilisation and stable coexistence. Ecology Letters 22:1957–1975.

Brooks, M. L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. American Midland Naturalist 144:92–108.

Carter, S. K., D. Saenz, and V. H. W. Rudolf. 2018. Shifts in phenological distributions reshape interaction potential in natural communities. Ecology Letters 21:1143–1151.

Chesson, P. 2000. Mechanisms and maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–366.

Chesson, P., and N. J. Huntly. 1989. Short-term instabilities and long term community dynamics. Trends in Ecology and Evolution 4:293–298.

Chesson, P., R. L. E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, S. K. M. Ernest, A. Sher, A. Novoplansky, and J. F. Wetzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semiarid environments. Oecologia 141:236–253.

Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs 85:373–392.

Cleland, E. E., E. Esch, and J. McKinney. 2015. Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. Oikos 124:33–40.

Coomes, D. A., and P. J. Grubb. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. Trends in Ecology and Evolution 18:283–291.

D'Antonio, C. M., R. F. Hughes, and P. M. Vitousek. 2001. Factors influencing dynamics of two invasive C_4 grasses in seasonally dry Hawaiian woodlands. Ecology 82:89–104.

Donohue, K. 2003. Setting the stage: phenotypic plasticity as habitat selection. International Journal of Plant Sciences 164:S79–S92.

Donohue, K., R. R. de Casas, L. Burghardt, K. Kovach, and C. G. Willis. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution, and Systematics 41:293–319.

Dyer, A. R., A. Fenech, and K. J. Rice. 2000. Accelerated seedling emergence in interspecific competitive neighbourhoods. Ecology Letters 3:523–529.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884.

Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annual Review of Ecology, Evolution, and Systematics 46:1–23.

Germain, R. M., and B. Gilbert. 2014. Hidden responses to environmental variation: maternal effects reveal species niche dimensions. Ecology Letters 17:662–669.

Germain, R. M., T. Grainger, N. Jones, and B. Gilbert. 2018*a*. Maternal provisioning is structured by species' competitive neighborhoods. Oikos 128:45–53.

Germain, R. M., M. M. Mayfield, and B. Gilbert. 2018*b*. The "filtering" metaphor revisited: competition and environment jointly structure invasibility and coexistence. Biology Letters 14: 20180460.

Germain, R. M., J. T. Weir, and B. Gilbert. 2016. Species coexistence: macroevolutionary relationships and the contingency of historical interactions. Proceedings of the Royal Society B 283:20160047.

Godoy, O., and J. M. Levine. 2014. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology 95:726–736.

Goldberg, D. E., R. Turkington, L. Olsvig-Whittaker, and A. R. Dyer. 2001. Density dependence in an annual plant community: variation among life history stages. Ecological Monographs 71:423–446.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C.

Grman, E., and K. N. Suding. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. Restoration Ecology 18:664–670.

Harper, J. L., J. N. Clatworthy, I. H. McNaughton, and G. R. Sagar. 1961. The evolution and ecology of closely related species living in the same area. Evolution 15:209–227.

HilleRisLambers, J., S. G. Yelenik, B. P. Colman, and J. M. Levine. 2010. California annual grass invaders: the drivers or passengers of change? Journal of Ecology 98:1147–1156.

Hoste, I. 2013. The Jepson manual. Vascular plants of California. Plant Ecology and Evolution 146:140–141.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

IPCC (Intergovernmental Panel on Climate Change). 2014. Climate change 2014: synthesis report. Presented at the 40th session of the Intergovernmental Panel on Climate Change. Copenhagen, November 1.

Ke, P.-J., and A. D. Letten. 2018. Coexistence theory and the frequency-dependence of priority effects. Nature Ecology and Evolution 2:1691–1695.

Kharouba, H. M., J. Ehrlén, A. Gelman, K. Bolmgren, J. M. Allen, S. E. Travers, and E. M. Wolkovich. 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy of Sciences of the USA 115:5211–5216.

Kimball, S., A. L. Angert, T. E. Huxman, and D. Lawrence Venable. 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. Global Change Biology 16:1555–1565.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the USA 112:797–802.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. Global Change Biology 20: 170–182.

Levine, J. M., A. K. McEachern, and C. Cowan. 2011. Seasonal timing of first rain storms affects rare plant population dynamics. Ecology 92:2236–2247.

Lortie, C. J., and R. Turkington. 2002. The effect of initial seed density on the structure of a desert annual plant community. Journal of Ecology 90:435–445.

McKane, R. B., D. F. Grigal, and M. P. Russelle. 1990. Spatiotemporal differences in ^{15}N uptake and the organization of an old-field plant community. Ecology 71:1126–1132.

