Stage-mediated priority effects and species life history shape long-term competition dynamics

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Abstract

The relative arrival time of species affects their interactions and can thus determine which species persist in a community. Although this phenomenon, called priority effect, is ubiquitous in natural communities, how it depends on species' life history is unclear. Using a seasonal stage-structured model, we show that differences in stages of interacting species could generate priority effects by altering the strength of stabilizing and equalizing coexistence mechanisms, changing outcomes between exclusion, coexistence, and positive frequency dependence. However, these priority effects are strongest in "slow" systems with just one or a few generations per season and diminish in "fast" systems where many overlapping generations per season dilute the importance of stage-specific interactions. Our model reveals a novel link between the "pace of life" and the consequences of priority effects, suggesting that consequences of phenological shifts driven by climate change should depend on specific life histories of organisms.

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 have highlighted the importance of priority effects in seasonal communities by demonstrating the role of seasonal timing, or phenology, in determining outcomes 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 systems with different life histories. Yet, making this prediction is crucial to fully understand the mechanism that maintains biodiversity in natural systems and predict how natural communities respond to a changing climate and which species are most vulnerable.

While various mechanisms have been proposed for priority effects, many are generated by the physiological differences between interacting species that arise by arriving earlier or later. For instance, differences in arrival time alter the traits of species that determine competition, such as resource competition mediated by the size difference between early and late arrivers (Lawler and Morin 1993; Schwinning and Weiner 1998; Brown and Cahill Jr 2022), behavioral interference on late arrivers (Van Buskirk 1992; Poulos and McCormick 2014), altered defense of prey/host of the early-arriving predator/pathogen (Hoverman and Relyea 2008; Hoverman et al. 2013), or even size-dependent intraguild predation (Rasmussen et al. 2014; Sniegula et al. 2019). Here, the outcome of interactions strongly depends on relative arrival time (phenology) because timing determines the per-capita effects of interacting species which in turn determines the persistence and coexistence of species. Collectively termed *trait-mediated priority effects* (Rasmussen et al. 2014; Rudolf 2019), they describe changes in per-capita effects mediated by a shift in the traits of interacting species, and priority effects arise because the shift in timing determines what outcome is possible.

Trait-mediated priority effects represent a category that is different from priority effects defined by classic theory, where they arise because the per-capita effects of interacting species result in bistability (alternative states) due to positive frequency dependence (species' growth rate scales positively with its relative abundance; Ke and Letten 2018). In this case, priority effects arise when the more frequent species is always able to maintain a numeric advantage over other species regardless of relative arrival time (phenology), and a difference in arrival time therefore only matters if it allows the population of early arriving species to increase relative to the late arriver and thus gain a numerical advantage. Traditionally, this type of "numeric" priority effect has dominated ecological theory on long-term dynamics and species coexistence, assuming no effects of seasonal reassembly on community composition (e.g., Fukami and Nakajima 2011; Gerla and Mooij 2014; Ke and Letten 2018). Although trait-mediated priority effects have been known for decades in empirical systems, they have received surprisingly little attention until recently, as empirical studies find more mechanisms and consequences of trait-mediated priority effects (Rudolf 2018; Blackford et al. 2020; Fragata et al. 2022). Therefore, we are only starting to understand when and how these different types of priority effects influence the 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 trait-mediated priority effects can depend on species' life histories, specifically the number of generations per growing season (hereafter "season"; Figure 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 the difference in interacting traits (e.g., ontogenetic stages) is preserved until the end of the season (Figure 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 (Figure 1B). In the latter scenario, the long-term outcome of competition should depend less on relative arrival time but more on initial abundances (Toju et al. 2018) and average interaction strengths. 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 season) of natural systems.

To explore the role of 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. Specifically, we assumed that the interspecific competition is mediated by stage classes of the two species ("stage-mediated interspecific competition"). We asked how changing relative arrival time would shift outcomes of competition, and how life history (number of generations per season) would affect this shift. We then investigated the contribution of trait-mediated priority effects by including or excluding stage-mediated interspecific competition. To examine the long-term dynamics of seasonal communities in nature, we further investigated the effect of seasonal variation on 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 the long-term dynamics of communities and ultimately persistence and coexistence of competing species.

Methods

Stage-structured Model

To capture the potential change in traits of interacting species with different arrival times, we used an age-classified matrix population model with a Beverton-Holt type density dependence (Travis et al. 1980; Caswell 2006). In this model, the age/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 (Figure 1; Yang and Rudolf 2010). We included five juvenile stages, one adult stage, and one dormant stage. 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. The dormant stage accounts for individuals before they arrive within a season.

We used season as a general term that refers to the duration of time between two periodic disturbances. We tracked the seasonal process and species arrival with two functions of time: $b(t) = 0$ when a season ends, and $b(t) = 1$ otherwise; $a_i(t) = 1$ if species i arrives at t, and $a_i(t) = 0$ otherwise. At the beginning of each season, all individuals of species i enter the community as stage 1 juveniles with density $N_{i,1}$. Juveniles in stage k of species i have density $N_{i,k}$ and survive

to the next stage with probability $P_{i,k}$. Adults ($N_{i,6}$) can live for more than one time step, with a survival probability of V, and produce stage 1 juveniles with a density-independent fecundity (R). At the end of the season, adults produce offspring that are subject to mortality (μ); all other individuals die. These offspring then enters a dormant stage ($N_{i,7}$) and re-emerge at the assigned arrival time of the next season, with no additional mortality. We let N_i denote the vector of densities $(N_{i,1}, \ldots, N_{i,7})$ for species i.

We let Δs denote the difference between the arrival time of species 2 and species 1. $\Delta s = 1$ means that stage m individuals of species 1 interact with stage $m+1$ individuals of species 2. Differences in arrival time lead to corresponding differences in what stages interact first; once both species are present, competition is determined by the stage structure of each species. We let $|\Delta s| \leq 4$ such that the two species can still interact as juveniles even with the latest arrival.

