



Tropical forests can maintain hyperdiversity because of enemies

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Explaining the maintenance of tropical forest diversity under the countervailing forces of drift and competition poses a major challenge to ecological theory. Janzen–Connell effects, in which host-specific natural enemies restrict the recruitment of juveniles near conspecific adults, provide a potential mechanism. Janzen–Connell is strongly supported empirically, but existing theory does not address the stable coexistence of hundreds of species. Here we use high-performance computing and analytical models to demonstrate that tropical forest diversity can be maintained nearly indefinitely in a prolonged state of transient dynamics due to distance-responsive natural enemies. Further, we show that Janzen–Connell effects lead to community regulation of diversity by imposing a diversity-dependent cost to commonness and benefit to rarity. The resulting species-area and rank-abundance relationships are consistent with empirical results. Diversity maintenance over long time spans does not require dispersal from an external metacommunity, speciation, or resource niche partitioning, only a small zone around conspecific adults in which saplings fail to recruit. We conclude that the Janzen–Connell mechanism can explain the maintenance of tropical tree diversity while not precluding the operation of other niche-based mechanisms such as resource partitioning.

niche theory | neutral theory | ecological drift | Janzen–Connell | biodiversity

Tropical forests can contain over 1,000 sympatric tree species, posing a major challenge to ecological theory, given that they all depend on the same suite of resources. Early attempts to explain the maintenance of tropical diversity were rooted in the idea of niche assembly based on functional differences between species (1–5). However, models based on niche diversification and minimum similarity have failed to explain observed levels of diversity (6). Hubbell's (7) neutral theory of biodiversity offered an alternative based on the assumption that individuals of all species have the same probabilities of birth and death independent of species identity. Each species undergoes a random walk, either to extinction or monodominance, which is counteracted by speciation or dispersal of new species from a metacommunity. A third approach is offered by the Janzen–Connell (J-C) mechanism (8, 9), in which host-specific natural enemies, including arthropods and fungi operating both above and below ground, restrict the recruitment of juveniles near conspecific adults. J-C is strongly supported empirically (10–13), and recent work has suggested that global plant diversity is associated with increased conspecific negative density dependence in local tree neighborhoods (14–16).

Despite strong empirical support for the J-C mechanism, existing theory predicts that J-C effects are unlikely to allow for the coexistence of more than a few species at equilibrium (one, two, or three tree crown diameters between conspecific adults supports only 3, 7, or 12 species) (17). Becker et al. (18) criticized the equilibrial approach by demonstrating that extinctions occur more slowly with Janzen–Connell effects, but stated that “the question of whether this effect is sufficiently strong to help explain the coexistence of many tree species in tropical forests is not so easily answered.” MacArthur (19) suggested that J-C

effects could only maintain diversity if they resulted in empty canopy space that allowed a new species to recruit. Armstrong (20) showed that, in principle, negative density dependence could lead to a stable equilibrium among tree species, but his nonspatial model allows an indefinite number of trees despite finite canopy space in tree communities. More-recent simulations have included dispersal from a metacommunity (21), speciation (22), or estimates of rare species advantage (23) to offset ecological drift toward extinction, but it remains unknown whether the J-C mechanism is sufficient to allow for the coexistence of hundreds of sympatric tropical forest trees. If so, then how strong must J-C effects be to maintain observed levels of tree species richness?

The most straightforward way to assess whether J-C effects can maintain observed levels of tropical tree diversity is to simulate large landscapes of trees initialized with high species richness for enough time to allow ecological drift to cause extinctions. Even if the J-C mechanism can only maintain a few species at equilibrium, sufficiently long transient dynamics could, in principle, lead to practical maintenance of species richness on evolutionary time scales. Such a simulation has been hindered due to substantial computational challenges associated with operating on long temporal and large spatial scales. In addition, the absence of a solvable analytical model has led to weak understanding of how the J-C effect influences the maintenance of tropical forest diversity.

We used high-performance computing to simulate distance-responsive natural enemies assuming neutral tree death and birth turnover with the simple addition of exclusion zones in

Significance

Biologists have long sought to explain how tropical forests can support as many as 1,000 tree species at a single site. Such high diversity presents a paradox in that two well-documented mechanisms, competition and drift, both erode diversity over time. Much imagination has gone into the quest to find a countervailing force of sufficient strength to counterbalance competition and drift. We show here that the 48-year-old Janzen–Connell mechanism, in which natural enemies restrict tree recruitment near conspecific adults, is capable of maintaining high levels of diversity indefinitely via a stabilizing mechanism that favors rare species and hinders common ones. Diversity maintenance requires only a small zone around conspecific adults in which saplings fail to recruit.

