Supporting Information for

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

Meike J. Wittmann and Tadashi Fukami

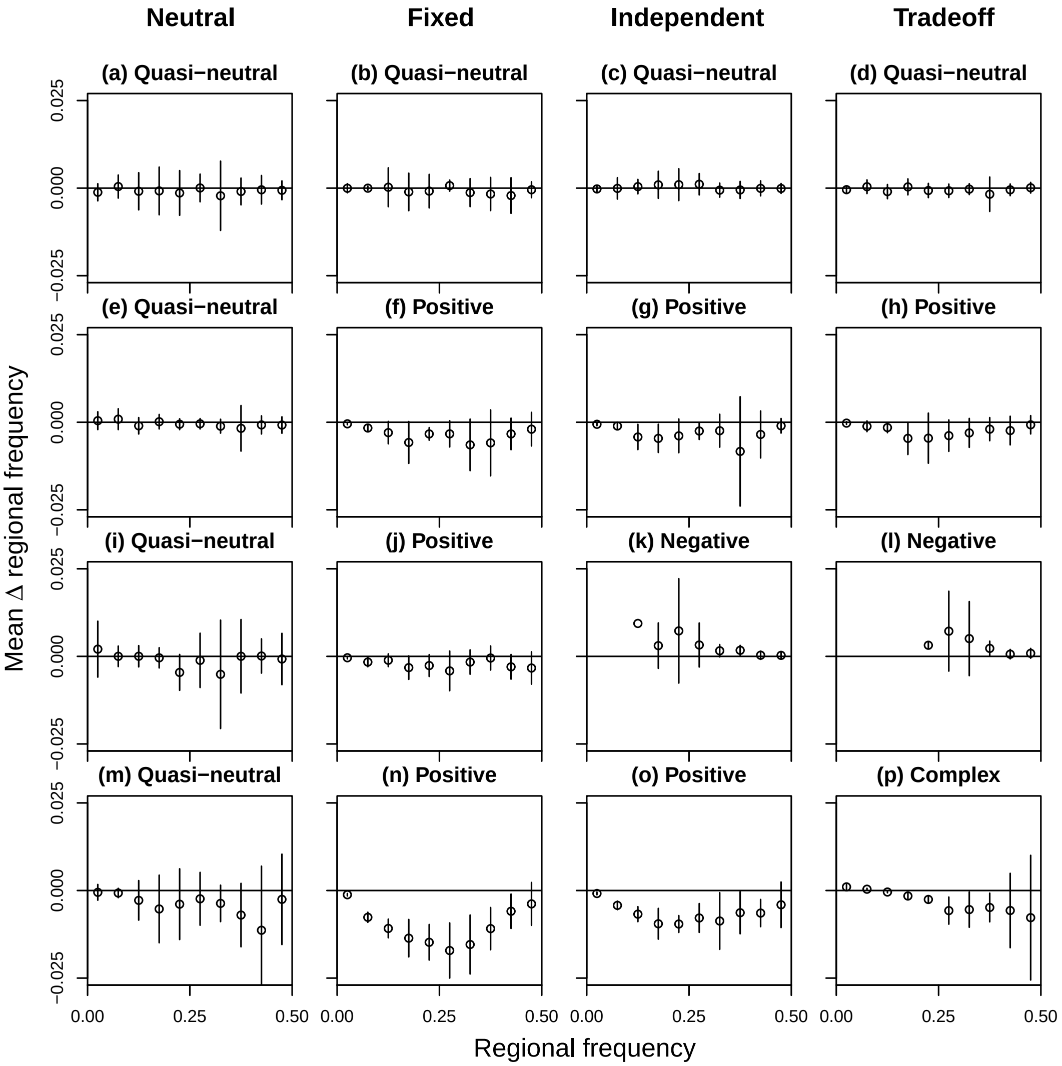

Figure S1: Frequency-dependence plots, i.e. intervals of mean regional frequency change ±3.83 standard errors for the various frequency bins between 0 and 0.5, corresponding to the the time series in Fig. 2.