Overall, the population dynamics of species i can be described as:

$$N_i(t+1) = A_i(t) N_i(t),$$

where

$$A_i(t) = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & b(t)R & a_i(t) \\ b(t)P_{i,1} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & b(t)P_{i,2} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & b(t)P_{i,3} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & b(t)P_{i,4} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & b(t)P_{i,5} & b(t)V & 0 \\ 0 & 0 & 0 & 0 & 0 & R(1-\mu)(1-b(t)) & 1-a_i(t) \end{bmatrix}. \quad (1)$$

Since the length of each generation is fixed, season length (T) determines the number of generations per season. A longer season permits more generations and the community is considered "fast", while a shorter season only allows for a few generations and is considered "slow". See Appendix I for the determination of season lengths in actual simulations.

Stage-mediated Interspecific Competition

We assumed that competition only occurs during the five juvenile stages. This represents a wide range of organisms that experience an ontogenetic niche shift, such as fish, amphibians, and insects (Werner and Gilliam 1984; Miller and Rudolf 2011; Nakazawa 2015). The transition probability of species 1, stage m to the next stage is reduced from baseline (P_0) by intra- and interspecific competition from all other individuals:

$$P_{1,k} = \frac{P_0}{1 + \underbrace{\sum_{\ell=1}^{5} \alpha_{1k,1\ell} N_{1\ell}}_{\text{intraspecific}} + \underbrace{\sum_{\ell=1}^{5} \beta_{1k,2\ell} N_{2\ell}}_{\text{interspecific}}}. \tag{2}$$

Following previous approach (Rudolf 2019), the strength of interspecific competition scales according to a sigmoidal function with midpoint (d), maximum interspecific competition (B) and a scaling constant that determines its shape (c):

$$\beta_{1k,2\ell} = f(\ell - k) = \frac{B}{1 + \exp\left((d - (\ell - k))/c\right)}. \tag{3}$$

For $\beta_{2k,1\ell}$ (interspecific competition coefficient from stage ℓ of species 1 to stage k of species 2), the sign of c is flipped to create a scaling function of the same shape but in a different direction (Figure 2A). This relationship assumes that later stages are more competitive than early stages, is well supported in plant and animal systems (Shorrocks and Bingley 1994; Rudolf 2018; Blackford et al. 2020), and can arise from various mechanisms such as resource preemption (Schwinning and Weiner 1998; Connolly and Muko 2003) or interference competition (Rudolf 2006; Narvaez et al. 2020). We set $d = 0$ such that the two interspecific competition coefficients are equal when the two species arrive simultaneously. Without this stage-mediated interspecific competition, β values are not dependent on Δs; we therefore calculated interspecific competition as if both species arrive simultaneously: $\beta_{1k,2\ell} = \beta_{2\ell,1k} = B/2$. Using Eqn. 3 this way ensures the consistency between scenarios with and without stage-mediated interspecific competition. We assumed that intraspecific competition (α) does not change with differences in interacting stages, an assumption that we relaxed in Appendix III.

Quantifying Competitive Outcomes

We determined outcomes of competition by calculating the invasion growth rates of each species (MacArthur and Levins 1967; Hofbauer and Sigmund 1998; Schreiber 2000; Roth et al. 2017; Chesson 2018). The invasion growth rate r_i of species i corresponds to its average per-capita growth rate when it is rare and the other species $j \neq i$ is common. We restricted to parameters where each species can persist in the absence of interspecific competition (see Appendix I for details). Through the classic mutual invasiability criterion (MacArthur and Levins 1967; Turelli 1978; Chesson 2018), the invasion growth rates can be used to classify competitive outcomes into three types. When both invasion growth rates are positive ($r_1 > 0$ and $r_2 > 0$), both species increase from being rare and, therefore, coexist. When both invasion growth rates are negative ($r_1 < 0$ and $r_2 < 0$), there is a numerical priority effect in which the more common species tends to exclude the less common species. When the invasion growth rates are of opposite sign (e.g., $r_1 > 0 > r_2$), one species tends to exclude the other (e.g., species 1 excludes species 2). The proofs and a detailed description of numerically estimating the invasion growth rates r_1 are discussed in Appendix I. Briefly, we numerically determined the resident's periodic stable state in the absence of the other species, then approximated the invasion growth rate using a linearization of the other species dynamics and the power method from numerical matrix theory (cf. Roth et al. 2017; Benaïm and Schreiber 2019).

While the signs of the invasion growth rates determine *whether* coexistence occurs or not, they do not provide insights into *why* it does or does not occur. To gain insights about why Δs matters for coexistence, we calculated niche difference (ND) and relative fitness difference (RFD) by calculating the sensitivity to competition (Narwani et al. 2013; Godwin et al. 2020). The sensitivity of species 1 is calculated using the long-term growth rate of its monoculture (r_1) and its invasion growth rate at the stable distribution of species 2 (r_{12}):

$$S_1 = \frac{r_1 - r_{12}}{r_1}. \tag{4}$$

A smaller sensitivity implies higher competitive ability; when both $S < 1$, both species coexist, whereas neither species can invade the other when both $S > 1$. We then used sensitivities of each species to calculate the niche and relative fitness differences (Godwin et al. 2020):

$$\begin{cases} ND = 1 - \sqrt{S_1 S_2} \\ RFD = \sqrt{S_1 / S_2} \end{cases} . \tag{5}$$

Chesson's criterion for coexistence requires that:

$$1 - ND < RFD < \frac{1}{1 - ND}. \tag{6}$$

We mapped the calculated ND and RFD values under each Δs and season length onto a "coexistence space" where ranges of coexistence, competitive exclusion, and numeric priority effects (positive density dependence) are marked by the above inequality.

Simulation

All simulations were conducted in R (R Core Team 2021). We changed season length (T), intraspecific competition (α), initial stage difference (Δs), and its variation (v) to explore their effects on competition outcomes. Each season was at least two-generation long to make sure at least one generation can finish development with a maximum $|\Delta s|$. We calculated invasion growth rates (r) of each species for each parameter combination. We imposed a competitive hierarchy by setting different intraspecific competition coefficients, i.e., species with lower intraspecific competition is competitively superior (Table 1). We specifically chose intraspecific competition coefficients much smaller than the average interspecific competition coefficient, $B/2$, to promote numeric priority effects (positive frequency dependence).

