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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, metacommunity, 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 and Wilsey 2012; Fukami and 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 and Pimm 1983; Lockwood et al. 1997; Morton and 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 and Schemske 2015). In other words, the regional pool is not external, but internal (*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. In their specific model, patches differ in the concentrations of two essential resources. Two species may then engage in priority effects in patches with relatively balanced resource composition while there is strict competitive exclusion of one or the other species in patches with more extreme resource composition. The extreme patches then serve as refuges from which species continue

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to disperse into patches where priority effects occur. In this sense, invoking spatial 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 and 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, Lankau (2009) and Vasseur et al. (2011) suggest that evolution along a trade-off between intra- and inter-specific competitive ability can prevent local extinction even when there is some positive frequency dependence, i.e. a common-species advantage. However, these studies did not consider coexistence at the metacommunity level.

Here we use a simple metacommunity model inspired by empirical examples of priority effects to determine whether rapid evolution can allow coexistence in metacommunities when species engage in local priority effects. Previous work that considered other types of spatial habitat structure (Vellend and Litrico 2008; Lankau 2009) calls into question whether rapid evolution can promote coexistence when there are multiple local communities that only occasionally exchange immigrants rather than one well-mixed community. Moreover, even if rapid evolution does promote coexistence in a metacommunity, it might also promote coexistence in local communities and thereby eliminate local priority effects altogether. Thus, it is far from obvious whether and how local priority effects and regional species coexistence can be maintained simultaneously. Our model is designed to generate hypotheses on this fundamental question.

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),

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another case of inhibitory priority effects via habitat modification. In plant communities, local positive feedbacks have been found to operate in some landscapes with interspersed patches of forest and heathland, mediated in this case by fire frequency and nutrient cycling (Petraitis and 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 and Ridenour 2004).

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). Inspired by these empirical examples, we built a simple metacommunity simulation model with priority effects via interspecific interference and evolution along trade-offs as key ingredients.

Model

Overview

Our simulation model is stochastic, individual-based, and considers a large number of patches. 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 (fig. 1, see also Table A1). In this model, local and regional dynamics are linked via migration and recolonization, making the species pool internal rather than external. If regional coexistence is not possible for two species, it is unlikely to be possible with more species. We therefore focus on metacommunities consisting of two species as a simplest case. 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. All species have the same dispersal ability. Our goal is to explore whether ecologically similar species engaging in local priority effects can coexist due to rapid evolution alone, that is in the absence of

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other coexistence mechanisms. We therefore assume that parameters are identical across patches. This means that there is no spatial environmental heterogeneity relevant to the coexistence of the species, although patches may differ in all other respects.

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, i.e., there is never any empty space in the patches. We assume patches are small enough for inhabitants to be affected by interference effects from 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 their individual level of competitive pressure, 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, with all trait values non-negative. A low value of G indicates a high general competitive ability (i.e., low mortality in a patch fully occupied by conspecifics), 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 having traits G and H_j

$$C = \underbrace{G \cdot k}_{\text{general competition}} + \sum_{j \neq i} \underbrace{H_j \cdot N_j}_{\text{interference from species } j}, \tag{1}$$

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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 within the same species may differ in G, H_j and consequently also C. Since C is smallest if all heterospecific abundances, N_j, are zero and increases with each N_j, interspecific competition is always stronger than intraspecific competition and coexistence would be impossible in a single homogeneous community with fixed species traits. Only in the extreme case where all H_j are zero, interspecific competition and interspecific competition would be equally strong. 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 interspecific sensitivities, H_j, and the general sensitivity to competition, G. For a specific member of species i:

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

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. In the main text, we focus on linear trade-offs ($y = 1$, fig. 1 b, but see Fig A6 for an exploration of nonlinear trade-offs).

To better understand the trade-off (fig. 1 b), let us consider the two extreme types for a given species (say species 1) sharing the landscape with one other species (species 2). On the one extreme, we have individuals of species 1 that are fully susceptible to heterospecific interference ($H_2 = h_{max}$) but have the smallest possible sensitivity to general competition, g_{min}. Those might be individuals that do not invest in costly resistance pathways and are thus better at competing for resources. Such individuals experience little competitive pressure when surrounded by conspecifics ($g_{min}k$, see (1)) and thus survive longer and produce on average more offspring, but they experience high competitive pressure when surrounded by heterospecifics ($g_{min}k + h_{max}(k-1)$). On the other extreme, we have species-1 individuals that are fully resistant to heterospecific interference ($H_2 = 0$) but at the cost of the highest possible general sensitivity to competition, $g_{min} + \Delta g$. As an illustration, they might invest a lot of energy into defenses, which makes them weak competitors for resources. The total competition experienced by such individuals does not depend on whether they are surrounded by conspecifics or heterospecifics, it is always $(g_{min} + \Delta g)k$. If $h_{max} > \Delta g$, which is fulfilled throughout this study, this is higher than what individuals at the other extreme experience in conspecific environments, but lower than what they experience in heterospecific environments. In other words, there is a trade-off between

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intraspecific and interspecific competitive ability.

Via mutations in individuals' traits, populations can evolve along the trade-off (fig. 1 b). Specifically, every new offspring experiences mutation, which adds a small, normally distributed increment with mean 0 and standard deviation d to the parent's value of G_j. If there are multiple interacting species, this is done independently for each of them. The values of H_j then follow from the trade-off equation. The parameter d can be interpreted as the sum over all relevant loci of effect size and mutation rate. If a trait overshoots the minimum or maximum possible value, it is set to the minimum or maximum (0 or Δg for the G_j, and 0 or h_{max} for the H_j). Note that even in cases where one extreme of the trade-off is optimal, mutations will prevent the population from becoming monomorphic and the average trait values will reflect a balance between selection pressure and mutations.

To investigate the metacommunity consequences of trait evolution and the trade-off between general sensitivity to competition and sensitivity to heterospecific interference, we compare the "trade-off evolution" scenario just described to three alternative 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, by default at the midpoint of the trade-off curve. Third, in the "independent evolution" scenario (evolution, but no trade-off), the G_j and H_j evolve independently. Mutations for H_j work exactly as described above for mutations in G_j, but the standard deviation of mutational steps is multiplied by $h_{max}/\Delta g$ to account for the different scale of the trait space. In the independent-evolution scenario, selection acts to reduce both the H_j and the G_j.

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 and 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 (fig. 1 c). 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

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of individuals elsewhere in the metacommunity. For the interplay between local and regional dynamics that is central to this study, it may be important where in the metacommunity the f recolonizing individuals originate. We therefore 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, such that they reflect the local species composition of one other patch. Under this model, a regionally rare species will often be absent among the initial colonizers of a patch but can sometimes be common. In the migrant-pool model, by contrast, the source patch is drawn independently for each of the f individuals such that the recolonizing individuals are more representative of the regional species composition. In the presence of local priority effects, migrant-pool recolonization should therefore benefit the regionally more common species.

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, see fig. 1) by drawing independently from the distributions given in Table A1. 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 A1.

In choosing these parameter ranges, we kept in mind both computational efficiency and biological relevance. Because individual-based simulations are computationally intensive, we were limited to simulating metacommunities with on the order of 10,000 individuals. Given this constraint, we decided to focus on metacommunities with hundreds of small patches rather than metacommunities with few larger patches. With our parameter choice, we expect fast and highly stochastic dynamics at the local scale, compared to slower and more deterministic dynamics at the regional scale. Also, we chose relatively frequent migration to ensure that evolution should occur at the regional scale rather than at the local scale (Lenormand 2002). We want to avoid evolution at the local scale because it might lead to local coexistence and thereby eliminate priority effects. In summary, our metacommunity set-up should be conducive to achieving both regional

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coexistence and local priority effects, if this is possible at all. Metacommunities of herbaceous plants or sessile aquatic animals might be the best empirical examples for metacommunities in this parameter range (see also Mouquet and Loreau 2002; Fukami and Nakajima 2013; Zee and Fukami 2015). However, as we discuss below, some of our results may also apply to other types of metacommunities and even 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).

Code and scripts

We provide C++ code for the simulation program in Online Appendix B, and R scripts to initiate and analyze the simulation studies in Online Appendix C.

Results

Probability of coexistence and outcome types

For a first impression of whether regional coexistence of two species is stable, we considered the proportion of replicate metacommunities that still contained both species at the end of a simulation run. 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, 9, and 18 % of the cases in the neutral, fixed-trait, and independent-evolution scenarios, respectively (fig. 2).

In some cases where species coexisted until the end of the simulation, 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. To determine whether or not this is the case in our simulations, we computed average changes in regional frequency for various frequency ranges. Based on these results, we then assigned a parameter combination to one of four frequency-dependence classes (see fig. 2, Online Appendix A.1). Under positive frequency-dependence, regionally more common species have an advantage and regionally rare species are expected to become even more rare and eventually go extinct. Such parameter combinations do not allow

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for regional coexistence. Under negative-frequency dependence, by contrast, regionally rare species have an advantage and are expected to become more common again. Coexistence at intermediate frequencies is expected. Under complex frequency-dependence, very rare species have an advantage and are expected to increase in regional frequency, but moderately rare species are at a disadvantage. Therefore, we do expect coexistence, but in an asymmetric fashion where one species is relatively rare in the landscape and the other common. Finally, we assigned parameter combinations without clear frequency dependence to the quasi-neutrality class. In this class, we do not expect long-term coexistence because one or the other species will drift to extinction. Because we did not want to erroneously conclude that regional coexistence is possible when it is not, we were very conservative in assigning scenarios to one of the "interesting" classes and assigned many scenarios to the quasi-neutral class even if they showed a slight tendency for rare species to become more common again and diversity to be maintained for longer than under strict neutrality.

Under fixed traits or independent evolution, some parameter combinations were classified as quasi-neutral, but most fell into the positive frequency dependence class (fig. 2). That is, the regionally rare species tended to become even rarer and eventually dropped out of the metacommunity. The results on frequency-dependence and coexistence were qualitatively robust with respect to the point along the trade-off to which the traits were fixed (fig. A7). With increasing general sensitivity to competition, coexistence and quasi-neutrality became only slightly more common. 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.

As expected, 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. 2). Parameter combinations that were classified as quasi-neutral under trade-off evolution had a substantially larger coexistence probability than quasi-neutral parameter combinations in the fixed-trait or independent-evolution. This indicates that our conservative classification scheme may indeed have classified many scenarios as quasi-neutral that do have some tendency to maintain diversity.

For each of the four outcome classes that occurred under trade-off evolution, fig. 3 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 fre-

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quency dependence was symmetric, with both species at regional frequencies around 0.5 (fig. 3 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 in the region than the other (fig. 3 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. 4 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. 4 a–d). However, common species tended to be more sensitive to interspecific interference (fig. 4 f). In the corresponding independent evolution scenario, both G and H_j were low at equilibrium but still responded weakly to regional frequency (fig. A3). Under complex frequency dependence (fig. 4 g,h), regionally rare species remained relatively resistant to the other species (low H_j), whereas 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. 4 g,h).

Strength of priority effects

To quantify priority effects, we explored how often the most abundant species among the initial colonists of a newly disturbed patch retained its dominant status over time. Specifically, we took all intervals between local disturbance events for all the patches in a simulation run and computed the proportion of such intervals for which the same species was locally most common both at the beginning and at the end of the interval. This proportion 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 make the results comparable across scenarios, we therefore controlled for regional frequency. For this, we used regional frequency bins of size 0.025 and computed the strength of priority effects separately for each bin. We performed the same analyses for the corresponding neutral scenario. If the resulting value for a certain frequency range is larger than in neutral scenario, we take this as evidence for inhibitory priority effects.

