Janzen-Connell effects and habitat-induced aggregation synergistically promote species coexistence

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Abstract

1. Janzen-Connell (JC) effects and habitat partitioning (HP) are two leading hypotheses for the maintenance of tropical forest diversity. There is strong empirical evidence that both mechanisms operate in forest communities, but the consequences of their joint operation remain poorly understood.

2. I develop a spatially explicit model that incorporates JC-effects, HP, and dispersal limitation. The model tracks propagules subject to habitat filtering and conspecific density dependence, and quantifies equilibrium species richness across a wide range of conditions.

3. JC-effects and HP each stabilize coexistence individually but fail to maintain high richness under biologically feasible parameter values. When both mechanisms operate together, the outcome depends on habitat spatial structure: if habitats are not spatially autocorrelated, their joint operation yields little more diversity than either mechanism alone, and sometimes less. In contrast, when habitats are positively autocorrelated, the two mechanisms interact synergistically and promote high species richness. This occurs because habitat specialization clusters conspecifics in favorable environments, concentrating JC-effects where species perform best. This interaction is quantified by the spatial JC-HP covariance, a simple and empirically measurable metric.

4. The relationship between species aggregation and richness qualitatively differs depending on the mechanism generating aggregation. Aggregation driven by dispersal limitation decreases the ability of JC-effects to maintain coexistence. By contrast, when JC-effects and HP operate together in spatially autocorrelated habitats, richness increased with conspecific aggregation.

5. *Synthesis.* The interaction between JC-effects and habitat specialization can maintain high species richness — potentially on par with levels observed in tropical forests —

when neither mechanism alone nor the sum of their parts does so. Habitat autocorrelation concentrates density dependence in species' favorable environments, generating a positive relationship between aggregation and species richness. This overturns the common expectation that strong JC-effects should produce overdispersion and instead shows that JC-mediated coexistence can be positively associated with intraspecific aggregation. By identifying the JC-HP covariance as the key measure of this interaction, results provide a framework for linking trees' spatial patterns to abiotically and biotically driven spatially-dependent processes that sustain forest diversity.

Introduction

Elucidating the mechanisms that maintain high diversity in species-rich forest communities remains a central challenge in theoretical ecology. This challenge is rooted in the competitive exclusion principle: in the absence of stabilizing niche differences, the species with the highest fitness is expected to exclude all others (Hardin, 1960; Levine & HilleRisLambers, 2009). This has motivated extensive empirical and theoretical work aimed at identifying and quantifying the mechanisms that promote stable coexistence.

Two major hypotheses — Conspecific Negative Density Dependence (CNDD) and habitat partitioning (HP) — are frequently invoked to explain high tree diversity in tropical forests (Fig. 1A). CNDD refers to the tendency of juvenile trees (seeds, seedlings, saplings) to experience reduced survival or growth near conspecific adults. CNDD is thought to stabilize diversity by generating negative frequency dependence: as a species becomes more common, the environment becomes increasingly inhospitable to its offspring. Many studies report evidence of CNDD in forest systems (e.g. Hyatt *et al.*, 2003; Petermann *et al.*, 2008; Mangan *et al.*, 2010; Swamy & Terborgh, 2010; Zhu *et al.*, 2010; Johnson *et al.*, 2012, 2014; Comita *et al.*, 2014; Bever *et al.*, 2015; Song *et al.*, 2021; Hülsmann *et al.*, 2024). CNDD is often attributed to host-specific enemies such as pathogens (e.g., fungi), or arthropods, and is commonly referred to as Janzen-Connell (JC) effects (Janzen, 1970; Connell, 1971; Terborgh, 2012). While CNDD may encompass broader mechanisms, I use the term "JC-effects" throughout the manuscript to emphasize local biotically mediated processes. JC-effects, then, are a form of biotically induced spatial heterogeneity.

In contrast to JC-effects, habitat partitioning depends on abiotic environmental heterogeneity. Habitat partitioning posits that species-specific environmental tolerances promote coexistence across spatially heterogeneous environments (Chesson, 2000; Hortal *et al.*, 2009; Stein *et al.*, 2014; Leibold & Chase, 2017). In forests, fine-scale variation in topography (e.g. elevation, convexity) and edaphic conditions (e.g., soil moisture, pH, nutrients) shapes species distributions and affects demographic performance (e.g. Clark *et al.*, 1998; Debski

et al., 2002; Phillips *et al.*, 2003; Palmiotto *et al.*, 2004; Gunatilleke *et al.*, 2006; Baldeck *et al.*, 2013a; Brown *et al.*, 2013). Coexistence is stabilized when species are sufficiently specialized in their habitat associations relative to interspecific fitness differences (Chesson, 2000; Snyder & Chesson, 2003).

Despite strong empirical support for both JC-effects and habitat partitioning, theoretical considerations cast doubt on whether either mechanism alone is sufficient to maintain the high levels of diversity observed in tropical forests. JC-effects, for example, can maintain high diversity in otherwise neutral communities (Levi *et al.*, 2019), but are likely insufficient when species differ in fitness (Chisholm & Fung, 2020). Interspecific variation in enemy susceptibility can further undermine coexistence (Stump & Comita, 2018; May *et al.*, 2020).

Similarly, although habitat partitioning clearly influences species' spatial distributions and demography, it is unclear if it creates a sufficient number of niches to allow for high diversity. Classical niche theory suggests that the number of coexisting species cannot exceed the number of limiting factors (Levin, 1970; Armstrong & McGehee, 1980). Given the relatively dimensionality of abiotic variation and relative to the high number of species in tropical forests, habitat partitioning alone appears insufficient to explain observed diversity (Wright, 2002; Silvertown, 2004; Terborgh, 2015).

While both JC-effects and habitat partitioning appear too weak to explain the extraordinary diversity of tropical forests, it is possible that their joint interaction could provide stronger stabilization. JC-effects and habitat effects frequently co-occur in empirical systems: many studies find that both conspecific density and environmental variables impact seedling survival and growth (e.g. Hubbell *et al.*, 2001; Wright, 2002; Uriarte *et al.*, 2004; Freckleton & Lewis, 2006; Queenborough *et al.*, 2009; Chen *et al.*, 2010; Bagchi *et al.*, 2011; Bai *et al.*, 2012; Piao *et al.*, 2013; Lu *et al.*, 2015; Wu *et al.*, 2016; Johnson *et al.*, 2017; Pu *et al.*, 2017; Cao *et al.*, 2018; Yao *et al.*, 2020; Magee *et al.*, 2021; Huang *et al.*, 2022; Liu *et al.*, 2022; Feng *et al.*, 2023). Broadly, these studies show that the survival of a life history stage (typically seedlings) is shaped jointly by conspecific density (whether of nearby adults

or seedlings) and by local habitat conditions. Because both JC-effects and habitat partitioning influence — and are themselves influenced by — the spatial distribution of trees, their interaction may yield non-additive effects. In particular, habitat specialization generates intraspecific aggregation, which in turn may modify the strength of local density-dependent processes (Chen *et al.*, 2010; Fortunel *et al.*, 2018). Thus, understanding how aggregation arises and how it interacts with JC-effects is central to predicting their joint consequences for coexistence.

Tree species are almost universally aggregated in tropical forests (Condit *et al.*, 2000), and both dispersal limitation and habitat specialization contribute to this pattern (Baldeck *et al.*, 2013b). Topographic and edaphic features strongly shape the aggregation patterns of tree species in a variety of tropical forest communities (Andersen *et al.*, 2010; Jones *et al.*, 2011; Bagchi *et al.*, 2011; Baldeck *et al.*, 2013b; Brown *et al.*, 2013; John *et al.*, 2007; Potts *et al.*, 2002; Umarani *et al.*, 2024). In contrast, JC-effects, which operate locally, are expected to generate conspecific repulsion and overdispersion of adults (Chave *et al.*, 2002; Wiegand & Moloney, 2013). Habitat specialization complicates empirical efforts to detect negative density dependence: the positive effects of favorable environments that aggregate conspecifics potentially mask or counteract negative effects of conspecific proximity (Wright, 2002; Chen *et al.*, 2010; Bagchi *et al.*, 2011; Wu *et al.*, 2016; Liu *et al.*, 2022; Feng *et al.*, 2023). Dispersal limitation also produces aggregation. As a result, spatial point-pattern analyses must disentangle overlapping influences of dispersal, abiotic filtering, and density-dependent mortality (Detto & Muller-Landau, 2013; Zhu *et al.*, 2013). Recent analyses at the Barro Colorado Island (BCI) forest dynamics plot illustrate this challenge: strong conspecific repulsion is detectable only after controlling for clustering due to dispersal limitation (Kalyuzhny *et al.*, 2023).

Despite advances in statistical techniques parsing out negative density dependence from dispersal limitation and habitat specialization, theoretical work has yet to fully clarify how their joint operation and the aggregation patterns they generate shape species coexistence.

Importantly, spatial aggregation is not a neutral backdrop: depending on the ecological context, it can either promote or hinder species richness (Chesson & Neuhauser, 2002; Murrell *et al.*, 2002; Bolker *et al.*, 2003), potentially via its interaction with distance- and density-dependent processes (Detto & Muller-Landau, 2016; Stump & Comita, 2020; Wiegand *et al.*, 2025) or with habitat partitioning (Snyder, 2008; D'Andrea & O'Dwyer, 2021). While dispersal limitation and habitat specialization both generate aggregation, they do so through distinct pathways. Dispersal limitation leads to clustering that is potentially independent of environmental heterogeneity, while habitat specialization causes species to aggregate in locations where they experience high fitness. These differences are crucial, as they likely influence how each aggregation-generating mechanism interacts with JC-effects (Fig. 1C vs. Fig. 1D, sub-panel iii), but they have not been theoretically explored.

