Revising the tolerance-fecundity tradeoff, or On the consequences of discontinuous resource use for limiting similarity, species diversity, and trait dispersion

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Abstract

The recently proposed tolerance-fecundity tradeoff model represents a step forward in the study of seed size diversity in plant communities. However, it uses a oversimplified picture of seed tolerance, with an infinitely sharp threshold: the probability that a seed tolerate a given stress level is either 1 or 0. This invites a revision of the model, presented here. We demonstrate that this simplification has large impacts on model behavior, including altering predictions regarding limiting similarity, raising expected diversity levels, and lessening expected spacing between species along the trait axis. Such dramatic impacts ultimately stem from the fact that a discontinuity in the probability of tolerating a site drastically reduces competition between similar species. This is one example of a class of models with a non-differentiable peak in the competition kernel, which we recently showed is produced by resource use unrealistically modeled as discontinuous, and affects fundamental predictions regarding limiting similarity. This paper illustrates those general results, and offers a revised model of the tolerance-fecundity tradeoff.

Keywords: competition-colonization tradeoff, continuous coexistence, discontinuous resource use, diversity, nonsmooth competition kernel, species packing

Introduction

In ecologists' never-ending quest to understand coexistence of competing species, tradeoffs are often assumed to be key (Kinzig et al. 1999, Bonsall et al. 2004, Adler et al. 2007). In the context of competition in plant communities mediated by seed size, the most commonly used approach is to postulate an exchange between competitive ability and fecundity (or colonization ability): smaller seeds are cheap and thus produced in great numbers, whereas larger seeds provide for stronger competitive ability and thus the capacity to displace weaker individuals (Levins 1969, Tilman 1994, Kinzig et al. 1999). This competition-colonization tradeoff idea has been utilized by several authors since at least the 70s (see Kinzig et al. 1999 and their references). However, the assumption that larger seeds have a fixed competitive advantage over smaller seeds regardless of environmental conditions lacks empirical support (Yu and Wilson 2001, Coomes and Grubb 2003, Eriksson 2005). Motivated by this mismatch between theory and empirical observation, Muller-Landau (2010) proposed a novel type of tradeoff model of seed size diversity, according to which a tradeoff between fecundity (as measured by number of seeds) and tolerance to stressful conditions such as drought and shade guarantee coexistence of species with seeds of different sizes. Here, the advantage of the large seed over its lower-sized competitor is contingent upon the stress level of the particular site they land on: the big seed is favored only if the stress level is beyond the tolerance threshold of the small seed.

Although representing an improvement over competition-colonization models of seed size diversity that did not contain an empirically supported element of contingency to competitive advantage, the TFM as proposed by Muller-Landau is based on a highly simplified picture of seed tolerance, and effectively, species' use of habitat. In the model, the size of a seed is associated with a tolerance threshold that defines its ability to survive in a given patch: if the stress level in the patch is below that threshold, the seed can fully tolerate the conditions in that patch, and its survival is limited only by competition with other seeds; otherwise, the seed is simply unable to recruit. In other words, each species' seed tolerance switches from 100% to 0% as stress increases past a threshold value, with nothing in between. It is highly unlikely such an infinitely sharp transition would occur in nature, where immanent small amounts of variation in phenotype or environmental conditions experienced within a species would suffice to smooth out the transition.

Muller-Landau acknowledges this simplifying assumption and argues that it would likely be of little consequence for the fundamental coexistence-generating nature of the tradeoff described by the model (Muller-Landau 2010). We agree. However, we point out that the assumption has potential consequences to the level of coexistence that is possible. In this scenario, no matter how similar the seed sizes of two given species, there will always be patches perfectly accessible to species A, but utterly out of reach for species B. In other words, niche overlap between two species is always limited, however similar they may be. Thus, though the assumption may not be essential to guarantee coexistence per se, it may have significant impacts on how much coexistence is allowed, and hence may impact how much diversity can be explained in practice by the tolerance-fecundity tradeoff.

It is the purpose of this article to demonstrate the strong implications of the discontinuity in the tolerance function onto the tolerance-fecundity tradeoff model. First, we highlight the implications of this assumption for predictions regarding coexistence of a continuum of arbitrarily similar species (*continuous coexistence*, or *tight packing* in the real-world case of a finite number of species) and the related concept of limits to similarity, which itself has had a broad influence in ecology and evolution (Schoener 1974, Rosenzweig 1978, Futuyma 1988, Chesson 1991, Grant and Grant 2006). We then examine how this assumption bears on predicted levels of diversity and trait dispersion. To do so, we develop a revised model where the assumption is dropped, and examine how predictions are affected by this change.

The notion that continuous coexistence is not possible in nature began with the work of MacArthur and Levins (1967), who showed that, in a simple model of Lotka-Volterra competition, stable coexistence of a set of three species requires some minimum spacing between them on a trait axis. Despite later work showing that in fact continuous coexistence can be produced in that simple model (Roughgarden 1979), ultimately it was proven that, for a wide class of competition models, any possible continuous coexistence is not robust to small changes in parameters, and in this sense these models always predict system-specific limits to the similarity of stably and robustly coexisting species (Gyllenberg and Meszéna 2005). Although technically possible given that the proof does not extend to all possible competition models, examples of models that actually predict robust tight packing have not been presented previously.

Here we show that Muller-Landau's tolerance-fecundity tradeoff model predicts robust continuous coexistence. Upon removal of the discontinuity in the model, however, the model no longer admits continuous coexistence at all. Hence the original version sees no fundamental limits to the similarity of species coexisting through this mechanism, whereas the revised version predicts such limits. Further, we find that the revised model predicts lower diversity and more detectable even spacing among species. Our demonstration that the shape of the tolerance function, a central feature of the model, has a profound and consistent influence on predicted levels of diversity and trait dispersion adds to Muller-Landau's contribution, and provides guidance to future empirical work regarding the link between this shape and the degree to which maintenance of observed diversity and dispersion in seed size can actually be attributed to the tolerance-fecundity tradeoff.

We note that the considerable differences in predictions found here are an example of more general results from our recent work on the relationship between continuity in resource use and robust continuous coexistence (Barabás et al. 2012). We thus argue that our results extend to any model with this offending property, of which Muller-Landau's model is by no means the sole example. The general results we illustrate here using the tolerance-fecundity tradeoff model as an example suggest caution when constructing models to study limiting similarity, diversity, and patterns of trait dispersion.

The tolerance-fecundity tradeoff model

Original formulation

The dynamics of the tolerance-fecundity tradeoff model (Muller-Landau 2010) are as follows. The community is assumed to be saturated with adult individuals which pre-empt establishment of propagules. Every time step, however, some individuals die, making sites available to propagules and enabling competition among them – in fact, in this model competition only occurs at the establishment phase. The number of seeds of a given species landing on a site is assumed to be proportional to the product of the fraction of sites occupied by that species, p_k, and its fecundity, f_k (i.e., no dispersal limitation is being considered – Muller-Landau also examined chance dispersal limitation through a Poisson-distributed seed rain and found no qualitative change in model behavior). Species are ordered by fecundity level from f_1 to f_n, with species 1 being the least fecund (and most tolerant) and species n being the most fecund (and least tolerant). In a fraction h_k of the sites, species k can fully tolerate the stress level, and in the remaining fraction it cannot tolerate it at all. Then given all the seeds that reach and tolerate the same site, a lottery decides which seed eventually recruits into an adult (Figure 1A). Given those conditions, the population growth rate of species k can be written as

$$\frac{dp_k}{dt} = m\left(f_k \sum_{i=k}^{n} \frac{h_i - h_{i+1}}{\sum_{j=1}^{i} f_j p_j} - 1 \right) p_k. \tag{1}$$

The first term on the right-hand side corresponds to recruitment of new individuals, and the second term reflects mortality. Both terms are proportional to species abundance p_k and mortality rate m (assumed constant across species for simplicity). The recruitment term is proportional to the species' fecundity f_k, and total recruitment is a sum over recruitment in colonizable patches, which include all the patches colonizable by species coming further down the hierarchy. For each fraction of patches colonizable by one species i $(i > k)$ but not the subsequent species, $h_i - h_{i+1}$, recruitment there is weighted by the total number of seeds that could potentially colonize, $\Sigma f_j p_j$. Notice that $h_n < h_{n-1} < \cdots < h_1$ and $h_{k>n} = 0$ are assumed.

