Supporting Information

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Stability and Invasibility of Equilibria

Stability of Coexistence Equilibria. We can formally verify that a two-species equilibrium is stable by examining the derivative of $\frac{dp_1}{dt}$ with respect to p_1 and the derivative of $\frac{dp_2}{dt}$ with respect to p_2 at the equilibrium $(p_1,p_2)=(\widehat{p}_1,\widehat{p}_2)$; both must be negative for the equilibrium to be stable. Starting from the equations given in the main text,

$$\frac{dp_1}{dt}=m\left[(h_1-h_2)+h_2f_1\frac{p_1}{f_1p_1+f_2p_2}-p_1\right]$$

$$\frac{dp_2}{dt}=m\left[h_2f_2\frac{p_2}{f_1p_1+f_2p_2}-p_2\right].$$

We obtain

$$\frac{d\left(\frac{dp_1}{dt}\right)}{dp_1}=m\left[h_2f_1\frac{(f_1p_1+f_2p_2)-f_1p_1}{(f_1p_1+f_2p_2)^2}-1\right]=m\left[h_2f_1\frac{f_2p_2}{(f_1p_1+f_2p_2)^2}-1\right]$$

$$\frac{d\left(\frac{dp_2}{dt}\right)}{dp_2}=m\left[h_2f_2\frac{(f_1p_1+f_2p_2)-f_2p_2}{(f_1p_1+f_2p_2)^2}-1\right]=m\left[h_2f_2\frac{f_1p_1}{(f_1p_1+f_2p_2)^2}-1\right].$$

At the two-species coexistence equilibrium, where $\widehat{p}_1=\frac{f_2(h_1-h_2)}{f_2-f_1}$ and $\widehat{p}_2=\frac{h_2f_2-h_1f_1}{f_2-f_1}$,

we have

$$\left.\frac{d\left(\frac{dp_1}{dt}\right)}{dp_1}\right|_{p_1=\widehat{p_1},p_2=\widehat{p_2}}=m\left[h_2f_1\frac{f_2\left(\frac{h_2f_2-h_1f_1}{f_2-f_1}\right)}{(f_2h_2)^2}-1\right]=m\left[\frac{f_1(h_2f_2-h_1f_1)}{f_2h_2(f_2-f_1)}-1\right]$$

$$\left.\frac{d\left(\frac{dp_2}{dt}\right)}{dp_2}\right|_{p_1=\widehat{p_1},p_2=\widehat{p_2}}=m\left[h_2f_2\frac{f_1\left(\frac{f_2(h_1-h_2)}{f_2-f_1}\right)}{(f_2h_2)^2}-1\right]=m\left[\frac{f_1(h_1-h_2)}{h_2(f_2-f_1)}-1\right].$$

Thus the conditions for stability are

$$f_2h_2(f_2-f_1)>f_1(h_2f_2-h_1f_1)$$

$$h_2(f_2-f_1)>f_1(h_1-h_2).$$

Or equivalently

$$h_2f_2^2-2f_1f_2h_2+h_1f_1^2>0$$

$$h_2f_2>h_1f_1.$$

Because we have $h_2f_2>h_1f_1$ as a condition of coexistence, the second condition holds. And because $h_1>h_2$, we have

$$h_2f_2^2-2f_1f_2h_2+h_1f_1^2>h_2f_2^2-2f_1f_2h_2+h_2f_1^2=h_2(f_2-f_1)^2>0.$$

Thus the first condition holds. The equilibrium is stable.

The same procedure shows that the coexistence equilibria for three or more species are also stable.

Invasibility of Other Equilibria. We can formally evaluate whether a given equilibrium is invasible by species i by examining $\frac{dp_i}{dt}$ and its derivative with respect to p_i at the equilibrium. Here, I provide an example demonstrating the invasibility of both one-species equilibria in the case of two species that can coexist.

