Priority effects determine how dispersal affects biodiversity in seasonal metacommunities

Heng-Xing Zou[1*], Volker H. W. Rudolf[2]

Program in Ecology and Evolutionary Biology, Department of BioSciences, Rice University, Houston, TX 77005

[*] Corresponding author. Emails: [1] hengxingzou@rice.edu, [2] volker.rudolf@rice.edu.

Statement of authorship: H.-X.Z. conceived the idea, designed, and performed the research with assistance from V.H.W.R. H.-X.Z. wrote the first draft, and both authors contributed to revisions.

Data accessibility: No new data were used. Code is available at GitHub (https://github.com/hengxingzou/Zou2022bioRXiv) during the peer review process and will be archived to an online repository upon acceptance.

Running title: Priority effects in Metacommunities

Keywords: priority effects, metacommunity, dispersal-diversity relationships, phenology, seasonal variation

Number of words in the abstract: 150

Number of words in the main text: 4956

Number of references: 55

Number of figures: 6

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, diversity measurements are highly sensitive to initial conditions and high dispersal homogenizes communities. However, when local priority effects arise from phenological shifts that alter species interaction strength (trait-mediated priority effects), local, regional, and temporal diversity are higher and are surprisingly robust to variation in dispersal and initial conditions, given spatiotemporal variations in phenology. Our results highlight that accounting for the 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 through 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 early arriver advantage, individuals that arrive at a patch may either successfully establish themselves if they arrive first, or they could perform poorly and even be excluded by earlier arriving competitors. 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 the often-unexpected dispersal-diversity relationships found in different systems.

Priority effects can be generated by at least two fundamentally different mechanisms, broadly categorized as “numeric” or “trait-mediated” (Rudolf 2019; Zou and Rudolf 2020). Numeric priority effects arise from the positive frequency dependence of the species with higher abundance (Ke and Letten 2018). As one species arrives early, it is more likely to establish a numeric advantage over late arrivers and maintain this advantage through a positive feedback. On the other hand, trait-mediated priority effects assume that per-capita interactions between species change with their relative arrival times (Rudolf 2019). In nature, this occurs through altered traits that could 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). These changes in interacting traits often result in a change of species’ competitive interactions that correlate with their relative arrival times (Rudolf 2019; Zou and Rudolf 2020). Therefore, if trait-mediated priority effects occur, the competitive outcome of early and late arrivers are not only determined by their numeric difference but also their relative arrival times.

Differences in local community dynamics between different types of priority effects also 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 arrivers 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, competitive outcomes are not only driven by relative abundances but also relative arrival times. Early arrivers therefore will not be excluded even if other species are more abundant. This effect of relative arrival times should be particularly important in systems with periodic species assembly ("seasonal" communities), as the frequent 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 species 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 the system with realistic spatial and temporal variations in phenology and compared the observed dispersal-diversity relationships with numeric and trait-mediated priority effects across different initial distributions of 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? (3) How sensitive are patterns of biodiversity to initial heterogeneity in population sizes among local communities?

Methods

Model Setup

We modeled natural habitats with seasonal disturbance, such as annual grassland or ephemeral ponds, in which species survive periodic, unfavorable environments (e.g., winter, droughts) and reemerge at the beginning of the next season. We define a season as the growth period between a previous disturbance to the next disturbance. For instance, a “season” for annual plants would start with the emergence in spring or summer and end with senescence in fall or winter, while a “season” for ephemeral ponds would be when they hold water. At the beginning of the season, each species emerges from dormancy in a patch at an assigned time. Patches are homogeneous throughout the landscape and are not spatially structured. The average time of emergence in a season ($\overline{p}$, for phenology) is fixed for each species, but the exact emergence time is randomly determined at each patch by drawing from a uniform distribution centered around the species-specific average time of emergence (Figure 1). Therefore, despite fixed average times of emergence, the exact order of arrival in the model varies among patches and between seasons. This reflects variations in the phenology of co-

occurring species arising from species-specific responses to 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).

Within each season, local population dynamics in a given patch are determined with a modified Beverton-Holt model (Rudolf 2019):

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

where the population of the next season, $N_i(t+1)$, is determined by population growth of species *i*, $\lambda_i N_i(t)$, which negatively scales with densities of all species with respective competition coefficients α_{ij}, and the proportion surviving to the next season, $s_i N_i(t)$. All interspecific competitions are pairwise.

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

$$\alpha_{ij}(\Delta p) = \frac{B}{1+e^{(d-\Delta p)/c}} \text{ (Eqn. 2)}$$

where Δp is the relative time of emergence between species *i* and *j*, calculated as $t_j - t_i$, and *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). If the community is only driven by numeric priority effects, the interspecific competition does not depend on the relative time of emergence, and Δp is effectively 0. In this scenario, the interspecific competition becomes a constant: $\alpha_{ij}(0) = \frac{B}{2}$.

We modeled the dispersal process as follows: first, *D* emigrating patches are randomly

selected, and emigrating populations of each species are determined by the number of successes of a binomial draw with n trials and probability r; n is the population of that species in that patch (Thompson et al. 2020). Emigrants are then pooled by species and redistributed to D randomly selected patches; D is hereafter termed patches with dispersal. This spatially implicit method has been widely used in empirical studies that often manually transfer individuals between patches (Grainger and Gilbert 2016) and theoretical models (e.g. DeMalach et al. 2021) and assumes that dispersal is not affected by distance or patch choice. After dispersal, the season ends with a disturbance event, in which an end-of-season survival rate (s_i in Eqn. 1) determines the proportion surviving to the next season.

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. This number of species allows for a competitive hierarchy and meaningful values for species richness while still being tractable. Each simulation was run for 100 seasons, long enough for us to discern population dynamics driven by competition, as patterns such as extinction and dominance qualitatively stabilized within 25-50 seasons, and we confirmed these observed patterns by simulating each set of parameters 50 times. In our model, dispersal is dependent on both dispersal rate (r) and patches with dispersal (D). Therefore, we varied them independently across a wide range (Table S1) to ensure that we observe the full range of possible dynamics under biologically realistic scenarios. We considered these two parameters as separate processes since they reflect different aspects of dispersal. The proportion of population being dispersed under the lowest combination of dispersal parameters (r = 0.001, D = 10) is approximately 1%-2%, while this

proportion is 20-30% under the highest combination (r = 0.1, D = 40).

We created a competitive hierarchy across all five species by differentiating intraspecific competition (intensity of self-limitation), with species 1 having the highest and species 5 having the lowest intraspecific competition coefficient. We set the average order of emergence time in reverse order to the competitive hierarchy, where species 1 emerges the earliest and species 5 the latest. Additional simulations show whether the competitive hierarchy matches with the order of emergence does not qualitatively change results. Note that with trait-mediated priority effects interspecific competition (and thus competitive hierarchies) also depend on the order of emergence (Eq. 2). We chose intraspecific competition coefficients that are smaller than baseline interspecific competition coefficients ($\frac{B}{2}$) to promote numeric priority effects, but our results are not sensitive to higher intraspecific competition strengths, which promote coexistence as shown by additional simulations. 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 no patch undergoes extinction. To determine the robustness of observed patterns, we relaxed each of the assumptions and did not find a qualitative change in observed differences in population dynamics and dispersal-diversity relationships between mechanisms of priority effects. Specific model parameters are listed in Table S1.

All simulations were performed in R version 4.1.1 (R Core Team 2021). Simulation code is available at GitHub (https://github.com/hengxingzou/Zou2022bioRXiv) during the peer review process and will be archived to an online repository upon acceptance.

