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Janzen-Connell Effects Are a Weak Impediment to Competitive Exclusion

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ABSTRACT: A goal of ecology is to identify the stabilizing mechanisms that maintain species diversity in the face of competitive exclusion and drift. For tropical forest tree communities, it has been hypothesized that high diversity is maintained via Janzen-Connell effects, whereby host-specific natural enemies prevent any one species from becoming too abundant. Here we explore the plausibility of this hypothesis with theoretical models. We confirm a previous result that when added to a model with drift but no competitive exclusion—that is, a neutral model where intrinsic fitnesses are perfectly equalized across species—Janzen-Connell effects maintain very high species richness that scales strongly with community size. However, when competitive exclusion is introduced—that is, when intrinsic fitnesses vary across species—the number of species maintained by Janzen-Connell effects is substantially reduced and scales much less strongly with community size. Because fitness variation is pervasive in nature, we conclude that the potential of Janzen-Connell effects to maintain diversity is probably weak and that the mechanism does not yet provide a sufficient explanation for the observed high diversity of tropical forest tree communities. We also show that, surprisingly, dispersal limitation can further reduce the ability of Janzen-Connell effects to maintain diversity.

Keywords: tropical forest diversity, Janzen-Connell effects, fitness variation, competitive exclusion, drift, selection.

Introduction

Two processes erode the species diversity of ecological communities over time: competitive exclusion and drift. Competitive exclusion occurs because selection favors species with higher fitness, leading to the extinction of species with lower fitness (Hardin 1960; Levine and HilleRisLambers 2009). Drift occurs because of the discrete nature of individuals and the finite nature of populations, which leads to randomness in the birth-death process that causes fluctuations in species abundance and leads to the chance extinction of some species. In the absence of niche-stabilizing mechanisms, immigration, or speciation, any community will collapse to a state with zero or one species given enough time. The observation that most ecological communities have more than one species—and sometimes hundreds or thousands (Roberts et al. 2002; Wright 2002; Smith et al. 2005)—has motivated ecologists to search for stabilizing mechanisms.

Proposed stabilizing mechanisms invoke niches of various kinds, including variation in resource or habitat requirements across species (Tilman 1980, 1981), temporal niches (Chesson 2000), and Janzen-Connell effects (Janzen 1970; Connell 1971). The commonality is that all of these stabilizing mechanisms cause a species' population growth rate to decline below the intrinsic rate of increase as the species becomes more abundant. Resource niche models show that n species can coexist at a stable equilibrium on n resources (Armstrong and McGehee 1980). But in plankton communities (Smith et al. 2005) or tropical forest tree communities (Wright 2002), the number of species can be orders of magnitude higher than the number of resources. In theory, more than n species can coexist on limit cycles or chaotic attractors (Huisman and Weissing 1999), but the mathematical criteria for multispecies coexistence in such scenarios become ever more restrictive as species are added (Goh and Jennings 1977; Schippers et al. 2001). Temporal niches allow species to coexist in a temporally variable environment, but there are limits to how finely the temporal coexistence axis can be partitioned.

Janzen-Connell effects provide a potential solution to the niche stabilization problem. If each species has its own specialized natural enemy, then the resulting recruitment failure near conspecifics will most heavily impact common species, which by definition have more conspecifics. The resulting rare-species advantage can stabilize community diversity. Theoretically, infinitely many species can coexist via this mechanism (Chisholm and Muller-Landau

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2011). But as in resource models, the mathematical criteria for coexistence become ever more restrictive as more species are added (Chisholm and Muller-Landau 2011). Hubbell (1980) showed that relatively few species could exist at equilibrium via Janzen-Connell effects (see his fig. 3*A*).

Recently, Levi et al. (2018) examined what happens if a Janzen-Connell rule is introduced to an otherwise neutral model—that is, a model in which fitnesses are perfectly equalized—such that there is drift but no competitive exclusion. They found long transient states in which species richness is very high: on a 200 × 200 grid with a Janzen-Connell rule prohibiting recruitment of conspecifics within a Moore neighborhood (a cell and its eight nearest neighbors), the community has more than 100 species after 5 million generations (see Levi et al. 2018, their fig. 2*A*). At larger scales, they found that, again in the transient regime, species richness scales roughly with the square root of area (Levi et al. 2018), which is more than sufficient to explain the observed Amazon tree diversity of more than 10,000 species (Hubbell et al. 2008). Note that because the Levi et al. (2018) results pertain to long transients, they do not contradict Hubbell's (1980) result that few species can be maintained by Janzen-Connell effects at equilibrium.

One limitation of the Levi et al. (2018) analysis is its assumption that, as in a neutral model, all species have equal intrinsic fitness (we take "intrinsic fitness" to be synonymous with the intrinsic rate of increase, i.e., the expected population growth rate when rare or the expected population growth rate in the absence of density dependence mechanisms; Adler et al. 2007; Caughley and Birch 1971; Cortés 2016). Critics of neutral theory have repeatedly pointed out that the fitness equivalence assumption is implausible and that neutral theory is not robust to slight violations of the assumption (Zhang and Lin 1997; Fuentes 2004; Purves and Turnbull 2010). The fitness equivalence assumption means that there is no competitive exclusion in a neutral model and the only diversity-eroding force is drift, which is weak (table 1). The model of Levi et al. (2018) with Janzen-Connell effects inherits the fitness equivalence assumption from neutral theory. Whether it also inherits neutral theory's fragility to violation of the assumption remains to be investigated.

Our goal here is to explore the potential for the Janzen-Connell mechanism to maintain diversity in a model where both drift and competitive exclusion act. This is a crucial test for the mechanism because interspecific intrinsic fitness variation is pervasive in nature and competitive exclusion can occur rapidly in the absence of stabilizing mechanisms (Gause 1934; Tilman 1981; Levine and HilleRisLambers 2009; Kraft et al. 2015). We first develop general theoretical arguments by making the simplifying assumption that there is just one rare species in a community of multiple common species each with approximately equal abundance, allowing us to invoke analogies with two-allele drift-selection models from population genetics. We then relax the simplifying assumption and test the rigor of our general arguments with a multispecies Markov chain model.

Methods

General Theoretical Arguments

For Janzen-Connell effects to maintain diversity, they must be strong enough to allow a species to recover from rarity. A rare species obtains an advantage under Janzen-Connell effects because by definition it has few conspecifics and thus recruitment seldom fails as a result of competition with conspecific neighbors. Let us assume that the rest of the community consists of S common species each with approximately equal relative abundance $1/S$. Therefore, if the Janzen-Connell exclusion zone, within which recruitment of conspecifics is not allowed, has k individuals, then the probability of recruitment failure for a common species will be roughly k/S. This is approximately

Table 1: Classification of mechanisms that have positive and negative effects on diversity in ecological systems

Process	Effect on diversity	Strength
Drift	Negative	Usually weak; strong only in small communities
Selection:		
Competitive exclusion	Negative	Often strong
Janzen-Connell effects	Positive	Usually weak; strong only when a species becomes relatively common
Other stabilizing mechanisms (e.g., resource niches, temporal niches)	Positive	Variable
Immigration	Positive	Strongest in terms of fraction of propagules at small scales; strongest in terms of numbers of species at large scales

equal to the selection coefficient attributable to Janzen-Connell effects α_{JanCon}, which is the expected change in log abundance over one time step (Chevin 2011; app. A; apps. A–C are available online). Thus, we have $\alpha_{\text{JanCon}} \approx k/S$ (we derive this formula as a linearization of a more exact expression and verify it using simulations in app. A).