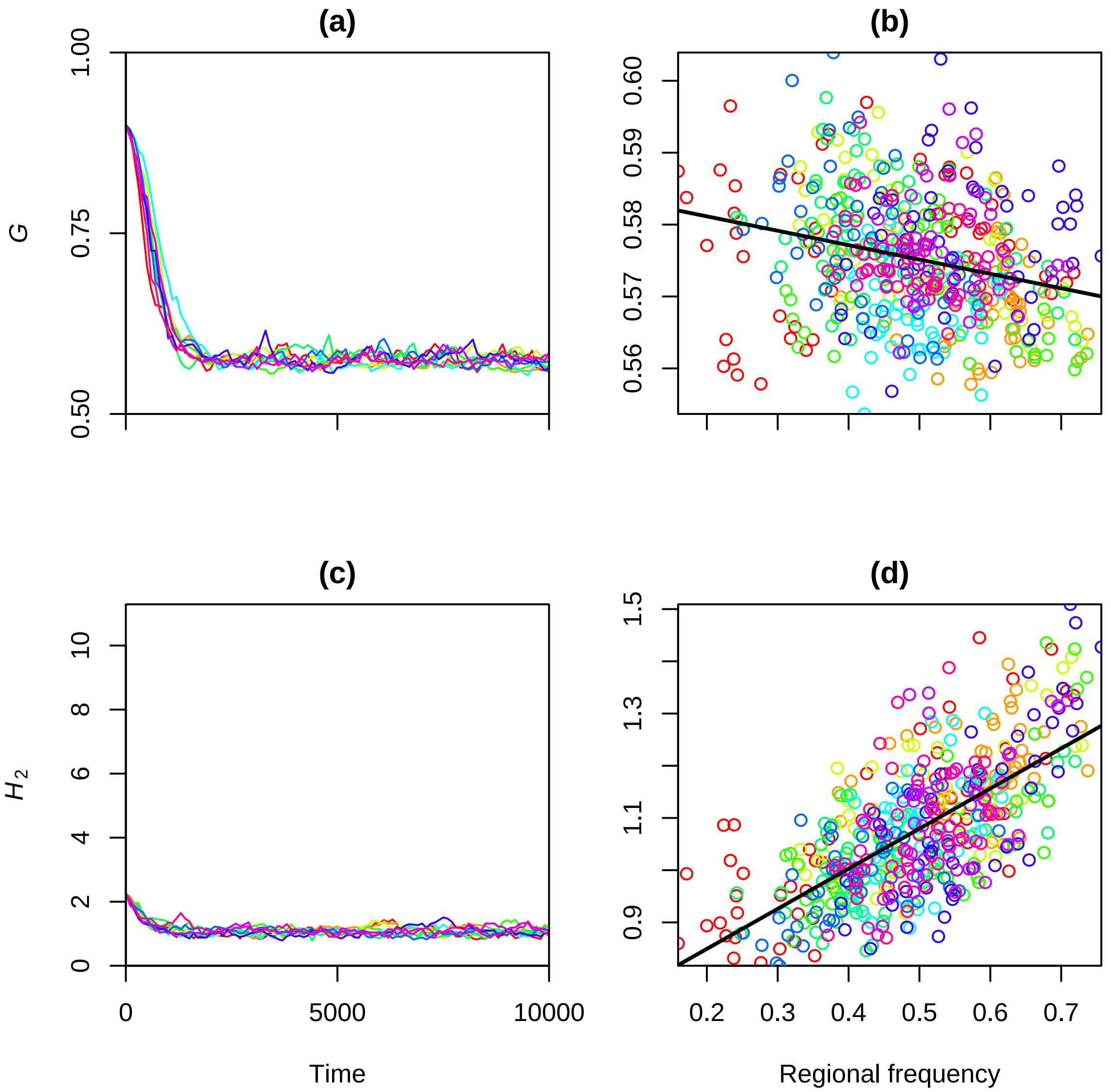

Figure S2: Example illustrating evolutionary dynamics under independent evolution. (a) Average sensitivity to general competition G for a focal species (species 1). (c) Corresponding average sensitivity to heterospecific interference H_2. (b) and (d) show how G and H, respectively, respond to regional frequency. Parameters as in Fig. 2 l (negative frequency dependence example).

Appendix S3 Additional results on parameter sensitivity

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. S3 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. S3 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.

