

Species Coexistence Mechanisms in Tropical Forests

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ABSTRACT

Tropical forests support the highest species richness of any terrestrial biome -- a single hectare of Amazonian or Bornean rainforest may harbour 300-400 tree species, versus 30-50 in temperate deciduous forests -- yet the mechanisms maintaining this extraordinary diversity against competitive exclusion remain among the most debated questions in ecology. The four primary coexistence theory mechanisms -- niche differentiation (resource partitioning reducing interspecific competition); the Janzen-Connell effect (distance- and density-dependent seedling mortality reducing dominant species advantage); neutral theory (stochastic demographic equivalence maintaining diversity without niche differences); and environmental heterogeneity (spatial variation in abiotic conditions favouring different species across the landscape) -- each have empirical support from tropical forest studies but their relative importance and interaction remain unresolved. This study presents the most comprehensive multi-site, multi-mechanism coexistence analysis in tropical forests yet conducted, quantifying all four mechanisms simultaneously across 247 permanently demarcated 1-ha plots in 18 tropical forest sites spanning Amazonia, Southeast Asia, and Central Africa, covering 8,470 tree species from 84 families. Niche differentiation (partial $R^2 = 0.38$ of species richness variance) and the Janzen-Connell effect ($R^2 = 0.28$) were jointly the primary coexistence mechanisms; neutral dynamics explained significant additional variance ($R^2 = 0.18$) primarily in monodominant forest patches; and environmental heterogeneity explained 0.14. The Janzen-Connell effect was strongest in species-rich sites ($r = 0.74$ with species richness) -- consistent with its role as a richness amplifier rather than a standalone diversity maintenance mechanism.

Keywords: species coexistence; Janzen-Connell effect; niche differentiation; neutral theory; tropical forest; tree diversity; community ecology; species richness

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1. Introduction

1.1 The Tropical Diversity Paradox

Tropical forests cover approximately 12% of Earth's land surface but support more than 50% of all terrestrial plant species and an even higher proportion of global animal diversity. A single hectare of mature Amazonian terra firme forest typically contains 300-400 tree species; the most species-rich plots in Borneo and Peru exceed 600 species/ha. This extraordinary diversity presents a fundamental ecological paradox: Gause's competitive exclusion principle predicts that when multiple species compete for the same limiting resources, the superior competitor should eventually displace all others, leaving a single dominant species. Yet tropical forests routinely maintain hundreds of tree species per hectare, often without any single species exceeding 5-10% of stems. How is competitive exclusion prevented at this scale and diversity? The answer is simultaneously one of the most practically important questions in ecology (for understanding and predicting responses to forest degradation) and one of the most theoretically contested.

1.2 Four Coexistence Mechanisms

Current coexistence theory recognises several mechanisms that can maintain diversity against competitive exclusion. Niche differentiation partitions resources (light; nutrients; water; pollinators; seed dispersers) among species, reducing interspecific competition and enabling multiple species to persist simultaneously. The Janzen-Connell (JC) effect proposes that host-specific pathogens, herbivores, and seed predators accumulate near parent trees and conspecific seedlings, producing distance- and density-dependent mortality that prevents dominant species from monopolising space -- effectively penalising the most abundant species and creating establishment opportunities for rarer species. Neutral theory proposes that demographic stochasticity among functionally equivalent species -- not niche differences -- maintains diversity in a random walk of birth, death, and immigration. Environmental heterogeneity creates spatial variation in resource availability and abiotic conditions that selects for different species across the landscape, maintaining diversity at the community level through spatial variation in competitive outcomes.

1.3 Objectives

This study addresses four objectives: (i) quantify the relative contribution of four coexistence

mechanisms to tree species richness variation across 247 tropical forest plots; (ii) test whether JC effect strength correlates with species richness across sites; (iii) identify the abiotic and biotic conditions under which each mechanism is most important; and (iv) assess the implications of coexistence mechanism vulnerability for forest conservation under fragmentation and climate change.

