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Revising the Tolerance-Fecundity Trade-Off; 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 trade-off model represents a step forward in the study of seed size diversity in plant communities. However, it uses an 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 nondifferentiable 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 article illustrates those general results and offers a revised model of the tolerance-fecundity trade-off.

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

Introduction

In ecologists' never-ending quest to understand coexistence of competing species, trade-offs 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 trade-off idea has been utilized by several authors since at least the 1970s (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 trade-off model of seed size diversity, according to which a trade-off 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 on 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 tolerance-fecundity model (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 trade-off 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 impact on how much coexistence is allowed and hence may impact how much diversity can be explained in practice by the tolerance-fecundity trade-off.

It is the purpose of this article to demonstrate the strong implications of the discontinuity in the tolerance function onto the tolerance-fecundity trade-off 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 trade-off model predicts robust continuous coexistence. On 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 trade-off.

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 trade-off model as an example suggest caution when constructing models to study limiting similarity, diversity, and patterns of trait dispersion.

The Tolerance-Fecundity Trade-Off Model

Original Formulation

The dynamics of the tolerance-fecundity trade-off model (Muller-Landau 2010) are as follows. The community is assumed to be saturated with adult individuals which preempt establishment of propagules. At every time step, however, some individuals die, making sites available to propagules and enabling competition among them—in fact, in this model, competition occurs only 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 (fig. 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 $h_n < h_{n-1} < \ldots < h_1$ 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 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 equation (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 to 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 trade-off 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 (fig. 1B).
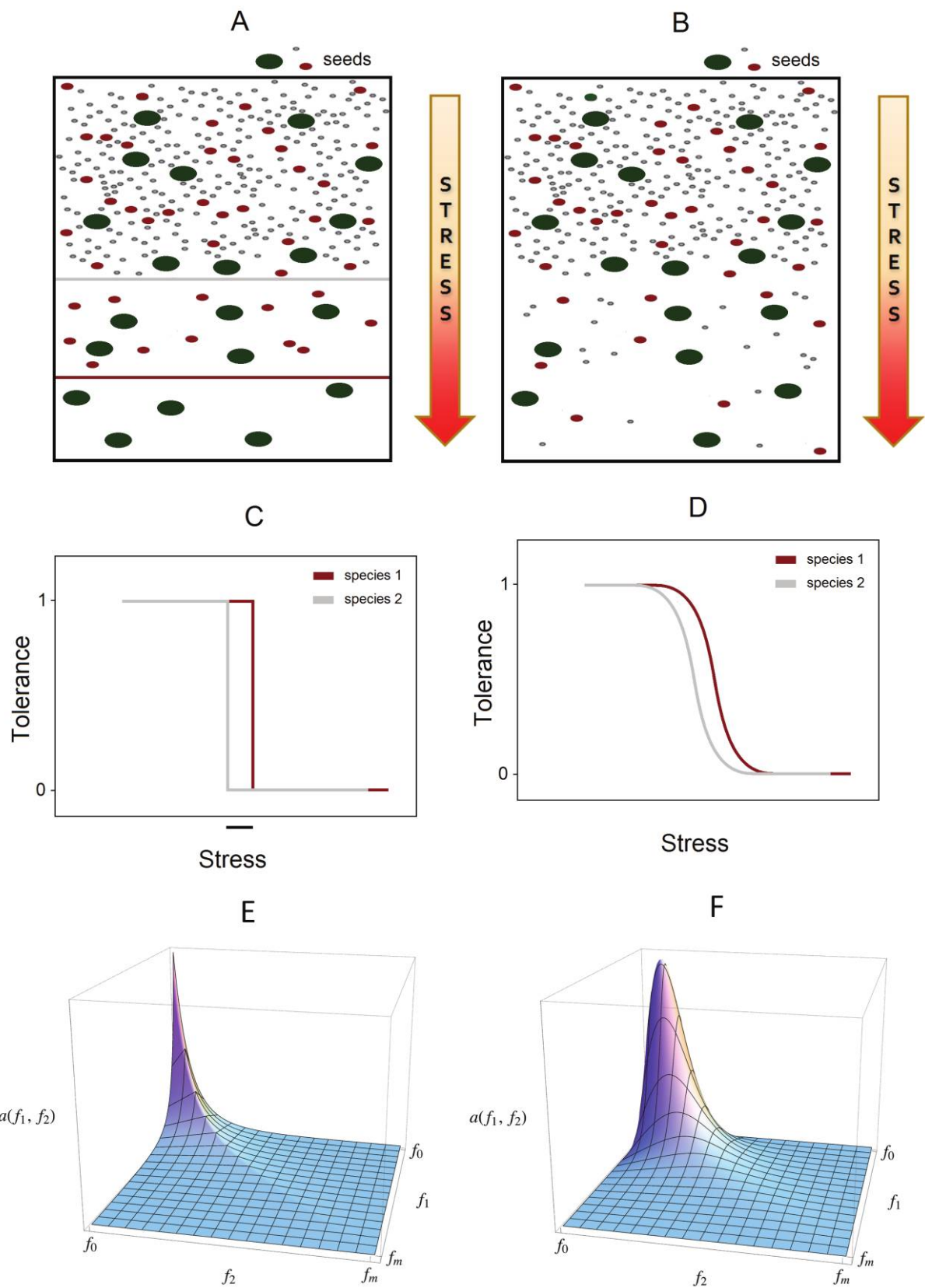
We first note that for mathematical convenience we consider a pool of species forming a continuum, with all possible fecundity values in the range $[f_0, f_m]$ represented, because we will later study the potential for coexistence of arbitrarily similar species ("continuous coexistence"). Although such continuum is a mathematical abstraction that cannot 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

