On the interaction between Janzen-Connell effects and habitat partitioning in spatially structured environments

Daniel J. B. Smith[a,1]

[a]Committee on Evolutionary Biology, The University of Chicago

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Janzen-Connell Effects and Habitat Partitioning have both been proposed as potential stabilizing mechanisms in species-rich forest communities. Janzen-Connell Effects describe the process in which specialized predators are attracted to adult trees, which reduce the survivorship of nearby conspecific juveniles. This is thought to generate stabilizing negative frequency dependence. Habitation Partitioning describes when species exhibit different fitness responses to spatially heterogeneous environmental factors, typically causing species to aggregate into favorable habitat types. Despite substantial empirical evidence that both processes occur simultaneously in empirical systems, the theoretical implications of how their interactions shape species diversity remain underdeveloped. In this study, I examine a spatially explicit model that incorporates both processes. I show that Janzen-Connell Effects and Habitat Partitioning can act synergistically to promote coexistence such that their contribution to species coexistence is greater than the sum of their parts when environmental spatial heterogeneity is positively autocorrelated. The results of this study highlight the need to explicitly model the interaction between co-occurring spatially dependent coexistence mechanisms to understand the role they play in the maintenance of species diversity.

Janzen-Connell effects | Habitat partitioning | Habitat heterogeneity | Coexistence theory | Species diversity | Tropical forests

The maintenance of diversity in species-rich forest communities has long captured the interest of ecologists. Janzen-Connell Effects (JCEs) and Habitat Partitioning (HP) are two leading hypothesis both frequently invoked to explain the high diversity of tropical forests. However, their ability to promote diversity while operating simultaneously remains understudied.

JCEs are based on observation that host-specific natural enemies attracted to adult trees (insects, pathogens, fungi, etc.) reduce juvenile conspecific offspring survivorship (1–3). JCEs are thought to maintain species diversity by inducing negative frequency dependence: the more common a species is, the greater the proportion of the environment that is rendered inhospitable to its offspring. Many empirical systems show evidence of JCEs (e.g. 4–12). HP is based on the observation that species differ in their tolerances of environmental conditions that vary in space (13–15). Environmental factors such as topography (e.g. elevation, convexity) and soil composition (e.g. soil moisture, pH, nutrient composition) have been observed to differentially affect species-specific demographic traits. HP can stabilize coexistence if species are sufficiently different in their environmental fitness associations (16). Empirical evidence strongly suggests that JCEs and HP co-occur in a variety of forest communities (e.g. 17–28).

Superficially, JCEs and HP seem to operate through opposing forces: HP allows for coexistence by aggregating species into favorable habitat types whereas JCEs function because adults render nearby areas inhospitable to conspecifics. In particular, if both mechanisms simultaneously operate, environmental spatial structure (i.e. autocorrelation in spatially varying environmental conditions) may impact the patches on which species experience JCEs (Fig. 1C). Current theory does not examine interactions between JCEs, HP, and spatial structure affect species coexistence (but see 29, 30).

Previous work shows that JCEs alone are sufficient to maintain high species diversity in an otherwise neutral community (31). However, this result is not robust to when communities exhibit realistic levels of inter-specific fitness variation (32) (although see 33). In this study, I explore the question: can JCEs and HP jointly maintain high diversity in communities that experience high inter-specific fitness variation when a single mechanism is insufficient?

To address this question, I develop a simple spatially explicit lottery model that incorporates JCEs and HP. Simulations were conducted on a 500×500 grid in which each grid cell represents a patch containing single adult tree (Fig. 1). Communities started with 300 species, with each species randomly assigned a level of intrinsic fitness according to a log-normal distribution (as in 32). JCEs were implemented by assuming adult trees reduce the survivorship of all conspecific juveniles on patches within the surrounding $M \times M$ Moore neighborhood (Fig. 1C). HP was integrated into the model by assigning each species a preferred habitat type on a one-dimensional trait

Significance Statement

A primary goal of ecology is to explain the maintenance of species diversity. However, the mechanisms that underlie the coexistence of highly diverse tropical rainforests remain contentious. Two leading hypotheses are Janzen-Connell Effects and Habitat Partitioning. Both hypotheses are based on space. Janzen-Connell Effects are based on the observation that natural enemies attracted to adult trees reduce the survival of their nearby seeds and seedlings. In contrast, Habitation Partitioning states that diversity can be maintained when species exhibit different responses to spatially varying environmental conditions such that species congregate into their preferred habitat types. In this paper, I demonstrate that these mechanisms can interact synergistiacally to promote high species diversity.

DBJS performed the study and wrote the paper.

I declare no competing interests.

