

Nonlinear effects of phenological shifts link interannual variation to species interactions

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Abstract

1. The vast majority of species interactions are seasonally structured and depend on species' relative phenologies. However, differences in the phenologies of species naturally vary across years and are altered by ongoing climate change around the world.
2. By combining experiments that shifted the relative hatching of two competing tadpole species across a productivity gradient with simulations of inter-annual variation in arrival times I tested how phenological variation across years can alter the strength and outcome of interspecific competition.
3. Shifting the relative timing of hatching (phenology) of a species fundamentally altered interspecific competition, and the effect of shifting the timing on competition was highly non-linear for most demographic rates. Furthermore, this relationship varied with productivity of the system. As a consequence, (a) shifts in relative timing of phenologies had small or large effects depending on the average natural timing of interactions, and (b) changes in the inter-annual variation in onset of interaction alone can alter species interactions in simulations even when mean phenologies (timing) remain unchanged across years.
4. Studies on phenologies traditionally focus on directional shifts in the mean of phenologies, but these results suggest that we also need to consider inter-annual variation in phenologies of interacting species to predict dynamics of natural communities and how they will be modified by climate change.

KEYWORDS

amphibian, climate change, competition, mistiming, phenological mismatch

1 | INTRODUCTION

The strength of species interactions is a key driver of the dynamics and structure of natural communities; it can determine which species coexist, their relative abundances, and how they respond to environmental change (McCann, Hastings, & Huxel, 1998; Wootton & Emmerson, 2005). In seasonal communities, many interactions are initiated by the "appearance" of offspring in a habitat and occur among growing individuals (De Roos, Persson, & McCauley, 2003; Godoy & Levine, 2014; Rasmussen, Van Allen, & Rudolf, 2014; Urban, 2007; Wilbur, 1997; Wissinger, 1992; Yang & Rudolf, 2010). Furthermore, in most competitive and predator-prey systems, interaction strength depends on the relative size differences in

individuals. Shifts in the relative timing of species' phenologies (e.g. hatching) can therefore alter the strength of species interactions by altering the size ratio of interacting offspring in these systems (Rasmussen et al., 2014; Rudolf & Singh, 2013; Yang & Rudolf, 2010). However, the timing of interactions naturally varies across years because interacting species typically differ in the suite of environmental cues that determine phenologies (Diez et al., 2012; Iler et al., 2013; McKinney et al., 2012). Furthermore, climate change causes shifts in the relative phenologies of interacting species world-wide (Ovaskainen et al., 2013; Parmesan & Yohe, 2003; Thackeray et al., 2016). Therefore, the timing of species interactions inherently varies across years and this interannual variation is likely to increase with climate change (Thackeray et al., 2016; Walther et al., 2002).

However, previous studies have been focused on changes in the mean of phenological events and it remains unclear when and how temporal variation in relative phenologies will affect dynamics and structure of natural communities.

To connect annual variation in phenologies to community dynamics, we first need to understand the relationship between phenological overlap and outcome of species interactions (e.g. linear vs. nonlinear). Recent studies clearly indicate that relative shifts in the mean phenologies of interacting species can alter the outcome of interactions (Both, Bouwhuis, Lessells, & Visser, 2006; Morin, Sharon, & Johnson, 1990; Rasmussen et al., 2014; Rudolf & Singh, 2013; Urban, 2007; Visser, Holleman, & Gienapp, 2006), but we lack a basic understanding of how interaction strengths scale with (e.g. linearly vs. nonlinearly) shifts in mean timing of phenologies of interacting species. Specifically, if interaction strength changes linearly with shift in relative arrival time of two interacting species, then the average interaction strength will only be affected by changes in the mean timing of interactions while interannual variation around that mean has no effect (Figure 1). In contrast, if the relationship is highly nonlinear, an increase in interannual variation around a phenological event can alter mean interaction strengths, even if the mean of the phenological event remains unchanged (stationary) across years (Figure 1). Furthermore, given some natural level of phenological variation across years, a nonlinear relationship would also indicate that predictions solely based on the mean would either over- or underestimate the true effect of phenological shifts depending on the monotonic curvature of the relationship at the mean (Jensen, 1906) (Figure 1). Identifying the relationship (e.g. linear vs. nonlinear scaling) between the timing and strength of interactions

is therefore crucial to predict how natural variation of phenologies affect long-term dynamics of communities and how they will respond to climate change (Ruel & Ayres, 1999).

Nonlinear relationships between relative arrival time and interaction strength could arise from several nonexclusive mechanisms. For instance, if body size scales proportionally with per-capita competitive ability, nonlinear growth rates could lead to nonlinear relationship between interaction strength and relative arrival time by altering the relative size-trajectories of interacting species over time (Figure 1). This nonlinear pattern could further be enhanced by positive feedbacks between growth rates, size and competitive abilities, that is larger individuals could be competitively dominant (Yang & Rudolf, 2010), allowing them to grow disproportionately faster. In addition, the strength of interspecific competition should eventually become negligible if the temporal overlap becomes very small. At this point, delaying arrival of the competitor even more would have no consequence. While this may suggest that the relationship between relative phenologies and interspecific competition should often be nonlinear, it remains unclear whether the nonlinearity is strong enough to have biologically meaningful consequences and what shape it might be (e.g. saturating vs. sigmoidal). For instance, interannual variation in relative arrival time may not play an important role in natural systems if the relationship is only weakly nonlinear, or nonlinearity only arises at relative arrival times that are very unlikely to occur in nature. In addition, changes in environmental conditions that alter growth rates or the strength of competition (e.g. resource availability) could furthermore modify these relationships and either strengthen or weaken nonlinear patterns.