Note that Muller-Landau postulated an unambiguous association between a given fecundity value (defined as the number of seeds produced by each individual of a certain species) and a unique

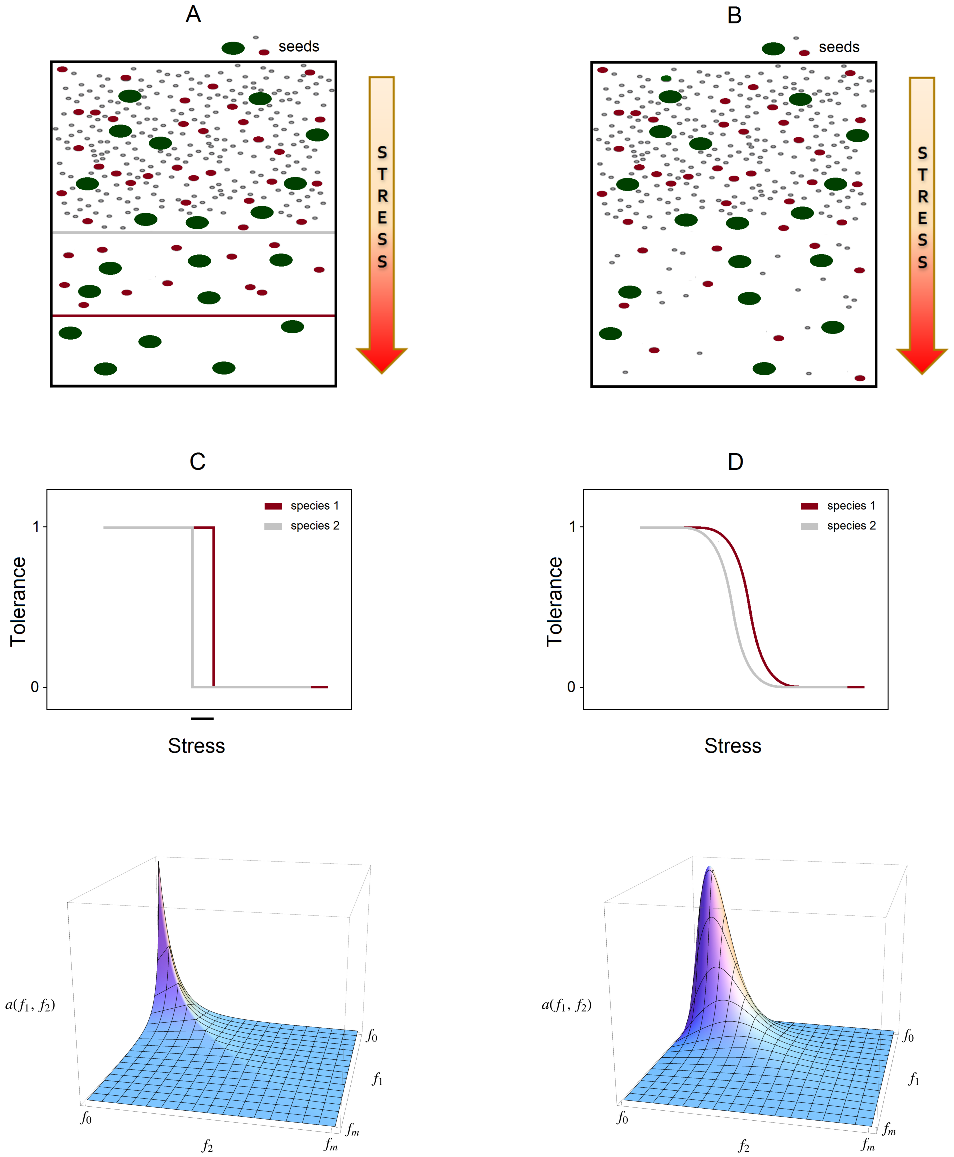

Figure 1: **A**: Cartoon representation of the distribution of seeds given a gradient in habitat stress according to Muller-Landau's assumption of all-or-nothing tolerance. Three seed sizes are represented. Density in seed numbers across habitat represents tolerance levels. The smallest seeds (light grey) occur with uniform density (constant tolerance) through sites with increasing stress levels, up to a threshold – marked by the gray line – beyond which no small seeds are found (zero tolerance). Intermediate-sized seeds (red), occur with uniform density until their own stress threshold is reached – red line – beyond which no medium-sized seeds occur. Large seeds (green) occur uniformly throughout the patch, as its particular threshold is never reached. **B**: Analogous representation in the case where the tolerance function varies continuously. Here, all seeds occur in increasingly lower densities as stress levels increase, and there is no sharp threshold separating sites where seeds occur from sites where they are absent. **C**: When tolerance curves of different species are overlaid, it becomes clear that given any pair of species, no matter how similar, there is always a range of stress levels (resources) that is at once perfectly accessible to the more tolerant of the pair and absolutely out of reach to the other. This range is indicated in the figure by the black bar. **D**: When the tolerance function is continuous, that range disappears. Instead, the way arbitrarily similar species use resources becomes arbitrarily similar, thus making for higher competition than in the previous case. **E**: Illustration of the competition kernel $a(f,f')$ when the tolerance function is discontinuous, showing an infinitely sharp ridge at $f=f'$. A 2D projection of this surface would show a curve with a kink at its peak. **F**: When the tolerance function is continuous – here modeled as $T(\sigma,f)=\frac{1}{2}(1+\mathrm{erf}[\nu(s(f)-\sigma)])$ – the ridge is absent, and the surface is smooth across its domain.

seed size. In other words, she assumed no noise in the relationship between seed size and species fecundity. This enabled her to focus on fecundity as the trait axis but draw from it conclusions about maintenance of seed size diversity. We will keep this simplified scenario, and regard the fecundity axis as the trait axis for the remainder of this article.

As just described, in Eq. 1 the recruitment term is a sum over the prevalence of different types of sites, categorized by the number of species that can tolerate them. The fact that the recruitment term can even be organized this way is the telltale sign of the simplified picture of seed tolerance used in the model. Note that no matter how similar two species i and $i+1$ are in their seed size and fecundity, species i has unfettered access to a proportion of the sites that species $i+1$ has no access whatever, namely $h_i - h_{i+1}$ of them. If seeds have some likelihood of tolerance of a given stress level other than 100% or 0%, then that must be factored into a species' probability to colonize a given site, and subsequently sites cannot be sorted by who can or cannot tolerate them as above; instead the stress level at each site must be considered.

Revised formulation

We now describe our revised version of the tolerance-fecundity tradeoff model. We rewrite the model from first principles, maintaining the same basic dynamics as Muller-Landau's model, except that we now allow for species' tolerance of a site to be a continuous function of the stress level at that site (Figure 1B).

We first note that for mathematical convenience we consider a pool of species forming a continuum, with all possible fecundity values in the range $[f_0, f_m]$ represented, because we will later study the potential for coexistence of arbitrarily similar species ('continuous coexistence'). Although such continuum is a mathematical abstraction that can't occur in nature, where only a finite number of species are available, we want to know how tightly packed that finite number of species can be, or correspondingly whether there are limits to the similarity of a finite set of coexisting species. Considering the possibility of continuous coexistence enables us to see whether such limits exist.

Let us divide our total area into sites (each colonizable by at most one individual), characterized by their stress level σ. Let c be the total number of sites. Let $n(f)$ be the number of individuals with fecundity f. Then

$$\frac{dn}{dt}(f) = \underbrace{(\text{\# of seeds that recruit})}_{fn(f)\int Q(\sigma,f)\,d\sigma} - \underbrace{(\text{death})}_{m(f)\,n(f)}. \tag{2}$$

Here $m(f)$ is the mortality rate, and $Q(\sigma, f)$ is the probability that a given seed from an individual of fecundity f germinates in a site of stress level σ. Following Muller-Landau, we do not include displacement terms: once an individual occupies a site, it cannot be displaced by another until it dies. This reflects the assumption that competition occurs only at the seed stage.