We found that local priority effects under trade-off evolution were generally stronger than in the corresponding neutral simulations, at least while both species had a regional frequency of 20 % or more (gray regions in fig. 3, see also fig. A4). However, when one species dominated

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the metacommunity, priority effects were often nearly identical or slightly weaker in strength compared to those in the neutral scenario (white regions in fig. 3, left side of fig. A4 d). 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 (fig. A4 a–d). In the long run, however, priority effects were visible only in scenarios with evolution and negative or complex frequency dependence (e.g., fig. 3 l,p). In the remaining cases, priority effects eventually disappeared along with species diversity (e.g., fig. 3 g,h).

Sensitivity to individual parameters

To better understand how the joint maintenance of regional diversity and local priority effects arises and how it depends on the model parameters, we focused on one scenario with negative-frequency dependence (fig. 3 l) and ran additional simulations varying two parameters systematically at a time while keeping the other parameters constant. Here we ran 50 replicates per parameter combination.

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. 5 d). The average time between disturbance events, τ, did not have a strong effect on the distribution of outcome types (fig. 5 c). The region of parameter space with stable coexistence grew slightly with increasing convexity of the trade-off (fig. A6).

For additional information on the role of the various parameters, we also considered their distributions among the outcome classes in the random parameter study. For k and m, the results are consistent with those described in the previous paragraph, but not for d and τ (fig. A5), indicating that these parameters may have opposing effects for different combinations of the other parameters. We also found that 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. A5 h). This finding is consistent with our expectation that migrant-pool recolonization is beneficial for the regionally common species.

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More than two species

For two parameter combinations with clear regional coexistence, we additionally ran simulations with 3, 4, 5, and 10 species, this time for 20,000 generations. Under a parameter combination with negative frequency dependence (third row in fig. 3), 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 when controlling for regional community composition as measured by Simpson's diversity index (fig. A9). The slightly more complex outcomes in a parameter combination with complex frequency-dependence (last row in fig. 3) are explored in Online Appendix A.4.

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 (e.g., cycles in fig. 4). Exploiting this loss of tolerance, other species recover in abundance.

Previous studies have explored similar coexistence mechanisms in a single local community, rather than in a metacommunity (Levin 1971; León 1974; Pease 1984; Vasseur et al. 2011). Here we have shown that such coexistence is also possible in metacommunities consisting of many small patches and in the face of demographic and genetic stochasticity, important factors especially in the recovery of rare species. Moreover, while previous studies have focused on two-species systems, our results show that eco-evolutionary buffering can stabilize a regional pool of at least up to four species (fig. 6). Most importantly, however, we have shown that even if metacommunities evolve toward traits that allow for regional coexistence, local coexistence does not necessarily follow. Neither is one species competitively superior at any time. Rather strong local priority effects are often maintained (figs. A4 and A9). Thus our new hypothesis can explain how multi-

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ple 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 and requirements of eco-evolutionary buffering

Our results indicate that eco-evolutionary buffering can result in either negative frequency dependence where the regionally rare species is always favored and coexistence is symmetric, or complex regional frequency dependence where only very rare species have an advantage and coexistence is generally asymmetric (fig. 2). Negative frequency dependence is particularly likely when local patches are small and when they are connected by infrequent migration (figs. 5 and A5). Under these conditions, a small evolutionary response seems sufficient to stabilize regional coexistence (fig. 4 e,f). In Online Appendix A.5, we offer a detailed heuristic explanation for this observation. 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 the balance between mutations and selection, is apparently 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 slight shift in mutation-selection balance does not appear to be sufficient to give an advantage to regionally rare species. We speculate that 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. 2). 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 and using our conservative classification scheme.

Under many of the parameter combinations leading to complex frequency dependence, regional frequencies oscillate (see, e.g., fig. 3 p). 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 common species has an advantage. Under negative frequency dependence, how-

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ever, local priority effects can be strong while at the same time regionally rare species have an advantage. We propose 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 might benefit from priority effects when it is substantially more common locally, but in patches where multiple species have a similar local frequency, regionally rare species might 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. A11 and Online Appendix A.5 for more detail).

Based on our explorations of the parameter space (figs. 5 and A5, see Online Appendix A.3 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. The requirements for eco-evolutionary buffering by complex frequency dependence are less restrictive and may be fulfilled even in some microbial communities. Although spatial heterogeneity is obviously common in natural systems, often a large number of species coexists in a landscape with surprisingly homogeneous environmental conditions (e.g., Sogin et al. 2006), and eco-evolutionary buffering may contribute to explaining such observations.

Future directions

This study is only a proof of concept, 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 for parameters relevant to microbial systems, 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 conspecifics that 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.

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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 and Croy 1993). Second, if patches differ in environmental conditions, regionally rare species may be better at evolutionary monopolization of patches (Urban and 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 and Fukami 2014; Pu and 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.

Conclusion

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 effects maintained at all times, or alternative attractors where species coexist regionally, but fluctuate around different frequencies, with local priority effects occurring only at

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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.

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References

Bais, H. P., R. Vepachedu, S. Gilroy, R. M. Callaway, and J. M. Vivanco. 2003. Allelopathy and exotic plant invasion: From molecules and genes to species interactions. Science 301:1377–1380.

Baquero, F., T. M. Coque, and F. de la Cruz. 2011. Ecology and evolution as targets: the need for novel eco-evo drugs and strategies to fight antibiotic resistance. Antimicrobial Agents and Chemotherapy 55:3649–3660.

Callaway, R., and W. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436–443.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia 136:489–498.

———. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328:1388–1391.

De Meester, L., J. Vanoverbeke, L. J. Kilsdonk, and M. C. Urban. 2016. Evolving perspectives on monopolization and priority effects. Trends in Ecology & Evolution 31:136–146.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. The American Naturalist 137:1–26.

bioRxiv preprint doi: https://doi.org/10.1101/040659; this version posted June 3, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder. All rights reserved. No reuse allowed without permission.

Fukami, T. 2005. Integrating internal and external dispersal in metacommunity assembly: preliminary theoretical analyses. Ecological Research 20:623–631.

———. 2015. Historical contingency in community assembly: Integrating niches, species pools, and priority effects. Annual Review of Ecology Evolution and Systematics 46:1–23.

Fukami, T., H. J. E. Beaumont, X.-X. Zhang, and P. B. Rainey. 2007. Immigration history controls diversification in experimental adaptive radiation. Nature 446:436–439.

Fukami, T., and M. Nakajima. 2013. Complex plant-soil interactions enhance plant species diversity by delaying community convergence. Journal of Ecology 101:316–324.

Gagneux, S., C. D. Long, P. M. Small, T. Van, G. K. Schoolnik, and B. J. M. Bohannan. 2006. The competitive cost of antibiotic resistance in *Mycobacterium tuberculosis*. Science 312:1944–1946.

Hairston, N. G., S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters 8:1114–1127.

Hanski, I. 1983. Coexistence of competitors in patchy environment. Ecology 64:493–500.

Hughes, R., and M. Croy. 1993. An experimental analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. Journal of Animal Ecology 62:341–352.

Knope, M. L., S. E. Forde, and T. Fukami. 2012. Evolutionary history, immigration history, and the extent of diversification in community assembly. Frontiers in Microbiology 2:273.

Knowlton, N. 2004. Multiple "stable" states and the conservation of marine ecosystems. Progress in Oceanography 60:387–396.

Lankau, R. 2008. A chemical trait creates a genetic trade-off between intra- and interspecific competitive ability. Ecology 89:1181–1187.

Lankau, R. A. 2009. Genetic variation promotes long-term coexistence of *Brassica nigra* and its competitors. The American Naturalist 174:E40–E53.

———. 2011. Rapid evolutionary change and the coexistence of species. Annual Review of Ecology Evolution and Systematics 42:335–354.

Lankau, R. A., V. Nuzzo, G. Spyreas, and A. S. Davis. 2009. Evolutionary limits ameliorate the negative impact of an invasive plant. Proceedings of the National Academy of Sciences 106:15362–15367.

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Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends in Ecology & Evolution 17:183–189.

León, J. A. 1974. Selection in contexts of interspecific competition. The American Naturalist 108:739–757.

Levin, B. R. 1971. Operation of selection in situations of interspecific competition. Evolution 25:249–264.

Lockwood, J. L., R. D. Powell, M. P. Nott, and S. L. Pimm. 1997. Assembling ecological communities in time and space. Oikos 80:549–553.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, USA.

Martin, L. M., and B. J. Wilsey. 2012. Assembly history alters alpha and beta diversity, exotic-native proportions and functioning of restored prairie plant communities. Journal of Applied Ecology 49:1436–1445.

Mittelbach, G. G., and D. W. Schemske. 2015. Ecological and evolutionary perspectives on community assembly. Trends in Ecology & Evolution 30:241–247.

Molofsky, J., and J. D. Bever. 2002. A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. Proceedings of the Royal Society B-Biological Sciences 269:2389–2393.

Molofsky, J., J. D. Bever, and J. Antonovics. 2001. Coexistence under positive frequency dependence. Proceedings of the Royal Society B-Biological Sciences 268:273–277.

Molofsky, J., R. Durrett, J. Dushoff, D. Griffeath, and S. Levin. 1999. Local frequency dependence and global coexistence. Theoretical Population Biology 55:270–282.

Morton, R. D., and R. Law. 1997. Regional species pools and the assembly of local ecological communities. Journal of Theoretical Biology 187:321–331.

Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: The regional similarity hypothesis. The American Naturalist 159:420–426.

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Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology 98:96–105.

Pál, C., B. Papp, and V. Lázár. 2015. Collateral sensitivity of antibiotic-resistant microbes. Trends in Microbiology 23:401–407.

Palumbi, S. R. 2001. Humans as the world's greatest evolutionary force. Science 293:1786–1790.

Pease, C. M. 1984. On the evolutionary reversal of competitive dominance. Evolution 38:1099–1115.

Peay, K. G., M. Belisle, and T. Fukami. 2012. Phylogenetic relatedness predicts priority effects in nectar yeast communities. Proceedings of the Royal Society B-Biological Sciences 279:749–758.

Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points. The American Naturalist 124:127–133.

Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. Ecology 80:429–442.

Post, W. M., and S. L. Pimm. 1983. Community assembly and food web stability. Mathematical Biosciences 64:169–192.

Pu, Z., and L. Jiang. 2015. Dispersal among local communities does not reduce historical contingencies during metacommunity assembly. Oikos 124:1327–1336.

Riley, M. A. 1998. Molecular mechanisms of bacteriocin evolution. Annual Review of Genetics 32:255–278.

Schoener, T. W. 2011. The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. Science 331:426–429.

Shurin, J., P. Amarasekare, J. Chase, R. Holt, M. Hoopes, and M. Leibold. 2004. Alternative stable states and regional community structure. Journal of Theoretical Biology 227:359–368.

Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128–134.

———. 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. Theoretical Population Biology 12:253–262.

Sogin, M. L., H. G. Morrison, J. A. Huber, D. M. Welch, S. M. Huse, P. R. Neal, J. M. Arrieta, and G. J. Herndl. 2006. Microbial diversity in the deep sea and the underexplored "rare biosphere". Proceedings of the National Academy of Sciences 103:12115–12120.

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Sutherland, J. P. 1974. Multiple stable points in natural communities. The American Naturalist 108:859–873.

Taneyhill, D. E. 2000. Metapopulation dynamics of multiple species: The geometry of competition in a fragmented habitat. Ecological Monographs 70:495–516.