Seasonal variation in arrival time often occurs in natural systems (Sheriff et al. 2011; Diez et al. 2012; Carter et al. 2018) and can have important consequences on long-term community dynamics (Rudolf 2019). We modeled one simple scenario of such variations where species phenology changes periodically over seasons. To acheive this periodicity, we made Δs periodically alternate between $\overline{\Delta s} - v$ and $\overline{\Delta s} + v$ where $\overline{\Delta s}$ is the mean value and v is a positive integer. We required that $|\overline{\Delta s} \pm v| \leq 4$, which is the range of Δs explored in simulations without variations. We determined outcomes of competition for using the same method outlined above.

Code Availability

Full simulation code is deposited at github.com/hengxingzou/Zou2020bioRXiv.

Results

Trait-Mediated Priority Effects and Season Length

We found that outcomes of competition were driven by interactive effects between differences in arrival times and season length. When interspecific competition was stage-mediated, the initial stage difference (Δs) affected the competition outcomes, indicating a trait-mediated priority effect (Figure 3A). When species 1 arrived early ($\Delta s < 0$) it generally excluded species 2; when species 2 arrived early ($\Delta s > 0$), it either excluded or coexisted with species 1. We expected this asymmetry because we chose $\alpha_{11} < \alpha_{22}$ (Table 1), giving species 1 a competitive advantage. However, these trait-mediated priority effects, or changes of competitive outcomes over Δs, were strongly dependent on season length (T). With short seasons (2-4 generations per season), even the smallest difference in initial stage difference shifted the outcome from alternative stable states (numeric priority effects) to a single state (competitive exclusion), but this shift in outcome required larger Δs with longer seasons (Figure 3A). As expected, these interactions were contingent on the strength of intraspecific competition. If both intraspecific competition coefficients were smaller than 0.05, each species generally limited the other more than itself; longer seasons therefore expanded the region of alternative stable states (Figure S1A). Conversely, α values larger than 0.06 promoted coexistence, and the two species coexisted regardless of their initial stage differences when each season contained more than 8 generations (Figure S1B). When we removed stage-mediated interspecific competition, outcomes were mostly driven by numeric priority effects (the species with a larger initial population won; Figure 3C), except when $T = 2$ generations. Overall, the interaction of arrival time and season length indicates longer seasons (i.e. "faster" systems) remove trait-mediated priority effects.

While these results confirmed our hypothesis that trait-mediated priority effects are dependent on season lengths, we nevertheless observed some unexpected patterns. In Figure 3A, when $T = 2$ generations, species 1 had an early arriver advantage when it arrived moderately early ($-3 \leq$

$\Delta s \leq 0$) but not when extremely early ($\Delta s = -4$), where it coexisted with species 2 instead of excluding it. Furthermore, we expected that the absence of stage-mediated interspecific competition would remove any signal of trait-mediated priority effects, i.e., all values of Δs and T would lead to numeric priority effects. Results in Figure 3C did not agree with this expectation as Δs still changed outcomes of competition with $T = 2$ generations, indicating a trait-mediated priority effect. We investigated the cause of these unexpected patterns by examining the population dynamics of the model. We found that changing Δs in our discrete stage-structured model altered not only interspecific competition coefficients but also the breeding adult population size at the end of the season, both of which would determine species fitness (Appendix IV). If a season ends one time step before the late arriver could produce adults ($|\Delta s| = 1$), the overall adult population would be smaller, leading to smaller population at the beginning of the next season. Conversely, if a season ends one time step after the production of adults (e.g., $|\Delta s| = 4$), the overall adult population would be larger, so would the initial population of the next season (Figure S4). These effects diminished with longer seasons because the population approached a stable stage distribution, leading to less variations of adult population between time steps (Figure S5). Despite these unexpected patterns, season length still altered outcomes of competition, emphasizing the interaction of arrival time and species life history.

Coexistence Space

Phenological shifts (initial stage differences; Δs) and season length (T) changed both niche and relative fitness differences between species, further demonstrating the complex nature underlying the early arriver advantage observed in Figure 3. With shorter seasons ($T = 2$ generations), changing the initial stage difference from -4 (species 1 at stage 5 when species 2 arrived) to 4 (species 2 at stage 5 when species 1 arrived) strongly shifted niche differences (ND) and relative fitness differences (RFD) from promoting coexistence to species 1 winning, numeric priority effects, species 2 winning, and coexistence again (Figure 4A). In general, smaller difference in arrival times ($|\Delta s|$) led to a smaller niche difference, meaning that the early arriver had less competitive advantage; when both species arrived together ($\Delta s = 0$), the niche difference become negative, indicating a higher probability of numeric priority effects from positive frequency dependence Ke and Letten 2018. This is consistent with numeric priority effect we observed from our simulations.

On the other hand, changes in relative fitness differences corresponded to the effect of Δs on the adult populations described above (see also Appendix IV). When the initial stage difference is small ($|\Delta s| = 1$), the late arriver was strongly disadvantaged because of a smaller adult population, reflected by a large fitness difference from the early arriver. When the initial stage difference is large ($|\Delta s| = 4$), the late arriver was slightly advantageous because of a larger adult population, reflected by a small fitness difference from the early arriver, leading to coexistence (Figure 4A). Longer seasons eliminated these effects and as expected: larger $|\Delta s|$ increased both niche and fitness differences due to the early arriver advantage (Figure 4B).

Without stage-structured interspecific competition, we observed the same qualitative patterns: with shorter seasons ($T = 2$ generations), larger initial stage differences led to larger niche and relative fitness differences, except when $|\Delta s| = 1$ or 4, which marked the effect of Δs on adult population (Figure 4C). With all Δs examined $ND < 0$, indicating a strong tendency toward numeric priority effects (Ke and Letten 2018). With longer seasons ($T = 4$ generations), the effect of Δs on the adult population diminished, and initial stage difference affected niche and relative fitness differences mostly by changing interspecific competition coefficients. As expected, competition outcomes were determined by initial abundance (numeric priority effects), and larger $|\Delta s|$ increased both niche and relative fitness differences (Figure 4D).