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which conspecifics are not allowed to replace any tree that dies (although we additionally examined the effect of forced replacement by an excluded species) (Fig. 1). Such an exclusion zone occurs, for instance, when adult trees harbor specialist herbivores or pathogens that are fatal to conspecific seeds or seedlings nearby (10, 11). We simulated 200 billion (200×10^9) tree replacements [~ 40 trillion tree-years given tree lifespan of ~ 200 y (24)] using no exclusion zone (i.e., classic neutral theory), excluding trees only of the species of the dead tree, or also excluding species of trees within one, two, or three crown diameters of the dead tree on four increasingly large landscapes (200 \times 200 trees, 400 \times 400 trees, 800 \times 800 trees, and 1,600 \times 1,600 trees). On each of the progressively larger landscapes, 40 trillion tree-years corresponds to roughly 1 billion, 250 million, 62.5 million, and 15.6 million years, all of which we take to represent evolutionary time scales of diversity maintenance. We additionally developed analytical models based on tractable simplifying assumptions and projected results from these models using an absorbing Markov chain.

Results

As expected, diversity drifted toward monodominance under neutral dynamics (Fig. 2, black curves). However, even a small exclusion zone led to an unexpectedly large pseudoequilibrium diversity, and broader exclusion zones resulted in still higher species richness, especially on larger landscapes (Fig. 2). We observed more-rapid initial species losses when starting with 3,000 species, but species richness then tended to converge on the same value as with 1,000 initial species (Fig. 2B). Thus, the imposition of an exclusion zone imposes a stabilizing force to regulate diversity such that species richness declines toward a pseudoequilibrium that is influenced by the size of the exclusion zone and the size of the landscape.

To assess how increasing the force rate (probability of allowing a replacement violating an exclusion zone) impacts our results, we simulated 200 billion tree replacements with force rates of 5%, 20%, and 50%, and compared the results to those with the 5% force rate used in Fig. 2. Species richness declines more

quickly as the force rate increases, but diversity is still maintained, even with high force rates (Fig. 3). Even a small exclusion zone ($E = 1$) with a force rate of 50% can maintain far more diversity than neutral dynamics (Fig. 3, red dashed curves), indicating that exclusion need not be strong to maintain diversity.

To illustrate the machinery behind our numerical results, we derive approximate equations for the probability of increase and decrease of focal species i (abundance N_i) assuming that all other species have equal abundances. Consider a large landscape with J trees of S species. If there is no exclusion, as in neutral theory, then species i increases for a given replacement if it is not the tree that dies (probability $1 - N_i/J$), and it is the tree selected to replace it [probability $N_i/(J - 1)$], so $\text{Pr}(N_i + 1|N_i) = (1 - N_i/J)N_i/(J - 1)$. Similarly, the probability that it decreases is the probability that the dead tree is species i and the replacement is not, which has probability $\text{Pr}(N_i - 1|N_i) = (N_i/J)(1 - [N_i - 1]/[J - 1])$, which is the same as the probability of increase.

Now assume that only the site of the newly dead tree is unavailable to conspecifics due to very weak J-C effects. To increase in abundance, species i must not include the tree that died, which again has probability $1 - N_i/J = 1 - f_i$, where $f_i = N_i/J$ is the frequency of species i . If so, the probability that the dead tree's replacement on the first attempt is species i is $P_1 = N_i/(J - 1) \approx f_i$ (since $J \gg 1$). If species i is not selected on the first try, but the prohibited species of the dead tree is, which has probability $P_2 \approx (1 - f_i)/(S - 1)$ (since the dead tree's species is one of $S - 1$ equally abundant species), species i has another chance to colonize. This again has probability P_1 , and if the prohibited dead tree's species is again selected randomly, species i gets a third chance with probability P_2 , and so on. The probability of species i replacing the dead tree (given that it is a different species) is the sum of the probability that i is chosen on the first or subsequent tries, which is a geometric series. Thus, the probability that species i increases in abundance is the product of the probability defined by the geometric series and the probability that the dead tree is not of species i , which is