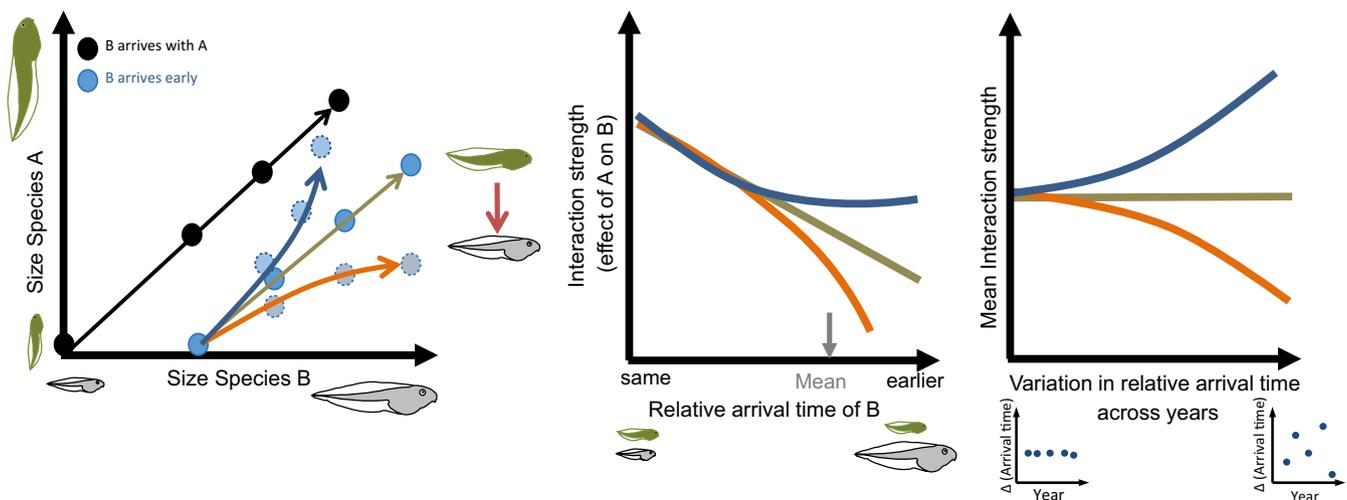


FIGURE 1 The relationship between interaction strength and phenological shifts determines the consequences of variance in relative phenologies. The middle panel shows hypothetical examples of competition between offspring of two species where competitiveness scales positively with size. In this scenario, delaying arrival (e.g. hatching) of species B alters the relative size ratio of both species and thereby increases the per-capita effect of species A (green tadpole) on species B (grey tadpole). If the relationship is linear, increasing interannual variation in relative arrival times will not affect interactions strength (right panel). However, if the relationship is nonlinear (dashed lines), then increasing variance in relative phenologies across years can either increase or decrease interaction strength depending on the curvature of the relationships. Such nonlinear relationship can easily arise when shifts in relative timing alter the relative growth trajectories and thus size ratios of competing species, for example due to nonlinear growth rates and/or positive feedback of growth rates, size and competitive ability (left panel). The right panel indicates how increasing variation in relative arrival time across years around a mean arrival time (indicated by grey line in middle panel) can alter mean interaction strength across years [Colour figure can be viewed at wileyonlinelibrary.com]

Here, I take an experimental approach to identify how interaction strength scales with shifts in the relative phenologies of species across an environmental gradient. I experimentally manipulated the relative hatching phenology of two competing tadpole species and measured how this variation altered key life-history traits along a productivity gradient. This allowed me to determine whether the relationship between phenological shift and interspecific competition is nonlinear, what the exact shape of this relationship is, and how robust it is to variation in a key environmental component. Resource limitation is likely to alter both the strength of competition and initial growth rates of species (Morin & Johnson, 1988) and could therefore alter the strength of size-mediated priority effects and potentially how phenological shifts alter interaction strength.

2 | MATERIALS AND METHODS

2.1 | Study system

To examine effects of phenological shifts on species interactions, I used tadpoles of the Southern Leopard Frog, *Rana sphenoccephala*, and the Western Chorus frog, *Pseudacris triseriata* as focal species. Tadpoles of both species are widespread in the eastern United States and commonly co-occur in temporary and semipermanent fishless ponds in late winter and spring in the study region in South East Texas (December–March). Competition among tadpoles frequently depends on the relative hatching time of species, although the outcome of phenological shifts varies among species and studies (Alford, 1989a; Alford & Wilbur, 1985; Lawler & Morin, 1993; Morin et al., 1990). Previous experiments demonstrated that both focal tadpole species compete for shared, limited resources and that the effect of competition on survival and growth rates is strongly influenced by shifts in relative hatching phenologies (Rudolf & Singh, 2013). Furthermore, breeding of *P. triseriata* is associated with temperature but not rainfall, while breeding of *R. sphenoccephala* is mostly associated with rainfall and typically not with temperature in the study area (Saenz, Fitzgerald, Baum, & Conner, 2006). This could explain why relative hatching phenologies (and thus timing of species interactions) of both species vary substantially among years (assuming that hatching differences are proportional to differences in timing of breeding) with changes in temperature and rainfall regimes (Supporting Information Figure S1). Finally, I can experimentally delay hatching of *R. sphenoccephala* for several weeks, allowing me to examine a wide range of relative arrival times that cover most of the variation in arrival time observed in natural populations (Supporting Information Figure S1). This long time span provides me with the necessary power to identify the shape of the relationship between phenological shifts and the strength of species interactions.

2.2 | Experimental design

To examine the effect of relative arrival time on competition between species, I manipulated the relative hatching time of both species across a productivity gradient, using a factorial, repeated-regression

design with 5 arrival times \times 3 productivity treatments and four replicates per treatment combination (=60 communities). Experimental communities were setup in mesocosms in a spatially randomized complete block design and all blocks were started simultaneously.

Each mesocosm consisted of a 340 L cylindrical PVC container (70 cm \times 91 cm) that was designed to closely mimic fishless temporary pond communities inhabited by both species. The mesocosms overlap in size with the bodies of water that these species naturally colonize, making these containers a useful venue for studying interactions between these species. Mesocosms were set up in an open field at the South Campus Research Facility of Rice University, Houston, TX. Each unit was filled with dechlorinated well water on 17 January, 2015, and immediately covered with 60% shade cloth to provide natural shade levels, and to prevent colonization by amphibians or large predatory invertebrates, and prevent amphibian metamorphs from escaping from the mesocosm. This setup still allowed small nonpredatory invertebrates to colonize tanks naturally. On 21 January, 2015, I inoculated tanks with 70 ml of concentrated phytoplankton and zooplankton and added 1.9 L of dried leaf litter (c. 95% oak leaves) that I collected from the margins of local fishless ponds. In addition, I added 500 ml concentrated zooplankton and pond water collected from the same pond on 28 January, 2015. This setup assured a diverse community of primary producers and small invertebrates that characterize the natural habitats of both species.

I manipulated relative arrival time of both species by introducing *R. sphenoccephala* hatchlings at five times spaced in 5 day intervals; it either “arrived” at the same time as its competitor *P. triseriata* or 5 day, 10 day, 15 day or 20 days later. This covered most of the natural variation observed at the study sites (Supporting Information Figure S1). Previous studies indicate that *R. sphenoccephala* is clearly competitively dominant when both species arrive together and can completely exclude *P. triseriata* when it arrives earlier (Rudolf & Singh, 2013). Thus, I only focused on the more interesting scenarios where *R. sphenoccephala* arrives at the same time or later than *P. triseriata*.