Overall, these patterns demonstrated that initial stage differences strongly affected outcomes of competition by changing both niche and relative fitness differences of interacting species. This effect was stronger when seasons were short and became weaker with longer seasons, which allowed for overlapping generations and many coexisting stages.

Periodic Environment

Periodic variations in relative arrival times (Δs) allowed for each species to arrive early at alternate seasons, shifting outcomes of competition compared to simulations with constant Δs. In most cases with a change of outcomes, these variations switched competitive exclusion or alternative stable states (numeric priority effects) to coexistence, although in some cases periodic variations also switched coexistence to competitive exclusion (Figure 3A, 3B). Without stage-mediated interspecific competition, periodic variations of Δs mostly promoted numeric priority effects, except when species 1 arrived much earlier (Figure 3D). Closer inspection showed that in general, periodic

variations strongly reduced the late arriver's sensitivity to interspecific competition (calculated by (4)), but this reduction was strongest when the season length was short ($T = 2$ generations). Indeed, we observed strongest shifts in the coexistence space when $T = 2$ generations both with and without stage-mediated interspecific competition (Figure 5A, 5C). These shifts were mostly caused by the concurrent changes of niche difference and relative fitness difference.

With stage-mediated interspecific competition, periodic variations equalized the two species by reducing the absolute values of relative fitness differences between the early and the late arriver (Figure 5A). Periodic variations also increased their niche differences when they arrive within one time step of each other ($|\Delta s| \leq 1$). These equalizing and stabilizing forces lead to shifts from competitive exclusion or numeric priority effects to coexistence (Figure 4A-B, Figure 5A-B). Without stage-mediated interspecific competition, the magnitude of shifts in niche differences and relative fitness differences were smaller in magnitude but much more context-dependent. The only case where periodic variations changed competitive outcomes was with a short season ($T = 2$ generations): a reduction of relative fitness differences again equalized the early and late arrivers, but they only shifted from competitive exclusion to numeric priority effects due to strong destabilization ($ND < 0$; Figure 4C, Figure 5C).

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. Using a stage-structured competition model that accounts for the seasonal nature of ecosystems, we show that the phenological differences within seasons (initial stage difference) and their fluctuations between seasons determine the long-term dynamics of two competing species, generating trait-mediated priority effects. Furthermore, these effects are dependent on the life histories of competing species (number of generations per season). 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 priority effects that altered the outcome of interactions. This observation was dampened and even 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 different mechanisms of priority effects could be important for systems operating at different time scales, and emphasize the role of seasonality, phenological shifts, and variations in long-term community dynamics.

Effects of Relative Arrival Time and Season Length

Phenological differences could lead to trait-mediated priority effects, as identified by many studies in various systems (Lawler and Morin 1993; Geange and Stier 2010; Rasmussen et al. 2014; Alexander and Levine 2019; Blackford et al. 2020; Fragata et al. 2022), but the long-term consequences of these effects remain poorly resolved. Recent theory suggests 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). By incorporating stage structure and stage-mediated interspecific competition, we provided a mechanistic resolution of the above result: shifts in initial stage differences can alter the long-term dynamics and coexistence patterns of competing species. Furthermore, we showed that this result is strongly influenced by the life histories of species, specifically the number of generations in a season. Indeed, shifting initial stage differences (Δs) in our model changes the niche difference and relative fitness difference between the two species, but this change weakens with more generations per season. By accommodating multiple overlapping generations, longer seasons allow all stages to interact with each other (Figure 1). The more generations overlap, the less important the initial trait differences become, as the stage distributions of two species become more similar, leaving little room for stage-specific interspecific competition. Thus, changing relative arrival time increases initial trait (stages in our model) differences and thereby "pushes" the system to a new potential outcome, while increasing season length "pulls" the system back, constraining the range of potential outcomes by reducing the effective trait differences.

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 could be increasing with climate change (Parmesan 2006; Diez et al. 2012; Post 2013; Wolkovich et al. 2014; Pearse et al. 2017; but see Stemkovski et al. 2022). Our results indicate that seasonal fluctuation in relative arrival time could change competition outcomes, especially when trait-mediated mechanisms are present:

periodic arrival times enable either species to harness early arriver competition advantage in alternating seasons, contributing to both equalizing and stabilizing mechanisms in the presence of stage-mediated interspecific competition. As in the cases without fluctuations, these effects are strongest when a season consists of only a few generations (short seasons) because of more accentuated trait-mediated priority effects. Thus, whether and how seasonal variation in species phenology changes long-term community composition is highly dependent on the type of priority effect and species life histories.

Together, these results also suggest that species can systematically differ in the sensitivity to climate-mediated shifts in phenology. Systems with more generations per season should be more buffered against seasonal variation in phenology, as the contribution of relative arrival time to community dynamics decreases with the number of generations per season. 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 histories and the ability to buffer against phenological variation is rarely explored. Our results call for more empirical work that compares the effects of phenological shifts across this slow-fast continuum, especially as warmer climates could affect life history traits such as developmental rates and voltinism (Altermatt 2010; Brans and De Meester 2018).

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 would likely alter realized niches of both species. Indeed, the calculated niched and relative fitness differences values changed with initial stage differences in our model, demonstrating the effect of relative arrival times on niches. On the other hand, a recently developed quantitative framework of priority effects (Fukami et al. 2016; Ke and Letten 2018) 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. By mapping competition at different initial stage differences onto the coexistence space, our results indicated the difference between numeric and trait-mediated priority effects. While a species pair exhibiting the former falls into a region in the coexistence space, the latter is marked by a *shift* of niche and fitness differences in this space: greater differences in arrival times generally increase niche difference and absolute values of relative fitness difference, leading to a shift in outcomes of competition. This difference demonstrates the underlying assumptions of numeric and trait-mediated priority effects: the former is one outcome of competition (out of three possibilities), while the latter is the shift of such outcomes. This difference is highlighted by a recent empirical study that did not find numeric priority effects via positive frequency dependence but found a trait-mediated priority effect via preemption of spatial niches, detected through the shift from competitive exclusion to coexistence (Fragata et al. 2022).

