Priority effects and season length shape long-term competition dynamics

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Abstract

The relative arrival time of species often affects species interactions within a community, contributing to priority effects. Recent studies on phenological shifts under climate change have generated renewed interest on priority effects, but their role in shaping long-term dynamics of seasonal communities is poorly resolved. Here we use a general stage-structure competition model to determine how different types of priority effects influence long-term coexistence of species in seasonal systems. We show that while shifts in mean and variance of relative arrival time can alter persistence and coexistence conditions of species, these effects depend on season length and type of priority effect. In "slow" systems with one or a few cohorts per season, changes in mean and seasonal variation of relative arrival time strongly altered species persistence through trait-mediated priority effects. In contrast, competition outcome in "fast" systems is largely determined by numeric priority effects due to interaction between many overlapping generations. These results suggest that empirically observed priority effects may arise from fundamentally different mechanisms, and that fast-generating systems may be less impacted by seasonal variation in phenology. Our model provides important insight into how natural communities respond to increasing variation in phenology over seasons under climate change.

Introduction

The relative timing of species' arrival during community assembly often determines the outcome of species interactions. Generally termed priority effects, this phenomenon is ubiquitous in animal, plant, and microbe systems (Alford and Wilbur 1985; Drake 1991; Louette and De Meester 2007; Kardol et al. 2013; Rasmussen et al. 2014; Clay et al. 2019) and plays a key role in structuring community composition (Chase 2003), species diversity (Fukami 2004), and ecosystem function (Burkle and Belote 2015; Weidlich et al. 2018; Bittleston et al. 2020). Recent studies on phenological shifts have prompted renewed interest in priority effects by emphasizing the importance of seasonal timing of species interactions (Alexander and Levine 2019; Rudolf 2019; Blackford et al. 2020; Waters et al. 2020). However, despite important advances in identifying mechanisms promoting priority effects (Chase 2003, 2010; Fukami 2004; Tucker and Fukami 2014; Grainger et al. 2019), we still have a poor understanding of how priority effects influence the long-term dynamics and structure of seasonal communities across different systems. Yet, making this prediction is crucial to fully understand the mechanism that maintain biodiversity in natural systems and predict how natural communities respond to a changing climate.

While various mechanisms have been proposed for priority effects, they can be divided into two broad categories: numeric and trait-mediated (Rasmussen et al. 2014; Rudolf 2019). Numeric priority effects arise when the competition outcome is determined by initial difference in densities. If one species' growth rate scales positively with its relative abundance (positive frequency dependence; Ke and Letten 2018), it is able to maintain a numeric advantage over other species regardless of variable phenology. On the other hand, trait-mediated priority effects are based on shifts in traits of interacting species. Relative arrival time changes those interacting traits (e.g. behavior, defense mechanism or size; Van Buskirk 1992; Lawler and Morin 1993; Hoverman and Relyea 2008; Yang and Rudolf 2010; Rasmussen et al. 2014; Poulos and McCormick 2014; Rudolf 2018; Carter and Rudolf 2019, Sniegula et al. 2019), subsequently changing species interactions. The outcome of interactions therefore depends on relative changes in per-capita effects driven by changes in relative

timing (phenology) of interactions, and is more likely to result in seasonal variation in community composition with variable phenology. Traditionally, numerical priority effects have dominated ecological literature on long-term dynamics and species coexistence, assuming no effects of seasonal reassembly on community composition. Although trait mediated priority effects have been known for decades, they have received surprisingly little attention until recently. As a consequence, we are only starting to understand when and how these different types of priority effects influence long-term dynamics of seasonal communities and species coexistence, especially when phenology varies over seasons and causes variation of community compositions between seasons (Rudolf 2019).

In nature, the importance of the two types of priority effects can be system-specific regarding number of generations per season (fig. 1). If a season consists of only a few generations (e.g. annual grassland with a single, non-overlapping generation), trait-mediated priority effects persist because difference in interacting traits is preserved until the end of the season (fig. 1A; Rudolf 2019; Blackford et al. 2020). On the other hand, if many overlapping generations take place in one season (e.g. fast-generating zooplankton communities), the correlation between initial arrival time and trait should be weakened because individuals from multiple generations with different trait values interact simultaneously (fig. 1B). In the latter scenario, the long-term outcome of competition should depend less on relative arrival time but on numeric advantages (Toju et al. 2018). Thus, the relative importance of trait-mediated priority effects on the long-term dynamics of communities could vary across a "slow-fast" continuum (few to many generations per seasons) of natural systems.

To explore the importance of numeric and trait-mediated priority effects in seasonal systems, we constructed a two-species, stage-structured model to examine how priority effects contribute to the long-term competition dynamics. We asked how changing relative arrival time would shift competition outcome, and how season length (number of generations per season) would affect this shift. We then investigated the contribution of trait-mediated and numeric priority effects by including or excluding stage-mediated interspecific competition. To examine the long-term dynamics of seasonal systems, we further investigated the effect of seasonal variation of relative

arrival time. Together, this allowed us to examine how relative arrival time and season length interact to mediate the importance of priority effects and their role in long-term dynamics of communities and ultimately persistence and coexistence of competing species.

Methods

The Model

To capture the potential change in traits of interacting species with different arrival time, we used a stage-structured competition model with Beverton-Holt type density dependence (Travis et al. 1980, Caswell 2006). In this model, stage of interacting species is the trait that changes with arrival time; the early-arriving species is at a later stage when the competing species arrives, creating the potential for trait-mediated priority effects (fig. 1). We included five juvenile stages and one adult stage to examine a wider range of interacting stages. With a fixed developmental period, using more stages gives a finer scale of arrival time, but does not affect the underlying mechanism of stage-mediated interspecific competition.

We used season as a general term that refers to the duration of time between two periodic disturbances. At the beginning of each season, all individuals enter the community as stage 1 juveniles and have probability (P_1) to survive to the next stage. At each time step, the population dynamics of both species follow:

$$\begin{pmatrix} J_1 \\ J_2 \\ J_3 \\ J_4 \\ J_5 \\ A \end{pmatrix}_{(t+1)} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & R \\ P_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & P_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & P_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_5 & S \end{bmatrix} \cdot \begin{pmatrix} J_1 \\ J_2 \\ J_3 \\ J_4 \\ J_5 \\ A \end{pmatrix}_{(t)} \tag{1}$$

At the end of season, adults reproduce to form a group of stage 1 juveniles that are subject to

a mortality (μ); all other individuals die. Since length of each generation is fixed, season length (T) determines number of generations per season. Longer season permits more generations and the community is considered "fast", while shorter season only allows for a few generations and is considered "slow".

We assumed that competition only occurs during the juvenile stage. This represents a wide range of natural systems that experience an ontogenetic niche shift to different resources, habitats or both, such as many fish, amphibians and insects that undergo metamorphosis (Werner and Gilliam 1984; Miller and Rudolf 2011; Nakazawa 2015). The survival for species 1, stage i to the next stage is reduced from baseline ($\mathbb{P}_{1,i}$) by intra- and interspecific competition summed across all stages:

$$P_{1,i} = \frac{\mathbb{P}_{1,i}}{1 + \underbrace{\sum_{j=1}^{s} \alpha_{1,i|1,j} N_{1,j}}_{\text{intraspecific}} + \underbrace{\sum_{j=1}^{s} \beta_{1,i|2,j} N_{2,j}}_{\text{interspecific}}} \tag{2}$$

Following previous approach (Rudolf 2019), we assumed that interspecific competition changes with relative arrival time (Δp) according to a sigmoidal function with midpoint (d), maximum interspecific competition (B) and scaling constant (c). Relative arrival time (Δp) is defined as the arrival time of species 1 minus that of species 2. A $\Delta p = 1$ means that species 1 arrives later than species 2 by one time step, or stage 1 individuals of species 1 encounters stage 2 individuals of species 2. We let $|\Delta p| \leq 5$ such that the two species arrive within the same generation. Δp can be either fixed (deterministic) or variable (stochastic) between each season. Interspecific competition from stage j of species 2 to stage i of species 1 is:

$$\beta_{1,i|2,j} = f(\Delta p) = B/(1 + \exp(d - (\Delta p)/c) \tag{3}$$

For $\beta_{2,i|1,j}$ (interspecific competition coefficient from stage j of species 1 to stage i of species 2), the sign of c is flipped to create a scaling function of the same shape but in different direction (fig. 2). This scaling function implies an early arrival advantage for both species (Rudolf 2019).