Thompson, J. N. 1998. Rapid evolution as an ecological process. Trends in Ecology & Evolution 13:329–332.

Tucker, C. M., and T. Fukami. 2014. Environmental variability counteracts priority effects to facilitate species coexistence: evidence from nectar microbes. Proceedings of the Royal Society B-Biological Sciences 281:20132637.

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 276:4129–4138.

Vannette, R. L., M.-P. L. Gauthier, and T. Fukami. 2013. Nectar bacteria, but not yeast, weaken a plant–pollinator mutualism. Proceedings of the Royal Society B-Biological Sciences 280:20122601.

Vasseur, D. A., P. Amarasekare, V. H. W. Rudolf, and J. M. Levine. 2011. Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. The American Naturalist 178:E96–E109.

Vellend, M., and I. Litrico. 2008. Sex and space destabilize intransitive competition within and between species. Proceedings of the Royal Society B-Biological Sciences 275:1857–1864.

Wang, Z.-L., D.-Y. Zhang, and G. Wang. 2005. Does spatial structure facilitate coexistence of identical competitors? Ecological Modelling 181:17–23.

Zee, P. C., and T. Fukami. 2015. Complex organism–environment feedbacks buffer species diversity against habitat fragmentation. Ecography 38:370–379.

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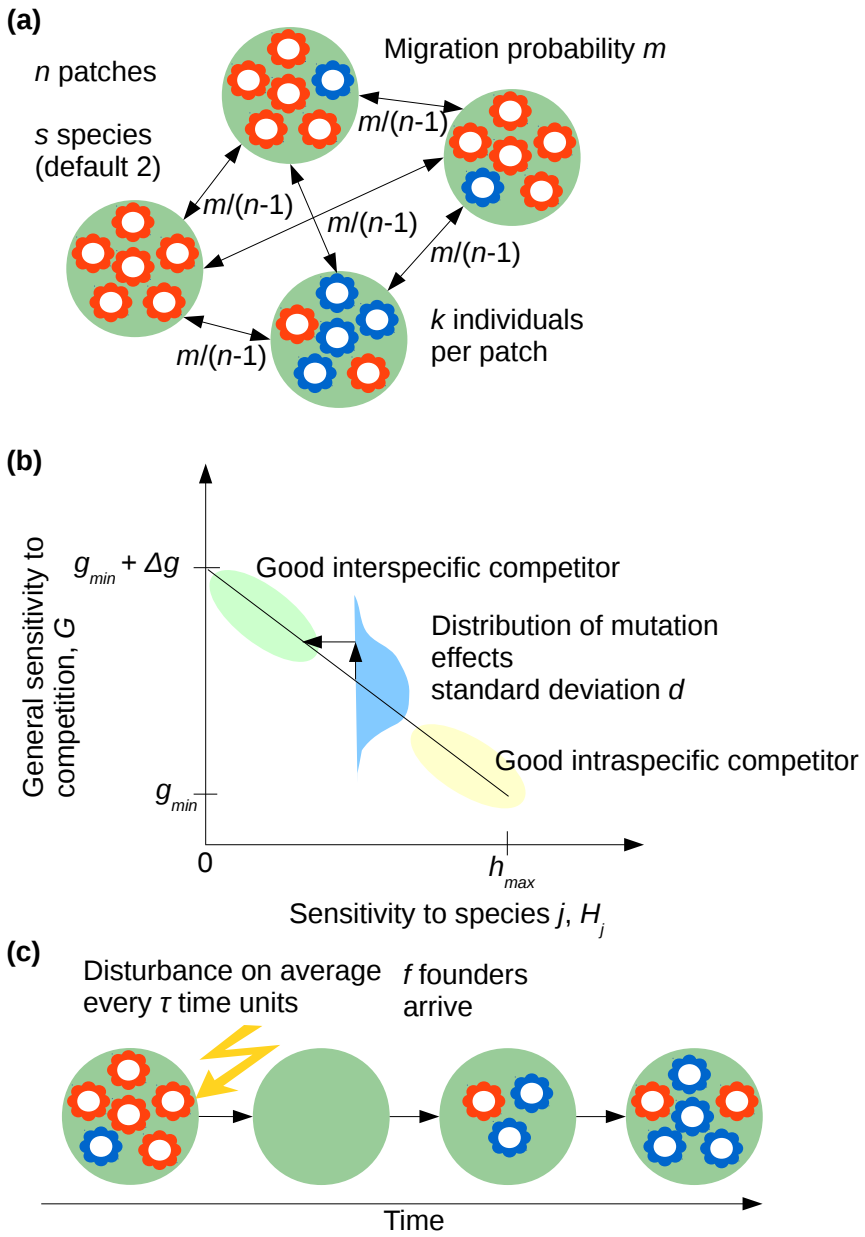

Figure 1: Illustration of the metacommunity model with its key parameters and processes. (a) Landscape set-up. In the actual simulations, the number of patches is on the order of hundreds. (b) Trade-off between individual competitive traits and mutation process. It is assumed here that there are just two species such that $G = g_{min} + G_j$. (c) Patch disturbance and recolonization. See Table A1 for sampling distributions for the various parameters in our simulation experiments.

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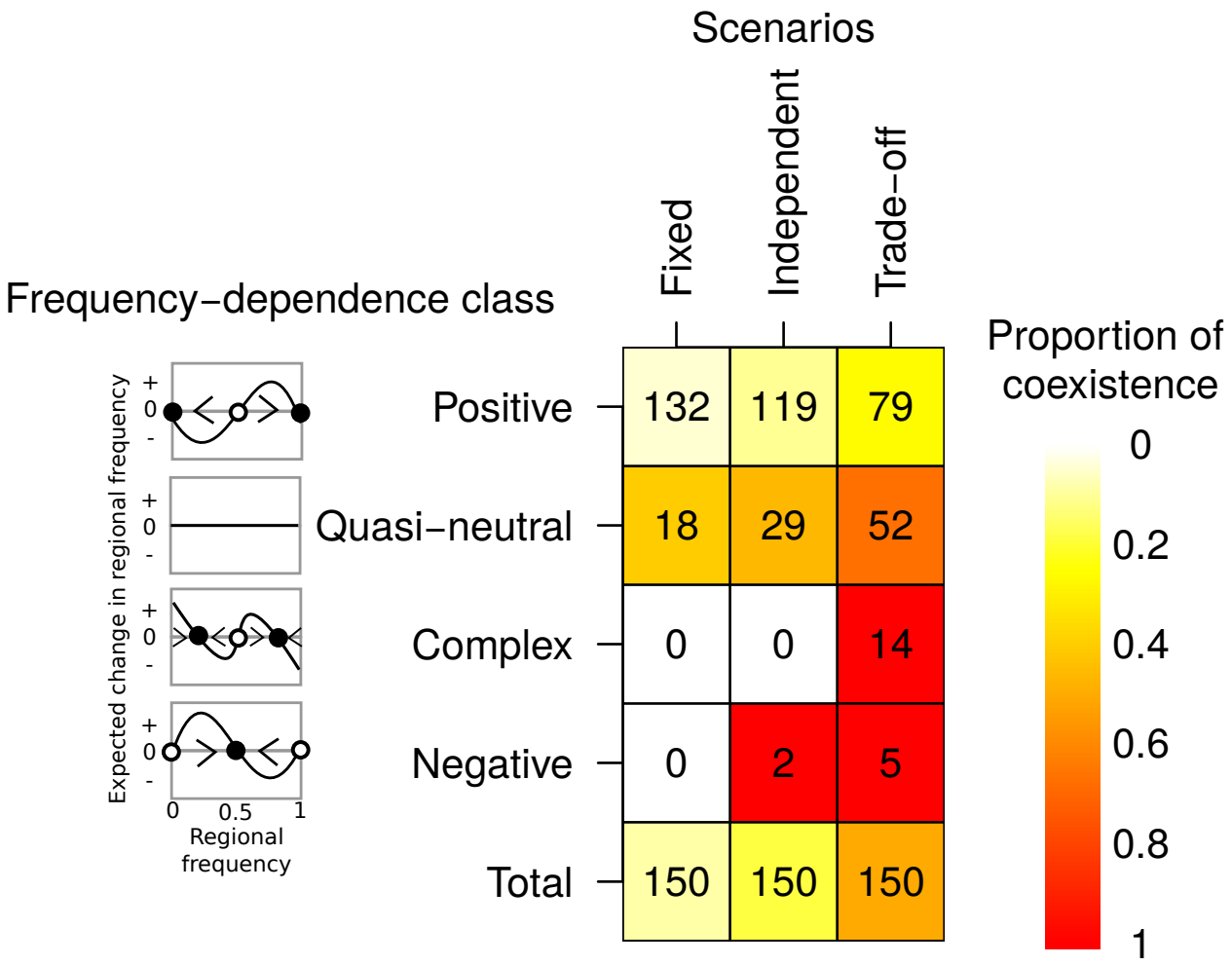

Figure 2: Number of parameter combinations under fixed parameters, independent evolution, and trade-off evolution that were assigned to the different regional frequency classes, and the corresponding proportion of replicates in which both species coexisted until the end of the simulation. The frequency-dependence cartoons depict the average change in the regional frequency of a focal species in various frequency ranges between 0 and 1. Filled circles indicate what would be stable equilibria in a deterministic system, and open circles denote unstable equilibria. Arrows indicate the expected direction of change. See Online Appendix A.1 for more detail on the classification of regional frequency dependence.

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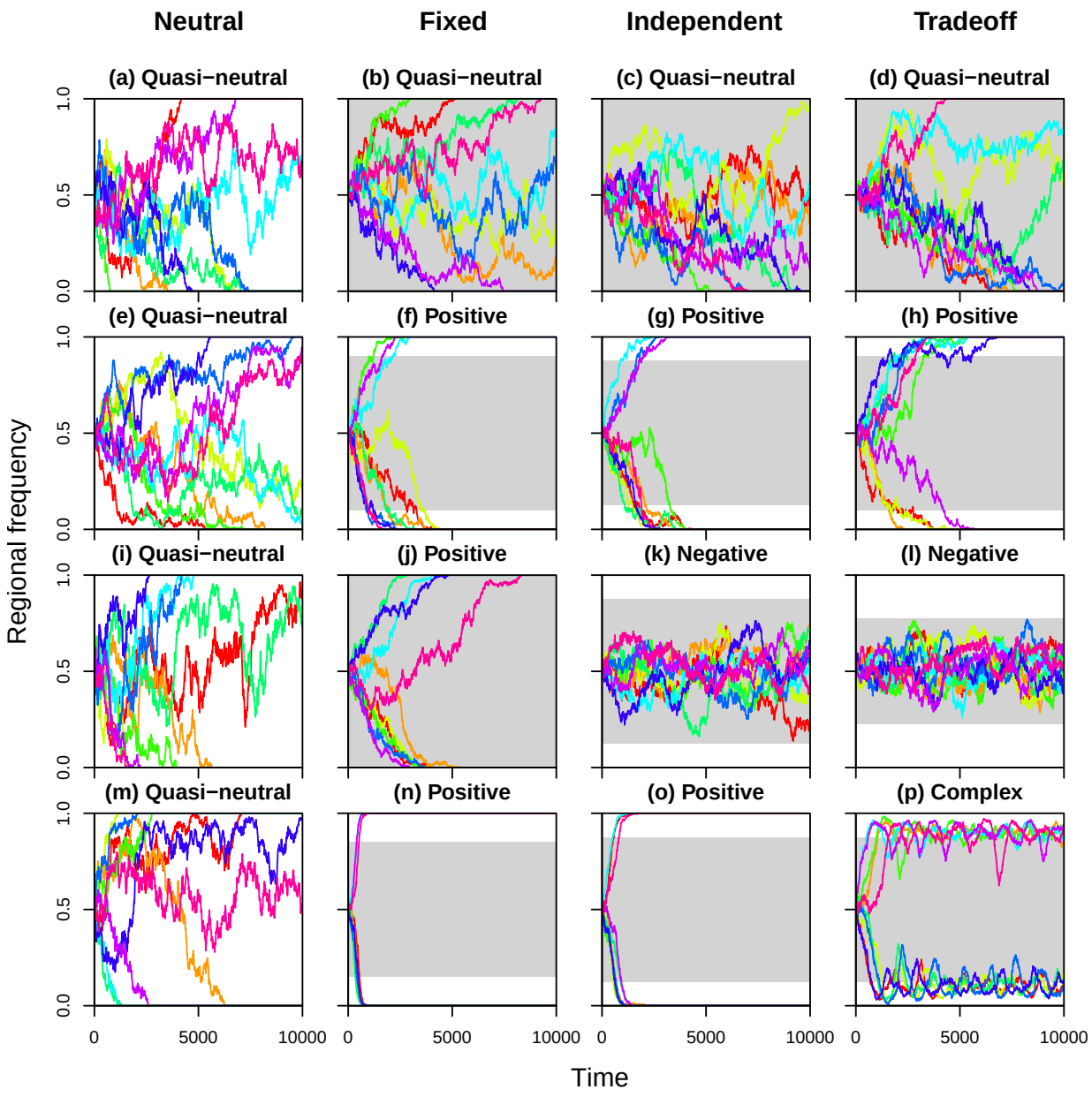

