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Eco-evolutionary buffering: rapid evolution facilitates regional coexistence of species engaged in local priority effects

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Abstract

Priority effects, in which early-arriving species exclude competing species from local communities, are thought to enhance regional species diversity by promoting community divergence. Theory suggests, however, that these same priority effects make it impossible for species to coexist in the region unless individuals are continuously supplied from an external species pool, often an unrealistic assumption. Here we develop an eco-evolutionary hypothesis to solve this conundrum. Using a metacommunity model in which priority effects occur via interspecific interference, we show that species can coexist regionally even in the absence of an external species pool if resistance to other species evolves rapidly under a trade-off with competitive ability. With this trade-off, species become less resistant as they become regionally more common. Rare species can then invade and dominate some local patches and consequently recover in regional frequency. Intriguingly, rare species recovery is possible even while local priority effects remain strong. This eco-evolutionary buffering of rare species appears especially effective when many small communities are connected by infrequent dispersal.

Keywords: priority effect, frequency dependence, metacommunity, interference, allelopathy, habitat modification, eco-evolutionary dynamics, competition, coexistence, species pool

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Introduction

There is now ample evidence that the effects that species exert on one another in a local habitat patch often depend on the order and initial abundance in which species arrive (Sutherland 1974; Drake 1991; Chase 2003). Known as priority effects (Slatkin 1974), such historical contingency in local community assembly is increasingly recognized as a major factor influencing species diversity (Fukami 2015). In particular, recent research has shown that local priority effects can enhance beta diversity, i.e., the variation in species composition among local communities, by driving communities onto divergent successional trajectories (e.g., Chase 2010; Martin & Wilsey 2012; Fukami & Nakajima 2013).

Founded in large part on MacArthur and Wilson's (1967) theory of island biogeography, much of this research has traditionally assumed an external species pool (e.g., Post & Pimm 1983; Lockwood *et al.* 1997; Morton & Law 1997). That is, immigrants entering local patches are drawn from a regional pool whose species composition is static and is not influenced by local community dynamics. However, at large spatial and temporal scales, the regional pool consists of immigrants originating from a collection of local patches themselves (Mittelbach & Schemske 2015). In other words, the regional pool is internal, rather than external (*sensu* Fukami 2005, 2015), as depicted by the metacommunity concept (Leibold *et al.* 2004).

To explain species diversity at these scales, it is therefore necessary to understand how a diverse species pool can be maintained as a collective result of local community dynamics. This task is particularly challenging when species engage in inhibitory priority effects, where species that are initially common hinder colonization by competing species (Shurin *et al.* 2004). In many cases, species are likely to arrive at a newly created or disturbed patch in proportion to their regional abundances within the metacommunity. This correspondence between regional frequency and arrival probability can result in neutral population dynamics at the regional scale (Taneyhill 2000), with all but one species eventually drifting to regional extinction. In other cases, regionally common species can benefit disproportionately from the local priority effects and regionally rare species tend to become even rarer and eventually disappear from the region (Shurin *et al.* 2004).

Thus, to maintain both local priority effects and a diverse regional pool of species, there has to be a mechanism that buffers species from regional extinction. In a pioneering study, Shurin *et al.* (2004) suggested that spatial environmental heterogeneity could be one such mechanism. If the environment varies among local habitat patches, each species may have a set of patches where it is favored over others and can dominate irrespective of initial composition. Individuals of each species can then continue to disperse from their respective refuges to those patches where local priority effects occur. In this sense, invoking spatial

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refuges is conceptually no different from assuming an external species pool. As a consequence, it remains unknown whether regional species diversity can be maintained in the presence of local priority effects without recourse to an external species pool.

The goal of this paper is to suggest that this maintenance is possible when species traits responsible for priority effects evolve rapidly. Many previous studies of priority effects have assumed that species traits are fixed (but see, e.g., Urban & De Meester 2009; Knope *et al.* 2012). Growing evidence indicates, however, that traits often evolve at a speed comparable to that of ecological population dynamics (Thompson 1998; Schoener 2011). Effects of such rapid evolution (*sensu* Hairston *et al.* 2005) on species coexistence are emerging as an active area of research (Lankau 2011). For example, Vasseur *et al.* (2011) suggested that evolution along a trade-off between intra- and inter-specific competitive ability could prevent local extinction even when there is positive frequency dependence at intermediate frequencies. However, this study did not explicitly consider coexistence at the metacommunity level.

Here we use a simple metacommunity model inspired by many empirical examples of priority effects in order to investigate how rapid evolution may influence regional coexistence of species that locally engage in inhibitory priority effects. We find that species can coexist in a metacommunity even in the absence of environmental heterogeneity if species traits responsible for priority effects evolve rapidly under a trade-off with other fitness components. By presenting this new "eco-evolutionary buffering" hypothesis and exploring the conditions under which it operates, we seek to stimulate more research that incorporates rapid evolution into the study of priority effects and their consequences for species diversity at large spatial and temporal scales.

Methods

Empirical motivation

In this study, we focus on inhibitory priority effects via interspecific interference, of which there are many empirical examples in microbes, animals, and plants. Microbes inhabiting floral nectar, for example, appear to change the chemical properties of nectar in a way that makes it harder for other, late-arriving species to colonize (Peay *et al.* 2012; Vannette *et al.* 2013). This type of self-serving habitat modification causes inhibitory priority effects. Similarly, in marine soft-bottom sediments, ghost shrimps and bivalves each modify grain size and oxygen content, and each group thrives better in its self-modified environment (Peterson 1984; Knowlton 2004), another case of inhibitory priority effects via habitat modification. In plant communities, local positive feedbacks have been found to operate in some landscapes

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with interspersed patches of forest and heathland, mediated in this case by fire frequency and nutrient cycling (Petraitis & Latham 1999; Odion *et al.* 2010). More generally, many species of microbes and plants engage in "chemical warfare" with their competitors, causing inhibitory priority effects by habitat modification. Bacteria, for example, produce bacteriocins, compounds that inhibit or kill closely related strains or species, but do not affect the producing strain itself (Riley 1998). Many plants, including invasive species can produce allelopathic chemicals that harm heterospecific individuals more than conspecifics (Bais *et al.* 2003; Callaway & Ridenour 2004). In addition to habitat modification, another form of interspecific interference that can cause inhibitory priority effects is intraguild predation. For example, the classic work by Park (1954) and Park *et al.* (1965) demonstrated that two competing species of flour beetle each preyed preferentially on heterospecific eggs and pupae, causing a common-species advantage.