Note that Eqn. 3 is a phenomonological generalization of stage-mediated interspecific competition, which could arise from various biological mechanisms (Yang and Rudolf 2010). Our stage-structured model simply assumes that the trait determining competition is closely correlated to the age/stage of individuals.

We explored two scenarios, that adults survive with probability S to the next time step within a season, and that adults are short-lived with $S = 0$. The former scenario enables adults to reproduce more than once in a lifetime (e.g. microcrustaceans), producing overlapping generations, while the latter does not allow for overlapping generations (e.g. annual plants, short-lived insects). Comparing both scenario allows us to further isolate the mechanisms driving trait-mediated priority effects.

Determination of Competition Outcome

Theoretically, coexistence is determined by comparing intra- and interspecific competition: one species has to limit itself more than limiting the other (Broekman et al. 2019). However, weighted arithmetic means by population of each stage cannot fully represent competition experienced by a species in the current model: The most abundant stage (stage 1 juveniles) always experiences the most intense interspecific competition, resulting in overestimation of interaction strengths (Supporting Information, Section 2.1). To avoid this issue, we directly measured each species' growth when invading the other species to determine competition outcome (Chesson 2018; Barabás et al. 2018). The resident grew for one season (sufficient to reach equilibrium) before the invader was introduced at low density. The invader grew without intraspecific competition, and invasion growth was measured as the difference between the initial population at the second season (N_{inv+1}) after invasion and the invading population (N_{inv}). If $N_{inv+1} > N_{inv}$, invasion growth is positive. Species coexist if both have positive invasion growth; if both negative, numeric priority effects happen; if one positive and one negative, the one with positive invasion growth wins.

Evaluation of Potential Mechanisms

We expected that trait-mediated priority effects alter interspecific competition with different relative arrival time, and that this effect is mediated by number of generations per season (i.e. season length). Therefore, we characterized two possible mechanisms that could determine competition outcome: realized interaction strengths and adult mortality; the latter is a proxy of reproduction potential.

The overall interaction strengths experienced by stage i individuals (I_i) is the sum of intra- ($I_{11,i}$) and interspecific ($I_{12,i}$) interactions:

$$I_{1,i} = I_{11,i} + I_{12,i} = \sum_{j=1}^{5} \alpha_{1,i|1,j} N_{1,i} + \sum_{j=1}^{5} \beta_{1,i|2,j} N_{2,j} \tag{4}$$

The overall interaction strength experienced by species 1 (all stages) ($\bar{I}_1$) is the weighted average of $I_{1,i}$s by the population of each stage:

$$\bar{I}_1 = \bar{I}_{11} + \bar{I}_{12} = \frac{\sum_{i=1}^{5} I_{11,i} N_{1,i}}{\sum_{i=1}^{5} N_{1,i}} + \frac{\sum_{i=1}^{5} I_{12,i} N_{1,i}}{\sum_{i=1}^{5} N_{1,i}} \tag{5}$$

In simulations, intra- and interspecific interaction strengths were calculated separately. Note that only 5 stages are counted in weighted means because adult stage is not involved in competition.

The long-term mortality of adults over several seasons ($\bar{\mu}_A$) is not related to competition. It is calculated by the number of time steps at which adults experience mortality (m), number of time steps at which adults are present (τ), number of full cycles (n) and adult survival (S in Eqn. 2):

$$\bar{\mu}_A = \frac{m(1-S)+n}{\tau} \tag{6}$$

$m(1-S)$ is the within-season mortality over the time period and n is the simplification of $n * 1$ (end-of-season mortality) as all adults die at the end of a full season. Within each season, $\tau = T - |\Delta p| - 5$ because adults do not emerge after development through stage 1-5; $m = \tau - 1$ because adults do not experience mortality at first emergence.

Simulation

All simulations were run in R (R Core Team 2019). We changed season length T, intraspecific competition α, relative arrival time Δp and its variation v to explore their effects on competition outcomes. Each season was at least two-generation long (minimum 12 time steps) to make sure at least one generation finish development with maximum Δp. Simulations for deterministic scenarios (no seasonal variation of Δp) were run once for each parameter combination and each species as invader; competition outcome was then determined by invasion growth. We examined two variants of the model, with or without overlapping generations (adult survival $S > 0$ or $S = 0$) when conducting deterministic simulations.

Seasonal variation in arrival time often occurs in natural systems, and previous study suggests that this variation can be important for long-term species coexistence (Rudolf 2019). To model this seasonal variation, Δp was drawn randomly from a uniform distribution bounded by v (a positive integer) and mean relative arrival time, $\overline{\Delta p}$: $[\overline{\Delta p} - v, \overline{\Delta p} + v]$; each random Δp was rounded to nearest integer to include both bounds. Because we required that two species arrive within the same generation, $|\overline{\Delta p}| + v \leq 5$. 30 simulations were run for each parameter combination and each species as invader, each for at least 10 seasons. Multiple preliminary trials showed that 30 replications could sufficiently capture possible outcomes. Instead of N_{inv+1} in deterministic scenario, we used final population to determine invasion success. Final population is conservatively defined as the minimum of end-of-season population for the last three seasons in a simulation and represents the realized long-term average stochastic invasion growth rate.

We calculated intra- and interspecific interaction strengths at each time step separately according to Eqn. 4-5. To better examine the overall trend, we then averaged each within each season or over the whole simulation (30 seasons, sufficient for patterns to emerge). We further calculated adult mortality over the period of simulation according to Eqn. 6.

We included two alternative scenarios regarding species interactions. We replaced stage-mediated interspecific competition with a constant interspecific competition ($\beta_{12} = \beta_{21} = B/2$) for cases

without trait-mediated priority effects. We also relaxed the assumption of a constant intraspecific competition and allowed it to change with interacting stages in addition to stage-mediated interspecific competition, as substantial intraspecific variation in ecology could occur between stages (Miller and Rudolf 2011; Rudolf and Rasmussen 2013*a*, 2013*b*; Rudolf et al. 2014; Murillo-Rincón et al. 2017). We report specific methods and results of the latter scenario in Supporting Information, Section 1 as it did not change our general conclusions. See table 1 for all parameters used. Changing specific parameters affected the simulated populations and calculated values but did not affect qualitative results.

Code Availability

Full simulation code is available upon request.

Results

Trait-Mediated Priority Effects and Season Length

Both relative arrival time and season length determined the competition outcome, indicating strong but context dependent trait-mediated priority effects (fig. 3A, 3B, left). For instance, in "symmetric" systems where species have equivalent competitive abilities ($\alpha_{11} = \alpha_{22} = 0.06$), even the smallest delay in relative arrival time shifted the outcome from alternative stable states (numeric priority effects) to a single state (competitive exclusion of late arriver) with short seasons (T = 12-48, or 2-8 generations per season; fig. 3A, left). But this shift in outcome required larger differences in relative arrival time (Δp) with longer seasons (T = 60-120) and eventually disappeared from the analyzed parameter space for systems with very long seasons ($T \geq 240$, or 40+ generations per season; fig. 3A, left).