Figure 3: Regional frequency time series of a representative example for each outcome type. In each panel, each line represents one of the ten replicate simulation run. Regional frequency ranges for which priority effects are stronger than in the corresponding neutral scenario, i.e. where the initially dominant species after a recolonization is more likely to remain dominant than under neutrality, are highlighted in gray (see fig. A4 for more detailed information). *Legend continues on next page.*

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Fig. 3 legend continued: Note that in (k) and (l), we do not have information on the strength of priority effects at extreme frequencies because they were not represented in the simulation runs, but for all frequency ranges represented, priority effects were stronger than under neutrality. 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. A2 for the corresponding frequency-dependence plots, which are the basis for classification.

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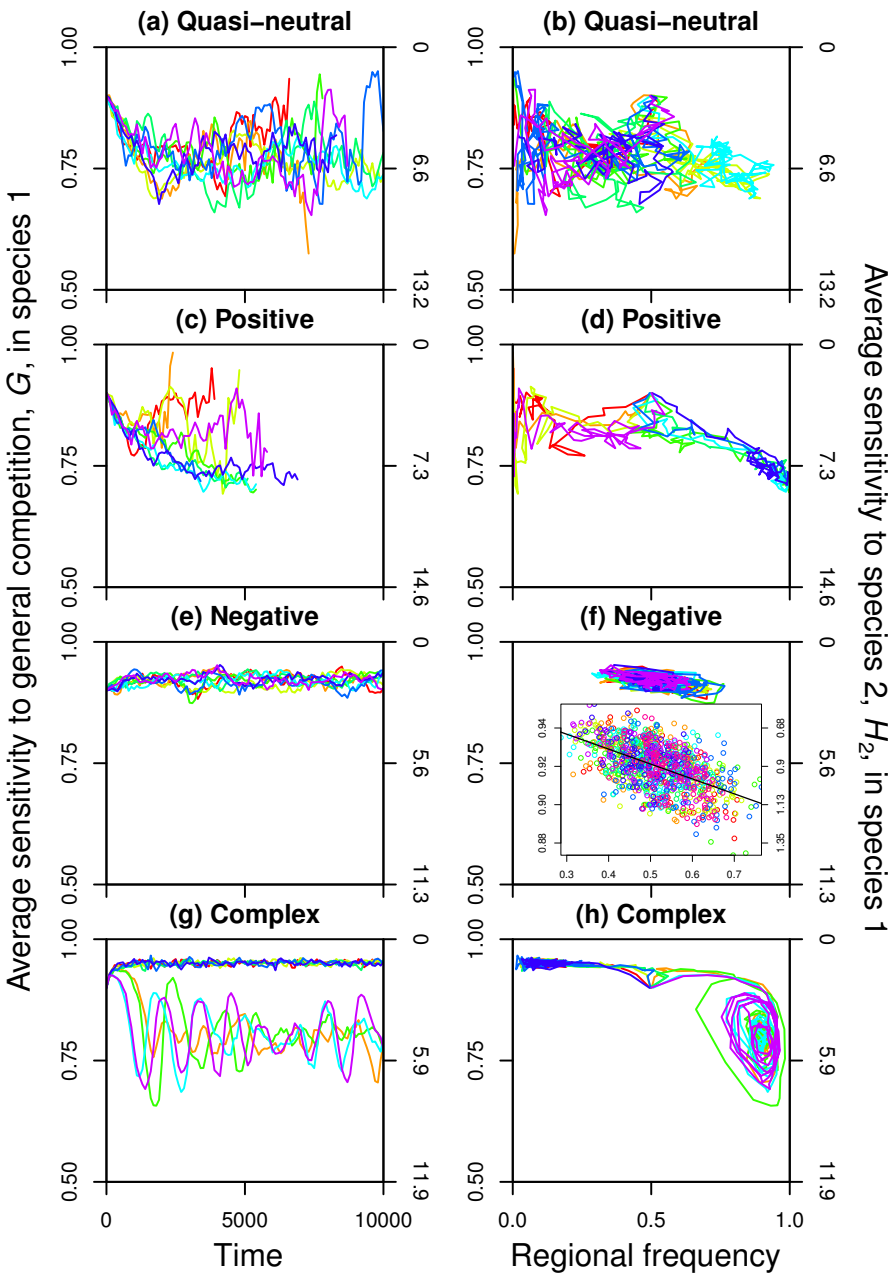

Figure 4: Time series of the average values of the evolving traits in the focal species (species 1, whose regional frequency is shown in fig. 3) for the example scenarios from fig. 3 under trade-off evolution. The inset in (f) zooms in on the response of G to regional frequency. The same colors are used for the corresponding replicates as in fig. 3. In (g), the upper, less variable lines correspond to replicates where species 1 is the regionally rare species, whereas the lower, more variable lines correspond to replicates where it is the regionally common species.

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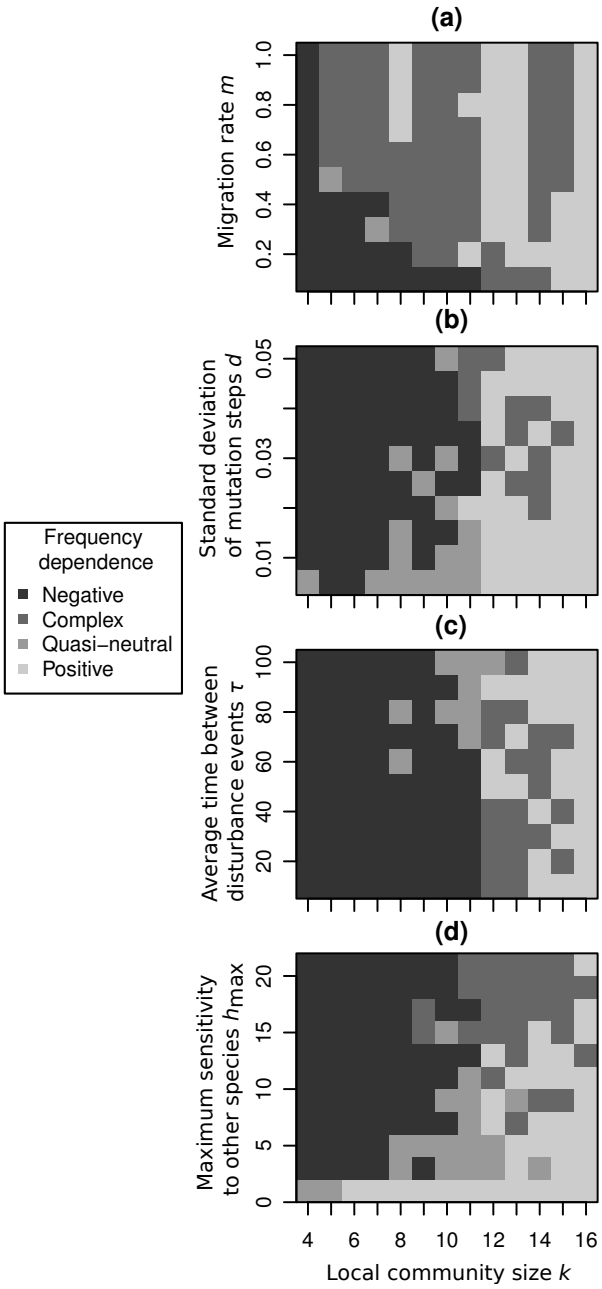

Figure 5: Effects of varying two parameters simultaneously while holding all other parameters constant at the values from fig. 3 l. (a) Migration probability m and local community size k are varied, (b) mutational standard deviation d and k are varied, (c) average time between disturbances τ and k are varied, (d) maximum sensitivity to heterospecific interference h_{max} and k are varied.

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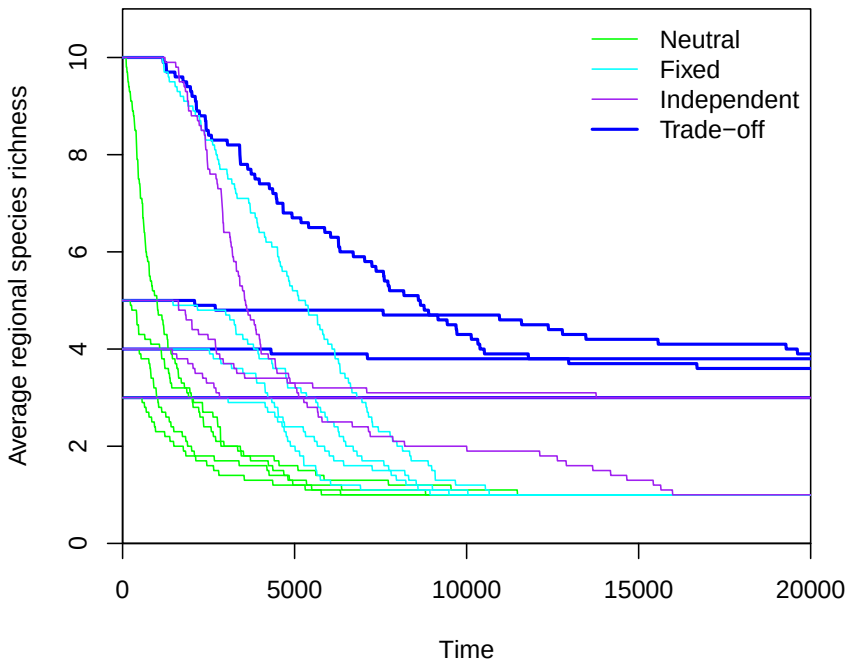

Figure 6: Time series of regional species richness for different initial numbers of species. Each point is the average over 10 replicate simulations. Parameters are the same as in the third row in fig. 3.

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Online Appendix A: Supplementary methods and results

Table A1: Model variables (capital letters) and parameters (small letters) and their default values or sampling distributions.