In our model, trait-mediated priority effects are achieved by stage-mediated interspecific competition: interactions are affected by the ontogenetic stages of the two species (Yang and Rudolf 2010; Rudolf 2019). However, we found that trait-mediated priority effects can attenuate and even disappear when longer seasons allow for multiple overlapping generations. This indicates that priority effects based on numeric and trait-mediated mechanisms impact slow- and fast-generating systems differently. Furthermore, fundamentally different mechanisms may generate priority effects. 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 by numeric priority effects (e.g. positive frequency dependence; Fukami 2004; Grainger et al. 2019); they are less likely to display trait differences (e.g., stage classes) and more likely to reach equilibrium within one season.

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 or 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 random dispersal (Pu and Jiang 2015).

The study observed changes in interspecific competition due to different assembly processes, indicating the presence of trait-mediated priority effects. In this case, the change of interacting traits from different assembly processes counteracted the homogenizing effects of dispersal, potentially maintaining beta diversity among communities. Two recent theoretical studies that explicitly incorporated trait-mediated priority effects highlighted this consequence: in these models, dispersal was unable to homogenize the metacommunity with their presence (Miller and Allesina 2021; Zou and Rudolf 2022).

Next Steps

Trait-mediated priority effects are common and can be driven by various mechanisms. Our model considered the ecological differences between ontogenetic stages of interacting species, which correlate with relative arrival times and 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; Brown and Cahill Jr 2022). How age or stage is related to changes in interaction strength depends on the specific mechanisms and thus can vary across systems. For instance, the competitive ability may change quickly or slowly with differences in stages in fast- versus. 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 the number of generations needed to remove the effect of arrival time), they are unlikely to change the general patterns presented here.

Our model is based on several important assumptions. We assumed no competition between adults and no reproduction from juveniles. Competition between adults is relevant to systems such as plants and will likely affect the fecundity, subsequently the initial population of the next season. Including reproduction of late juvenile stages, such as in some zooplanktons, may promote overlapping generations and possibly further decrease the importance of initial phenological difference. More importantly, we assumed the same number of stages and duration of each stage and therefore similar developmental rates for both species. Competition may negatively impact physiological development (Park 1938; Morin and Johnson 1988), undermining this assumption. This is especially relevant because climate change may also accelerate vital processes such as ontogenetic development and reproduction timing (Brans and De Meester 2018; Keller and Shea 2020), but how the

two contrary effects interact in competitive communities is less explored (Lancaster et al. 2017).

Stage differences are also not the only mechanism that could cause trait-mediated priority effects. For instance, priority effects in plants could arise from light competition (Schwinning and Weiner 1998), plant-soil feedbacks (Kardol et al. 2007; Van der Putten et al. 2013) or plant-pollinator interactions (Waters et al. 2020); arrival time of competing predators or parasites can also alter defensive traits of common prey or 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 of these alternative mechanisms could lead to a different competition-phenology function (different shape or direction of curves in Figure 2A) 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 to phenological shifts (Rudolf 2019) and seasonality (White and Hastings 2020) raises the need of rethinking priority effects in seasonal ecosystems. By incorporating stage-mediated interspecific competition, our model shows that the importance of trait-mediated priority effects depends on the position of the community on the slow-fast continuum. These results provide a much-needed link between priority effects and species life histories. As we face pressing global change, we need a better resolution on how communities respond to the simultaneous shifts in phenology and life history. Future studies should continue to investigate such synergistic effects under season- and time-explicit frameworks.

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Tables and Figures

Table 1: Major parameters and values used in simulation.

Parameter	Definition	Range/Values
Δs or $\overline{\Delta s}$	(Mean) initial stage difference	Integers; $[-4, 4]$ (constant) or $[-2, 2]$ (periodic)
v	Seasonal variation of Δs	0 (constant) or 2 (periodic)
B, d, c	Baseline interspecific competition, midpoint and scaling constant for $f(\Delta s)$, respectively	0.225, 0, ± 0.85
α	Intraspecific competition coefficient	$\alpha_{11} = 0.05$, $\alpha_{22} = 0.06$; see results with other values in Appendix II
β	Interspecific competition coefficient	Determined by $f(\Delta s)$ or $B/2 = 0.1125$
T	Season length	2, 4, 8, 16, 20 generations
R	Fecundity of adults	12
S	Survival rate of adults after one time step	0.8
μ	Seasonal mortality of newly produced J_1	0.2
$\mathbb{P}_i$	Baseline survival from juvenile stage i to i+1	0.8