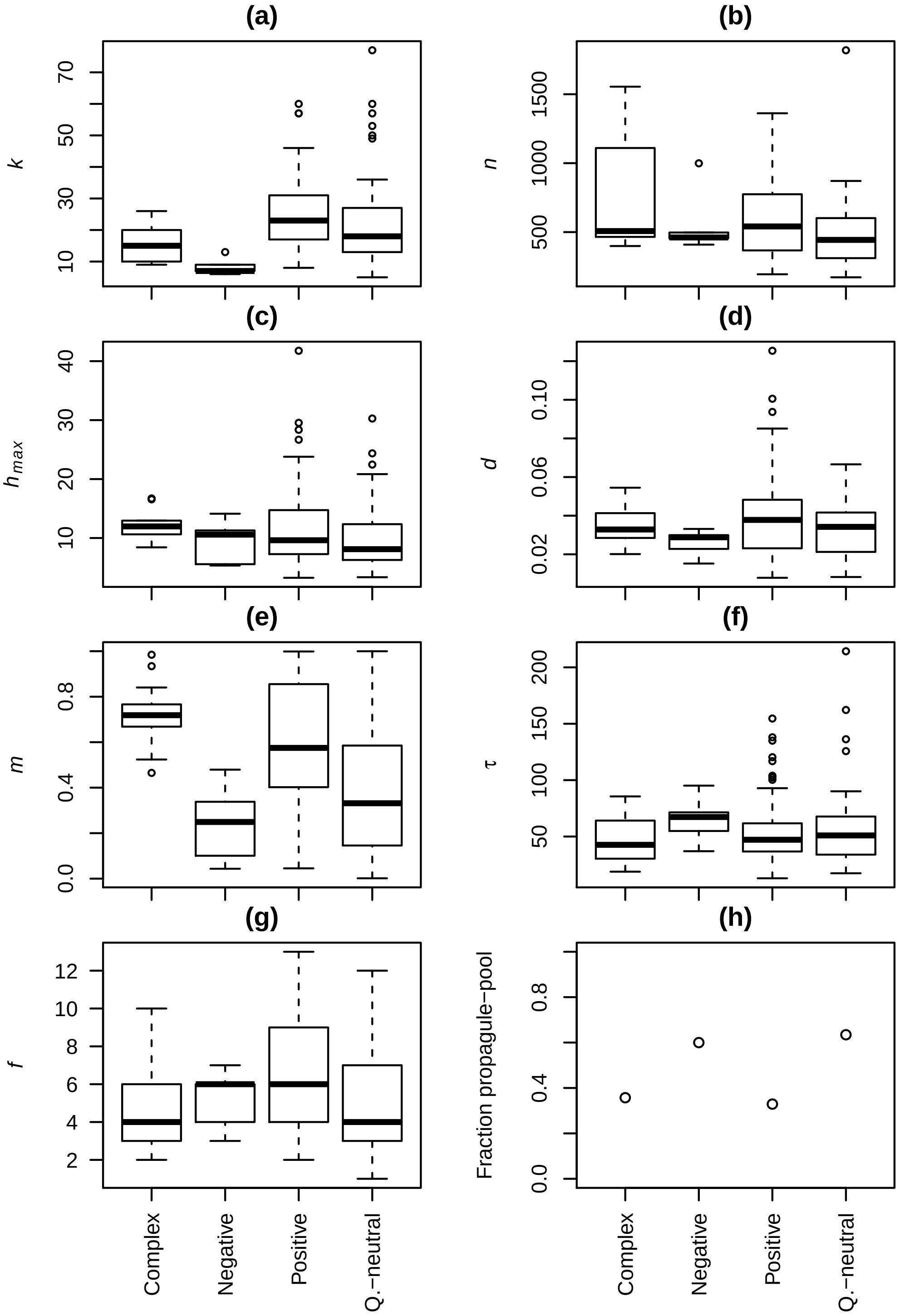

Figure S3: Distribution of parameter values for trade-off simulations classified as having complex, negative, or positive frequency dependence, or quasi-neutrality. Since it is a binary parameter whether recolonization happens according to the propagule-pool or migrant-pool model, (h) shows the fraction of simulations in each class that follow the propagule-pool model.