Furthermore, empirical evidence suggests that traits involved in inhibitory priority effects often evolve rapidly along a trade-off with other aspects of fitness. For example, microbial resistance to bacteriocins or antibiotics evolves so rapidly that it is a pressing medical and economic problem (Palumbi 2001; Baquero *et al.* 2011). But rapid evolution of microbial resistance often comes at a cost such as reduced growth rate (Riley 1998), reduced competitive ability (Gagneux *et al.* 2006), or "collateral sensitivity" to other types of antimicrobials (Pál *et al.* 2015), at least until compensatory mutations alleviate it (Riley 1998). Similarly, in some plants, such as species of *Brassica*, both allelotoxin production and growth rate can evolve rapidly, but along a trade-off between the two traits (Lankau 2008; Lankau *et al.* 2009; Lankau 2011). Building on these empirical examples, the modeling study we describe below examines scenarios where traits responsible for priority effects evolve under a trade-off with another key trait, general competitive ability.

Model

Overview

Our simulation model is stochastic, individual-based, and spatially implicit. The key processes are birth and death events, migration between patches, evolution of two traits involved in priority effects (general sensitivity to competition and sensitivity to interference by other species), disturbance, and recolonization of patches (see Table 1 for a list of all parameters and variables). In this model, local and regional dynamics are linked via migration and recolonization, making the species pool internal rather than external. Because we wish to explore whether species can coexist without spatial environmental heterogeneity, parameters are identical across patches. Throughout we focus on metacommunities consisting of two

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species as a simplest case to consider. However, to investigate the potential generality of our findings, we also explore some cases where up to 10 species are initially present in the metacommunity. We assume that all species have the same dispersal ability.

Death, birth, and migration

In our model, there are n patches, each of which is always fully occupied by a local community of k individuals. We assume patches are small enough for individuals to "feel" the presence of all other inhabitants. Time is continuous and death events occur at rate k in each patch such that one time unit roughly corresponds to one generation. For each death event, we first pick an individual to be killed. Individuals are picked in proportion to the total competitive pressure they experience, C, which results from actual competition and interference effects. As explained below, C may vary between individuals and its parameters evolve over time. Second, we choose an individual to reproduce asexually. With probability $1 - m$, the parent individual comes from the same patch where the death event has just occurred (no migration), and with probability m it comes from a randomly chosen other patch (migration). Finally, we randomly draw one of the k individuals in the selected patch as a parent, including, in the case of no migration, the individual that has just died.

Individual traits, trade-offs, and competitive pressure

Individuals are haploid and each of them has its own set of quantitative traits: general sensitivity to competition, G, and sensitivity to interference or habitat modification by each of the other species j, H_j. A low value of G indicates a high general competitive ability (e.g., high ability to survive under low resource availability), whereas a low value of H_j indicates a high tolerance or resistance to species j. We assume that each species interferes or modifies the habitat in a unique way, for example by producing different toxins. The strength of interference, e.g. the rate of toxin production, is assumed constant across individuals, species, and time.

The total competitive pressure, C, experienced by a focal individual is the sum of general competitive effects of all individuals in the local community and the additional effects of interference. For a specific individual of species i that has traits G and H_j

$$C = G \cdot k + \sum_{j \neq i} H_j \cdot N_j, \tag{1}$$

where N_j is the local population size of species j. To avoid excessive indexing, we did not include indices for individual and deme number in (1). But keep in mind that individuals

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within the same species may differ in G, H_j and consequently also C. Also note that interspecific competition is always stronger than intraspecific competition, such that coexistence would be impossible in a single homogeneous community. Competitive pressure only depends on the current community composition and not on past inhabitants of the patch. This is realistic for all types of direct interspecific interference and also for many types of habitat modification, for example for toxins that rapidly decay or diffuse away.

In our full model, we assume a trade-off between each of the H_j and G. For a specific member of species i:

$$G = g_{min} + \sum_{j \neq i} \underbrace{\left(1 - \frac{H_j}{h_{max}}\right)^y \cdot g_{max}}_{G_j}, \tag{2}$$

where G_j is the cost in terms of general sensitivity to competition that the individual pays for reduced sensitivity to species j. The exponent $y > 0$ defines the shape of the trade-off curve. By default, we assume a linear trade-off ($y = 1$). In our simulations, h_{max} will be substantially larger than g_{max}. Thus, if we compare two members of species i, one with a low H_j and one with a high H_j, the one with a low H_j will be fitter in a patch with many individuals of species j, but the one with the high H_j will be fitter in a patch with many conspecifics, i.e., individuals of species i. In other words, there is a trade-off between intraspecific and interspecific competitive ability.

To investigate the metacommunity consequences of trait evolution and the trade-off between general sensitivity to competition and sensitivity to heterospecific interference, we compare four different scenarios. First, in the "neutral" scenario (no trade-off, no evolution), all individuals in the metacommunity have the same general sensitivity to competition ($G = 1$) and are completely resistant to heterospecific interference ($H_j = 0$ for all j). Second, in the "fixed trait" scenario (trade-off, but no evolution), there is no mutation such that all G_j and H_j stay at their initial values. Third, in the "independent evolution" scenario (evolution, but no trade-off), we draw the offspring's trait values for each of the G_j and H_j independently from normal distributions with the parent's trait values as mean and standard deviations d and $d \cdot h_{max}/g_{max}$, respectively. That is, every new offspring experiences some mutation. The value of d can be interpreted as the sum over all relevant loci of effect size and mutation rate. If one of the traits overshoots the minimum or maximum possible value, it is set to the minimum or maximum (0 or g_{max} for the G_j, and 0 or h_{max} for the H_j). In this scenario, selection acts to reduce both the H_j and the G_j. Finally, in the "trade-off evolution" scenario, only the G_j mutate, as described for the independent-evolution scenario, and the corresponding H_j are determined by the trade-off equation (2).

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Patch disturbance and recolonization

As in Shurin *et al.* (2004), we assume that entire patches can be destroyed and recolonized. Without such disturbance or when disturbance occurs at a smaller scale than local positive feedbacks, the landscape may settle into a configuration where each patch is dominated by one species. The regional dynamics then come to a halt and species can coexist for extended periods of time, as demonstrated by Molofsky *et al.* (1999, 2001) and Molofsky & Bever (2002) for spatially explicit models. However, since there is no disturbance to initiate new rounds of local community assembly, priority effects will no longer be operating.

In our model, disturbance events occur at rate $1/\tau$ in each patch, i.e. τ is the average time between disturbance events. When a patch is disturbed, all its inhabitants die. The patch is then recolonized immediately by a founder population of size f, consisting of offspring of individuals elsewhere in the metacommunity. We use two recolonization variants, the "propagule-pool model" and the "migrant-pool model" (Slatkin 1977). In the propagule-pool model, all f recolonizing individuals come from the same randomly drawn other patch. In the migrant-pool model, the source patch is drawn independently for each of the f individuals. After drawing the source patch(es), parents in the source patch(es) are drawn independently and with replacement to produce an offspring for the founder population. The founder population of size f then gives rise to a population of size k in one round of reproduction, i.e. for each of the k places to be filled, a parent individual is drawn independently and with replacement from the f recolonizers. Mutations can happen in each reproduction event during recolonization.