To determine $Q(\sigma, f)$, we need to examine the probability of a given seed to arrive at an available site, and then consider its probability of successfully recruiting. Let $T(\sigma, f)$ denote the probability that a seed produced by an individual of fecundity f arriving at a site of stress σ successfully recruits there. Let $c(\sigma)$ be the number of sites of stress level σ (thus $c = \int c(\sigma)d\sigma$). The total number of colonizable sites of stress σ is equal to $c(\sigma)$ minus the number of occupied sites, or $(c(\sigma) - \int n(\sigma, f)\,df)$, where $n(\sigma, f)$ is the number of individuals of fecundity f occupying sites of stress σ (note that $n(f) = \int n(\sigma, f)d\sigma$). Therefore, the a priori probability of a given seed landing on any of the empty sites of stress level σ per unit time is $(c(\sigma) - \int n(\sigma, f)\, df)/c$. However, the seed has to survive the stress level of the site, so this has to be weighted by $T(\sigma, f)$. Additionally, we need to consider the probability that, once this seed gets there and is able to survive the local stress level, it wins over the competition with rival seeds. This probability is just the inverse of the total number of seeds arriving at the site and able to recruit there as well, namely $(\int f\, n(f) T(\sigma, f)\, df)/c$. We therefore arrive at the stress-dependent probability of colonization:

$$Q(\sigma, f) = \frac{T(\sigma, f)\big(c(\sigma) - \int_{f_0}^{f_m} n(\sigma, x)\, dx\big)/c}{\big(\int_{f_0}^{f_m} y\, n(y) T(\sigma, y)\, dy\big)/c} = \frac{T(\sigma, f)\big(c(\sigma) - \int_{f_0}^{f_m} n(\sigma, x)\, dx\big)}{\int_{f_0}^{f_m} y\, n(y) T(\sigma, y)\, dy},$$

where f_0 and f_m are, respectively, the minimum and maximum fecundity within the community.

We should have an intuitive idea of the functional form of the function $T(\sigma, f)$: the species with fecundity f should be able to tolerate stress levels below a certain threshold $s(f)$ fairly well, but should be less successful at levels above that threshold. $T(\sigma, f)$ should tend to one at low σ and zero at high σ, and the transition between these extremes should center at $s(f)$.

Putting together what we have so far, our model reads

$$\frac{dn}{dt}(f) = \left(f \int_{\sigma_0}^{\sigma_m} \frac{T(\sigma, f)(c(\sigma) - \int_{f_0}^{f_m} n(\sigma, x)\, dx)}{\int_{f_0}^{f_m} y\, n(y) T(\sigma, y)\, dy}\, d\sigma - m(f) \right) n(f), \tag{3}$$

where σ_0 and σ_m are respectively the lowest and highest stress levels in the patch. It is convenient to convert the absolute population abundances to proportions. This is done by defining $p(f) = n(f)/c$, so that $\int p(f) \leq 1$. Eq. 3 becomes

$$\frac{dp}{dt}(f) = \left(f \int_{\sigma_0}^{\sigma_m} \frac{T(\sigma, f)(c(\sigma)/c - \int_{f_0}^{f_m} p(\sigma, x)\, dx)}{\int_{f_0}^{f_m} y\, p(y) T(\sigma, y)\, dy}\, d\sigma - m(f) \right) p(f). \tag{4}$$

The model can be simplified by assuming saturation: each site is occupied and will only become available through deaths. In this case, the proportion of sites of stress σ being made available at any moment, $c(\sigma)/c - \int p(\sigma, x)\, dx$, is expressible as the number of deaths that occurred, $\int p(\sigma, x) m(x)\, dx$. In the saturated case, therefore, we have

$$\frac{dp}{dt}(f) = \left(f \int_{\sigma_0}^{\sigma_m} \frac{T(\sigma, f) \int p(\sigma, x) m(x) dx}{\int_{f_0}^{f_m} y\, p(y) T(\sigma, y)\, dy}\, d\sigma - m(f) \right) p(f). \tag{5}$$

We can further simplify things by assuming uniform mortality across species: $m(f) = m$. We then get

$$\frac{dp}{dt}(f) = m \left(f \int_{\sigma_0}^{\sigma_m} \frac{r(\sigma) T(\sigma, f)}{\int_{f_0}^{f_m} y\, p(y) T(\sigma, y)\, dy}\, d\sigma - 1 \right) p(f), \tag{6}$$

where $r(\sigma) = \int p(\sigma, f)\, df$ is the proportion of occupied sites of stress level σ within the full habitat (which in the saturated case is the total proportion of sites of level σ).

In words, Eq. 6 tells us that the dynamics of a species labelled by its fecundity f is determined by a recruitment term and a mortality term, both of which are proportional to the mortality given our saturation assumption. Mortality is being assumed a species-independent parameter, and recruitment is the sum of successful recruitment in each class of sites (defined by their stress level σ). Eq. 6 is our revised tolerance-fecundity tradeoff model.

In Online Appendix A, we show that Muller-Landau's original formulation of the model can be obtained from our revised formulation if to each species f there is an associated stress threshold, $s(f)$, and $T(\sigma, f)$ is defined as the unit step function $\Theta(s-\sigma)$, defined as 1 if $\sigma \leq s$ and 0 if $\sigma > s$. Importantly, this characterizes a discontinuous transition in stress tolerance (Figure 1C). Clearly, this state of affairs is a caricature of nature: site colonization by plants mediated by seed size is not truly expected to rely on stress thresholds that determine absolutely the fate of the seed (Muller-Landau 2010).

If, conversely, we define $T(\sigma, f)$ as a continuously varying function, then sites of increasing stress levels present correspondingly increasing levels of difficulty to a seed. Habitat (resource) partitioning between two species becomes increasingly similar with species similarity (Figure 1D). Competition is presumably much stronger in this scenario. In order to gauge the consequences of relaxing Muller-Landau's assumption to important predictions in the model such as levels of species diversity and patterns of species trait distribution, below we compare results from simulations of the model using both the step-like $T(\sigma, f)$ and an alternative continuous form.

Comparisons between continuous and discontinuous tolerance function

Tight packing

If, as in Muller-Landau (2010), $T(\sigma, f)$ is chosen to be a step-like function as above, then the model is greatly simplified, and the fixed points and their stability can be determined analytically. Of particular interest, we can find solutions $p(f)$ where species of arbitrarily similar traits can coexist – a scenario which here will be called *tight packing*, and is also known as *continuous coexistence* (strictly speaking, tight packing as referred to here should be defined as the *potential* for continuous coexistence, as a finite number of species does never truly make up a continuum). In equilibrium, $dp(f)/dt$ in Eq. 6 must vanish for all f. For tight packing, $p(f) \neq 0$ for all f in $[f_0, f_m]$. Thus, for tight packing, the expression in parenthesis in Eq. 6 must vanish identically. If we define the quantity $h(f)$, representing the proportion of land whose stress level is equal to or less than the threshold $s(f)$ of species f (see Online Appendix A),

$$h(f) = \int_0^{s(f)} r(\sigma)\, d\sigma,$$

then a necessary condition for tight packing is (see details in Online Appendix B)

$$f h''(f) + 2h'(f) + p(f) = 0, \tag{7}$$

where the prime is standard shorthand notation for differentiation with respect to a function's argument. Mathematically, the tradeoff consists in imposing that $h(f)$ be a monotonically decreasing function. There are many acceptable functions $h(f)$ for which the solution to this equation $p(f)$ is of the tight packing kind. Thus, tight packing is supported in this model. Although we do not perform formal stability analysis here, we note that all tight packing solutions we tried proved dynamically stable in our simulations.

Previous work has shown that for a wide class of competition models, tight packing, when present, is fragile to changes in model parameters (Abrams 1983, Gyllenberg and Meszéna 2005). Fragile states are not expected in nature since fluctuations in parameters are inevitable in natural systems. To our knowledge, robust tight packing is unheard of in the theoretical literature; the slightest change in parameters suffices to destroy tight packing entirely, in the sense that after such perturbation no continuous range of species remains. Nevertheless, we show with simulations that this is not the case here. Given tight packing solutions, we perturb $h(f)$ at either a single fecundity value or many, and observe that the effects of such perturbations remain close to the perturbations (single-point case depicted in Figure 2). Tight packing proves robust to parametrization changes.

In contrast, if the tolerance function loses its discontinuity, the model's predictions regarding tight packing changes qualitatively. In fact, we provide proof in Online Appendix B that there is no tight packing solution to Eq. 6 if the tolerance function is analytic—a mathematical result that should apply generally to any smooth tolerance function and could be argued to hold for more general conditions as well, such as non-uniform mortality (see Online Appendix B).