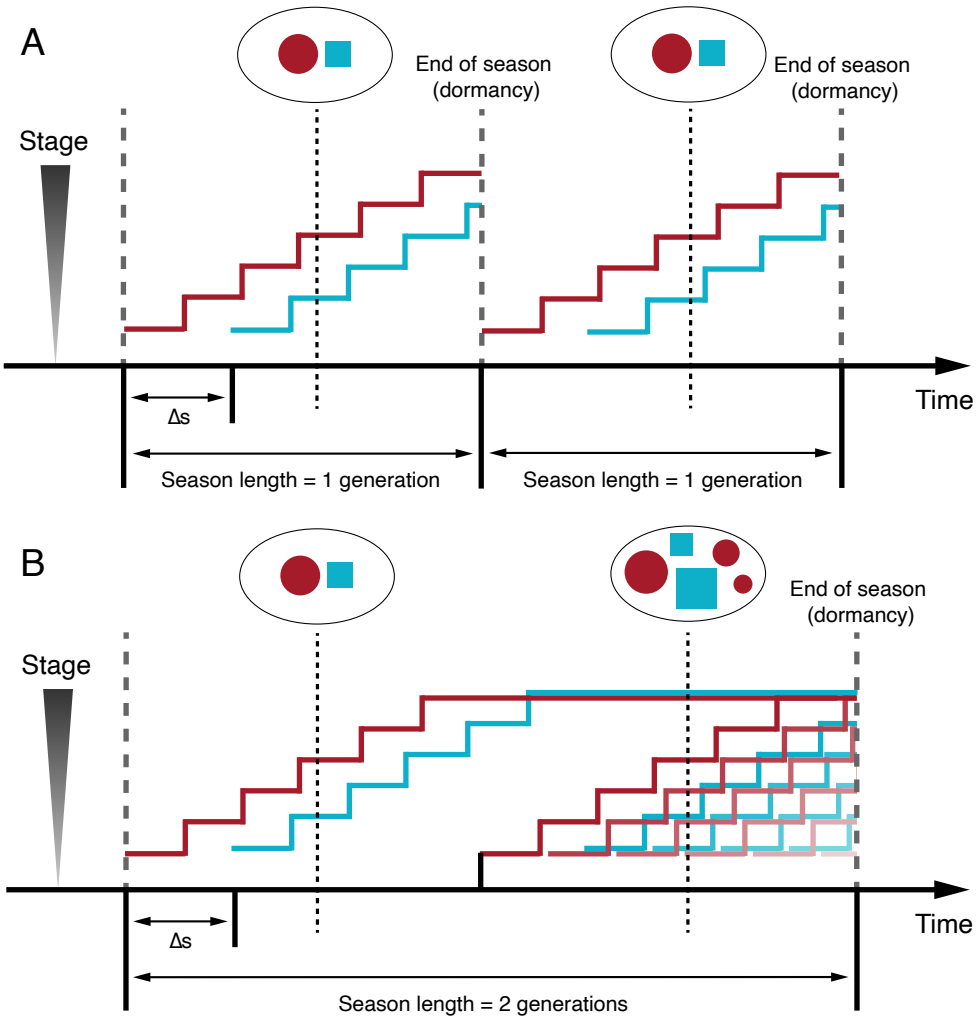

Figure 1: Conceptual drawing of interacting individuals at a given time with single (A) or multiple overlapping (B) generations in a season, indicated by "season length" and thick dashed lines. If a season has only one generation, then the initial size/stage differences caused by different arrival times (phenological difference) persist until the end of the season. If a season is long enough for completion of multiple generations (two shown in B) and individuals continue to reproduce once they mature, populations gradually become mixtures of all different size classes, diluting the effect of initial phenological difference on species interactions. Colored circles and squares indicate two different species; their sizes correspond to sizes of individuals in the population. Thick colored lines show the size distribution in the community; blue lines in B are slightly raised for visibility. Thin dashed lines shows the community composition at a particular time.

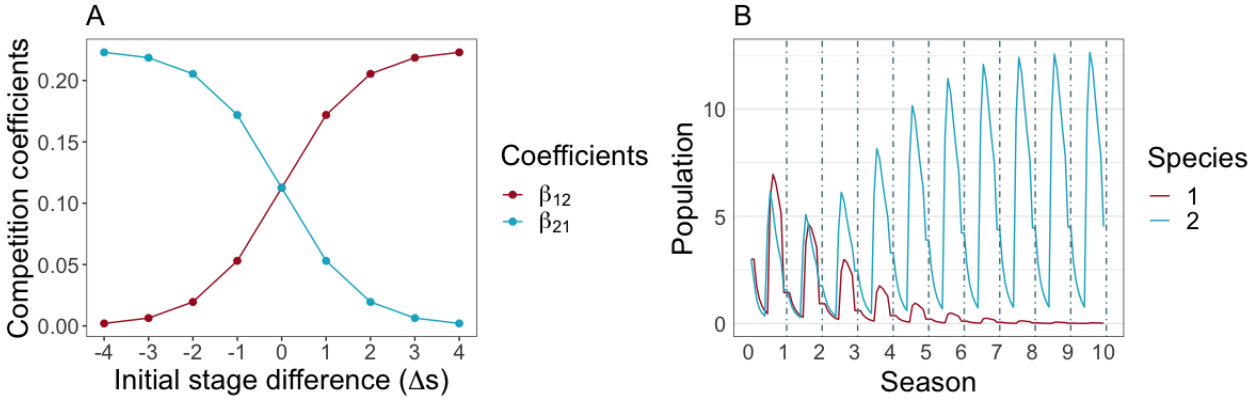

Figure 2: A. The scaling function of stage-mediated interspecific competition. Both per-capita competition coefficients are determined by Δs. The function assumes an early arriver advantage. B. An example of population dynamics generated by the model, with initial population of both species at 3, $\Delta s = 0$, and $T = 2$ generations. Vertical dashed line marks the beginning of each season. See Table 1 for other parameters used.