Simulations

To explore the parameter space for two-species metacommunities, we generated 150 combinations of seven parameters (number of patches n, local community size k, migration probability m, maximum sensitivity to heterospecific interference h_{max}, the standard deviation of mutation effect sizes d, average time between disturbance events τ, and founder population size f) by drawing independently from the distributions given in Table 1. In addition, recolonization followed either the propagule-pool or migrant-pool model, with equal probability. The remaining parameters were fixed to the values given in Table 1. In choosing these parameter ranges, we had metacommunities of macro-organisms in mind as potential examples, with hundreds of relatively small local communities. In such metacommunities we expect fast and highly stochastic dynamics at the local scale, compared to slower and more deterministic dynamics at the regional scale. We focused on metacommunities with frequent dispersal between patches such that evolution should occur at the regional scale rather than in the form

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of local adaptation (Lenormand 2002). Potential examples of such metacommunities include herbaceous plants and sessile aquatic animals (see also Mouquet & Loreau 2002; Fukami & Nakajima 2013; Zee & Fukami 2015). However, as we discuss below, our results may also apply to microorganisms.

For each parameter combination, we ran 10 replicate simulations. At the beginning of each simulation run, we assigned individuals randomly to species. All individuals in the metacommunity initially had the same general sensitivity to competition $G_j = g_0$ for all j and corresponding values of H_j. Storing regional frequencies every ten time units, we then ran each simulation for 10,000 time steps (generations).

To better understand the role of individual parameters, we ran additional simulations varying two parameters at a time and keeping the other parameters fixed at one of the original parameter combinations. Here we ran 50 replicates per parameter combination.

For some parameter combinations, we additionally ran simulations with 3, 4, 5, and 10 species, this time for 20,000 generations.

Analyses

Classification of regional frequency dependence

For a first impression of whether the regional species pool is stable for a given parameter combination, we can simply consider the proportion of replicate metacommunities that still contain all species at the end of the simulation. However, sometimes the regional dynamics may be slow and there may simply not have been enough time for one species to go extinct. For the regional species pool to be actually stable in the long run, a regionally rare species must on average become more common again. We therefore developed a heuristic framework that allowed us to classify parameter combinations with respect to their regional frequency dependence in the two-species simulations.

Specifically, we divided the frequency interval between 0 and 0.5 into 10 equally sized bins (from 0 to 0.05, from 0.05 to 0.10 etc.). After discarding the first few sampling points (before time 50), we assigned each of the remaining ones to a frequency bin according to the regional frequency of the regionally less common species. For each bin, we then computed the average change in regional frequency until the next sampling point, i.e. ten time units later. We did this for all replicates separately and then computed an interval of mean $\pm c$ standard errors for each bin, where c is a positive constant.

Based on these intervals, we assigned a simulated scenario to one of five regional frequency dependence classes (Fig. 1 a). If all intervals overlapped with zero, we assigned the scenario to the "quasi-neutral" class. After confirming independently that our neutral simulations indeed

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exhibit neutral regional frequency dependence, we chose c such that 95% of neutral simulations were classified as quasi-neutral. We then used the resulting value $c = 3.83$ throughout the study.

For scenarios that were not classified as quasi-neutral, we considered the most marginal frequency bin whose interval was not overlapping with zero (Fig. 1 a). A positive average change in this frequency bin indicates that a rare species can increase in frequency and that the regional species pool may be stable. Depending on whether or not there were any intervals with negative average change, we assigned such scenarios either to the "complex frequency dependence" class or to the "negative frequency dependence" class. Under negative frequency dependence, coexistence is expected to be symmetric, and under complex frequency dependence asymmetric with one species at high and one at low regional frequency. Analogously, scenarios whose most marginal interval not overlapping zero was negative were assigned to either the "inverse complex frequency dependence" class or the "positive frequency dependence" class (Fig. 1 a). In both cases, a regionally rare species would be expected to go extinct, but under inverse complex frequency dependence two species that are initially equally common might coexist for a long time.

Quantification of the strength of local priority effects

As a measure of the strength of priority effects, we used the proportion of disturbance events across time and patches for which the locally most common species was the same among the f founding individuals and also immediately before the next disturbance event. This probability tends to be higher if the regional pool has an uneven composition because different immigrants to a focal patch then belong to the same species more often. To control for this effect in the two-species case, we binned observations according to regional frequency. In the multi-species case, we binned according to Simpson's index $\sum_{i=1}^{s} p_i^2$, where p_i is the regional frequency of species i. In both cases, we used bins of size 0.025 and computed the strength of priority effects separately for each bin. Cases where both species were equally common locally, either at the beginning or at the end, were discarded.

For each regional frequency bin, the strength of priority effects under the neutral scenario serves as a baseline expectation. If the strength of priority effects under another scenario is stronger than the neutral expectation for the same frequency bin, this result provides evidence for the existence of inhibitory priority effects under that scenario, where the initially most abundant species in the local patch is more likely to retain a dominant status in that patch than expected solely by demographic drift.

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Code and scripts

We provide C++ code for the simulation program in Appendix S1 in Supporting Information, and R scripts to initiate and analyze the simulation studies in Appendix S2.

Results

Probability of coexistence and outcome types

Across all of the simulation runs we carried out, regional species coexistence was most likely under trade-off evolution. Specifically, averaged over all 150 randomly generated parameter combinations, the two species coexisted until the end of the simulation in 50 % of the cases under trade-off evolution, whereas they coexisted in only 25, 13, and 19 % of the cases in the neutral, fixed-trait, and independent-evolution scenarios, respectively (Fig. 1 b).

Under fixed traits or independent evolution, some parameter combinations were classified as quasi-neutral, but most fell into the positive frequency dependence class (Fig. 1 b). That is, the regionally rare species tended to become even rarer and eventually dropped out of the metacommunity. Under trade-off evolution, many parameter combinations still exhibited positive frequency dependence or quasi-neutrality, but a sizable number of parameter combinations (19 out of 150) were classified as having either complex or negative frequency dependence, meaning that there was a clear tendency for the regionally rare species to become more common again and that such systems are stable. These coexistence outcomes did not appear in any of the other scenarios, except for two independent-evolution scenarios that showed negative frequency dependence.

Coexistence until the end of the simulation was most likely under complex or negative frequency dependence (100 % in both cases) and least likely under positive frequency dependence (Fig. 1 b).

Regional frequency dynamics

For each of the four outcome classes that occurred under trade-off evolution, Fig. 2 shows time series for one representative parameter combination, together with time series for the corresponding three other scenarios for comparison. As expected, coexistence under negative frequency dependence was symmetric, with both species at regional frequencies around 0.5 (Fig. 2 l). Additional simulations with initial regional frequencies closer to 0 or 1 suggest that this symmetric coexistence equilibrium is indeed globally attracting. By contrast, under complex frequency dependence, coexistence was asymmetric, with one species more abundant

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in the region than the other (Fig. 2 p). Within each outcome class, parameter combinations differed in the magnitude of fluctuations around the respective mean frequencies.