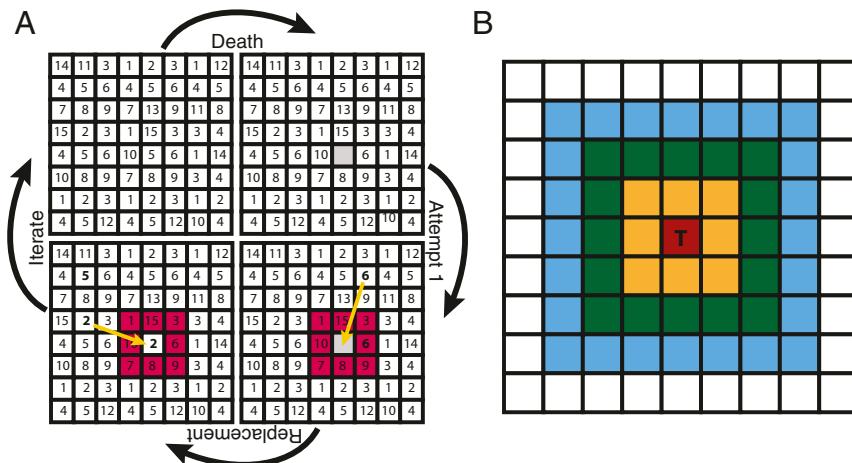


Fig. 1. Simulation of tree turnover and resulting equilibria. (A) A tree randomly dies, and another is randomly selected to replace it (orange arrow). If the opening is within one exclusion distance of a conspecific of the selected tree, the selected species will be rejected and another will be selected until an allowable species is chosen. In the case illustrated, tree species "6" is selected initially but is excluded, and tree species "2" then successfully replaces the dead tree. In our simulations, we allow an excluded replacement 5% of the time. (B) A tree creates exclusion zones within which it, or a conspecific, cannot replace a dead tree. By symmetry, if the target tree for replacement is denoted T , then any species within its exclusion zone represents a tree that cannot replace the target tree because the replacement's exclusion zone also overlaps the target. The red square represents exclusion of conspecifics from replacing T ($E = 1$), species within the red and orange squares ($E = 9$) are within an exclusion zone of one tree crown of the target and so cannot replace the target tree, red, orange, and green squares are within an exclusion zone of two tree crowns ($E = 25$), and squares colored red, orange, blue, or green are within an exclusion zone of three tree crowns ($E = 49$). The tree targeted for death cannot be replaced by a conspecific, or a tree conspecific to any species within the exclusion zone. The program is described in *SI Appendix, section S4*.