Here, I analyze a spatially explicit model that incorporates JC-effects, habitat partitioning, and dispersal limitation. I assess the ability of each mechanism (JC-effects and habitat partitioning), as well as their joint operation, to maintain high species richness. I report the following results. On their own, JC-effects and habitat partitioning are unlikely to sustain the high levels of diversity observed in tropical forests when realistic interspecific fitness differences are present. Spatial aggregation caused by dispersal limitation further reduces the ability of JC-effects to maintain coexistence. By contrast, aggregation driven by habitat specialization interacts synergistically with JC-effects and strongly promotes coexistence, often far exceeding the combined effects of each mechanism in isolation. As a surprising consequence, the extent to which JC-effects maintain coexistence can increase with intraspecific aggregation. The synergistic interaction is governed by the spatial covariance between JC-effects and habitat partitioning ("the JC–HP covariance"): species richness is highest when trees disproportionately generate JC-effects in the habitats where they also have high fitness. This covariance provides a simple, empirically measurable metric for quantifying the strength of JC–HP interactions and their contribution to coexistence.

Methods

Model description

I use a discrete-time site occupancy model similar to those developed by Levi *et al.* (2019), Chisholm & Fung (2020), and Smith (2022). The model tracks the dynamics of a local forest community composed of P patches, each occupied by a single adult tree. The local community contains N species, which draw from a regional pool of R species. Each time step proceeds through four stages: (1) Adults disperse propagules (i.e., seeds) throughout the landscape. (2) Propagules experience mortality due to habitat effects and JC-effects. (3) Each adult dies with probability δ. (4) Vacant patches are recolonized either by a propagule from the local seed rain or by an immigrant drawn from the regional species pool.

To model propagule arrival, let x denote a patch (i.e., a discrete grid cell) in space. At each time step, species i ($i = 1, 2, \ldots, N$) disperses propagules across the landscape in proportion to its intrinsic fitness parameter Y_i. This parameter scales the number of propagules contributed by the species and reflects underlying demographic traits such as fecundity, baseline density-independent offspring survival, and competitive ability. Dispersal occurs either globally, with propagules distributed uniformly across all patches, or locally according to a Gaussian kernel with standard deviation σ_D (in grid-cell units), which determines the spatial scale of dispersal. The expected propagule density of species i arriving at patch x is denoted $d_i(x)$. Full details of the dispersal kernel are provided in the Supplementary Information (see "General model derivation and details").

Once propagules arrive, their survival depends on two factors: abiotic habitat effects and JC-effects. I begin by describing habitat effects. Each patch $x \in [0, 1]$ is assigned a habitat value that influences species' demographic performance. The survival of species i's seedlings on patch x is higher when the patch habitat is close to its optimum $h_{\text{opt},i}$ and declines with

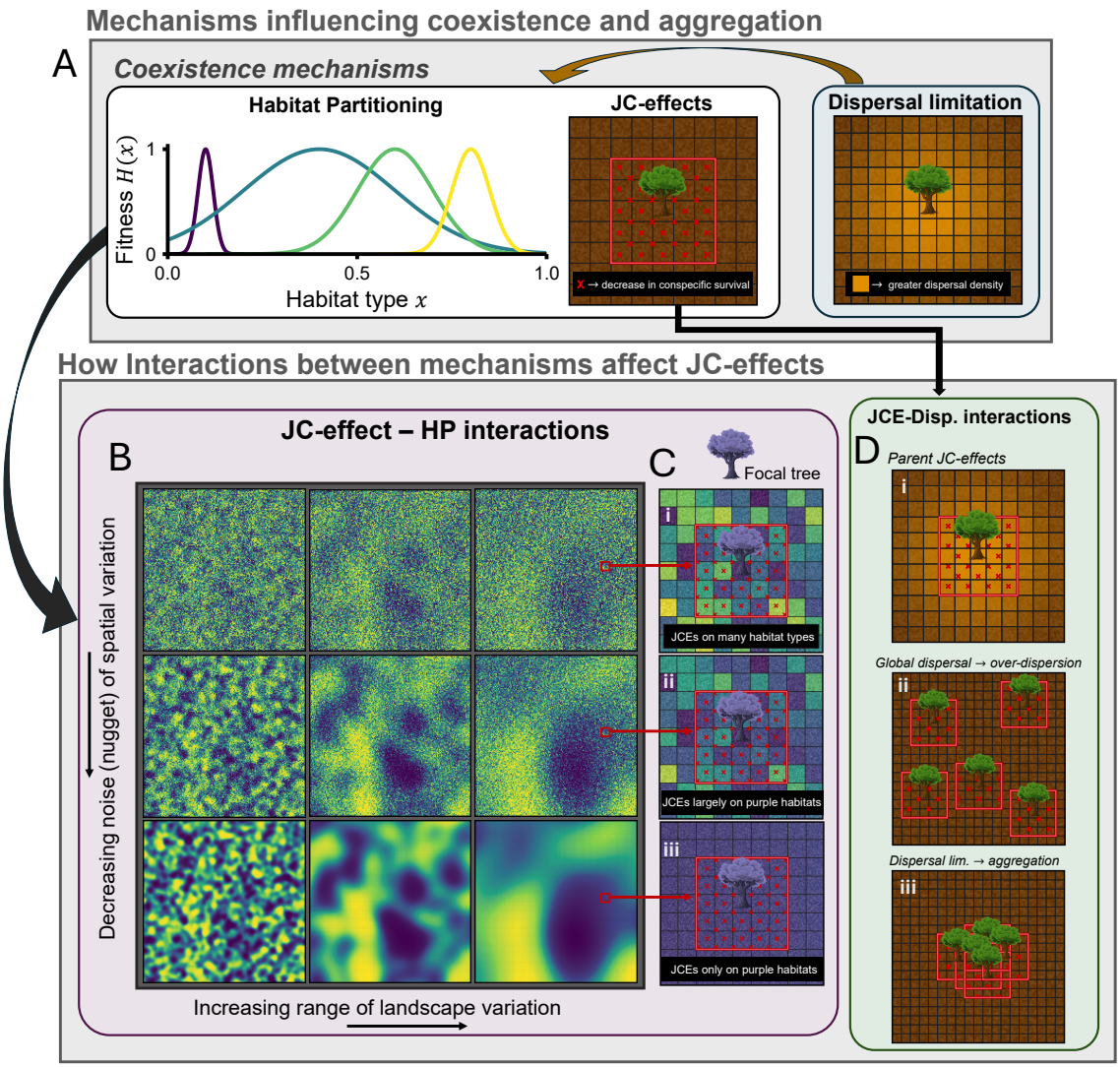

Figure 1: **Conceptual overview of coexistence mechanisms and their interactions.** (A) The mechanisms influencing coexistence and aggregation: habitat partitioning, JC-effects, and dispersal limitation. "Habitat partitioning" shows species responses to the environment $H(x)$, with niche breadth values $\sigma_h = 0.02, 0.2, 0.1$, and 0.05 (left to right). "JC-effects depict" the $M \times M$ Moore neighborhood of influence (red) around a focal tree, with $M = 5$. "Dispersal limitation" shows the relative propagule pressure from a focal tree (orange shading). (B) Spatial distributions of habitat under varying nugget and range parameters. The nugget controls fine-scale heterogeneity (decreasing from top to bottom); the range controls the size of habitat patches (increasing from left to right). Nugget values are 10, 1, and 0 (top to bottom) and range values are 0.05, 0.2, 0.5 (left to right). (C) JC–HP interactions depend on the level of spatial autocorrelation. Consider a focal tree positively associated with purple habitat patches. When noise is high (nugget large, i), the tree induces JC-effects on many non-purple patches, where its fitness is low. With lower noise and greater autocorrelation (ii and iii), the tree induces JC-effects primarily on purple patches, where it performs best. (D) JC-effects interact with dispersal. (i) When a tree is dispersal-limited, some of its locally dispersed propagules are subject to its own JC-effects. (ii) Under global dispersal, JC-effects generate overdispersion . (iii) With dispersal limitation, conspecifics may instead aggregate, altering the spatial distribution over which JC-effects are expressed (spread out vs. concentrated).

distance according to a Gaussian response function:

$$H_i(x) = \exp\left(-\frac{(x - h_{\mathrm{opt},i})^2}{2\sigma_h^2}\right). \tag{1}$$

Here, $h_{\mathrm{opt},i}$ is species i's habitat optimum ($0 \leq h_{\mathrm{opt},i} \leq 1$), and σ_h determines niche breadth; smaller σ_h indicates greater specialization. The function $H_i(x)$ ranges between 0 and 1 and captures the relative survival probability of propagules across the habitat axis.

In the main text, I examine the above Gaussian habitat response, in which all species share the same value of σ_h. However, species may also display specialist–generalist trade-offs and exhibit non-Gaussian environmental responses. To test if results were robust to this possibility, I also performed analyses based on the so-called "stress–tolerance–fecundity trade-off" (Muller-Landau, 2010; D'Andrea *et al.*, 2013; D'Andrea & O'Dwyer, 2021), in which seed size mediates a trade-off between fecundity and tolerance of stressful environments (e.g., drought or low resource availability; Moles *et al.*, 2003; Moles & Westoby, 2004). The full stress–tolerance–fecundity trade-off and related results are described in the Supplementary Information ("Tolerance–fecundity trade-off model"). The central result from the main text — that JC-effects and habitat partitioning can interact synergistically — is robust to this alternative formulation.