Evolutionary dynamics

In the negative frequency dependence class under trade-off evolution (Fig. 3 e), both species remained highly tolerant of interspecific interference (low H_j) and therefore had a high sensitivity to general competition (high G) compared to species under the quasi-neutral and positive frequency dependent classes (Fig. 3 a–d). However, common species tended to be more sensitive to interspecific interference (Fig. 3 f). In the corresponding independent evolution scenario, both G and H_j were low at equilibrium but still responded weakly to regional frequency (Fig. S2). Under complex frequency dependence (Fig. 3 g,h), the regionally rare species remained relatively resistant to the other species (low H_j), whereas the common species evolved to become more competitive (lower G) and thus more sensitive to the other species (higher H_j). When species frequencies fluctuated, trait values fluctuated also, particularly in the regionally common species (Fig. 3 g,h).

Strength of priority effects

Local priority effects under trade-off evolution were generally stronger than in the corresponding neutral simulations, at least while both species were relatively common (Fig. 4). When one species dominated the metacommunity, with regional frequency of more than 0.8, priority effects were often nearly identical in strength to those in the neutral scenario. For a given regional frequency, there were no substantial differences in the strength of priority effects between trade-off evolution, independent evolution, and fixed-trait scenarios. However, priority effects were maintained only in scenarios with evolution and negative or complex frequency dependence. In the remaining cases, local priority effects could be observed while multiple species were still present in the region, but since the regional species pool was not stable, priority effects eventually disappeared.

Sensitivity to individual parameters

By varying parameters systematically around the parameter combination in Fig. 2 l, we found that negative frequency dependence generally occurs for small local community sizes k, with quasi-neutrality or complex frequency dependence at intermediate values of k, and positive frequency dependence for large k (Fig. 5). The range of k values with negative frequency dependence was largest with small migration rates m (Fig. 5 a), large standard deviations of mutational effects d (Fig. 5 b), and large maximum sensitivity to interference h_{max} (Fig.

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5 d). The average time between disturbance events, τ, did not have a strong effect on the distribution of outcome types (Fig. 5 c). For k and m, these observations are consistent with the distributions among the outcome classes in the random parameter study, but not for d and τ (Fig. S3), indicating that these parameters may have opposing effects for different combinations of the other parameters. The complex and positive frequency dependence classes contained more parameter combinations with migrant-pool recolonization, whereas the negative and quasi-neutral classes contained more parameter combinations with propagule-pool recolonization (Fig. S3 h). The region of parameter space with stable coexistence grew slightly with increasing convexity of the trade-off (Fig. S4).

More than two species

We examined multi-species dynamics for two of the parameter combinations used in the two-species simulations. Under a parameter combination with negative frequency dependence (third row in Fig. 2), three species coexisted until the end of the simulation in all cases under trade-off evolution, and most of the replicate metacommunities that started with four, five, or ten species maintained four species until the end (Fig. 6). In all cases, regional species diversity in the neutral and fixed-trait scenarios decayed more rapidly than in the trade-off evolution scenario. But as in the two-species case, some independent-evolution simulations also resulted in coexistence. Again, priority effects were usually stronger under trade-off evolution than under neutrality (Fig. S6). The slightly more complex outcomes in a parameter combination with complex frequency-dependence (last row in Fig. 2) are explored in Appendix S4.

Discussion

Taken together, our results suggest a new hypothesis for the maintenance of a multi-species regional pool in the presence of local priority effects. This "eco-evolutionary buffering" hypothesis can be summarized as follows. Assuming resistance to heterospecific interference is costly and evolves along a trade-off with general competitive ability, the strength and direction of selection will depend on regional frequencies of species. When other species are common in the region, members of a species experience strong selective pressure to be tolerant of heterospecific interference. However, as a species approaches regional dominance as a cumulative result of local priority effects, its members lose the costly resistance to other species (Fig. 3). Exploiting this loss of tolerance, other species recover in abundance. Our results show that eco-evolutionary buffering can stabilize a regional pool of at least up to four species (Fig. 6). Intriguingly, despite species evolving this way, strong local priority effects are often maintained, particularly when multiple species remain common in the region

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(Figs. 4 and S6). While similar coexistence mechanisms have been suggested before at the scale of local communities (Levin 1971; León 1974; Pease 1984; Vasseur *et al.* 2011), our new hypothesis considers metacommunity dynamics, explaining how multiple species that engage in local priority effects can stably co-exist even under an internal species pool and even in the absence of environmental heterogeneity across local habitat patches.

Types, requirements, and consequences of eco-evolutionary buffering

Our results indicate that eco-evolutionary buffering can result in either negative or complex regional frequency dependence (Fig. 1). Negative frequency dependence is particularly likely when local patches are small and when they are connected by infrequent migration (Figs. 5 and S3). Under these conditions, a small evolutionary response seems sufficient to stabilize regional coexistence. In Appendix S5, we offer a detailed heuristic explanation. Briefly, under small community size and low migration rate, the variance in local community size relative to its expectation is large. Hence many individuals of regionally rare species are in patches where they are locally common. Therefore, these individuals do not suffer much from local interference by the regionally common species, and a small evolutionary change, e.g., a slight shift in mutation-selection balance, is sufficient to tip the balance in favor of the regionally rare species. This explanation is consistent with the observation that, for small local communities and rare migration, even some independent-evolution scenarios exhibit negative frequency dependence.

In other parts of parameter space in our model, a shift in mutation-selection balance is not sufficient to give an advantage to regionally rare species. Instead, they have to become rare enough for the direction of selection to change in the common species. In some of these cases, rapid evolution buffers rare species from extinction via complex frequency dependence. In other cases, either because evolution is too slow or because selection changes direction only at an extreme regional frequency, positive frequency dependence or quasi-neutrality ensues and species cannot coexist in the long run. However, the proportion of species that coexisted until the end of the simulation was still elevated in the trade-off evolution scenario compared to the other scenarios (Fig. 1 b). We suspect that deterministic models with simplified genetic assumptions might indicate stable coexistence for many of the cases that we classified as unstable in the face of demographic and genetic stochasticity.

Under many of the parameter combinations leading to complex frequency dependence, regional frequencies oscillate. Times during which the rare species has an advantage and priority effects are weak alternate with times during which priority effects are strong and the

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common species has an advantage. Under negative frequency dependence, however, local priority effects can be strong while at the same time regionally rare species have an advantage. It appears that a slight asymmetry in the strength of interspecific competition and local priority effects is key to understanding why priority effects remain strong. Each species benefits from priority effects when it is substantially more common locally, but in patches where multiple species have a similar local frequency, regionally rare species have an advantage even if they are slightly less common locally. For example, if local communities consist of six individuals, each species may have an advantage when it has four or more individuals in the patch, but if both species have three individuals then the regionally rare species has an advantage (see Fig. S8 and Appendix S5 for more detail).