The equilibrium abundance of species 1 when it is the only species present is simply h_1. Thus, substitution into the equations obtained in the previous section shows that

$$\left.\frac{dp_2}{dt}\right|_{p_1=h_1,p_2=0}=0$$

and

$$\left.\frac{d\left(\frac{dp_2}{dt}\right)}{dp_2}\right|_{p_1=h_1;p_2=0}=m\left[\frac{h_2f_2}{f_1h_1}-1\right].$$

Because we have $h_2f_2>h_1f_1$ as a condition of coexistence, this derivative is positive. Thus, the growth rate of species 2 is increasing away from zero at $p_2=0$, which means species 2 can invade.

Similarly, the equilibrium abundance of species 2 when it is the only species present is simply h_2. At this equilibrium,

$$\left.\frac{dp_1}{dt}\right|_{p_1=0,\,p_2=h_2}=m[(h_1-h_2)];$$

that is, species 1 is increasing. (This reflects the simplistic assumptions of the basic model, which assume there is no seed limitation.) Thus, species 1 can invade.

The same procedure can be used to evaluate invasibility for systems of three or more species.

Invasion and Coexistence Conditions in the Basic Tolerance–Fecundity Model

Two Species. Two species satisfying $h_1>h_2$ and $f_2>f_1$ can coexist if and only if $f_2h_2>f_1h_1$. Thus, if there is single resident species (f_1,h_1), then a more tolerant and less fecund species (f,h) can always invade. It will coexist with (rather than exclude) the resident if and only if $fh<f_1h_1$ or, equivalently, $h<\frac{f_1h_1}{f}$ (Fig. 2*D*). A more fecund and less tolerant species can invade if and only if $fh>f_1h_1$ or, equivalently, $h>\frac{f_1h_1}{f}$ (Fig. 2*D*). It is able to coexist with the resident under all conditions that allow invasion.

Three Species. Three species satisfying $h_1>h_2>h_3$ and $f_3>f_2>f_1$ can coexist if and only if $f_3h_3>f_2h_2>f_1h_1$ and $\frac{(f_2h_2-f_1h_1)}{(f_2-f_1)}>\frac{(f_3h_3-f_2h_2)}{(f_3-f_2)}$. Suppose there are two coexisting resident species (f_1,h_1) and (f_2,h_2) and an invader (f,h). If the invader is more tolerant and less fecund than both residents, it can always invade. It will coexist with both residents if and only if $\frac{(f_1h_1-fh)}{(f_1-f)}>\frac{(f_2h_2-f_1h_1)}{(f_2-f_1)}$, equivalently, $fh<f_1h_1-\frac{(f_1-f)(f_2h_2-f_1h_1)}{(f_2-f_1)}$, or $h<\frac{f_1h_1}{f}-\frac{(f_1-f)(f_2h_2-f_1h_1)}{f(f_2-f_1)}$. An invader that is more fecund and less tolerant than both residents can invade if and only if $fh>f_2h_2$ or, equivalently, $h>\frac{f_2h_2}{f}$. It will coexist with both residents rather than excluding the less tolerant one if and only if $\frac{(f_2h_2-f_1h_1)}{(f_2-f_1)}>\frac{(fh-f_2h_2)}{(f-f_2)}$, equivalently, $fh<f_2h_2+\frac{(f_2h_2-f_1h_1)(f-f_2)}{(f_2-f_1)}$, or $h<\frac{f_2h_2}{f}+\frac{(f-f_2)(f_2h_2-f_1h_1)}{f(f_2-f_1)}$. A potential invader that is of intermediate fecundity and tolerance will be able to invade only if $\frac{(fh-f_1h_1)}{(f-f_1)}>\frac{(f_2h_2-fh)}{(f_2-f)}$ or, equivalently, $h>\frac{f_1h_1}{f}+\frac{f_2h_2(f-f_1)}{f(f_2-f)}$. It will coexist with both residents, rather than excluding the less tolerant species, if and only if $fh < f_2 h_2$ or, equivalently, $h < \frac{f_2 h_2}{f}$ (Fig. 2*E*).