Parameter or variable	**Explanation**	**Default value/distribution**[a]
	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
Δg	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[b]
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

[a] $\ln\mathcal{N}$ stands for the log-normal distribution. $\lfloor\rceil$ denotes rounding to the nearest integer. [b] 0.25 in the fixed-parameter scenario.

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Online Appendix A.1 Classification of regional frequency dependence

To assess regional frequency dependence, 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. A1). If all intervals overlapped with zero, we assigned the scenario to the "quasi-neutral" class. After confirming independently that our neutral simulations indeed 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.

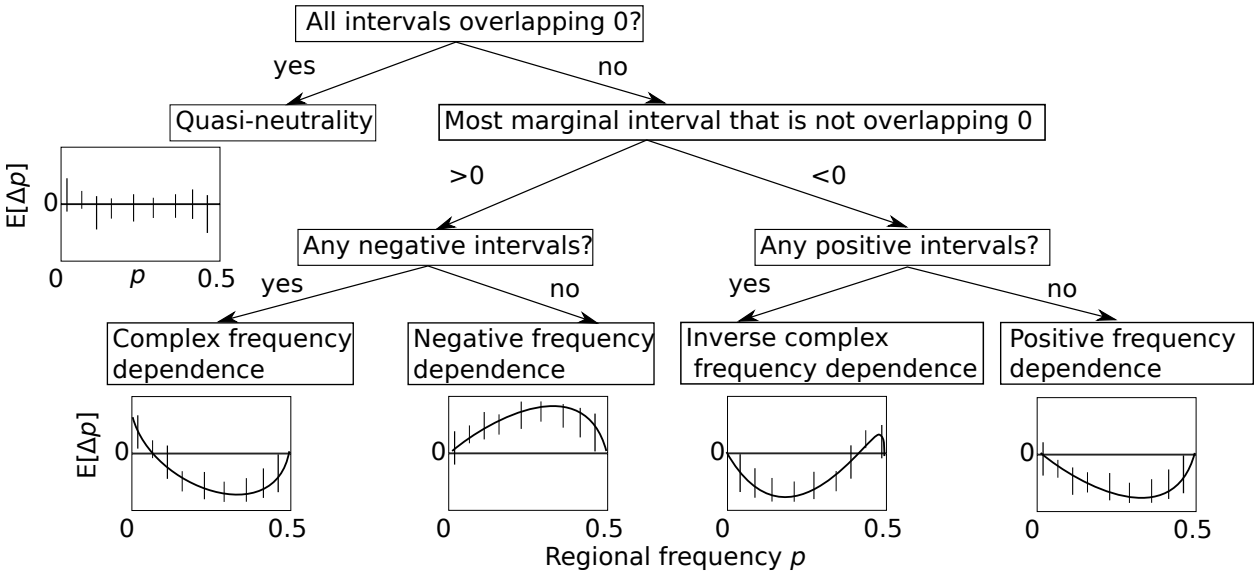

Figure A1: Classification algorithm based on the intervals of average regional frequency change, $\mathbf{E}[\Delta p], \pm$ 3.83 standard errors for various regional species frequencies. Since our model is symmetric, we only need to consider the regional frequency of the species that is currently less frequent in the metacommunity, i.e. we consider only regional frequencies between 0 and 0.5.

For scenarios that were not classified as quasi-neutral, we considered the most marginal frequency bin whose interval was not overlapping with zero (fig. A1). 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 nega-

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tive 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. A1). 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. However, no parameter combination in our study exhibited inverse complex frequency dependence.

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Online Appendix A.2 Additional results for two species

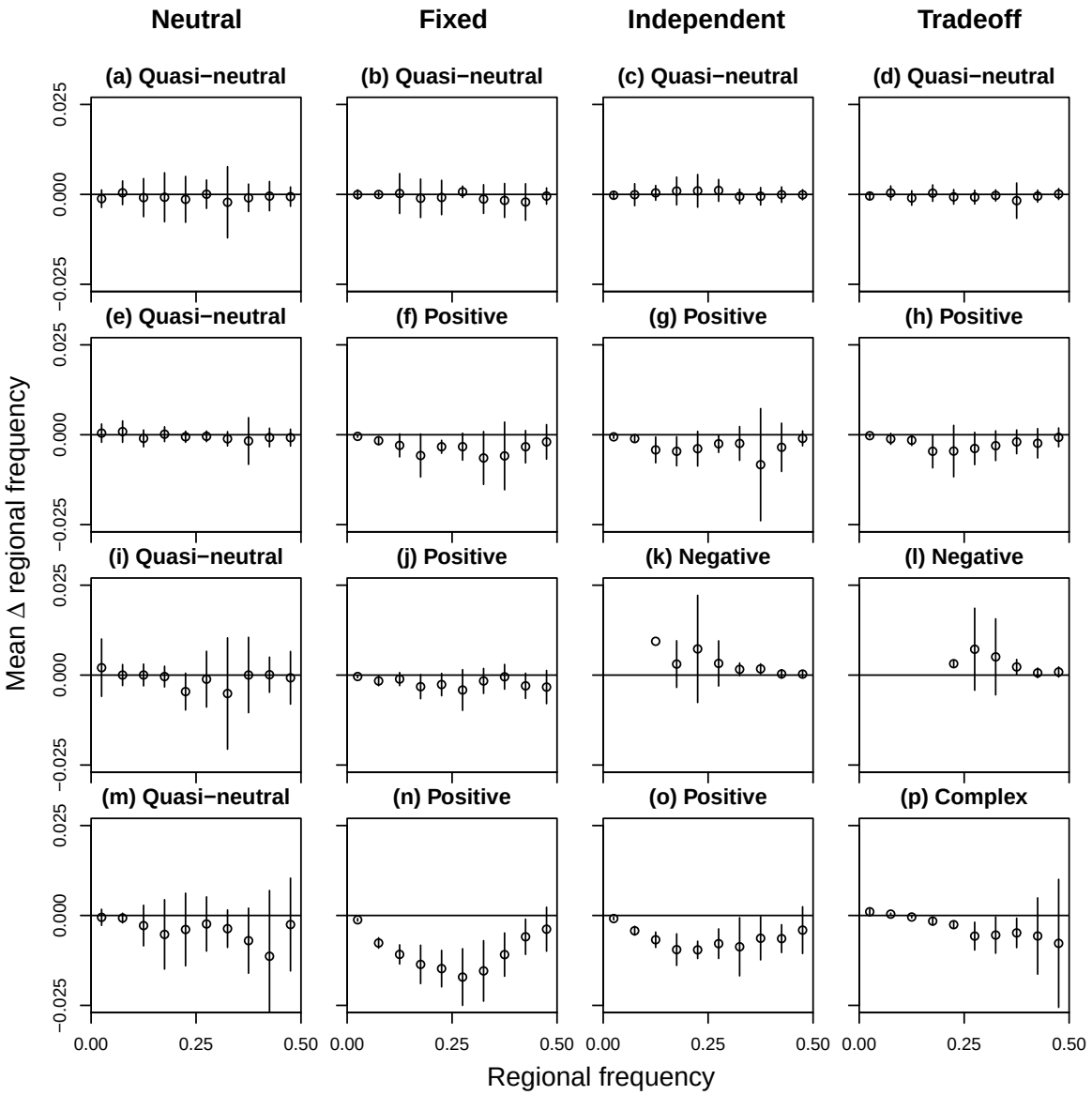

Figure A2: Frequency-dependence plots, i.e. intervals of mean regional frequency change ±3.83 standard errors for the various frequency bins between 0 and 0.5, corresponding to the the time series in fig. 3.

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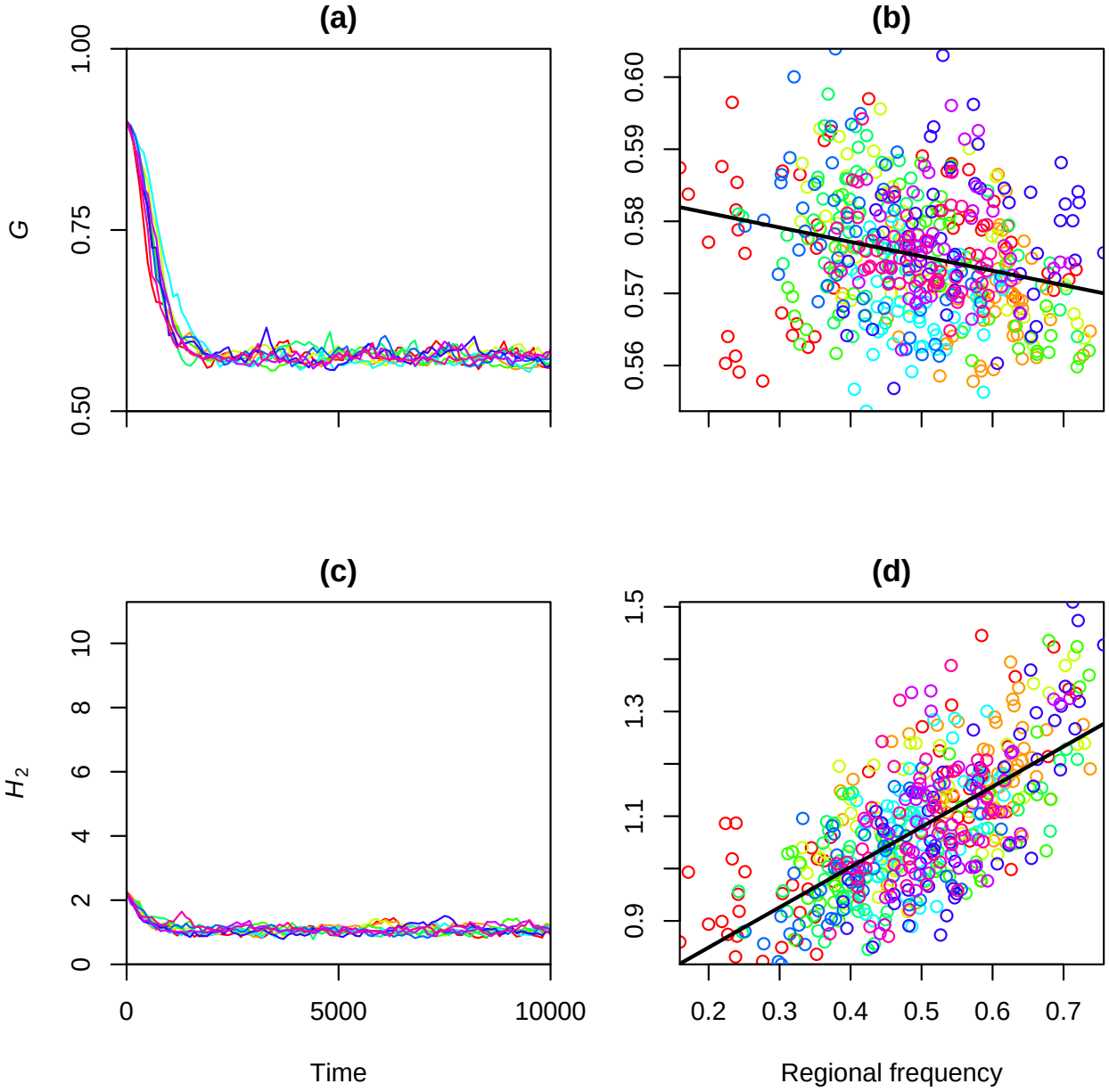

Figure A3: Example illustrating evolutionary dynamics under independent evolution. (a) Average sensitivity to general competition G for a focal species (species 1). (c) Corresponding average sensitivity to heterospecific interference H_2. (b) and (d) show how G and H, respectively, respond to regional frequency. Parameters as in fig. 3 l (negative frequency dependence example).