Measuring Biodiversity

We examined dispersal-diversity relationships by calculating local species richness (# of

species in each patch; alpha diversity), dissimilarity in community composition among patches (beta diversity), and regional species richness (# of species in the metacommunity; gamma diversity) at the end of simulations. Alpha diversity was averaged among all patches within each repetition. We quantified beta diversity (dissimilarity in community composition based on numeric abundances of species) by averaging all pairwise Bray-Curtis distances between patches using 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. A high dissimilarity index indicates that relative abundances of species vary greatly over time.

Scenarios and Results

The heterogeneity in initial population densities among patches strongly affects measured dispersal-diversity patterns (Grainger and Gilbert 2016; Lu 2021) and priority effects are likely to further amplify these differences. Therefore, we set three scenarios that varied in initial relative abundances of species within and across patches and compared the resulting biodiversity measures with and without trait-mediated priority effects.

Scenario 1: Initial populations are separated across patches

We first consider a simple baseline scenario in which each patch is initially colonized by only one species and each species colonized the same number of patches. Therefore, the initial alpha diversity is low (one species per patch), while beta and gamma diversities are high.

Results of this scenario immediately highlight the difference between dynamics with and without trait-mediated priority effects. With numeric priority effects, the initial resident remains dominant in a given patch for low and medium levels of dispersal since the number of immigrants is small compared to the resident's population (Figure 2A, 2C). This pattern only changes when dispersal (dispersal rate, *r*, and patches with dispersal, *D*) is high enough to boost immigrant populations to a size that allows them to overcome the numeric advantage of the resident species (Figure 2E). The difference in final population size between species simply reflects species-specific differences in strength of intraspecific competition (Figure 3A, 3C), except when high dispersal homogenizes the metacommunity (Figure 3E). In contrast, with trait-mediated priority effects, immigrants can successfully invade and even achieve dominance in new patches (Figure 2B, 2D). This invasion is possible because the relative timing of emergence (and not initial densities) determines per-capita effects and thus competitive dominance. Therefore, metacommunities with trait-mediated priority effects show a clear hierarchy of final population and regional dominance, reflecting early-arriver advantage (Figure 3B, 3D, 3F).

These differences in patch dynamics between both types of priority effects (numeric vs. trait-mediated) strongly affect the local and regional dispersal-diversity relationships. Alpha diversity shows a clear hump-shaped relationship with total dispersal (combined effect of *r* and *D*) in metacommunities with numeric priority effects (Figure 4A). At a lower dispersal rate (r = 0.001) alpha diversity increases with higher *D* (more patches with dispersal) but decreases with higher *D* at the highest dispersal rate (r = 0.1; Figure S6-8A). In contrast, alpha diversity monotonically increases with dispersal (both *r* and *D*) in metacommunities with trait-mediated priority effects (Figure 4B; Figure S6-8A).

With numeric-mediated priority effects, beta diversity decreases with higher dispersal (both *D* and *r*), indicating that dispersal homogenizes the metacommunity and leads to regional dominance of a single species (Figure 5A; Figure S6-8D). This negative dispersal-diversity relationship is present but weaker in systems with trait-mediated priority effects (Figure 5B). Furthermore, the overall dissimilarity is lower with trait-mediated compared to numeric priority effects, as patches quickly gain species from the initial monoculture (Figure 5A-B; Figure S6-8D). Gamma diversity remains high in metacommunities with numeric priority effects, as some species are locally extinct, but no species goes extinct regionally unless overall dispersal is very high (r=0.1, D=40, or 80% of all patches; Figure S5A, S6-8G). With trait-mediated priority effects, no regional extinction occurs, and gamma diversity is always at maximum even under high overall dispersal (Figure S5A, Figure S6-8G).

Scenario 2: Initial populations are equal across all patches

We next explored a scenario where all five species start with equal population sizes in all patches. This starting condition is often used in lab experiments (Grainger and Gilbert 2016). Similar to Scenario 1, we found a striking difference in population dynamics with and without trait-mediated priority effects. With numeric priority effects, the competitively superior species (species 5) dominates most patches, and the dominance is promoted by dispersal, although in rare cases other species can rise to dominance as well (Figure S1C). With trait-mediated priority effects, the observed pattern is very similar to that of Scenario 1: all species coexist, the dominant species in a patch changes quickly over time, but the species with the earliest time of emergence on average (species 1) still has the largest total population (Figure S1, S3).

In this scenario, we also found a weak hump-shaped pattern between alpha (Figure 4C;

Figure S6-8B), beta (Figure 5C; Figure S6-8E), and gamma (Figure S5, S6-8H) diversity and overall dispersal in metacommunities with numeric priority effects. However, alpha diversity of metacommunities with trait-mediated priority effects consistently increases with higher dispersal (Figure 4D; Figure S6-8B). This results in a concurrent decrease in beta diversity (Figure 5D; Figure S6-8E), although the change of both diversity values is small compared to that with numeric priority effects. Finally, gamma diversity remains constant since no regional extinction occurs with trait-mediated priority effects (Figure S5C; Figure S6-8H).

Scenario 3: Initial populations vary randomly across patches

Finally, we consider a scenario where populations of each species vary among patches, which is often the case in field experiments with heterogeneous starting conditions (Kneitel and Miller 2003; Howeth and Leibold 2010a; 2010b). We simulated this heterogeneity in initial conditions by allowing all five species to occupy all patches, but their initial population is randomly drawn from a normal distribution with a mean of 50 (initial population used in Scenario 1 and 2) and a standard deviation of 10.

In metacommunities with numeric priority effects, the species with an initial numeric advantage may be able to maintain its dominance in a given patch, but increasing dispersal (high D or r) also allows competitively stronger species to replace the initially most abundant species over time (Figure 2E). When r or D is small, the final total population of each species reflects their initial population and strength of intraspecific competition (Figure S4A, C), but higher dispersal quickly homogenizes the metacommunity (Figure S4E). In contrast, metacommunities with trait-mediated priority effects again display very similar patterns to those in Scenarios 1 and 2, with highly variable dynamics over time regardless of spatial

dispersal (Figure S2) and species 1 (earliest emergence) having the highest local dominance (Figure S4).

With numeric priority effects, alpha diversity displays a unimodal relationship with dispersal (Figure 4E), while it consistently increases with dispersal with trait-mediated priority effects (Figure 4F). Higher dispersal contributes to more regional extinction and thus reduced gamma diversity with numeric priority effects (Figure S5E). In contrast, gamma diversity remains at maximum with trait-mediated priority effects, even under high dispersal levels (Figure S5F). Metacommunities with both numeric and trait-mediated priority effects show decreasing beta diversity with higher dispersal, although the change is much more obvious for those with numeric priority effects, indicating that they have received a stronger homogenizing effect from dispersal (Figure 5E-F; Figure S6-8F).