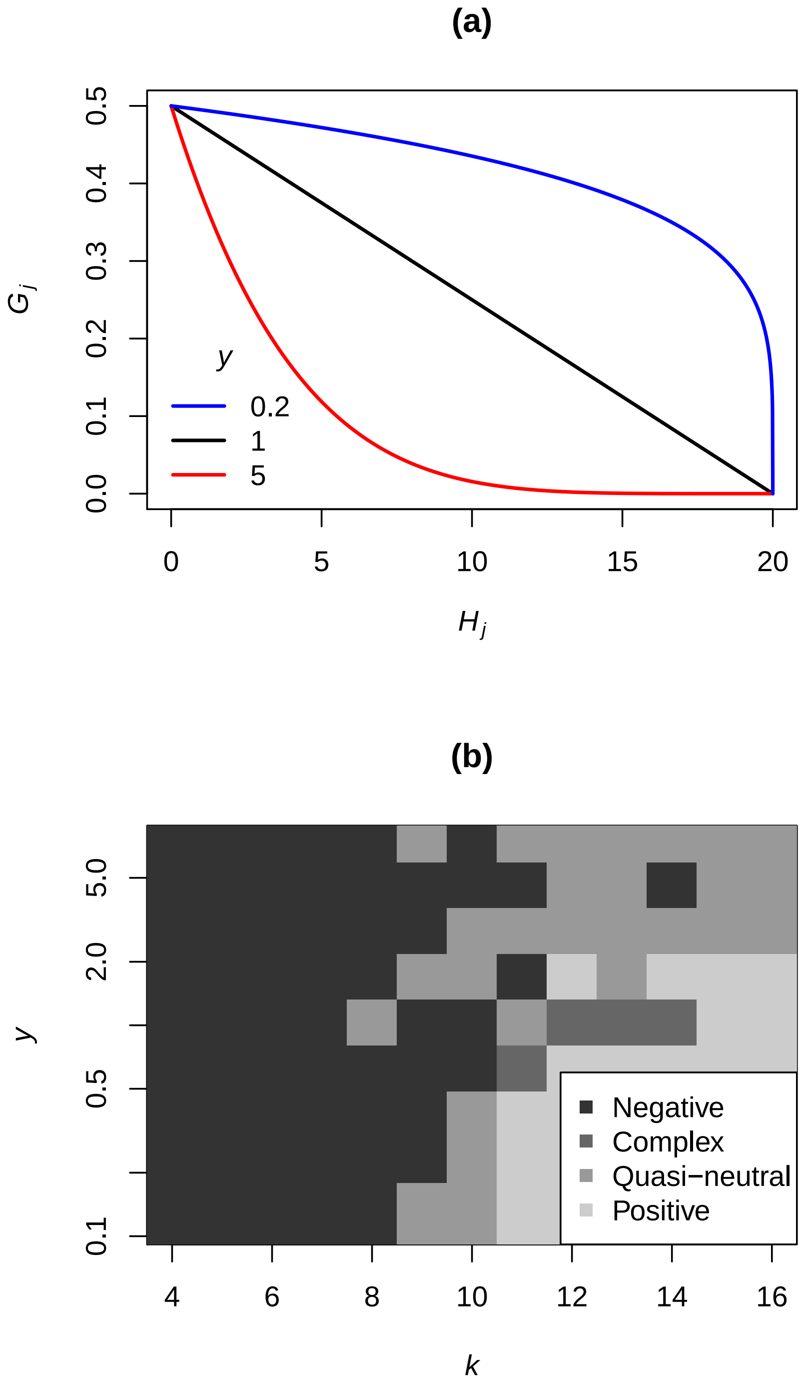

Figure S4: Role of the trade-off shape parameter y (see 2). (a) The trade-off is concave for $y < 1$, linear for $y = 1$, and convex for $y > 1$. (b) Classification of parameter combinations with various values of y and local community size k. All other parameters are held constant at the values from Fig. 2 l. Note the log-scale on the y axis.

Appendix S4 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. 2). 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. S5). 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. S5). 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. S5). These additional results indicate that it is mutational noise at sensitivity traits affecting interactions with extinct species that destabilized coexistence in the original model.