In addition to habitat effects, propagule survival is reduced by JC-effects. These capture mortality imposed by nearby conspecific adults, such as from host-specific pathogens or natural enemies. JC-effects act within an $M \times M$ Moore neighborhood around each patch x, which includes the focal patch and its surrounding neighbors (including diagonals; Fig. 1A). Let $A_i(M(x))$ denote the number of conspecific adults of species i within this neighborhood. The probability that propagules of species i on patch x die due to JC-effects is given by

$$J_i(x) = 1 - \exp\big(-a_i A_i(M(x))\big), \tag{2}$$

where a_i is the baseline strength of JC-effects. The total JC-effect pressure induced by a

single adult of species i is therefore $a_i M^2$ (baseline strength $\times$ spatial scale). The term $1-e^{-a_i}$ corresponds to the mortality rate experienced when a single conspecific adult is present ($A_i = 1$). Larger values of A_i or stronger baseline sensitivity a_i increase the probability of mortality, while the complementary term $1 - J_i(x)$ gives the probability of surviving JC-effects. This exponential form provides a minimal but biologically reasonable representation of distance- and density-dependent mortality (see Supplementary information "General model derivation and details").

Combining dispersal, habitat effects, and JC-effects, the expected number of viable propagules of species i on patch x is

$$S_i(x) = d_i(x) Y_i H_i(x) \big(1 - J_i(x)\big) \tag{3}$$

where survival after JC-effects is represented by $1 - J_i(x)$. Thus, a species' recruitment on a patch depends on its dispersal pressure ($d_i(x)$), its intrinsic fitness Y_i, habitat suitability $H_i(x)$, and its probability of surviving JC-effects $1 - J_i(x)$.

Following propagule survival, adult dynamics proceed in three steps. First, at each time step every adult dies with probability δ. Second, if a patch becomes vacant, it is recolonized either from local propagules or by an immigrant drawn from the species in the regional pool. Local recolonization occurs with probability $1-\nu$, while immigration occurs with probability ν. Third, when local lottery competition occurs, species i claims patch x with probability

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

where $S_i(x)$ is the number of surviving propagules from Equation (3). Immigration ensures that the local community reaches a dynamic quasi-equilibrium.

Parameterizations for simulations

I used empirical data — largely from the 50-ha Forest Dynamics Plot at BCI — to roughly parameterize key quantities within a biologically feasible range

The spatial scale of JC-effects M strongly influences their ability to maintain species richness (Smith, 2022). In the model, M is the side length (in patches) of the Moore neighborhood within which conspecific adults reduce offspring survival. Its value is determined by two biological quantities: (1) the radius r (in meters) over which JC-effects operate (the focal center of a patch where effects end), and (2) the density of reproductive adults per square meter, g. Field studies indicate JC-effects typically decline rapidly beyond 10–20 m from conspecific adults (Hubbell *et al.*, 2001; Johnson *et al.*, 2014), though Kalyuzhny *et al.* (2023) report effects extending further. I assume a JC-effect radius of $r \sim 5$–15 m. To connect r to M, it is necessary to define how many trees typically fall within r. At BCI, Comita *et al.* (2007) reported approximately 30,000 reproductive adult trees. Other estimates vary depending on the cutoff for reproductive maturity: assuming a 5 cm dbh threshold yields $\sim$ 50,000 woody plant adults (D'Andrea & O'Dwyer, 2021), while species-specific thresholds yield $\sim$ 80,000 (Chisholm & Fung, 2020). Given that the BCI plot spans 50 hectares (5×10^5 m^2), these values imply adult densities of $g \sim 0.06$–0.10 individuals per m^2. In the model's square-lattice geometry, neighboring patches are separated by $1/\sqrt{g}$ m (i.e., each patch has area $1/g$ m^2 and each side length is $1/\sqrt{g}$ m). $M/2$ can be interpreted as the number of patch-lengths spanning the JC-effect radius and, thus, thus, a Moore neighborhood of size M covers a spatial radius of $(M/2)(1/\sqrt{g})$ m. Rearranging gives $M = 2r\sqrt{g}$. Using the empirical ranges of r and g yields approximate values of M between 1 and 9. Slightly more conservatively, I typically ran simulations using $M \in 1, 3, 5, 7$, spanning small-scale to relatively large neighborhood effects.

The baseline strength of JC-effects, a, also plays a central role in determining species richness (Smith, 2022). Meta-analyses suggest that seedling survival near a conspecific adult is reduced by roughly 60%, which corresponds to $a \approx 1$ under the exponential mortality

function (Comita *et al.*, 2014; Song *et al.*, 2021). For most simulations, I adopted a more conservative baseline value of $a = 0.5$. Unless otherwise noted, species were assumed to share the same baseline JC-effect strength. Because empirical studies also document substantial interspecific variation in sensitivity to conspecific density (Comita *et al.*, 2010; Song *et al.*, 2021), I additionally ran simulations in which a varied among species, with values drawn from a gamma distribution (see Supplementary Information "Interspecific variation in baseline JC-effect strength).

Substantial interspecific variation in fitness-related demographic rates (e.g., fecundity, density-independent survival, and growth) is well documented in tropical forests such as BCI. In particular, fecundity and related rates often exhibit fat-tailed distributions (Dalling *et al.*, 2002; Wright *et al.*, 2005; Chisholm & Fung, 2020). Following Chisholm & Fung (2020) and D'Andrea & O'Dwyer (2021), I represent intrinsic fitness (Y) as a log-normally distributed variable: $Y \sim \text{lognormal}(\mu = 0, \sigma_Y)$. Y captures multiple life-history traits and demographic rates, including fecundity, density-independent juvenile survival, seedling growth, and general competitive ability. For most simulations, I adopt a value of $\sigma_Y = 0.3$, which produces roughly an order of magnitude of variation in fitness among species — sufficient to test the robustness of coexistence mechanisms.

Species' responses to abiotic heterogeneity — quantified by the niche-breadth parameter σ_h — are difficult to estimate directly because they integrate over multiple environmental factors that are rarely directly measured for most tropical tree species. I therefore explored a broad range of σ_h values in simulations, spanning from $\sigma_h = 0.02$ to $\sigma_h = 0.2$. Lower values (e.g., $\sigma_h = 0.02$; Fig. 1A, blue curve) represent relatively specialized species, while higher values (e.g., $\sigma_h = 0.2$; Fig. 1A, red curve) represent generalized responses. Unless otherwise noted, all species shared the same value of σ_h. In simulations, each species' habitat optimum, $h_{\text{opt},i}$, was drawn uniformly on $[0, 1]$. As noted earlier, I also considered an alternative formulation in which species experience a stress–tolerance–fecundity trade-off to test robustness (Supplementary Information).

I explored a range of dispersal limitation values, characterized by the dispersal kernel standard deviation σ_D, from highly limited local dispersal ($\sigma_D = 1$) to global dispersal ($\sigma_D = \infty$). For simplicity, all species were assumed to share the same value of σ_D.

I used a low immigration rate of $\nu = 0.3 \times 10^{-5}$, which yields $\sim$ 1–3 species at equilibrium in a neutral community. This ensures that effectively all species richness in simulated communities can be attributed to JC-effects, habitat partitioning, or their interaction. Simulations with larger and smaller ν had qualitative identical results.

Simulations were run on a 175×175 grid, yielding $\sim$ 30,000 patches, each occupied by a single adult tree — comparable to the number of reproductive adults at BCI. Each patch was assigned a habitat value between 0 and 1. To investigate the effects of habitat-driven aggregation, I generated spatial habitat landscapes as Gaussian random fields using the Julia package GaussianRandomFields (Robbe, 2023), and rescaled values to a uniform $[0, 1]$ distribution (preserving spatial ranks). These fields are parameterized by three quantities: the sill, the range, and the nugget. The sill sets the total variance of the field at large distances (fixed at 1 here for convenience), while the range specifies the distance at which sites become effectively uncorrelated (Fig. 1B, left to right) — formally, the range is the point where the variogram rises to 95% of the sill (Cressie, 1993; D'Andrea & O'Dwyer, 2021). The nugget adds microscale white-noise variance to each point, producing local roughness without altering large-scale patchiness (Fig. 1B, top to bottom). In practice, the range controls the size of habitat patches, while the nugget controls their fine-scale heterogeneity.

Analysis and simulations

I combined mathematical analyses with forward-time simulations of the spatial model. First, I derived an approximate analytical condition under which a rare species deterministically increases in abundance when introduced into a community of N resident species in the local community. This was accomplished by deriving when the quantity $\tilde{\lambda}_i = (\lambda_i - 1)/\delta > 0$ as $p_i \to 0$ where $\lambda_i = \frac{p_i(t+1)}{p_i(t)}$ is the finite rate of increase and δ is the adult mortality rate.

I refer to $\tilde{\lambda}_i$ as the weighted growth rate of species i (Chesson, 2003). See Supplementary Information "Invasion criteria" for more information and derivations.

Next, I conducted forward-time simulations on the 175×175 grid, on a torus to eliminate edge effects. The local community was initialized with species drawn from the regional pool. In most simulations, I assumed the regional pool contained 500 species, although I also tested how the regional pool size affects local community species richness. Species were randomly assigned to patches, but the probability of assignment at a given location was proportional to their performance in the local habitat. Simulations were run for $\sim$ 10,000 generations — sufficient for species richness to reach a dynamic equilibrium maintained by the balance of extinction and immigration.

With these specifications, I conducted four main sets of simulations. **(1) Regional pool size and local species richness.** I performed simulations varying the regional pool size under five different scenarios: when only JC-effects occur, when only habitat partitioning occurs, and when both occur under low, intermediate, and high levels of spatial autocorrelation (defined by the nugget). **(2) Baseline contributions.** Using the above-specified parameterizations, I examined how JC-effects, habitat partitioning, and their joint operation affect species richness, and how these effects are mediated by habitat autocorrelation and dispersal limitation. **(3) Drivers of aggregation and coexistence.** I investigated how different processes that affects the level of intraspecific aggregation — dispersal limitation, JC-effect strength (a), and the level of spatial autocorrelation — combine to influence species coexistence. **(4) The spatial scale of JC-effects.** Because the overall strength of JC-effects depends on both their baseline intensity and their spatial extent, I normalized total JC-effect pressure as $aM^2 = K$, where M is the neighborhood size and K is a constant. This allowed me to isolate the effect of spatial scale *per se* by varying M while holding total JC-effect pressure fixed.