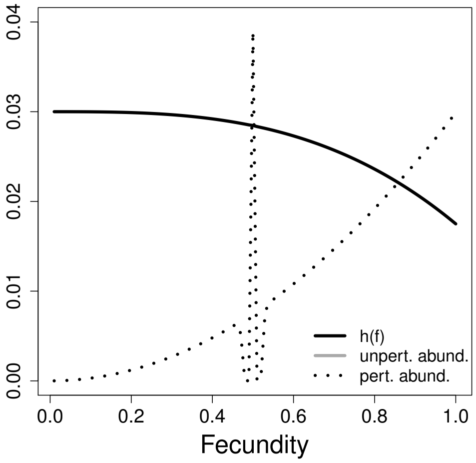

Figure 2: Tight packing. The gray solid line shows one possible solution of Eq. 7, $p(f) = 3f^2$ (gray line), obtained when $h(f) = 1 - f^3/4$ (black solid line). The dotted line shows what happens to the community upon a small local disturbance at $h(f = 5)$. The abundance of species $f = 5$ is greatly affected, and so are those of its immediate neighbors, which go extinct. The remainder of the community, however, is left intact. In the end, tight packing survives the disturbance. This is in striking contrast with known results for a great variety of models (MacArthur and Levins 1967, Gyllenberg and Meszéna 2005).

Species diversity

When tight packing is not allowed (or not robust), we say there is *limiting similarity* to coexisting species. We now ask how the model with a continuous tolerance function differs from Muller-Landau's discontinuous version in terms of diversity when limiting similarity occurs in both formulations. To find out, we perform the following test: starting with 100 species of equal initial abundances uniformly distributed in the fecundity range [0,1] and a given parametrization $h(f)$, we simulate the model dynamics until equilibrium is reached. We then take species richness and evenness (defined as the ratio between the obtained Shannon diversity index and its maximum possible value given the number of species present) and compare these diversity metrics between the discontinuous and the continuous case. This test is replicated many times, each for a different parametrization.

The parameters $h(f)$ in each run are determined randomly as follows: we draw 100 real numbers between 0 and 1 from a uniform distribution, spline-interpolate them (cubic spline), calculate their partial cumulative sums, normalize these by the total cumulative sum, and then subtract them from 1 – thus generating a cascade of numbers in decreasing order, ending in 0. Each value is then assigned to each of the species in order, as the proportion of sites below their stress threshold. This set of steps was taken to ensure that the parametrization would be random and smooth at the same time, with the intent of reproducing a typical real-world case and avoiding results that depend on any special parametrization. The dynamics is completely deterministic, meaning that a certain set of initial species abundances and site-stress parametrization $h(f)$ uniquely determines the outcome. Thus by averaging out the parametrization, we get an overall comparison of diversity levels across model types. We start with a species-rich state with evenly spaced species at equal abundances to represent an initial community in a tight packing state.

Results are shown in Figure 3A and 3B. A very clear and strong distinction in diversity levels between the two models is observed under both metrics: the model with continuous tolerance function almost invariably allows for considerably less diversity in the equilibrium community.

We note that in our simulations species are not allowed to evolve and there is no immigration. The addition of new types can bring in better competitors that could drive out hitherto coexisting inferior types (Metz et al. 1996). Thus it is likely that, should mutation and immigration be implemented, diversity would come out even lower in the continuous formulation, while the discontinuous formulation would show less change, as that scenario typically sees pockets of tight packing where all species can coexist. The results reported here should thus be seen as conservative estimates of the disparate diversity levels across these two formulations of the tolerance-fecundity tradeoff.

It should be noted that the discontinuous case is a limit of the continuous case. For instance, our expression of choice for the continuous tolerance function used in the tests, $T(\sigma, f) = \frac{1}{2}(1 + \mathrm{erf}[\nu(s(f) - \sigma)])$, approaches the step function as $\nu \to \infty$. Thus, it behooves us to check how diversity levels in the continuous case behave as the limit is approached. Figure 3C shows a progression of species richness in the equilibrium community as a function of the parameter ν. The curve rises to no limit, again confirming the tendency towards higher diversity as the tolerance function becomes steeper and nears the discontinuity.

Trait dispersion

Finally, we examine how the models differ regarding the distribution of species along the trait axis. Recently, community ecologists have been interested in finding evidence for the role of species differences in allowing for competitive coexistence, and employ several different metrics of trait dispersion to that purpose (Stubbs and Wilson 2004, Schamp et al. 2008, Ingram and Shurin 2009, Thompson et al. 2010). Here we focus on one of such metrics, the coefficient of variation in adjacent-neighbor trait distances (Stubbs and Wilson 2004). For each of the simulated runs, we take the differences in fecundity between consecutive (adjacent) neighbors on the trait axis. The coefficient of variation is then defined as the ratio between the standard deviation and the mean of such distances. A value significantly lower than expected by the null hypothesis implies overdispersion – species are more separated than expected by chance – and the opposite indicates clustering – species clump together.

The test is perfomed as follows: for each of one hundred simulation runs, we set up model parametrization with a random small perturbation around $h(f) = exp(-f)$ and run the continuous