[1]E-mail: smithdj4uchicago.com

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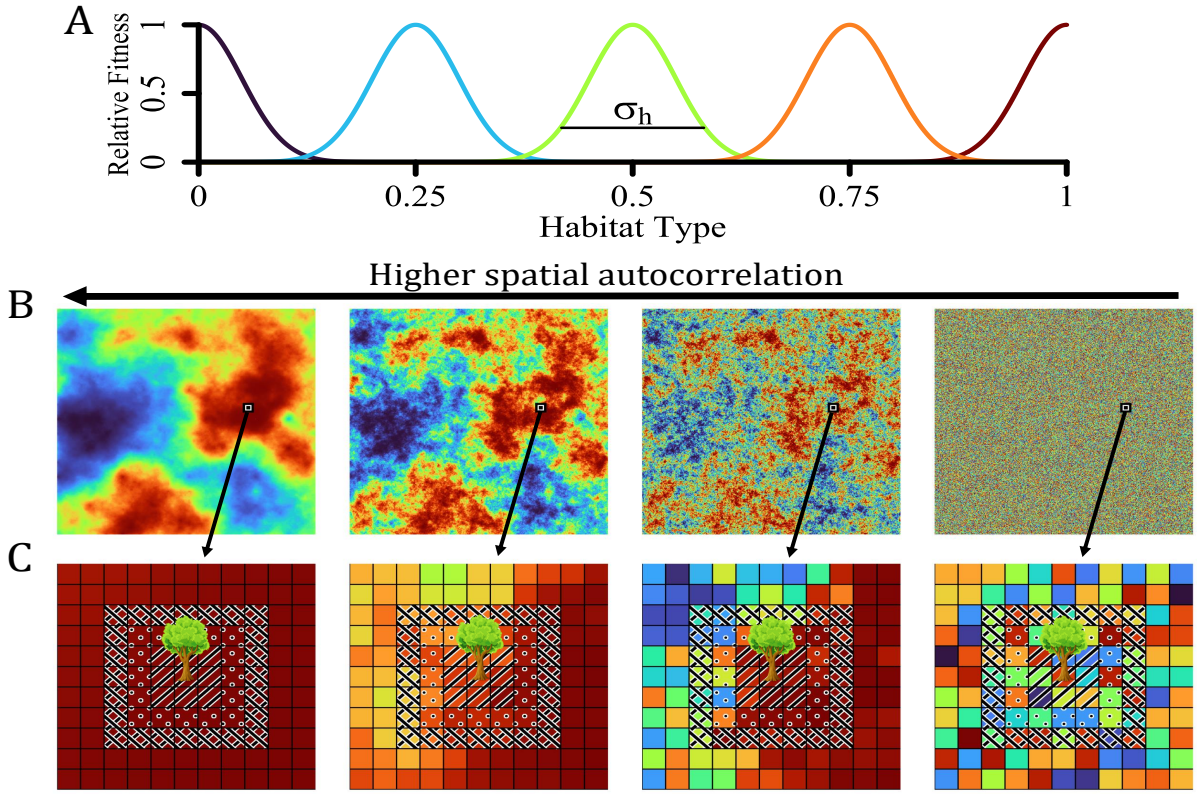

Fig. 1. Visualization of species responses to spatial environmental heterogeneity, habitat structure, and its potential interaction with Janzen-Connell Effects (JCEs). (A) shows how species-specific habitat associations are implemented in the model: fitness is a Gaussian function of habitat type (Eq. 3) with response breadth defined by σ_h. Environmental type affects the probability a species' offspring (seeds and seedlings) survive on a patch. Responses depict when $\sigma_h = 0.05$. (B) shows the different landscapes examined, which vary in their level of spatial autocorrelation. Different colors represent a different value of an environmental variable, ranging from $0 - 1$. Environments range from highly positively autocorrelated (left hand side) to randomly distributed (zero autocorrelation; right hand side). (C) depicts a small portion of the habitat. Each grid-cell is a patch which contains a single adult tree; only a single tree is depicted for simplicity. Patterns around the tree depict the area of which JCEs occur, spanning a 3×3 Moore neighborhood (lines), a 5×5 Moore neighborhood (dots), and a 7×7 Moore neighborhood (crosshatches). If the focal tree has a preference for red habitat types, then the autocorrleation of the environment affects how many favorable (red) patches on which it induces JCEs. When autocorrelation is high, the tree induces JCEs almost entirely on favorable patches. When autocorrelation is low, the tree induces JCEs on relatively few favorable patches.

axis in which juvenile survivorship depends on habitat type (Fig. 1A). Simulations were run on landscapes with different levels of spatial autocorrelation (Fig. 1B). Simulations were run until the number of species approximately saturated to a constant value.

Results

In the presence of a single coexistence mechanism (JCEs or HP only) a relatively small portion of the initial community persisted (Fig. 2). For JCEs alone, diversity increased with increasing Moore neighborhood size (M). For HP alone, diversity increased with greater specialization (smaller σ_h, species habitat response breadth; Eq. 3).