To quantify intraspecific spatial aggregation of adult trees, I computed the index

$$\kappa_{i,M} = \frac{\sigma^2_{i,M}}{\mu_{i,M}}$$

where $\mu_{i,M}$ and $\sigma^2_{i,M}$ are the mean and variance of species i's abundance across all $M \times M$ Moore neighborhoods. $\mu_{i,M} = p_i M^2$, where p_i is the proportion of patches occupied by species i. This index is a local variance-to-mean ratio: $\kappa_{i,M} = 1$ implies spatial randomness, $\kappa_{i,M} > 1$ indicates aggregation, and $\kappa_{i,M} < 1$ indicates regular (overdispersed) spacing. As a community-level summary metric, I used the average aggregation across species

$$\overline{\kappa}_M = \frac{1}{N} \sum_{k=1}^{N} \kappa_{k,M} \tag{4}$$

The spatial scale M used to compute aggregation is the same as that used to define the neighborhood over which JC-effects operate, allowing direct quantification of the tension between processes that generate aggregation (habitat partitioning and dispersal limitation) and the local repulsion imposed by JC-effects.

All simulations were implemented in Julia version 1.11 (Bezanson *et al.*, 2017), and figures were produced in R version 4.3.2 (R Core Team, 2021).

Results

Invasion criteria

This invasion analysis has two goals: (1) to examine stabilizing effects due to JC-effects, habitat partitioning, and their interaction scale with N the number of resident species in the local community and (2) to distinguish the effects of aggregation driven by dispersal limitation vs. by habitat specialization. To this end, I explore two cases: (1) JC-effects with habitat partitioning under global dispersal and (2) JC-effects alone with dispersal limitation. While

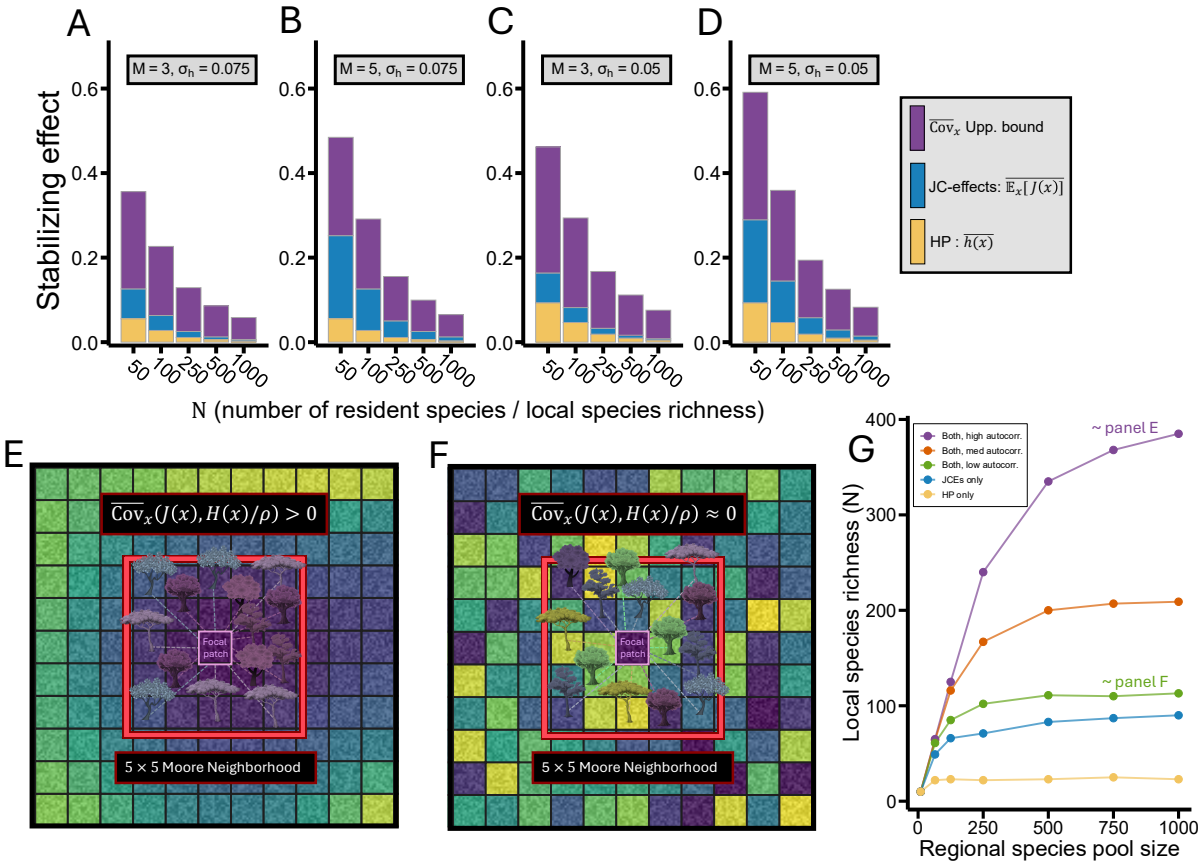

Figure 2: **The JC–HP covariance can generate substantial stabilization in highly diverse communities.** (A-D) Stabilizing contributions due to habitat partitioning (HP; yellow), JC-effects (blue), and the upper bound of the JC–HP covariance (purple) as a function of resident species richness (N), shown for different values of M and σ_h. All plots use $a = 0.5$. (E) Illustration of positive JC–HP covariance when habitats are spatially autocorrelated. Individuals within the central square induce JC-effects on the labeled focal patch. Bluer/purpler species prefer bluer/purpler patches. (F) Illustration of near-zero JC–HP covariance when habitats are distributed randomly (high noise). (G) Simulations of the model. The x-axis shows the number of species in the regional pool, and the y-axis shows local species richness at equilibrium N. Colored lines correspond to five simulation scenarios: JC-effects only (no habitat partitioning), habitat partitioning only (no JC-effects), and joint operation of both mechanisms under low, medium, and high spatial autocorrelation. In all simulations, dispersal was global, $a = 0.5$, $\nu = .3 \times 10^{-5}$, $Y \sim \text{lognormal}(\mu = 0, \sigma_Y = 0.3)$, $M = 7$ (except for the HP only case), $\sigma_h = 0.02$ (except for the JCEs only case), and habitat range = 0.5. Autocorrelation was varied by setting nugget = 10, 0.1, or 0 (low autocorrelation — similar to panel E; medium autocorrelation; and high autocorrelation — similar to panel F, respectively).

dispersal also interacts with HP, these two cases capture the essential contrasts and keep the analysis tractable. For simplicity, I present when species have the same habitat response breadths (σ_h), although results are robust to relaxing this assumption (see Supplementary Information "Invasion Criteria").

JC-effects and habitat partitioning

I first consider an invader i under global dispersal. The invasion criteria should be interpreted as the propensity of invasion of a species with a randomly chosen optimum $h_{\text{opt},i}$ between 0 and 1 (i.e., imagine a species randomly selected from the regional pool invading the N species local community). Suppose species i is a rare invader with intrinsic fitness Y_i. Let ρ_i be the mean performance of species i across space, $\rho_i = \overline{H_i(x)}$ Then, to a first approximation $\rho_i = \rho_k = \rho$ ($k = 1, 2, ..., N$; this is true because spices are assumed to have the same response breadth).

Under these assumptions, species i invades if its weighted growth rate is positive:

$$\tilde{\lambda}_i \approx \underbrace{\ln Y_i - \overline{\ln Y}}_{\text{Fitness differences}} + \underbrace{\overline{\mathbb{E}_x[J(x)]}}_{\text{JC-effects}} + \underbrace{\overline{h(x)}}_{\text{Habitat effects}} + \underbrace{\overline{\text{Cov}_x}\Big(J(x), H(x)/\rho\Big)}_{\text{JC–HP covariance}} > 0, \tag{5}$$

where $\overline{\ln Y} = \frac{1}{N}\sum \ln Y_k$ is the mean log-scaled fitness of the local resident species. See Supplementary Information "JC-effects and habitat partitioning, no dispersal limitation" for the derivation.

The direct contribution of JC-effects $\overline{\mathbb{E}_x[J(x)]}$ is the mean JC-effect strength over space x, averaged over the resident species:

$$\overline{\mathbb{E}_x[J(x)]} \approx (1 - e^{-a})\frac{M^2}{N}. \tag{6}$$

a is the baseline strength of JC-effects, M^2 is their spatial scale, and N is the total number of species in the local community. This approximation assumes adults are randomly distributed.

Intuitively, stronger baseline JC-effect strength (a) and larger neighborhoods (M) promote coexistence. However, effect scales inversely with N, and thus decline rapidly with the number of species in the community (Fig. 2A, blue bars).

The habitat effect term $\overline{h(x)}$ should be interpreted as the direct contribution habitat partition makes to an invader with a randomly selected optima.

$$\overline{h(x)} \approx \frac{1}{N}\left(\tfrac{1}{\rho\sqrt{2}} - 1\right) \tag{7}$$

where it is assumed $\rho \ll 1$ (i.e., species are somewhat specialized, which is the case of interest). Stabilization via habitat partitioning increases with the degree of habitat specialization (smaller ρ). However, like JC-effects, stabilizing effects are inversely proportional to N (Fig. 2A, yellow bars).