This interaction between relative arrival time and season length was qualitatively robust to variation in absolute and relative strength of competition (fig. 3B, left; fig. S11A, S11B). The specific parameter combination of intra- and interspecific competition only determined which out-

comes were possible. For instance, in an asymmetric case ($\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$), the outcome of competition changed similarly with relative arrival time and this effect was modified by season length, except longer seasons shifted the outcome from competitive exclusion (early arriving species 2 wins) to stable coexistence, and eventually to the opposite competitive exclusion scenario (species 1 wins; fig. 3B, left).

We observed a small range of Δp and T leading to coexistence that did not conform to early arriver advantage (fig. 3A, 3B, left). This coexistence region arises in our stage-structured model because average adult population actually increased with larger difference in arrival time within a given season for systems with shorter seasons (see Supporting Information, Section 2.2 for detailed analysis and discussion).

The interaction of relative arrival time and season length can be explained by concurrent shifts in interspecific interaction strengths and competitive dominance (fig. 4, 5). In systems with short seasons, earlier arrival of species 1 increased its competitive ability over species 2 (due to stage-mediated interspecific competition). This allowed species 1 to invade when rare, and ultimately changed which species can persist (fig. 3A, 3B). However, increasing the number of generations per season (season length) lead to concurrent increase in the average interspecific competition pressure on the early arriver across and within seasons, while simultaneously weakening interspecific competition for the late arriver (fig. 4, 5). Average adult mortality decreased with longer seasons, causing changes in species fecundity, subsequently affecting population density and interaction strengths (fig. S12). Together, increasing season length therefore effectively reduced and eventually removed the competitive advantage gained from early arrival, returning the system to the outcome expected without differences in arrival time.

The effect of season length completely disappeared in systems with non-overlapping generations (i.e. adults reproduce once per lifetime): relative arrival time again determined the outcome of competition, but season length had no effects (fig. S13). This result makes intuitive sense; without overlapping cohorts, the initial differences in relative arrival time (Δp) and its effect on interaction strength are preserved across each generation, and hence indefinitely retained regardless of season

length. Overall, these patterns clearly demonstrate that trait-mediated priority effects strongly affect outcome of competition when seasons are short, but this effect becomes weaker when seasons allow for many coexisting stages due to overlapping generations.

Finally, when we fixed interspecific competition regardless of Δp (effectively removing stage-mediated interspecific competition), neither season length nor relative arrival time altered the outcome except when one species arrived very early with shorter seasons (fig. 3C). The exception was driven by a temporal refuge effect between early and late arrivers: When species 1 arrives earlier, its early stages are exempted from interspecific competition before species 2's arrival; this exemption increases species 1's survival, subsequently increases its possibility of invasion success (see Supporting Information, Section 2.3 for details). Taking out this effect, these simulations indicate that trait-mediated priority effects were solely responsible for changes in competition outcomes (fig. 3B, 3C, left).

Variation in Arrival Time

In natural systems, relative arrival time of species varies across years. We found that variation in Δp across seasons introduced the potential of alternative competition outcomes, and this potential was again influenced by season length. In many cases, adding seasonal variation to Δp promoted species coexistence by turning population dynamics to long-term transients where population of both species fluctuated but never reached zero (fig. S14). However, this effect was dependent on season length. Variation in relative arrival time promoted coexistence with shorter seasons: while species 1 could not invade species 2 at $T = 18$ with fixed Δp, increasing seasonal variation of Δp increased the final invading population of species 1, promoting coexistence (fig. 6A). Variation of Δp did not lead to changes in competition outcome with intermediate season length ($T = 24$; fig. 6B) but promoted competitive exclusion with longer seasons ($T = 48$): species 2 could invade species 1 Δp (fig. 6C). The effect of varying relative arrival time at the start of the season (Δp) therefore had opposite effects on competition outcome depending on season length.

While seasonal variation of Δp significantly changed what outcomes are possible and the rela-

tive probability that each will occur, the outcome predicted in deterministic scenarios was usually the most likely outcome to occur. However, under some parameter combinations, the outcome predicted under constant (deterministic) conditions was completely absent from the range of observed outcomes with seasonal variation in Δp (e.g. $\overline{\Delta p} = 0$, $T = 18$ and 24, fig. 3A, S15A; $\overline{\Delta p} = 1$, $T =$ 18-36, fig. 3B, S15B). This was likely driven by the same synergistic effects of season lengths and relative arrival time on interaction strengths observed in deterministic cases. Some season lengths and relative arrival times led to specific interaction strengths that enabled a slow but successful invasion, but the invader stayed at a very small population size during the invasion process, increasing risk of extinction with seasonal variation of Δp. Therefore, the invading species could go extinct even if the initial invasion is successful. For instance when $\overline{\Delta p} = 1$, $T = 36$, $\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$, the small but positive invasion growth rate of species 2 led to a long period with small population, during which a variation in Δp could result in unsuccessful invasion and therefore species 1's competitive dominance (fig. S15B, S16).

We also observed changes in competition outcomes due to variable relative arrival time when we removed stage-mediated interspecific competition (fig. 3C). However, the change in probability of different competition outcomes was very limited and mechanistically different from changes observed with stage-mediated interspecific competition. This was caused by the change of deterministic competition outcome with relative arrival time, which was due to temporal refuge effect rather than stage-mediated interspecific competition (Supporting Information, Section 2.3). Therefore, trait-mediated priority effects were the only contributing factor in changes observed between deterministic and stochastic simulations (fig. 3B, 3C).

Discussion

Priority effects can greatly influence community structure and functions (Chase 2003; Fukami 2004; Burkle and Belote 2015; Weidlich et al. 2018; Bittleston et al. 2020), but their long-term implications on seasonal community dynamics and underlying mechanisms are poorly understood.

Here, we show that season length (number of generations per season), together with relative arrival time, determines the long-term dynamics of two competing species, and this effect is dependent on the type of priority effects and potential for overlapping generations. In "slow" systems with only one or a few generations per season, changes in mean and seasonal variation of relative arrival time (phenology) at the onset of the season led to trait-mediated (but not numerical) priority effects that altered outcome of interactions. This effect was dampened and disappeared in "fast" systems with many overlapping generations per season. Thus, slow systems with short seasons are much more sensitive to climate mediated changes in phenology. Together, these results suggest that numeric and trait-mediated priority effects both shape community structure but contribute differently along a continuum of slow- to fast-generating systems.

Effects of Relative Arrival Time and Season Length

Many studies have identified trait-mediated priority effects, highlighting its prevalence in nature (Lawler and Morin 1993; Rasmussen et al. 2014; Alexander and Levine 2019; Blackford et al. 2020). Recent theory suggest that trait-mediated priority effects can play a key role in determining long-term dynamics in seasonal communities, but this work focused on systems with one reproductive event per season (Rudolf 2019). Using a very different model formulation, we found the same general pattern: shifts in relative arrival can alter the long-term dynamics and coexistence patterns of competing species. Furthermore, we found that these effects (1) are absent without trait-mediated priority effects and (2) attenuate and even disappear when longer seasons allow for multiple overlapping generations. Note that numerical priority effects are still possible but would require that relative arrival time exceeds one generation within a given season. This condition is unlikely when species have similar phenology and compete for the same seasonal resources. Overall, these results reveal that both the type of priority effects and season length (number of generations per season) are important to the long-term dynamics of communities.