Méndez, M., and P. S. Karlsson. 2005. Nutrient stoichiometry in *Pinguicula vulgaris*: nutrient availability, plant size, and reproductive status. Ecology 86:982–991.

Milbau, A., B. J. Graae, A. Shevtsova, and I. Nijs. 2009. Effects of a warmer climate on seed germination in the subarctic. Annals of Botany 104:287–296.

Mondoni, A., G. Rossi, S. Orsenigo, and R. J. Probert. 2012. Climate warming could shift the timing of seed germination in alpine plants. Annals of Botany 110:155–164.

Peay, K. G., M. Belisle, and T. Fukami. 2012. Phylogenetic relatedness predicts priority effects in nectar yeast communities. Proceedings of the Royal Society B 279:749–758.

Rabinowitz, D., J. K. Rapp, V. L. Sork, B. J. Rathcke, G. A. Reese, and J. C. Weaver. 1981. Phenological properties of wind- and insect-pollinated prairie plants. Ecology 62:49–56.

Ross, M. A., and J. L. Harper. 1972. Occupation of biological space during seedling establishment. Journal of Ecology 60:77–88.

Rudolf, V. H. W. 2019. The role of seasonal timing and phenological shifts for species coexistence. Ecology Letters 22:1324–1338.

Satyanti, A., L. K. Guja, and A. B. Nicotra. 2019. Temperature variability drives within-species variation in germination strategy and establishment characteristics of an alpine herb. Oecologia 189:407–419.

Scranton, K., and P. Amarasekare. 2017. Predicting phenological shifts in a changing climate. Proceedings of the National Academy of Sciences of the USA 114:13212–13217.

Siepielski, A., and M. A. McPeek. 2010. On the evidence for species coexistence: a critique of the coexistence program. Ecology 91:3153–3164.

Thomson, D. M., R. A. King, and E. L. Schultz. 2017. Between invaders and a risky place: exotic grasses alter demographic tradeoffs of native forb germination timing. Ecosphere 8: e01987.

Wainwright, C. E., E. M. Wolkovich, and E. E. Cleland. 2011. Seasonal priority effects: implications for invasion and restoration in a semi-arid system. Journal of Applied Ecology 49: 234–241.

Waterton, J., and E. E. Cleland. 2016. Trade-off between early emergence and herbivore susceptibility mediates exotic success in an experimental California plant community. Ecology and Evolution 6:8942–8953.

Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters 13:1–10.

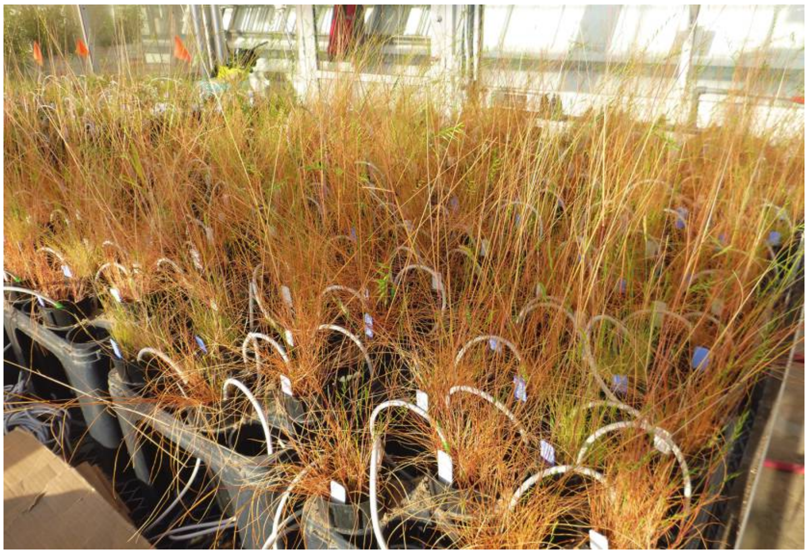
Young, J., R. Evans, C. Raguse, and J. Larson. 1981. Germinable seeds and periodicity of germination in annual grasslands. Hilgardia 49:1–37.

Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly. Ecological Restoration 19: 5–18.

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

Zhang, H., H. Wu, Q. Yu, Z. Wang, C. Wei, M. Long, J. Kattge, M. Smith, and X. Han. 2013. Sampling date, leaf age and root size: implications for the study of plant C∶N∶P stoichiometry. PLoS ONE 8:e60360.

Associate Editor: Janneke Hille Ris Lambers
Editor: Alice A. Winn



Vulpia microstachys and *V. octoflora* growing in the greenhouse. Photo credit: Christopher Blackford.