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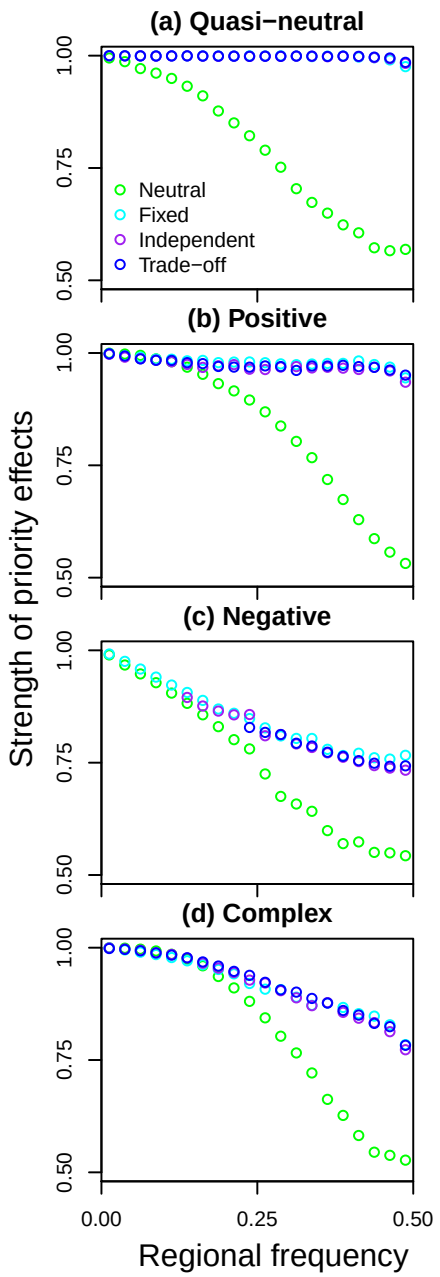

Figure A4: Strength of priority effects for the representative examples from fig. 3, i.e. the probability that the locally dominant species directly after a disturbance event is also the dominant species before the next disturbance event. The x axis represents the regional frequency of the regionally 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 (c), 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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Online Appendix A.3 Additional parameter sensitivity analyses for two species

Among the two outcome types that do not allow for stable coexistence, quasi-neutrality was more likely under propagule-pool recolonization and small migration rates, where the early inhabitants of a patch mostly consist of just one species (fig. A5 e,h). Positive frequency dependence was more likely under migrant-pool recolonization and large migration rates, where the early inhabitants of a patch are a more representative sample from the whole metacommunity (fig. A5 e,h). This makes intuitive sense because in the first case species recolonize patches in proportion to their regional frequencies, whereas in the second case the regionally common species wins disproportionately more often.

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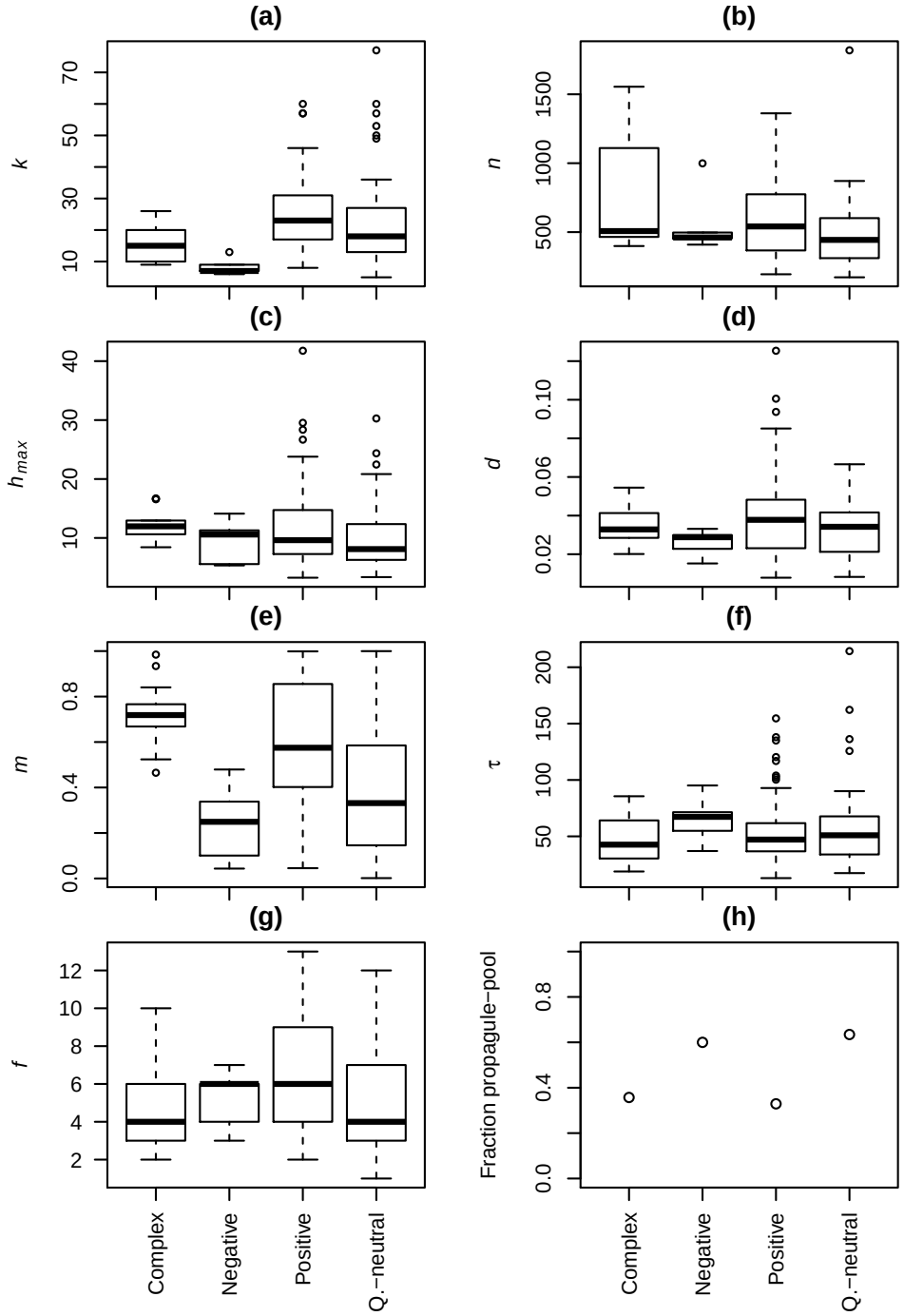

Figure A5: Distribution of parameter values for trade-off simulations classified as having complex, negative, or positive frequency dependence, or quasi-neutrality. Since it is a binary parameter whether recolonization happens according to the propagule-pool or migrant-pool model, (h) shows the fraction of simulations in each class that follow the propagule-pool model.

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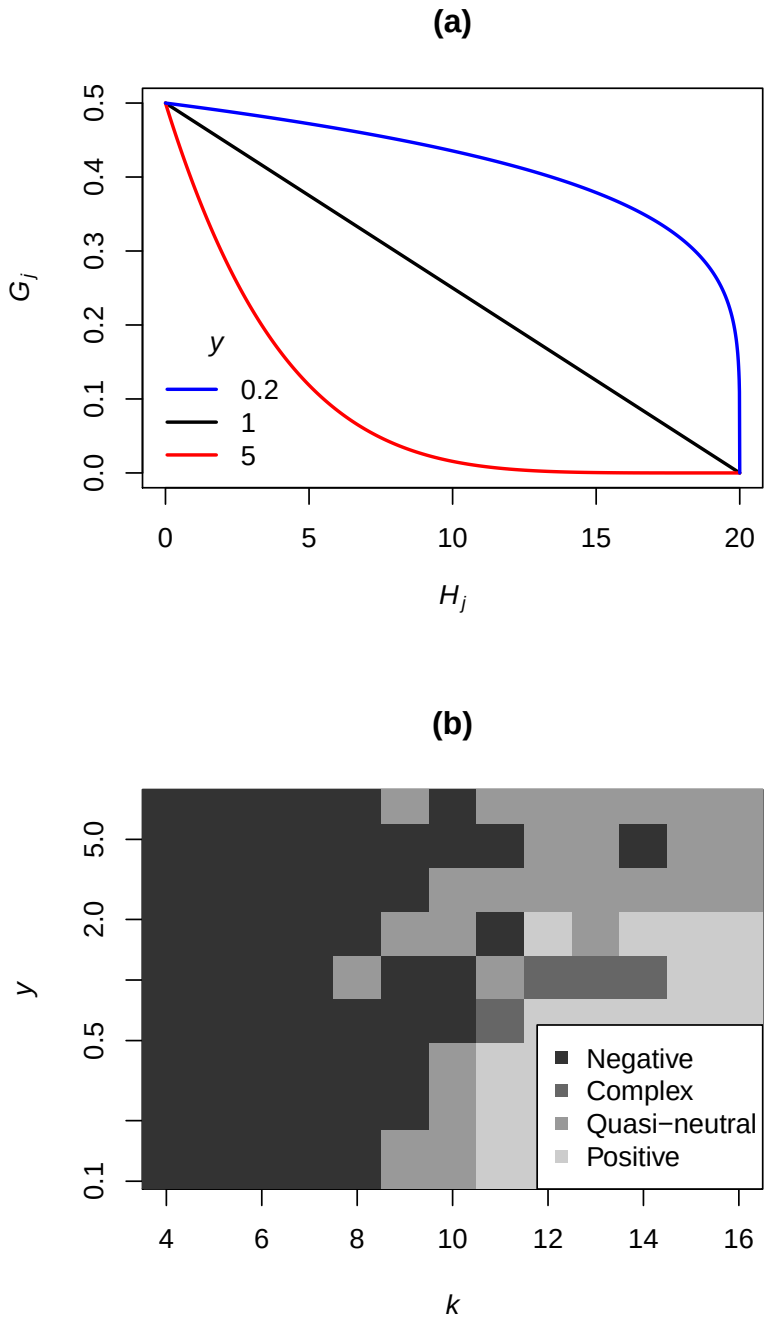

Figure A6: Role of the trade-off shape parameter y (see 2). (a) The trade-off is concave for $y < 1$, linear for $y = 1$, and convex for $y > 1$. (b) Classification of parameter combinations with various values of y and local community size k. All other parameters are held constant at the values from fig. 3 l. Note the log-scale on the y axis.