The interaction between relative arrival time and season length arises because they have opposing effects on interaction strength. Changing relative arrival times alters outcome of competition

when stages (age classes) differ in their per-capita effects. Longer seasons accommodate multiple overlapping generations, allowing all stages to interact with each other (fig. 1). The more generations overlap, the smaller the initial trait differences become. We found that this reduction in trait differences also reduces the change in realized interaction strength that is initiated by difference in arrival time. Thus, changing relative arrival time increases initial trait differences and thereby "pushes" the system to a new potential outcome, while increasing season length reduces initial trait-differences and "pulls" the system back to the outcome expected when species arrive simultaneously (fig. 7). In contrast, this interaction is not expected (and did not occur) with just numerical priority effects.

Temporal variation can play an important role in shaping the outcome of species interactions (Chesson 2000; Adler et al. 2006; Barabás et al. 2018; Rudolf 2019). In nature, relative arrival time fluctuates across seasons, and this fluctuation of phenology is increasing with climate change (Parmesan 2006; Diez et al. 2012; Post 2013; Wolkovich et al. 2014; Pearse et al. 2017). Our results indicate that seasonal variation in relative arrival time could change what competition outcomes are possible and how likely each outcome is, but only when trait-mediated priority effects are present. In our model, different relative arrival times at the beginning of each season enable either species to harness early arriver competition advantage in some seasons, and this advantage is boosted by trait-mediated priority effects. As in the deterministic case, this boost is strongest when a season consists of only a few generations (short seasons) because of more accentuated trait-mediated priority effects. When seasons become longer (fast-generating systems), the probability for a given outcome changes, and the potential for alternative outcomes overall decreases and eventually disappears. Thus, whether and how seasonal variation in species relative phenology changes long-term community composition is highly dependent on type of priority effects and number of generations per season.

Together, these results also suggest that species can systematically differ in how sensitive they are to climate mediated shifts in phenology. The interactive effect of season length implies that fast-generating systems (more generations per season) may be buffered more against seasonal variation in

phenology given the insignificant contribution of relative arrival time to community dynamics. Previous studies have discovered several mechanisms that could buffer against mismatch arising from phenological variation, such as decreased competition (Reed et al. 2013), intrinsic flexibility in phenology and resource use (Salido et al. 2012), or dispersal across heterogeneous patches (Phillimore et al. 2012; Post 2013). However, the relationship between life cycle and ability of buffering against phenological variation is rarely explored. Our results suggest that slow-generating systems may be highly susceptible to seasonal variations in phenology, while fast-generating systems may be less susceptible due to overlapping generations, although more empirical investigation is needed.

Mechanisms of Priority Effects

Until recently, the distinction between numeric and trait-mediated mechanisms has received little attention. The niche-based mechanistic framework of priority effects, namely niche preemption and niche modification (Vannette and Fukami 2014; Fukami 2015), aligns well with our definition of trait-mediated priority effects because changes in interacting traits likely alter realized niches of both species. The use of a competition-phenology function (e.g. Eq. 3) reflects this change in competition coefficients (Rudolf 2019). On the other hand, a recently developed quantitative framework of priority effects requires fixed competition coefficients regardless of arrival time; it is therefore unable to fully address niche-based mechanisms and can only be applied to numeric priority effects arising from positive frequency dependence (Fukami et al. 2016; Ke and Letten 2018). Our results indicate that priority effects based on numeric and trait-mediated mechanisms have different importance to slow- and fast-generating systems. While the effect of relative arrival time could persist throughout short seasons with only a few generations, it diminished with longer seasons that spans many overlapping generations, at which numeric mechanisms determine the competition outcome. These results suggest that priority effects observed in nature may be generated by fundamentally different mechanisms: trait-mediated priority effects are more likely in slow-generating systems while numeric priority effects are observed in fast-generating systems. In slow systems (e.g. annual grassland, ephemeral ponds), trait differences caused by relative arrival time may persist and mediate species

interactions for the whole season (Rasmussen et al. 2014; Blackford et al. 2020). In fast systems, priority effects observed are likely generated from pure numeric mechanism (e.g. positive frequency dependence; Grainger et al. 2019); they are also more likely to reach equilibrium within one season, therefore less affected by seasonality.

The two underlying mechanisms of priority effects could lead to different community dynamics in the long term; one such example is the persistence of priority effects in spatial communities over several dispersal/colonization events. Dispersal could homogenize local community composition regardless of different assembly history, lowering the impact of priority effects (Mouquet and Loreau 2002; Fukami 2015; Grainger and Gilbert 2016; but see Vannette and Fukami 2017). Nevertheless, this homogenizing effect was not discovered in freshwater protist communities, in which the assembly history determined community composition despite of random dispersal (Pu and Jiang 2015). The study observed changes of interspecific competition due to different assembly processes, indicating the presence of trait-mediated priority effects. In this case, change of interacting traits from different assembly processes counteracted the homogenizing effects of dispersal, potentially maintained beta diversity among communities. Although numeric advantage could also persist over several dispersal events (Toju et al. 2018), whether this advantage can be maintained under constant dispersal until reaching stable equilibria is unclear.

Next Steps

Trait-mediated priority effects are common and can be driven by various mechanisms. Our model specifically considered age/ontogenetic stage, which is associated with arrival time and leads to changes in traits that determine species interactions in both animal and plant systems (Alford and Wilbur 1985; Van Buskirk 1992; Lawler and Morin 1993; Rasmussen et al. 2014; Godoy and Levine 2014; Carter and Rudolf 2019). Clearly, how age is related to changes in interaction strength depends on the specific mechanisms and thus can vary across systems. For instance, competitive ability may change quickly or slowly with difference in age in fast- vs. slow-growing systems respectively. While these relationships will determine the quantitative results (e.g. the absolute

difference in arrival time needed to change competition outcome, or number of generations needed to remove effect of arrival time), they are unlikely to change the general patterns presented here.

Age/stage is nevertheless not the only mechanism that could cause trait-mediated priority effects. For instance, priority effects in plants could arise from plant-soil feedback (Kardol et al. 2007) or plant-pollinator interaction (Waters et al. 2020); arrival time of competing predators/parasites can also alter defensive traits of common prey/host, subsequently affecting competition (Olito and Fukami 2009; Clay et al. 2019) and sometimes generate late arriver advantage (Hoverman and Relyea 2008; Clay et al. 2020). All these alternative mechanisms could lead to a different competition-phenology function (different shape and/or direction of curves in Figure 2) that often is poorly documented or unknown in natural systems. Our study provides a baseline of how trait-mediated priority effects from one specific mechanism (stage-mediated interspecific competition) could affect community dynamics that can easily be expanded to explore the long-term effects of these different systems once more information is available.

Recent attention on phenological shifts and species competition raises the need of rethinking priority effects from different mechanisms in seasonal systems. By incorporating stage-mediated interspecific competition, our model shows that trait-mediated priority effects are different from numeric priority effects in mechanisms and implications to long-term community dynamics. This result represents a much-needed theoretical exploration of trait-mediated priority effects and calls for more investigations of priority effects under a changing climate. Future studies should focus on the various mechanisms of trait-mediated priority effects and their long-term implications to community structure, especially with seasonal variation of phenology.

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Tables

Table 1: Major parameters and values used in simulation.