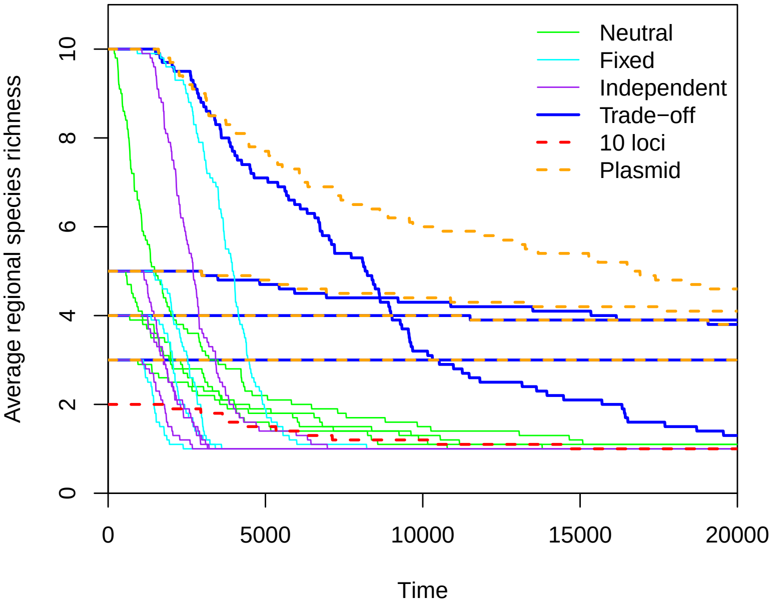

Figure S5: Time series of regional species diversity (gamma diversity) for different initial numbers of species. Each point is the average over 10 replicate simulations. Parameters are the same as in the last row in Fig. 2.

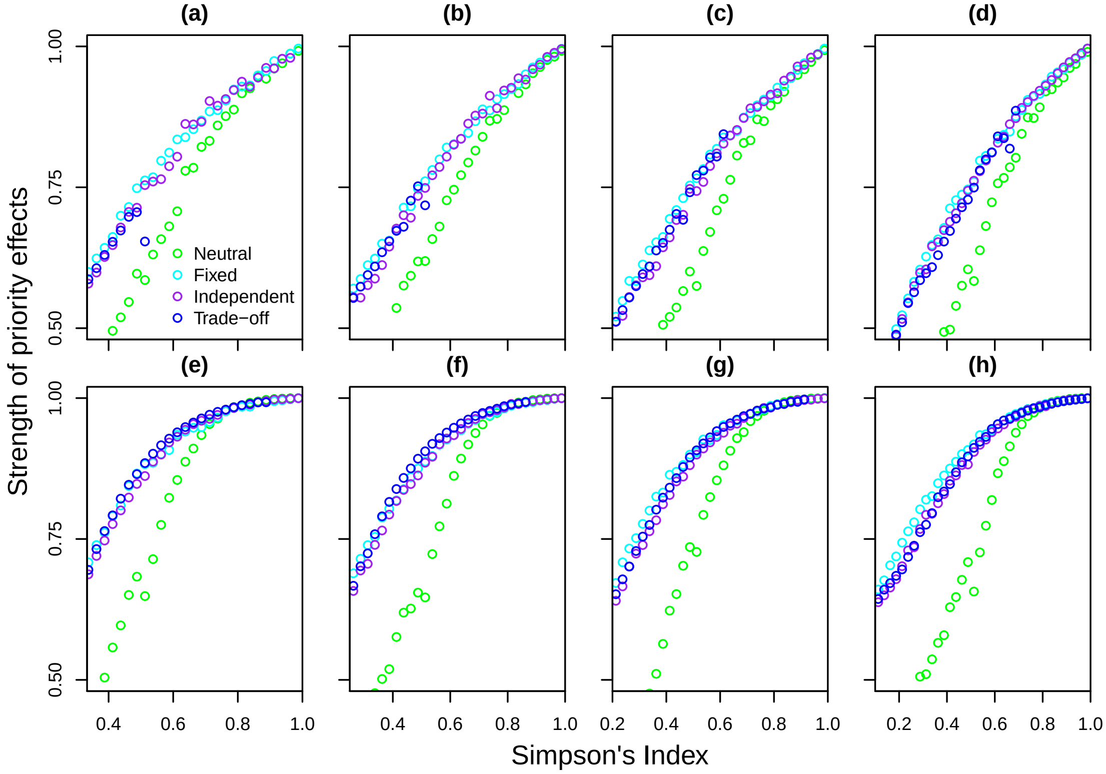

Figure S6: Strength of priority effects in the multi-species simulations. The first and second row correspond to Figs. 6 and S5, respectively. There are 3 species in the first column, four species in the second column, five species in the third column, and ten species in the fourth column.