In a model where Janzen-Connell effects are added to neutral processes and become the only selective force operating in the model, α_{JanCon} represents the entirety of the overall selection coefficient α, that is, $\alpha = \alpha_{\text{JanCon}}$. A species will tend to recover from rarity providing that this selection coefficient is strong enough to offset drift—the only diversity-eroding process operating in the model. A rule of thumb, analogous to similar rules in population genetics (Moran 1959; Kimura 1962, 1983), is that a species will tend to escape rarity if

$$J\alpha \gg 1, \tag{1}$$

where J is the community size and α is the selection coefficient for the rare species (see app. A for a more detailed justification). In a neutral model $\alpha = 0$, and so the rule of thumb never holds—drift always dominates, and diversity tends to be eroded over time.

In a neutral model plus Janzen-Connell effects (Levi et al. 2018), the rule of thumb translates to $J\alpha = J\alpha_{\text{JanCon}} \approx Jk/S \gg 1$. This rule is easy to satisfy because $S \leq J$ by definition. In addition, J increases as area increases, and hence the inequality is easier to satisfy for larger S; this results in S scaling strongly with area.

The situation changes qualitatively if we allow species to vary in their intrinsic fitnesses, which would lead to competitive exclusion in the absence of any stabilizing mechanisms (Zhang and Lin 1997; Purves and Turnbull 2010). Suppose we have a focal species with an intrinsic fitness that is low relative to the community average, perhaps because its fecundity is inherently low or its mortality rate is inherently high. Let $-\alpha' < 0$ represent the corresponding component of the overall selection coefficient (app. A). When this focal species is rare, can it be saved from extinction by Janzen-Connell effects? Using a linearization approximation that holds for small α' and small α_{JanCon} (app. A), our rule of thumb becomes $J(-\alpha' + \alpha_{\text{JanCon}}) \approx J(-\alpha' + k/S) \gg 1$, which is qualitatively different from the previous rule and much harder to satisfy. For a given value of α', there is now a limit to how many species can be maintained by Janzen-Connell effects regardless of the size of the community (the rule of thumb becomes impossible to satisfy for $S > k/\alpha'$). This reveals two important results, both in contrast to the case with no intrinsic fitness differences: (i) the ability of Janzen-Connell effects to save rare species from competitive exclusion is weak and (ii) this ability does not increase strongly with community size and thus with spatial scale.

Mechanistic Markov Chain Model

In this section we describe a Markov chain model that implements explicit multispecies dynamics characteristic of a tropical forest tree community and allows us to test the robustness of the general theoretical principles just outlined. A comprehensive model would allow intrinsic fitnesses to vary across species, time, and space. But the complexity of such a model would make it difficult to analyze and understand. Here we take a first step and consider a model in which intrinsic fitnesses vary across species but are fixed across time and space. This is a better approximation to reality than a neutral model, but we acknowledge that it is an approximation nonetheless. Operationally, we induce fitness variation by varying reproduction rates across species (Zhang and Lin 1997; Adler et al. 2007; Levine and HilleRisLambers 2009; Purves and Turnbull 2010).

Our model is a mechanistic multispecies Markov chain model that includes drift, dispersal limitation, Janzen-Connell effects, and interspecific intrinsic fitness variation. The community in the Markov chain model comprises $J = L^2$ individuals on a square grid and S species, with the abundance and intrinsic fitness of species i denoted by n_i and f_i, respectively. In each discrete time step of the model, one individual is chosen at random to die. Each existing individual then produces a number of propagules proportional to its species' intrinsic fitness f_i (Zhang and Lin 1997), and these are rained down on the surrounding landscape in a two-dimensional spatial pattern following a bivariate normal distribution with means and covariance equal to zero and standard deviations equal to σ_d, in units of grid cells. A replacement individual is chosen randomly from the propagules landing on the vacated cell, subject to the constraint of Janzen-Connell effects; that is, the recruit cannot be conspecific with one of the k individuals in the dead individual's Janzen-Connell exclusion zone. If $k = 0$ (as in a neutral model), then the recruitment event always succeeds; if $k > 0$, the recruitment event will sometimes fail. We defined the parameter k such that it excludes the individual that just died (i.e., a dying tree can be replaced by a conspecific) in order to avoid situations where the last individual of a species dies and the vacated cell cannot be filled by any extant species without violating the Janzen-Connell exclusion rule.

After studying the model mathematically, we implemented it numerically in C++. We used periodic boundary conditions to minimize edge effects and restricted the community grid size to powers of two for optimization purposes. We drew the intrinsic fitness parameter f_i of each species i from a lognormal distribution with parameters $\mu_f = 0$ and σ_f. We ran simulations with all combinations of $L \in \{2^2, 2^3, \ldots, 2^8\}$ and $\sigma_f \in \{0.0, 0.2, \ldots, 1.0\}$. The largest grid size corresponds to a total adult tree community size ($J = L \times L = 2^{16} = 65{,}536$ individual trees) on the order of the number of reproductive trees in a 50-ha forest plot (see the next subsection).

To allow the system to reach a dynamic equilibrium with a nontrivial number of species, we introduced a small per capita speciation rate of $\nu = 10^{-6}$. The speciation rate is sufficiently low such that the corresponding neutral scenarios spend most of their time as monocultures at the dynamic equilibrium, which means we can attribute all diversity in the simulation output to Janzen-Connell effects. We initialized each simulation at high diversity, with each individual's identity being drawn randomly from a pool of $S_0 = 1{,}000$ species. We ran each simulation for $T_{\max} = 10^7$ generations and verified convergence to a dynamic equilibrium independent of the initial condition by confirming that species richness changed little after 10^6 generations. We explored two values of the Janzen-Connell exclusion zone parameter: $k = 8$, corresponding to a 3×3 Moore neighborhood, and $k = 24$, corresponding to a 5×5 neighborhood. In our initial simulations, there was no dispersal limitation ($\sigma_d = \infty$); we subsequently repeated the simulations with $k = 8$ for four different finite values of dispersal limitation ($\sigma_d \in \{1, 5, 10, 15\}$).