Parameter	Definition	Range/Values
Δp or $\overline{\Delta p}$	(Mean) relative arrival time	Integers; $[-5, 5]$ (deterministic) or $[-2, 2]$ (stochastic)
v	Seasonal variation of Δp	0 (deterministic) or 3 (stochastic)
B, d, c	Baseline interspecific competition, midpoint and scaling constant for $f(\Delta p)$, respectively	0.225, 0, ± 0.85
α	Intraspecific competition coefficient	A wide range (0.04-0.15) examined; results presented were with $\alpha_{11} = \alpha_{22} = 0.06$ and $\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$
β	Interspecific competition coefficient	Determined by $f(\Delta p)$ or $B/2 = 0.1125$
J_i, A	Population of juvenile stage i and adult stage	Resident initial population $J_1 = 3$; invading population $J_1 = 0.01$
T	Season length	12, 18, 24, 36, 48, 60, 96, 120; 240 (deterministic only)
R	Fecundity of adults	10
S	Survival rate of adults after one time step	0.6
μ	Seasonal mortality of newly produced J_1	0.2
$\mathbb{P}_i$	Baseline survival from juvenile stage i to i+1	0.8

Figure legends

Figure 1. Conceptual drawing of interacting individuals at a given time with single (A) or multiple (B) generations in a season, indicated by "season len" and thick dashed lines. If a season has only one generation, then size differences caused by relative arrival time (Δp) persists. Individuals of different sizes interact until both species all reach adulthood, before which trait-mediated priority effects persist. If a season consists of several generations (two shown in B), because of the continuous reproduction of adults, a mixture of different size classes emerges, diluting the effect of Δp on species interaction. Colored circles and squares indicate two different species; their sizes correspond to sizes of individuals in the population. Curves show the size distribution within one generation. Thin dashed lines shows the community composition at a particular time.

Figure 2. The scaling function of stage-mediated interspecific competition. Both per-capita competition coefficients are determined by Δp. The function assumes an early arriver advantage. Parameters used: $B = 0.225$, $c = 0.85$, $d = 0$.

Figure 3. Phase diagrams of competition outcomes across different season lengths (T) and relative arrival times (Δp). Left: deterministic (constant p across seasons); right: stochastic (varying Δp across seasons), shown by composition of outcomes from 30 simulations. Black rectangles on deterministic results show the parameter space examined by stochastic simulations. Numeric PE means that competition outcome is determined by numeric priority effects. A, symmetric case with $\alpha_{11} = \alpha_{22} = 0.06$; B, asymmetric case with $\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$; C, asymmetric case with constant intra- and interspecific competition ($\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$, $\beta_{12} = \beta_{21} = 0.1125$. See Table 1 for other parameters used.

Figure 4. Average interaction strengths over 30 seasons change with season length. I_{11} and I_{22} means intraspecific competition of species 1 and 2, respectively; I_{12} and I_{21} means interspecific competition from species 2 to 1, and from species 1 to 2, respectively. Coexistence region is $T = 24$-96, before which species 2 wins and after which species 1 wins (see fig. 3B, left). Parameters used: $\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$, $\Delta p = 2$, initial population $N_1 = N_2 = 3$. Note that this is not an invasion

scenario, but the change of realized interaction strength with season length still holds.

Figure 5. Average interaction strengths within season change with different season lengths. Species 1 cannot invade with shorter season ($T = 12$) but can invade with longer season ($T = 36$); Species 2 can invade with both season lengths and excludes resident with shorter season. Interactions "on itself" refers to intraspecific competition, "on others" to interspecific competition from the focal species to the other. Competition outcome cannot be simply inferred by comparing the two interaction strengths because they are weighted means over population of all juvenile stages (Supporting Information, Section 2.3). A zero interaction means zero population; a constant nonzero interaction means equilibrium. A, species 1's interaction strengths when invading. B, species 2's interaction strengths when invading. C, species 2's interaction strengths when species 1 invades. D, species 1's interaction strengths when species 2 invades. Vertical lines indicate start of invasion. Parameters used: $\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$,$\Delta p = 2$, $T = 12$ and 36.

Figure 6. Distribution of final populations of 30 stochastic simulations (in triangles), comparing to final population of deterministic simulation (in circle). Increasing season length changes the effect of stochasticity from stabilizing (decreasing difference between populations of two species) to destabilizing (increasing the difference). Note that these are not exactly the same simulations as represented in Figure 3B; there may be minor differences due to stochasticity. Left: species 1 invades; right: species 2 invades. Parameters used: A, $T = 18$; B, $T = 24$; C, $T = 48$. Shared parameters: $\alpha_{11} = 0.06$, $\alpha_{22} = 0.07$, $\Delta p = 2$.

Figure 7. Conceptual drawing showing synergistic effects of relative arrival time (Δp) and season length (T) on competition outcome, assuming fixed intraspecific competition. Axes are interspecific competition between species 1 and 2, and 2 and 1 (β_{12} and β_{21}, respectively). Dashed diagonal represents when $\beta_{12} = \beta_{21}$, i.e. the two species arrive simultaneously. Solid circles represent interspecific competition coefficients under simultaneous arrival, empty circles show coefficients in alternative scenarios. The parameter space is divided into four quadrants by possible competition outcomes; numeric PE means that competition outcome is determined by numeric priority effects. Shifting Δp (dashed arrows) "pushed" the system to alternative outcomes: from coexistence (A) to

competitive exclusion of either species (B and C). Longer T (more generations per season) "pull" the system back to the condition when both species arrives simultaneously (solid arrows). This pattern is quantitatively robust with different intraspecific competition used, which only changes the outcome under simultaneous arrival from coexistence to numeric priority effects (A to D); shifts in competition outcomes due to Δp and T (E and F) still hold.

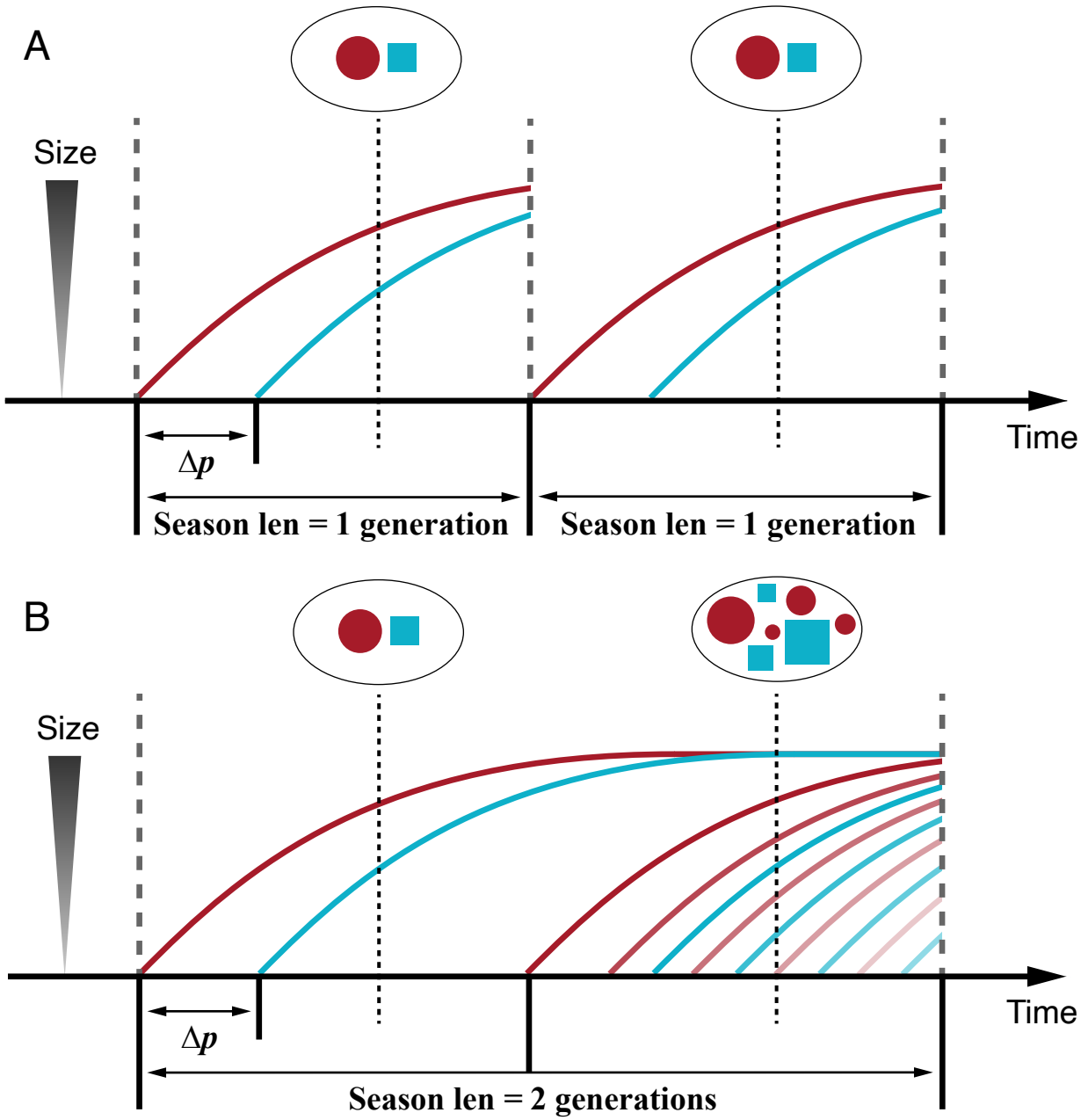
A
Size
Time
Δp
Season len = 1 generation
Season len = 1 generation
B
Size
Time
Δp
Season len = 2 generations