Based on our explorations of parameter space (Figs. 5 and S3, see Appendix S3 for more detail), we expect to observe eco-evolutionary buffering at intermediate frequencies (negative frequency dependence) in metacommunities consisting of numerous local patches with only few individuals per patch, which may be possible in plants or sessile aquatic organisms. However, qualitative dynamics in subdivided populations or communities depend on the product of local population size and migration rate (see e.g., Hartl & Clark 2007). It is therefore possible that negative frequency dependence occurs even in microbial communities characterized by many individuals per patch when among-patch dispersal is rare. The requirements for eco-evolutionary buffering by complex frequency dependence are less restrictive and may be fulfilled more readily in many microbial communities. Eco-evolutionary buffering may thus help to explain the high diversity of microbial species in habitats with apparently homogeneous environmental conditions (e.g., Sogin *et al.* 2006).

Future directions

This study is only a first step toward understanding the role of eco-evolutionary buffering in the maintenance of species diversity. Questions that should be addressed in future work include (1) how the total number of species that can coexist in a landscape depends on ecological and evolutionary parameters, (2) whether eco-evolutionary buffering also works for diploid sexual organisms, and (3) how eco-evolutionary buffering interacts with spatial and temporal environmental heterogeneity to affect regional coexistence. In addition, it would be useful to consider evolution of the rate of habitat modification in addition to the sensitivity to habitat modification. A mutation that reduces sensitivity to heterospecific habitat modification directly reduces the death rate of the focal individual. In contrast, a mutation that increases the rate of habitat modification first influences the death rate of heterospecific individuals. Indirectly, the mutation may then benefit the focal individual, but also non-mutated

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conspecifics who do not pay the fitness cost of an increased rate of habitat modification. Hence habitat modification can be an altruistic trait in this case, and cheating may play a role in regional species coexistence. It is unclear at this point how readily eco-evolutionary buffering occurs in these circumstances.

Besides the specific eco-evolutionary buffering mechanism we have studied in this paper, a number of other mechanisms could potentially buffer regional diversity in the presence of priority effects. Simple patch-occupancy models seem to suggest that, by virtue of spatial structure alone, two identical competitors can coexist in a region even if there is some local inhibition (Slatkin 1974; Hanski 1983). However, this requires doubly-occupied patches to send out the same number of colonists of both species (Taneyhill 2000), an assumption that gives an "unfair" advantage to the regionally rare species and even leads to logical inconsistencies (Wang *et al.* 2005). We list three more promising examples for possible buffering mechanisms. First, a predator that forages on a regional scale may either exhibit behavioral plasticity or evolve rapidly to preferentially prey on regionally common species (e.g., Hughes & Croy 1993). Second, if patches differ in environmental conditions, regionally rare species may be better at evolutionary monopolization of patches (Urban & De Meester 2009; De Meester *et al.* 2016) as they suffer less from the inflow of maladapted migrants (Lankau 2011). Finally, at a long evolutionary time scale, any factor that accelerates speciation rate would help to maintain a speciose regional pool. Speciation rate itself may be affected by local priority effects (Fukami *et al.* 2007). Interactive effects of speciation and priority effects on the generation and maintenance of species pools are a particularly interesting topic for future research.

Of course, empirical tests should accompany theoretical exploration of the mechanisms and conditions for eco-evolutionary buffering. Because of computational constraints, we were not able to explore the parts of parameter space directly relevant to microbes in our simulation. However, because many microbes have short generation times, they may be particularly amenable to experimental tests of the eco-evolutionary buffering hypothesis. In such an experiment, spatial conditions (number of patches, migration rate, disturbance and recolonization parameters) could be manipulated (e.g., Tucker & Fukami 2014; Pu & Jiang 2015). Other parameters, like the shape of the trade-off and the mutation parameters, could be measured in laboratory assays. One would then need to monitor regional frequencies over time and regularly assess the traits of the various species in sensitivity assays.

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Conclusions

We have shown that species engaged in local priority effects can coexist in a metacommunity if their sensitivity to heterospecific interference evolves rapidly, especially under a trade-off with competitive ability. Rapid evolution can lead to one globally attracting coexistence state, with local priority effect maintained at all times, or alternative attractors where species coexist regionally, but fluctuate around different frequencies, with local priority effects occurring only at times when both species are relatively common. The eco-evolutionary buffering hypothesis we have developed here provides the first mechanism, to our knowledge, that can maintain regional species diversity in the presence of local priority effects even under an internal species pool. By offering this new perspective on a phenomenon that has been difficult to explain, we hope this work will stimulate future research on eco-evolutionary buffering in metacommunities.

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Table 1: Model variables (capital letters) and parameters (small letters) and their default values or sampling distributions. $\ln\mathcal{N}$ stands for the log-normal distribution. $\lfloor\rceil$ denotes rounding to the nearest integer.

Parameter or variable	**Explanation**	**Default value/ distribution**
	Metacommunity level	
s	Number of species	2
n	Number of patches	$\ln\mathcal{N}(\ln(500), 0.5)$
m	Migration probability per birth event	Beta(1,1)
	Community level	
N_i	Number of individuals of species i in a local community	
k	Size of local communities	$\lfloor\ln\mathcal{N}(\ln(20), 0.5)\rceil$
τ	Average time between disturbance events	$\ln\mathcal{N}(\ln(50), 0.5)$
f	Founder population size	$\min(\lfloor\ln\mathcal{N}(\ln(5), 0.5)\rceil, k)$
	Individual level	
G	General sensitivity to competition, i.e. from conspecifics and heterospecifics	
G_j	Contribution to G due to resistance to species j	
H_j	Sensitivity to species j	
g_{min}	Minimum sensitivity to general competition	0.5
g_{max}	Maximum per-species contribution to sensitivity to general competition	0.5
h_{max}	Maximum sensitivity to another species	$\ln\mathcal{N}(\ln(10), 0.5)$
g_0	Initial value of the G_j	0.4
d	Standard deviation of mutation effect size (on the scale of G_j)	$\ln\mathcal{N}(\ln(0.032), 0.5)$
y	Trade-off shape parameter	1