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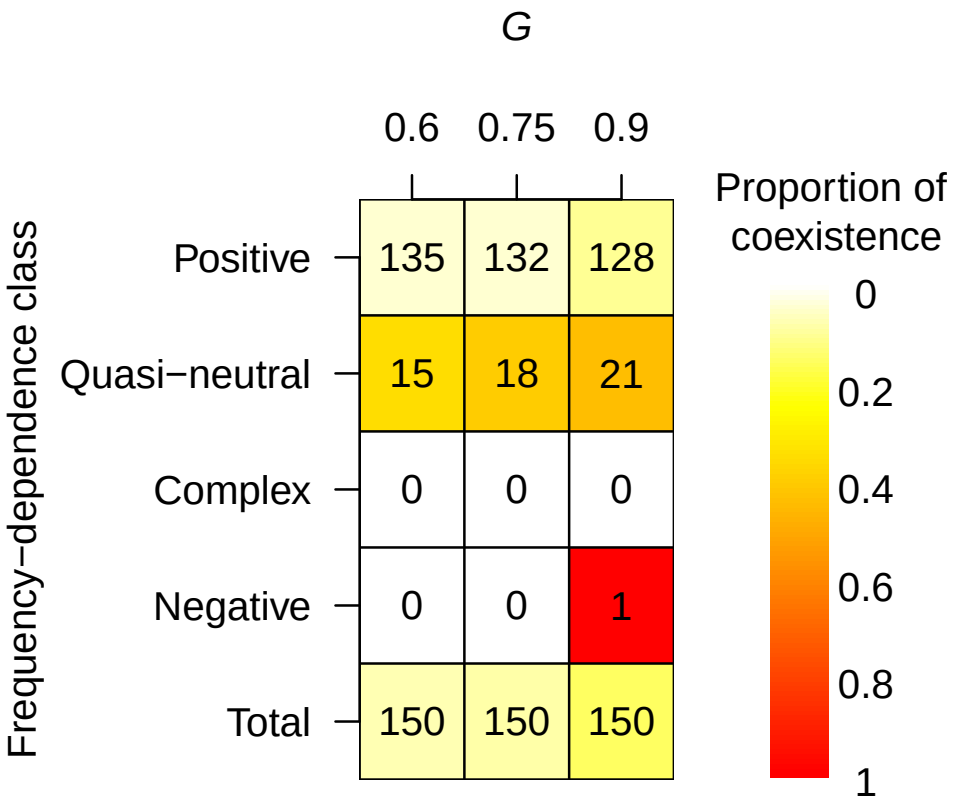

Figure A7: Coexistence and frequency dependence in the fixed-trait scenario with individual traits fixed to three different points along the trade-off. The middle column corresponds to the results in the main text. The parameter combination classified as having negative frequency dependence is likely a misclassification.

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Online Appendix A.4 Additional results for more than two species

Here we consider metacommunities of more than two species under a parameter combination that exhibited complex frequency dependence with two species (last row in fig. 3). As in the negative frequency dependence example in fig. 6, metacommunities starting with three species generally maintained all three species until the end. Metacommunities starting with four or five species maintained four species (fig. A8). However, metacommunities starting with ten species often had only one or two species left at the end. To better understand this result, we performed two additional types of control simulation. In the "10-species" control, we started the metacommunity with only two species, but individuals had sensitivity traits H_j for 9 interacting species, as in the 10-species case. The two species in this control generally did not coexist until the end of the simulation (fig. A8). In the "plasmid" control, we made the loci corresponding to extinct species no longer contribute to the overall competitive pressure. Qualitatively, this scenario represents a situation where the relevant loci are on plasmids that can be rapidly discarded once they are no longer advantageous. With this modification, metacommunities starting at ten species stabilized at four species (fig. A8). These additional results indicate that it is mutational noise at sensitivity traits affecting interactions with extinct species that destabilized coexistence in the original model.

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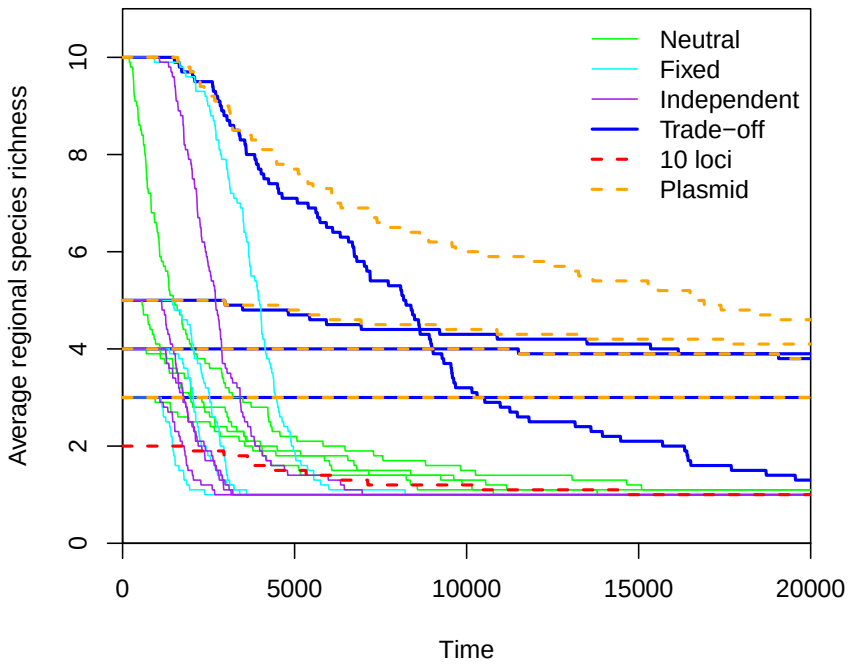

Figure A8: Time series of regional species diversity (gamma diversity) for different initial numbers of species. Each point is the average over 10 replicate simulations. Parameters are the same as in the last row in fig. 3.

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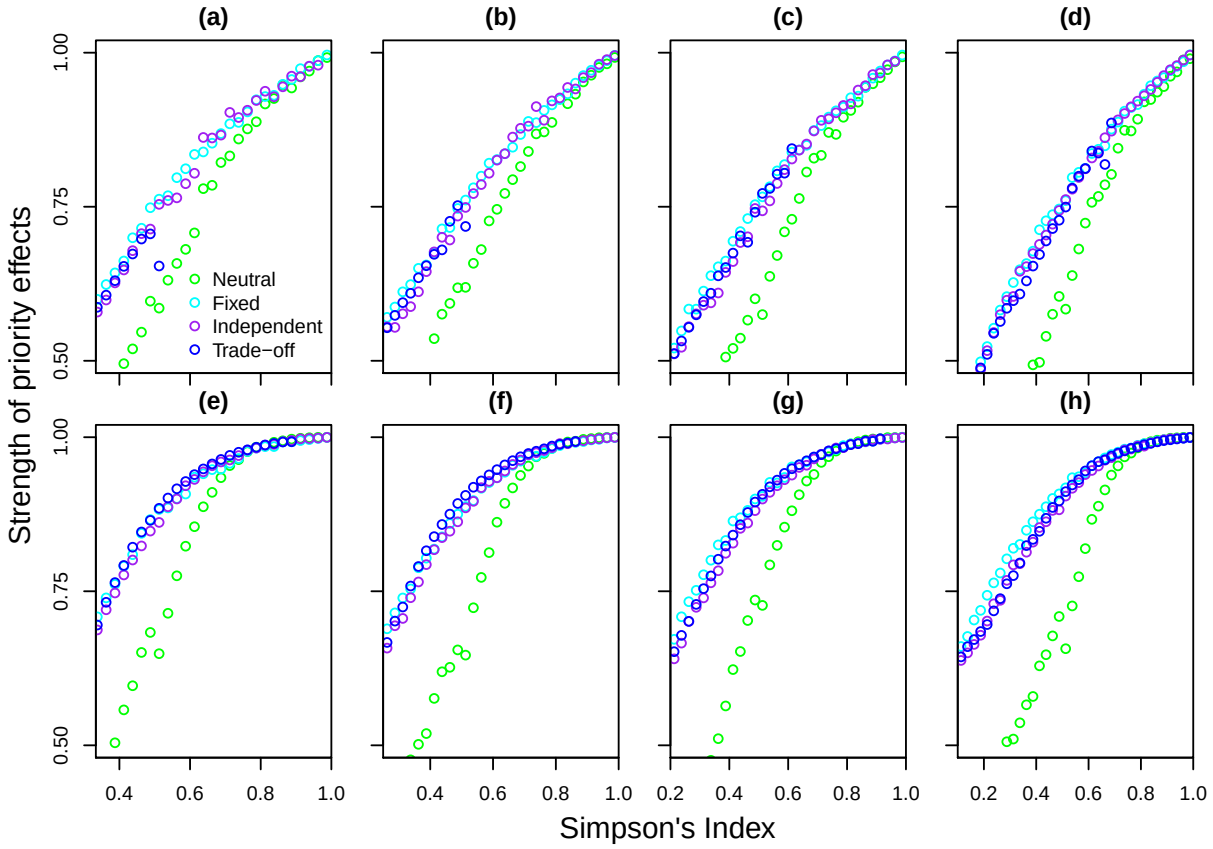

Figure A9: Strength of priority effects in the multi-species simulations. The first and second row correspond to figs. 6 and A8, respectively. There are 3 species in the first column, four species in the second column, five species in the third column, and ten species in the fourth column.

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Online Appendix A.5 Additional analysis on regional coexistence

In the following two sections, we will show that (1) in metacommunities with small local communities and a low migration rate, the regionally rare species tends to be "subjectively" common locally, and (2) the more common a rare species is locally, the smaller is the difference in trait values between regionally common and rare species for the average member of the rare species to be at an advantage in its local environment. The reason is that individuals do not suffer as much from heterospecific interference if they are locally common. From these two points, we can conclude that with small community sizes and with small migration rates, a smaller difference in trait values is sufficient to tip the balance towards the regionally rare species. Thus negative regional frequency dependence is more likely under smaller local community sizes and lower migration rates.

1. "Subjective" local frequency

Consider a metacommunity where all patches have the same total community size k, as we assume in our simulations. The mean local frequency of a species averaged over all patches is equal to its regional frequency. However, the mean local frequency might not adequately portray the community composition experienced by the average individual of the focal species. For example, consider a metacommunity with a local community size of 10 and a focal species at a regional frequency of 0.1. Let us also imagine that most patches are dominated by a single species as a result of local priority effects and that only a small fraction of patches contains both species. In this scenario, the negative effects of interference by the common species will only be felt by a small fraction of individuals of the rare species. Had we assumed that most local frequencies are close to the regional frequency, we would have erroneously concluded that most members of the rare species are in patches where the other species is locally common and that they would therefore suffer strongly from the negative effects of interference by the other species.

To formalize this intuition, we define the "subjective" local population size of a focal species as the local population size experienced by the average individual of this species

$$\mathbf{E}[N^*] := \frac{\sum_{i=1}^{k} i^2 \pi(i)}{\sum_{i=1}^{k} i \pi(i)}, \tag{A1}$$

where $\pi(i)$ is the proportion of patches containing i individuals of the focal species. In other words, when computing the average, patches are weighed by the local population size of the focal species. This way of averaging is formally known as size-biasing.

The mean subjective local population size can be easily computed from the mean and variance

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across patches of local population sizes N:

$$\mathbf{E}[N^*] = \frac{\mathbf{E}[N^2]}{\mathbf{E}[N]} = \frac{\mathbf{E}[N]^2 + \mathbf{Var}[N]}{\mathbf{E}[N]} = \mathbf{E}[N] + \frac{\mathbf{Var}[N]}{\mathbf{E}[N]}. \tag{A2}$$

As (A2) shows, the difference between size-biased expectation and un-biased expectation increases with the variance in local community sizes. Intuitively, the larger variance in local community sizes, the more heavily are patches dominated by a single species, and the larger is the subjective local population size of the own species. To consider a specific example, let us assume that local population sizes are binomially distributed with parameters p and k. We then obtain

$$\mathbf{E}[N^*] = pk + 1 - p \tag{A3}$$

and the subjective local frequency is

$$p^* = p + \frac{1-p}{k}. \tag{A4}$$

The smaller the local community size k is, the larger is the subjective local frequency for a given regional frequency (fig. A10 a). The increase in subjective local frequency compared to the regional frequency in small patches can be substantial, especially for small regional frequencies.