Four or More Species. n species satisfying $h_1 > \ldots > h_k > \ldots > h_n$ and $f_n > \ldots > f_k > \ldots > f_1$ can coexist if and only if $f_n h_n > \ldots > f_k h_k > \ldots > f_1 h_1$ and also $\frac{f_2 h_2 - f_1 h_1}{f_2 - f_1} > \frac{f_3 h_3 - f_2 h_2}{f_3 - f_2} > \ldots > \frac{f_k h_k - f_{k-1} h_{k-1}}{f_k - f_{k-1}} > \frac{f_{k+1} h_{k+1} - f_k h_k}{f_{k+1} - f_k} > \ldots > \frac{f_n h_n - f_{n-1} h_{n-1}}{f_n - f_{n-1}}$. Suppose there are $n > 3$ resident species (f_1, h_1), (f_2, h_2), … (f_n, h_n), and an invader (f, h). As in all cases, an invader that is more tolerant and less fecund than all residents can always invade. As in the three-species case, it will coexist with all residents if and only if $\frac{(f_1 h_1 - fh)}{(f_1 - f)} > \frac{(f_2 h_2 - f_1 h_1)}{(f_2 - f_1)}$ or, equivalently, $h < \frac{f_1 h_1}{f} - \frac{(f_1 - f)(f_2 h_2 - f_1 h_1)}{f(f_2 - f_1)}$. As in all cases, an invader that is more fecund and less tolerant than all residents can invade if and only if the product of its fecundity and stress tolerance exceeds that of the most fecund resident, i.e., if $fh > f_n h_n$ or, equivalently, $h > \frac{f_n h_n}{f}$. As in the three-species case, it will coexist with all residents rather than excluding the least tolerant one if and only if $\frac{(f_n h_n - f_{n-1} h_{n-1})}{(f_n - f_{n-1})} > \frac{(fh - f_n h_n)}{(f - f_n)}$, equivalently, $fh < f_n h_n + \frac{(f_n h_n - f_{n-1} h_{n-1})(f - f_n)}{(f_n - f_{n-1})}$, or $h < \frac{f_n h_n}{f} + \frac{(f_n h_n - f_{n-1} h_{n-1})(f - f_n)}{f(f_n - f_{n-1})}$. A potential invader that is of intermediate fecundity and tolerance between species k and species $k + 1$ will be able to invade if and only if $\frac{(fh - f_k h_k)}{(f - f_k)} > \frac{(f_{k+1} h_{k+1} - fh)}{(f_{k+1} - f)}$ or, equivalently, $h > \frac{f_k h_k}{f} + \frac{f_{k+1} h_{k+1}(f - f_k)}{(f_{k+1} - f)}$. If there is only one resident with higher fecundity, then it will coexist with this resident (rather than exclude it) if and only if $fh < f_n h_n$ or, equivalently, $h < \frac{f_n h_n}{f}$. If there are two or more residents with higher fecundity, it will coexist with them (rather than excluding the next more fecund species, species $k + 1$), if and only if $\frac{f_{k+1} h_{k+1} - fh}{f_{k+1} - f} > \frac{f_{k+2} h_{k+2} - f_{k+1} h_{k+1}}{f_{k+2} - f_{k+1}}$ or, equivalently, $h < \frac{f_{k+1} h_{k+1}}{f} - \frac{(f_{k+1} - f)(f_{k+2} h_{k+2} - f_{k+1} h_{k+1})}{f(f_{k+2} - f_{k+1})}$.

If there are two or more residents with higher tolerance, it will coexist with them both (rather than excluding the next more tolerant, species k), if and only if $\frac{f_k h_k - f_{k-1} h_{k-1}}{f_k - f_{k-1}} > \frac{fh - f_k h_k}{f - f_k}$ or, equivalently, $h < \frac{f_k h_k}{f} + \frac{(f - f_k)(f_k h_k - f_{k-1} h_{k-1})}{f(f_k - f_{k-1})}$ (Fig. 2*F*).