When communities experienced both JCEs and HP, species diversity increased relative to either mechanism in isolation. However, the degree of spatial autocorrelation dramatically affected the extent of this increase. For zero or low autocorrelation, the diversity maintained under JCEs and HP together only modestly increased diversity relative to either mechanism in isolation (Fig. 3, columns 3 and 4). The number of species maintained by JCEs and HP simultaneously under zero autocorrelation (red dots, Fig. 3 column 4) was similar to the sum of species maintained by each JCEs and HP in isolation (the sum of the dashed line and grey dots, Fig. 3) with their simultaneous operation increasing species diversity by up to 32%. When spatial autocorrelation was high, the combination of JCEs and HP produced considerably greater diversity than either mechanism in isolation (Fig. 3, columns 1 and 2). Simultaneous operation HP and JCEs (red dots, Fig. 3, column 1) maintained up to 277% more diversity than the sum of species diversity maintained by the mechanisms in isolation (the sum of the dashed line and grey dots, Fig. 3). Results were qualitatively identical when examining Shannon diversity (SI Appendix, Fig. S12).

To provide some insight into these results, I derived an invasion criterion that quantifies the condition under which a rare species can invade a community of N resident species:

$$Y_i \gtrsim \underbrace{\overline{Y}}_{\substack{\text{mean}\\ \text{intrinsic}\\ \text{fitness}}} \underbrace{\left(1 + \text{cov}(Y, p)\phi\right)}_{\substack{\text{relative}\\ \text{competition}\\ \text{term}}} \underbrace{R(\sigma_h, N)}_{\substack{\text{HP}\\ \text{term}}} \underbrace{e^{-(1-e^{-a})\frac{M^2}{N}R(\sigma_h,N)k_M}}_{\substack{\text{JCE} - \text{HP}\\ \text{term}}} \quad [1]$$

The left had side of Eq. 1 represents the intrinsic fitness of a rare invading species (Y_i; a composite trait of seed fecun-

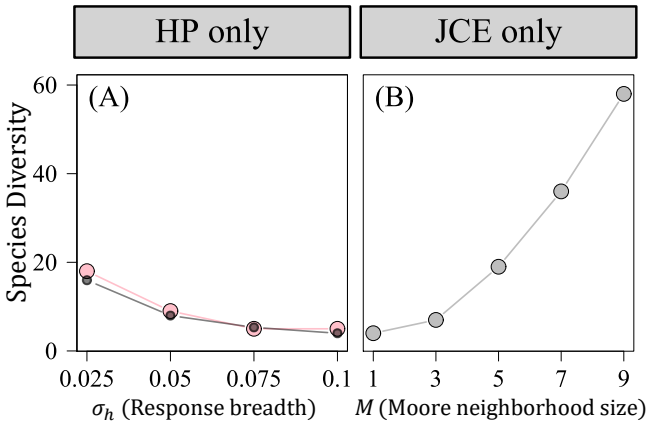

Fig. 2. Diversity maintained by either Habitat Partitioning (HP) or Janzen-Connell Effects (JCEs) in isolation. (A) shows the diversity maintained by HP under different values of σ_h (the breadth of environmental response; Eq. 3). Higher diversity is maintained for smaller σ_h because species are more specialized (more species can persist in the community because of relatively small niche overlap). The pink points show the exact values from model simulations. The grey points show the approximate predicted level species diversity noted in the main text ($1/\sigma_h\sqrt{2\pi}$). (B) shows species diversity when only JCEs are present for different Moore neighborhood sizes (M). Diversity increases with M. However, species diversity is overall low: out of an initial pool of 300 species, up to 58 species are maintained.

dity and baseline seed/seedling survivorship; see Material and Methods). The right hand side of Eq. 1 can be interpreted as the mean fitness of the resident community, with smaller values more easily allowing a rare species to invade. The right hand side consists of several key terms. $\overline{Y}$ is the mean intrinsic fitness of the resident community. The relative competition term (which is equal to or greater than 1) quantifies the degree to which invaders tend to compete against species of high fitness. The mean intrinsic fitness and relative competition terms are quantitatively important for determining invasion, but not qualitatively important concerning how JCEs and HP interact to shape affect invasion (see SI Appendix). I henceforth focus on the HP and JCE−HP terms.

$R_i(\sigma_h, N)$, the HP term, quantifies the extent to which HP in isolation promotes invasion. If it is assumed species' habitat preferences are randomly distributed, then

$$R(\sigma_h, N) \approx 1 - e^{-N\sigma_h\sqrt{2\pi}} \qquad [2]$$

(see SI Appendix). $R_i(\sigma_h, N)$ quantifies the expected proportion of habitat overlap between an invader (species i) and the N residents ($0 \leq R_i(\sigma_h, N) \leq 1$). $R_i(\sigma_h, N)$ increases with the number of species in the community, N, rapidly saturating to 1 (Fig. 4A). This reflects how unless species are highly specialized (σ_h is very small) potential habitat preferences (i.e. spatial niches) quickly saturate such that a species invading a diverse community is likely to compete against species with near-complete habitat preference overlap. Therefore, HP directly contributes to invasion when there are relatively few species in the community, but not when it is diverse. Under the assumption that species evenly partition the environment, it can be derived that approximately $1/(\sigma_h\sqrt{2\pi})$ species coexist in the community when HP operates in isolation (see SI Appendix, Eq. 50). The simulation outputs are approximately consistent with this value (Fig. 2).