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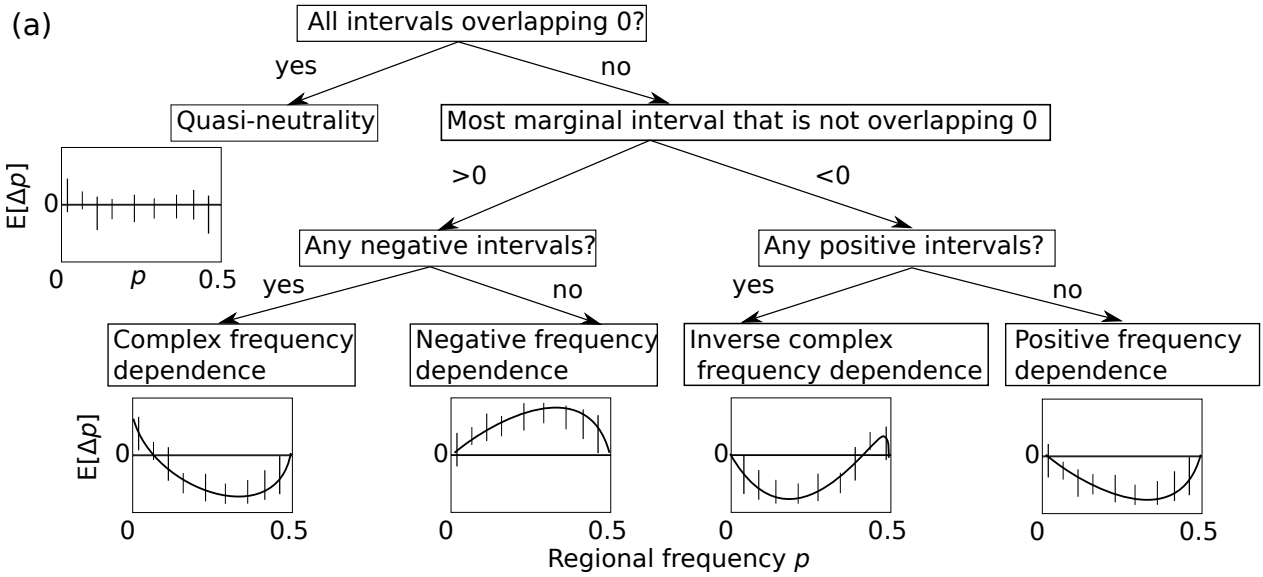

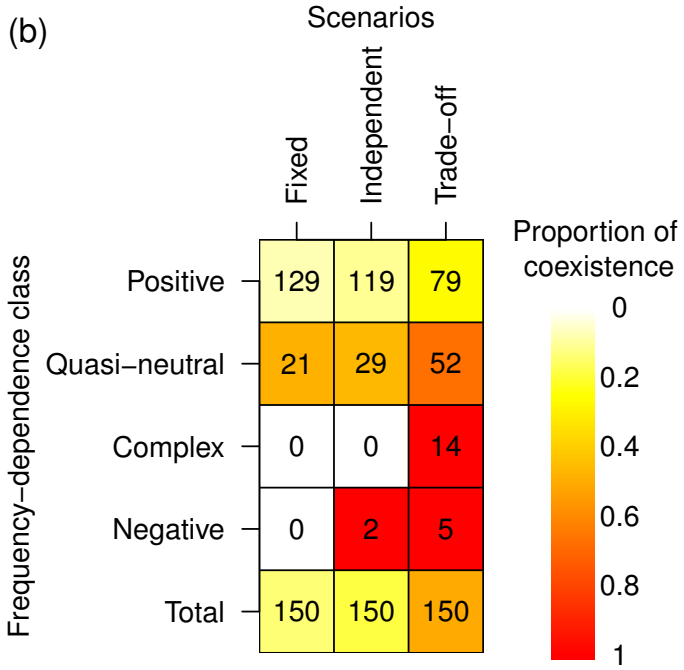

Figure 1: Classification of simulation runs. (a) Classification algorithm based on the intervals of mean regional frequency change ± 3.83 standard errors for the various frequency bins between 0 and 0.5 (see text). (b) Number of parameter combinations under fixed parameters, independent evolution, and trade-off evolution that were assigned to the different outcome classes, and the corresponding proportion of replicates in which both species coexisted until the end of the simulation. No parameter combination exhibited inverse complex frequency dependence.

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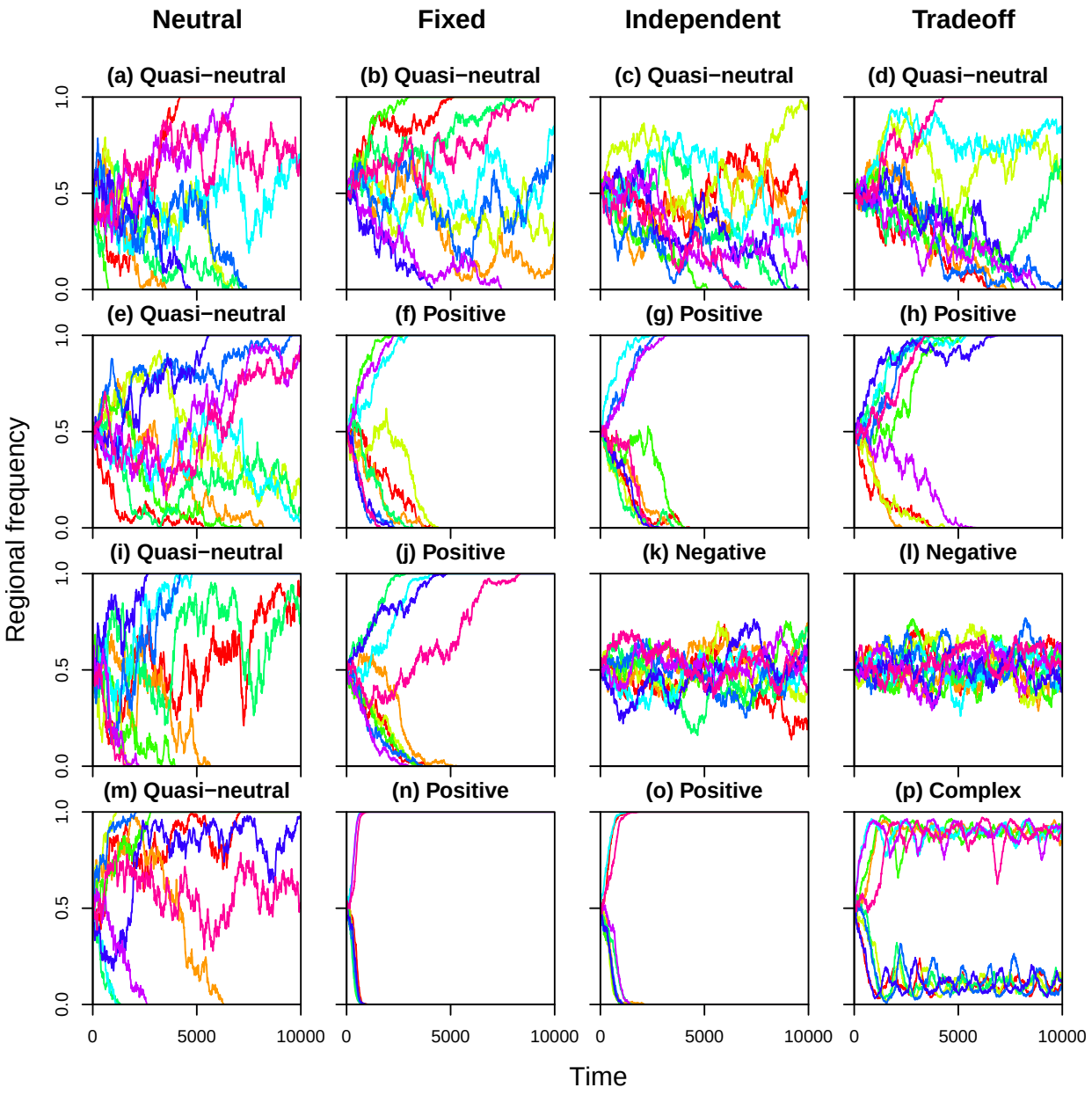