$$\frac{dn}{dt}(f) = \underbrace{(\text{no. seeds that recruit})}_{fn(f)\int Q(\sigma, f)d\sigma} - \underbrace{(\text{death})}_{m(f)n(f)}. \tag{2}$$

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

A

B

seeds

STRESS

seeds

STRESS

C

D

Tolerance

1

0

Stress

species 1
species 2

Tolerance

1

0

Stress

species 1
species 2

E

F

$a(f_1, f_2)$

f_0
f_1
f_m
f_0
f_2
f_m

$a(f_1, f_2)$

f_0
f_1
f_m
f_0
f_2
f_m

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$(\int fn(f)T(\sigma,f)df)/c$. We therefore arrive at the stress-dependent probability of colonization:

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

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

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. function $T(\sigma,f)$ should tend to 1 at low σ and 0 at high σ, and the transition between these extremes should center at $s(f)$.

Putting together what we have so far, our model reads

$$\frac{dn}{dt}(f) =$$

$$\left[f\int_{\sigma_0}^{\sigma_m} \frac{T(\sigma,f)(c(\sigma) - \int_{f_0}^{f_m} n(\sigma,x)dx)}{\int_{f_0}^{f_m} yn(y)T(\sigma,y)dy} d\sigma - m(f) \right]n(f),$$

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 $\int p(f) \leq 1$. Equation (3) becomes

$$\frac{dp}{dt}(f) =$$

$$\left[f\int_{\sigma_0}^{\sigma_m} \frac{T(\sigma,f)(c(\sigma)/c - \int_{f_0}^{f_m} p(\sigma,x)dx)}{\int_{f_0}^{f_m} yp(y)T(\sigma,y)dy} d\sigma - m(f) \right]p(f).$$

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

$$\frac{dp}{dt}(f) =$$

$$\left(f\int_{f_0}^{f_m} \frac{T(\sigma,f)\int_{f_0}^{f_m} p(\sigma,x)m(x)dx}{\int_{f_0}^{f_m} yp(\sigma,y)T(\sigma,y)dy} d\sigma - m(f) \right)p(f).$$

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

$$\frac{dp}{dt}(f) =$$

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

where $r(\sigma) = \int_{f_0}^{f_m} p(\sigma,f)df$ 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, equation (6) tells us that the dynamics of a species labeled 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). Equation (6) is our revised tolerance-fecundity trade-off model.

In appendix A, available online, we show that Muller-Landau's original formulation of the model can be obtained from our revised formulation if to each species f

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 gray) 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 two-dimensional projection of this surface would show a curve with a kink at its peak. *F,* When the tolerance function is continuous—here modeled as $T(\sigma,f) = (1/2)\{1 + \text{erf}[\nu(s(f) - \sigma)]\}$—the ridge is absent, and the surface is smooth across its domain.