The JCE−HP term quantifies how JCEs and their interactions with HP facilitate species invasion. Invasion becomes easier as $(1 - e^{-a})\frac{M^2}{N}R(\sigma_h, N)k_M$ increases. M is the dimension of the Moore Neighborhood and a is the baseline reduction in juvenile survival induced by conspecific trees (see Material and Methods). Larger values of a and M therefore increase the baseline strength and spatial scale over which JCEs occur, respectively, making invasion easier.

Species invasion also becomes easier with increasing k_M (Fig. 4). k_M is a metric of the autocorrelation of habitat types at the $M \times M$ Moore neighborhood scale similar to Ripley's K (34). Numerically, $1 \leq k_M \leq 1/\sigma_h\sqrt{2\pi}$ for which $k_M = 1$ indicates zero autocorrelation and $k_M = 1/\sigma_h\sqrt{2\pi}$ indicates arbitrarily high autocorrelation (noting $\sigma_h\sqrt{2\pi} < 1$; see Materials and Methods). To understand this, first consider how HP affects the spatial composition of adult trees. For each species, a proportion of approximately $\sigma_h\sqrt{2\pi}$ of the environment is favorable (Materials and Methods, Eq. 8) and, consequently, each of the resident species mainly inhabit patches favorable to them. Now consider a patch in the environment of habitat type x that is favorable to the invader, species i. Species i competes mainly against resident species that also have a positive habitat association with x. Species i experiences a competitive advantage colonizing the patch due to JCEs induced by the surrounding M^2 adult trees. However, species i benefits from these JCEs only when the surrounding adults have a positive habitat association with x. Because species tend to occupy favorable patches, JCEs most strongly promote invasion if species tend to neighbor favorable patches – i.e., if habitats types are positively autocorrelated (Fig. 1C). $k_M = 1$ corresponds to when all species are equally likely to neighbor all habitat types. In this case, JCE strength rapidly weakens with increasing N (the number of species in the community) because many resident species induce JCEs on unfavorable patches (Fig. 4B). $k_M = 1/\sigma_h\sqrt{2\pi}$ approximately corresponds to when species only neighbor the $\sigma_h\sqrt{2\pi}$ proportion of patches they find favorable. This reduces the impact of N on JCE strength because all resident species induce JCEs only on favorable patches (Fig. 4B).

How HP promotes invasion through its mediation of JCEs (i.e. k_M) is potentially more quantitatively important than the direct effect of HP on invasion (i.e. Eq. 2; see Fig. 4). Consistent with this, variation in species diversity between simulations depicted in Fig. 3 are almost entirely explained by the key quantity of the JCE−HP term, $(1 - e^{-a})M^2R(\sigma_h, N)k_M$ (Fig. 5).

Discussion

How Janzen-Connell Effects and Habitat Partitioning interact. Janzen-Connell Effects (JCEs) and Habitat Partitioning (HP) are thought to contribute to the maintenance of diversity in species-rich tree communities. Despite considerable theoretical attention given to both JCEs (e.g. 31, 32, 35–37) and HP (e.g. 16, 38–43) in isolation and the strong evidence of their joint presence in numerous communities (17–28), their potential interactions have received relatively little theoretical attention (although see 29). In this paper, I show that JCEs and HP can synergistically interact to promote high species diversity if habitat types exhibit positive spatial autocorrelation.

This result stems from how HP and autocorrelation modify the spatial composition of competitors and the patches they neighbor. First, consider the case of only JCEs: all species

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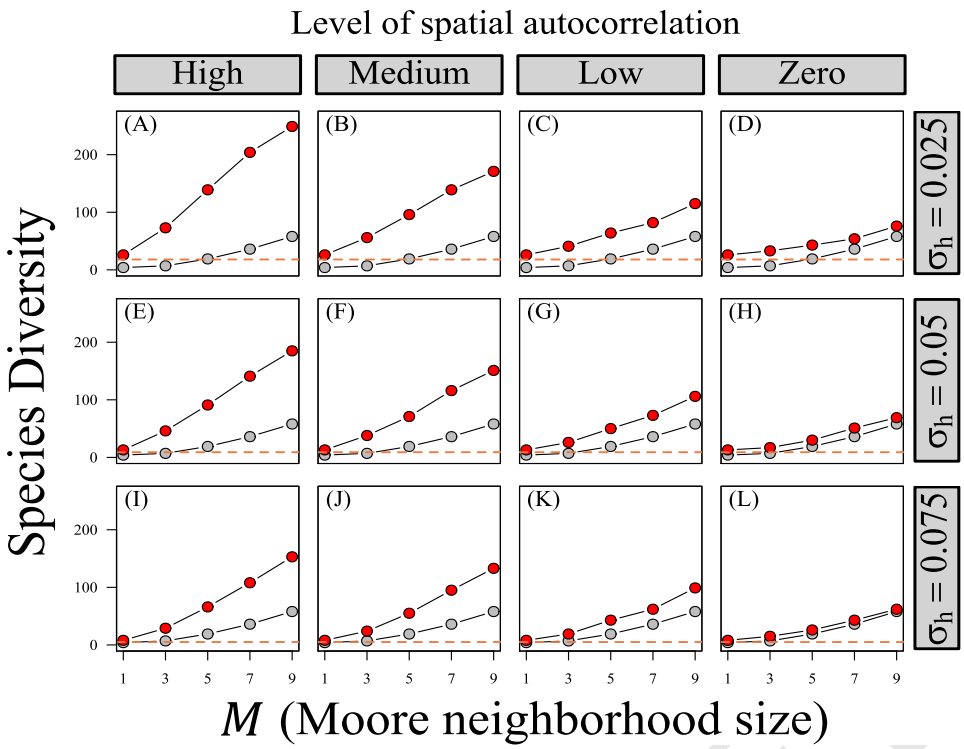