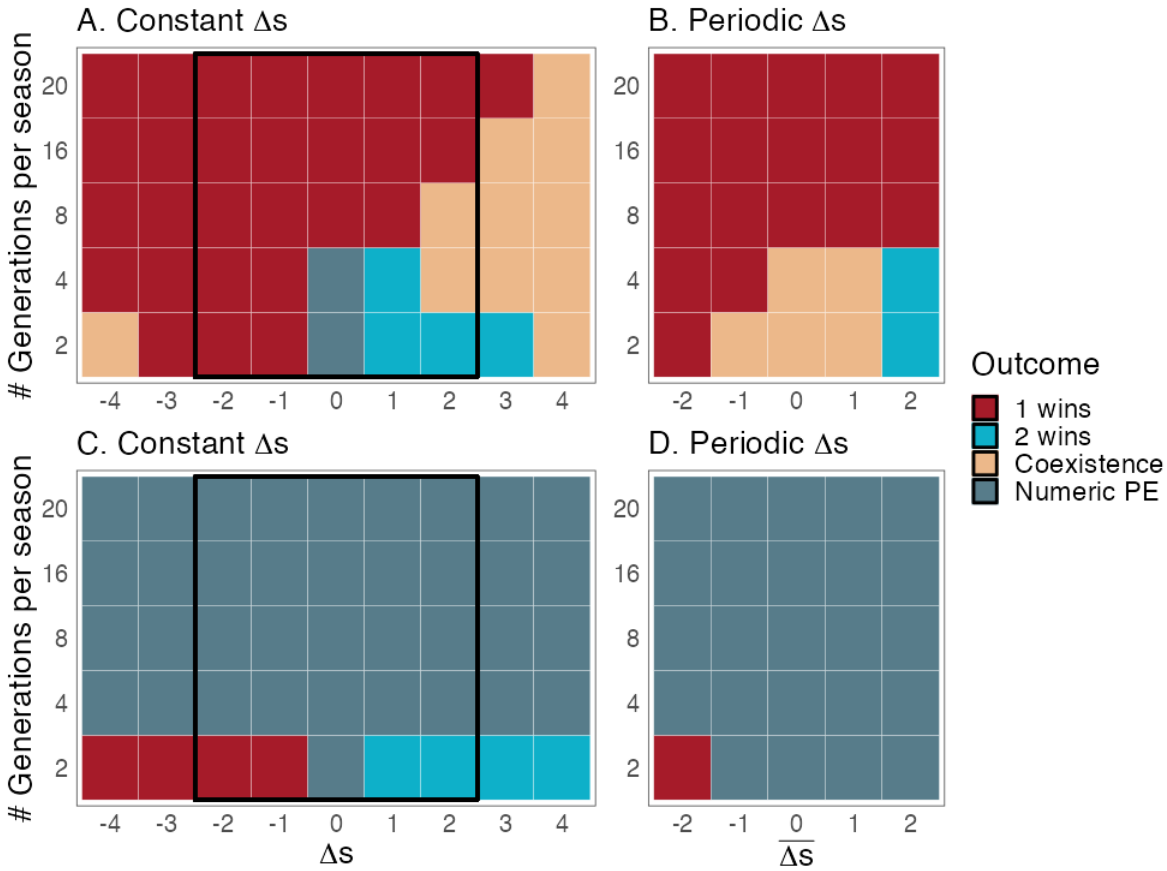

Figure 3: Phase diagrams of competition outcomes across different season lengths (T; in number of generations per seasons) and stage differences (Δs). A and B show results with stage-mediated interspecific competition, C and D show results without stage-mediated interspecific competition. Left panels show results from simulations with constant Δs across seasons; the rectangle marks the parameter space used in simulations with periodic variations of Δs across seasons, shown in right panels. Black rectangles in panels A and C show the parameter space examined by periodic simulations presented in panels B and D. Numeric PE means that competition outcome is determined by numeric priority effects generated by positive frequency dependence. See Table 1 for other parameters used.