Figure 1

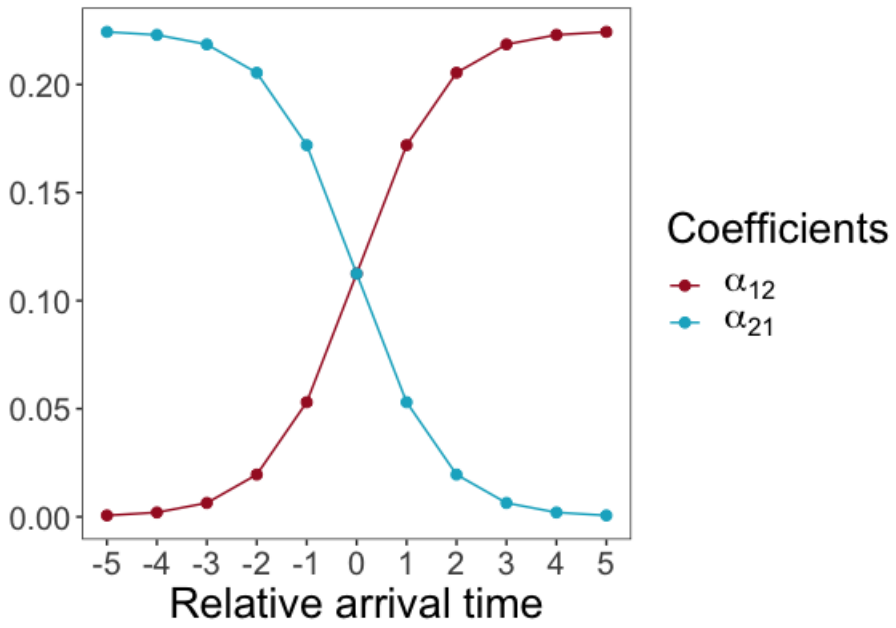
0.20
0.15
0.10
0.05
0.00
-5 -4 -3 -2 -1 0 1 2 3 4 5
Relative arrival time
Coefficients
α_{12}
α_{21}

Figure 2

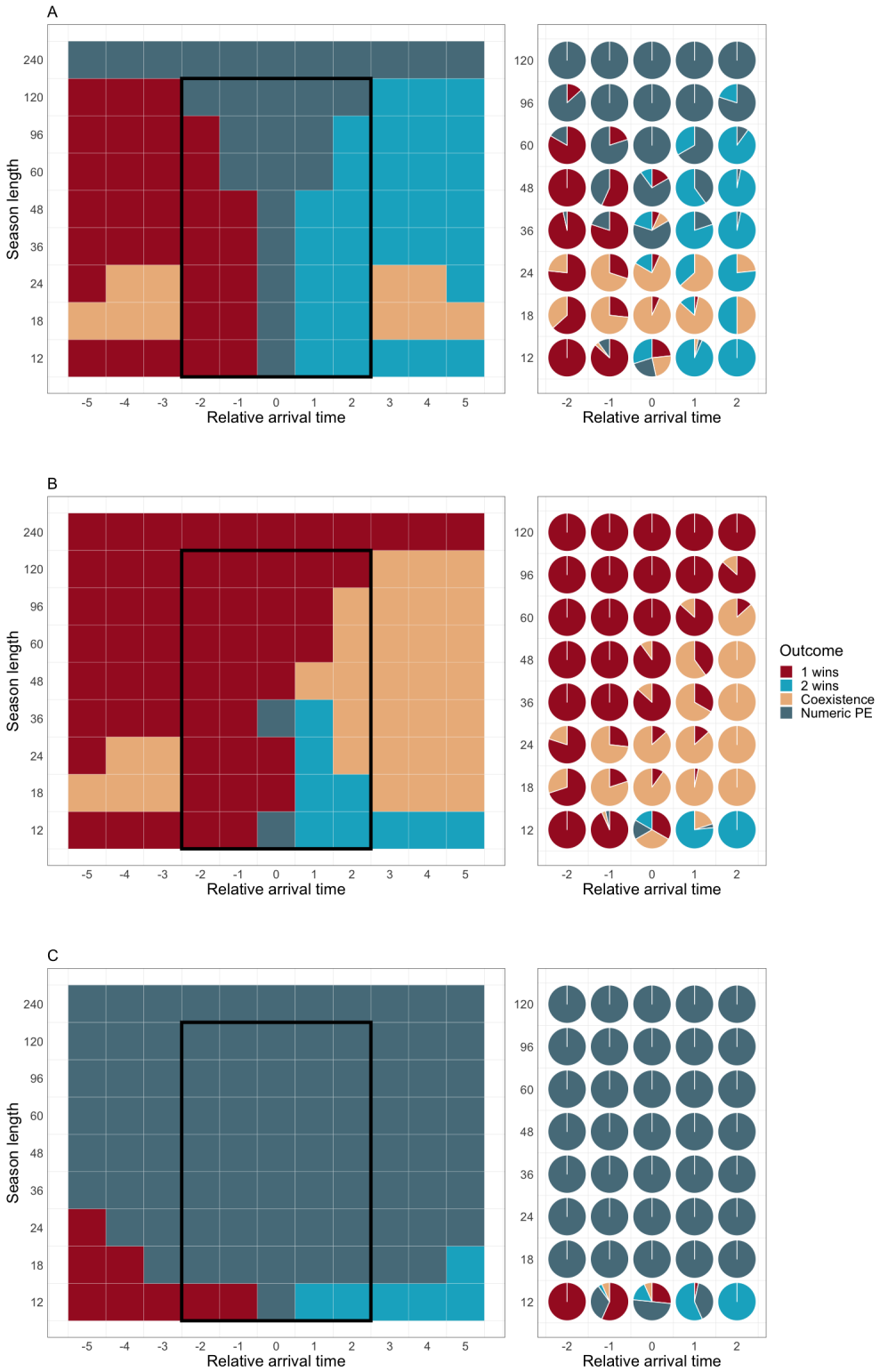
A
B
C
Season length
240
120
96
60
48
36
24
18
12
-5 -4 -3 -2 -1 0 1 2 3 4 5
Relative arrival time
-2 -1 0 1 2
Relative arrival time
Outcome
1 wins
2 wins
Coexistence
Numeric PE