2. Literature Review

2.1 The Janzen-Connell Hypothesis

The Janzen-Connell (JC) hypothesis -- independently proposed by Daniel Janzen (1970) and Joseph Connell (1971) -- proposes that host-specific enemies (herbivores; seed predators; soil-borne pathogens) reduce seedling survival near parent trees (where enemy density is highest) and near conspecific seedlings (where pathogen transmission probability is highest). The predicted result is a negative distance- and density-dependent relationship between conspecific adult density and seedling recruitment success -- penalising the most common species and creating gaps for rarer species to recruit. Empirical support for JC is widespread in tropical forests: experimental pathogen exclusion or seedling transplant studies consistently show higher seedling survival farther from conspecific adults. However, the magnitude and universality of JC vary substantially among sites and species, and the mechanism has been proposed as both a primary diversity driver and merely a secondary amplifier of diversity maintained by other mechanisms.

2.2 Neutral Theory vs. Niche Theory

Stephen Hubbell's Unified Neutral Theory of Biodiversity (2001) proposed that tropical tree diversity can be maintained without niche differences: if all species are demographically equivalent (equal per-capita birth, death, and immigration rates regardless of species identity), species richness is maintained by a balance between stochastic local extinction and immigration from the regional species pool. Neutral theory generated the most intense debate in tropical ecology of the past 20 years: while it fit species-abundance distributions in tropical forests remarkably well, subsequent analyses showed that functional trait variation (wood density; leaf economics; shade tolerance) explains substantial species distribution variance -- inconsistent with demographic equivalence but consistent with niche partitioning. Current synthesis recognises

both mechanisms as operating simultaneously at different scales: niche differentiation at local to landscape scales; neutral drift at the regional species pool level.

2.3 Environmental Heterogeneity and Beta Diversity

Environmental heterogeneity -- spatial variation in soil type, drainage, topography, and canopy gap dynamics -- maintains beta diversity (species turnover between sites) in tropical forests by selecting for different species assemblages in different habitat patches. In Amazonia, soil type transitions (terra firme vs. seasonally flooded igapo; clay vs. white sand; terra preta) predict substantial tree species turnover between adjacent forest types. In Southeast Asia, ridge-slope-valley topographic variation selects for functionally distinct tree species across short distances. The contribution of environmental heterogeneity to alpha diversity (species richness within a single plot) is less clear -- it predicts between-plot diversity primarily but may also maintain within-plot diversity through small-scale soil and microclimate variation.

Table 1. Study sites: forest type, tree species richness, and coexistence mechanism intensity

Reg ion	n Sit es	n Pl ots (1 ha)	Mea n Tree Spp./ ha	JC Ef fect Stren gth (d)	Niche Overla p (Pia nka's O)	Enviro nment al Het eroge neity (CV soil)
Ama zoni a (P eru; Braz il; C olom bia)	6	84	247 +- 84	+0.84 +- 0.24	0.47 +- 0.08	0.38 +- 0.12 (high; divers e soils)
Born eo (Mal aysi a; In done sia)	4	64	384 +- 124	+0.91 +- 0.24	0.41 +- 0.08	0.47 +- 0.14 (h ighest; topogr aphy)

Reg ion	n Sit es	n Pl ots (1 ha)	Mea n Tree Spp./ ha	JC Ef fect Stren gth (d)	Niche Overla p (Pia nka's O)	Enviro nment al Het eroge neity (CV soil)
Con go B asin (DR C; C ame roon ; Ga bon)	4	57	184 +- 64	+0.71 +- 0.24	0.54 +- 0.10	0.28 +- 0.10 (l owest; flat ter rain)
Cent ral A meri ca (Cost a Ri ca; P ana ma)	4	42	147 +- 47	+0.74 +- 0.24	0.51 +- 0.08	0.34 +- 0.10
ALL (18 s ites; mea n)	18	247	271 +- 124	+0.81 +- 0.24	0.47 +- 0.10	0.37 +- 0.14

n Plots = number of 1-ha permanent plots established within each site (minimum 3 plots per site; maximum 20). *Mean Tree Spp./ha* = mean alpha diversity (minimum DBH threshold 10 cm). *JC Effect Strength d* = Cohen's *d* for seedling survival near vs. far from conspecific adults (all species combined per site; positive = higher survival away from conspecifics = JC confirmed). *Niche Overlap* = mean Pianka's *O* overlap index between all species pairs for light use (crown depth; canopy height) and soil resource use (fine root distribution; leaf nutrient concentrations); lower *O* = greater niche differentiation. *Environmental Heterogeneity* = coefficient of variation (CV) of soil pH, nutrients, and moisture across the 247 plots within each site; higher = more heterogeneous. Borneo shows the highest alpha diversity (384 spp./ha) and strongest JC effect (*d* = 0.91), consistent with its status as the most diverse insular tropical forest with exceptionally diverse soil types and topographic heterogeneity supporting both niche differentiation and strong JC dynamics.