Fig. 3. Species diversity maintained by Janzen-Connell Effects (JCEs) and Habitat Partitioning (HP) simultaneously. Plots show how the level of spatial autocorrelation (columns), response breadth (σ_h; rows), and Moore neighborhood size (M; x-axis) affect species diversity. The four levels of spatial autocorrelation are the same as those depicted in Fig. 1. Red points depict when JCEs and HP operate simultaneously, grey point depict when only JCEs are present, and dashed lines depict when only HP is present. As in the case of JCEs alone, species diversity increases with increasing M and decreasing σ_h. The magnitude of this increase depends on the level of spatial autocorrelation. For zero and low autocorrelation, the diversity maintained at various Moore neighborhood sizes is very similar to that of the JCEs only case (grey points) regardless of σ_h. In contrast, when under medium and high spatial autocorrelation, diversity increases rapidly with M, particularly under lower σ_h. This indicates that the level of spatial autocorrelation mediates the interaction between JCEs and HP. Results were qualitatively identical examining Shannon diversity (SI Appendix, Fig. S12).

in the community compete equally (in that no habitat preferences exist) so the particular patches on which a species induces JCEs does not matter. This is not the case when HP is considered: species experience high fitness only on patches with suitable habitat types and compete primarily with species sharing similar habitat preferences. When there is little or no spatial autocorrelation, species do not tend to neighbor patches on which they experience high fitness (Fig. 1C) which means they induce JCEs on many patches they are already unlikely to colonize. When habitat types are positively autocorrelated, this is reversed: species tend to neighbor and induce JCEs on patches where they have high fitness. This increases the strength of frequency dependence, allowing for the maintenance of relatively high species diversity (Fig. 3). In cases where there is high autocorrelation and species are highly specialized (Fig. 3A), the community acts like it is structured with several sub-communities comprising primarily of competitors sharing habitat preferences. This increases diversity because the strength by which JCEs promote invasion is a decreasing function of the total number of species in the community (Eq. 1). How the spatial scale over which which spatial heterogeneity is autocorrelated compares to the spatial scale over which JCEs occur, k_M, defines the strength of this effect. Measuring k_M is therefore of key importance in determining the interaction between mechanisms.

Realism of the model and future avenues. This model makes several simplifying assumptions. A considerable limitation is that I considered a one-dimensional axis on which the spatial environment varies; in reality, species-specific adaptations to spatial environmental heterogeneity are multidimensional. Different spatially varying environmental factors may exhibit differing (and independent) levels of autocorrelation, which may factor into how JCEs and HP interact. In addition, spatial variation was assumed to be fixed (habitat structure was invariant with time). However, some forms of spatial environmental heterogeneity emerge from short-term spatial-temporal fluctuations (e.g. flooding that occurs periodically at different locations) such that changes in the environment are faster than the life-span of trees. JCEs and HP may interact differently in these situations.

All species were assumed have the same degree of habitat specialization, σ_h. However, the breadth of environmental tolerance varies between species. For example, larger seeded species tend to be tolerant of more stressful environmental conditions (large seeded species are thus habitat generalists with respect to stress; 44, 45) and previous work shows that a trade-off between seed size and fecundity can maintain diversity in communities with spatial heterogeneity in environmental stress levels (the tolerance–fecundity trade-off; 46). Future work explicitly integrating the effects of variable stress levels, the tolerance–fecundity trade-off, and the model of this study might be a fruitful avenue to examine how interactions between JCEs and HP manifest themselves in empirical communities. Empirical evidence also indicates large-seeded species are less sensitive to JCEs (47), which offers a potential means of integrating JCEs into life history theory.