We then ran further simulations on larger grid sizes for comparison with previously published results by Levi et al. (2018), whose model is similar to ours but always assumes intrinsic fitness equivalence across species. In these simulations, for consistency with Levi et al. (2018), we excluded speciation, turned off dispersal limitation ($\sigma_d = \infty$), and modified the definition of k such that a dying individual cannot be replaced by a conspecific (this has little effect on model behavior at high species richness). Our use of periodic boundary conditions instead of a buffer zone (Levi et al. 2018) has only minor effects on the results. We ran five baseline scenarios of the model, one neutral ($k = 0$) and four with Janzen-Connell effects ($k \in \{1, 9, 25, 49\}$), over $T_{\max} = 10^6$ generations. Each scenario was run on four different grid sizes $L \in \{2^8, 2^9, 2^{10}, 2^{11}\}$ (the largest grid here represents a ≈100 km^2 area of tropical forest). At the initial condition, each individual's identity was randomly drawn from a pool $S_0 = 1{,}000$ species with equal intrinsic fitnesses. The $S_0 = 1{,}000$ initial condition was used here because these scenarios lack speciation and so high initial diversity is a necessary precondition for high diversity maintenance via Janzen-Connell effects. We repeated these large-grid simulations with low ($\sigma_f = 0.1$) and high ($\sigma_f = 1$) intrinsic fitness variation. Thus, in total for the large-grid simulations we ran 15 scenarios at each of four grid sizes. This required a total of more than 83 trillion birth-death time steps, which took several months of processing time (split into multiple jobs) on a high-performance cluster.

Estimating Model Parameter Values for the Barro Colorado Island Plot

To establish which region of parameter space in the simulated models is appropriate for real tropical forests, we estimated the Janzen-Connell exclusion zone size (k) and intrinsic fitness variation (σ_f) for the well-studied 50-ha forest plot on Barro Colorado Island (BCI) in Panama (Condit et al. 2017). To estimate k, we first defined an adult tree as a tree with diameter at breast height (DBH) greater than or equal to the reproductive DBH threshold for the corresponding species reported by Wright et al. (2005*a*). With this definition, there were 86,069 adult trees in the plot in the 1995 census. We counted how many conspecifics c_k the average adult tree had within its k nearest adult neighbors, where $k = 8$ or $k = 24$. For a strict Janzen-Connell exclusion zone, we should have $c_k = 0$. To the extent that $c_k > 0$, this indicates that the true exclusion zone size is less than k or that the exclusion rule is not strict (i.e., conspecific trees may sometimes recruit there). A caveat here is that neighboring conspecifics could also be the result of simultaneous recruitment events. This caveat aside, our method provides a rough idea of how large and/or strict the Janzen-Connell exclusion zone is in practice. In these calculations, we considered only the 30 most abundant tree species (all of which have more than 250 adult individuals in the plot): these species are common enough that one might reasonably expect their recruitment to be limited by Janzen-Connell effects.

We empirically estimated interspecific intrinsic fitness variation σ_f from published data on seed production rates and seedling recruitment rates (Wright et al. 2005*b*) for 15 tree species at BCI collected over the periods 1987–2003 and 1995–2003, respectively (note that *Thinouia myriantha* is listed as a tree species in table 2 of Wright et al. 2005*b*, but it is actually a liana [Kitajima et al. 2013]). We estimated relative intrinsic fitness for each of the 15 species by dividing the seed production or seedling recruitment by the corresponding number of reproductive adult trees in the BCI plot in the 1995 census (Wright et al. 2005*a*).

Note that these seed production and recruitment estimates are meaningful in relative terms but not in absolute terms because they were estimated from, respectively, a series of traps that covered only 100 m^2 and a series of plots that covered only 600 m^2 of the 50-ha plot and because the timeframes over which the data were collected are arbitrary. However, the interspecific standard variation in the logarithm of the estimates is invariant to multiplication by a constant. Thus, the estimated interspecific variation corresponds to the parameter σ_f in our model.

Other sources of error are the sampling error inherent in the estimates of seed production and seedling recruitment and the imperfect correspondence between the trees in the 50-ha plot in 1995 that were classified as reproductive and those that contributed to seed production. Although adult tree abundances have been fairly consistent across species from the first census in 1981–1983 to the seventh in 2010 (Spearman's $\rho = 0.91$), some trees contributing to seed reproduction may be outside the plot, and our assignments of reproductive status based on DBH thresholds are not precise. These errors propagate through to our estimates of the σ_f parameter.

A final caveat is that our estimates of σ_f—one based on seed production and one on seedling recruitment—do not capture all factors influencing intrinsic fitness variation, that is, all factors differentially affecting species' prospects in the absence of density dependence. Of the two estimates, the one based on seedling recruitment is more informative because it accounts for interspecific variation in both seed production and germination success.

Results

Mechanistic Markov Chain Model: Analytical Results

We derived the following approximation for the selection coefficient for a rare focal species i in our model under a scenario with no dispersal limitation ($\sigma_d = \infty$; app. B):

$$\alpha_i \approx \frac{f_i}{\langle f \rangle_J}\left(1 + \frac{k}{S}\frac{\langle f \rangle_J}{\langle f \rangle_S}(1 + \mathrm{CV}^2_{x,f})\right) - 1, \qquad (2)$$

where $\langle f \rangle_J$ and $\langle f \rangle_S$ are the mean intrinsic fitnesses across, respectively, all individuals and all species in the community and $\mathrm{CV}^2_{x,f}$ is the coefficient of variation in abundance across species weighted by species' intrinsic fitnesses. If the community is composed mainly of common species having roughly equal abundance, then we have $\mathrm{CV}^2_{x,f} \approx 0$ and $\langle f \rangle_J \approx \langle f \rangle_S$, and equation (2) reduces to $\alpha_i \approx f_i/\langle f \rangle_J - 1 + k/S$ (app. B). In this case, if there are Janzen-Connell effects but there is no intrinsic fitness variation ($f_i = \langle f \rangle_J$), then the selection coefficient is always positive with $\alpha_i \approx k/S$ (solid curves in fig. 1), consistent with our earlier general theoretical arguments. But if intrinsic fitness variation is present and a focal rare species has lower than average intrinsic fitness ($f_i < \langle f \rangle_J$), then the selection coefficient is much lower and becomes negative for sufficiently high species richness (dashed and dotted curves in fig. 1), in which case the condition $J\alpha_i \gg 1$ becomes impossible to satisfy for any community size J, again consistent with our general theoretical arguments. Relaxing the assumption of negligible variation in species' abundances—that is, allowing $\mathrm{CV}^2_{x,f} \gg 0$—leads to higher rare species advantages but qualitatively similar results (fig. 2). Relaxing the assumption of global dispersal by allowing finite σ_d reduces rare species advantages but again gives qualitatively similar results (app. B).

Mechanistic Markov Chain Model: Simulations

Our simulations on scales roughly up to that of a 50-ha forest plot showed that Janzen-Connell effects could maintain high diversity in an otherwise neutral system, that is, a system in which species' intrinsic fitnesses are perfectly equalized (bottom of each panel in fig. 3). With the small exclusion zone ($k = 8$) about 200 species could be maintained at the largest grid size, and with the larger exclusion zone ($k = 24$) more than 300 species could be maintained. This is on the order of the number of tree species present in the BCI 50-ha plot (Condit et al. 2017).

However, as interspecific intrinsic fitness variation σ_f is increased from zero (moving upward on fig. 3), diversity drops sharply as species with lower fitness are eliminated and species with higher fitness come to dominate. If $\sigma_f = 0.2$, the number of species maintained with small and large exclusion zones drops by 65% and 49%, respectively, relative to the equal-fitness case; if $\sigma_f = 1.0$, the number of species maintained drops by 88% and 78%. Thus, Janzen-Connell effects can maintain high diversity only if interspecific intrinsic fitness variation is low, that is, if species are already nearly perfectly equalized.

