Priority effects determine how dispersal affects biodiversity in seasonal metacommunities

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Abstract

The arrival order of species frequently determines the outcome of their interactions. This phenomenon, called the priority effect, is ubiquitous in nature and determines local community structure, but we know surprisingly little about how it influences biodiversity across different spatial scales. Here, we use a seasonal metacommunity model to show that biodiversity patterns and the homogenizing effect of high dispersal depend on the specific mechanisms underlying priority effects. When priority effects are driven by a numeric advantage only, dispersal-diversity relationships are sensitive to initial conditions but generally show a humped shaped relationship: biodiversity declines when dispersal rates become high and allow the dominant competitor to overcome the numerical advantage of residents, excluding species across patches. In contrast, when local priority effects can also arise from phenological shifts that alter species interaction strength (trait-mediated priority effects), local, regional, and temporal diversity are surprisingly insensitive to variation in dispersal and initial conditions given spatiotemporal variations in phenology. Thus, trait-mediated priority effects can strongly reduce the effect of dispersal on biodiversity, preventing homogenization of metacommunities. Our results highlight that accounting for the different mechanisms underlying priority effects is fundamental to understanding the maintenance of regional biodiversity.

Introduction

Dispersal promotes the exchange of individuals between communities and thus links local population and community dynamics to regional patterns of species distributions. As a consequence, dispersal can play a key role in shaping biodiversity patterns at both local and regional scales (Kerr et al. 2002; Cadotte 2006; Grainger and Gilbert 2016). However, the relationship between dispersal and biodiversity patterns is also shaped by local conditions and processes, including biotic interactions (e.g. Kneitel and Miller 2003; Shurin et al. 2004; Altermatt et al. 2011; Carrara et al. 2012; Vanschoenwinkel et al. 2013; Catano et al. 2017). Although recent studies identify local competitive interactions as a major contributor to dispersal-diversity relationships (Pu and Jiang 2015; Lu 2021; Miller and Allesina 2021), one ubiquitous biotic process in metacommunities, the temporal sequence of community assembly, has been largely neglected.

Communities are not assembled all at once; instead, species arrive at different times and differences in the sequence of arrival times can alter the outcome of species interactions and thereby also community composition. Such priority effects (or historical contingencies) are widespread in nature and occur in systems ranging from microbes to plants and vertebrates (Alford and Wilbur 1985; Drake 1991; Kardol et al. 2013; Fukami 2015). In a metacommunity context, priority effects become important because they can alter the fate of immigrating individuals into a patch. For instance, with an early arriver advantage, individuals that arrive at a patch may either successfully establish themselves if they arrive before competitors, or they could perform poorly and even be excluded if the arriver after them. By altering the outcome of local competitive interactions, priority effects have the potential to shape the relationship between dispersal and diversity patterns at local and regional scales. Although several theories

predict that priority effects could affect how regional dispersal shapes biodiversity (e.g. Shurin et al. 2004; Fukami 2015; Grainger and Gilbert 2016; Miller and Allesina 2021), few have incorporated the diverse mechanisms that can generate priority effects in natural systems. Yet accounting for these mechanisms may be key to explaining why dispersal-diversity relationships are often contrary to theoretical expectations (e.g., Pu and Jiang 2015; Vannette and Fukami 2017; Toju et al. 2018).

Priority effects can be generated by at least two fundamentally different mechanisms, broadly categorized as “numeric” and “trait-mediated” (Rudolf 2019; Zou and Rudolf 2020). Traditionally, numeric priority effects have received the most attention and dominate the theoretical literature. They arise when fitness differences between species are small and destabilizing differences are large (i.e., positive frequency-dependent growth rates; Ke and Letten 2018). If conditions are met, the system exhibits alternative stable states, where neither species can invade when rare. Arrival time itself does not affect any per-capita rates and only matters if differences in arrival time allow for shifts in the relative frequency of species when interactions start. In contrast, trait-mediated priority effects arise when per-capita interactions between species change with their relative arrival times (Rudolf 2019). In nature, this occurs when differences in arrival time are correlated with changes in traits that affect species interactions, such as size and behavior, or modified environment from the difference in arrival times (Poulos and McCormick 2014; Rasmussen et al. 2014; Rudolf 2018; Blackford et al. 2020). In contrast to numeric priority effects, trait-mediated priority effects shift what outcomes are possible (e.g., from coexistence to competitive exclusion) by altering the parameter space (e.g., changes in interspecific competition) itself instead of favoring one of two possible states (Rudolf 2019; Zou and Rudolf 2020).

These two mechanisms or priority effects are not mutually exclusive but operate at different temporal scales. Numeric priority effects require that arrival times are separated by several generations to allow populations to reproduce multiple times and increase before competitors arrive (Figure 1A; Fukami 2004; Grainger et al. 2019). Trait-mediated priority effects typically occur when arrival times are separated by less than one generation, e.g., when phenological differences between competitors lead to differences in traits such as body size (Figure 1B; Shorrocks and Bingley 1994; Rudolf 2018; Blackford et al. 2020). This distinction is especially important in a seasonal context where both can occur. Consider a community where species complete one generation per year (Figure 1C). Here, numerical priority effects can arise when one species colonizes a patch several years before others (Figure 1C), but a later colonizing species may have an earlier phenology (e.g., earlier germination, emergence from dormancy, or reproduction) and thus become “active” first within a year, allowing for trait-mediated priority effects in a year (Figure 1D). Therefore, both the different timing among and within years can determine the local outcomes of competition.

These differences in local priority effects have the potential to alter local and regional dispersal-diversity relationships. With numeric priority effects, positive frequency dependence could enable the more abundant early arriver to spread over the landscape through dispersal and competitively exclude late arrivers. High dispersal will therefore decrease both local and regional diversity because one or a few regionally dominant species will eventually establish and maintain a numeric advantage in all patches, similar to the classic prediction that dispersal homogenizes (Tilman 1994; Mouquet and Loreau 2003; Leibold et al. 2004; Vanoverbeke et al. 2016; Fodelianakis et al. 2019). Following this premise, alpha diversity is likely highest at intermediate dispersal while beta and gamma diversity likely decreases with dispersal

(Mouquet and Loreau 2002; 2003; Cadotte 2006). However, regional diversity may be retained even under high dispersal if priority effects are driven by trait-mediated mechanisms, such as when early species alter the environment or rapidly adapts to the habitat (Shurin et al. 2004; Fukami 2015; Grainger and Gilbert 2016; Leibold et al. 2019; Miller and Allesina 2021). In these cases, outcomes of competition are not only driven by relative abundances but also by within-year arrival times, or phenology. Early arrivers therefore will not be excluded even if other species are more abundant. Consequences of this process should be particularly important in seasonal systems, as the frequent, periodic assembly of local communities creates many opportunities for spatial and temporal variations in arrival orders (Sheriff et al. 2011; Diez et al. 2012; Theobald et al. 2017; Carter et al. 2018; Rudolf 2019). In these seasonal systems, trait-mediated priority effects and natural variations in phenology could lead to high temporal turnover of local and regional community composition despite the homogenizing effect of dispersal. Thus, local priority effects and variations in phenology should strongly shape the dispersal-diversity relationship in seasonal metacommunities, but the specific relationship should depend on the mechanism of priority effects.