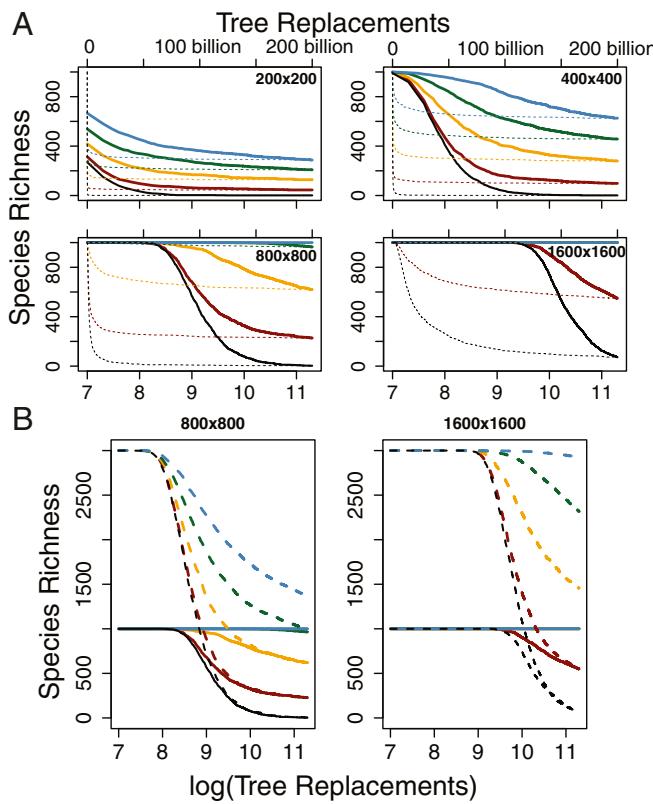


Fig. 2. Simulation results from 200 billion (200×10^9) tree replacements (~40 trillion tree-years given tree lifespan of ~200 y) using no exclusion zone (i.e., classic neutral theory; black), excluding trees only of the species of the dead tree (red), or also excluding species of trees within one (orange), two (green), or three (blue) crown diameters of the dead tree on four increasingly large landscapes (200×200 trees, 400×400 trees, 800×800 trees, and $1,600 \times 1,600$ trees, each with a 10% buffer on all sides to mitigate edge effects; *SI Appendix, section S4*). On each of the progressively larger landscapes, 40 trillion tree-years corresponds to roughly 1 billion, 250 million, 62.5 million, and 15.6 million years, all of which we take to represent evolutionary time scales of diversity maintenance. (A) Species richness for model runs initialized with 1,000 species on linear (dashed lines, top labels) and base-10 logarithmic (solid lines, bottom labels) temporal scales. Runs with no exclusion zone (black) led to monodominance through ecological drift. Modest exclusion only limiting replacement of the dead tree by a conspecific (red) maintained substantial species richness, while increasing the exclusion to one (orange), two (green), or three (blue) crown diameters apparently led to a pseudoequilibrium state with prolonged transient dynamics due to an increasing rare species advantage and common species disadvantage as species richness declines. On the largest landscape, no tree species went extinct with the imposition of any exclusion zone beyond excluding a conspecific from replacing the dead tree. (B) When the model was initialized with 3,000 species (dashed lines), the richness declined relatively rapidly and approached convergence with the corresponding simulation initialized with 1,000 species (solid lines). On the largest landscape, species richness declined even with exclusion zones, in contrast to the simulation initialized with 1,000 species, but the richness always remained above 1,000 species for simulations with at least an exclusion zone of one crown diameter.

$$\Pr(N_i + 1|N_i) \approx (1 - f_i) \sum_{n=0}^{\infty} P_1 P_2^n = \frac{(1 - f_i)P_1}{1 - P_2}$$

$$\approx (1 - f_i) \left(\frac{f_i}{1 - [1 - f_i] \frac{1}{S-1}} \right) = \frac{(1 - f_i)f_i(S-1)}{S-2+f_i}.$$

Species i decreases in abundance if it dies, which has probability $\Pr(N_i - 1|N_i) = N_i/J = f_i$, since, by assumption, a dead tree cannot be replaced by another of the same species. The ratio between the probability of increase and of decrease is therefore

$$\Pr(N_i + 1|N_i)/\Pr(N_i - 1|N_i) \approx (1 - f_i)(S - 1)/(S - 2 + f_i).$$

If species i is rare, then $f_i \approx 0$, and $\Pr(N_{i+1}|N_i)/\Pr(N_{i-1}|N_i) = (S - 1)/(S - 2)$, giving the rare species an advantage of this magnitude. At very high species richness, rare species have little advantage, but the advantage increases as S declines, causing extinction to slow.

Generalizing beyond a single-cell exclusion zone to an exclusion zone of E cells (*SI Appendix, section S1*), we obtain

$$\frac{\Pr(N_{i+1}|N_i)}{\Pr(N_{i-1}|N_i)} \approx (1 - Ef_i) \left(\frac{1}{1 - [1 - f_i] \frac{E}{S-1}} \right)$$

$$= (1 - Ef_i) \left(\frac{S-1}{S-1-E+Ef_i} \right).$$

The probability of decrease is still f_i , and the rare species advantage is $(S - 1)/(S - E - 1)$, which increases as E increases or S decreases (i.e., rare species advantage increases as richness declines; Fig. 4A). Similarly, it can be shown that a more common species, such as one twice as abundant as the others, $N_i = 2J/(S + 1)$ or $f_i = 2/(S + 1)$, has a ratio of increase to decrease probability of $(S - 2E + 1)/(S - E + 1)$, which is less than 1 and declines as richness declines (Fig. 4A), giving a bigger penalty for an abundant species. In general, the probability of increase relative to the probability of decrease $\Pr(N_{i+1}|N_i)/\Pr(N_{i-1}|N_i)$ is a decreasing function of f_i (Fig. 4B). It is equal to 1 for $f_i = 1/S$ (for which species i has the same abundance as the others), greater than 1 for lower f_i , and less than 1 for higher f_i , so that a species more rare than all others has an advantage, and a species more common than all others has a disadvantage (Fig. 4B). This approximation assumes that there are E different species in the exclusion zone, so E nonfocal species are excluded, and the probability that one of these is selected as replacement is $E/(S - 1)$. For larger E , this assumption is less accurate, but it can be reasonable as long as S is fairly large. For example, if $S > 100$ and $E = 9$, there should be an average of over 8.6 different species in an exclusion zone, rather than the assumed 9 (*SI Appendix, section S2*). This makes the approximation slightly overstate the rare species advantage. However, heterogeneity in nonfocal species abundances has the opposite effect. If $S - 1$ nonfocal species abundances have a coefficient of variation of cv , then the effect