Note that in general, invasion conditions for interior species in the n-species case depend only on the single next more fecund and single next less fecund species. In contrast, whether such an invader coexists with all of the residents depends on the two next more fecund and the two next less fecund species. The reason is that the abundance of an interior species always depends on its parameter values and the parameter values of its first nearest neighbor species on both sides. Invasion requires only that the invader's abundance is greater than zero and thus depends only on these first nearest neighbors. In contrast, coexistence requires also that the species on each side of the neighbor continue to have abundances greater than zero, and this depends on their nearest neighbors as well.

The Tolerance–Fecundity Model with Poisson Seed Rain

Here I consider how Poisson seed rain alters dynamics and coexistence conditions under the tolerance–fecundity model. This is the simplest formulation of seed limitation and is the one commonly used in the competition–colonization model. Poisson seed rain captures only seed limitation due to limited population-level seed production (source limitation), not additional limitation due to clumping and limited dispersal (dispersal limitation). For convenience, let us denote the equilibrium abundance under Poisson seed rain of species i as $\tilde{p}_i$ and refer to it as the seed-limited equilibrium abundance, thus distinguishing it from the equilibrium abundance under uniform seed rain, denoted $\widehat{p}_i$, and referred to as the seed-saturated equilibrium abundance.

One-Species Case. It is useful to begin by considering persistence conditions for a single species in isolation. Because seed rain is not uniform, seeds will fail to reach a proportion of sites equal to $\exp(-f_1 p_1)$. Thus, at equilibrium,

$$\tilde{p}_1 = h_1(1 - \exp(-f_1 \tilde{p}_1))$$

That is, species 1 occupies that fraction of the habitat in which it can recruit, h_1, at which its seeds arrive. We can obtain an approximate solution to this by first substituting in the second-order Taylor expansion of the exponential function [that is, $\exp(x) \approx 1 + x + x^2/2$], which leads to the equation

$$\tilde{p}_1 \approx h_1\left(1 - \left(1 - f_1 \tilde{p}_1 + \frac{(f_1 \tilde{p}_1)^2}{2}\right)\right).$$

The solution to this equation is

$$\tilde{p}_1 \approx \frac{2(f_1 h_1 - 1)}{f_1^2 h_1^2}.$$

This approximate solution is good for $f_1 p_1$ close to zero and becomes progressively worse as this quantity increases, as shown by comparisons with simulation results (Fig. S1). Note that this is quite different from the solution in the case of uniform seed rain, which is simply $\widehat{p}_1 = h_1$ (Fig. S1).

The equilibrium abundance of a single species will be greater than zero only if $f_1 h_1 > 1$. Thus, this species can invade an empty habitat only if this condition is met. In the case of uniform seed rain with no seed limitation, equilibrium abundance and the possibility of invading and persisting are insensitive to the absolute value of the fecundity. Here, in contrast, they depend directly on absolute fecundity. Note also that the condition for invasion and persistence can equivalently be written $f_1 \widehat{p}_1 > 1$, that is, as a requirement that the product of a species' fecundity and its seed-saturated equilibrium abundance be greater than one. I conjecture that this will prove to be a general condition for a species to invade under Poisson seed rain.

Two-Species Case. When considering the dynamics of two interacting species under Poisson seed rain, we need to account for the probabilities of each seed winning each type of site under all possible combinations of numbers of seeds arriving of each species. Thus, at equilibrium,

$$\tilde{p}_1 = (h_1 - h_2)(1 - \exp(-f_1 \tilde{p}_1)) + h_2 \sum_{i=1}^{\infty} \sum_{j=0}^{\infty} \left[\left(\frac{(f_1 \tilde{p}_1)^i \exp(-f_1 \tilde{p}_1)}{i!}\right)\left(\frac{(f_2 \tilde{p}_2)^j \exp(-f_2 \tilde{p}_2)}{j!}\right)\left(\frac{i}{i+j}\right)\right]$$

$$\tilde{p}_2 = h_2 \sum_{i=0}^{\infty} \sum_{j=1}^{\infty} \left[\left(\frac{(f_1 \tilde{p}_1)^i \exp(-f_1 \tilde{p}_2)}{i!}\right)\left(\frac{(f_2 \tilde{p}_2)^j \exp(-f_2 \tilde{p}_2)}{j!}\right)\left(\frac{j}{i+j}\right)\right].$$