Figure 2: Regional frequency time series of a representative example for each outcome type. In each panel, each line represents one replicate simulation run ($n = 10$ runs). First row parameter values: $k = 32, n = 294, h_{max} = 13.212, d = 0.05 \cdot 2h_{max}, m = 0.161, \epsilon = 0.017, f = 4$, propagule-pool recolonization. Second row parameter values: $k = 60, n = 355, h_{max} = 14.55, d = 0.052 \cdot 2h_{max}, m = 0.897, \epsilon = 0.023, f = 5$, propagule-pool recolonization. Third row parameter values: $k = 6, n = 461, h_{max} = 11.287, d = 0.023 \cdot 2h_{max}, m = 0.101, \epsilon = 0.015, f = 6$, migrant-pool recolonization. Fourth row parameter values: $k = 13, n = 1379, h_{max} = 12.393, d = 0.054 \cdot 2h_{max}, m = 0.728, \epsilon = 0.012, f = 4$, propagule-pool recolonization. See Fig. S1 for the corresponding frequency-dependence plots, which are the basis for classification.

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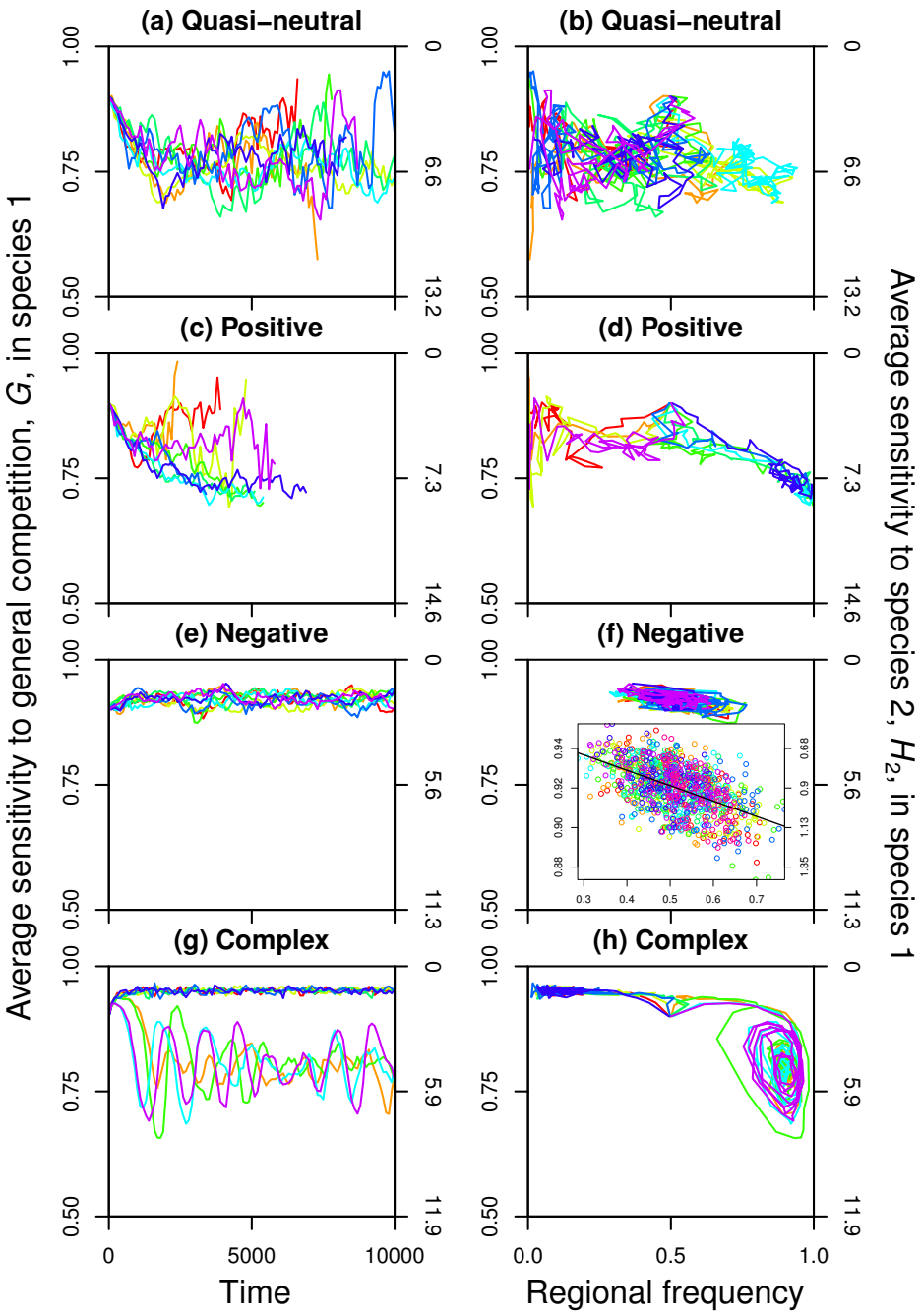

Figure 3: Time series of the average values of the evolving traits in the focal species (species 1, whose regional frequency is shown in Fig. 2) for the example scenarios from Fig. 2 under trade-off evolution. The inset in (f) zooms in on the response of G to regional frequency. The same colors are used for the corresponding replicates as in Fig. 2.