Here, we use a spatially implicit, multispecies metacommunity model to reveal how different mechanisms of priority effects interact with dispersal to shape biodiversity at local and regional scales in competitive metacommunities. We modeled a seasonal system with spatial and temporal variations in annual emergence times (representing species phenology) and compared the observed dispersal-diversity relationships with numeric and trait-mediated priority effects across different initial distributions of the population. We asked the following questions: (1) How will different mechanisms of priority effects change dispersal-diversity relationships? (2) When will local and regional diversity be maintained under high dispersal?

Methods

Model Setup

We modeled natural habitats with seasonal disturbance, such as temperate grassland or ephemeral ponds, in which species survive periodic, unfavorable environments (e.g., winter, droughts) and reemerge at the beginning of the next growing season. We define a growing season as the growth period between a previous periodic disturbance to the next disturbance. At the beginning of the growing season (hereafter season for short), each species emerges from dormancy in a patch at an assigned time (phenology). Patches are homogeneous throughout the landscape and are not spatially structured.

Within each season (before dispersal and end-of-season disturbance), local population dynamics of species *i* in a given patch are modeled with a modified Beverton-Holt model (Rudolf 2019):

$$N_i(t+1) = \frac{s_i \lambda_i N_i(t)}{1+\sum_{j=1}^{n} \alpha_{ij} \lambda_i N_j(t)} \text{ (Eqn. 1)}$$

where the population of the next season, $N_i(t+1)$, is determined by population growth of species *i*, $s_i \lambda_i N_i(t)$, where s_i is the end-of-season survival and λ_i the intrinsic growth rate. Population growth is dependent on densities of all species with respective pairwise competition coefficients α_{ij}.

If the community is driven by trait-mediated priority effects, interspecific competition is a function of the relative emergence time:

$$\alpha_{ij}(\Delta p_t) = \frac{\mathrm{B}}{1+\exp((\mathrm{d}-\Delta \mathrm{p_t})/\mathrm{c})} \text{ (Eqn. 2)}$$

where Δp_t is the difference between actual emergence times between species *i* and *j* at the start of season *t*, calculated as $p_{it} - p_{jt}$. *B*, *d*, and *c* are constants that determine the asymptotic

maximum, midpoint (when two species emerge simultaneously), and shape of the sigmoidal function. This nonlinear competition-phenology function assumes an early arriver advantage and has been validated by several empirical studies in animal and plant systems (Shorrocks and Bingley 1994; Rudolf 2018; Blackford et al. 2020).

At the end of the season, species disperse in the metacommunity, and all patches are subject to an end-of-season disturbance. We modeled the dispersal process as follows: first, emigrating populations of each species in each patch are determined by the number of successes of a binomial draw with m trials and probability r; m is the population of that species in that patch (Thompson et al. 2020), and r represents the dispersal rate. Emigrants are then pooled and randomly redistributed to all patches. This spatially implicit method assumes that dispersal is not affected by distance or patch choice. Spatially implicit models have been widely used in theoretical studies (e.g. Mouquet and Loreau 2002; 2003) and represent a group of empirical studies that manually transfer individuals between patches (Pu and Jiang 2015; Grainger and Gilbert 2016). We modeled the end of the season by a reduction in survival (s_i in Eqn. 1), as it usually represents a period when individuals face harsh environmental conditions (drought, cold). We allowed s_i to vary stochastically across seasons and patches by drawing it from a normal distribution with a mean of 0.5 and standard deviation of 0.05. Each species then emerges at its assigned times in the next season.

Generating Emergence Times

We randomly selected the emergence time (phenology) of a species from a normal distribution with mean $\overline{p}$ and standard deviation v. We fixed v for all species but varied $\overline{p}$ among species. We repeated this process each season and for each patch and species (Figure

S1). As long as $v = 0$, this creates variations in the phenology of co-occurring species and mimics the environmental stochasticity across space and time in natural systems (Sheriff et al. 2011; Diez et al. 2012; Theobald et al. 2017; Carter et al. 2018). We separated $\overline{p}$ of each species by a constant interval along an arrival gradient, with species 1 arriving on average the earliest and species 5 the latest (Figure S1).

Based on field and experimental data, the phenological variation (v) can be up to 5-10 times the pairwise difference between emergence times of interacting species (Menzel et al. 2006; Kharouba et al. 2018; Rudolf 2018). Because emergence times are in a sequence with fixed intervals in our model, the pairwise differences depend on the specific species combination. To encompass possible scenarios of natural variation, we explored a wide range of v and picked three representative values, 0.5 (= smallest pairwise difference in $\overline{p}$), 2 (= largest pairwise difference in $\overline{p}$), and 8 (= four times the largest pairwise difference in $\overline{p}$), corresponding small, medium, and large variations (Table 1). We report results with $v = 2$ in the main text and the other scenarios in the supplement.

Model Simulations

Although our model can be extended to any number of species and patches, we simulated metacommunities with 5 competing species and 50 patches. We focus on results with 5 species here to highlight the individual populations within each patch. Additional simulations with 10 species showed qualitatively the same dispersal-diversity patterns, indicating the results reflect dynamics of more diverse systems (Appendix I). Each simulation was run for 110 seasons, including a 10-season burn-in period, long enough for us to discern population dynamics driven by competition, as patterns such as extinction and dominance qualitatively stabilized

within 25-50 seasons. We ran 50 simulations under the same set of parameters.

If the community is only driven by numeric priority effects, the interspecific competition does not depend on the relative emergence time, and Δp is effectively 0. In this scenario, interspecific competition (Eqn. 2) is a constant: $\alpha_{ij}(0) = \frac{B}{1+e^{d/c}}$. We set interspecific competition coefficients to be equal when two species emerge simultaneously (i.e., d = 0), which simplifies competition to $\alpha_{ij}(0)=\frac{B}{2}$. With trait-mediated priority effects, α_{ij} is calculated based on the respective Δp of a given patch at time t. Using Eqn. 2 in this way ensures the consistency between the presence and absence of trait-mediated priority effects.

We created the competitive hierarchy across all five species by differentiating intraspecific competition (intensity of self-limitation). For each simulation, we drew intraspecific competition coefficients from a normal distribution around a mean that is smaller than the average interspecific competition coefficients ($\frac{B}{2}$) to promote numeric priority effects (Table 1). Additional simulations indicate that our results are qualitatively not sensitive to the specific strength of intraspecific competition strengths (Appendix I).