Essentially, species 1 occupies that fraction of $(h_1 - h_2)$ in which its seeds arrive, plus a fraction of h_2 that reflects the probability that i of its seeds arrive (the first term in parentheses after the summation), j seeds of species 2 arrive (the second term), and its probability of winning under those arrivals (the last term), summed over all possible seed arrivals i and j. The fraction of h_2 occupied by species 2 is calculated in like fashion. Note that now $p_1 + p_2 < h_1$, because there is nonzero probability that both species will fail to arrive in sites where both can recruit, and that species 1 will fail to arrive in sites where only it can recruit.

These equations cannot be solved for the equilibrium abundances in closed form, but they can be solved numerically through iteration (essentially simulation). Simulations show that two species whose respective stress tolerances and the ratio of whose fecundities together enable coexistence in the case of uniform seed rain can also coexist under Poisson seed rain provided that $f_1\hat{p}_1 > 1$ and $f_2\hat{p}_2 > 1$; that is, the product of fecundity and seed-saturated equilibrium abundance must be greater than one for both species. Whereas before the lifetime of individual species and the units of fecundity were irrelevant, now we must consider these as well. Fecundity here is the number of seeds produced per site occupied by an adult per year (or, equivalently, regeneration season).

It is instructive to specifically examine the dynamics of a typical pair of interacting and potentially coexisting species as we scale the fecundities of both species up and down (Fig. 3*B*, Fig. S2). Recall that in the case of uniform seed rain, the absolute values of fecundities were unimportant, and thus such scaling would make no difference to equilibrium abundances. With Poisson seed rain, in contrast, very low fecundities do not admit the persistence of either species (Fig. S2 *A* and *F*). As fecundities of both species are increased in parallel, the more fecund species first becomes able to persist, and then at still higher fecundities both species coexist, converging eventually on seed-saturated equilibrium abundances (Fig. S2).

Coexistence conditions under the case of Poisson seed rain are more restrictive than in the case of uniform seed rain (Fig. 3*A*). In particular, the requirements $f_1\hat{p}_1 > 1$ and $f_2\hat{p}_2 > 1$ can be rewritten $\hat{p}_1 > 1/f_1$ and $\hat{p}_2 > 1/f_2$. In contrast, under uniform seed rain these quantities need only be greater than zero. Thus, coexistence requires that $f_2 h_2 > f_1 h_1 + \frac{f_2 - f_1}{f_2}$ (not simply $f_2 h_2 > f_1 h_1$) and $h_1 > h_2 + \frac{f_2 - f_1}{f_1 f_2}$ (not simply $h_1 > h_2$). A species that is more tolerant and less fecund than the resident species 1 can invade only if its stress tolerance h and fecundity f satisfy $h > h_1 + \frac{f_1 - f}{f f_1}$, and it will coexist with the resident only if $fh < f_1 h_1 - \frac{f_1 - f}{f_1}$. A more fecund (and less tolerant) species can invade only if $fh > f_1 h_1 + \frac{f - f_1}{f}$, and it will coexist only if $h < h_1 - \frac{f - f_1}{f f_1}$. This represents a distinct narrowing of the parameter range that enables coexistence relative to that for uniform seed rain (compare Figs. 2*D* and 3*A*).

***n*-Species Case.** For $n > 2$ species under Poisson seed rain, the equations for abundances at equilibrium are straightforward, if long, to write down. Now the conjectured conditions for coexistence are $f_k\hat{p}_k > 1$ for $1 \le k \le n$. This means that $\hat{p}_k > 1/f_k$ for all k—effectively setting minimum abundances for all species. Using the equations for the seed-saturated equilibrium for the n-species case, the conjectured conditions for coexistence are thus $h_1 - h_2 > \frac{f_2 - f_1}{f_1 f_2}$, $f_n h_n > f_{n-1} h_{n-1} + \frac{f_n - f_{n-1}}{f_n}$, and $\frac{h_k f_k - h_{k-1} f_{k-1}}{f_k - f_{k-1}} > \frac{h_{k+1} f_{k+1} - h_k f_k}{f_{k+1} - f_k} + \frac{1}{f_k}$ for $1 < k < n$.