Appendix S5 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

$$\mathbf{E}[N^*] := \frac{\sum_{i=1}^{k} i^2 \pi(i)}{\sum_{i=1}^{k} i \pi(i)}, \tag{S1}$$

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 across patches of local population sizes N:

$$\mathbf{E}[N^*] = \frac{\mathbf{E}[N^2]}{\mathbf{E}[N]} = \frac{\mathbf{E}[N]^2 + \mathbf{Var}[N]}{\mathbf{E}[N]} = \mathbf{E}[N] + \frac{\mathbf{Var}[N]}{\mathbf{E}[N]}. \tag{S2}$$

As (S2) 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

$$\mathbf{E}[N^*] = pk + 1 - p \tag{S3}$$

and the subjective local frequency is

$$p^* = p + \frac{1-p}{k}. \tag{S4}$$

The smaller the local community size k is, the larger is the subjective local frequency for a given regional frequency (Fig. S7 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

$$p^* = \frac{\mathbf{E}[N^*]}{k} = p + \frac{\mathbf{Var}[N]}{k^2 p}. \tag{S5}$$

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. S7 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

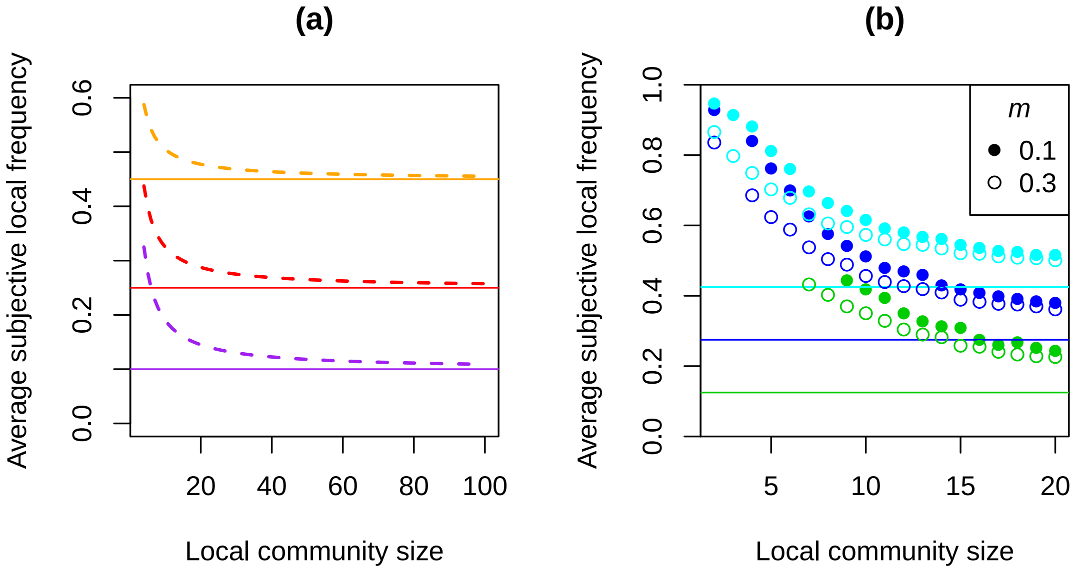

Figure S7: Average subjective frequency as a function of local community size k for different regional frequencies. As the local community size increases, the average subjective frequency approaches the respective regional frequency (indicated by horizontal lines). In (a) a binomial distribution of local population sizes is assumed, (b) represents distributions of local community sizes from our simulations, specifically those underlying Fig. 5 a.

subjective frequency decreased with migration rate (Fig. S7 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 $\Delta G > 0$. 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

$$H(G) = \left(1 - \frac{G - g_{min}}{g_{max}}\right) \cdot h_{max}. \tag{S6}$$

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

$$H(G) = 2(1 - G) \cdot h_{max}. \tag{S7}$$

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

$$C^r = G^r k + 2(1 - G^r) h_{max}(k - i) \tag{S8}$$

and the death rate for members of the common species is

$$C^c = G^c k + 2(1 - G^c) h_{max} i = (G^r - \Delta G)k + 2(1 - G^r + \Delta G) h_{max} i. \tag{S9}$$

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

$$G^r(k - 2h_{max}(k - i)) + 2h_{max}(k - i) < (G^r - \Delta G)(k - 2h_{max} i) + 2h_{max} i \tag{S10}$$

$$\Leftrightarrow G^r(-2h_{max}(k - 2i)) + 2h_{max}(k - 2i) < \Delta G(2h_{max} i - k) \tag{S11}$$

$$\Leftrightarrow 2h_{max}(k - 2i)(1 - G^r) < \Delta G(2h_{max} i - k). \tag{S12}$$