We assumed that each season consists of one generation, dispersal happens once at the end of a season, all species have equal dispersal rates (r), and we did not impose additional spatial disturbance. To determine the robustness of the results, we repeated simulations but relaxed each of the assumptions. Overall, we did not find a qualitative change in observed differences in population dynamics and dispersal-diversity relationships between mechanisms of priority effects. Model parameters for the corresponding results in the main text are listed in Table 1. All simulations were performed in R version 4.1.1 (R Core Team 2021).

Measuring Biodiversity

We examined dispersal-diversity relationships by calculating alpha, beta, and gamma diversity of the metacommunity at the end of each simulation. We calculated alpha and gamma diversity using the Shannon's index on local patches and the whole metacommunity respectively. Alpha diversity was averaged among all patches of a metacommunity. We quantified beta diversity (dissimilarity in community composition based on numeric abundances of species) by averaging all pairwise Bray-Curtis distances between patches. We calculate these metrics for each of the 50 simulations of a given parameter combination using respective functions in the R package *vegan* (Oksanen et al. 2013).

We also calculated temporal beta-diversity to quantify changes in metacommunity composition over time using the R package *adespatial* (Dray et al. 2018). Specifically, we calculated the dissimilarity (*D* metric in Legendre 2019) in species composition of a metacommunity between consecutive time steps separated by 10 seasons, excluding the first 10 seasons as burn-in. A high dissimilarity index indicates that relative abundances of species vary greatly over time.

Scenarios and Results

To better identify the different and combined effects of each type of priority effects (numeric vs. trait) we examined the model under two different initial scenarios. The first scenario assumes that the early species colonizes a patch for several seasons before others arrive, establishing a numeric advantage. This scenario, therefore, maximizes the impact of numeric priority effects as resident species always start with a numeric advantage over rare immigrants. For the first 10 seasons (burn-in), we ran simulations with only one species per patch and no dispersal, with each species occupying equal numbers of patches; this ensures that

the early colonizer or the “resident” species reached quasi-equilibrium abundance in the patch and only varied over time due to stochastic end-of-season survival rates (Table 1). We then allowed dispersal for other species to colonize. The second scenario removes this numeric advantage by starting each path with all five species at the same initial population. We compared the resulting population dynamics and biodiversity measures with and without trait-mediated priority effects under each scenario.

Scenario 1: Numeric Advantage

The local population dynamics in a given patch immediately highlight the difference between dynamics with and without trait-mediated priority effects. Without trait-mediated priority effects, the resident remains dominant in a patch at low dispersal rates (r = 0.01) since the number of immigrants is always small compared to the resident’s population, preventing them from outcompeting the early colonizer in a patch (Figure 2). This pattern only changes when dispersal rates are so high (r = 0.1) that immigrating species are abundant enough to overcome the numeric advantage of the resident. Once this condition is met, immigrants can invade and exclude the resident. This pattern is also reflected in the proportion of patches “occupied” by the dominant species, defined as patches in which the dominant species has the highest population (Figure 3). At a low dispersal rate, the resident maintains its numeric advantage in each patch such that the dominant species always occupy 1/5 of all patches, identical to the starting condition. However, with a high dispersal rate, the dominant competitor species occupies all patches.

In contrast, when trait-mediated priority effects are also possible, immigrants can successfully establish and potentially achieve dominance in new patches even at the lowest

level of dispersal rates (Figure 2). This establishment is possible because the relative timing of emergence in a season (not initial densities) determines per-capita effects and thus competitive dominance. This can lead to a high turnover in community composition within each patch (Figure 2), given sufficient seasonal variation in phenology (Figure S3). The rank of overall population size therefore reflects the sequence of the average emergence times, where the species that emerges the earliest also generally has the highest population. The local patch dynamics do not qualitatively change with dispersal rates (Figure S2). Higher dispersal only slightly decreases the patch occupancy of the dominant species (Figure 3).

These differences in within-patch dynamics strongly affect the local and regional dispersal-diversity relationships with and without trait-mediated priority effects. In metacommunities without trait-mediated priority effects, alpha diversity shows a clear hump-shaped relationship with dispersal rates. In contrast, alpha diversity increases with dispersal rates in metacommunities with trait-mediated priority effects (Figure 4). In the absence of trait-mediated priority effects, beta diversity starts highest due to both the numeric advantage and low dispersal (Figure 2) but decreases with higher dispersal rates, indicating that dispersal homogenizes the metacommunity and leads to regional dominance of a single species. In contrast, with trait-mediated priority effects, beta diversity remains largely constant and is not influenced by dispersal rates (Figure 4). Beta diversity is lower at low dispersal with trait-mediated priority effects because immigrants can establish in patches occupied by the resident (Figure 2, 4). Without trait-mediated priority effects, gamma diversity decreases rapidly at higher dispersal rates as species are driven to extinction by competitive exclusion. In contrast, gamma diversity slightly increases with higher dispersal under trait-mediated priority effects (Figure 4). Although the exact diversity values of metacommunities with trait-mediated priority

effects are dependent on how much phenology varies across years (i.e., the magnitude of *v*), they are all remarkably different from diversity patterns in metacommunities without trait-mediated priority effects which are not influenced by this variation (Figure S3).

Scenario 2: Equal Initial Population

Like Scenario 1, we found a striking difference in population dynamics with and without trait-mediated priority effects. Without trait-mediated priority effects, all species have an approximately equal chance of dominating a patch because no species has an initial numeric advantage, and the competitive hierarchy is randomly determined for each simulation. This pattern is not affected by dispersal rates, which only increases the fluctuation of populations (Figure S4). Furthermore, the absence of an initial numeric advantage facilitates the competitive exclusion of species other than the dominant species which also promotes the homogenization effect of dispersal, reflected by a higher occupancy of the dominant species that increases with dispersal (Figure 3). With trait-mediated priority effects, the observed pattern is very similar to that of Scenario 1: the local community composition fluctuates over time, but the species with the earliest emergence time on average (species 1) still has the largest total population (Figure S4, S5); the occupancy of the dominant species again decreases slightly with dispersal (Figure 3).

Without trait-mediated priority effects, we found a weak hump-shaped pattern between alpha, beta, and gamma diversity and dispersal rates in metacommunities (Figure 4). This is different from dispersal-diversity relationships under Scenario 1 due to the absence of initial numeric advantage. However, with trait-mediated priority effects, all dispersal-diversity relationships are strikingly similar to those observed under Scenario 1 (compare left and right

panels of Figure 4): alpha diversity increases, beta diversity slightly decreases, and gamma diversity remains the same with dispersal. Note that in the absence of the initial numeric advantage in Scenario 1 that boosted beta diversity without trait-mediated priority effects, beta diversity of metacommunities with trait-mediated priority effects is consistently higher. Overall, this shows that systems with trait-mediated priority effects are not sensitive to initial conditions, which is opposite to observations from systems with only numeric priority effects.