The last condition takes the place of the less restrictive condition $\frac{h_k f_k - h_{k-1} f_{k-1}}{f_k - f_{k-1}} > \frac{h_{k+1} f_{k+1} - h_k f_k}{f_{k+1} - f_k}$ found for uniform seed rain. This reduces the range of parameters compatible with coexistence relative to the case of uniform seed rain and, in particular, admits of parameter combinations for two resident species that make it impossible for any intermediate species to invade and coexist with them.

Simulations confirm that these conditions correspond to parameter combinations at which species are able to invade and coexist. As in the two-species case, it is instructive to consider how the equilibrium changes as fecundity is scaled up for a group of three species whose habitat tolerance values and ratio of fecundities allow coexistence for high enough values of fecundity (Fig. S3). As fecundity is increased in parallel for all species starting from very low values, species 3 is the first to be able to persist (Fig. S3 *A* and *B*), then species 2 (Fig. S3*C*), and then species 1 (Fig. S3*D*), with equilibrium abundances eventually converging on seed-saturated values (Fig. S3 *E* and *F*).

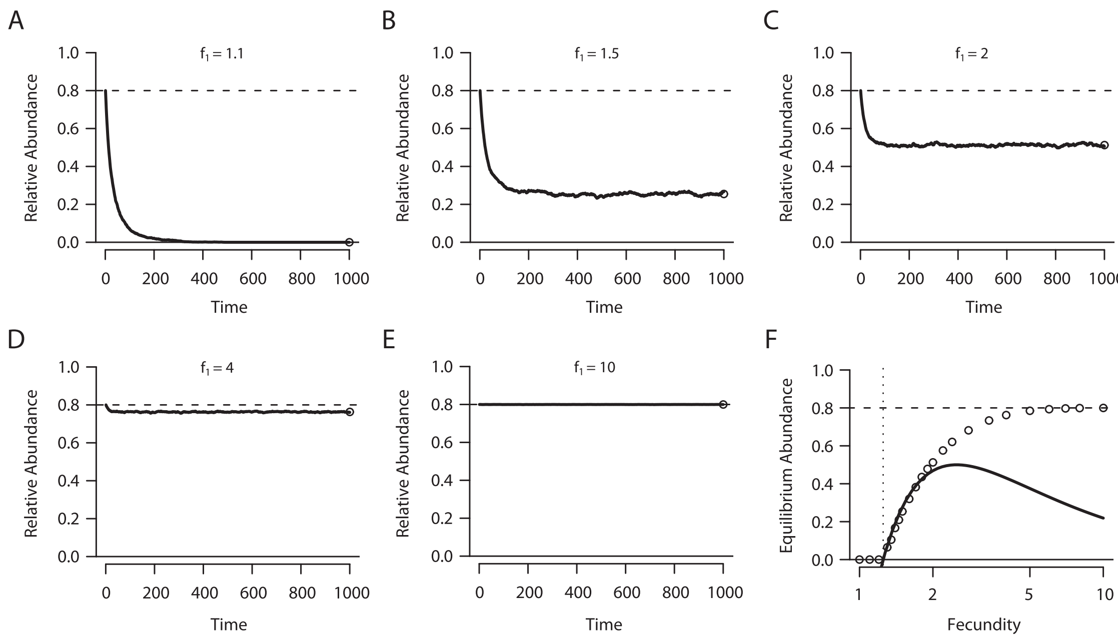

Fig. S1. Simulation results for abundance of a single species when dynamics are governed by the tolerance–fecundity model with Poisson seed rain. Here the single species has habitat tolerance $h_1 = 0.8$, and thus its seed-saturated equilibrium abundance (as a proportion of total area that it occupies) is 0.8 (dashed line). If its fecundity, $f_1 < 1/h_1$ (vertical dotted line in *F*), then the species cannot maintain itself and quickly dies out (*A*). For fecundities above this threshold, the equilibrium abundance under Poisson seed rain (circles) gradually increases (*B*–*E*) toward