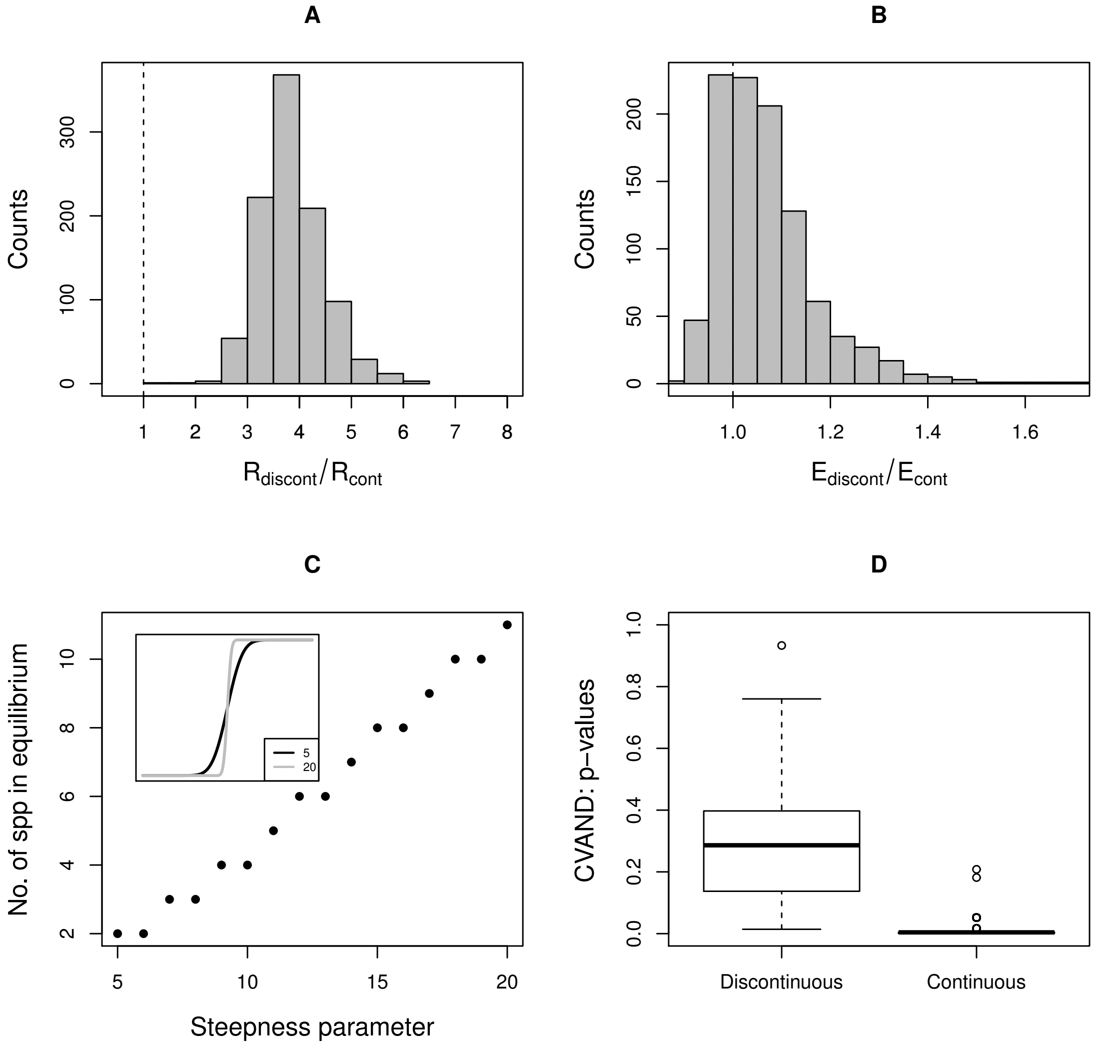

Figure 3: **A**: histogram with the distribution of richness R ratios between runs of the discontinuous and continuous versions of the model ($R_{discont}/R_{cont}$)for 1,000 runs. If the continuity of the tolerance function does not significantly affect diversity outcomes, we should obtain a distribution centered around $R_{discont}/R_{cont} = 1$. Results, however, are strongly skewed towards $R_{discont}/R_{cont} > 1$, indicating that the discontinuous formalization consistently leads to a higher species count in equilibrium (see main text for explanations). **B**: histogram showing the distribution of evenness E ratios ($E_{discont}/E_{cont}$) for the same runs as in A. Again, results deviate from the null hypothesis ($E_{discont}/E_{cont} = 1$); the discontinuous version of the model tends to produce more evenly distributed species abundances in equilibrium. **C**: trend in species richness with the steepness of the continuous tolerance function. As the steepness parameter ν in the function $T(\sigma, f) = \frac{1}{2}(1 + \mathrm{erf}[\nu(\sigma(f) - \sigma)])$ increases while all other parameters are kept fixed, so does the number of species in equilibrium after the community reaches equilibrium, starting with 100 species uniformly distributed in the [0,1] fecundity range. This indicates that diversity grows as the continuous formulation approaches its discontinuous limit. Inset shows how the tolerance function looks like for two examples, $\nu = 5$ and $\nu = 20$. **D**: comparison of the distribution of coefficients of variation between adjacent-neighbor distances (CVAND) throughout 499 runs of each version of the model, parametrized as described in the main text. The CVAND gives an indication of how closely surviving species distribute themselves along the trait axis in equilibrium. We see a striking distinction between results for each model: although both tend towards overdispersion (median below 0.5), the pull of the continuous model is much stronger. In addition to a much narrower scatter, the continuous version yields a median p-value of 0.004, in contrast with 0.286 in the discontinuous case. 83% of the runs in the continuous model are within the $\alpha = 0.05$ significance level for overdispersion, compared to 4% in the discontinuous case.

and discontinuous versions to equilibrium (this is a different approach to parametrization than used in the tests above, but was necessary because completely random $h(f)$ tends to yield very few species in the continuous case, which brings in power issues). We then take the corresponding coefficient of variation of adjacent-neighbor distances along the fecundity axis (henceforth referred to simply as CVAND for brevity) for each and establish the probability that these values would be obtained by chance (p-value) by comparing with a pool of null CVANDS. We end up with a distribution of one hundred p-values for each formulation of the model, which are summarized in the box plots on Figure 3D.

The pool of null CVANDs is generated and used to arrive at p-values as follows: for every number between 3 and 99, we randomly draw that number of species from the pool of 100 species of the initial community used in the simulations, and take the CVAND. This is repeated 100,000 times, thus obtaining a pool of null CVANDs for all richness values between 3 and 99. Then, for each run of each model, we compare the resulting CVAND with the corresponding pool of null CVANDs (i.e., that with the same number of surviving species). The proportion of times (out of 100,000) that the null CVANDs are lower than the observed value is the p-value, representing the probability that randomly generated CVANDs be lower than the observed one. As low CVANDs indicate overdispersion, this is in effect the probability that a random assemblage would be at least as much overdispersed as the observed assemblage.

Upon comparing the box plots for the discontinuous and continuous versions (Figure 3D), the distinction in trait dispersion becomes clear. Although both tend towards overdispersion in that both result in median p values less than 0.5, the pull of the continuous model is much stronger. In fact, 83% of the runs in the continuous model are within the $\alpha = 0.05$ significance level for overdispersion, compared to 4% in the discontinuous case. Results do vary quantitatively with different parameter implementations, but importantly the two formulations consistently lead to quite disparate trait dispersion regardless of how we parametrized the models. We should note that while different metrics could exist that may be better suited to capture the spread in fecundity among surviving species than the coefficient of variation of adjacent-neighbor distances, our test suffices to capture the dramatic differences in trait dispersion across the two model formulations under analysis here.

In order to further ensure generality of our results, we performed the tests described above for different initial conditions (namely, more species and unevenly spaced initial species). Indeed, although outcomes vary quantitatively, the continuous model invariably produces less diverse communities and shows stronger tendency for overdispersion than the continuous model.

Relation to competition kernel and generalization to other models

Our comparisons indicate that a discontinuity in the tolerance function has a strong, qualitative impact on model predictions regarding the distribution of species along the fecundity (or seed size) axis. This phenomenon is in fact an example of a more general result recently shown by us (Barabás et al. 2012) regarding the influence of a non-differentiable sharp peak in the competition kernel on model predictions of competitive outcomes.

The *competition kernel* is the function that determines the level of competition between two species given their traits. It can be defined as $a(f_1, f_2) = \frac{\delta R(f_1)}{\delta p(f_2)}$, where $R(f) = \frac{1}{p(f)} \frac{dp}{dt}$ is the per capita growth rate of species f. (Note that alternative definitions are also in use; see, e.g., Rueffler et al. 2007. The definition we employ is the most pertinent to our analysis, and has the added benefit of, when applied to Lotka–Volterra models, being equivalent to the collection of all the competition coefficients.) In Online Appendix C we show that the competition kernel in our tolerance-fecundity tradeoff model (Eq. 6) has a point of non-differentiability – a *kink* (Figure 1E, 1F) – at its peak if and only if $T(\sigma, f)$ has a discontinuity. In our recent work (Barabás et al. 2012), we show that coexistence of arbitrarily similar species is robust to changes in parameters when the competition-kernel is kinked, and nonexistent or fragile when the competition kernel is smooth (no kinks). The results shown here for tight packing in the TFM are in good accord with that generalization. Above and beyond this, here we have shown for the TFM additional model behavior that is strongly affected by a discontinuous tolerance function, namely species diversity and patterns of spacing between species on the trait axis.

When the kernel is expressible in terms of the overlap of resource utilization curves (MacArthur and Levins 1967), kinked competition kernels arise from discontinuities in those functions (Barabás et al. 2012). More generally, competition kernels can be written in terms of functions describing species' sensitivity to and impact on *regulating factors* (i.e. factors that influence and are in turn influenced by the population sizes of species; Meszéna et al. 2006), and we show in Barabás et al. (2012) that kinked competition kernels arise from discontinuities in those functions. Clearly, the tolerance function $T(s, f)$ is related to these functions, and a discontinuity in the former must be tantamount to a discontinuity in the latter. Informally it is apparent that the tolerance function is reflective of resource use, where the resources can be seen as patches of a given stress level.

To further make the point that the impacts of non-differentiability in the competition kernel extend beyond the particulars of any given model, in Online Appendix D we provide the same analysis shown above for a different model of seed size diversity which turns out to have a kinked kernel: the hierarchical competition-colonization model (Levins 1969, Tilman 1994, Kinzig et al. 1999). In this model, the non-differentiability arises from the assumption that the hierarchy is absolutely strict, with a clearly dominant competitor arising out of any two species considered, no matter how similar they are in colonization ability. Results of the analysis are much alike: when the model's original non-differentiability is removed, much lower levels of diversity are obtained, tight packing is no longer supported, and tendencies for species overdispersion are much stronger. We note that Adler and Mosquera (2000) showed previously that predicted diversity dramatically decreases when strictly hierarchical competition is relaxed for a similar mechanism, namely the competition-mortality tradeoff. Their finding can be now understood in the context of the severe consequences of a kinked kernel to model behavior.

Discussion

We have examined the importance of relieving Muller-Landau's tolerance-fecundity tradeoff model of the discontinuity in resource use that it previously contained. Our work on this model can be viewed as a case study on the consequences of modeling *resource use* (interpreted broadly as described above) as discontinuous. We can understand the general consequences of discontinuous resource use analogously to our understanding of the importance of the tolerance function: if resource use is discontinuous, then two species, no matter how close in traits, stand apart in their use of resources. Hence competition among similar species is relatively lax compared to models with continuous resource utilization, which explains the greater permissivity to coexistence in the former.

We would like to impress upon the reader the unnaturalness of the discontinuity in tolerance level. For one, any small variation in intraspecific trait expression or environmental conditions, which are inevitable in any biological system, suffices for this theoretical scheme to break down (Barabás et al. 2012). More importantly, the infinitely sharp transition is hopelessly unrealistic because ultimately in nature there is no such thing as a continuous change in the cause bringing about a discontinuous change in the effect.

Muller-Landau acknowledged the discontinuous tolerance regime as unrealistic, but argued that this assumption was not central to her demonstration that this tradeoff can generate coexistence. Nevertheless, one cannot ignore the implications of this assumption for the amount of diversity that the mechanism can explain. All else being equal, the smoother the tolerance function is, the lower the number of species that will coexist in this model. As is the case with any model of coexistence, it remains an empirical question whether conditions in nature are such that this tradeoff actually explains observed diversity. Our work here highlights the importance of the tolerance function for assessing the existence and potential importance of the tolerance-fecundity tradeoff.