Temporal Turnover of Metacommunity

The difference between local population dynamics of numeric and trait-mediated priority effects is further reflected by the temporal turnover of metacommunities. Without trait-mediated priority effects, the temporal dissimilarity depends on the dispersal rate *r* and initial scenarios (Figure 5). Under Scenario 1 (numeric advantage), low dispersal rates lead to little dissimilarity over time, which reflects the stochastic “noise” of random dispersal events (Figure 2). With a higher dispersal rate, populations change initially much more over time, and the decrease in dissimilarity reflects the dominant species spreading within the meta-community and driving others to local extinction. Under Scenario 2 (equal initial population), the absence of numeric advantage allows for faster competitive exclusion by the dominant species, leading to the initial decline in temporal turnover. With trait-mediated priority effects, metacommunities show a consistently higher temporal dissimilarity under both low and high dispersal rates and across all initial scenarios (Figure 5). This observation corresponds to the high species turnover observed in population dynamics (Figure 2, Figure S2). Under Scenario 1, the initial decrease corresponds to the influx of immigrating species, which lowers the relative abundance of the resident. Overall, these temporal trends are consistent with the observed local

population dynamics and highlight the importance of the specific mechanism that produces priority effects in determining biodiversity patterns across all spatial and temporal scales.

Discussion

Priority effects are ubiquitous in natural systems, yet their role in shaping biodiversity patterns is still poorly understood (Fukami 2015). Here we show that priority effects can play a key role in shaping the local and regional biodiversity of seasonal communities and how they are influenced by dispersal. However, the shape of this dispersal-diversity relationship depends on what type of priority effects are present. Metacommunities with only numeric priority effects are highly sensitive to the initial conditions and exhibit high spatial diversity at low dispersal rates but become homogenized as dispersal increases. In contrast, trait-mediated priority effects promote local and regional species coexistence even under very high levels of dispersal and the patterns are highly robust to variation in initial conditions. Together, these results provide novel insights into how priority effects shape the dispersal-diversity relationships in nature and highlight the importance of considering the seasonal nature of local community assembly to predict regional patterns.

Positioning Priority Effects in Current Dispersal-Diversity Framework

Classic models predict that the dispersal-diversity relationship should be maximized at intermediate dispersal, while between-patch and regional diversity should constantly decrease with dispersal (Mouquet and Loreau 2002; 2003). This prediction still qualitatively holds when local dynamics are not driven by trait-mediated priority effects in our model, but with different mechanisms. In classical models, diversity peaks at intermediate dispersal because species are

present in both source and sink habitats, and the population in the latter can be rescued by immigration from the former (Leibold et al. 2004). Traditionally, source-sink dynamics are expected to be driven by spatial heterogeneity in habitat conditions (Pulliam 1988). However, source-sink dynamics are still possible in our model, even in the absence of any environmental heterogeneity because the numeric advantage poses a barrier for rare immigrating species to establish themselves. These patches serve as sources for numerically dominant species and sinks for all other (immigrating) species. At low to moderate dispersal rates, numeric priority effects thus maintain high beta diversity within metacommunities. This is especially visible under Scenarios 1, where each species is initially numerically dominant in some patches.

This source-sink dynamic diminishes when dispersal is high enough for competitively superior species to reach patches in large enough numbers to overcome the numeric priority effects. Once this threshold is reached, dispersal works as a homogenizing force that decreases local and regional diversity (Mouquet and Loreau 2003; Grainger and Gilbert 2016; Catano et al. 2017). Furthermore, we found that the shape of this relationship is highly sensitive to initial conditions (i.e., the presence or absence of initial numeric advantage) in metacommunities without trait-mediated priority effects. Notably, our Scenario 2 (equal initial population) coincides with a design often used in lab experiments (Grainger and Gilbert 2016), but the resulting population dynamics and dispersal-diversity relationships are different from those obtained under Scenario 1 (numeric advantage). This result is not previously emphasized in theory (but see Lu 2021) and could at least partly help explain why the diversity-stability relationship differs among studies that use different initial settings (Grainger and Gilbert 2016).

On the contrary, diversity patterns in metacommunities with trait-mediated priority effects are much less affected by dispersal or initial conditions. In these metacommunities, immigrants

may successfully colonize a patch regardless of their numeric disadvantage as their colonization success is more dependent on the order of emergence. If an immigrating species emerges early enough within a season, this advantage (relative increase in interspecific competitive ability) can overcome its numeric disadvantage toward the resident species, allowing it to establish in the patch. Given the temporal and spatial variation in within-season emergence times (phenology), trait-mediated priority effects can promote local and regional coexistence of species by preventing competitive exclusion and homogenization at a high dispersal rate. Our results suggest that seasonality and phenological variations are important factors promoting coexistence in spatial communities, in addition to other classic mechanisms such as spatial heterogeneity (Leibold et al. 2004; Schreiber and Killingback 2013). This result agrees with a recent study that models patch memory, which is a source of environmental heterogeneity that can arise from trait-mediated priority effects via habitat modification (the previous resident modifies the habitat and therefore affects colonization success of other species): with patch memory, any number of species stably coexist despite dispersal (Miller and Allesina 2021).

The trait-mediated priority effect in our model appears conceptually similar to processes implemented by some previous models (e.g. biotic heterogeneity in Shurin et al. 2004; monopolization effects by local adaptation in Vanoverbeke et al. 2016). Yet, they found that positive feedback of early arrivers enables their regional dominance. This result represents what we found in metacommunities with high dispersal, but not in those with trait-mediated priority effects. This discrepancy arises because we incorporated seasonality and realistic spatial and temporal phenological variations in our model. These variations lead to a constant reshuffling of competitive hierarchies across time and space that reduces or prevents local and

regional extinction, as predicted by previous theoretical results in non-spatial models (Rudolf 2019; Zou and Rudolf 2020). When aggregated on a spatial or temporal scale, this reshuffling of competitive hierarchies can also lead to intransitive competition, which is predicted to stabilize multispecies systems (Allesina and Levine 2011; Levine et al. 2017).