The interaction between JC-effects and HP (henceforth the JC-HP covariance) is captured by

$$\overline{\mathrm{Cov}_x}\Big(J(x), H(x)/\rho\Big) = \frac{1}{N}\sum_{k=1}^{N} \mathrm{Cov}_x\Big(J_k(x), H_k(x)/\rho_k\Big), \tag{8}$$

where Cov_x is the spatial covariance between the strength of JC-effects and habitat effects scaled by the degree of specialization. A positive JC-HP covariance promotes invasion. The mechanism reflects a key principle: invaders compete most intensely in habitats favorable to them, which are also the habitats of resident species with similar optima. If those residents disproportionately generate JC-effects in those same habitats — which occurs when habitats are spatially autocorrelated — the resident species' fitness is reduced more strongly than if JC-effects are induced in unfavorable habitats. This is captured by $\overline{\mathrm{Cov}_x}\Big(J(x), H(x)/\rho\Big) > 0$ (Fig. 2E). In contrast, if habitats are randomly distributed, $\overline{\mathrm{Cov}_x}\Big(J(x), H(x)/\rho\Big) \approx 0$ and JC-effects and HP act do not interact (Fig. 2F).

The JC-HP covariance term can exceed the direct effects. An approximate upper bound is

$$\overline{\mathrm{Cov}_x}\big(J(x), H(x)/\rho\big) \lesssim \ (1 - e^{-aM^2})\sqrt{\tfrac{1}{N}\big(1 - \tfrac{1}{N}\big)}\,\sqrt{\tfrac{1}{\rho\sqrt{2}} - 1} \tag{9}$$

which is derived using the Cauchy–Schwarz inequality, and arises when species' JC-effects are highly concentrated in habitats favorable to them (Fig. 2E; see Supplementary Information "Upper bound on JC–HP covariance "). At this bound, the contribution to invasion decays with $1/\sqrt{N}$, slower than either JC-effects or HP alone ($\sim 1/N$). Thus, even when the direct effects are weak — which occurs when N is large — their interaction can provide substantial stabilization (Fig. 2A-D; purple vs. blue and yellow bars).

JC-effects and dispersal limitation

I next consider how dispersal limitation affects the ability of JC-effects to stabilize coexistence. With local dispersal, propagules deposited near a parent tree are subject to its JC-effects (Fig. 1D, i). Let d denote the proportion of propagules that disperse far enough to avoid JC-effects within the $M \times M$ Moore neighborhood of the parent tree. In this case, invasion occurs when

$$\tilde{\lambda}_i \approx \ln Y_i - \overline{\ln Y} + \overline{\mathbb{E}_x[J(x)]}\Big(d + (1-d)e^{-a}\Big) > 0. \tag{10}$$

See Supplementary Information "JC-effects, dispersal limitation, and no habitat partitioning" for the derivation. Dispersal limitation reduces stabilizing effects relative to global dispersal through two mechanisms. First, the loss of locally dispersed propagules weakens the stabilizing effect (also see Stump & Chesson, 2015). The stabilizing term $\overline{J(x)}$ is multiplied by the factor $d + (1-d)e^{-a} \leq 1$. Stabilization thus declines as dispersal becomes more limited (smaller d). With limited dispersal, a fraction $1-d$ of propagules remain near the parent and experience JC-effects, weakening the advantage of rarity.

Second, dispersal limitation can lead to intraspecific aggregation. Aggregation directly reduces $\overline{\mathbb{E}_x[J(x)]}$. To see this, I derived an alternative first order approximation

$$\overline{\mathbb{E}_x[J(x)]} \;\approx\; \frac{aM^2}{N}\left(1 \;-\; \frac{a}{2}\overline{\kappa}_M\right) \tag{11}$$

which is valid when a and $\overline{\kappa}_M$ are not large (i.e., the expression cannot be negative for the parameters space in which the approximation applies) and N is not small. Here, $\overline{\kappa}_M$ is the mean intraspecific aggregation of residents at the $M \times M$ scale (equation 4). Aggregation ($\overline{\kappa}_M > 1$) reduces $\overline{J(x)}$. Thus, aggregation *per se* reduces the ability of JC-effects to stabilize coexistence (see Supplementary Information "Moment-based approximation of $\overline{\mathbb{E}_x[J(x)]}$" for more details). This also implies that aggregation due to habitat partitioning may weaken the direct stabilization due to JC-effects, even if it is overall boosted by the JC-HP covariance.

Simulations

JC-effects and habitat partitioning in isolation

Consistent with the analytical results, simulations suggest that neither JC-effects nor habitat partitioning were sufficient on their own to maintain high species richness under feasible parameterizations. Local species richness N maintained by JC-effect alone or habitat partitioning alone saturated rapidly to a maximum value as a function of the regional pool size (Fig. 2G, blue and yellow curves). This reflects how the contribution to coexistence of JC-effects and habitat partitioning are inversely proportional to the number species N.

When only JC-effects operated, the number of coexisting species increased with the spatial scale of JC-effects (M), but only up to ∼80—90 species (Fig. 3A-B "No HP" row, $M = 7$; Fig. 2G). Dispersal limitation decreased species richness (compare Fig. 3A-B "No HP" row to those of Fig. 3C-D). When only habitat partitioning was present, richness increased with greater habitat specialization (smaller σ_h; Fig. 3 "no JCEs" column). On the order of $20 - 30$ species persisted when niches were narrow and dispersal was global ($\sigma_h = 0.02$; see the purple curve in Fig. 1A for a visualization of niche width). Unlike with JC-effects, species richness was higher under dispersal limitation (compare 'No JCEs" columns in Fig. 3A and 3B to those of 3C and 3D). On the order ∼30—40 species coexisted with the narrowest niches examined (Fig. 3C,D "No JCEs" columns).

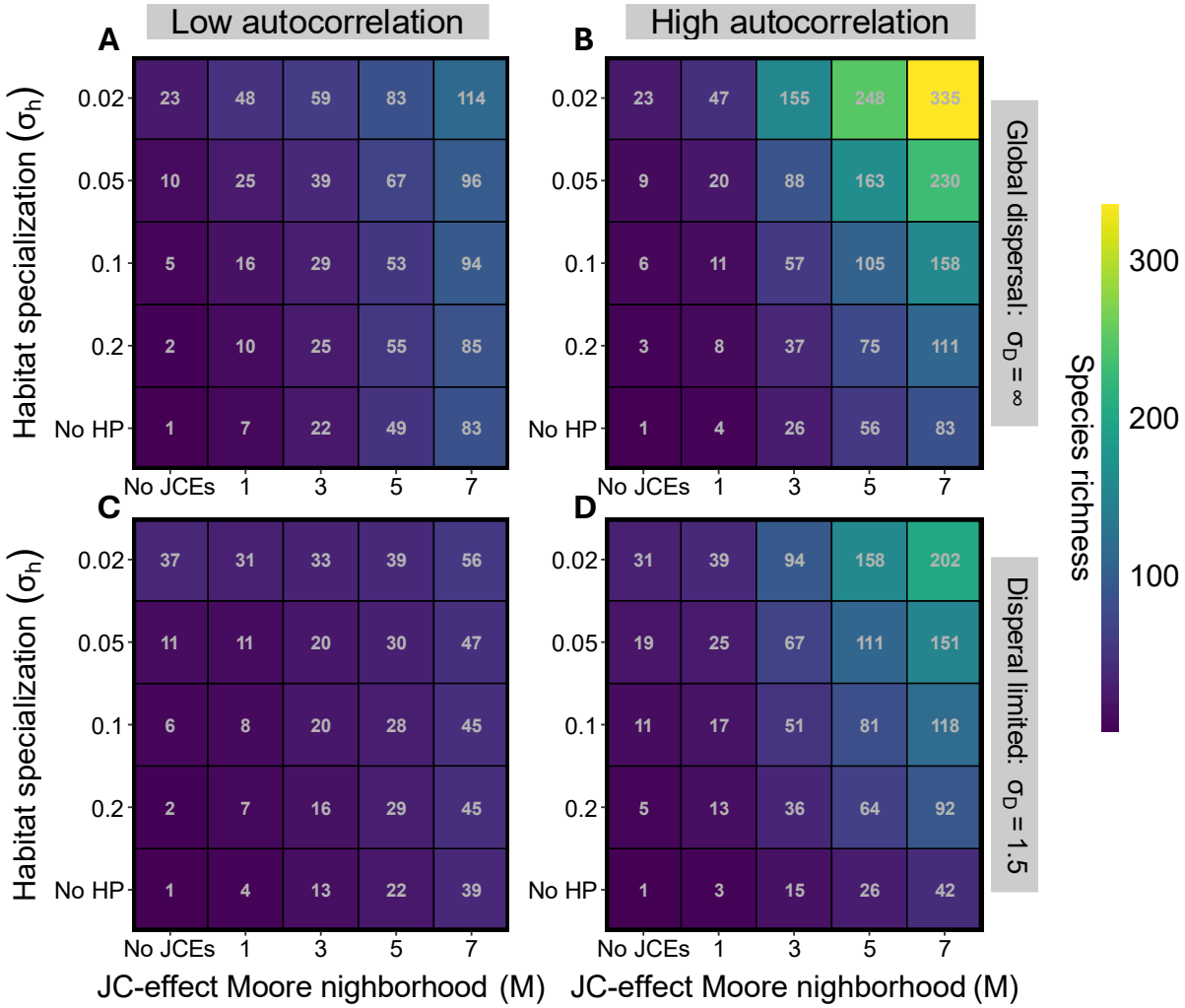

Figure 3: **Positive spatial autocorrelation in the abiotic environment maintains high species richness with both JC-effects and habitat partitioning operate, whereas dispersal limitation typically reduces it.** All plots show equilibrium species richness (color scale) across combinations of JC-effect scale (M, x-axis) and niche breadth (σ_h, y-axis). (A) Global dispersal with low spatial autocorrelation. (B) Global dispersal with high spatial autocorrelation. (C) Dispersal limitation ($\sigma_D = 1.5$) with low spatial autocorrelation. (D) Dispersal limitation ($\sigma_D = 1.5$) with high spatial autocorrelation. In all simulations, $a = 0.5$, $\nu = 0.3 \times 10^{-5}$, $Y \sim \text{lognormal}(\mu = 0, \sigma_Y = 0.3)$, and habitat range $= 0.5$. High spatial autocorrelation corresponds to nugget $= 0$, while low autocorrelation corresponds to nugget $= 10$.