Adding dispersal limitation to the model reduces diversity (fig. 4), although these reductions are appreciable only for the strongest dispersal-limited scenarios ($\sigma_d = 1$; fig. 4*A*). We ran dispersal-limited simulations only for the case of a small exclusion zone ($k = 8$), but we expect this result would generalize to larger exclusion zone sizes, consistent with our corresponding analytical results (app. B).

In our simulations on larger grid sizes, we again found that Janzen-Connell effects could substantially boost diversity in an otherwise neutral model. In these simulations we turned off speciation, for consistency with the model of Levi et al. (2018). Whereas diversity decays to monodominance by the end of each neutral simulation (fig. 5, solid black curves), it decays much more slowly in the Janzen-Connell simulations (fig. 5, solid gray curves). With $k = 9$, even after 10^6 generations there were still well over 100 species in the simulations with grid size $L = 2^8$ (fig. 5*A*; see fig. C1 for other values of k; figs. A1, C1, C2

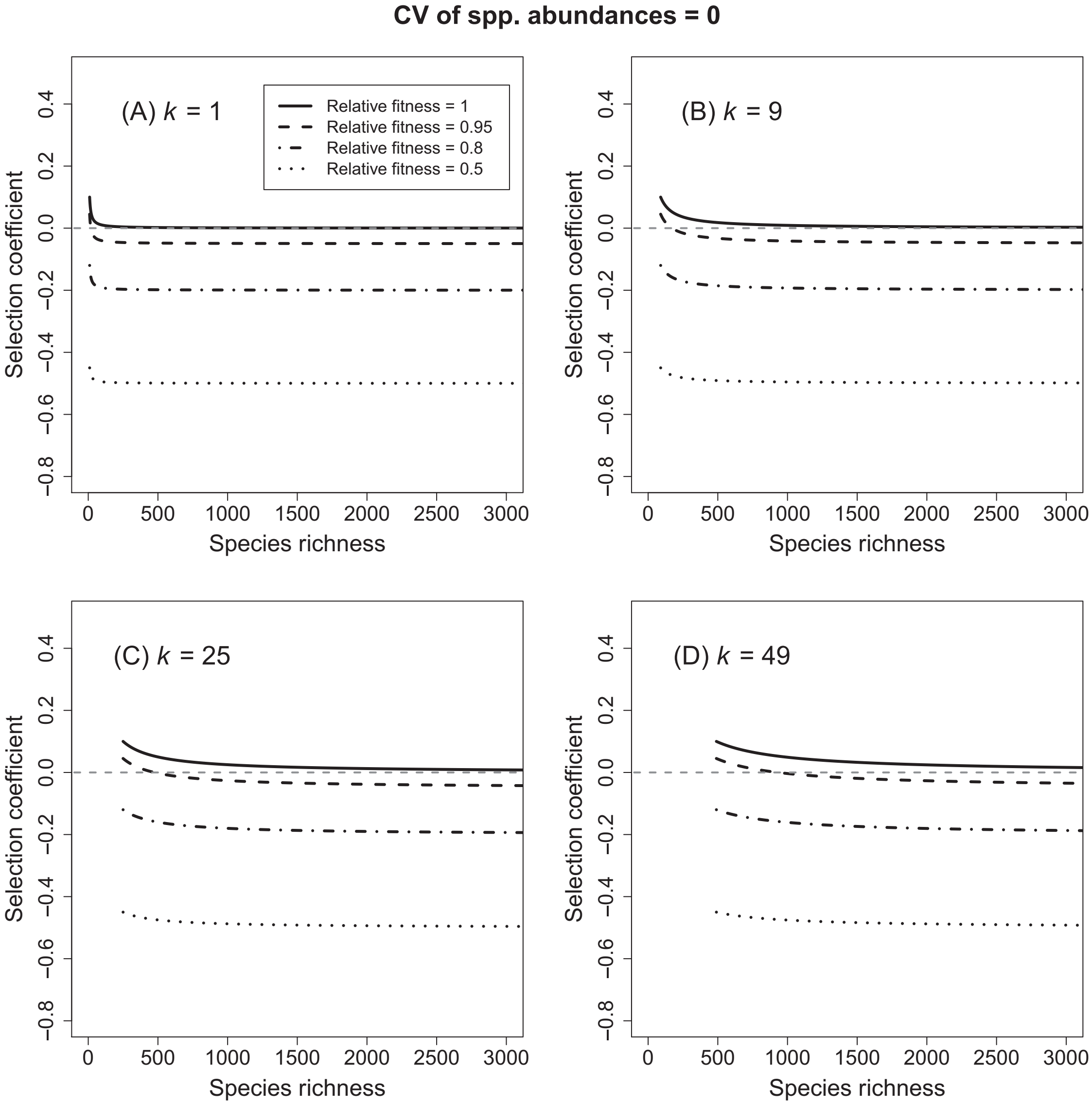

Figure 1: Selection coefficient α_i for a rare focal species versus species richness S for different strengths of stabilizing Janzen-Connell effects (measured by size of the exclusion zone k, varying across panels) and different values of the focal species' intrinsic fitness relative to the community mean ($f_i/\langle f\rangle_J$; separate curves on each panel). In the scenarios illustrated, we make the approximation that variation in abundances across species can be ignored ($\mathrm{CV}_{x,f=0}$ and $\langle f\rangle_J/\langle f\rangle_S = 1$ in eq. [2]). The gray horizontal dashed lines denote $\alpha_i = 0$, corresponding to a neutral baseline with no Janzen-Connell effects and equal intrinsic fitness across species. The curves are drawn starting from species richness $S = 10k$, to fulfil the assumption of $S \gg k$ used in the derivation of the equation for α_i (app. B). To assess whether a rare species with relative intrinsic fitness $f_i/\langle f\rangle_J$ can recover from rarity in a community of J individuals and S species, one reads the corresponding selection coefficient α_i off the appropriate graph and checks whether the rule $J\alpha_i \gg 1$ holds (eq. [1]).

are available online) and still close to the original 1,000 species in the simulations with grid size $L = 2^{11}$ (figs. 5*D*, C1). Accordingly, at the end of the simulations the species-area curve (using community size as a proxy for area) is strongly positive (fig. 6, solid curve), with richness scaling roughly as the square root of area, that is, $S \sim A^{0.5}$ (as in Levi et al. 2018). Adding interspecific intrinsic fitness variation qualitatively changed the results, as in the earlier simulations on small grids. In scenarios with low intrinsic fitness variation, there was a moderate reduction in diversity on the $L = 2^8$ grid (fig. 5*A*, dashed gray curve for $k = 9$; see fig. C1 for other values of k) and a massive reduction in diversity on the $L = 2^{11}$ grid (figs. 5*D*, C1) relative to the respective cases without intrinsic fitness variation (solid gray curves