I collected egg clutches of both species from two fishless temporary ponds in the Davy Crockett National Forest, TX, where both species co-occur naturally. I then randomly assigned egg clutches of *R. sphenoccephala* to one of the five hatching time (phenology) treatments. Within a given hatching treatment, tadpoles from all clutches were distributed evenly among all replicates. Following established protocols (Rudolf & Singh, 2013), eggs of *R. sphenoccephala* were incubated at 10°C at 10:14 light:dark cycle in controlled environmental chambers to delay development and hatching. Eggs were then moved to 20°C walk-in environmental chambers 5 days before their respective arrival time treatment to accelerate hatching and growth and to standardize the sizes of introduced tadpoles across treatments. Previous studies demonstrated that this hatching protocol allows tadpoles to develop without any detectable side effects or mortality in all hatching treatments (Rudolf & Singh, 2013). In addition to the 60 competition treatments, I reared 20 *R. sphenoccephala* from each of the five introduction times in absence of *P. triseriata* as a control to detect potential effects of hatching treatment.

To examine how robust effects of phenological shifts are to variation in environmental conditions (i.e. resource availability), I crossed each arrival treatment with three productivity levels. Following previous studies (Chase, 2003), I manipulated primary productivity by fertilizing mesocosms with nitrogen (N) as NaNO_3 and phosphorus (P) as NaH_2PO_4 , which are known to be limiting in this system. I created three levels of productivity that maintained constant N and P ratios across all three productivity levels: low levels only received well water (no N or P addition, ambient N = 0.9 mg/L and P = 0.02 mg/L), medium levels received 1.9 g NaNO_3 and 0.0795 g NaH_2PO_4 (N = 4.5 mg/L, P = 0.1 mg/L) and high levels received 3.86 g NaNO_3 and 0.1587 g NaH_2PO_4 (N = 9 mg/L, P = 0.2 mg/L). Analysis of periphyton densities indicates that this nutrient treatment successfully increased primary producer biomass by up to 10-fold between low and high nutrient treatments (see Supporting Information Figure S2).

Each competition treatment received 80 (0.36 Ind/L) *P. triseriata*, and 20 (0.09 Ind/L) *R. sphenocéphala*. The difference in density between species accounts for the four times larger per-capita biomass of *R. sphenocéphala* at hatching. Both densities are well within the range of natural densities for both species. The experiment started when I added *P. triseriata* and the first arrival of *R. sphenocéphala* to the respective treatment on 21 February, 2015, and was completed 4-month later on 18 June, 2015, after the last *P. triseriata* had emerged. The experiment thus covered the entire larval period of *P. triseriata* in all treatments.

2.3 | Response variables

I monitored tanks daily and collected all metamorphs (i.e. individuals with at least one forelimb). Metamorphs were brought to the laboratory and weighed once the tail was fully absorbed after which they were released at the field site where I had collected the eggs. In addition, I subsampled tanks after the 2nd and 4th introduction to estimate changes in size of *P. triseriata*. For each subsample, I photographed 20 randomly selected tadpoles from four randomly selected tanks from each nutrient and arrival treatment. I subsampled all tanks on 20 March and 2 April and photographed 20 *P. triseriata* and 10 *R. sphenocéphala* per tank to calculate body size and growth rates as: growth rate = $(\text{SVL}_{t_x} - \text{SVL}_{t_0})/t_x$, where SVL = snout vent length, t_x = days since introduction of tadpoles to the experiment, t_0 . Note that t_0 accounts for any delay in arrival for a given treatment. Tadpoles were photographed in the field and immediately returned to their respective mesocosm after the pictures were taken. For each treatment, I also calculated the total biomass of each species produced during the course of the experiment. For *R. sphenocéphala*, this included both tadpoles and metamorphs. Thus, I used established relationships to convert wet mass (of metamorphs) and SVL (of tadpoles) to dry mass for both species (Rudolf & Rasmussen, 2013a,b).

2.4 | Statistical analysis

For each response variable, I first fit and compared three different polynomial models (1st, 2nd, 3rd order) to determine whether the

response was linear or nonlinear, and if nonlinear, whether a 2nd or 3rd order fit was best. Polynomial regressions modelled the number of survivors, time to metamorphosis and total biomass as a function of relative arrival time, productivity treatment and their interaction as fixed effects and block as random effect. Survival was modelled with binomial error and logit link function. To account for heterogeneity in variances, I log-transformed total biomass. For *P. triseriata*, I additionally modelled error variances as a combination of functions of arrival time of *R. sphenocéphala* and nutrient treatments (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) (Supporting Information Table S1). I then compared models (1st vs. 2nd, 2nd vs. 3rd order) using lack-of-fit-likelihood ratio tests. The lack-of-fit test indicates what minimum level of complexity (i.e. 1st, 2nd or 3rd degree) is required to describe the relationship between difference in arrival time and interaction strength, that is whether the relationship is linear or nonlinear.

Once the best polynomial model was identified for each response variable, I examined evidence of treatment effects and their interaction in these models. Survival was analysed with the “glmer” function, size with “lmer” and all other variables with the “lme” function. I used the “car” package to obtain *p*-statistics based on type II Wald chi-square statistics. Analyses of growth rates and periphyton densities (initial polynomial final analyses) additionally included time (days since experiment initiation) as a continuous predictor and its interaction with nutrient and arrival treatment, and replicate as a random factor to account for nonindependence of repeated measures. To account for differences in variation across treatments and time, I modelled error variance as a function of all three predictors.