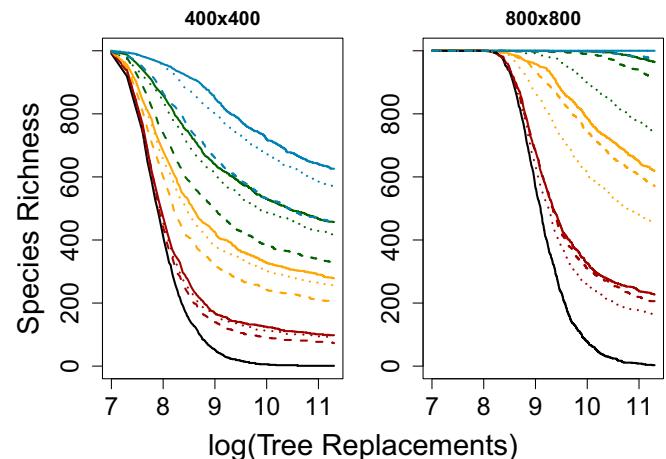


Fig. 3. Probability of allowing prohibited species to replace the dead tree 5% (solid lines), 20% (dotted lines), and 50% (dashed lines) of iterations. Black, red, yellow, green, and blue refer to no exclusion, exclusion of dead tree only, and one, two, and three tree crowns of exclusion ($E = 0, 1, 9, 25$, and 49).

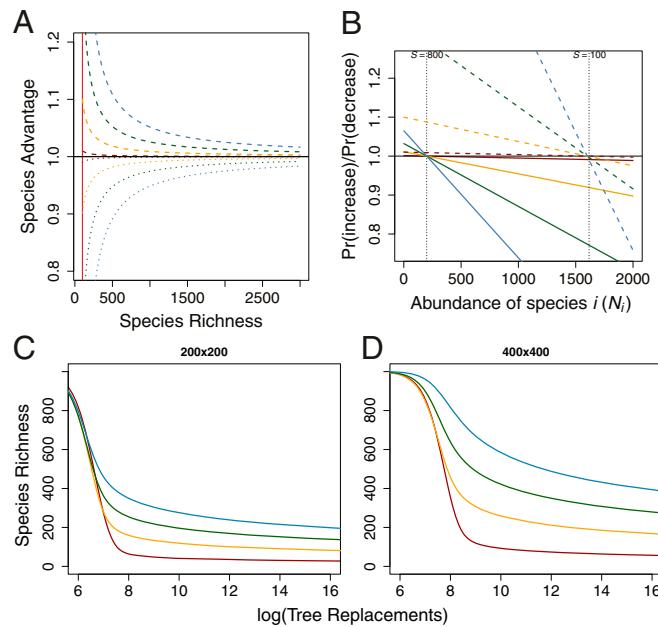


Fig. 4. (A) The species advantage/disadvantage (probability of a species increasing in abundance relative to the probability that species decreases in abundance) as a function of species richness. Dashed lines indicate rare species advantage (as the abundance of a species approaches zero), and dotted lines indicate common species disadvantage (for a species twice as abundant as all other species). As the size of the exclusion zone increases from $E = 1$ (no replacement of dead tree by conspecifics; red) to $E = 9$ (one tree crown; yellow) to $E = 25$ (two tree crowns; green) to $E = 49$ (three tree crowns; blue), the size of the advantage/disadvantage increases. The red vertical line demarcates $S = 100$ species. The rare-species advantage and abundant-species disadvantage produces the stabilizing mechanism leading to observed pseudoequilibrium. (B) Ratio of the probability that a species with abundance N_i increases in abundance relative to the probability that it decreases for a 400×400 landscape ($J = 160,000$) with either species richness of $S = 800$ (solid lines) or $S = 100$ (dashed lines), and exclusion zones of $E = 1$ (red line), $E = 9$ (orange line), $E = 25$ (green line), or $E = 49$ (blue line). The ratio crosses 1 (no advantage or disadvantage) at abundance equal to J/S (vertical black dotted line), but the slope increases with increasing E . For the same landscape size and exclusion zone, reducing S causes the curve to move up and to the right with similar slope. If all species start at equal abundances, for one to become extinct, it must drift from its initial density (where the curve crosses 1) to 0 despite the fact that, as it does so, the probability that it increases in abundance becomes increasingly more than the probability that it decreases. (C and D) The analytical approximate probabilities can be used to define an absorbing Markov chain and projected to over 10 quadrillion (10^{16}) tree replacements without the need for simulation. Results are qualitatively concordant with the simulation model, although it is now evident that the extinction rate is slowed to such a degree that species are essentially maintained indefinitely, and the number of species is dependent on the size of the exclusion zones (colors as before) and the size of the interacting landscape.