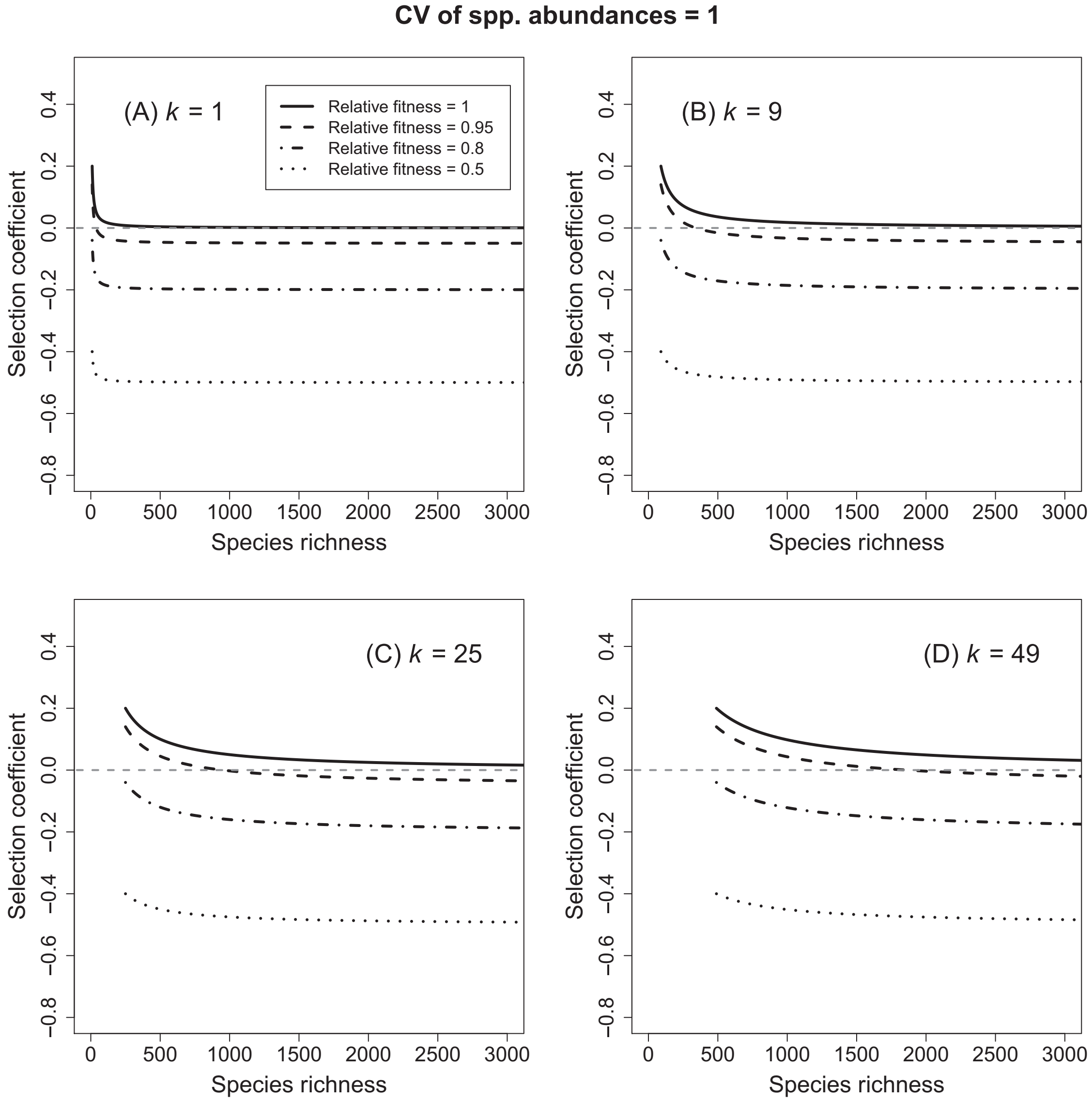

Figure 2: Selection coefficient α_i for a focal rare species versus species richness S for different strengths of stabilizing Janzen-Connell effects (k) and different values of the focal species' relative intrinsic fitness ($f_i/\langle f\rangle_J$). In contrast to figure 1, here we account for variation in abundance across species ($\mathrm{CV}_{x,f} = 1$ in eq. [2] but still assuming $\langle f\rangle_J/\langle f\rangle_S \approx 1$ as in fig. 1). Other details are as for figure 1.

on same panels). In scenarios with large intrinsic fitness variation, the reductions in diversity were much starker (fig. 5, dotted gray curves; fig. C1). For these scenarios, species richness was far below the values in the scenarios with only Janzen-Connell effects and no fitness variation (fig. 5, dotted gray curves vs. solid gray curves) and much closer to the values in the scenarios with only intrinsic fitness variation and no Janzen-Connell effects (fig. 5, dotted gray curves vs. dotted black curves). The species-area curves were much shallower in the scenarios with intrinsic fitness variation: roughly $S \sim A^{0.13}$ for the low intrinsic fitness variation scenarios and $S \sim A^{0.09}$ for the high intrinsic fitness variation scenario (fig. 6). Qualitatively similar results were obtained for other values of k (figs. C1, C2), with a steep species-area curve only for very large k and low σ_f (fig. C2).

Estimating Model Parameter Values for the Barro Colorado Island Plot

For the 30 most common tree species in the BCI 50-ha tropical forest plot, the average adult tree has $c_8 = 1.9$ conspecific adults within its eight nearest adult neighbors and $c_{24} = 5.9$ conspecific adults within its 24 nearest