2.5 | Simulating phenological variation

To quantify effects of phenological variation around a mean, I simulated different levels of variation in the late competitor for a range of mean arrival times. The polynomial analysis indicated a clear nonlinear relationship (Table 1), and further model fitting (Supporting Information Table S2) indicated that this relationship was best modelled by a logistic function that allowed the respective shape parameters to vary across nutrient treatments (see Supporting Information for details). Fitting the function to empirical data allowed me to predict natural survival for any given arrival time combination. I then simulated different interannual variation scenarios for a given mean arrival time (X) by selecting arrival times within the interval $[X - \Delta, X + \Delta]$ from a uniform distribution. Increasing Δ allowed me to increase the variation in relative arrival time while the mean arrival time remained constant. I focused simulations on survival of the early competitor because all tadpoles had completed their development in all treatments while this was not the case for late arriving competitor. Variation (V) is measured as the average absolute deviation based on $V = \sum_{i=1}^{i=k} |x - d_i|/k$ where k indicates the number of simulations and d_i the simulated arrival time for simulation i and x the mean arrival time. So a $V = 2$ indicates that the late competitor arrived typically 2 days before or after the mean arrival time of the early competitor. Mean survival rates (averaged across “years”) are

TABLE 1 Fit statistics of polynomial regression models used to determine model complexity needed to describe functional relationship between shift in relative arrival time and survival (% individuals that survived until end of experiment), total biomass (summed across all individuals of each species), emergence (days until metamorphosis) and size of the early competitor (*Pseudacris triseriata*) and late competitor (*Rana sphenoccephala*). All models included nutrient and arrival treatments and their interaction as fixed predictors, and block as random effect and for emergence and size also replicate as random effect, and time as fixed effect for size. Note that analyses for growth rates and emergence do not include replicates that had no survivors. For details, see “statistical analyses” in methods. The selected best fitting model is indicated in bold based on lack-of-fit test (indicated by chi-square statistic and *p* values) between model pairs with increased complexity (e.g. 1st order vs. 2nd order, 2nd order vs. 3rd order). *df* indicates numerator degrees of freedom for a given model. *R* – *LR*² indicates the likelihood ratio-based pseudo-*R*-squared which quantifies the variance explained by fixed effects in the model (see Materials and Methods for details)

Species	Response	Polynomial model	<i>df</i>	χ^2	<i>p</i>	<i>R</i> – <i>LR</i> ²
Early arriver (PT)	Survival	1st order	14			0.490
		2nd order	17	93.94	<0.0001	0.590
		3rd order	20	14.77	0.0020	0.615
	Log(total biomass) ^a	1st order				0.867
		2nd order	17	20.38	0.0001	0.905
		3rd order	20	0.64	0.8864	0.915
	Emergence ^{a,b}	1st order	14			0.602
		2nd order	17	10.32	0.016	0.673
		3rd order	20	4.21	0.240	0.699
	Size ^c	1st order	15			0.734
		2nd order	21	5.26	0.5110	0.746
		3rd order	27	0.56	0.9971	0.747
Late arriver (RS)	Survival	1st order	8			0.309
		2nd order	11	6.51	0.0892	0.380
		3rd order	14	4.80	0.1879	0.428
	Log(total biomass)	1st order	8			0.461
		2nd order	11	1.61	0.6568	0.476
		3rd order	14	2.48	0.4782	0.497
	First emergence	1st order	8			0.685
		2nd order	11	5.20	0.1574	0.711
		3rd order	14	6.64	0.0842	0.741
	Size ^c	1st order	15			0.819
		2nd order	21	15.22	0.0186	0.841
		3rd order	27	2.69	0.8464	0.844
Early vs. late arriver	Size ratio	1st order	15			0.737
		2nd order	21	8.26	0.2198	0.754
		3rd order	27	3.81	0.7030	0.762

Notes. ^aVariances allowed to vary across nutrient and arrival treatments. ^bDoes not include treatment with low nutrient and 0 delay arrival as it had no survivors. ^cIncludes two repeated samples and time as predictor.

based on 99,000 simulations of a given mean arrival and variation combination.

3 | RESULTS

3.1 | Effects on early competitor

Survival and total biomass of the early competitor, *P. triseriata*, differed significantly across treatments and largely followed the same pattern (Figure 2, Table 1, 2). In low nutrient treatments when both

species arrived at the same time, no early competitor survived to the end of the experiment, while most (75%) survived in treatments with high productivity levels and a 15-day delay of its competitor, *R. sphenoccephala* (Figure 2). Model selection indicated that survival and biomass of *P. triseriata* scaled nonlinearly with relative arrival time of its competitor *R. sphenoccephala* and required a 3rd-order polynomial (Table 1). Note that biomass was log-transformed for the analysis, so 2nd-order polynomial on a log scale is equivalent to 3rd-order polynomial on an untransformed scale. Consistent with this results, further model fitting indicated that logistic function