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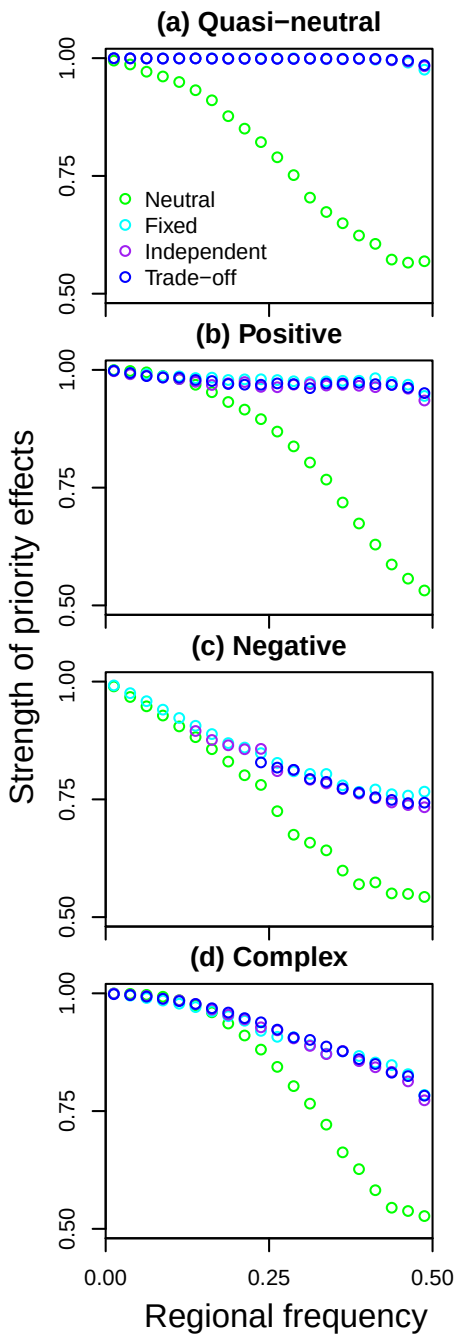

Figure 4: Strength of priority effects for the representative examples from Fig. 2, i.e. the probability that the locally dominant species directly after a disturbance event is also the dominant species before the next disturbance event. The x axis represents the regional frequency of the regionally rare species at the time of the disturbance event. The symbols for the trade-off scenario, the fixed-traits scenario, and the independent-evolution scenario often overlap. In some cases, coexistence is so stable that regional frequencies never reach very marginal values and therefore we do not have data on the strength of priority effects in this frequency range.

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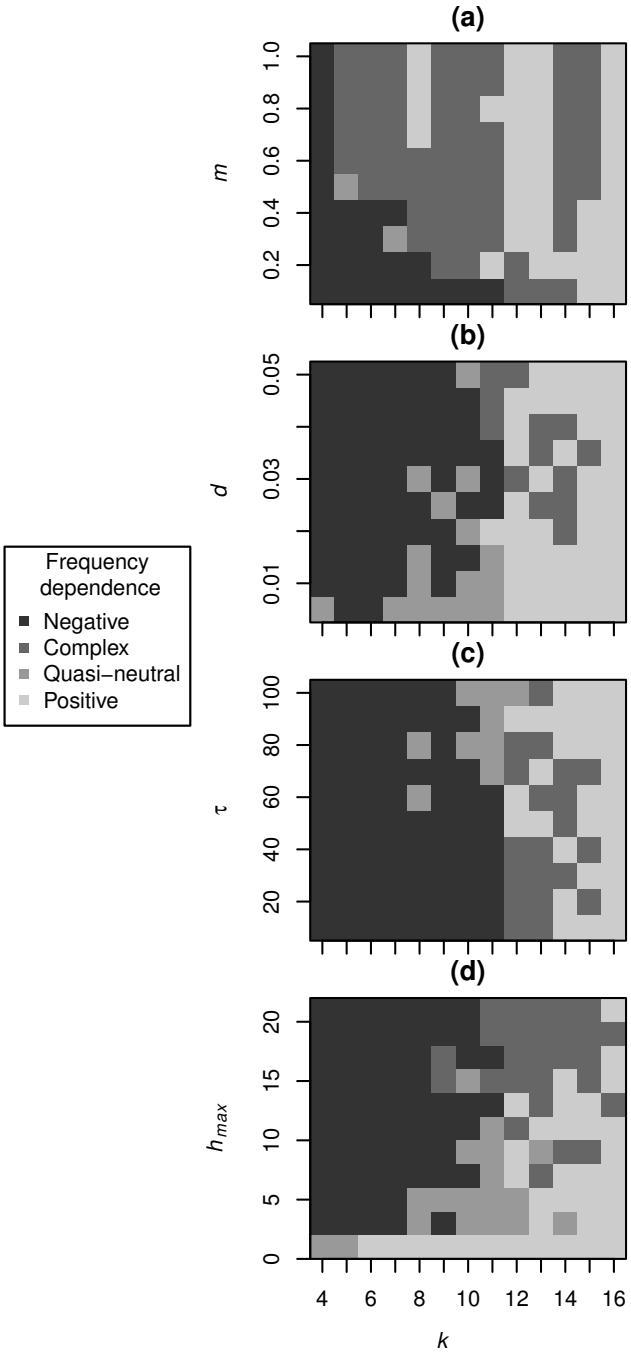

Figure 5: Effects of varying two parameters simultaneously while holding all other parameters constant at the values from Fig. 2 l. (a) Migration probability m and local community size k are varied, (b) mutational standard deviation d and k are varied, (c) average time between disturbances τ and k are varied, (d) maximum sensitivity to heterospecific interference h_{max} and k are varied.

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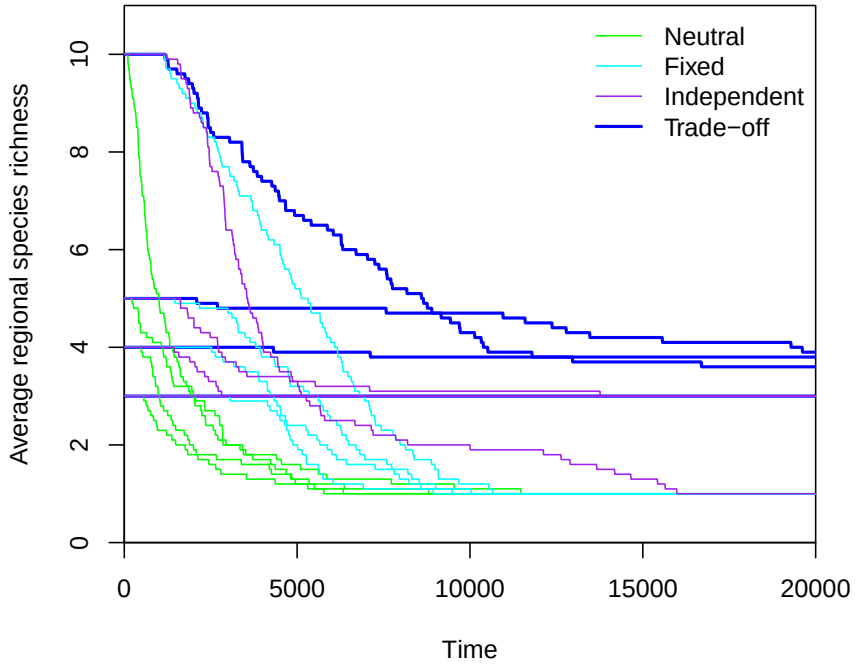

Figure 6: Time series of regional species richness for different initial numbers of species. Each point is the average over 10 replicate simulations. Parameters are the same as in the third row in Fig. 2.