We need to consider two cases:

a) $k > 2h_{max} i$. Since $i < k/2$, it follows from (S12) that

$$\Delta G < \frac{2h_{max}(k-2i)(1-G^r)}{2h_{max}i-k} < 0. \tag{S13}$$

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

$$\Delta G > \frac{2h_{max}(k-2i)(1-G^r)}{2h_{max}i-k} > 0. \tag{S14}$$

Since the common species will generally have a lower G and $\Delta G > 0$, (S13) 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}.

In case b), we get a critical trait difference

$$R_{crit} := \frac{2h_{max}(k-2i)(1-G^r)}{2h_{max}i-k} \tag{S15}$$

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

$$\frac{\partial R_{crit}}{\partial i} = 2h_{max}(1-G^r)\frac{-2(2h_{max}i-k)-(k-2i)2h_{max}}{(2h_{max}i-k)^2} = \frac{4(1-G^r)kh_{max}(1-h_{max})}{(2h_{max}i-k)^2}. \tag{S16}$$

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. S8, 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.

$$\frac{\partial R_{crit}}{\partial h_{max}} = 2(k-2i)(1-G^r)\frac{2h_{max}i - k - 2h_{max}i}{(2h_{max}i-k)^2} = \frac{-2k(k-2i)(1-G^r)}{(2h_{max}i-k)^2} < 0. \quad \text{(S17)}$$

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.

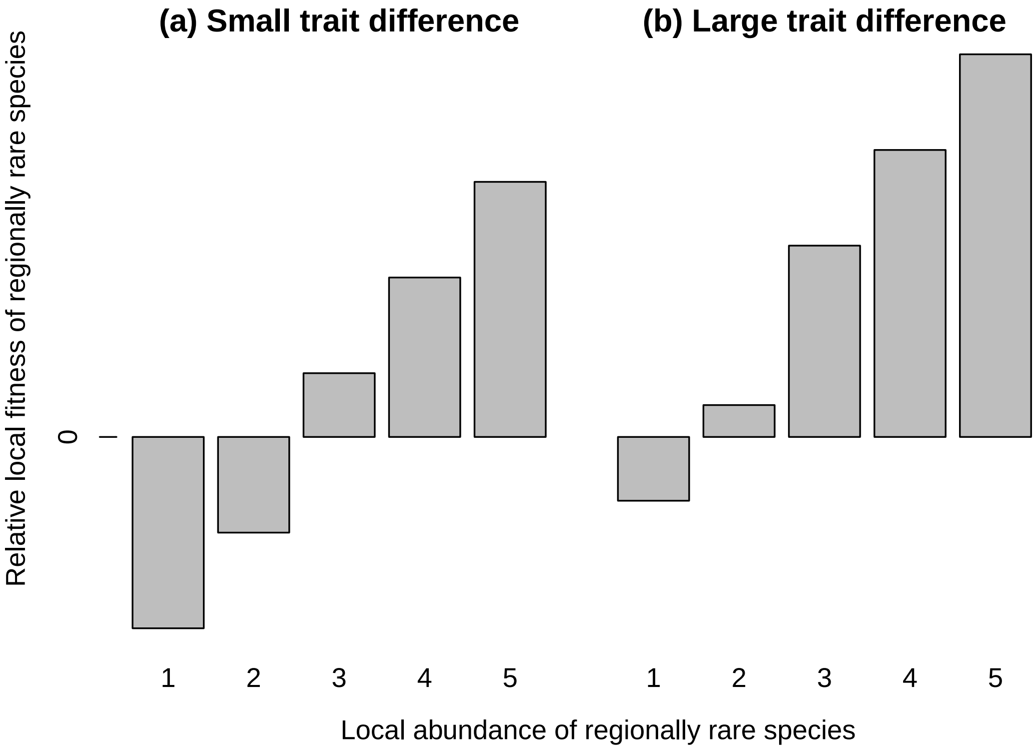

Figure S8: Cartoon illustrating a situation with priority effects at extremely unbalanced local species configurations and an advantage of the regionally rare species under more balanced configurations. The local community size k is 6. (a) Small evolutionary response, ΔG. (b) Large evolutionary response, ΔG.