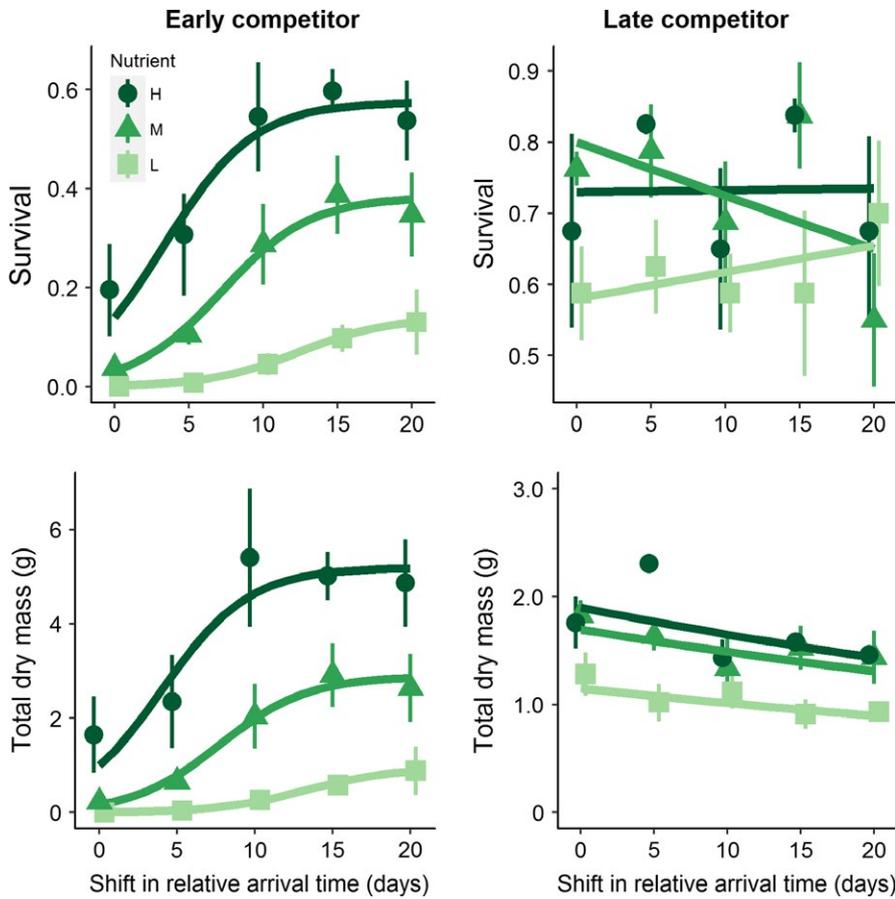


FIGURE 2 Change in survival and biomass (total dry mass) of two competing tadpole species with changes in relative arrival time and productivity (high = H, medium = M, low = L). Arrival time indicates the number of days by which the late competitor (*Rana sphenoccephala*) was delayed relative to arrival of the early competitor (*Pseudacris triseriata*). Large open symbols indicate $M \pm 1$ SE (not accounting for block effects), and small symbols indicate replicates. Lines indicate predictions of best fit nonlinear (logistic) model except for survival of late competitor which was not significantly affected by arrival times (Table 1). Note differences in y-axis scaling for biomass between left and right middle panels. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Effects of relative arrival time and nutrient treatments on survival, biomass, and emergence times of early arriving competitors (*Pseudacris triseriata*), and late arriving competitors (*Rana sphenoccephala*). Emergence indicates mean emergence time of metamorphs of the first arriving competitor and is based on developmental times relative to the start of experiment (i.e. introduction of early competitor), fastest development measures the number of days between first emergence of first metamorph of the late competitor and its respective introduction to account for differences in introductions times across arrival treatments of the late competitor. Significance tests are based on best fitting and most parsimonious polynomial model of arrival time (Table 1). χ^2 indicates type II Wald chi-square statistics

Early arriver			
Source	Survival	Total biomass	Mean emergence
Nutrient	$\chi^2_{2,45} = 78.2^{***}$	$\chi^2_{2,45} = 166.5^{***}$	$\chi^2_{2,37} = 16.8^{***}$
Arrival	$\chi^2_{3,45} = 66.9^{***}$	$\chi^2_{3,45} = 166.7^{***}$	$\chi^2_{3,37} = 3.9$
Nutrient × Arrival	$\chi^2_{6,45} = 31.0^{***}$	$\chi^2_{6,45} = 37.6^{***}$	$\chi^2_{6,37} = 20.9^{**}$
Late arriver			
Source	Survival	Total Biomass	Fastest development
Nutrient	$\chi^2_{2,48} = 15.2^{***}$	$\chi^2_{2,51} = 41.9^{***}$	$\chi^2_{2,51} = 88.1^{***}$
Arrival	$\chi^2_{3,48} = 0.4$	$\chi^2_{3,51} = 8.2^*$	$\chi^2_{3,51} = 33.9^{***}$
Nutrient × Arrival	$\chi^2_{6,48} = 6.4^*$	$\chi^2_{6,51} = 0.02$	$\chi^2_{6,51} = 3.1$

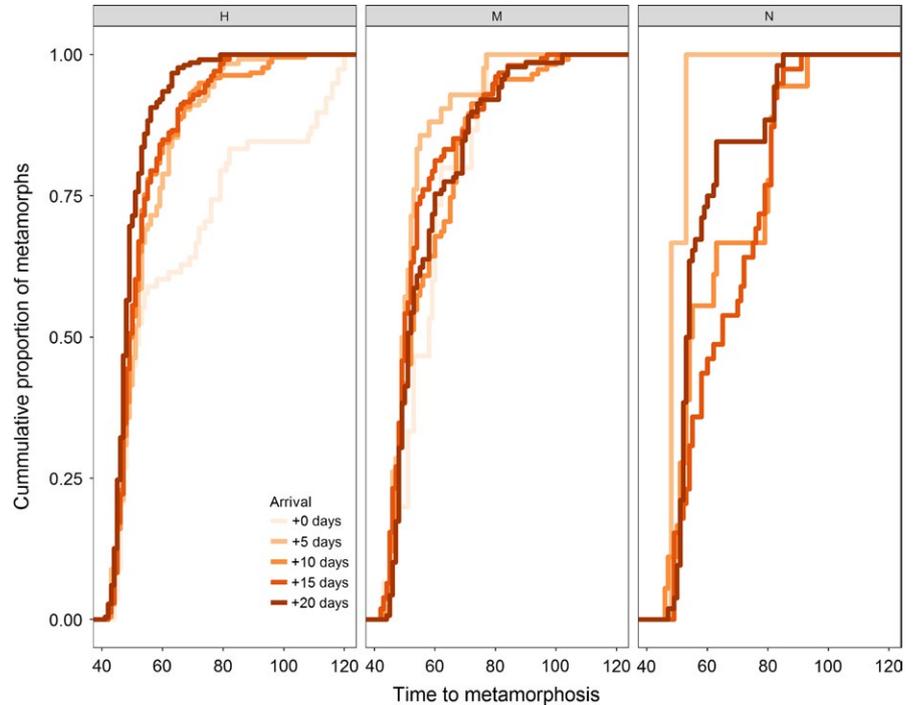
Notes. $^{***}p < 0.001$, $^{**}p < 0.01$, $^*p < 0.05$.

fitted the data much better than a simple asymptotic function (Supporting Information Table S2). Delaying arrival of the competitor by 5 and 10 days exponentially increased survival and biomass of *P. triseriata*, but a further delay (15–20 days) had weaker or no

effects, resulting in a sigmoidal relationship between survival or biomass and relative arrival time (Figure 2).

The specific relationship between phenological shift and survival or biomass was always nonlinear (sigmoidal), but varied significantly

FIGURE 3 Empirical cumulative distribution function curves of emergence (i.e. timing of metamorphosis) patterns of the early competitor *Pseudacris triseriata* as a function of productivity treatment (L = low nutrient levels, M = moderate nutrient levels, H = high nutrient levels) and “Arrival” treatment of the late competitor. Colours indicate different delays in arrival relative to the early competitor; +0 day indicates species arrived at the same time; and +20 day indicates the late competitor (*Rana sphenoccephala*) arrived 20 days later. Curves are normalized by total number of individuals that emerged in a given treatment. Note that no individuals emerged at N nutrient treatment and 0 day delay [Colour figure can be viewed at wileyonlinelibrary.com]



across productivity treatments (Table 2, Figure 2); survival and biomass increased faster and reached a higher maximum/plateau with less delay in arrival time of the competitor at higher productivity levels. As a consequence, delaying the competitor arrival had either no effect, a small effect or a very large effect depending on the productivity in the system. For instance, delaying arrival by 10 days increased (relative to 0 days delay treatment) survival by 5.6% at low vs. 57.8% at high productivity, and biomass by 2.5-fold and 10-fold at low vs. high productivity levels, respectively.