There are several further interesting avenues for future studies to explore. The model assumes species are not seed-limited. However, seed limitation can reduce species diversity (43, 48) and the parameter space over which coexistence mechanisms operate (46). An additional complication is dispersal limitation, which can interact with HP (e.g. 16, 41, 43, 49) and JCEs (29, 32, 50). Furthermore, this study assumes JCEs are perfectly specialized. While measurements show JCEs are indeed highly specialized (11, 51, 52) specialization is not perfect and often exhibits taxonomic spillover (53, 54). Whether species that share natural enemies are also more likely than random chance to have similar habitat associations is an additional

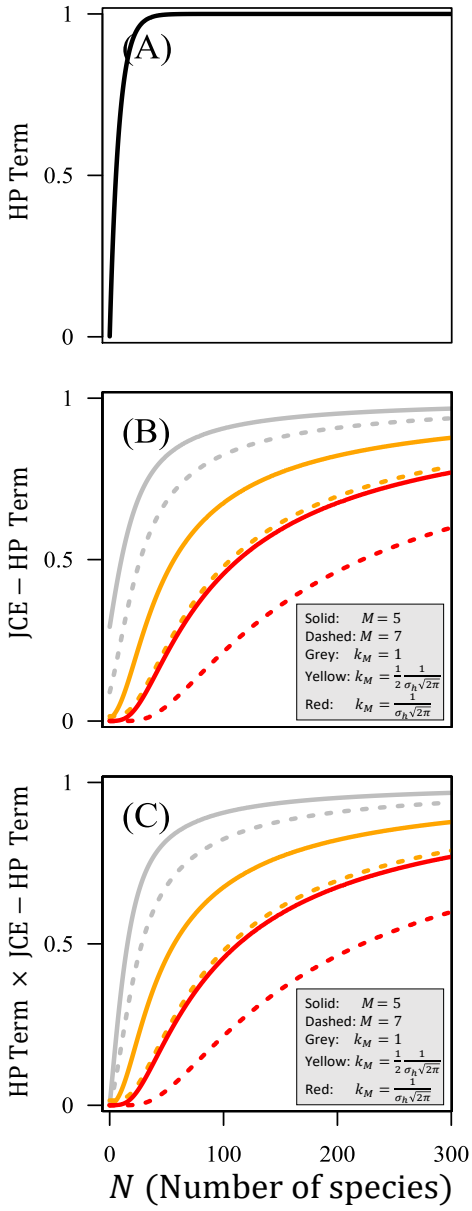

Fig. 4. Visualization of the different components of the invasion criterion (Eq. 1). The x-axis shows N, the number of species in the community. Note that N in this figure is a parameter input into the invasion criterion, not an output from a simulation. For all invasion criterion components (the y-axis of each plot) invasion is easier when the component is smaller; a value of 1 indicates the component does not make invasion easier. (A) depicts the HP term, $R(\sigma_h, N)$. Invasion is made easier only for relatively small N; $R(\sigma_h, N)$ rapidly saturates to 1 as N increases. (B) shows the JCE−HP term under three different values of k_M (spatial autocorrelation) and two different values of M (Moore neighborhood size). Grey shows $k_M = 1$ (no autocorrelation), orange shows $k_M = 1/2\sigma_h\sqrt{2\pi}$ (moderate autocorrelation), and red shows $k_M = 1/\sigma_h\sqrt{2\pi}$ (high autocorrelation; the upper bound of k_M). Invasion becomes more difficult with increasing N, but less so when the spatial environment is highly autocorrelated. Solid curves show $M = 5$ and dashed curves show $M = 7$. While invasion becomes easier with larger M in all cases, the effect is much more pronounced under high autocorrelation (compare the difference between solid and dashed curves in grey to the difference between solid and dashed curves in red). This reflects how positive autocorrelation mediates a synergistic interaction between JCEs and HP. (C) shows the product of (A) and (B). (B) and (C) look are almost identical, while different colored curves dramatically differ. Therefore, the effect of HP on species invasion through its mediation of JCEs (i.e. k_M) is more quantitatively important than the direct of effect of HP alone ($R(\sigma_h, N)$). This highlights the importance of the interaction between JCEs and HP in promoting species invasion and coexistence. Parameters are as follows: $\sigma_h = 0.05$, $a = 0.5$.

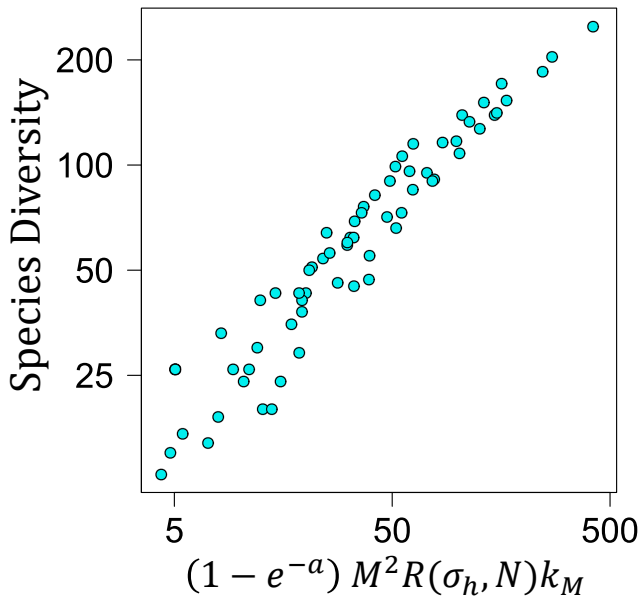

Fig. 5. The relationship between species diversity and the key metric from the JCE−HP term from Eq. 1, $(1 - e^{-a})M^2 R(\sigma_h, N)k_M$. Most of the variation in species diversity is captured by this quantity. M^2 and σ_h are set parameters from each simulation. k_M was calculated using Eq. 9 (Materials and Methods). $a = 0.5$ in all simulations.

axis on which HP and JCEs can interact (30).