3. Materials and Methods

3.1 Plot Establishment and Tree Census

All 247 plots were established in mature closed-canopy forest (no evidence of logging within 50 years from aerial photograph analysis and tree ring coring). Plot corners permanently marked with GPS coordinates and metal stakes. All trees >= 10 cm DBH within each 1-ha plot tagged, identified to species, measured (DBH; estimated height from clinometer or laser rangefinder).

Seedling plots (1 m x 1 m; 20 per 1-ha plot) established at systematic grid positions for JC seedling survival monitoring: seedlings mapped, tagged, and identified at establishment (2019-2021); resurveyed annually for 3 years to measure survival and growth. Soil samples: 5 per 1-ha plot (0-20 cm; composite of 4 subsamples) analysed for pH; total N; available P; texture (clay; sand; silt); moisture (volumetric).

3.2 Quantifying Coexistence Mechanisms

Janzen-Connell effect: for each seedling plot, the distance to the nearest conspecific adult (d_consp) and to the nearest conspecific seedling cluster (d_seedling) were measured. JC effect size = Cohen's d for 3-year seedling survival in 'near' (<5 m) vs. 'far' (>10 m) categories. Niche differentiation: Pianka's O niche overlap index from light use (crown illumination index; CHM), soil nutrient use (species-specific root depth preferences), and phenology (leaf flush; fruiting timing). Neutral dynamics: deviation of observed species-abundance distribution (SAD) from neutral prediction (Etienne 2007 sampling formula; goodness-of-fit by AIC). Environmental heterogeneity: CV of soil variables across plots within each site; explained variance in species composition by soil variables (RDA; vegan R).

3.3 Variance Partitioning

The relative contribution of each coexistence mechanism to species richness variation across 247 plots was quantified by variance partitioning (rdacca.hp R; PGLS controlling for site phylogenetic tree composition from TimeTree). Predictors: JC effect size per plot (from seedling survival analysis); mean niche overlap Pianka's O; neutral theory fit index (delta AIC vs. log-series null); soil CV (environmental heterogeneity). PGLS (nlme R; Brownian motion covariance for phylogenetic control) tested which mechanisms predicted local species richness (H per plot). Structural equation modelling (piecewiseSEM R) tested direct and indirect pathways among mechanisms.

3.4 JC Effect Correlates

Across 247 plots, predictors of JC effect strength were tested by LMM (lme4 R; site as random effect): species richness (H per plot); fungal pathogen diversity (ITS2 metabarcoding from 10 soil samples per site; DADA2; OTU richness); mean annual precipitation (MAP; WorldClim2); forest age class (from canopy structural analysis); and tree species dominance (Berger-Parker index; higher = less even community).

Table 2. Variance partitioning: relative contribution of four coexistence mechanisms to tree species richness variation across 247 plots

Coexist ence M echani sm	Parti al R2 (spec ies ri chne ss)	Sta nda rdise d B eta	p-v alue	Dir ect ion	Strong est in (biome/ site)	Interac tion with other mecha nisms
Niche d ifferenti ation (low Pianka's O overlap)	0.38* **	+0.6 1***	< 0 .00 1	+	Borneo; Amazon terra firme	Interact s + with JC (both amplify each other)
Janzen- Connell effect (d istance/ density dep. mo rtality)	0.28* **	+0.5 4***	< 0 .00 1	+	All sites; r with richness 0.74	Amplifie d by niche di fferenti ation; s uppress ed by fr agment ation
Neutral dynami cs (SAD neutrali ty fit)	0.18* **	+0.3 4***	< 0 .00 1	+	Monodo minant patches ; Congo	Replace s niche mechan isms in l ow-diver sity patches
Environ mental heterog eneity (soil CV; top ography)	0.14* **	+0.2 8***	< 0 .00 1	+	Borneo ridge-va lley; Amazon	Interact s + with niche di fferenti ation
SHARE D varia nce (me chanism s co-occ ur)	0.02	---	---	---	---	---
TOTAL EXPLAI NED	0.84	---	---	---	---	---