We do not purport to have purged Muller-Landau's model of all its unrealistic simplifications. Many others remain, such as no explicit spatial structure, uniform mortality, no dynamics to stress levels, and no stochasticity. One must keep in mind that any model is a limited representation of reality and must perforce rely on helpful, if simplistic, assumptions. Of course the trouble is that there is no general way to know beforehand the degree to which any given assumption impacts the quality of the model as a representation of the real world. Here we showed that discontinuous resource use has a very strong impact in the tolerance-fecundity tradeoff, and connected this result with the more general impact of modeling resource use as discontinuous on predictions regarding limits to similarity, species diversity, and patterns of trait dispersion.

In addition to cautioning against modeling resource use discontinuously, our study presented and at the same time cast aside a potential challenge to the widely influential theory of limiting similarity. We showed that a specific mechanism of coexistence seemingly indicates that tight packing of species can be robust, but eventually rooted this unexpected prediction to one of the simplifying and unrealistic assumptions of the model.

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Appendix A Constructing the tolerance-fecundity tradeoff model

Here, we show that Muller-Landau's 2010 tolerance-fecundity tradeoff model arises from Eq. 6 of the main text when a simpler picture of seed tolerance is assumed.

First, we must convert the sum over sites to a sum over fecundities. This can be done for the following reason: sweeping over the stress axis is equivalent to sweeping over fecundity values, as each stress level is the threshold associated with a given fecundity. Mathematically, we can always write

$$\int (\text{integrand})\, d\sigma = \int (\text{integrand})\, ds = \int (\text{integrand})\, \frac{ds}{dx}\, dx,$$

In our case, we will write

$$\int_{s_0}^{s_m} \frac{r(s)T(s,f)}{\int_{f_0}^{f_m} y\, p(y)T(s,y)\, dy}\, ds = -\int_{f_0}^{f_m} \frac{h'(x)g(x,f)}{\int_{f_0}^{f_m} y\, p(y)g(x,y)\, dy} dx. \tag{A.1}$$

where s_0 and s_m are the thresholds of the least and most tolerant species, respectively. The left-hand side of Eq. A.1 is simply the integral term in Eq. 6 (main text) with the stress threshold explicitly used as the integration variable, and the functions $h(x)$ and $g(x,f)$ are defined to have the properties

$$h'(x)dx = r(s)ds \qquad g(x,f) = T(s(x),f),$$

where $s(x)$ is the stress threshold of the species with fecundity x. Finally, the minus sign arises because of the change in the limits of the integration given the inverse relationship between stress thresholds and fecundity: $\int_{\sigma_0}^{\sigma_m} ds \to \int_{f_m}^{f_0} dx = -\int_{f_0}^{f_m} dx$.

To see what $h(x)$ means, let us write $r(s)$ as $\frac{d\gamma}{ds}$, where $\gamma(s)$ is some function of s. Then, using the chain rule, we see that

$$\frac{dh}{dx} = \frac{d\gamma}{dx},$$

whereby we can say $h(x) = \gamma(s(x))$. The function γ is easily interpretable: $\gamma(s) = \int^{s} r(\sigma)\, d\sigma$, that is, $\gamma(s)$ is the total proportion of sites in the community whose stress level is equal to or less than s. The function $h(f)$, then, is the proportion of land whose stress level is equal to or less than the threshold of species f. Its functional form is determined by both the environment and the biology of the organisms, as it depends on the distribution of stress in the land and on how a given fecundity translates to its stress threshold. Notice that the tolerance-fecundity tradeoff, which comprises the essence of the model, requires that $h'(f) < 0$ for all values of f.

The function g is just a renaming of function T, and is not hard to interpret: just as $T(s(x),f)$ is the probability that species f can tolerate in a site with stress s (which is the threshold of species x), $g(x,f)$ is the probability that species f can tolerate a site whose stress level is the threshold of species x. Notice that, for fixed f, $g(x,f)$ is a forward sigmoid function of x, while $T(\sigma,f)$ is a backwards sigmoid function of σ (i.e., g starts low and transitions to 1 as x increases, while T shows the opposite behavior with increasing σ). We change notation from $T(\sigma,f)$ to $g(x,f)$ to highlight this shift of focus from sites to species, which flips the function.

Having justified all terms in Eq. A.1, we can now render our model in the form

$$\frac{dp}{dt}(f) = m\left(-f\int_{f_0}^{f_m} \frac{h'(x)\, g(x,f)}{\int_{f_0}^{f_m} yp(y)g(x,y)\, dy}\, dx - 1\right)p(f). \tag{A.2}$$

If we further assume that all species have a similar transition regime around their specific stress threshold, then the transition function becomes a function of a single variable, $g(x-f)$. Although this greatly simplifies things, such an assumption unfortunately has no a priori biological foundation. It is, however, implicitly used by Muller-Landau, and we apply it here to show the compatibility between the models. With that assumption, Eq. A.2 reads

$$\frac{dp}{dt}(f) = m\left(-f\int_{f_0}^{f_m} \frac{h'(x)\,g(x-f)}{\int_{f_0}^{f_m} yp(y)g(x-y)\,dy}\,dx - 1\right)p(f). \tag{A.3}$$

In Muller-Landau (2010), the transition function is the unit step function $\Theta(x-f)$ (which is one for positive arguments and zero otherwise): $g(x-f) = \Theta(x-f)$. In biological terms, this means that species with fecundity values x equal to or higher than that of the focal species with fecundity f can tolerate sites whose stress level is that of the focal species with probability 1, and species whose fecundity x is less than f cannot tolerate that stress level at all. Thus Eq. A.3 finally becomes

$$\frac{dp}{dt}(f) = m\left(-f\int_{f}^{f_m} \frac{h'(x)}{\int_{f_0}^{x} yp(y)\,dy}\,dx - 1\right)p(f), \tag{A.4}$$

which is Muller-Landau's model put in the context of a continuum of species.

Appendix B Tight packing in the tolerance-fecundity model

Here, we analytically solve Muller-Landau's model for tight packing solutions. Simulations reported in the main text further demonstrate that tight packing is robust in this case. Additionally, we show that for a very general class of continuous transition functions g, namely analytic ones, tight packing is not a possible solution.

For tight packing to occur in any subset $[f_1, f_2]$ of the range $[f_0, f_m]$, $p(f)$ must satisfy the conditions $\frac{dp}{dt} = 0$, $p(f) > 0$ for all f in $[f_1, f_2]$. Applying these to Eq. A.4 – Muller-Landau's model written for a continuum of species – we obtain

$$\int_{f}^{f_m} \frac{h'(x)}{I(x)}dx + \frac{1}{f} = 0,$$

where $I(x) = \int_{f_0}^{x} dy\, yp(y)$. Differentiating twice the equation above with respect to f and performing appropriate substitutions gives

$$fh''(f) + 2h'(f) + p(f) = 0. \tag{B.1}$$

Eq. B.1 is our tight packing equation, and appears in the main text as Eq. 7. If it is satisfied in the subset $[f_1, f_2]$, then we get a continuum of coexisting species in that subset. Given that Eq. B.1 is a second-order differential equation, $h(f)$ must be further specified by two boundary conditions. Such boundary conditions are more easily obtained from the discrete version of the model, Eq. 1 of the main text. One such condition can be obtained by summing over all i's (recall that, in equilibrium, $\frac{dp_i}{dt} = 0$): $\sum_{i=1}^{N} p_i = h_1$ – which when extended for a continuum of species reads $\int_{f_0}^{f_m} dx\, p(x) = h(f_0)$. The other condition can also be obtained from Eq. 1 by substituting $i = N$: $f_N^{-1}\sum_{i=1}^{N} f_i p_i = h_N$ – which in the continuum is $f_m^{-1}\int_{f_0}^{f_m} dx\, x\, p(x) = h(f_m)$. Although in principle Eq. B.1 is an equation for $p(f)$, the easiest way to arrive at a solution for it is to posit $p(f)$ and solve for h, subject to the boundary conditions discussed above. If no suitable h can be found, than the posited $p(f)$ is not a possible solution. As it turns out, there are infinitely many functions $h(f)$ for which there is a corresponding tight packing solution $p(f)$. We give one example in Fig. 2 in the main text.

Having argued that the tight packing equation has a wealth of solutions in the discontinuous model, we now turn to show that it has no solution at all in the continuous case, at least if the transition function is analytic.