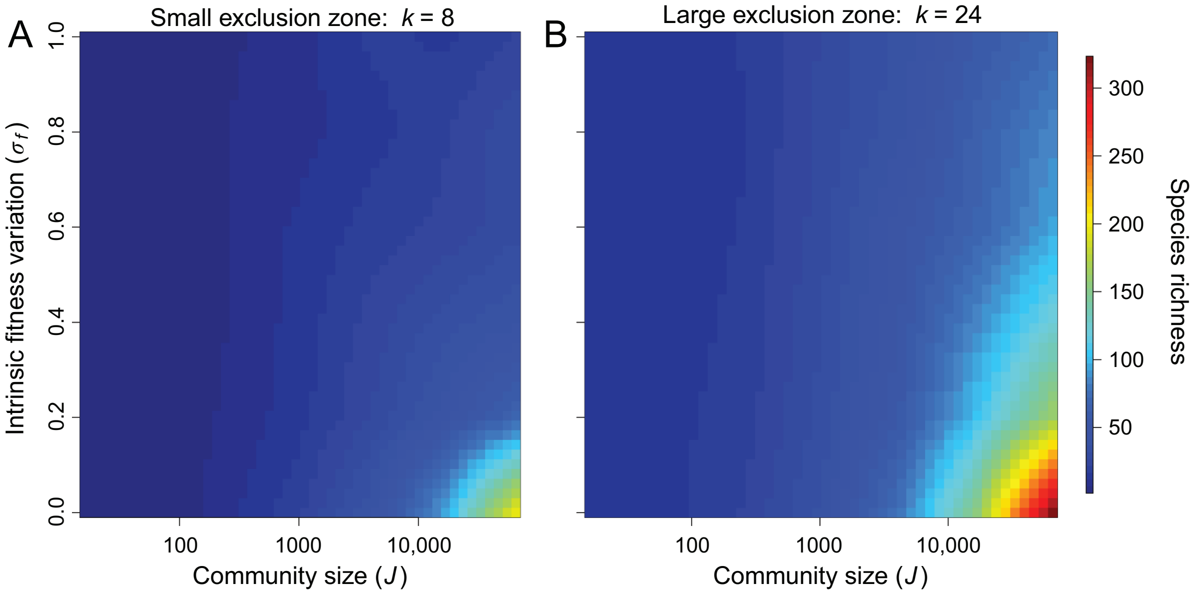

Figure 3: Species richness as a function of community size (J) and intrinsic fitness variation (σ_f) at dynamic equilibrium in a system with a speciation rate of $\nu = 10^{-6}$, no dispersal limitation ($\sigma_d = \infty$), and a Janzen-Connell exclusion neighborhood of size $k = 8$ (*A*) or $k = 24$ (*B*). The speciation rate is sufficiently low such that in a neutral system there would be only one species on average at the dynamic equilibrium (not shown). In the Janzen-Connell system shown, equilibrium species richness increases rapidly with area as community size increases when all species have equal fitness (i.e., $\sigma_f = 0$, implying equal intrinsic fitness; bottom of each panel), but this result is not robust to moderate interspecific intrinsic fitness variation (intrinsic fitness increases from bottom to top in each panel).

adult neighbors, suggesting that the true exclusion zone is either small or rather weak (or both).

For the 15 tree species considered at BCI with seed production and seedling recruitment data, interspecific variation in per-adult seed production and seedling recruitment was large and lognormally distributed (seed production: $\mu_f = 2.7$, $\sigma_f = 1.5$, with a one-sample Kolmogorov-Smirnov test of log-transformed values against a normal distribution giving $D = 0.11$ and $P = .98$; seedling recruitment: $\mu_f = 0.9$, $\sigma_f = 1.0$, $D = 0.13$, $P = .95$). Because our goal was to estimate components of variation in intrinsic fitness—that is, fitness in the absence of density-dependent factors—we repeated the calculations excluding the abundant species *Faramea occidentalis*, which comprised more than 10% of the reproductive trees in the plot. The remaining species all had relative abundance less than 1%, and the per-adult seed production and seedling recruitment estimates exhibited no correlation with adult abundance (seed production: Pearson's $r = -0.0013$, $P = 1.00$; seedling recruitment: $r = -0.059$, $P = .84$). The interspecific variation in seed production and seedling recruitment without *F. occidentalis* remained large and lognormally distributed (seed production: $\mu_f = 2.9$, $\sigma_f = 1.3$, $D = 0.14$, $P = .85$; seedling recruitment: $\mu_f = 1.0$, $\sigma_f = 0.9$, $D = 0.14$, $P = .92$).

We also estimated the standard deviation of dispersal distance at BCI to be roughly $\sigma_d = 50$ m (using data from Muller-Landau et al. 2008), which in units of grid cells in our model is $\sigma_d \approx 20$, comparable to our $\sigma_d = 15$ results (fig. 4*D*), which numerically are almost indistinguishable from our results without dispersal limitation ($\sigma_d = \infty$; fig. 3).

Discussion

A major goal of community ecology is to discover the stabilizing mechanisms that maintain species richness in the face of two diversity-eroding forces: drift and competitive exclusion (May et al. 2012; Terborgh 2012). Less commonly acknowledged is that of these two forces, drift is by far the weaker (McPeek and Gomulkiewicz 2005; table 1). Terborgh (2012, p. 303), for example, writes that "in the absence of compensatory mechanisms, two powerful forces, drift and competition, are expected to erode diversity quickly." But drift is a "powerful force" only in very small communities. In communities of any appreciable size, competitive exclusion and other selective forces dominate over drift, which becomes negligible. Showing that Janzen-Connell effects can maintain high diversity in the face of drift (Levi et al. 2018) is therefore a weak result. The key test of any proposed stabilizing

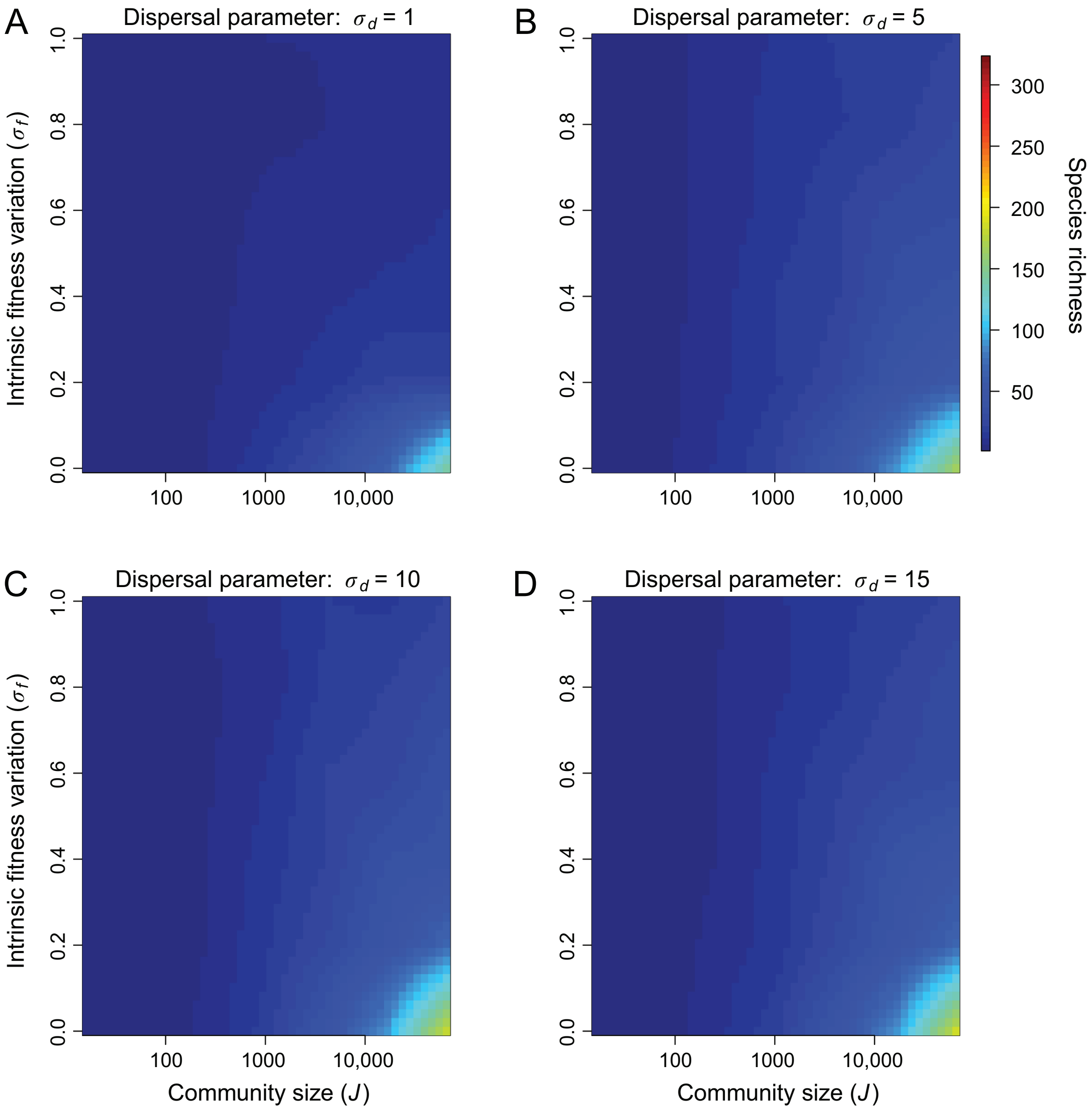

Figure 4: As for figure 3*A*, but with dispersal limitation (value of σ_d indicated at the top of each panel).

mechanism is whether it can oppose competitive exclusion. Our main result suggests that for realistic parameter values, Janzen-Connell effects only weakly oppose competitive exclusion.