the equilibrium in the absence of seed limitation (0.8). Overall, the Taylor series-based approximation (*F*, thick line) provides a good fit to the observed equilibrium abundance in the simulations (circles) for fecundities close to the threshold for persistence. In each simulation, the total area comprises 10,000 cells, each of which can support one adult; 10% of adults die each time step; and initial abundance is equal to the seed-saturated abundance. The equilibrium abundance of a species in a simulation is calculated as its mean abundance for time steps 501–1,000. Fecundity is defined as the mean seed production per adult per time step.

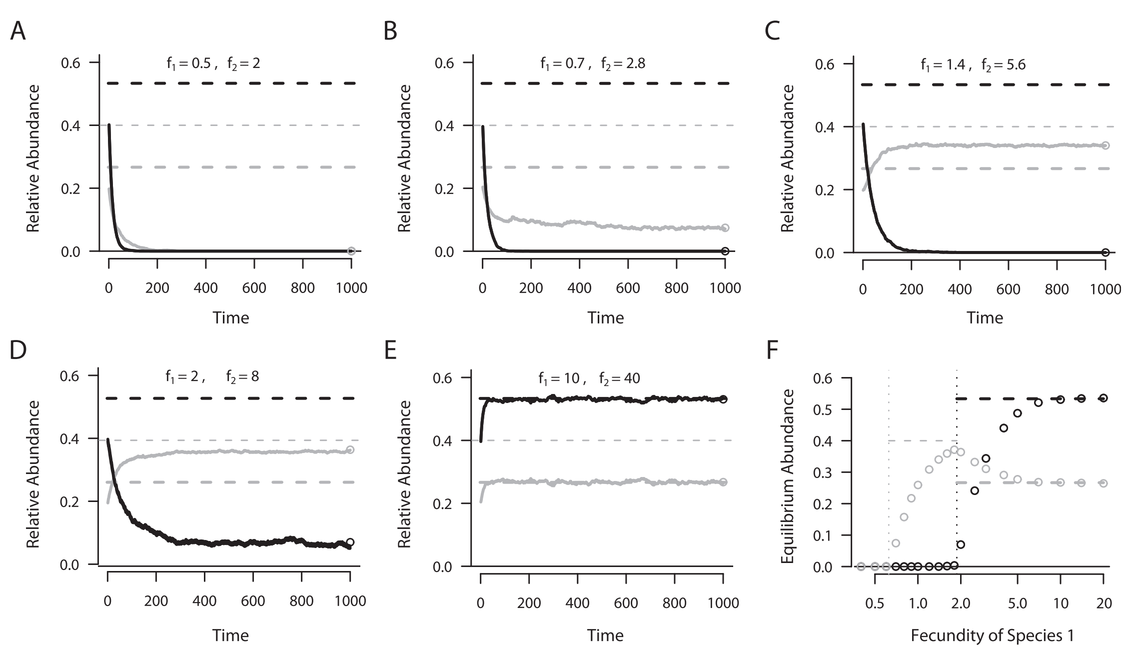

Fig. S2. Simulation results for abundances of two species when dynamics are governed by the tolerance–fecundity model with Poisson seed rain. Here the species have habitat tolerances $h_1 = 0.8$ and $h_2 = 0.4$, and the fecundity of species 2 is always four times that of species 1. Thus the seed-saturated equilibrium abundance of species 2 when alone is 0.4 (dashed thin gray line). If the fecundity of the more fecund species, $f_2 < 1/h_2$ (dotted gray line in *F*), then neither species can maintain itself (*A*). As fecundities are increased in parallel above this threshold, the seed-limited equilibrium abundance of species 2 initially increases toward its seed-saturated equilibrium abundance in isolation whereas species 1 remains unable to persist (*B* and *C*). Once the fecundities are increased such that $f_1 > 1/\widehat{p}_1$ (dotted black line in *F*), then species 1 can also persist (*D*). As fecundities increase further, the seed-limited equilibrium abundances approach the seed-saturated abundances under 2-species coexistence (thick dashed lines). Simulations were performed as for Fig. S1.