on the rare species advantage (or common species disadvantage) is equivalent to $(S - 1)/(1 + cv^2)$ nonfocal species with equal abundances (SI Appendix, section S1). Since this is a lower number of nonfocal species, the rare species advantage is increased by heterogeneity, and diversity maintenance is stronger.

To verify that these approximations adequately characterize the extreme slowing of extinctions seen in the simulations, we projected extinction times and species richness using these probabilities of increase and decrease (i.e., those assuming equal species abundances) to define an absorbing Markov chain (SI Appendix, section S3), which produced results that were concordant with the long transient dynamics evident in the simulations (Fig. 4 C and D). The dynamics defined by the analytical approximation continued to maintain species richness for over 10

quadrillion iterations, with more species again maintained by increasing the size of the exclusion zone or the interacting landscape (Fig. 4 C and D). Even a trivially small landscape of (400×400 trees) maintained ~ 200 species almost indefinitely with an exclusion zone of only one tree crown (Fig. 4D, yellow).

Although it is not our goal to reproduce biodiversity patterns observed in nature, which are produced by a more complex milieu of mechanisms than simply J-C exclusion zones, it is instructive to compare the results of our model with canonical relationships in ecology such as the species-area power law relationship and the lognormal relative abundance distribution. After 200 billion tree replacements, the resulting relationship between species richness and area was linear on a log-log scale (Fig. 5), indicating that these simple simulations reproduce the power law relationship of species-area curves in accordance with observation (25). Larger exclusion zones led to larger intercepts in the species-area relationship, but the species-area relationships for the four exclusion zones were parallel. This indicates that larger exclusion zones allowed for the maintenance of more trees in small areas, but the rate of species accumulation with area was invariant to the size of the exclusion zone. Although not necessarily diagnostic of the ecological mechanism (26), the resulting species abundance distributions also had a form resembling the lognormal with a log-left skew observed in nature (albeit with substantial more evenness) (7), even without the effect of dispersal, speciation, or resource niches (Fig. 6).

Discussion

Although the J-C hypothesis has been with us for nearly 50 y, the question of what forces maintain the high diversity of tropical forest tree communities in the face of ecological drift remains a lively and contentious topic (27–31). Doubts remain about the efficacy of the J-C mechanism, perhaps because it has heretofore lacked a convincing mathematical foundation (17, 19, 22, 32). Taken together, our simulation and analytical results demonstrate that the J-C model can maintain highly diverse communities via extremely prolonged transient dynamics, offsetting drift