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. The initial decrease of dissimilarity index in all cases is due to the stabilization process of local communities (see Figure 2). In metacommunities with numeric priority effects, the temporal trend of beta diversity depends on the dispersal rate *r* and initial scenarios (Figure 6; Figure S9-10). Under Scenario 1, low dispersal results in little (but nonzero) temporal turnover (Figure 6A) after the initial drop. This indicates the persistent but extremely low turnover brought by dispersal, while intermediate and high dispersal results in higher turnover due to a higher population flow in and out the patch (Figure 6C, 6E). Note that even when the metacommunity is dominated by a single species (as in Figure 2E), its population still fluctuates frequently due to high dispersal

rates, leading to relatively high temporal turnover (Figure 6E). However, with trait-mediated priority effects, metacommunities show a consistently high temporal beta diversity under low, medium, and high dispersal rates and across all initial scenarios (Figure 6; Figure S9-10). Under Scenario 1, even with the lowest dispersal rate, the temporal turnover is still higher than with numeric priority effects only (Figure 6A, 6B). This observation corresponds to the high species turnover observed in population dynamics regardless of initial conditions. Overall, these temporal trends are consistent with the observed local population dynamics and highlight the importance of the specific mechanism that produces priority effects for 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 local and regional biodiversity of seasonal communities and how they are influenced by dispersal. However, the shape of this dispersal-diversity relationship depends on the mechanisms underlying the priority effects, i.e., whether they are generated by numeric or trait-mediated effects. When relative arrival times (phenological differences) vary across space and time, metacommunities with numeric priority effects are highly sensitive to the initial conditions and become homogenized at high levels of dispersal with low local and regional diversity. 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 driven by numeric 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 with numeric priority effects, even in the absence of any spatial heterogeneity in habitat quality because the numeric advantage of resident species 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 and 3, 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 of residents and eventually exclude them both locally and regionally. 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 also found that the shape of this relationship is highly sensitive to initial conditions (i.e., how species are distributed among patches) in metacommunities with numeric priority effects. 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 arrival (emergence). If a species arrives early enough, its early arrival advantage (relative increase in interspecific competitive ability) can overcome its numeric disadvantage and allow it to invade the resident species. Given the temporal and spatial variation in arrival times (species phenology), trait-mediated priority effects can therefore promote local and regional coexistence of species by preventing competitive exclusion and homogenization at a high dispersal rate. This result agrees with a recent study that models patch memory, which is similar to trait-mediated priority effects via habitat modification (the previous resident modifies the habitat and therefore affects colonization success of the late arriver): with priority effects, 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 and numeric, but not trait-mediated

priority effects. This discrepancy arises because we incorporated seasonality and realistic spatial and temporal variations of arrival order 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. 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 an 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 ways, 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; plant communities, 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 variation (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 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). 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. Mechanistic understanding of this process is fundamental to our knowledge of how biodiversity responds to critical environmental processes in a changing world.

Acknowledgments

We thank members of Miller and Rudolf labs for their feedback on the project and Lydia Beaudrot, Joshua Fowler, Tom E. X. Miller, and Chuliang Song for commenting on the manuscript. Funding was provided by NSF DEB-1655626.

Figure Captions

Figure 1. Basic processes of the metacommunity model. In the hypothetical metacommunity each patch is occupied by one species and the season starts when species emerge in patches (step 1). Emergence time can vary across seasons and patches within a given species-specific range. After emergence, species compete locally (step 2) according to competition coefficients that either: (A) do not depend on the relative time of emergence (scenarios with numeric priority effects), or (B) depend on the pairwise difference in relative time of emergence (Δp) (scenarios with trait-mediated priority effects) and determine subsequent population dynamics in a given patch. These local patch dynamics together determine regional patterns (step 3) at the end of the season. Finally, the season ends with dispersal (step 4) and end-of-season disturbance.

Figure 2. Example of population dynamics of one randomly selected patch under Scenario 1 (each patch is initially occupied by a single species with the same starting population density) with different dispersal rates and mechanisms of priority effects. The left column (A, C, and E) shows dynamics with numeric priority effects, and the right column (B, D, and F) shows dynamics with trait-mediated priority effects. Each row shows results for low (0.001), medium (0.04), 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 log-transformed. All simulations were run with 40 dispersal patches (D = 40; 80% of all patches). See Table S1 for other parameters used.

Figure 3. The regional final population of all species among all 50 simulations under Scenario 1, with different dispersal rates and mechanisms of priority effects. The left column (A, C, and E) shows dynamics with numeric priority effects, and the right column (B, D, and F) shows dynamics with trait-mediated priority effects. Each row shows results with low (0.001), medium (0.04), and high (0.1) dispersal rates (*r*). All population densities are log-transformed. All simulations were run with 40 dispersal patches (*D* = 40; 80% of all patches). See Table S1 for other parameters used.

Figure 4. Relationship of alpha diversity (local species richness) and dispersal in metacommunities with numeric vs. trait-mediated priority effects for three scenarios that differ in initial conditions. Axes are parameters that determine dispersal; the x-axis is dispersal patches (*D*), shown in percentage of overall patches (*P* = 50), and the y-axis is dispersal rate (*r*). The color of the shaded region indicates local richness averaged among all patches and 50 simulations. The left column (A, C, and E) shows dynamics with numeric priority effects, and the right column (B, D, and F) shows dynamics with trait-mediated priority effects. Rows show differences in initial conditions of species distributions: A-B, Scenario 1 (one species per patch); C-D, Scenario 2 (equal abundance of species in all patches); E-F, Scenario 3 (different species abundances across patches). For specific distribution of alpha diversity values over dispersal patches, see Figure S6-8, panels A-C. See Table S1 for other parameters used.

Figure 5. Relationship of beta diversity (dissimilarity between patches) and dispersal in metacommunities with numeric vs. trait-mediated priority effects for 3 scenarios that differ in initial conditions. Axes are parameters that determine dispersal; the x-axis is dispersal patches

(*D*), shown in percentage of overall patches (*P* = 50) and the y-axis is dispersal rate (*r*). The color of the shaded region indicates dissimilarity averaged among 50 simulations. The left column (A, C, and E) shows dynamics with numeric priority effects, and the right column (B, D, and F) shows dynamics with trait-mediated priority effects. Rows show differences in initial conditions of species distributions: A-B, Scenario 1 (one species per patch); C-D, Scenario 2 (equal abundance of species in all patches); E-F, Scenario 3 (different species abundances across patches). For specific distribution of alpha diversity values over dispersal patches, see Figure S6-8, panels D-F. See Table S1 for other parameters used.

Figure 6. Temporal turnover calculated from one randomly selected simulation under Scenario 1 with different dispersal rates and mechanisms of priority effects. The left column (A, C, and E) shows dynamics with numeric priority effects, and the right column (B, D, and F) shows dynamics with trait-mediated priority effects. Rows show results with low (0.001), medium (0.04) and high (0.1) dispersal rates (*r*). The number of patches with dispersal (*D*) is shown as a percentage of total patches and represented by different shades of color. The dissimilarity index was calculated from metacommunities between consecutive time steps separated by 10 seasons.

Reference

Alford, R. A., and H. M. Wilbur. 1985. "Priority Effects in Experimental Pond Communities: Competition between Bufo and Rana." *Ecology*. https://doi.org/10.2307/1939161.

Allesina, Stefano, and Jonathan M. Levine. 2011. "A Competitive Network Theory of Species Diversity." *Proceedings of the National Academy of Sciences of the United States of America* 108 (14): 5638–42. https://doi.org/10.1073/pnas.1014428108.

Altermatt, F, S Schreiber, and M Holyoak. 2011. "Interactive Effects of Disturbance and Dispersal Directionality on Species Richness and Composition in Metacommunities." *Ecology*. https://doi.org/10.1890/10-1095.1.

Berlow, Eric L., and Sergio A. Navarrete. 1997. "Spatial and Temporal Variation in Rocky Intertidal Community Organization: Lessons from Repeating Field Experiments." *Journal of Experimental Marine Biology and Ecology* 214 (1–2): 195–229. https://doi.org/10.1016/S0022-0981(97)00023-3.

Blackford, Christopher, Rachel M Germain, and Benjamin Gilbert. 2020. "Species Differences in Phenology Shape Coexistence." *The American Naturalist* 195 (6). https://doi.org/10.1086/708719.