Models lacking the potential for competitive exclusion are unrealistic because they make the assumption of equal intrinsic fitness across species. This assumption is central to neutral theory, where it has rightly been the target of frequent criticism: the assumption is violated in practice, and neutral theory's predictions are not robust to deviations from it (Zhang and Lin 1997; Fuentes 2004; Purves and Turnbull 2010). Gause (1934) found that intrinsic fitnesses differed by more than 40% for two species of competing *Paramecium*, more than 30% for two species of *Saccharomyces* yeast, and more than 400% for two species of *Schizosaccharomyces* yeast—these observations inspired the competitive exclusion principle. In annual plant communities, intrinsic fitnesses can vary by orders of magnitude across species (Kraft et al. 2015), resulting in rapid competitive exclusion if the stabilizing effects of niches are removed (Levine and HilleRisLambers 2009). Similarly high interspecific variation in intrinsic fitness has been reported for coexisting diatom species (Tilman 1981). When realistic interspecific intrinsic fitness

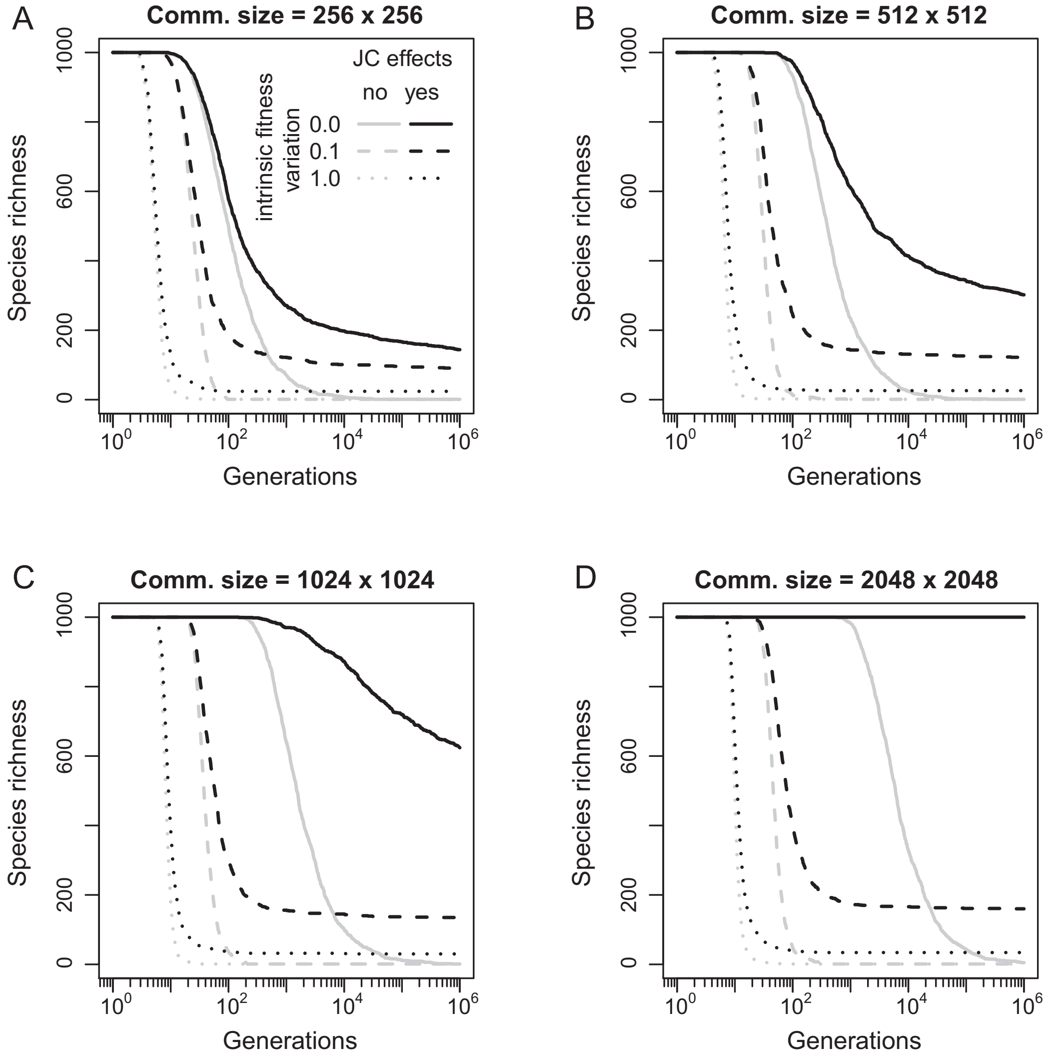

Figure 5: Time series of species richness from simulations of the Markov chain model with a Janzen-Connell exclusion zone size of $k = 9$. Each panel corresponds to a different community size (grid size; indicated at the top of each panel). The solid gray curves show neutral scenarios, and the solid black curves show scenarios with Janzen-Connell effects added to an otherwise neutral model (equal intrinsic fitness across species). The dashed and dotted curves show versions of these scenarios with, respectively, low and high interspecific intrinsic fitness variation. Diversity decays much faster when intrinsic fitness variation is present, especially on large grids (note the logarithmically transformed time axis). See figure C1 for the corresponding results for other values of k. JC = Janzen-Connell.

variation is added to otherwise neutral models, thus allowing competitive exclusion, diversity collapses (Zhang and Lin 1997; Fuentes 2004; Purves and Turnbull 2010).

Because our model of Janzen-Connell effects incorporates intrinsic fitness variation, it is more realistic than a previous model of Janzen-Connell effects in an otherwise neutral context (Levi et al. 2018). And in our model many fewer species can be maintained, broadly consistent with previous theory examining a generic stabilizing mechanism in a deterministic, nonspatial context (Chisholm and Muller-Landau 2011). Exactly how many species can be maintained in our model hinges largely on the values of two parameters: the strength of interspecific intrinsic fitness variation (σ_f) and the Janzen-Connell exclusion zone size (k). More species can be maintained for smaller σ_f and larger k (fig. 3).