Relative arrival time also altered timing of the next phenological event (emergence of metamorphs) in the life cycle of the early competitor (Figures 2 and 3), but the significant nonlinear (3rd-order polynomial) relationship (Table 1) varied substantially across productivity levels (Table 2). Individuals emerged earliest (mean (M) = 49 days) in high productivity treatments when the arrival of the competitor was delayed by 20 days, and latest (mean (M) = 73 days) in low nutrient treatments when competitors arrived with a 10-day delay (Figure 3). Note that there were no survivors that could emerge from the same productivity treatment where both species arrived at the same time. At the highest productivity treatment, development time was c. 27% shorter (by c. 20 days) when arrival time of the competitor was delayed by only 5 days and continued to shorten with further delay in arrival time of the competitor but at a much lower rate. In contrast, delaying arrival time of the competitor in intermediate productivity treatments did not clearly alter the timing of emergence and even delayed average emergence time at low productivity (Figure 3).

3.2 | Effect on late competitor

Survival and total biomass of the late arriving competitor, *R. sphenoccephala*, were on average much higher than survival of its early

arriving competitor (Figure 2). Survival of the late competitor was lowest at lowest productivity treatment and declined only noticeably with arrival at intermediate productivity, likely because of the substantial variation in survival in the other treatments (Table 2, Figure 2). In contrast, its total biomass significantly (Table 2) decreased linearly (Table 1) in all treatments when it arrived relatively later. Time to first emergence of *R. sphenoccephala* (i.e. number of days from introduction to first emergence) significantly declined with arrival time (Table 2, Figure 2) and differed by up to 1.6 times between treatments (55 days, high nutrient and 20-day delay vs. 88 days low nutrient and 0 delay).

3.3 | Shift in body sizes of competitors

Growth rates (and thus body sizes) of both species were significantly affected by nutrient and arrival treatments and their interaction and the effects largely increased over time (Table 3, Figure 3). Growth rates of both species were positively correlated with productivity, while arrival treatments had opposite effects on both species: delaying arrival of the late competitor increased growth rates of the early arriver while it decreased growth rates of the late arriving competitor. This negative effect on the late arriver increased with productivity (Table 3 Figure 4). In the late competitor, the relationship was significantly nonlinear, largely because effect sizes declined with increasing differences in relative arrival time (Table 1, Figure 4). Interestingly, tadpoles of the late arriving competitor (*R. sphenoccephala*) in control tanks without early arriving competitor species showed the opposite pattern, that is later arriving individuals had higher growth rates and larger body sizes (Figure 3), suggesting that this negative relationship between arrival time and growth rates was driven by interspecific competition and not simply late arrival time.

Source	Early arriver size	Late arriver size	Early/Late size ratio
Nutrient	$\chi^2_{2,51} = 45.1^{***}$	$\chi^2_{2,53} = 19.1^{***}$	$\chi^2_{2,51} = 8.3$
Arrival	$\chi^2_{2,51} = 22.5^{***}$	$\chi^2_{2,46} = 206.3^{***}$	$\chi^2_{9,51} = 172.0^{****}$
Date	$\chi^2_{1,54} = 261.9^{***}$	$\chi^2_{1,46} = 288.6^{***}$	$\chi^2_{1,54} = 61.7^{****}$
Nutrient \times Arrival	$\chi^2_{4,51} = 5.0$	$\chi^2_{4,46} = 9.9^*$	$\chi^2_{2,51} = 7.9^*$
Nutrient \times Date	$\chi^2_{2,54} = 3.1$	$\chi^2_{2,46} = 2.5$	$\chi^2_{2,54} = 3.1$
Arrival \times Date	$\chi^2_{2,54} = 5.9^*$	$\chi^2_{2,46} = 19.1^{***}$	$\chi^2_{4,54} = 4.1^*$
Nutrient \times Arrival \times Date	$\chi^2_{4,54} = 1.1$	$\chi^2_{2,46} = 3.1$	$\chi^2_{4,54} = 0.9$

Notes. **** $p < 0.0001$, *** $p < 0.001$, * $p < 0.05$.

TABLE 3 Treatment effects on body sizes of early (*Pseudacris triseriata*) and late (*Rana sphenoccephala*) arriving competitors. Body size was measured as mean snout vent length (SVL) within a replicate. Arrival was modelled as 2nd-order polynomial (see Table 1). χ^2 indicates type II Wald chi-square statistics

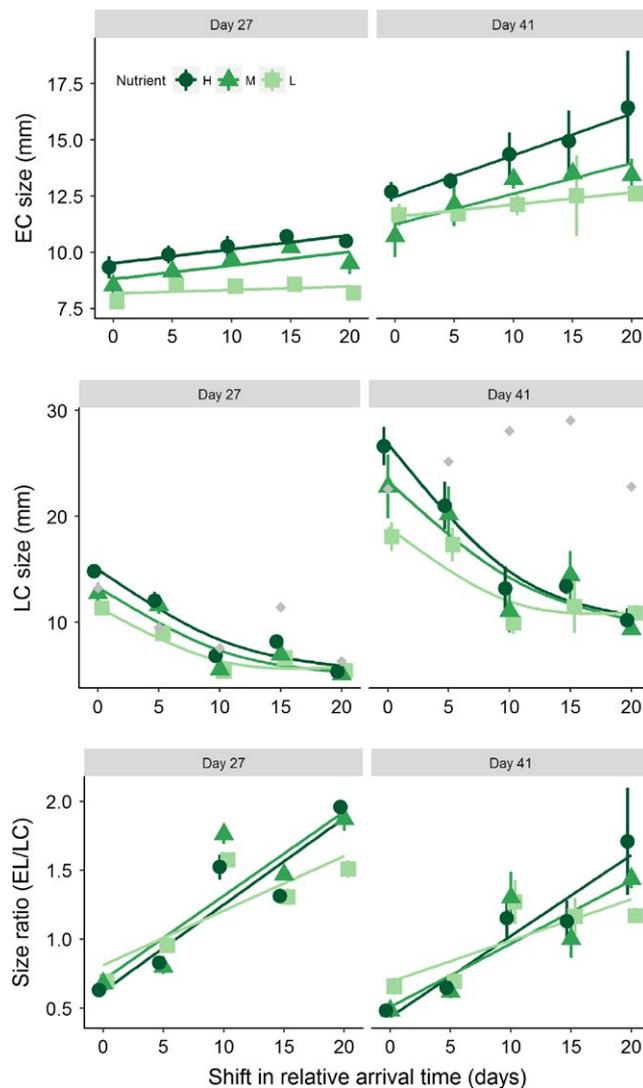


FIGURE 4 Mean body size (measured as snout vent length: SVL) and size ratio of early (EC) and late (LC) arriving competitors as a function of relative arrival time for different nutrient treatments 27 and 41 days after introduction of first competitor. Grey diamonds indicate size of late competitor in the corresponding control without early arriving competitors and low nutrient levels. Large symbols indicate $M \pm 1$ SE (not accounting for block effects), and small symbols indicate replicates. Lines indicate best fit model (see Table 1) [Colour figure can be viewed at wileyonlinelibrary.com]

Relative arrival time also changed the size asymmetry of early vs. late competitors over the first 41 days of the interaction period. Specifically, the size ratio increased with relative arrival time (Table 3) and this effect increased with productivity of the system (Table 3, Figure 4). As a consequence, early competitors were only $\frac{1}{2}$ the size of late arrivers when both species arrived at the same time, but they were almost 1.5–2 times larger if the late competitor was delayed by 20 days (Figure 4).