Overall, while the assumptions of this model leave room for refined biological realism and integration into life history theory, it is unlikely that any particular assumption qualitatively affected the main result that interaction between HP and JCEs is shaped by the degree of spatial autocorrelation in habitat types.

Broader significance of results and conclusion. Results are relevant to conservation concerns. Previous work shows habitat fragmentation reduces species diversity (55, 56) though the ecological processes that facilitate this are contentious. The results of this study suggest that fragmentation may reduce diversity through its interaction with JCEs. The degree of spatial autocorrelation is related to the extent of environmental fragmentation: lower autocorrelation implies that similar habitats are more fragmented in space. Therefore, habitat fragmentation may have particularly severe consequences for the maintenance of diversity of sessile organisms in systems for which JCEs and HP jointly operate. Indeed, JCEs have been measured to decrease in strength in more fragmented environments (nearer to the forest edge; 57) which can reduce their ability to stabilize coexistence (58). The results of this study provide a potential mechanism for these observations.

In conclusion, the primary result of this study, that JCEs and HP can work synergistically to promote species diversity in spatially autocorrelated environments, highlights the need to carefully model the interactions between spatially-dependent stabilizing mechanisms. Precise examinations of spatial coexistence mechanisms that elucidate the conditions under which they work in series or parallel are necessary to explain the high diversity of tropical forests and pinpoint environmental variables of high conservation concern.

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Materials and Methods

Here, I describe the model, simulations, and the calculation of k_M.

Model description. I consider a discrete-time site occupancy model. The community consists of a $X \times X$ grid, upon which each cell represents a single patch that contains a single adult tree. First, I describe the offspring dynamics on each patch type.

Each time-step, species i disperses Y_i offspring uniformly throughout the environment. $i = 1, 2, .., N$ such that there are N species in the community. Y_i is a composite parameter of the fecundity and basline density-independent mortality of species i's offspring. I refer to Y_i as "intrinsic fitnes". Because dispersal is global, the number of offspring species i disperses to a each patch is equal to $p_i Y_i$, where p_i is the proportion of patches in the environment occupied by species i. The number of offspring of species i on a given patch is modified by (1) habitat type and (2) Janzen-Connell Effects (JCEs). Let x represent the habitat type of a particular patch in space for which $0 \leq x \leq 1$. Similarly, let $H_i(x)$ be the probability that an offspring of species i survives on patch x (i.e. the relative fitness of species i on habitat type x). I assume fitness is a Gaussian function of habitat type:

$$H_i(x) = \exp(-(x - h_{\text{opt},i})^2/2\sigma_h^2) \qquad [3]$$

where $h_{\text{opt},i}$ is the optimal patch type of species i ($0 \leq h_{\text{opt},i} \leq 1$) and σ_h is the breadth of environmental response (smaller σ_h means species are more specialized).

JCEs are implemented by assuming adult trees within the $M \times M$ Moore neighborhood around a patch decrease the probability of conspecific offspring survival therein according to the function

$$J_i(x) = \exp\Big(- a \sum_{m=1}^{M(x)^2} \mathbf{1}_m(i)\Big) \qquad [4]$$

noting that M^2 trees are contained within an $M \times M$ Moore neighborhood. $M(x)$ refers to the Moore Neighborhood around the patch located at x. a is a constant that defines the baseline strength of JCEs. $\mathbf{1}_m(i)$ is an indicator function for which

$$\mathbf{1}_m(i) = \begin{cases} 1, & \text{if } m = i \\ 0, & \text{if } m \neq i \end{cases} \qquad [5]$$

Therefore, offspring survival declines exponentially with the number of conspecific adult trees within the area of effect. The number of offspring of species i on patch x, $S_i(x)$, is then equal to:

$$S_i(x) = p_i Y_i H_i(x) J_i(x) \qquad [6]$$

Now, I describe adult dynamics. Each time-step, each adult dies with probability δ. If the adult on a patch dies, the patch is immediately replaced by another individual. The identity of the species replacing the patch is determined by a lottery model (59) where the probability species i "wins" the lottery and colonizes the patch is equal to the relative abundance of its offspring on a patch. That is:

$$\text{P(species } i \text{ colonizes patch } x) = \frac{S_i(x)}{\sum_{j=1}^{N} S_j(x)} \qquad [7]$$

using the quantities from Eq. 6 for each of the N species.