Joint operation of JC-effects and habitat partitioning

When both mechanisms operated simultaneously, the outcome depended strongly on the degree of spatial autocorrelation in habitat structure. Local species richness N rapidly saturated to a maximum value as a function of the regional pool size when spatial autocorrelation was low (Fig. 2G, green curve). However, this saturation was much slower at intermediate and high levels of autocorrelation (Fig. 2G, blue and purple curves, respectively). For example — given otherwise identical parameters — simulations with highly autocorrelated environments maintained ~ 400 species while simulations with lowly autocorrelated environments maintained ~ 100 species (Fig. 2G purple curve vs. green curve when the regional species pool is 1000 species).

With low spatial autocorrelation, local species richness was similar to the sum of species richness maintained by the mechanisms in isolation, reflecting the minimal interaction (Fig. 2G yellow and blue curves vs. green curve; Fig. 3A, 3C). In contrast, when habitats were spatially autocorrelated, the combination of JC-effects and habitat partitioning substantially increased species richness relative to either mechanism alone (Fig. 3B, 3D). The distinction between high and low autocorrelation was present only when JC-effects extended beyond the local patch scale. When JC-effects only occurred on the patch of the occupant ($M = 1$), results were approximately the same under low and high autocorrelation (compare $M = 1$ in Fig. 3A and 3B). The strong influence of spatial autocorrelation occurred when JC-effects extended beyond the local patch (compare $M = 3, 5, 7$ in Fig. 3A vs. 3B). These results were qualitatively identical when species experienced a specialist-generalist trade-off (Supplementary Information, "Tolerance–fecundity trade-off model").

Dispersal limitation typically reduced species richness relative to global dispersal in communities structured by both JC-effects and habitat partitioning, except when JC-effects only occurred on the local patch (when $M = 1$; compare Fig. 3C and 3D to Fig. 3A and 3D, respectively). Under low autocorrelation, the operation of JC-effects on top of habitat partitioning only marginally increased species richness (Fig. 3C, examine figure rows reading left

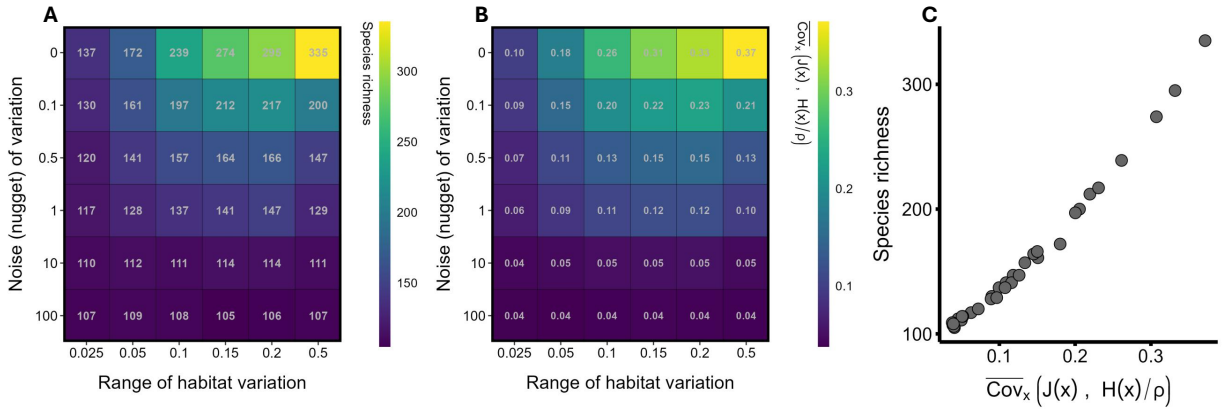

Figure 4: **When both JC-effects and habitat partitioning operate, species richness increases with abiotic habitat spatial autocorrelation, as reflected by the JC–HP covariance.** All panels depict simulations in which the range (x-axis, columns 1–2) and noise (nugget, y-axis) of habitat variation were varied. (A) and (B) show how the range and nugget influence species richness and the JC–HP covariance, respectively. (C) shows the relationship between species richness and the JC–HP covariance across simulations. Parameters are $a = 0.5$, $\nu = 0.3 \times 10^{-5}$, $\sigma_h = 0.02$, $Y \sim \text{lognormal}(\mu = 0, \sigma_Y = 0.3)$, $M = 7$, and dispersal is global.

to right). Under high specialization, the addition of small-to-moderate scale JC-effects on top of habitat partitioning reduced species richness (Fig. 3C, top row, compare "No JCEs" to $M = 1$ and $M = 3$). As in the global dispersal case, high spatial autocorrelation increased species richness when JC-effects extended beyond the local patch (compare $M = 3$, 5, 7 in Fig, 3C and 3D).

The increase in species richness associated with positive spatial autocorrelation reflects the JC-HP covariance. In simulations varying the range and nugget of spatial variation, species richness closely tracked $\overline{\mathrm{Cov}}_x\big(J(x), H(x)/\rho\big)$ (compare Fig. 4A and 4B). Richness increased approximately linearly with the JC-HP covariance term in these simulations (Fig. 4C). The approximately linear association was robust to when species experienced interspecific variation in baseline JC-effect strength a (Supplementary Information, "Interspecific variation in baseline JC-effect strength") and when species experienced a specialist-generalist trade-off (Supplementary Information, "Tolerance–fecundity trade-off model").

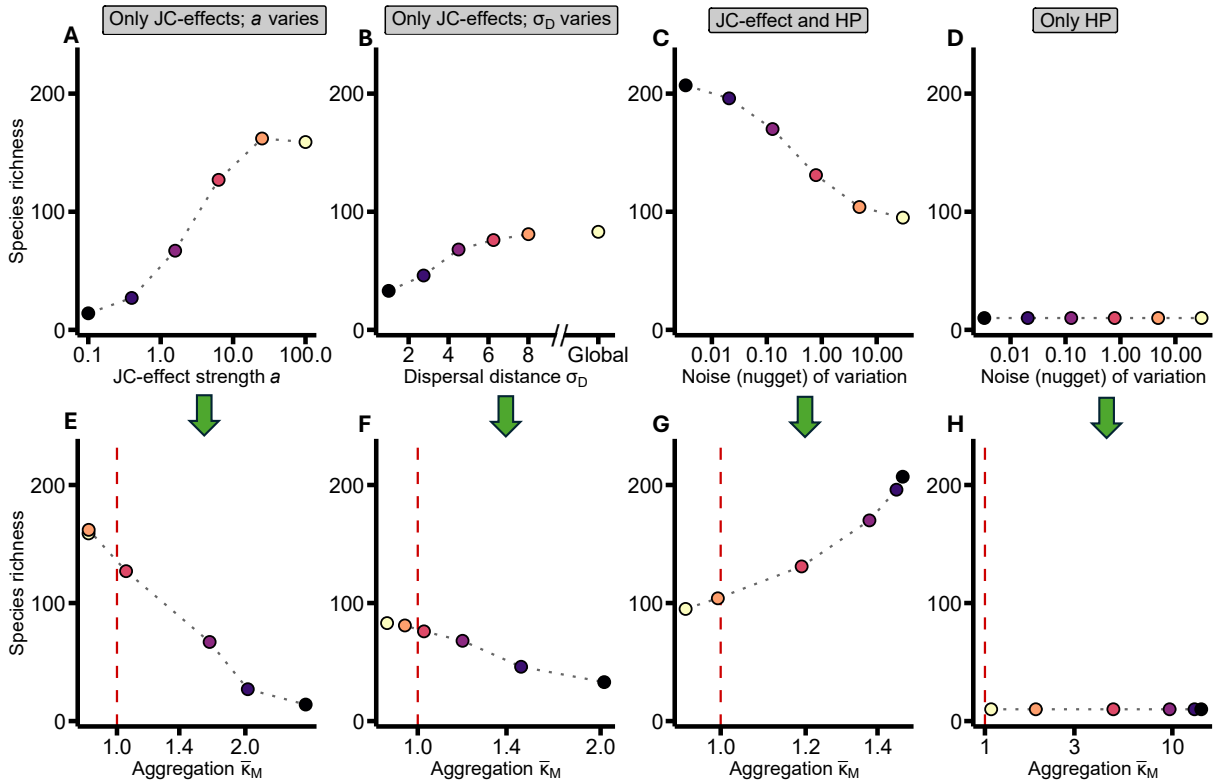

Figure 5: **Aggregation driven by habitat partitioning vs. dispersal limitation have qualitatively different effects on species richness when interacting with JC-effects.** Each column shows a pair of plots, with point colors indexing the same parameter values (e.g. the dark colored point on the far left of A is the same simulation as the dark colored point on the far right of E). The first row (A–D) shows species richness as a function of the varied parameter; the second row (E–H) shows species richness as a function of mean intraspecific aggregation $\overline{\kappa}_M$ of the corresponding simulations. Values to the left of the red dashed line indicate overdispersion; values to the right indicate greater aggregation than random. (A, E) JC-effects only (no habitat partitioning); simulations vary baseline JC-effect strength a; $\sigma_D = 1.0$. (B, F) JC-effects only; simulations vary dispersal distance σ_D; $a = 0.5$. (C, G) The joint operation of JC-effects and habitat partitioning; simulations vary the noise (nugget) of habitat variation (larger values = less spatial autocorrelation); dispersal is global. (D, H) Habitat partitioning only; simulations vary the nugget of habitat variation; dispersal is global. In all simulations, $\nu = 0.3 \times 10^{-5}$, $Y \sim \text{lognormal}(\mu = 0, \sigma_Y = 0.3)$. When JC-effects occur, $M = 7$. When habitat partitioning occurs, $\sigma_h = 0.05$ and habitat range = 0.5.