3.4 | Effect of interannual variation in relative timing of interactions

The simulations indicate that changes in the interannual variation of phenologies can substantially alter survival of the early competitor even when the mean remains unchanged (Figure 5). Furthermore, the effects could be positive or negative depending on the mean timing of interactions and the specific nonlinear relationship. For instance, when *R. sphenoccephala* arrives on average 10 days after *P. triseriata*, increasing the variance by 5 days can lead to a 15% proportional decrease in survival of *P. triseriata*. In contrast, if *R. sphenoccephala* arrives at the same time or 5 days later, the same variance can lead to a proportional increase in survival by c. 25%–150% depending on the productivity treatment (Figure 4). This context-dependent effect is driven by the sigmoidal shape of the empirical relationship between arrival time and survival (see Figure 1), that is the shift from convex to concave curvature with increasing delay in relative arrival time. The effect of interannual variance decreases when the relationship becomes more linear (e.g. at >20 days delay in arrival at high productivity treatment). Importantly, the simulations are well within the natural range of relative arrival time and interannual variation indicating that the effects are clearly biological relevant for this tadpole system.

4 | DISCUSSION

In seasonal communities, the vast majority of species interactions follow a “timetable” set by the relative phenologies of interacting species. However, this timetable naturally varies across years, species and communities (Diez et al., 2012; Forrest, Inouye, & Thomson, 2010; Wolkovich, Cook, McLauchlan, & Davies, 2014). Results presented

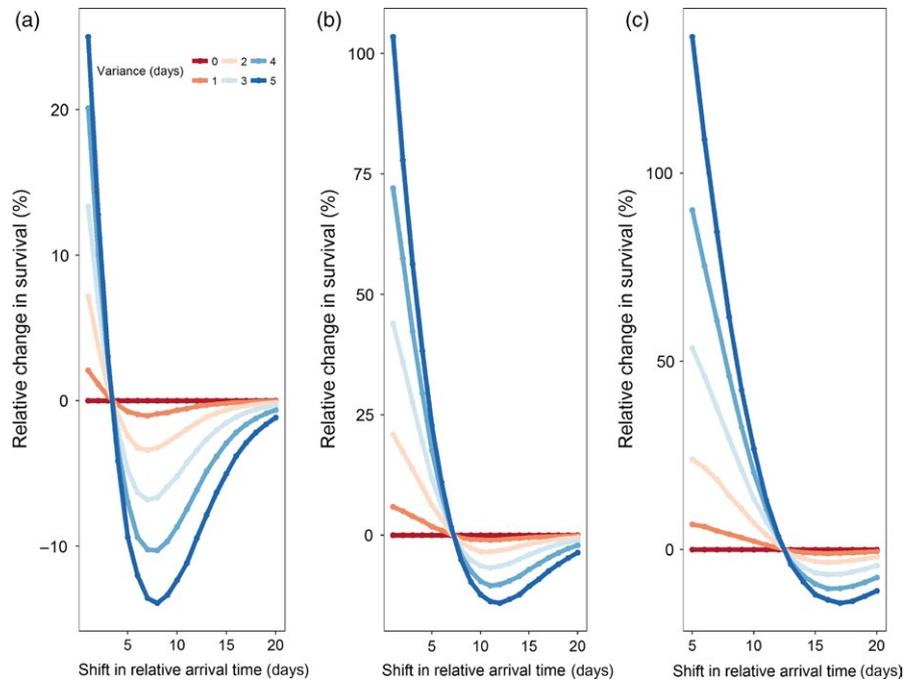


FIGURE 5 Predicted effect of variation in relative arrival time of two competing species on species interactions across three environments with three different productivity levels: (a) high, (b) medium, (c) low nutrient treatments. Lines/colours indicate proportional change (relative to scenario without interannual variation) in mean survival of early the arriving competitor (*Pseudacris triseriata*) under different simulated levels of variation (V) in relative arrival time of late competitor based on empirical survival patterns within a given nutrient treatment shown in Figure 2. Variance is well within the range observed in natural systems (Supporting Information Figure S1) and indicates the average (absolute) difference in relative arrival time of late competitor assuming a uniform distribution with a range twice the average. Means are average of 99,000 stochastic simulations (see Methods and Supporting Information for details). Left panel: high nutrient treatment, middle: medium nutrient, right panel: low nutrient treatment. Note differences in y-axis scale across the three panels [Colour figure can be viewed at wileyonlinelibrary.com]

here indicate that this phenological variation across years can have important consequences for species interactions. Specifically, I demonstrate that effects of delaying hatching phenologies of competing species have nonlinear effects on most demographic rates examined. As a consequence, (a) shifts in relative timing of phenologies can have small or large effects depending on the average natural timing of interactions and (b) changes in the interannual variation of phenologies alone can alter species interactions even if the mean would remain constant across years (i.e. remain stationary) (Figure 4). It also implies that we often cannot predict effects of phenological shifts simply based on the mean of phenologies given that phenologies typically vary across years in nature. Studies on phenologies traditionally focus on directional shifts in the mean of phenologies (McKinney et al., 2012; Ovaskainen et al., 2013; Todd, Scott, Pechmann, & Gibbons, 2011; Visser & Both, 2005; Walther, 2010), but my results suggest that we also need to consider variation in phenologies of interacting species to predict dynamics of natural communities and how they will be modified by climate change.