Our results provide a theoretical basis for interpreting many empirical results, especially those explicitly considering the role of priority effects. For instance, experiments in freshwater protists found that community composition in homogeneous patches was strongly correlated to the temporal sequence of assembly despite dispersal (Pu and Jiang 2015). Our results suggest that this counterintuitive pattern can be easily explained by trait-mediated priority effects. Consistent with this prediction, Pu and Jiang (2015) reported changes in interspecific competition based on arrival orders of species, indicating the presence of trait-mediated priority effects. Our observations also corroborate the result that local priority effects in nectar microbial communities help maintain beta diversity (Vannette and Fukami 2017), although we do not observe a consistent increase of beta diversity with higher dispersal, as in the experiment. Additionally, Toju et al. (2018) found a persistent numeric advantage of initially abundant species after prolonged dispersal in nectar microbial communities. This may indicate that dispersal in this empirical study was not high enough to homogenize all local patches or priority effects initiated by numeric advantage were maintained in other trait-mediated mechanisms, such as habitat modification.

Empirical Implications and Future Directions

Phenology and priority effects are key factors that structure population dynamics and coexistence patterns in natural communities. Although the importance of priority effects is

increasingly recognized (Fukami 2015; Rudolf 2019), they are rarely studied in an explicitly spatial context. Our model indicates the need to consider specific mechanisms of priority effects when studying spatial dynamics of metacommunities and vice versa. For instance, systems that display robust diversity measurements regardless of dispersal might be more influenced by trait-mediated processes. In these systems, considering specific trait-mediated mechanisms of priority effects may help to understand otherwise unexpected patterns (e.g. Pu and Jiang 2015; Vannette and Fukami 2017; Toju et al. 2018). Conversely, metacommunities with species known to display trait-mediated priority effects (e.g. amphibians, Rudolf 2018; dragonflies, Rasmussen et al. 2014; plants, Kardol et al. 2013; Blackford et al. 2020) may show different dynamics at a regional scale compared to metacommunities with numeric priority effects. Yet, few studies have considered this aspect when studying dispersal-diversity relationships in these systems, although many metacommunities are driven by stochastic processes that promote priority effects (e.g. Chase 2007).

Our model predicts that seasonal metacommunities under spatial and temporal variations in phenology may behave differently based on the mechanism of priority effects. This is relevant to many systems in nature, including ephemeral ponds, nectar microbiome, pitcher plant inquilines, rocky intertidal pools, and any other periodic communities where such variations could occur (Berlow and Navarrete 1997; Kneitel and Miller 2003; Chase 2007; Sheriff et al. 2011; Theobald et al. 2017; Vannette and Fukami 2017). Although recent studies of these systems indicate that phenology can vary considerably between communities (Sheriff et al. 2011; Diez et al. 2012; Theobald et al. 2017; Carter et al. 2018), few have addressed the local and regional level consequences of these variations. As climate change exacerbates phenological shifts and variations (Parmesan 2006; Diez et al. 2012; Wolkovich et al. 2014;

Pearse et al. 2017), the arrival order of species may differ greatly over space and time, leading to increasing opportunities for priority effects. Understanding how metacommunities respond to this increasing reshuffling of arrival order (and likely competitive hierarchy) in the long term could help evaluate the responses of biodiversity to climate change.

We have extensively investigated different forms of dispersal and incorporated variations in phenology, but the influence of another aspect of spatial communities, environmental heterogeneity, remains unexplored. Heterogeneous patches could serve as a spatial refuge for some species, promoting regional coexistence (Shurin et al. 2004; Schreiber and Killingback 2013). Environmental heterogeneity may also induce trait-mediated priority effects, leading to monopolization effects (Urban and De Meester 2009; De Meester et al. 2016) or legacy effects (Miller and Allesina 2021) in local patches. Furthermore, environmental heterogeneity could covary with other factors that are coupled with another process, such as spatial variation of arrival time (e.g., species may arrive early in warmer patches), leading to more complex dynamics. Collectively, our results emphasize that the temporal sequence of community assembly is a critical process shaping biodiversity in spatial communities. A mechanistic understanding of this process is fundamental to our knowledge of how biodiversity responds to critical environmental processes in a changing world.

Table 1. Major parameters and values used in simulations.

	Definition	Symbol	Value(s) Used
Population dynamics	Intrinsic growth rate	λ	100
	Intraspecific competition	α_{ii}	Randomly drawn from normal distribution $N(0.07, 0.01)$ (shown in main text), $N(0.10, 0.01)$ or $N(0.15, 0.01)$ (shown in Appendix II)
	Constants for calculating interspecific competition	B, d, c	0.225, 0, -0.5, respectively
	End-of-season survival	s	Randomly drawn from normal distribution $N(0.5, 0.05)$
Metacommunity	Number of patches	P	50
	Number of species	n	5 (shown in main text), 10 (shown in Appendix I)
	Number of generations in a season	T	1
	Initial population	N_0	10
	Dispersal rate	r	Range: 0.001-0.1; representative values: 0.01 (low) and 0.1 (high)
Emergence time	Average emergence time	$\overline{p}$	0, 0.5, 1, 1.5, 2 for species 1-5, respectively
	Seasonal variation	v	2 (shown in main text), 0.5, and 8 (shown in Appendix I)

Figure Captions

Figure 1. Illustration of numeric and trait-mediated priority effects and how they operate at different temporal scales. A species may arrive several seasons before its competitor, allowing it to reproduce and thus reach a higher population than the immigrating population of the late arriver (A, C). This represents a numeric advantage that, if species interactions allow for positive frequency dependence, can lead to numeric priority effects. However, species can also differ in their phenology, i.e., when they become "active" (or emerge) within a season (B, D). This within-season timing can lead to changes in species interaction via changes in traits (e.g., size; B) and therefore trait-mediated priority effects. Note that a species can arrive several seasons earlier at a patch, but it can still have a later phenology within a season (C, D): the species with a numeric priority effect does not necessarily imply a trait-mediated priority effect.

Figure 2. Example of population dynamics of one randomly selected patch under Scenario 1 (numeric advantage) and different dispersal rates, with and without trait-mediated priority effects. Line colors represent species. The left column shows dynamics without trait-mediated priority effects, and the right column shows dynamics with trait-mediated priority effects. Rows show results for low (0.01) and high (0.1) dispersal rates (*r*). Each line of the same color in a panel represents the population dynamics of that species from one out of 50 simulations. All population densities are transformed by natural log. Note that the identity of dominant species is different for each repetition because the competitive hierarchy is randomly determined. See Table 1 for other parameters used.

Figure 3. Patch occupancy of the dominant species, calculated as the proportion of all patches where the dominant species has the highest population, under low (0.01) and high (0.1) dispersal rates. Because the competitive hierarchy is random in each repetition, the dominant species is posteriorly determined as the species with the highest population in all patches. Left and right panels show results under Scenario 1 (numeric advantage) and 2 (equal initial population), respectively. Solid points and error bars show the mean and standard deviation, and translucent points show actual occupancy data. See Table 1 for other parameters used.