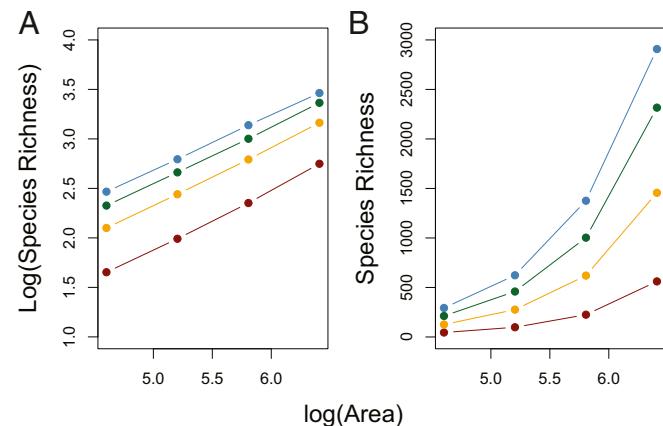


Fig. 5. Species-area curve after 200 billion iterations of the simulation model for the four landscape sizes (200×200 , 400×400 , 800×800 , and $1,600 \times 1,600$) and four exclusion zones. Red, yellow, green, and blue refer to exclusion of dead tree only, and one, two, and three tree crowns of exclusion ($E = 1, 9, 25$, and 49). (A) The species-area curve is linear on a log-log scale, indicating a power law relationship, and the curves are parallel in log-log space, indicating that the exponent in the power law relationship is approximately invariant to the size of the exclusion zone. (B) To illustrate the maintenance of diversity after 200 billion iterations across the four landscapes and exclusions zones, we additionally include results for untransformed species richness. Larger landscapes and/or exclusion zones maintain substantial species richness even exceeding the maximum observed richness of sympatric trees in tropical forests.

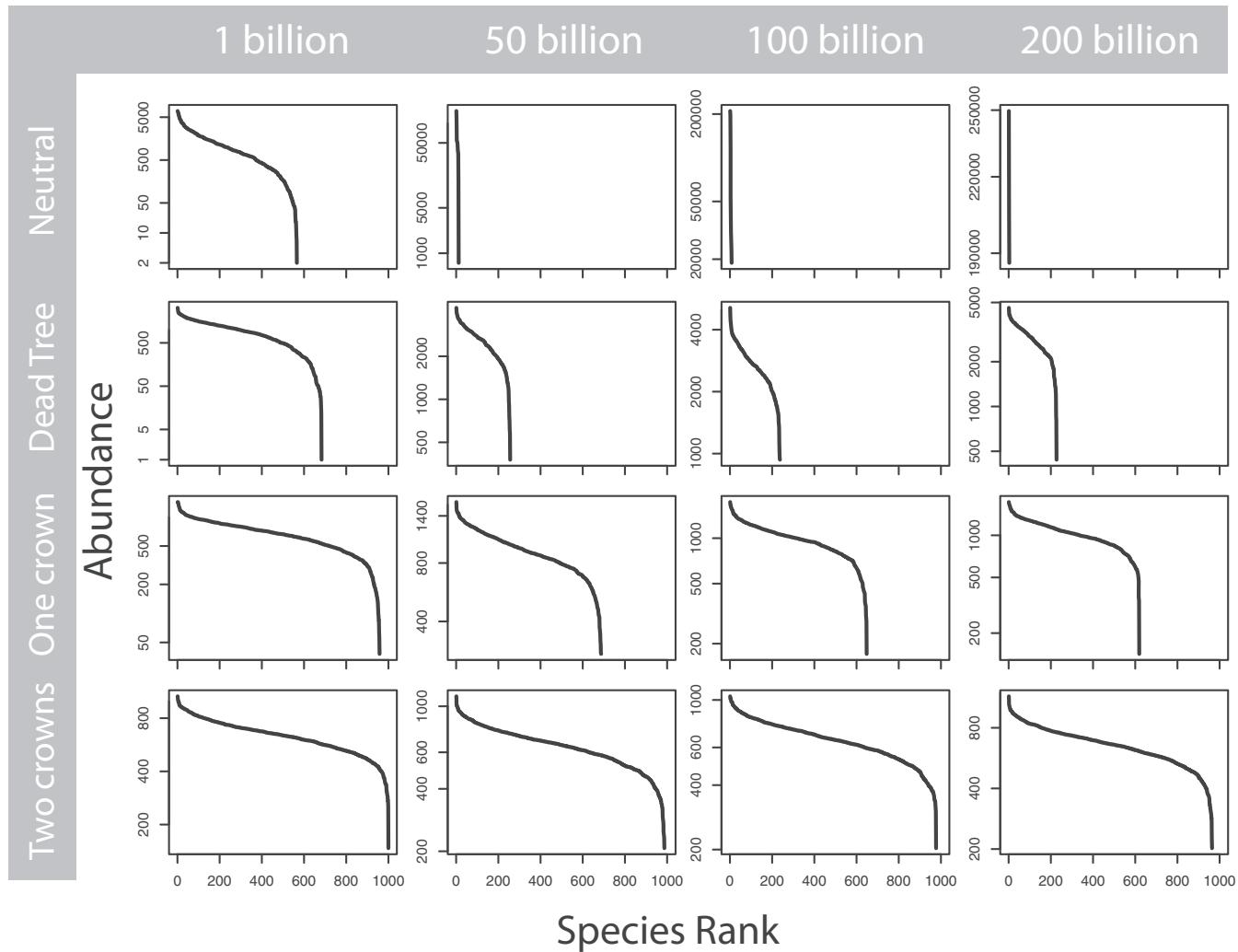


Fig. 6. Rank–abundance (log scaled y axis) curves for 1, 50, 100, and 200 billion tree turnovers on an 800×800 landscape with (Top to Bottom) no exclusion, equivalent to neutral theory in the absence of dispersal or speciation, exclusion of conspecifics from replacing the dead tree ($E = 1$), and exclusion zones of one tree crown ($E = 9$) and two crowns ($E = 25$). Neutral dynamics approach monodominance, while diversity is maintained at increasingly higher levels as the exclusion zone increases.