Bearing in mind that our model is only an approximation of reality, we can ask what values of these two parameters are realistic for tropical forest tree communities. For the BCI forest, we found large variation in interspecific intrinsic fitness based on seedling production and seedling recruitment data corresponding to $\sigma_f \approx 1.0$ or greater (Wright et al. 2005*b*). Although seed production and seedling recruitment are only two component of

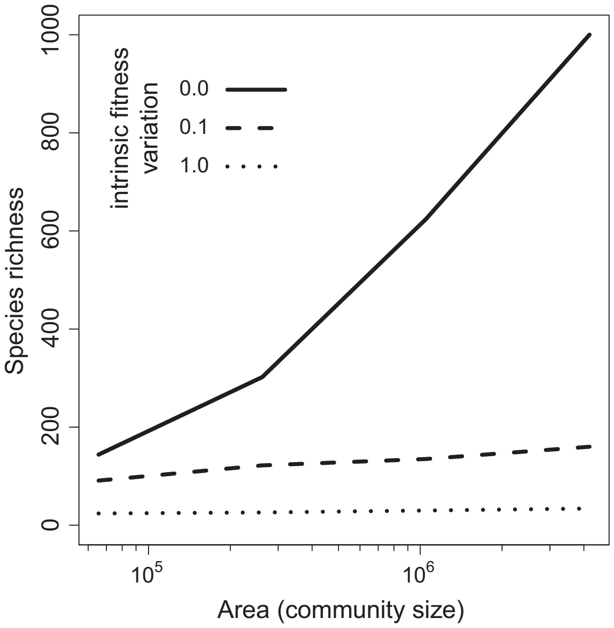

Figure 6: Species-area relationships from simulations of the Markov chain model with Janzen-Connell effects. The solid curve shows an otherwise neutral scenario (equal intrinsic fitness across species), and the other curves show scenarios with interspecific variation in intrinsic fitness (dashed curve = low intrinsic fitness variation; dotted curve = high intrinsic fitness variation) for an exclusion zone size of $k = 9$ (see fig. C2 for other values of k). Area is measured in units such that the density of individuals per unit area is equal to 1. For each simulation, species richness was computed after 10^6 generations (see fig. 5).

intrinsic fitness and although trade-offs in vital rates may mitigate this variation to some extent in practice, the hypothesis of perfectly equalizing trade-offs remains implausible (Purves and Turnbull 2010). The available evidence thus suggests that in tropical forest tree communities, as in annual plant and microbe communities (Gause 1934; Tilman 1981; Levine and HilleRisLambers 2009; Kraft et al. 2015), intrinsic fitness variation is high and rapid competitive exclusion of the less fit species would occur in the absence of niche-stabilizing mechanisms (or substantial immigration; table 1). Empirical data also suggest that the Janzen-Connell exclusion zone size k is not large. Hubbell (1980) found that for 30 common tree species in a dry forest in Costa Rica, the nearest neighbor distance between conspecific trees was less than 20 m for 16 species and less than 40 m for all species, pointing to a relatively small exclusion zone. Our counts of the number of conspecific adult trees within neighborhoods of $k = 8$ and $k = 24$ at BCI similarly suggest either that the true exclusion zone is small (i.e., $k < 8$) or that Janzen-Connell effects are weak within the zone (i.e., conspecifics may sometimes recruit)—or both. Although these estimates of the k and σ_f parameters are rough, they indicate that even our simulation scenarios with $k = 9$ and $\sigma_f = 1.0$ (corresponding to the top of fig. 3*A* or the dotted curves in fig. 5), in which diversity maintained by the Janzen-Connell mechanism was lowest, may overstate the true potential of this mechanism to maintain diversity in nature.

Our results also show that the ability of Janzen-Connell effects to maintain diversity scales weakly with area in the presence of interspecific intrinsic fitness variation (fig. 6, dashed and dotted curves). This contrasts with the equal-fitness scenario, where species richness scales roughly with the square root of area (fig. 6, solid curve; fig. C2; Levi et al. 2018). These results can be explained as follows. In an equal-fitness scenario, the only diversity-eroding force is drift, which quickly becomes negligible with community size, making it easy to oppose with a weak stabilizing force at larger scales. In a world with fitness variation, competitive exclusion is in operation and its substantial effects are felt in both small and large communities.

Our results are an important reminder that drift is a very slow process (Ricklefs 2003). Ironically, if we start with a drift-only model (i.e., a neutral model), then there is actually no need for stabilizing mechanisms at all because high diversity can easily be maintained just with realistic rates of immigration at the local scale and speciation at larger scales (Hubbell 2001; Chisholm and Lichstein 2009; Condit et al. 2012). But as noted earlier the fitness equivalence assumption inherent to neutral theory is not realistic and leads to various problems, including drift-only dynamics that are far too slow to account for observed temporal changes in species abundances on both ecological (Leigh 2007; Chisholm et al. 2014; Kalyuzhny et al. 2014) and evolutionary (Nee 2005; Chisholm and O'Dwyer 2014) timescales. These problems can be fixed by adding fitness variation in various ways (Kalyuzhny et al. 2014; Kalyuzhny et al. 2015; Fung et al. 2016), again pointing to the general need for incorporating such variation into ecological models.

One surprising result from our models is that dispersal limitation can reduce diversity maintained by Janzen-Connell effects. This contradicts the intuition that dispersal limitation increases encounters between conspecifics and thus should amplify Janzen-Connell effects and increase diversity. We can now point to the flaw in this intuition: dispersal limitation does amplify Janzen-Connell effects, but it can amplify them more for rare species than for common species. The reason is that relative to the global dispersal scenario, dispersal limitation increases the frequency of conspecific encounters for rare species more than for common species. Under global dispersal rare species can easily escape their conspecifics, but common species cannot because they are already usually widespread.

Curiously, these results are opposite those of Detto and Muller-Landau (2016*b*), who, using a point process model, found that greater dispersal limitation allows more diversity to be maintained by Janzen-Connell effects. We conjecture that these contrasting results are due to key differences in the assumptions of Detto and Muller-Landau (2016*b*): in their model, the location of a recruitment event is independent of that of the preceding death, and their Janzen-Connell effects act to elevate death rates (rather than lower recruitment rates, as in our model) in areas of high conspecific density. We encourage future work exploring the connections between our models and point process models (Detto and Muller-Landau 2016*a*, 2016*b*).

In conclusion, we find that the Janzen-Connell mechanism is generally unable to act strongly against competitive exclusion and maintain high diversity in competitive communities with realistic interspecific intrinsic fitness variation. We encourage future modeling exercises that test the robustness of our results to various factors, including age structure and spatial and temporal variation in intrinsic fitness. We also encourage empirical studies aimed at better quantifying interspecific intrinsic fitness variation itself, to firmly establish how strong the tendency toward competitive exclusion is and how strong stabilizing mechanisms need to be to offset it. In the meantime, it appears that the Janzen-Connell mechanism is an insufficient explanation for high tropical tree diversity. The search for niche-stabilizing mechanisms that could maintain high diversity in ecological communities must therefore continue.

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Statement of Authorship

R.A.C. conceptualized the project, conducted mathematical and empirical analyses, performed simulations, and wrote the first draft; T.F. conducted mathematical and empirical analyses and edited subsequent drafts.

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