Intraspecific aggregation and species richness

The relationship between species aggregation and species richness qualitatively differed depending on the mechanism generating aggregation. First consider the case of only JC-effects. Stabilization due to JC-effects alone increases with their baseline strength a (equation (6)). Correspondingly, species richness increases with a (Fig. 5A). When a is large (e.g. $a > 10$; Fig. 5A) conspecific recruitment is effectively impossible within the Moore neighborhood; this reduces aggregation and causes regular conspecific spacing. Thus, species richness decreased with increasing aggregation (Fig. 5F). Similarly, species richness decreased with dispersal limitation, leading to a negative relationship between richness and aggregation (Fig. 5B, 5F).

In contrast, when both JC-effects and habitat partitioning were present, aggregation driven by habitat specialization was associated with greater species richness. As in Fig. 4, species richness increased with decreasing environmental noise (the nugget; Fig. 5C). This generates a positive relationship between species richness and aggregation (Fig. 5G). This relationship does not arise from habitat partitioning *per se*: under global dispersal, aggregation driven by habitat specialization was unrelated to species richness when JC-effects were absent (Fig. 5D, 5H). Thus, the positive aggregation–richness association can be entirely attributed to how habitat partitioning modifies the operation of JC-effects.

The spatial scale of JC-effects and species richness

In simulations where the total JC-effect pressure was maintained ($aM^2 = K$), the relationship between the spatial scale of JC-effects (M) and species richness differed qualitatively depending on if JC-effects occurred alone or alongside habitat partitioning. In the case of JC-effects alone, species richness increased with the spatial scale of M, saturating to a maximum value for global JC-effects (Fig. 6A). This directly follows from equation (6): given constant JC-effects induced by each tree ($aM^2 = K$), stabilization due to JC-effects are proportional to $\left(1 - e^{-K/M^2}\right)M^2$. This quantity is a strictly increasing, concave (saturating)

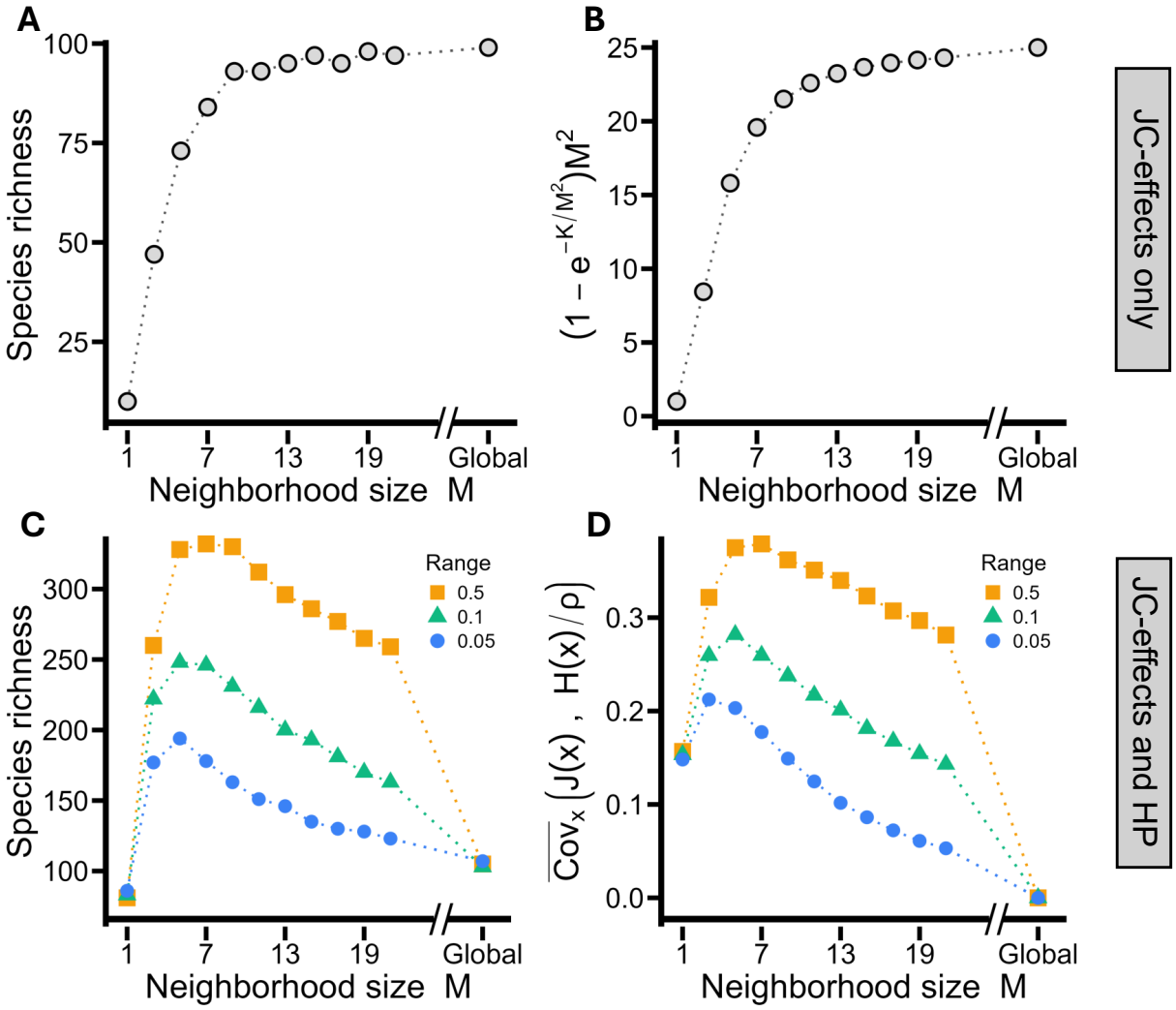

Figure 6: **The relationship between the spatial scale of JC-effects and species richness qualitatively differs depending on whether JC–HP covariance is present.** Panels depict how the spatial scale of JC-effects impact species richness; the total JC-effect pressure induced by each tree was held constant by setting $aM^2 = K$. (A) Species richness as a function of M (with $a = K/M^2$) when only JC-effects occur. (B) The quantity $\left(1 - e^{-a}\right)M^2 = (1 - e^{-K/M^2})M^2$ — which is proportional to the stabilization generated directly by JC-effects — as a function of M. (C) Species richness as a function of M when both JC-effects and habitat partitioning operate, shown for three different habitat range values. Habitats are positively autocorrelated in all cases (nugget = 0). (D) JC–HP covariance as a function of M. In all simulations, $\nu = 0.3 \times 10^{-5}$, $Y \sim \text{lognormal}(\mu = 0, \sigma_Y)$, and dispersal is global. In (C, D), $\sigma_h = 0.02$.

function of M (Fig. 6B).

By contrast, species richness peaked at an intermediate spatial scale M when both JC-effects and habitation partitioning operated (assuming habitats are spatially autocorrelated; Fig. 6C). This occurs because the JC-HP covariance also peaked at intermediate M (Fig. 6D). JC-effects stemming from a focal tree that occur at large spatial scales ($M > 5$ or $M > 7$, Fig. 6C) spill over into relatively poor habitat types, decreasing the JC-HP covariance. This decline occurs less rapidly when spatial autocorrelation has a relatively large range of variation (Fig. 6C-D; compare orange to yellow and green points).

Discussion

Quantifying how coexistence mechanisms interact is crucial for understanding their downstream effects on species richness. Here I show that two leading candidates for explaining tropical forest richness — Janzen–Connell effects (JC-effects) and habitat partitioning (HP) — can interact in a way that fundamentally changes their consequences. When habitat specialization causes species to aggregate in the environments where they perform best, JC-effects and HP act synergistically to promote high species richness. In contrast, aggregation generated by dispersal limitation weakens the ability of JC-effects to stabilize coexistence.

Conceptual and theoretical context

JC-effects and habitat partitioning each face limitations in maintaining coexistence when operating alone. JC-effects generate negative frequency dependence by reducing recruitment near conspecific adults, yet their ability to stabilize coexistence scales inversely with species richness ($\sim 1/N$; also see Chisholm & Fung, 2020; Smith, 2022). Habitat partitioning allows species differing in habitat preferences to coexist (Snyder & Chesson, 2003; Wright, 2002), but the impact on species coexistence similarly scales inversely with N and cannot maintain high species richness unless species are highly specialized.

When the two mechanisms act together, their interaction can greatly exceed the sum of their parts. In spatially autocorrelated habitats, species cluster in environments where they perform best, and resident adults disproportionately impose JC-effects on those same favorable locations. Invaders that share habitat preferences thus encounter weakened competitors, because residents are heavily suppressed precisely where they would otherwise hold the strongest advantage. The strength of this interaction is captured by the JC-HP covariance, which decays more slowly with the number of local resident species N than the direct effect of each mechanism — as slowly as $\propto 1/\sqrt{N}$ — and so remains strong even in highly diverse communities. This slower erosion allows habitat partitioning that might otherwise sustain only 10—30 species to maintain hundreds when coupled with JC-effects (Figs. 2G, 3B). Of course, one could theoretically select parameter values that allow any number of species to coexist under JC-effects alone (with sufficiently large a and M) or habitat partitioning alone (with sufficiently small σ_h). The key point is that JC-HP interactions require far less extreme parameter choices to maintain high species richness, because their contribution to invasion erodes much less rapidly with N.