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 $\sigma \le s$ and 0 if $\sigma > s$. Importantly, this characterizes a discontinuous transition in stress tolerance (fig. 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 (fig. 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 that 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 equation (6) must vanish for all f. For tight packing, $p(f) \ne 0$ for all f in $[f_0, f_m]$. Thus, for tight packing, the expression in parenthesis in equation (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 app. A),

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

then a necessary condition for tight packing is (see details in app. B)

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

where the prime is standard shorthand notation for dif-ferentiation with respect to a function's argument. Mathematically, the trade-off 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 fig. 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 appendix B, available online, that there is no tight packing solution to equation (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 nonuniform mortality (see app. B).[1]

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

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[1] An analytic function is a differentiable function that converges to a power series of its argument.
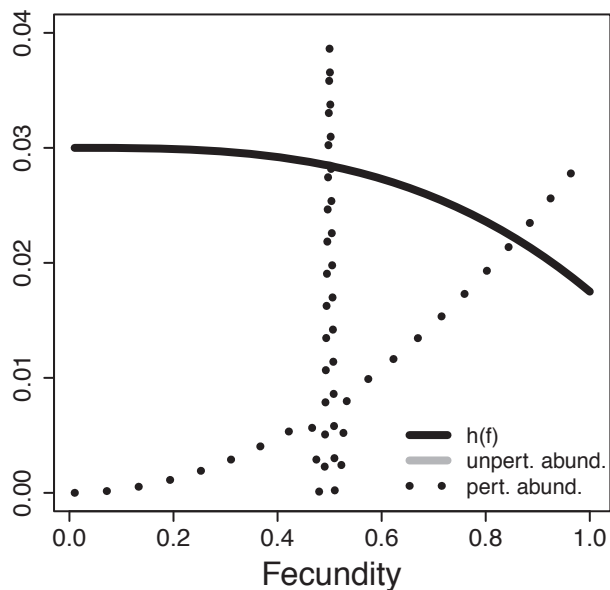
Figure 2: Tight packing. The solid gray line shows one possible solution of equation (7), $p(f) = 3f^2$ (gray line), obtained when $h(f) = (1 - f^3)/4$ (black solid line). The dotted line shows what happens to the community upon a small local disturbance at $h(f = 5)$. The abundance of species $f = 5$ is greatly affected, and so are those of its immediate neighbors, which become 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).

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 3*A* and 3*B*. 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 trade-off.