We can see from Eq. A.3 that for the tight packing conditions to hold, we must have

$$f \int_{f_0}^{f_m} \frac{h'(x)}{J(x)} g(x-f)\, dx = -1 \qquad \forall\, f \in [f_0, f_m], \tag{B.2}$$

where $J(x) = \int_{f_0}^{f_m} dy\, y\, p(y) g(x-y)$. We now make the assumption that g is analytic. We will also require that the function $\xi(x) \equiv \frac{h'(x)}{J(x)}$ be differentiable at all points and decay to zero at $|x| \to \infty$. This is expected to hold for any reasonable set of functions $h(x)$ and $J(x)$ which obey the constraints of the model. The integral above is a function of f, and given our assumptions about g and ξ, it can be shown that the Taylor series of the integral above converges, and therefore the integral is an analytic function. Since f itself is of course an analytic function and the product of analytic functions is analytic, then the entire left-hand side of Eq. B.2 is analytic. Thus Eq. B.2 can only be satisfied if

$$f \int_{f_0}^{f_m} \xi(x)\, g(x-f)\, dx = -1 \qquad \forall\, f \in \mathbb{R}$$

That, however, cannot be, as the equality cannot hold at $f = 0$. Now, since two analytic functions differing at a point can only coincide at a finite number of points, we conclude that Eq. B.2 does not have a solution for any continuous range $[f_0, f_m]$ if g is analytic.

Although this proves that no analytic transition function would allow tight packing (let alone robust tight packing!), it does not prove that the same should hold for *any continuous* transition function. However, if we restrict ourselves to *differentiable* transition functions (a reasonable and fairly general assumption), then we can approximate any such function with arbitrary precision by an analytic function. Then, given that Eq. B.2 cannot be satisfied if g is analytic, it stands to reason that no differentiable function g will work either. We believe a formal proof can be constructed, and leave it for future work.

We add that while here we can only ensure tight packing is not possible for analytic tolerance functions, we contend elsewhere (Barabás et al. 2012) that, for any model with a differentiable competition kernel, tight packing, if present, is necessarily fragile.

Finally, we speculate that this no-tight packing bound could probably be extended to more general conditions. For instance, we were able to show (unpublished results) that the proof developed here holds when mortality, rather than a constant, is an analytic function of species fecundity.

Appendix C The competition kernel

Here we show that the competition kernel in Muller-Landau's model, $a(f_1, f_2)$, possesses a discontinuous first derivative at $f_1 = f_2$ if and only if the tolerance function is discontinuous.

It follows from the definition of derivatives that the first derivative of a function is discontinuous at a point if and only if the second derivative diverges to infinity at that point. We will use that to show that the competition kernel has a divergent second derivative if and only if the tolerance function is discontinuous. We will use the transition function g defined in Online Appendix A, rather than the tolerance function T. Recall that $g(x,f)$ describes the probability that the species with fecundity f can tolerate stress level at the threshold of the species with fecundity x.

From Eq. A.2, if $g(x,f)=\Theta(x-f)$, the per capita growth rate is

$$R(f)=\frac{1}{p(f)}\frac{dp}{dt}=-m\left(f\int_{f_0}^{f_m}\frac{h'(x)\Theta(x-f)}{\int_{f_0}^{f_m}yp(y)\Theta(x-y)dy}dx-1\right)$$

From this we calculate the competition kernel:

$$a(f_1,f_2)=\frac{\delta R(f_1)}{\delta p(f_2)}=mf_1f_2\int_{f_0}^{f_m}\frac{h'(x)\Theta(x-f_1)\Theta(x-f_2)}{(I(x))^2}dx,$$

where $I(x)\equiv\int_{f_0}^{f_m}yp(y)\Theta(x-y)dy$, and take the first derivative with respect to f_2 (we could equally well pick f_1 instead):

$$\frac{\partial}{\partial f_2}a(f_1,f_2)=mf_1\left(\int_{f_0}^{f_m}\frac{h'(x)\Theta(x-f_1)\Theta(x-f_2)}{(I(x))^2}dx-f_2\int_{f_0}^{f_m}\frac{h'(x)\Theta(x-f_1)\delta(x-f_2)}{(I(x))^2}dx\right).$$

The second derivative is, then,

$$\begin{aligned}\frac{\partial^2}{\partial {f_2}^2}a(f_1,f_2) &= mf_1\Bigg(-2\int_{f_0}^{f_m}\frac{h'(x)\Theta(x-f_1)\delta(x-f_2)}{(I(x))^2}dx\\ &\qquad -f_2\frac{\partial}{\partial f_2}\left(\int_{f_0}^{f_m}\frac{h'(x)\Theta(x-f_1)\delta(x-f_2)}{(I(x))^2}dx\right)\Bigg)\\ &= mf_1\left(-2\frac{h'(f_2)}{(I(f_2))^2}\Theta(f_2-f_1)-f_2\frac{\partial}{\partial f_2}\left(\frac{h'(f_2)}{(I(f_2))^2}\Theta(f_2-f_1)\right)\right). \qquad \text{(C.1)}\end{aligned}$$

Since we are only interested in whether or not the second derivative diverges, we can stop here and look at the behavior of the terms. Since $h(f)$ is well behaved and $I(f)\neq 0$ for all $f>f_0$, the first term never diverges, and is therefore of no consequence. The second term, however, contains a derivative of $\Theta(f_2-f_1)$. The step function is discontinuous at $f_1=f_2$, and the derivative of a discontinuous function diverges at the point of discontinuity (more specifically, the derivative of a function at a point of discontinuity is proportional to the Dirac delta function, which is uniformly zero at all points except for where its argument vanishes, at which point it is infinite). Precisely at $f_1=f_2$, then, we have a singularity in Eq. C.1. This proves that the competition kernel has a discontinuous first derivative at the point where two species coincide if the transition function $g(x,f)$ is discontinuous when $x=f$.

In the same vein, the competition kernel when the transition function g is continuous can be shown to be smooth, i.e., it does not contain any point where the first derivative is discontinuous – no 'kinks'. To see that, we can follow the same steps as above and replace the discontinuous unit function with any continuous function g:

$$\begin{aligned}a(f_1,f_2) &= mf_1f_2\int_{f_0}^{f_m}\frac{h'(x)g(x-f_1)g(x-f_2)}{(J(x))^2}dx,\\ \frac{\partial}{\partial f_2}a(f_1,f_2) &= mf_1\left(\int_{f_0}^{f_m}\frac{h'(x)g(x-f_1)g(x-f_2)}{(J(x))^2}dx-f_2\int_{f_0}^{f_m}\frac{h'(x)g(x-f_1)g'(x-f_2)}{(J(x))^2}dx\right)\end{aligned}$$

where $J(x) \equiv \int_{f_0}^{f_m} yp(y)g(x-y)dy$. Proceeding to the second derivative, we have

$$\begin{aligned}\frac{\partial^2}{\partial {f_2}^2}a(f_1,f_2) &= mf_1\Bigg(-2\int_{f_0}^{f_m}\frac{h'(x)g(x-f_1)g'(x-f_2)}{(I(x))^2}dx \\ &\quad -f_2\frac{\partial}{\partial f_2}\Bigg(\int_{f_0}^{f_m}\frac{h'(x)g(x-f_1)g'(x-f_2)}{(I(x))^2}dx\Bigg)\Bigg).\end{aligned}$$

Now it should be easy to see that none of the terms above diverge at any point, since they contain only smooth, well-behaved functions and their derivatives. This proves that the kernel is smooth.

Appendix D The hierarchical competition-colonization model

To illustrate the generality of the impact of a kinked competition kernel on model predictions across different models, here we present a similar analysis for a different 'kinked model', the hierarchical competition-colonization model (Kinzig et al. 1999). We find that this model shares with Muller-Landau's the ability to support robust tight packing due to discontinuity in resource use. A continuous formulation of the model is presented, from which our simulations indicate robust tight packing is absent. Further tests verify that diversity levels and trait dispersion differ sharply between the original and the smooth formulations.