Figure 3

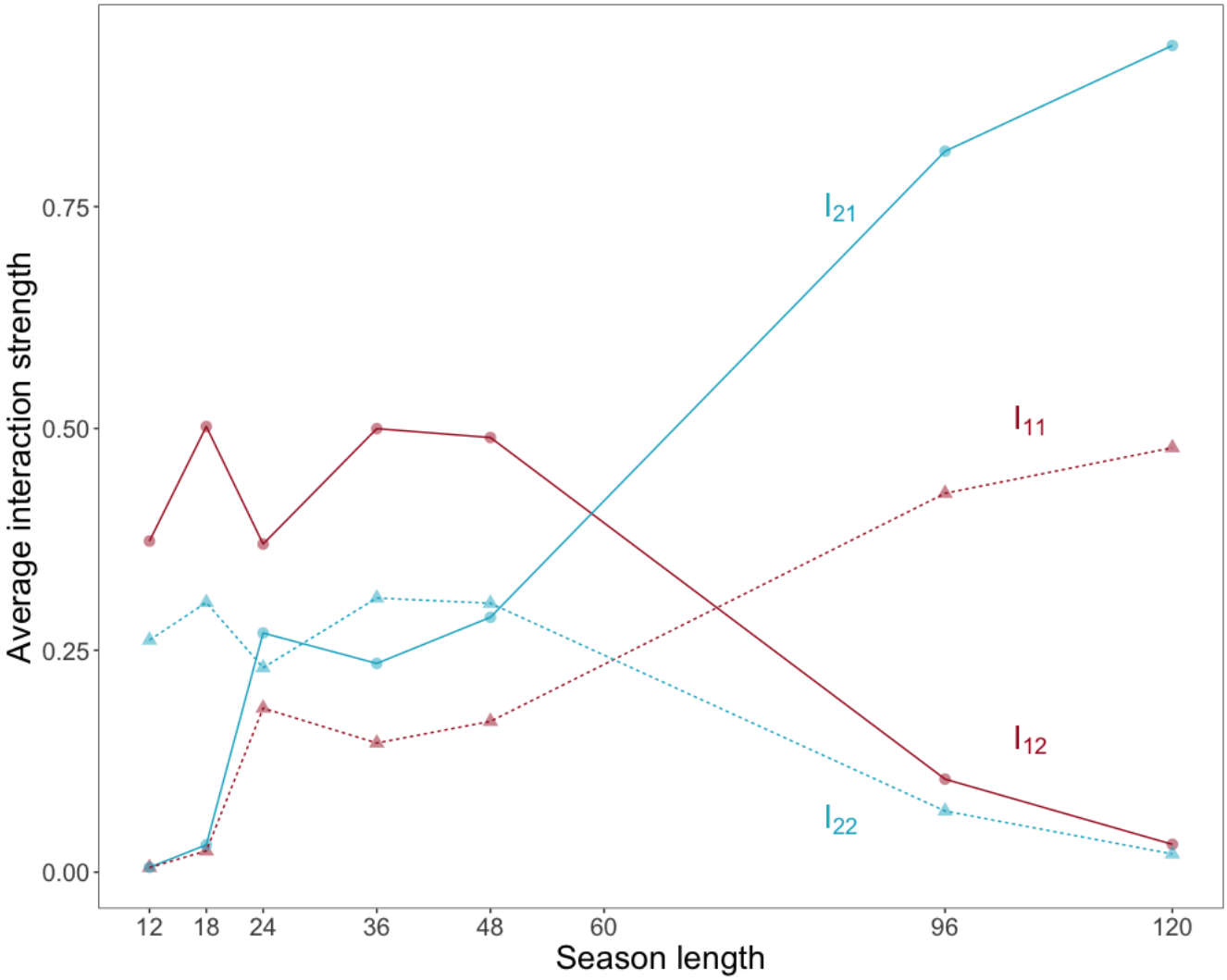
Average interaction strength
0.75
0.50
0.25
0.00
12
18
24
36
48
60
96
120
Season length
I21
I11
I12
I22

Figure 4

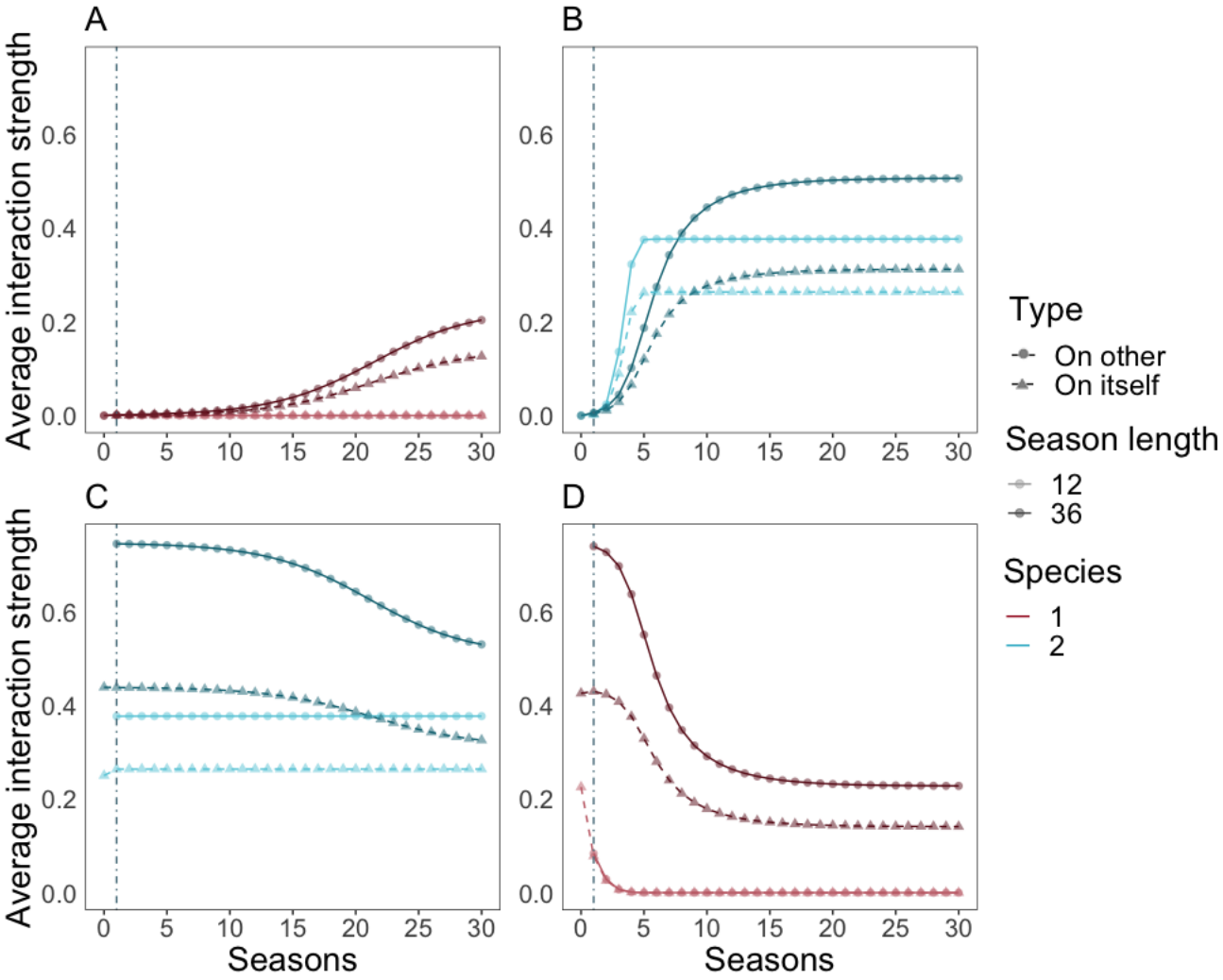
A
B
C
D
Average interaction strength
0.0
0.2
0.4
0.6
0
5
10
15
20
25
30
Seasons
Type
On other
On itself
Season length
12
36
Species
1
2