and reducing extinction to near zero as species richness declines toward a pseudoequilibrium. For larger landscapes, even the simple rule that a dead tree cannot be replaced by a conspecific can maintain >500 tree species for at least 200 billion tree turnovers, and an exclusion zone of only one tree crown is sufficient to maintain at least 1,000 tree species (Fig. 2), affirming the efficacy of the J-C mechanism in preventing drift and local extinction from eroding diversity.

Due to the increasing advantage of rarity with decreasing species richness (Fig. 4A), these dynamics produce community regulation of diversity such that simulations (and results from the analytical model) converge on the same species richness during prolonged transient dynamics regardless of the initial richness (Fig. 2B and *SI Appendix*, Fig. S1), as long as initial richness is sufficiently large (since we are concerned here with maintenance rather than generation of diversity). As species richness declines, a species achieves an advantage at a higher average population size (Fig. 4B), which also reduces stochastic extinction risk.

In light of our findings, it is no longer necessary to wonder how drift can be compensated to maintain species diversity (22). The J-C effect is a potent nonequilibrium (28, 33) mechanism for maintaining high species richness over extraordinarily long time

scales in forest ecosystems. Using high-performance computing and analytical solutions under simplifying assumptions, we can now state that the answer to Becker et al.’s (18) question as to whether J-C effects are sufficiently strong to explain the coexistence of many species in tropical forests is definitively affirmative. However, other stabilizing (e.g., resource niche partitioning) and equalizing (e.g., neutral theory) mechanisms contribute to the maintenance of diversity (32), and the effects of J-C can be attenuated by variance in the strength of conspecific exclusion (34, 35). Our model also incorporates neutrality, in that, when a given tree dies, all individuals of all species—other than itself—have an equal chance of providing a recruit to fill that empty spot. Nevertheless, a large body of empirical support (10) coupled with our theoretical and simulation results strongly suggest that J-C effects alone can explain the majority of tropical forest tree diversity maintenance. Future work should generalize our approach, for instance, incorporating distance-dependent dispersal in recruitment, and natural enemy effects that spillover among closely related taxa.

Tropical forest tree diversity increases markedly from dry forests to moist forests to everwet equatorial forests, a trend that parallels an affinity of fungal pathogens for humid environments

(36–38). We propose that J-C operates to maintain the diversity of speciose forests around the world, including warm temperate forests (16, 39). A requirement is that species in a community be limited by at least moderately host-specific mortality agents operating in a distance-dependent fashion (ref. 40, but see ref. 41 for conditions under which distance responsiveness is not necessary). These agents include arthropod pests and fungal pathogens that accumulate around reproductive adult trees (42), where they proliferate on abundant seeds and/or seedlings. The size of exclusion zones around seed-bearing adults remains an empirical unknown, although recent theoretical work suggests that more diversity can be accommodated when within-community variance in exclusion is low (34, 35). Our results demonstrate that exclusion need not be absolute, since even a modest exclusion zone that allows recruitment near conspecifics 50% of the time still maintains substantial species richness on even the modestly sized landscapes used in the simulations (Fig. 3).

Recent investigations in tropical forests have shown that undispersed seeds, and seedlings arising from them, experience

100% mortality within these exclusion zones (43). Recruitment distances, defined as the mean distance from saplings to the nearest adult conspecific, range from in the tens of meters for common species to >50 m for uncommon species (44). Any species that could resist enemies to reproduce in its own shadow would be able to monopolize space, as appears to be true of species comprising monodominant tropical forests (45). Given recent evidence of its operation in coral reefs, J-C may also function in other kinds of space-limited communities (46). In a still larger context, J-C belongs to a broader class of top-down mechanisms that suppress competition and are permissive of high diversity in both plant and animal communities around the world (47).

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