The original model is defined by the equations (Kinzig et al. 1999)

$$\dot{p}_i = f_i p_i\Big(1-\sum_{j=1}^{i}p_j\Big) - p_i\sum_{j=i}^{i-1}f_j p_j - m_i p_i, \tag{D.1}$$

which determines the growth of species i, characterized by fecundity f_i and mortality m_i. The first term represents recruitment, which can occur in any patch happening to be empty or occupied by any species j with $j \geq i$. In fact, species i sees patches occupied by species $j,\ j > i$ as empty patches. The second term represents the converse: species i is promptly displaced by any species $j,\ j < i$. The last term is the mortality term. When we extend Eq. D.1 to a continuous pool of species, we obtain

$$\frac{dp}{dt}(f) = \Bigg(f\Big(1-\int_{f_0}^{f}p(x)dx\Big) - \int_{f_0}^{f}xp(x)dx - m(f)\Bigg)p(f). \tag{D.2}$$

Let us first derive the conditions under which the solution to Eq. D.2 constitutes tight packing. For tight packing equilibrium, characterized by $dp/dt = 0,\ p(f) > 0$ for all f in $[f_0, f_m]$, we then must have

$$f\Big(1-\int_{f_0}^{f}p(x)dx\Big) - \int_{f_0}^{f}xp(x)dx - m(f) = 0. \tag{D.3}$$

We can turn this integral equation into a differential equation by differentiating twice with respect to f. The resulting equation, as found in Kinzig et al. (1999), is

$$3p(f) + 2p'(f) + m''(f) = 0. \tag{D.4}$$

If $m(f)$ satisfies Eq. D.4, then our equilibrium will consist of arbitrarily close species coexisting in the community. Since it is a second-order differential equation, it requires two boundary conditions for the solution to be completely specified. Here, such conditions can be found from Eq. D.3:

$$\begin{aligned}m(f_0) &= f_0, \\ m'(f_0) &= 1-2f_0p(f_0).\end{aligned}$$

The first is obtained by substituting $f = f_0$, and the second by taking the derivative with respect to f on both sides and then evaluating at $f = f_0$. Thus any solutions to Eq. D.4 subject to these initial conditions is a tight packing solution. We find one such solution and show with simulations that it is robust to small perturbations in $m(f)$ (Figure D.1.A).

Fixing the hierarchical competition-colonization model

As before, we take the model's equations to the species continuum, Eq. D.2, and introduce unit step functions to obtain

$$\frac{dp}{dt} = p(f)\Big(f - \int_{f_0}^{f_m} dx\,(f+x)\; p(x)\; \Theta(f-x) - m(f)\Big).$$

The discontinuity is again effectively removed by substituting the step function with a differentiable function:

$$\frac{dp}{dt} = p(f)\Big(f - \int_{f_0}^{f_m} dx\,(f+x)\; p(x)\; g(f-x) - m(f)\Big).$$

Whereas in the tolerance-fecundity tradeoff the function $g(x)$ introduces a continuous transition between full tolerance and absolute intolerance to stress, here it introduces a gradient of competitive effect across species. While in Kinzig et al.'s original model an individual could be displaced just as easily by any given seed from any outranking species, here a seed from a species higher up the hierarchy poses a stronger threat than another seed from a species closer down. The same goes for species being outranked by the focal species: the further down the hierarchy the other species is, the greater its competitive disadvantage per seed. In short, our reformulation of the model introduces degrees of competitive ability differences, thus replacing the binary {outranks, is outranked}.

Comparing tight packing, species diversity, and trait dispersion

The competition-colonization tredoff, in its discontinuous (i.e. with a kinked competition kernel) form as presented in Kinzig et al. 1999, supports robust tight packing (Figure D.1.A). As for its continuous, smooth kernel counterpart, though we are unable to produce analytical proof that tight packing is absent, we argue elsewhere (Barabás et al. 2012) that models with smooth competition kernels cannot bear robust tight packing. Thus, if tight packing occurs, the smallest fluctuation in model parameters suffices to break the assemblage. Since such fluctuations could be easily brought about by noise and stochasticity in natural systems, a model which forecloses robust tight packing effectively precludes tight packing altogether.

Analogous tests for diversity levels and species distribution along the trait axis as those performed for the tolerance-fecundity tradeoff model in the main text produce similar results (Figure D.1.B to D.1.D).

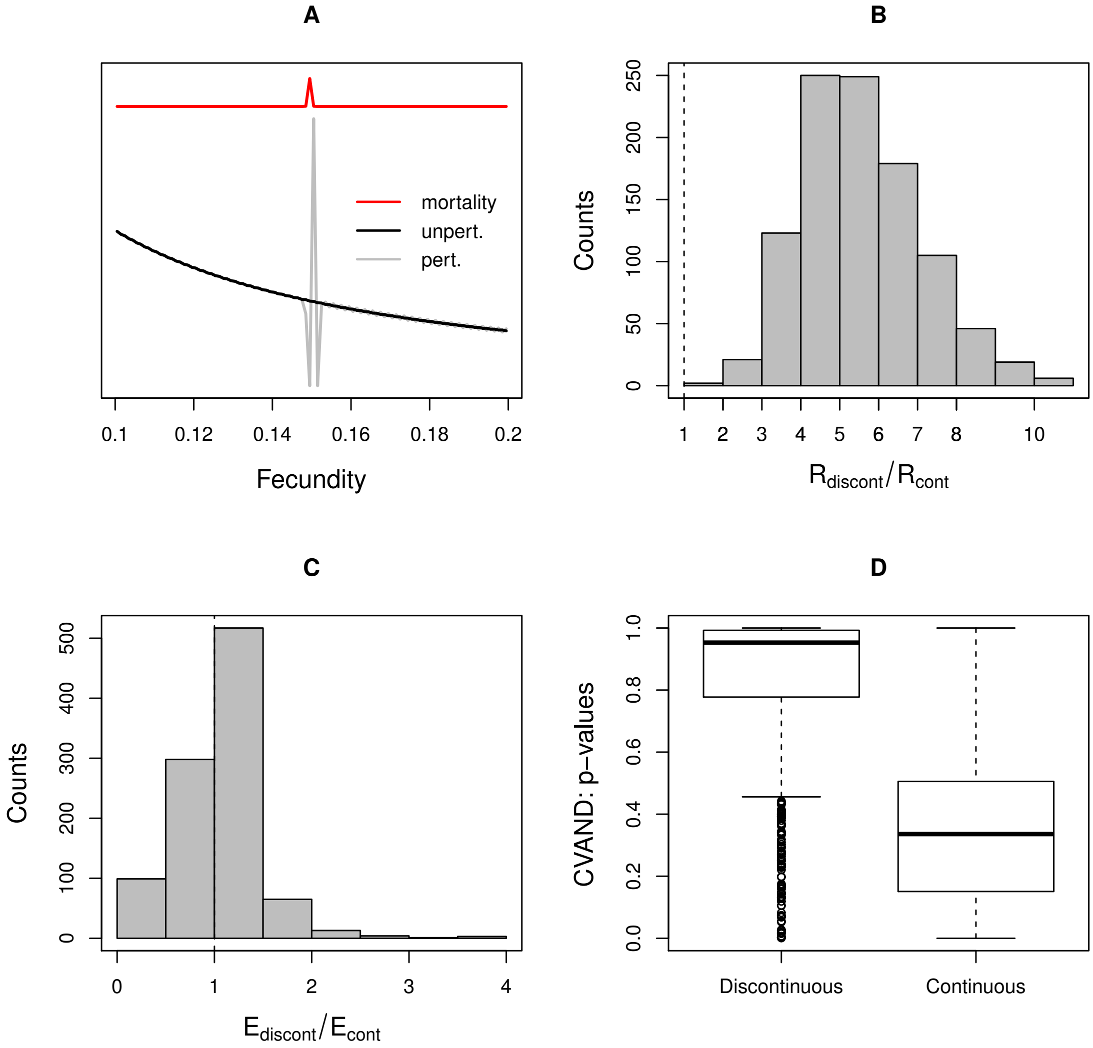

Figure D.1: **D.1.A**: tight packing solution for Kinzig et al.'s hierarchical competition-colonization tradeoff model with uniform mortality. As with Muller-Landau's model, the effect of a perturbation – represented here as a change in the death rate of one species – remains local and does not destroy the assemblage. **D.1.B** and **D.1.C**: comparison of diversity levels between the original and 'smooth' formulations of the competition-colonization tradeoff produce similar results as those performed with the tolerance-fecundity case, namely, the smooth version typically supports much lower diversity levels. **D.1.D**: trait dispersion differs markedly across the two formulations of the competition-colonization tradeoff. For perturbations around uniform mortality, the original model shows a consistent and strong tendency towards species clustering due to the formation of patches of continuous coexistence, whereas the smooth version shows no visible trend towards either overdispersion or clustering. As with the model analyzed in the main text, results depend quantitatively on model parameters (in this case, species mortality), but the two formulations consistently lead to quite disparate trait dispersion across parametrizations.