Cadotte, Marc W. 2006. "Dispersal and Species Diversity: A Meta-Analysis." *American Naturalist*. https://doi.org/10.1086/504850.

Carrara, Francesco, Florian Altermatt, Ignacio Rodriguez-Iturbe, and Andrea Rinaldo. 2012. "Dendritic Connectivity Controls Biodiversity Patterns in Experimental Metacommunities." *Proceedings of the National Academy of Sciences*.

Carter, Shannon K., Daniel Saenz, and Volker H.W. Rudolf. 2018. "Shifts in Phenological Distributions Reshape Interaction Potential in Natural Communities." *Ecology Letters* 21 (8): 1143–51. https://doi.org/10.1111/ele.13081.

Catano, Christopher P., Timothy L. Dickson, and Jonathan A. Myers. 2017. "Dispersal and Neutral Sampling Mediate Contingent Effects of Disturbance on Plant Beta-Diversity: A Meta-Analysis." *Ecology Letters* 20 (3): 347–56. https://doi.org/10.1111/ele.12733.

Chase, Jonathan M. 2007. "Drought Mediates the Importance of Stochastic Community Assembly." *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.0704350104.

De Meester, Luc, Joost Vanoverbeke, Laurens J. Kilsdonk, and Mark C. Urban. 2016. "Evolving Perspectives on Monopolization and Priority Effects." *Trends in Ecology and Evolution* 31 (2): 136–46. https://doi.org/10.1016/j.tree.2015.12.009.

DeMalach, Niv, Nadav Shnerb, and Tadashi Fukami. 2021. "Alternative States in Plant Communities Driven by a Life-History Trade-Off and Demographic Stochasticity." *The American Naturalist*, March, E000–E000. https://doi.org/10.1086/714418.

Diez, Jeffrey M., Inés Ibáñez, Abraham J. Miller-Rushing, Susan J. Mazer, Theresa M. Crimmins, Michael A. Crimmins, C. David Bertelsen, and David W. Inouye. 2012. "Forecasting Phenology: From Species Variability to Community Patterns." *Ecology Letters*. https://doi.org/10.1111/j.1461-0248.2012.01765.x.

Drake, J. A. 1991. "Community-Assembly Mechanics and the Structure of an Experimental Species Ensemble." *American Naturalist* 137 (1): 1–26. https://doi.org/10.1086/285143.

Dray, Stéphane, Guillaume Blanchet, Daniel Borcard, Guillaume Guenard, Thibaut Jombart, Guillaume Larocque, Pierre Legendre, Naima Madi, Helene H Wagner, and Maintainer Stéphane Dray. 2018. "Package 'Adespatial.'" *R Package Version*, 3–8.

Fodelianakis, Stilianos, Alexander Lorz, Adriana Valenzuela-Cuevas, Alan Barozzi, Jenny Marie Booth, and Daniele Daffonchio. 2019. “Dispersal Homogenizes Communities via Immigration Even at Low Rates in a Simplified Synthetic Bacterial Metacommunity.” *Nature Communications* 10 (1): 1314. https://doi.org/10.1038/s41467-019-09306-7.

Fukami, Tadashi. 2015. “Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects.” *Annual Review of Ecology, Evolution, and Systematics* 46: 1–23.

Grainger, Tess Nahanni, and Benjamin Gilbert. 2016. “Dispersal and Diversity in Experimental Metacommunities: Linking Theory and Practice.” *Oikos* 125 (9): 1213–23. https://doi.org/10.1111/oik.03018.

Howeth, Jennifer G., and Mathew A. Leibold. 2010a. “Prey Dispersal Rate Affects Prey Species Composition and Trait Diversity in Response to Multiple Predators in Metacommunities.” *Journal of Animal Ecology* 79 (5): 1000–1011. https://doi.org/10.1111/j.1365-2656.2010.01715.x.

———. 2010b. “Species Dispersal Rates Alter Diversity and Ecosystem Stability in Pond Metacommunities.” *Ecology* 91 (9): 2727–41. https://doi.org/10.1890/09-1004.1.

Kardol, Paul, Lara Souza, and Aimée T Classen. 2013. “Resource Availability Mediates the Importance of Priority Effects in Plant Community Assembly and Ecosystem Function.” *Oikos*.

Ke, Po Ju, and Andrew D. Letten. 2018. “Coexistence Theory and the Frequency-Dependence of Priority Effects.” *Nature Ecology and Evolution* 2 (11): 1691–95. https://doi.org/10.1038/s41559-018-0679-z.

Kerr, B, M A Riley, M W Feldman, and B J M Bohannan. 2002. “Local Dispersal Promotes Biodiversity in a Real-Life Game of Rock-Paper-Scissors.” *Nature*. https://doi.org/10.1038/nature00823.

Kneitel, Jamie M, and Thomas E Miller. 2003. “Dispersal Rates Affect Species Composition in Metacommunities of Sarracenia Purpurea Inquilines.” *American Naturalist* 162 (2): 165–71.

Legendre, Pierre. 2019. “A Temporal Beta□diversity Index to Identify Sites That Have Changed in Exceptional Ways in Space–Time Surveys.” *Ecology and Evolution* 9 (6): 3500–3514. https://doi.org/10.1002/ece3.4984.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. “The Metacommunity Concept: A Framework for Multi-Scale Community Ecology.” *Ecology Letters*. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Leibold, Mathew A., Mark C. Urban, Luc De Meester, Christopher A. Klausmeier, and Joost Vanoverbeke. 2019. “Regional Neutrality Evolves through Local Adaptive Niche Evolution.” *Proceedings of the National Academy of Sciences of the United States of America* 116 (7): 2612–17. https://doi.org/10.1073/pnas.1808615116.

Levine, Jonathan M., Jordi Bascompte, Peter B. Adler, and Stefano Allesina. 2017. “Beyond Pairwise Mechanisms of Species Coexistence in Complex Communities.” *Nature* 546 (7656): 56–64. https://doi.org/10.1038/nature22898.

Lu, Muyang. 2021. “Complex Relationships between Beta Diversity and Dispersal in Meta-Community Models.” *Ecography* n/a (n/a). https://doi.org/10.1111/ecog.05937.

Miller, Zachary R., and Stefano Allesina. 2021. “Metapopulations with Habitat Modification.” *Proceedings of the National Academy of Sciences* 118 (49).