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, $T(\sigma, f) = (1/2)\{1 + \text{erf}[\nu(s(f) - \sigma)]\}$, 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 3*C* 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 toward 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 performed as follows: for each of 100 simulation runs, we set up model parametrization with a random small perturbation around $h(f) = \exp(-f)$ and run
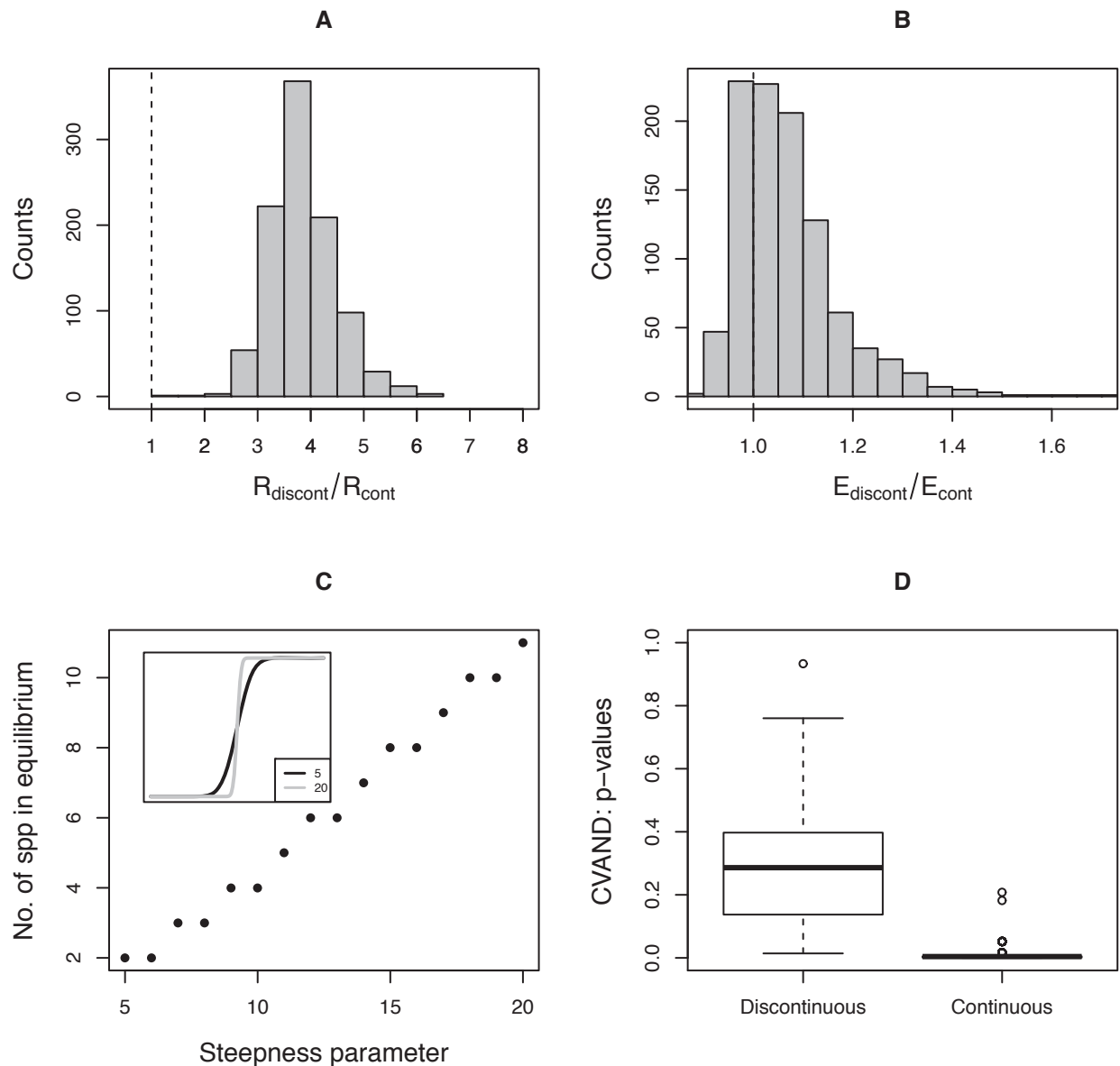
Figure 3: *A,* Histogram with the distribution of richness *R* ratios between runs of the discontinuous and continuous versions of the model ($R_{\mathrm{discont}}/R_{\mathrm{cont}}$) for 1,000 runs. If the continuity of the tolerance function does not significantly affect diversity outcomes, we should obtain a distribution centered on $R_{\mathrm{discont}}/R_{\mathrm{cont}} = 1$. Results, however, are strongly skewed toward $R_{\mathrm{discont}}/R_{\mathrm{cont}} > 1$, 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 ($E_{\mathrm{discont}}/E_{\mathrm{cont}}$) for the same runs as in *A*. Again, results deviate from the null hypothesis ($E_{\mathrm{discont}}/E_{\mathrm{cont}} = 1$); 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 $T(\sigma, f) = (1/2)\{1 + \mathrm{erf}\,[\nu(\sigma(f) - \sigma)]\}$ 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, parameterized 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 toward 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 .004, in contrast with .286 in the discontinuous case. Eighty-three percent of the runs in the continuous model are within the $\alpha = 0.05$ significance level for overdispersion, compared to 4% in the discontinuous case.

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the continuous 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 100 P values for each formulation of the model, which are summarized in the box plots on figure 3*D*.

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.

On comparing the box plots for the discontinuous and continuous versions (fig. 3*D*), the distinction in trait dispersion becomes clear. Although both tend toward overdispersion in that both result in median P values less than .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 parameterized 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 nondifferentiable 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 $a(f_1, f_2) = \delta R(f_1)/\delta p(f_2)$, where $R(f) = (1/p(f))(dp/dt)$ 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 appendix C, available online, we show that the competition kernel in our tolerance-fecundity trade-off model (eq. [6]) has a point of nondifferentiability—a kink (fig. 1*E*, 1*F*)—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 functions (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 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 nondifferentiability in the competition kernel extend beyond the particulars of any given model, in appendix D, available online, we provide the same analysis shown above for a different model of seed size diversity that turns out to have a kinked kernel: the hierarchical competition-colonization model (Levins 1969; Tilman 1994; Kinzig et al. 1999). In this model, the nondifferentiability 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 nondifferentiability 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 trade-off. 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 trade-off 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 trade-off 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 trade-off 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 trade-off.

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 trade-off, 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.

Acknowledgments

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