4.1 | Nonlinear effects of phenological shifts on interspecific competition

Relative shifts in the phenology of species play a key role in the outcome of interspecific interactions. For instance, phenological

shifts can alter predation (Alford, 1989b; Morin, 1984; Rasmussen & Rudolf, 2016; Rasmussen et al., 2014), herbivory (Liu, Reich, Li, & Sun, 2011), pollination (Rafferty & Ives, 2011) and interspecific competition (Godoy & Levine, 2014; Hernandez & Chalcraft, 2012; Rudolf & Singh, 2013; Wilbur & Alford, 1985). Consistent with these studies, I found that shifting the relative timing of hatching (phenology) of a species fundamentally altered interspecific competition, but the effect of shifting the timing on competition was highly nonlinear. As a consequence, shifts in relative timing of phenologies can have very different effects depending on the average natural timing of interactions. For instance, if species would typically hatch at the same time, even a small (e.g. 5 day) delay in hatching of the dominant competitor in the system could prevent competitive exclusion of the inferior competitor at all productivity levels and substantially increase its survival and biomass within a given season. In contrast, a similar shift has little consequence if both species naturally differ by 15–20 days in relative hatching times. This decline in effect size is consistent with arrival experiments in reef fish (Geange & Stier, 2009), dragonfly larvae (Rasmussen et al., 2014) and fruit fly larvae (Shorrocks & Bingley, 1994) suggesting that this nonlinear pattern may be wide spread. Furthermore, these results highlight that the timing of interactions can determine the strength and outcome of interspecific competition and thus play a key role in species coexistence.

The nonlinear scaling of competition with phenological shifts is likely driven by two interacting processes that are found in many natural systems. Delaying arrival of the competitor by 5–10 days exponentially increased survival and biomass of the early competitor. This initial nonlinear increase is most consistent with positive feedbacks between growth rates and relative competitiveness that arise with “size-mediated priority effects” (*sensu* Rasmussen et al., 2014). In this system and many others, larger individuals have a competitive advantage (Yang & Rudolf, 2010). Delaying the arrival of the late competitor frees up resources and allows individuals of the early competitor to grow faster. This increase in relative size should decrease the competitive effect of the late arriving competitor which in turn would allow individuals of the early arriver to grow faster, thereby creating a positive feedback between growth rates and relative competitiveness. Consistent with this prediction, I found significant differences in resource (i.e. periphyton) levels across arrival treatments, and higher levels during early periods with delayed arrival of late competitor. I also found higher growth rates of early competitors (at high resource levels) and lower growth rates of late competitors when arrival of the late competitor was delayed; this pattern even increased over time and was still detectable >20 days after the last introduction. It is important that, the reduction in growth rate of the late competitor at later arrival times did not occur in the absence of interspecific competition (Figure 4), providing additional support for the presence of size-mediated priority effects in this system.

Delaying the arrival of a competitor should, however, not indefinitely increase the performance of the early arriver. At some point, there will be little temporal overlap between co-occurring life stages of both species, and early arriver will be much larger, thereby decreasing per-capita effects of late competitors, at which point interspecific competition will become negligible for the early arriver. However, the release from interspecific competition will result in a concurrent increase in survival and total biomass and thus increase intraspecific competition. This shift from interspecific to intraspecific competition could explain why a further delay of the late competitor (i.e. 15–20 days) did not continue to increase performance of the early arriving species. These results are consistent with studies in plants (Godoy & Levine, 2014) and suggest that phenological shifts can alter the relative strength of intra- vs. interspecific interactions which ultimately determine the mechanisms that allow or prevent species coexistence (Chesson, 2000).

4.2 | Context-dependent outcomes of phenological shifts

Priority effects (e.g. due to phenological shifts) during community assembly can be modified by variation in environmental conditions if these conditions alter population growth rates (Chase, 2010; Fukami, 2015). Effects of phenological shifts should hence depend on environmental conditions if priority effects are important. Consistent with this prediction, I found that the scaling relationship between interspecific competition and phenological shifts varied substantially across environments with different primary productivities.

Reducing a limiting shared resource will inevitably intensify competition. Indeed, survival and total biomass of both species were clearly negatively correlated with resource levels in this experiment. Maybe more importantly, lower resource levels can also modify size-mediated priority effects because individuals will grow less before the arrival of other species. The benefits (i.e. relative increase in competitiveness) of arriving earlier should therefore decrease in low resource environments while competition increases (Kardol, Souza, & Classen, 2013), which explains why delaying the competitor had a much smaller proportional effect at low productivity levels. Overall, these results empirically support predictions about mechanisms driving priority effects in community assembly (Fukami, 2015; Rasmussen et al., 2014) and suggest that phenological shifts could have much stronger effects on species interactions and dynamics of seasonal communities in environments that are highly productive.

4.3 | Effects of interannual variation in phenologies

While much progress has been made in documenting shifts in the mean of phenological events, we know surprisingly little about when and how variation in phenologies across years affects populations and communities (Wolkovich et al., 2014). This study shows that interannual variation in phenologies can alter the outcome of species interactions even when mean phenologies may not change over time (i.e. in stationary systems) (Figure 5). Furthermore, given some level of natural interannual variation of phenologies, the simulations also demonstrate that predictions based on mean phenologies will typically either under- or overestimate the true interaction strength (Figure 4). These results should apply to a wide range of systems given that the nonlinear pattern arises from simple size-mediated priority effects that can occur whenever growing individuals interact. Overall, the results clearly indicate that variation in phenologies across years can be a key, but largely neglected, driver of species interactions and thus community dynamics.

The results highlight an important gap in our current understanding of the dynamics of natural communities and how they will be influenced by future climate change: we know very little about how much relative phenologies of interacting species vary across years, whether variation differs systematically across taxa and systems, and how this variation will change with climate change (Wolkovich et al., 2014). It is fortunate that, researchers have accumulated impressive long-term datasets of multiple coexisting and often interacting species (CaraDonna, Iler, & Inouye, 2014; Cook, Wolkovich, & Parmesan, 2012; Thackeray et al., 2016; Walther, 2010; Wolkovich et al., 2012) that could be analysed to quantify phenological variation across a wide range of taxa and systems to look for systematic patterns. However, predicting how this variation will affect communities will also require a general understanding of how interaction strength scales with relative arrival times. In this system, the magnitude and even direction of interannual variation effects were strongly dependent on this scaling relationship and the average arrival time in the system. Clearly, it is not feasible to measure this relationship for all possible interactions within a given ecological

network. However, my experiment demonstrates that if we understand the underlying mechanisms we can make at least qualitative predictions for a wide range species. Future studies that examine this scaling relationship and underlying mechanisms across a range of interaction types and taxonomic groups are therefore essential to develop a general mechanistic framework that allows us to incorporate temporal variation into community ecology models and predict how climate change will affect the structure of natural communities.

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DATA ACCESSIBILITY

All data used for this project and model simulation code are publicly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tn9775r> (Rudolf, 2018).

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