https://doi.org/10.1073/pnas.2109896118.
Mouquet, Nicolas, and Michel Loreau. 2002. “Coexistence in Metacommunities: The Regional Similarity Hypothesis.” *American Naturalist* 159 (4): 420–26. https://doi.org/10.1086/338996.
———. 2003. “Community Patterns in Source-Sink Metacommunities.” *American Naturalist*. https://doi.org/10.1086/378857.
Oksanen, Jari, F Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R Minchin, RB O’hara, Gavin L Simpson, et al. 2013. “Package ‘Vegan.’” *Community Ecology Package, Version* 2 (9): 1–295.
Parmesan, Camille. 2006. “Ecological and Evolutionary Responses to Recent Climate Change.” *Annual Review of Ecology, Evolution, and Systematics*. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.
Pearse, William D., Charles C. Davis, David W. Inouye, Richard B. Primack, and T. Jonathan Davies. 2017. “A Statistical Estimator for Determining the Limits of Contemporary and Historic Phenology.” *Nature Ecology and Evolution* 1 (12): 1876–82. https://doi.org/10.1038/s41559-017-0350-0.
Poulos, Davina E., and Mark I. McCormick. 2014. “Who Wins in the Battle for Space? The Importance of Priority, Behavioural History and Size.” *Animal Behaviour* 90: 305–14. https://doi.org/10.1016/j.anbehav.2014.02.003.
Pu, Zhichao, and Lin Jiang. 2015. “Dispersal among Local Communities Does Not Reduce Historical Contingencies during Metacommunity Assembly.” *Oikos* 124 (10): 1327–36. https://doi.org/10.1111/oik.02079.
Pulliam, H. Ronald. 1988. “Sources, Sinks, and Population Regulation.” *The American Naturalist* 132 (5): 652–61.
R Core Team. 2021. “R: A Language and Environment for Statistical Computing.”
Rasmussen, Nick L., Benjamin G. Van Allen, and Volker H.W. Rudolf. 2014. “Linking Phenological Shifts to Species Interactions through Size-Mediated Priority Effects.” *Journal of Animal Ecology* 83 (5): 1206–15. https://doi.org/10.1111/1365-2656.12203.
Rudolf, Volker H.W. 2018. “Nonlinear Effects of Phenological Shifts Link Interannual Variation to Species Interactions.” *Journal of Animal Ecology* 87 (5): 1395–1406. https://doi.org/10.1111/1365-2656.12850.
———. 2019. “The Role of Seasonal Timing and Phenological Shifts for Species Coexistence.” *Ecology Letters* 22 (8): 1324–38. https://doi.org/10.1111/ele.13277.
Sheriff, Michael J., G. Jim Kenagy, Melanie Richter, Trixie Lee, Øivind Tøien, Franziska Kohl, C. Loren Buck, and Brian M. Barnes. 2011. “Phenological Variation in Annual Timing of Hibernation and Breeding in Nearby Populations of Arctic Ground Squirrels.” *Proceedings of the Royal Society B: Biological Sciences* 278 (1716): 2369–75. https://doi.org/10.1098/rspb.2010.2482.
Shorrocks, Bryan, and Marc Bingley. 1994. “Priority Effects and Species Coexistence: Experiments with Fungal-Breeding Drosophila.” *Journal of Animal Ecology* 63 (4): 799–806.
Shurin, Jonathan B., Priyanga Amarasekare, Jonathan M. Chase, Robert D. Holt, Martha F. Hoopes, and Mathew A. Leibold. 2004. “Alternative Stable States and Regional Community Structure.” *Journal of Theoretical Biology* 227 (3): 359–68. https://doi.org/10.1016/j.jtbi.2003.11.013.
Theobald, Elli J., Ian Breckheimer, and Janneke HilleRisLambers. 2017. “Climate Drives

Phenological Reassembly of a Mountain Wildflower Meadow Community." *Ecology* 98 (11): 2799–2812. https://doi.org/10.1002/ecy.1996.

Thompson, Patrick L., Laura Melissa Guzman, Luc De Meester, Zsófia Horváth, Robert Ptacnik, Bram Vanschoenwinkel, Duarte S. Viana, and Jonathan M. Chase. 2020. "A Process-Based Metacommunity Framework Linking Local and Regional Scale Community Ecology." *Ecology Letters* 23 (9): 1314–29. https://doi.org/10.1111/ele.13568.

Tilman, David. 1994. "Competition and Biodiversity in Spatially Structured Habitats." *Ecology* 75 (1): 2–16. https://doi.org/10.2307/1939377.

Toju, Hirokazu, Rachel L. Vannette, Marie Pierre L. Gauthier, Manpreet K. Dhami, and Tadashi Fukami. 2018. "Priority Effects Can Persist across Floral Generations in Nectar Microbial Metacommunities." *Oikos* 127 (3): 345–52. https://doi.org/10.1111/oik.04243.

Urban, M C, and L De Meester. 2009. "Community Monopolization: Local Adaptation Enhances Priority Effects in an Evolving Metacommunity." *Proceedings of the Royal Society B-Biological Sciences*. https://doi.org/10.1098/rspb.2009.1382.

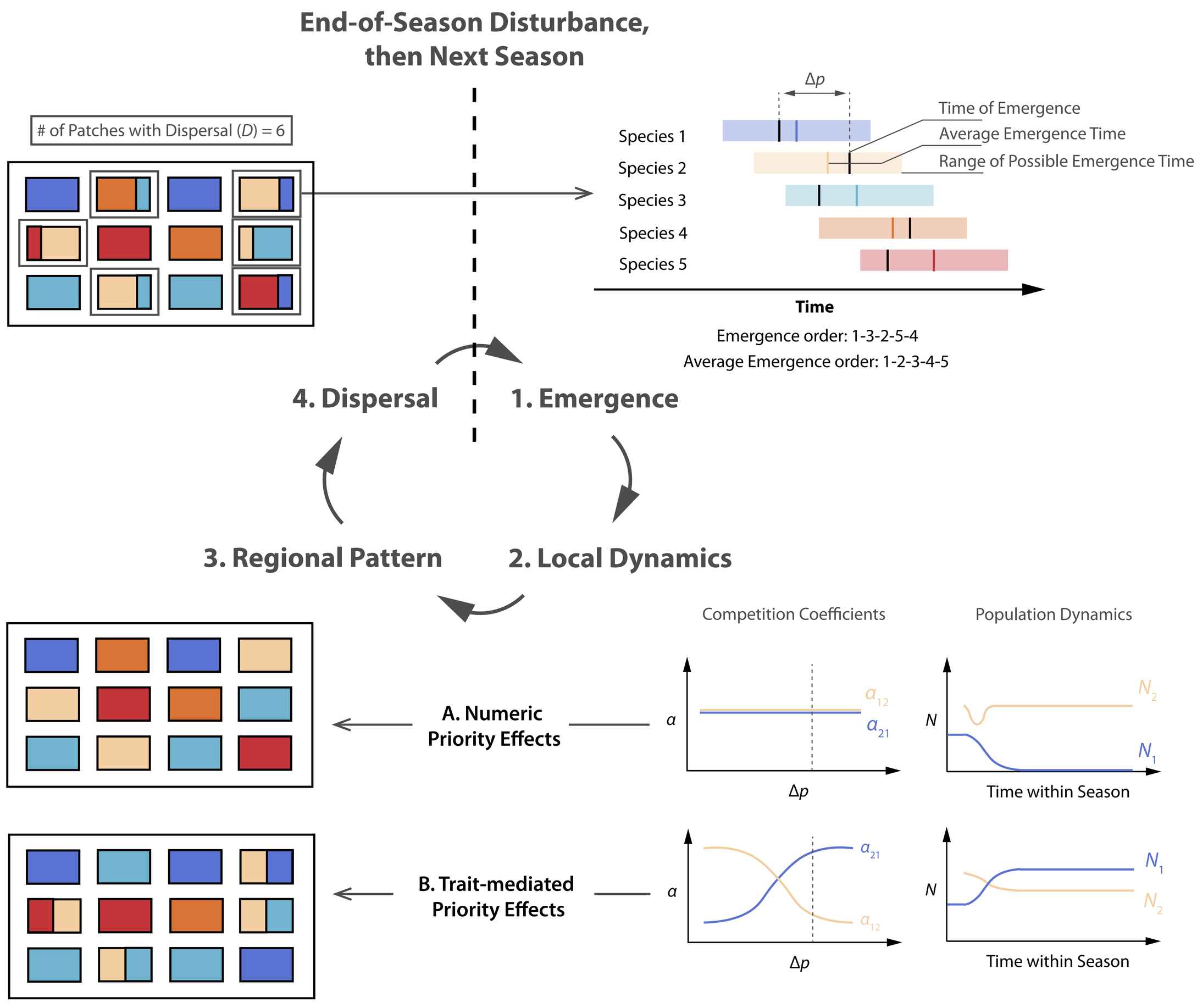
Vannette, Rachel L., and Tadashi Fukami. 2017. "Dispersal Enhances Beta Diversity in Nectar Microbes." *Ecology Letters* 20 (7): 901–10. https://doi.org/10.1111/ele.12787.