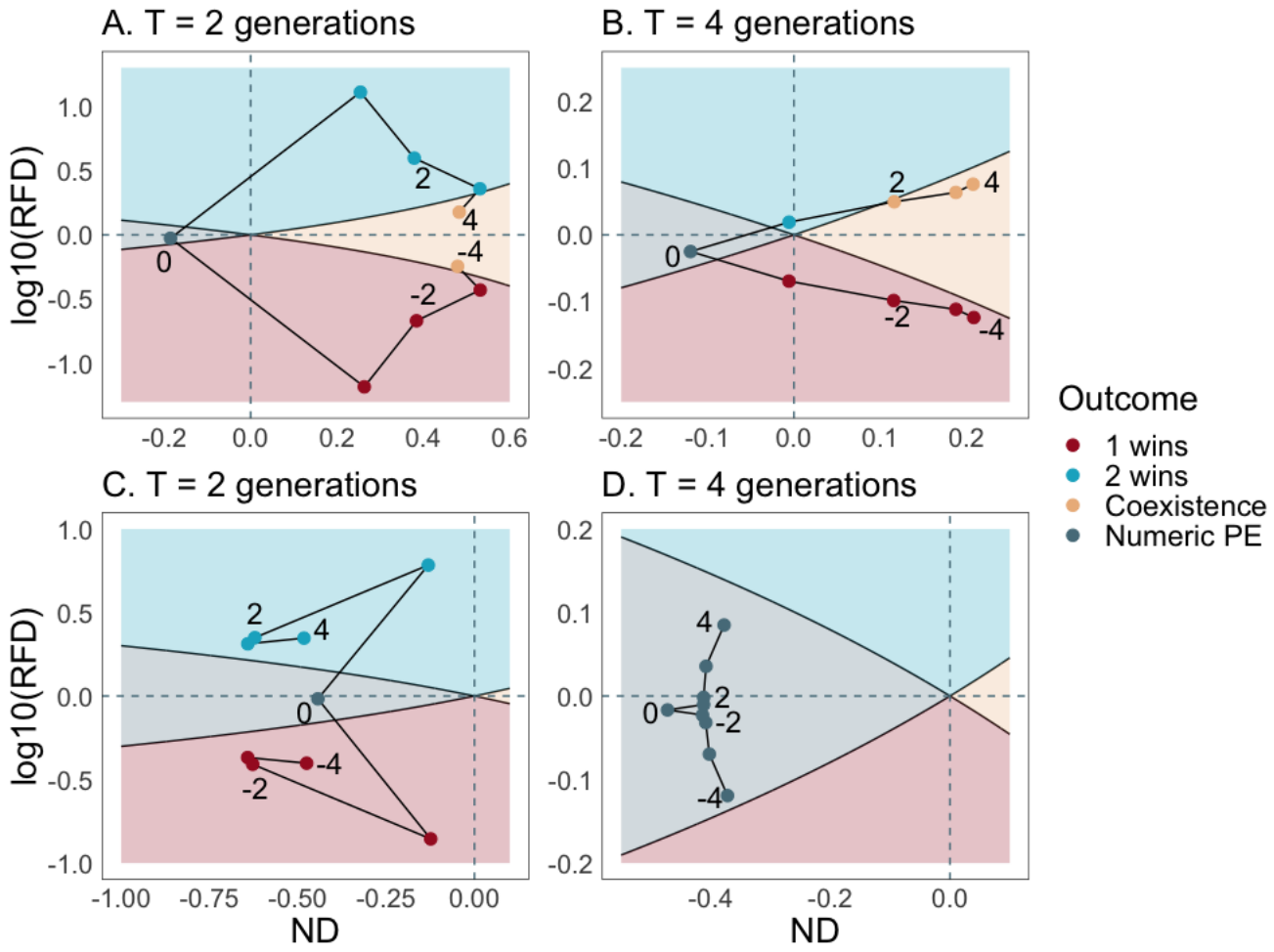

Figure 4: Calculated niche difference (ND) and relative fitness difference (RFD) for interactions at different Δs. Numbers next to points denote values of Δs as it changes from -4 to 4 following the trajectory, showing the movement of ND-RFD points in the coexistence space. Colors of each point and shades of the coexistence space indicate regions of each outcome. A and B show results with stage-mediated interspecific competition, C and D show results without stage-mediated interspecific competition. Left panels show results of $T = 2$ generations, right panels show results of $T = 4$ generations. Note that axis ranges of each panel are different for better visibility, but corresponding panels in Figure 4 and 5 have the same axes for better comparison between results without and with periodic fluctuations. See Table 1 for other parameters used.

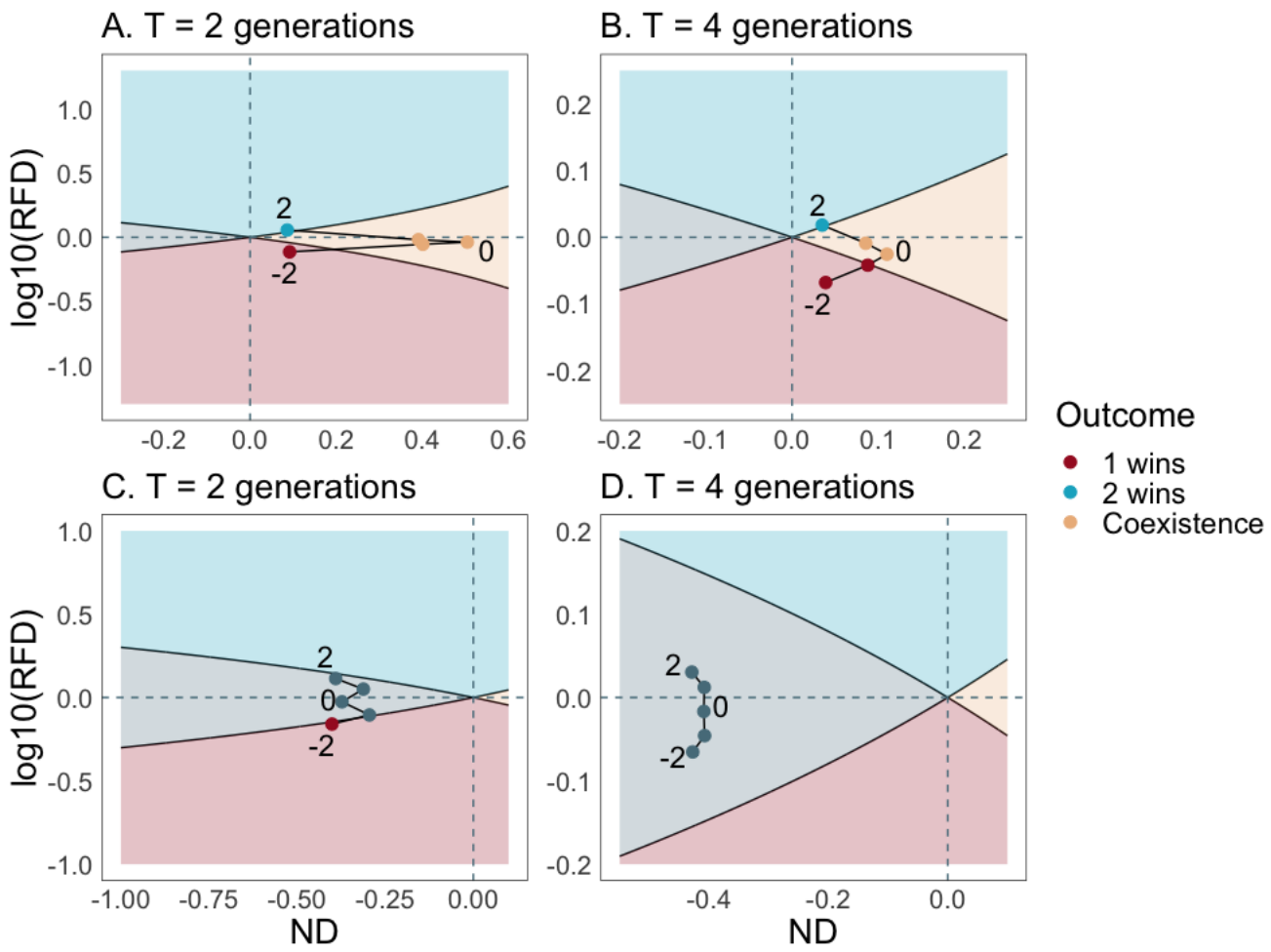

Figure 5: Calculated niche difference (ND) and relative fitness difference (RFD) for interactions at different Δs under periodic fluctuation. Numbers next to points denote values of Δs as it changes from -2 to 2 following the trajectory, showing the movement of ND-RFD points in the coexistence space. Colors of each point and shades of the coexistence space indicate regions of each outcome. A and B show results with stage-mediated interspecific competition, C and D show results without stage-mediated interspecific competition. Left panels show results of $T = 2$ generations, right panels show results of $T = 4$ generations. Note that axis ranges of each panel are different for better visibility, but corresponding panels in Figure 4 and 5 have the same axes for better comparison between results without and with periodic fluctuations. See Table 1 for other parameters used.