This result builds on and contrasts with previous theory. Stump & Chesson (2015) analyzed a simplified case where space was implicit and JC-effects operated only at the parent's patch, without explicit spatial structure. Under those assumptions, they found little interaction between JC-effects and habitat partitioning, and argued that distance-dependent specialized predation is less able to promote coexistence than globally dispersing predators. I recover this outcome when only JC-effects operate (Fig. 6A–B). However, once habitat partitioning is included, the conclusion reverses: local, distance-dependent JC-effects strongly stabilize coexistence (Fig. 6C–D). The reason is that global enemies generate no JC–HP covariance, whereas local enemies do. Thus, when space is modeled explicitly, the *local* nature of JC-effects greatly amplifies their ability to promote coexistence in the presence of habitat partitioning and autocorrelated habitats.

However, JC-HP interactions can also be antagonistic. When habitat partitioning acts

alone, dispersal limitation tends to increase species richness because rare species disproportionately recruit into favorable habitats, generating a fitness–density covariance (Chesson, 2000; Snyder, 2008). JC-effects may erode the fitness-density covariance by reducing conspecific recruitment in those favorable patches (see the first row of Fig. 3C). This only occurred when habitat structure did not generate a JC-HP covariance — when habitats exhibit low autocorrelation — (compare Figs. 3C and 3D) suggesting that habitat structure modifies multiple mechanisms by which JC-effects and habitat partitioning interact.

Aggregation, JC-effects, and coexistence

The results of this study suggest the need to reinterpret the relationship between intraspecific aggregation, JC-effects, and coexistence. JC-effects are associated with overdispersion (Janzen, 1970; Chave *et al.*, 2002; Wiegand & Moloney, 2013) which is used as an indicator of its strong operation. However, when habitat partitioning operates alongside JC-effects, I find that species richness increases with intraspecific aggregation (Fig. 5) as facilitated by the JC-HP covariance. Thus, findings that habitat partitioning and dispersal limitation explain spatial distributions more than JC-effects (e.g. Zhu *et al.*, 2013) are not inconsistent with JC-effects contributing substantially to diversity maintenance (also see Kalyuzhny *et al.*, 2023).

Importantly, the JC–HP interaction provides a more empirically plausible pathway to high diversity maintenance than JC-effects alone when spatial aggregation is taken into account. Chisholm & Fung (2020) argue that the close proximity of conspecific adults in sites such as the Barro Colorado Island (BCI) Forest Dynamics Plot make it implausible that JC-effects are strong enough to fully prevent local recruitment. However, I find that JC-effects on their own can maintain substantial richness only when their baseline strength a is very large; large a eliminates recruitment near adults (Fig. 5A) and generates pronounced overdispersion ($\overline{\kappa} < 1$; Fig. 5E). This overdispersion contrasts spatial patterns at e.g. BCI and the near-universal aggregation of tropical trees (Condit *et al.*, 2000). However, the pos-

itive aggregation-richness relationship associated with JC-HP covariance is not inconsistent with these empirical aggregation patterns.

Aggregation itself (or lack thereof) is not inherently indicative of strong or weak stabilization with respect to JC-effects; its consequences depend entirely on the mechanism that generates it. Aggregation arising through habitat specialization promotes coexistence by concentrating JC-effects on the patches where species otherwise perform best. By contrast, aggregation produced by dispersal limitation undermines coexistence: the average strength of JC-effects directly decreases with resident aggregation (equation 11) in the absence of a JC–HP covariance. Moreover, if dispersal limitation overrides the repulsion of JC-effects, it may signal effects are weak (Fig. 5A, 5E). In addition, dispersal limitation harms rare species' propagules, which cannot fully escape local negative conspecific effects, weakening the stabilizing role of JC-effects and reducing coexistence (Stump & Chesson, 2015; Chisholm & Fung, 2020). Interestingly, however, dispersal-based aggregation processes that decouple recruit clustering from parent locations can enhance coexistence when species experience density-dependence (Wiegand *et al.*, 2021, 2025) — this may interact with habitat partitioning in a different way.

Overall, simply documenting aggregation in empirical communities is insufficient to determine the importance of JC-effects. This echoes past work indicating that the relationship between intraspecific aggregation and coexistence is murky (Murrell *et al.*, 2002; Chesson & Neuhauser, 2002; Bolker *et al.*, 2003). To link spatial patterns to coexistence, it is essential to identify the processes that generate clustering (or its absence).

Empirical considerations for forest communities

These theoretical results suggest a promising empirical target: measuring the JC–HP covariance in field plots. The importance of habitat heterogeneity varies among forest sites (Shen *et al.*, 2013), and the interaction between local density-dependent processes and habitat-induced clustering likely varies accordingly. This can be illustrated by contrasting the BCI

Forest Dynamics Plot in Panama, which was intentionally selected for relatively low spatial heterogeneity (Hubbell *et al.*, 2024), with the Lambir Hills Forest Dynamics Plot in Malaysia, which exhibits sharp edaphic contrasts and steep species turnover and harbors roughly four times as many tree species as BCI in a similar area (52 ha vs. 50 ha; Palmiotto *et al.*, 2004; Russo *et al.*, 2005). Notably, stabilizing conspecific negative density dependence has been detected at both sites (Hülsmann *et al.*, 2024). It is possible that Lambir Hills' higher richness reflects not greater habitat heterogeneity *per se*, but the way that heterogeneity interacts with local density-dependent processes such as JC-effects.

A key task is to determine how variation among sites in habitat heterogeneity shapes the relative importance of JC-effects, habitat partitioning, and their interactions. Addressing this requires not only quantifying the strength of each mechanism, but also identifying the processes generating conspecific clustering. Targeted empirical approaches that parse both density-dependent and habitat-associated effects are needed. One promising avenue is to extend generalized linear mixed models (GLMMs) and spatial point-pattern analyses to incorporate environmental maps, allowing joint estimation of conspecific (and heterospecific) distance- and density-dependent effects alongside spatially varying abiotic factors (e.g., topography, elevation, soil chemistry; Yao *et al.*, 2020; Huang *et al.*, 2022; Wiegand & Moloney, 2013; Wiegand *et al.*, 2021). Because JC-effects and habitat partitioning are predicted to interact most strongly under positive spatial autocorrelation, captured by the JC–HP covariance, such approaches offer a tractable way to estimate the strength of JC–HP interactions and their stabilizing effect.

Experimental manipulations provide a complementary route. For example, factorial designs crossing conspecific proximity with fungicide treatments have already demonstrated the role of specialized pathogens in generating conspecific negative density dependence (Bagchi *et al.*, 2010, 2014; Liu *et al.*, 2012). Extending these experiments to account for habitat variation would provide a direct test of the JC–HP interaction by asking whether natural enemies suppress seedlings most strongly in habitats where they would otherwise have high

survival. Such designs would offer a direct empirical test of the spatial covariance between JC-effects and habitat suitability.

Limitations, future directions, and conclusion

Several simplifying assumptions in the model suggest avenues for extension. I considered a one-dimensional habitat axis, but real forests contain multiple abiotic gradients that vary independently and across scales; extending the model to multidimensional environments would capture this complexity. Similarly, JC-effect strength was modeled as independent of habitat type, although evidence suggests that habitat variables can modify the baseline strength of density dependence (e.g. Yang *et al.*, 2023). Therefore, certain environment types (e.g. moister environments; Milici *et al.*, 2020) may generate stronger JC-HP interactions. I also assumed natural enemies to be perfectly specialized, while in reality spillover across related species is common (Gilbert & Webb, 2007; Ødegaard *et al.*, 2005); incorporating natural enemy overlap may modify JC-HP interactions in ways that depend on whether species sharing habitat preferences also share natural enemies (see Stump, 2017). The coevolution of natural enemy specialization on host trees and tree habitat specialization (Fine *et al.*, 2004, 2013) is a particularly interesting avenue to explore in future models.

Functional traits such as seed size also trade off with density-dependence susceptibility: larger-seeded species tend to experience weaker CNDD (Lebrija-Trejos *et al.*, 2016). This axis of variation could be integrated into the tolerance-fecundity trade-off (see Supplementary Information; Muller-Landau, 2010; D'Andrea & O'Dwyer, 2021), helping connect the JC–HP mechanism to observed trait variation in tropical forests (but see Detto & Pacala, 2024). Incorporating interspecific variation in dispersal distances (Muller-Landau *et al.*, 2008) could be an additional avenue to link JC-HP interactions with life history trade-offs (Stump & Comita, 2020).

While these extensions may provide additional insights, the main result is likely robust: JC-effects and habitat partitioning are not independent forces but interact strongly through

the spatial structure of forests. When habitats are spatially autocorrelated, habitat specialization generates conspecific clustering in favorable environments, concentrating JC-effects where they matter most and producing a powerful stabilizing mechanism. By contrast, aggregation arising from dispersal limitation undermines coexistence. Thus, the consequences of aggregation depend critically on its underlying cause. Recognizing this distinction helps reconcile apparent contradictions in previous theory and highlights a clear empirical task. To understand how tropical forests sustain extraordinary diversity, we must go beyond documenting aggregation or testing for JC-effects and habitat partitioning in isolation. Instead, we need to identify and quantify the mechanisms that generate spatial patterns, and integrate these measurements with process-based theory to elucidate their contributions to species coexistence. Doing so will allow us to link the operation of local processes to the maintenance of community-level biodiversity.

Data availability

All code required to reproduce the analyses and results in this paper is available at: https://github.com/DanielSmithEcology/Janzen_Connell_Habitat_Partitioning_Interactions.

Acknowledgements

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