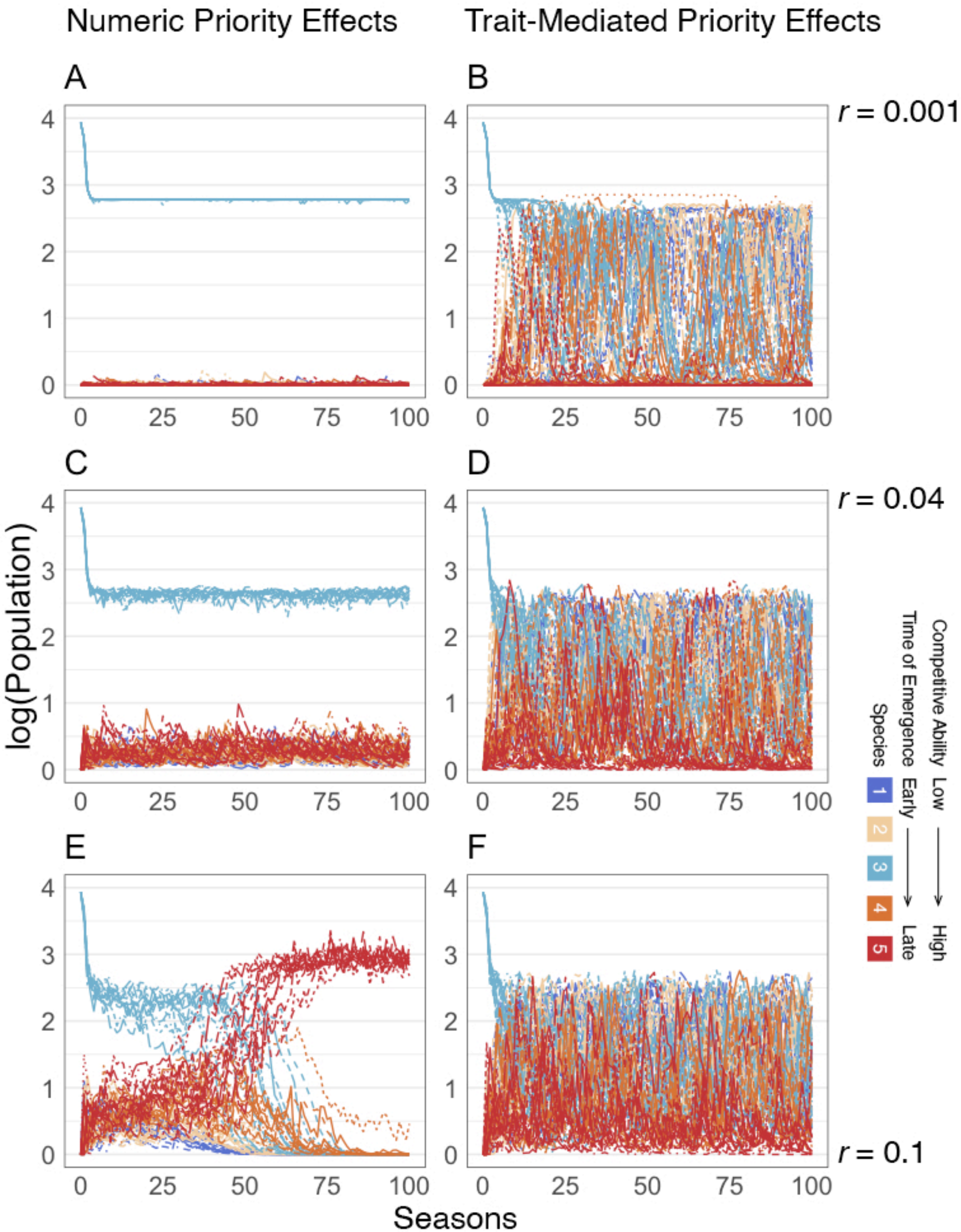
Vanoverbeke, Joost, Mark C. Urban, and Luc De Meester. 2016. "Community Assembly Is a Race between Immigration and Adaptation: Eco-Evolutionary Interactions across Spatial Scales." *Ecography* 39 (9): 858–70. https://doi.org/10.1111/ecog.01394.

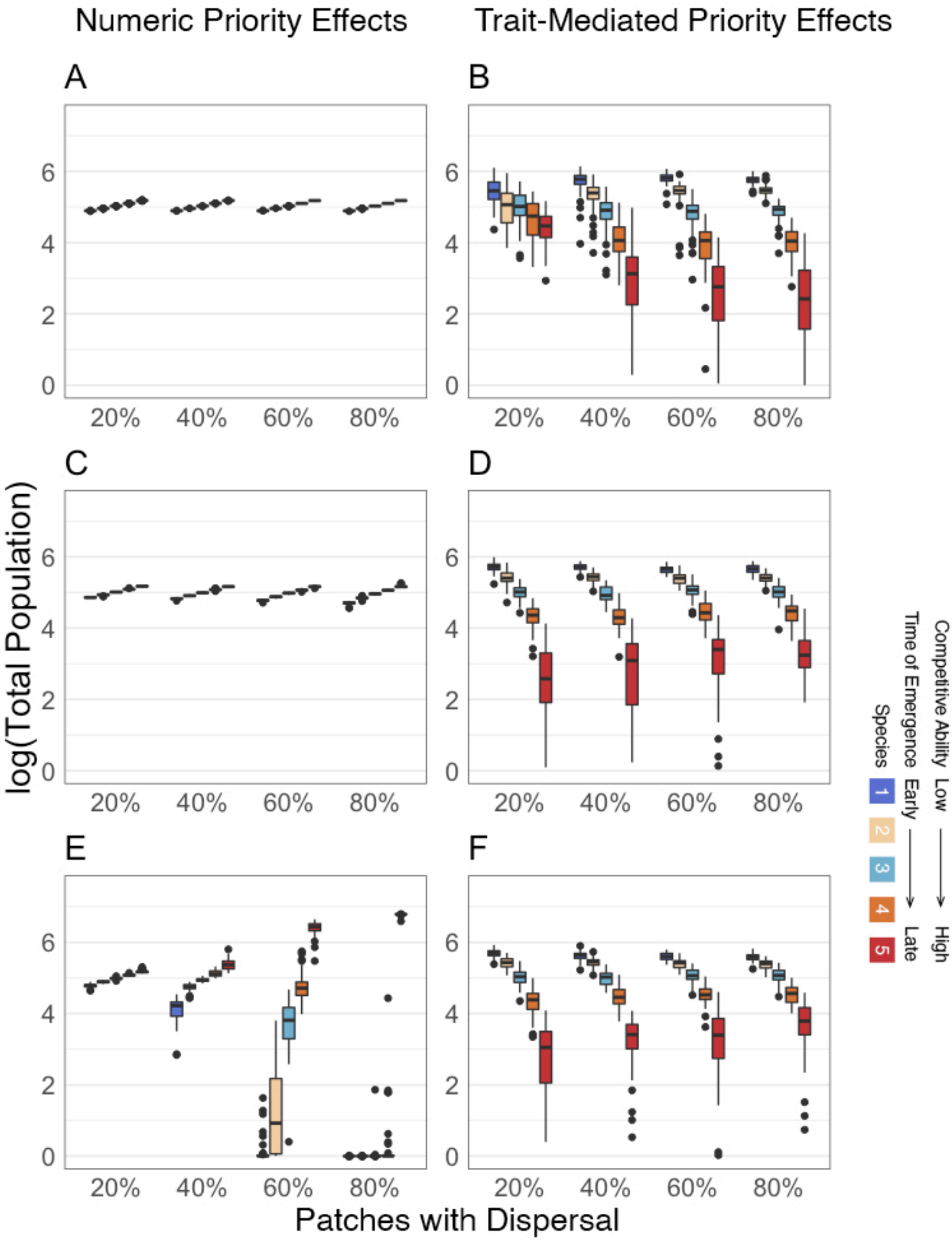
Vanschoenwinkel, Bram, Falko Buschke, and Luc Brendonck. 2013. "Disturbance Regime Alters the Impact of Dispersal on Alpha and Beta Diversity in a Natural Metacommunity." *Ecology* 94 (11): 2547–57. https://doi.org/10.1890/12-1576.1.