Spatially explicit simulations. Simulations were conducted on a 500×500 grid on which each grid-cell represents a patch containing a single adult tree (as noted above). The community was modeled on a torus to avoid edge effects. Landscapes (i.e. habitat structure) were generated by assigning a value between $0 - 1$ to each grid-cell, defining its habitat type. Autocorrelation was introduced using a midpoint displacement algorithm (60) by modifying the value of the Hurst exponent using the [R] package NLMR (61). The resulting landscape was subsequently modified such that frequency of habitat types was uniformly distributed between $0 - 1$.

All simulations began with 300 species at equal abundance. Intrinsic fitness (Y) was log-normally distributed such that $Y \sim \text{lognormal}[\mu = 0, \sigma_Y = 1.0]$. These values were chosen on the basis that recent analyses at Barro Colorodo Island indicate inter-specific variation in low-density seedling recruitment is of approximately this order (32). Simulations examined $\sigma_h \sim \{.025, .05, .075., 0.10\}$ (the breadth of environmental response) and $M \times M \sim \{1 \times 1, 3 \times 3, 5 \times 5, 7 \times 7, 9 \times 9\}$ (the size of the Moore neighborhood). $a = 0.5$ in all simulations, meaning that the presence of a single adult within the Moore neighborhood reduced offspring survivorship by approximately 40%. Simulations were run for approximately 125 generations (equivalent to over 3×10^7 tree replacements), sufficiently long for the transient dynamics to end (with species diversity and Shannon diversity in the community having approximately saturated to a constant number; see supplemental Figs. S4-S11). All simulations were conducted in [R] (62).

Calculation of k_M. k_M quantifies the level of spatial autocorrelation in habitat type with respect to the size of the Moore neighborhood size (M) and the response breadth of habitat specialization (σ_h). To quantify k_M, I make the approximation

$$H_i(x) \approx \begin{cases} 1, & \text{if } h_{\text{opt},i} - \frac{1}{2}\sigma_h\sqrt{2\pi} \leq x \leq h_{\text{opt},i} + \frac{1}{2}\sigma_h\sqrt{2\pi} \\ 0, & \text{otherwise} \end{cases} \qquad [8]$$

or, in words, species i experiences a relative fitness of 1 for the proportion of habitat types between $h_{\text{opt},i} - \frac{1}{2}\sigma_h\sqrt{2\pi}$ and $h_{\text{opt},i} + \frac{1}{2}\sigma_h\sqrt{2\pi}$ and 0 in other habitat types (see SI Appendix, Fig. S1). Therefore, a portion of approximately $\sigma_h\sqrt{2\pi}$ of the community is favorable to each species (ignoring edge cases). k_M is then calculated with the following summation:

$$k_M = \frac{1}{\sigma_h\sqrt{2\pi}M^2} \sum_{x=1}^{X^2} \sum_{j \in M^2} \frac{\mathbf{1}\big[j < f(x)\big]}{X^2} \qquad [9]$$

recalling X^2 is the number of patches in the community.

$$\mathbf{1}\big[j < f(x)\big] = \begin{cases} 1, & x - \frac{1}{2}\sigma_h\sqrt{2\pi} \leq j \leq x + \frac{1}{2}\sigma_h\sqrt{2\pi} \\ 0, & \text{otherwise} \end{cases} \qquad [10]$$

in which j represents the habitat type of one of the patches within the $M \times M$ around x ($j \in M^2$). Eq. 9 is essentially a discrete-space analogue to Ripley's K (34).

k_M quantifies how the habitat types of patches at the $M \times M$ Moore neighborhood scale deviate from random. Note that Eq. 9 is divided by $1/\sigma_h\sqrt{2\pi}M^2$. If $k_M = 1$, it means that

$$\sum_{x=1}^{X^2} \sum_{j \in M^2} \frac{\mathbf{1}\big[j < f(x)\big]}{X^2} = \sigma_h\sqrt{2\pi}M^2 \qquad [11]$$

which implies, on average, a proportion of $\sigma_h\sqrt{2\pi}$ of similar habitat types fall within M^2. This is identical to when patches are randomly distributed in the environment. Conversely, if $k_m = 1/\sigma_h\sqrt{2\pi}$, it follows that

$$\sum_{x=1}^{X^2} \sum_{j \in M^2} \frac{\mathbf{1}\big[j < f(h)\big]}{X^2} = M^2 \qquad [12]$$

which means all patches within M^2 are always of similar habitat types (high spatial autocorrelation). This is an upper bound to k_M. Therefore,

$$1 \leq k_M \leq \frac{1}{\sigma_h\sqrt{2\pi}} \qquad [13]$$

ranging from randomly distributed habitat types to highly spatially autocorrelated.

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Approximate invasion criterion and $R(\sigma_h, N)$. Derivations of the approximate invasion criterion, $R(\sigma_h, N)$ and numerical validation of their accuracy can be found in the SI Appendix.

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