Figure 5

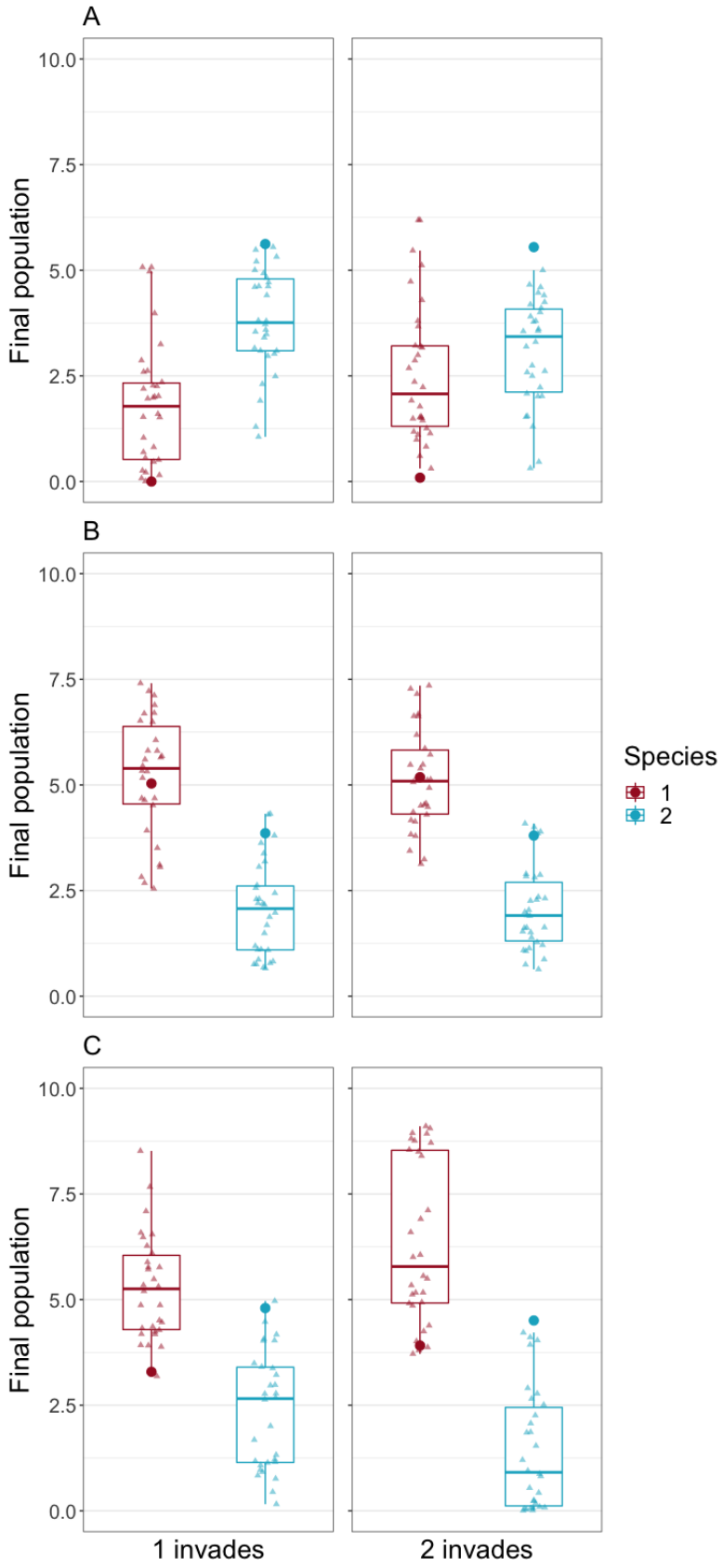
A
B
C
Final population
10.0
7.5
5.0
2.5
0.0
1 invades
2 invades
Species
1
2

Figure 6

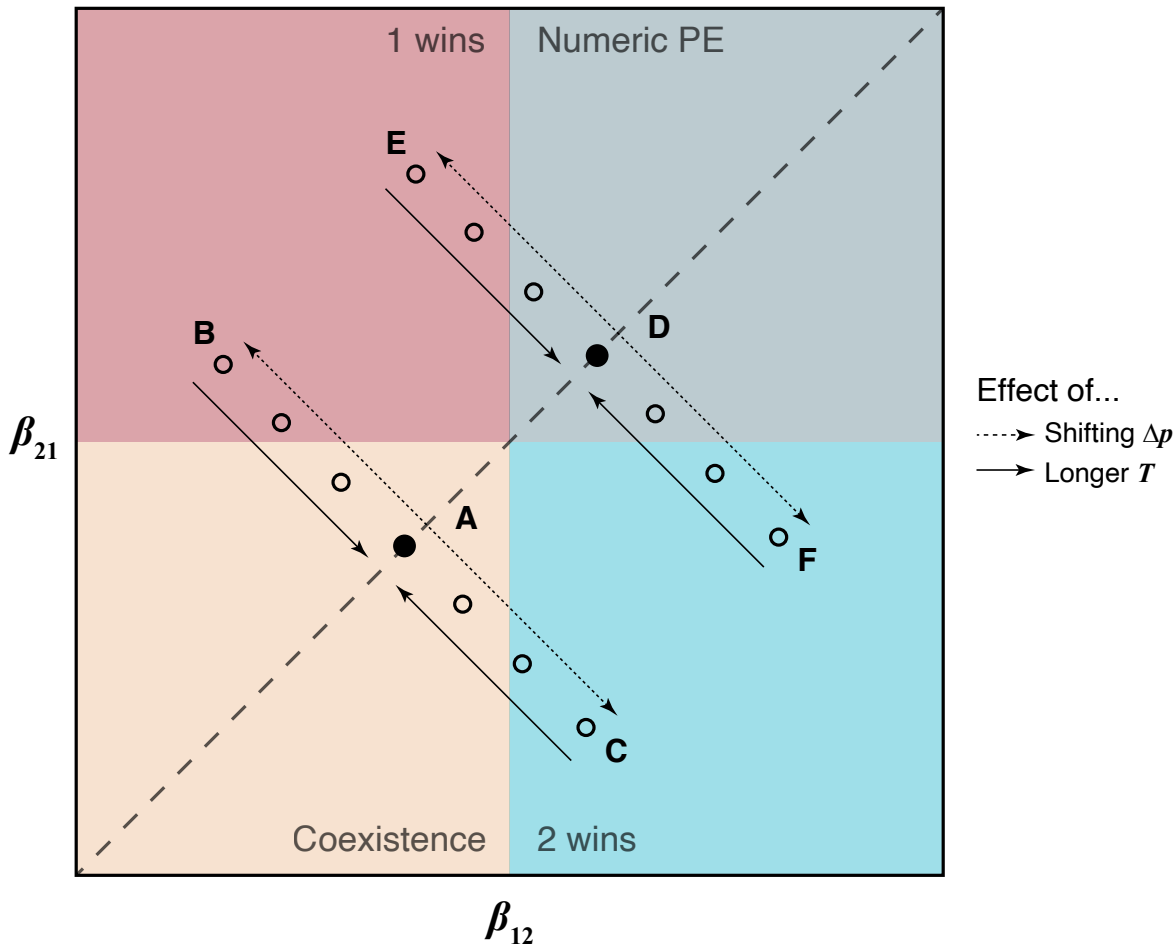
1 wins
Numeric PE
E
D
B
A
F
C
Coexistence
2 wins
β_{21}
β_{12}
Effect of...
Shifting Δp
Longer T

Figure 7