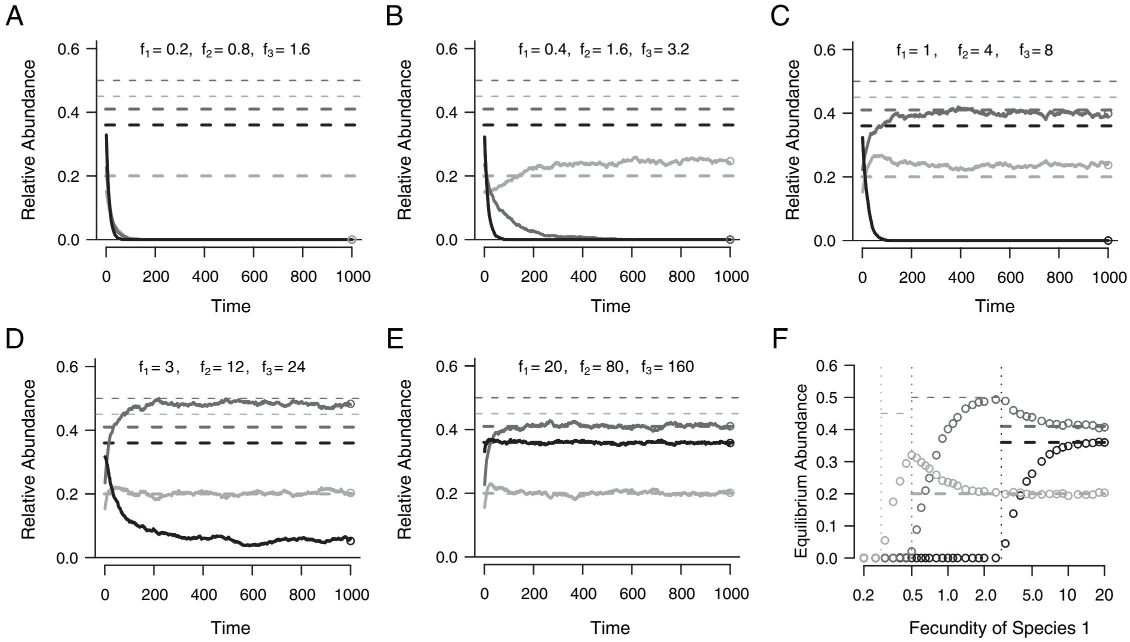

Fig. S3. Simulation results for abundances of three species when dynamics are governed by the tolerance–fecundity model with Poisson seed rain. Here the species have habitat tolerances $h_1 = 0.97$, $h_2 = 0.7$, and $h_3 = 0.45$, and the fecundities of species 2 and 3 are always four and eight times that of species 1, respectively. If the fecundity of the most fecund species, $f_3 < 1/h_3$, then none of the species can maintain itself (*A*). As fecundities are increased in parallel above this threshold (dotted light gray line in *F*), the seed-limited equilibrium abundance of species 3 initially increases toward its seed-saturated equilibrium abundance when alone (dashed thin light gray line), whereas species 1 and 2 remain unable to persist (*B*). Species 2 becomes able to persist and coexist with species 3 (*C*) once its fecundity exceeds a threshold (dotted dark gray line in *F*) that equals the inverse of its seed-saturated equilibrium abundance when coexisting with species 3 alone; with higher fecundities abundances of both species 2 and 3 first converge on their seed-saturated equilibria under two-species coexistence (dashed thin dark gray line for species 2; dashed thick light gray line for species 3). Once fecundities are further increased such that $f_1 > 1/\hat{p}_1$ (dotted black line in *F*), then species 1 can also persist and all three species coexist (*D*). As fecundities increase further, the seed-limited equilibrium abundances approach the seed-saturated abundances under three-species coexistence (thick dashed lines in *E* and *F*). Simulations were performed as for Fig. S1.