More generally

$$p^* = \frac{\mathbf{E}[N^*]}{k} = p + \frac{\mathbf{Var}[N]}{k^2 p}. \tag{A5}$$

Therefore, the average subjective frequency is a decreasing function of local community size not only for the binomial distribution but whenever $\mathbf{Var}[N]$ increases with k not faster than k^2. This appears to be the case in our simulated metacommunities. For small local communities, the size-biased local frequency was substantially larger than the respective regional frequency (fig. A10 b). As a further intuitive illustration why subjective frequency should increase with k, note that one is the minimum local abundance in which we can find members of the rare species. Thus, the smaller k is, the larger is the minimum possible local frequency of the rare species. For example, if $k = 4$, the minimum possible local frequency is 0.25. In our simulations, the average subjective frequency decreased with migration rate (fig. A10 b), which makes sense because frequent migration reduces variance in local species frequencies.

2. Critical evolutionary response

Consider a rare species with sensitivity to general competition G^r and a common species with sensitivity to general competition G^c, and let $\Delta G = G^r - G^c$. The common species should evolve to be a better intraspecific competitor or at least be under relaxed selection, so we expect $\Delta G > 0$.

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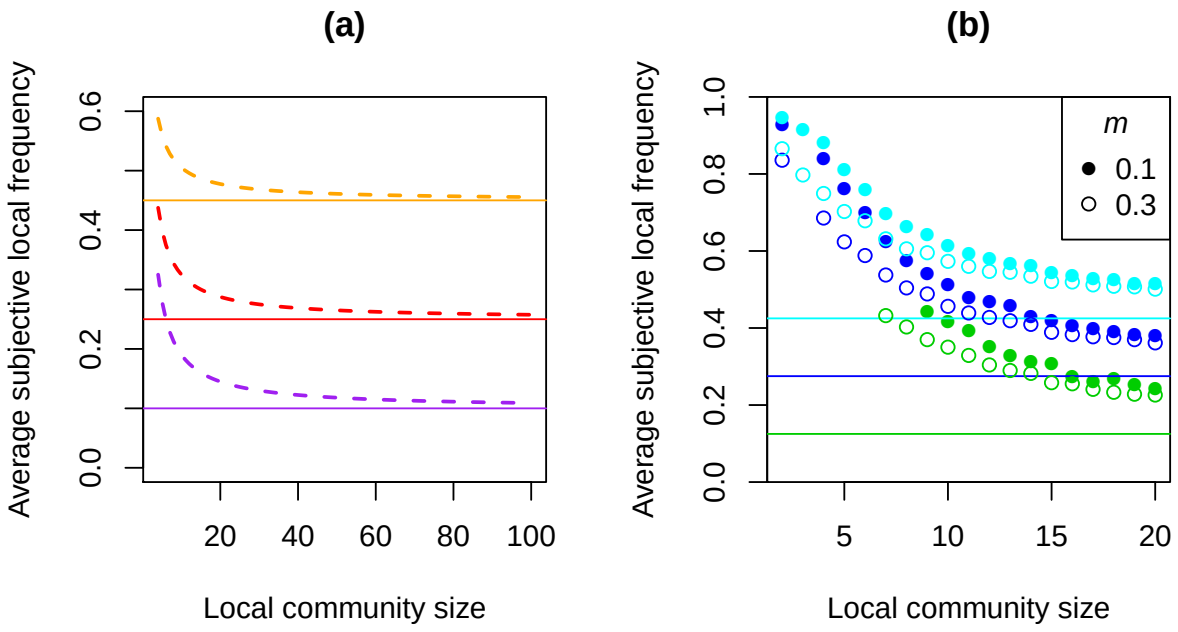

Figure A10: Average subjective frequency as a function of local community size k for different regional frequencies. As the local community size increases, the average subjective frequency approaches the respective regional frequency (indicated by horizontal lines). In (a) a binomial distribution of local population sizes is assumed, (b) represents distributions of local community sizes from our simulations, specifically those underlying fig. 5 a.

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Assuming a linear trade-off, we will now compute the critical value for ΔG such that the rare species has an advantage locally when it has i individuals in a community of size k, with $i < k/2$. Since the probability to reproduce is assumed to be the same for all species, a species has an advantage locally when its members have a lower death rate $C_i = G \cdot k + H(G)(k - N_i)$ with

$$H(G) = \left(1 - \frac{G - g_{min}}{\Delta g}\right) \cdot h_{max}. \tag{A6}$$

In our study, we used $g_{min} = 0.5$ and $\Delta g = 0.5$ so that

$$H(G) = 2(1 - G) \cdot h_{max}. \tag{A7}$$

With this, the death rate for rare-species individuals is

$$C^r = G^r k + 2(1 - G^r) h_{max}(k - i) \tag{A8}$$

and the death rate for members of the common species is

$$C^c = G^c k + 2(1 - G^c) h_{max} i = (G^r - \Delta G)k + 2(1 - G^r + \Delta G) h_{max} i. \tag{A9}$$

Members of the rare species have an advantage, i.e. a lower death rate, if

$$G^r(k - 2h_{max}(k - i)) + 2h_{max}(k - i) < (G^r - \Delta G)(k - 2h_{max} i) + 2h_{max} i \tag{A10}$$

$$\Leftrightarrow G^r(-2h_{max}(k - 2i)) + 2h_{max}(k - 2i) < \Delta G(2h_{max} i - k) \tag{A11}$$

$$\Leftrightarrow 2h_{max}(k - 2i)(1 - G^r) < \Delta G(2h_{max} i - k). \tag{A12}$$

We need to consider two cases:

a) $k > 2h_{max} i$. Since $i < k/2$, it follows from (A12) that

$$\Delta G < \frac{2h_{max}(k - 2i)(1 - G^r)}{2h_{max} i - k} < 0. \tag{A13}$$

b) $k < 2h_{max} i$

$$\Delta G > \frac{2h_{max}(k - 2i)(1 - G^r)}{2h_{max} i - k} > 0. \tag{A14}$$

Since the common species will generally have a lower G and $\Delta G > 0$, (A13) cannot be fulfilled. If $h_{max} < 1$ then $k > 2h_{max} i$ for all $i < k/2$, and it would be impossible for a locally rare species to have a local advantage, no matter how sensitive the common species is to heterospecific interference. This should prevent regional coexistence. However, in our simulations we did not consider such low values of h_{max}.

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In case b), we get a critical trait difference

$$R_{crit} := \frac{2h_{max}(k-2i)(1-G^r)}{2h_{max}i-k} \tag{A15}$$

such that a globally and locally rare species has a local advantage whenever the difference in G values is at least R_{crit}. The smaller R_{crit} is, the easier it is for evolution along the trade-off to stabilize regional coexistence.

The critical trait difference is a function of local population size i and

$$\frac{\partial R_{crit}}{\partial i} = 2h_{max}(1-G^r)\frac{-2(2h_{max}i-k)-(k-2i)2h_{max}}{(2h_{max}i-k)^2} = \frac{4(1-G^r)kh_{max}(1-h_{max})}{(2h_{max}i-k)^2}. \tag{A16}$$

If $h_{max} > 1$, which is the case if the condition of case b) is fulfilled and $k > 1$, then the critical evolutionary response necessary to give an advantage to the rare species decreases with its local population size i. As explained in the main text and illustrated in fig. A11, this can give an average advantage to the rare species while at the same time priority effects are maintained, but slightly asymmetric. However, not all values of k have the same potential for such slight asymmetry. For odd k, for example, there are no patches with a completely balanced species composition and to start having a regional advantage the regionally rare species needs to dominate even in patches where the regionally common species is slightly more abundant, which presumably requires a larger evolutionary response. Such "discreteness effects" may underlie the idiosyncratic relationship between k and outcome type in fig. 5 a.

$$\frac{\partial R_{crit}}{\partial h_{max}} = 2(k-2i)(1-G^r)\frac{2h_{max}i-k-2h_{max}i}{(2h_{max}i-k)^2} = \frac{-2k(k-2i)(1-G^r)}{(2h_{max}i-k)^2} < 0. \tag{A17}$$

Therefore, with increasing h_{max} the evolutionary response necessary to provide an advantage to the regionally rare species decreases. This is consistent with the finding in fig. 5 g: regional negative frequency dependence occurred only for sufficiently large h_{max}. Under a high h_{max}, the common species is punished heavily for neglecting to invest in heterospecific tolerance.

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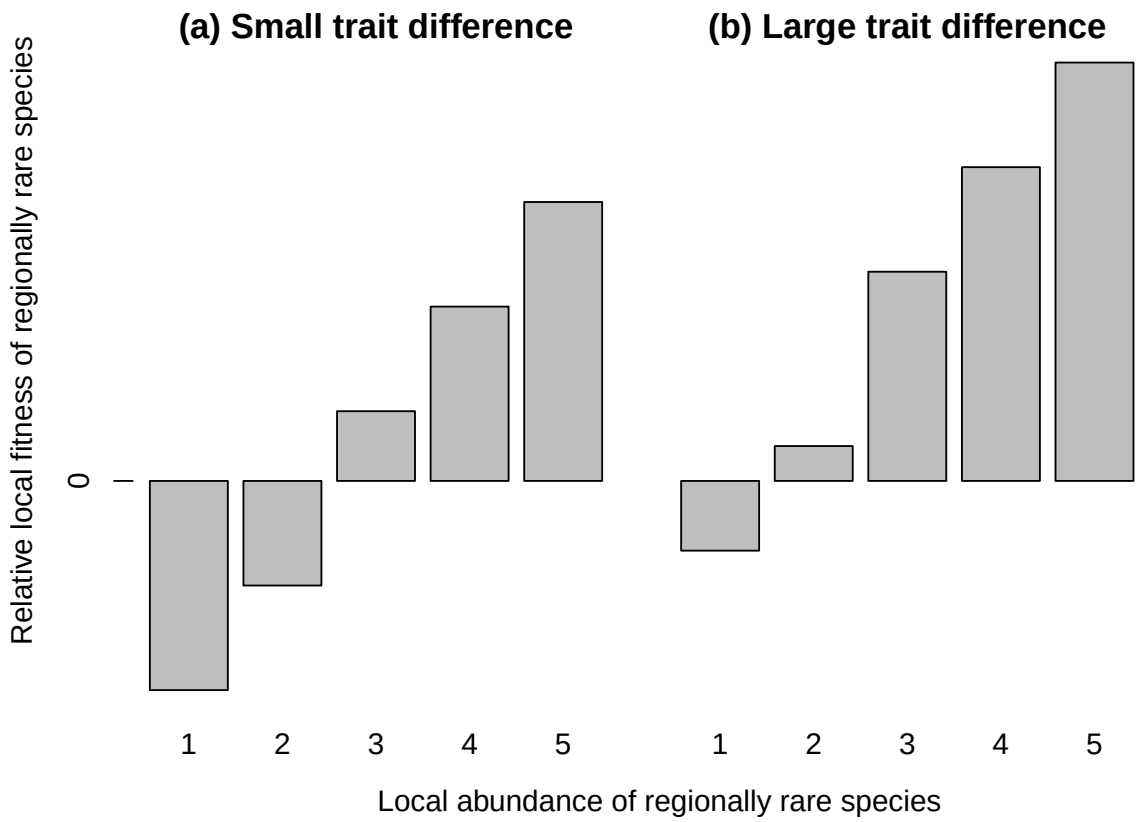

Figure A11: Cartoon illustrating a situation with priority effects at extremely unbalanced local species configurations and an advantage of the regionally rare species under more balanced configurations. The local community size k is 6. (a) Small evolutionary response, ΔG. (b) Large evolutionary response, ΔG.