Figure 4. Relationship of alpha, beta, and gamma diversity and dispersal rates under the two initial scenarios, with or without trait-mediated priority effects. Left and right columns show dispersal-diversity relationships under Scenario 1 (numeric advantage) and 2 (equal initial population), respectively. Each line is rendered from data of all 50 simulations. See Table 1 for other parameters used.

Figure 5. Temporal dissimilarity index calculated from one randomly selected simulation under Scenario 1 under different dispersal rates, with and without trait-mediated priority effects. Left and right columns show results under Scenario 1 (numeric advantage) and 2 (equal initial population), respectively. Rows show results for low (0.01) and high (0.1) dispersal rates (*r*). The dissimilarity index was calculated from metacommunities between consecutive time steps separated by 10 seasons, omitting the first 10 seasons as burn-in. Each line is rendered from data of all 50 simulations. See Table 1 for other parameters used.

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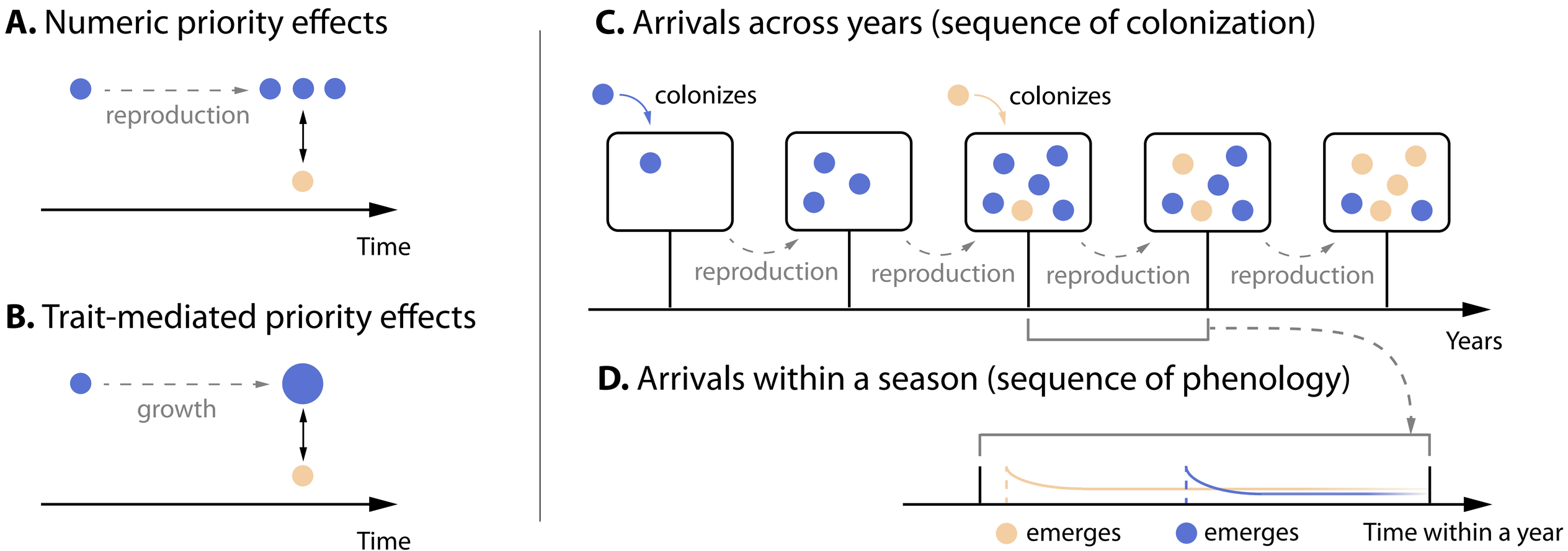
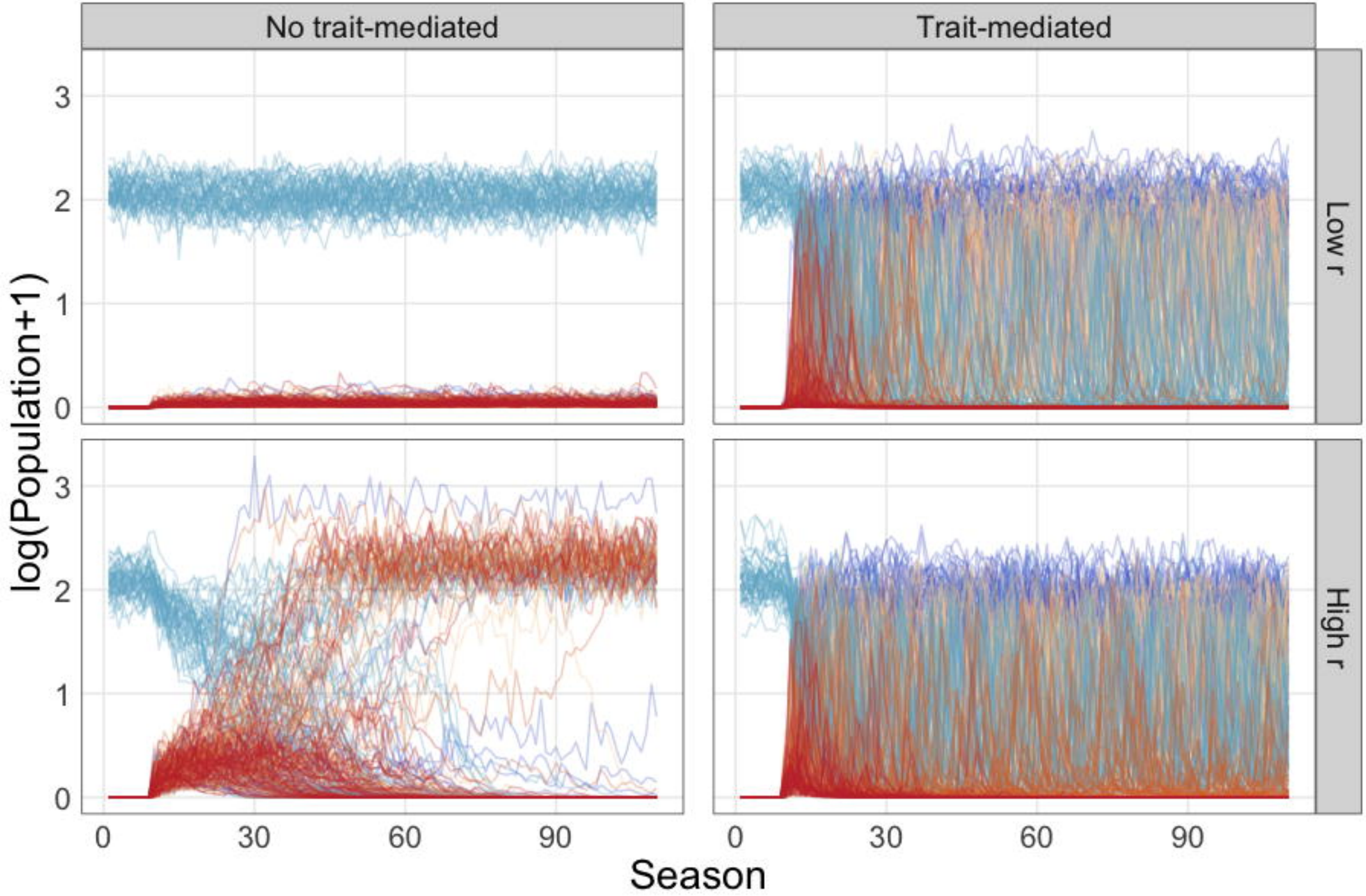
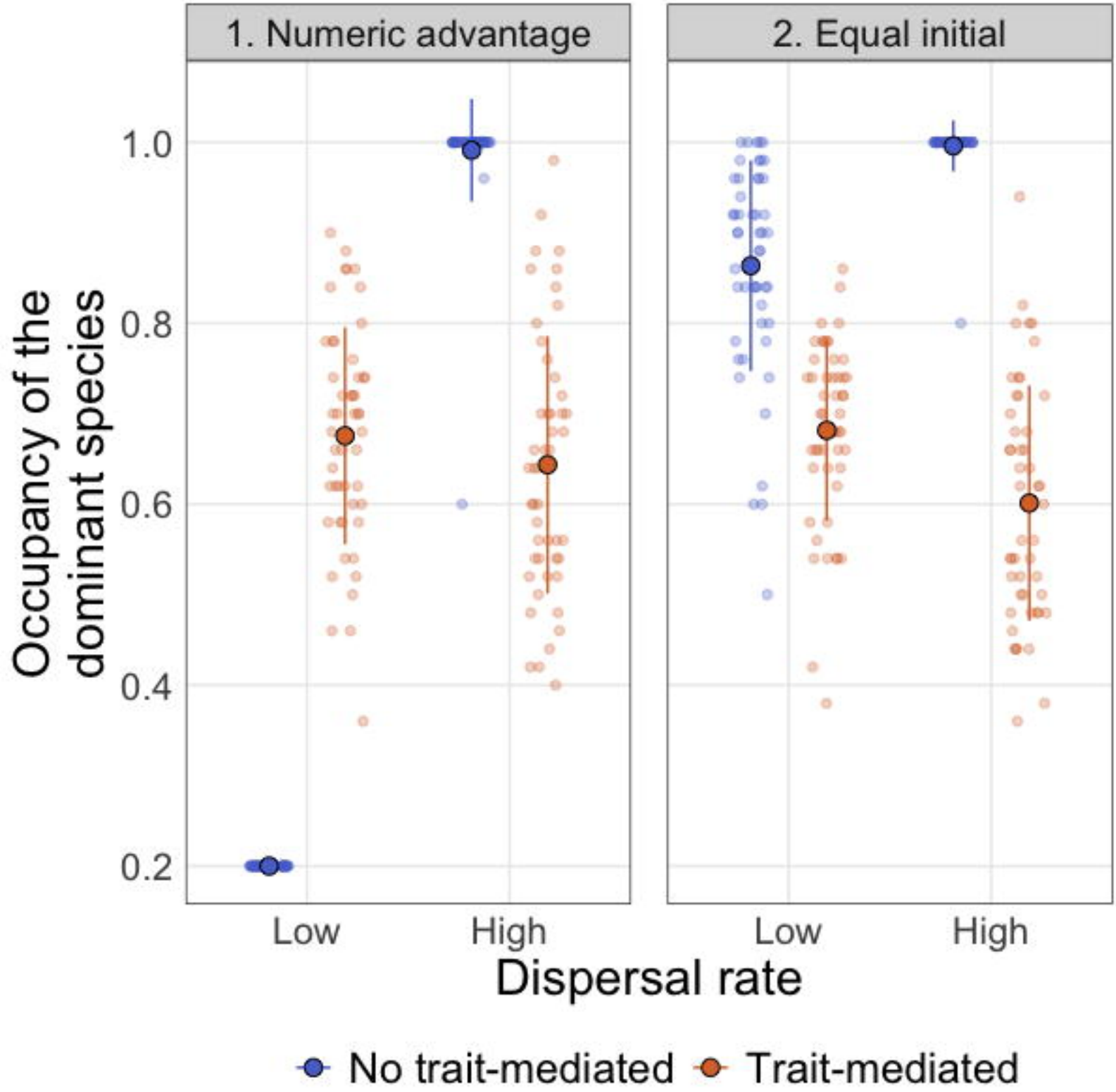
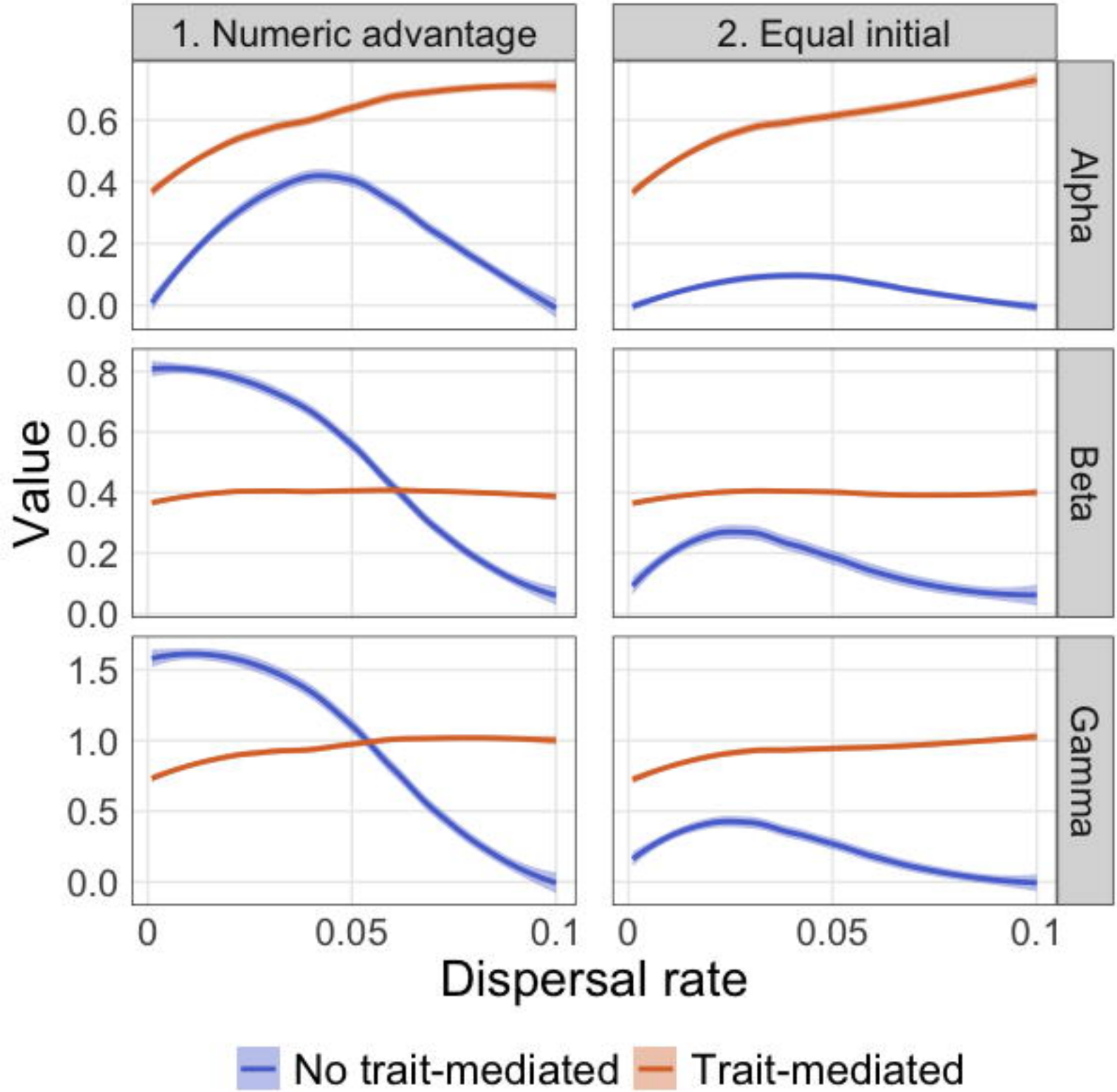
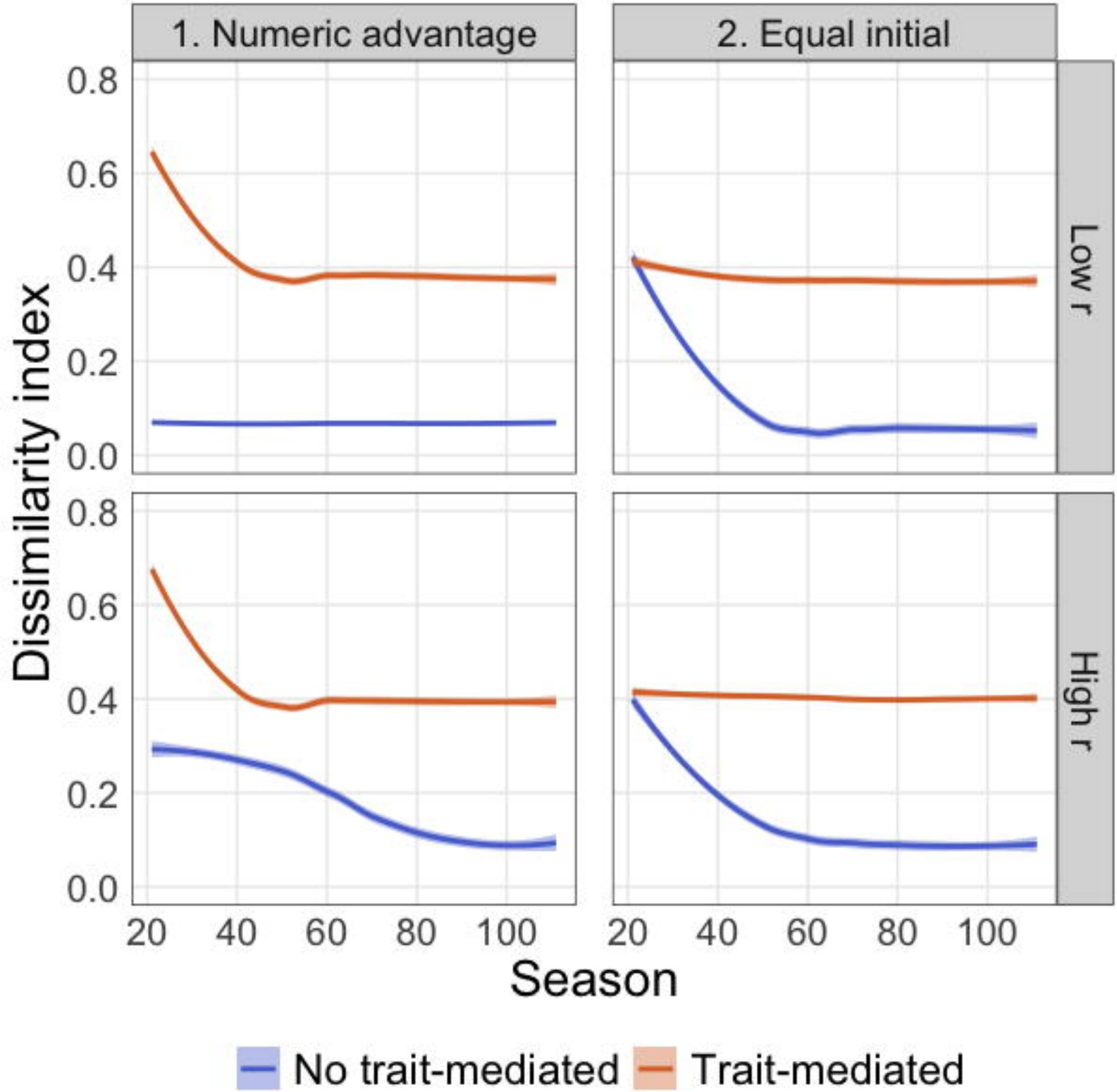

A. Numeric priority effects
reproduction
Time
B. Trait-mediated priority effects
growth
Time
C. Arrivals across years (sequence of colonization)
colonizes
colonizes
reproduction
reproduction
reproduction
reproduction
Years
D. Arrivals within a season (sequence of phenology)
emerges
emerges
Time within a year


No trait-mediated
Trait-mediated
Low r
High r
log(Population+1)
Season
0
1
2
3
0
30
60
90


1. Numeric advantage
2. Equal initial
Occupancy of the dominant species
1.0
0.8
0.6
0.4
0.2
Low
High
Low
High
Dispersal rate
No trait-mediated
Trait-mediated


1. Numeric advantage
2. Equal initial
Alpha
Beta
Gamma
Value
0.0
0.2
0.4
0.6
0.8
0.5
1.0
1.5
0
0.05
0.1
Dispersal rate
No trait-mediated
Trait-mediated


1. Numeric advantage
2. Equal initial
Low r
High r
Dissimilarity index
0.0
0.2
0.4
0.6
0.8
20
40
60
80
100
Season
No trait-mediated
Trait-mediated