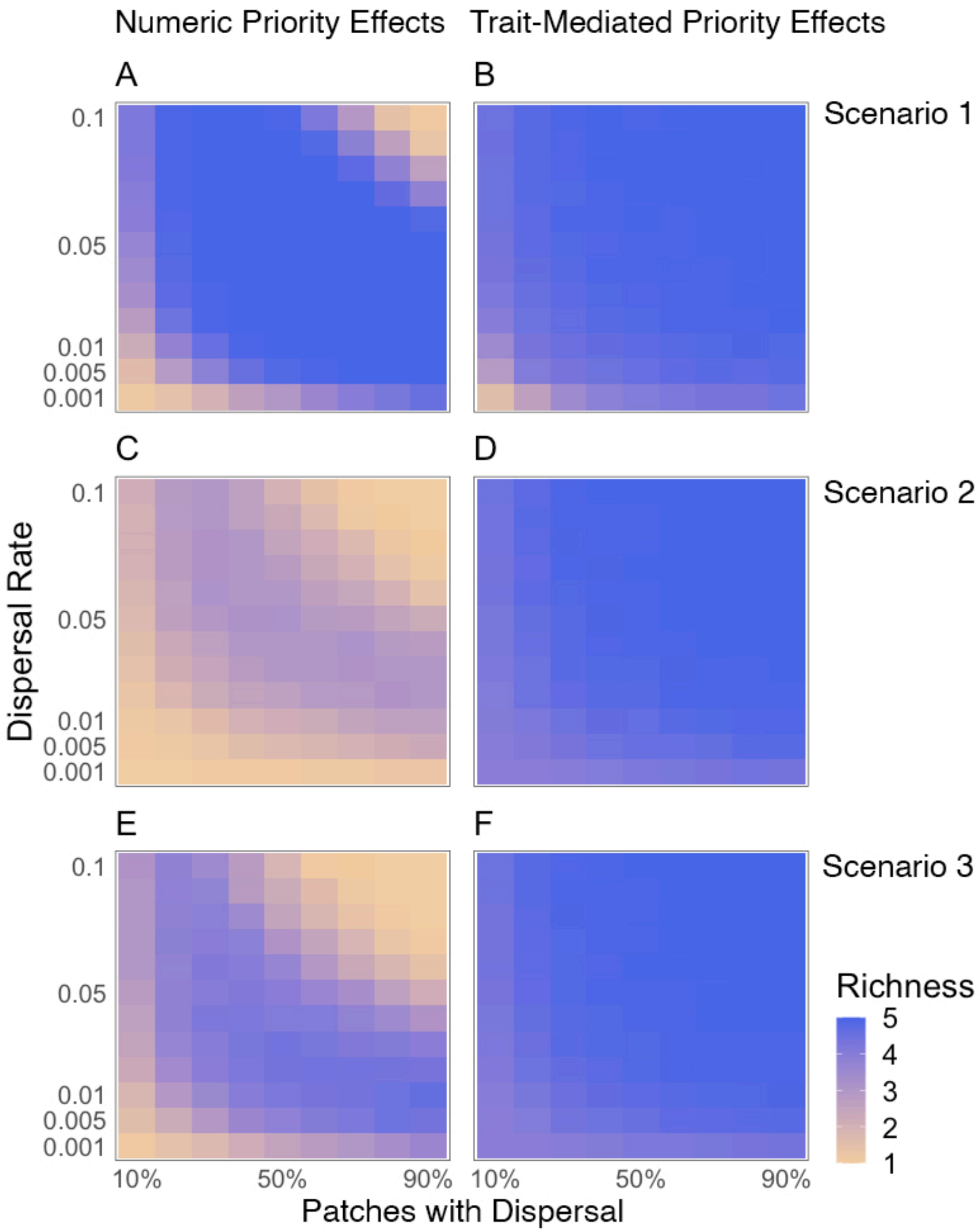
Wolkovich, E. M., B. I. Cook, K. K. McLauchlan, and T. J. Davies. 2014. "Temporal Ecology in the Anthropocene." *Ecology Letters*. https://doi.org/10.1111/ele.12353.

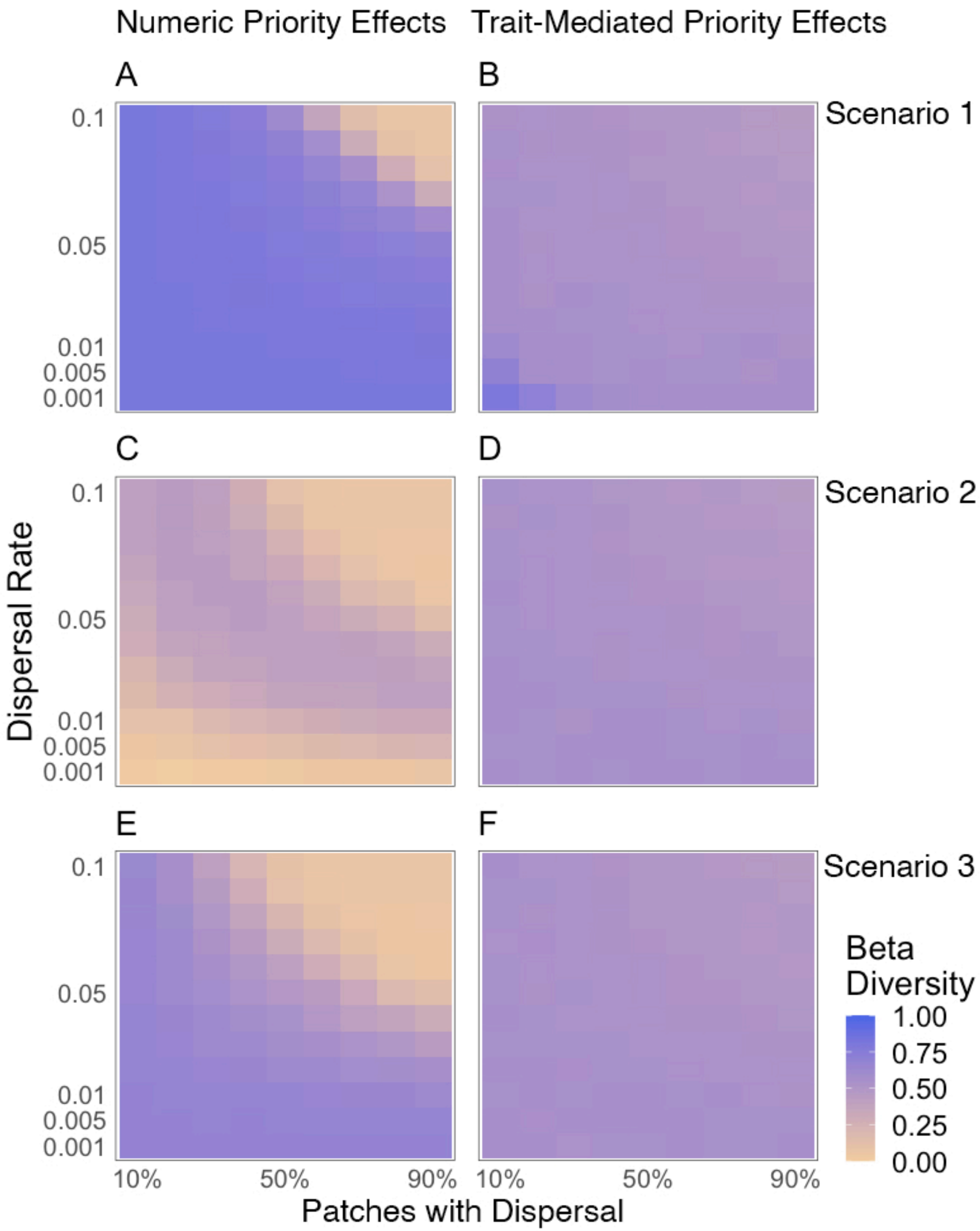
Zou, Heng-Xing, and Volker H. W. Rudolf. 2020. "Priority Effects and Season Length Shape Long-Term Competition Dynamics." *BioRxiv*, 2020.08.14.251926.

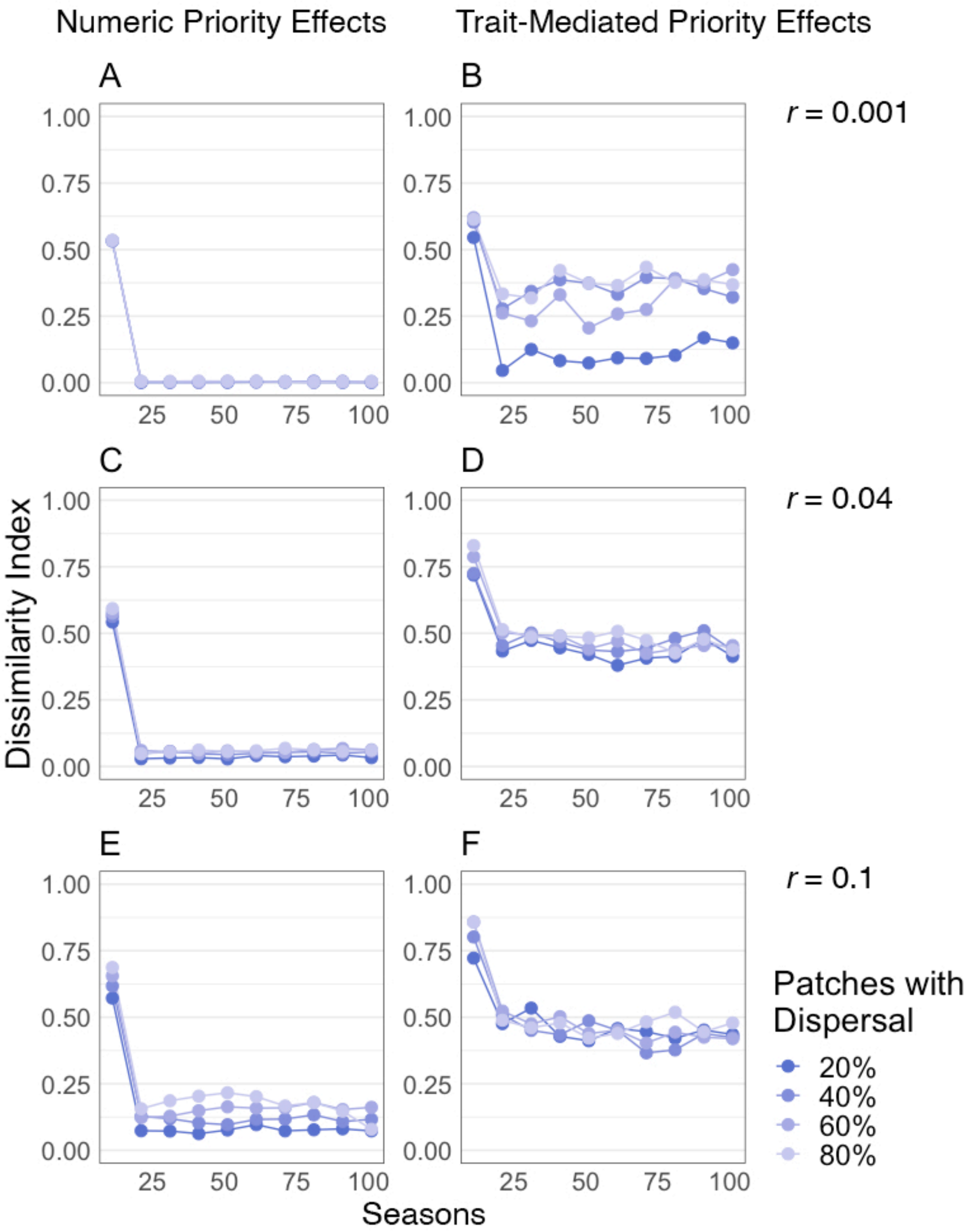

End-of-Season Disturbance,
then Next Season
# of Patches with Dispersal (D) = 6
Δp
Time of Emergence
Average Emergence Time
Range of Possible Emergence Time
Species 1
Species 2
Species 3
Species 4
Species 5
Time
Emergence order: 1-3-2-5-4
Average Emergence order: 1-2-3-4-5
4. Dispersal
1. Emergence
3. Regional Pattern
2. Local Dynamics
Competition Coefficients
Population Dynamics
A. Numeric
Priority Effects
α
α12
α21
Δp
N
N2
N1
Time within Season
B. Trait-mediated
Priority Effects
α
α21
α12
Δp
N
N1
N2
Time within Season


Numeric Priority Effects
Trait-Mediated Priority Effects
A
B
C
D
E
F
r = 0.001
r = 0.04
r = 0.1
log(Population)
Seasons
0
1
2
3
4
0
25
50
75
100
Species
1
2
3
4
5
Time of Emergence
Early
Late
Competitive Ability
Low
High


Numeric Priority Effects
Trait-Mediated Priority Effects
A
B
C
D
E
F
log(Total Population)
0
2
4
6
20%
40%
60%
80%
Patches with Dispersal
Competitive Ability
Low
High
Time of Emergence
Early
Late
Species
1
2
3
4
5


Numeric Priority Effects
Trait-Mediated Priority Effects
A
B
C
D
E
F
Scenario 1
Scenario 2
Scenario 3
Dispersal Rate
0.1
0.05
0.01
0.005
0.001
10%
50%
90%
Patches with Dispersal
Richness
5
4
3
2
1


Numeric Priority Effects
Trait-Mediated Priority Effects
A
B
C
D
E
F
Scenario 1
Scenario 2
Scenario 3
Dispersal Rate
0.1
0.05
0.01
0.005
0.001
10%
50%
90%
Patches with Dispersal
Beta Diversity
1.00
0.75
0.50
0.25
0.00


Numeric Priority Effects
Trait-Mediated Priority Effects
A
B
C
D
E
F
r = 0.001
r = 0.04
r = 0.1
Dissimilarity Index
Seasons
1.00
0.75
0.50
0.25
0.00
25
50
75
100
Patches with Dispersal
20%
40%
60%
80%