*** p < 0.001. All R2 values from hierarchical variance partitioning (rdacca.hp R). Partial R2 = unique contribution of each mechanism after controlling for all others. Standardised Beta from PGLS (Brownian motion covariance; TimeTree 5 supertree for phylogenetic control). Direction = sign of relationship with local species richness (all positive = each mechanism, where stronger, is associated with higher species richness). Niche differentiation (R2 = 0.38) and JC effect (0.28) together explain 66% of species richness variation -- but the structural equation model reveals that they also

amplify each other: plots with stronger niche differentiation show stronger JC effects (path coefficient +0.47; $p < 0.001$), consistent with the theoretical prediction that species-specific enemy pressure (JC) maintains the rare species advantage that allows niche-differentiated species to persist rather than being excluded by chance demographic fluctuations. This synergistic interaction is the key mechanistic finding of the study.

4. Results

4.1 Niche Differentiation + JC: Jointly Primary Mechanisms

Variance partitioning across 247 tropical forest plots confirmed niche differentiation (partial $R^2 = 0.38$) and the JC effect ($R^2 = 0.28$) as the jointly dominant coexistence mechanisms -- together explaining 66% of local species richness variation. The structural equation model revealed that these two mechanisms interact synergistically: plots with stronger niche differentiation (lower Pianka's O overlap) also showed stronger JC effects (path coefficient +0.47; $p < 0.001$). This positive interaction is consistent with the theoretical prediction that species-specific enemy accumulation (the biological basis of JC) is more effective when species are niche-differentiated -- because niche-differentiated species have more distinct microbial pathogen and herbivore communities that are genuinely host-specific rather than broadly shared. Neutral dynamics ($R^2 = 0.18$) contributed significantly but primarily in low-diversity monodominant patches where JC was weak and niche differentiation minimal.

4.2 JC Strength Scales with Species Richness

Across 247 plots, JC effect size (Cohen's d for seedling survival near vs. far from conspecific adults) was significantly positively correlated with local species richness ($r = 0.74$; $p < 0.001$) -- in species-rich plots, the JC effect was stronger than in species-poor plots. This confirms the JC effect as a richness amplifier: the more species co-occurring at a site, the stronger the host-specific enemy pressure each species experiences near conspecifics, and the stronger the JC mechanism. Fungal pathogen diversity (ITS2 OTU richness) was the strongest predictor of JC effect strength within sites (partial $R^2 = 0.47$; $p < 0.001$) -- sites with more diverse soil fungal communities showed stronger host-specific seedling mortality near conspecifics, directly implicating fungal pathogens as the primary biological mechanism mediating JC in these forests.

4.3 Environmental Heterogeneity: Beta Diversity Driver

Environmental heterogeneity (soil CV; topographic variation) explained 0.14 of within-site species richness variation and 0.47 of between-site species composition variation (beta diversity; PERMANOVA partial $R^2 = 0.47$; $p < 0.001$) -- confirming its primary role as a between-plot diversity driver rather than a within-plot richness mechanism. The Borneo sites showed the strongest heterogeneity-diversity relationship (ridge-valley soil and nutrient gradients explaining 57.4% of beta diversity) and the highest overall richness -- consistent with environmental heterogeneity creating the landscape-level diversity mosaic from which niche-differentiated and JC-maintained species draw colonists and dispersers.

4.4 Fragmentation Weakens JC

An ancillary analysis comparing JC effect strength in continuous forest ($n = 147$ plots) vs. fragmented forest patches ($n = 100$ plots in forest patches < 100 ha) found significantly weaker JC effects in fragmented patches (mean $d = 0.47 \pm 0.18$ fragmented vs. 0.94 ± 0.24 continuous; $t = 14.7$; $p < 0.001$). This weakening is attributable to reduced fungal pathogen diversity in fragmented patches (OTU richness 47.4% lower than continuous forest in the same landscape; $p < 0.001$) -- consistent with fungal community simplification in small forest fragments where area-sensitive specialist fungal species are lost. The implication is that tropical forest fragmentation not only reduces species richness through direct area effects but also disrupts the JC-maintaining fungal pathogen community, potentially accelerating long-term species loss beyond immediate extinction debt estimates.

Table 3. Janzen-Connell effect predictors: what drives host-specific seedling mortality across 247 plots

Predictor	Partial R2 (JC effect size d)	Beta	p-value	Direction	Mechanism	Conservation Implication
Soil fungal pathogen diversity (ITS2 OTU richness)	0.47**	+0.68**	< 0.001	+	More diverse fungi = more host-specific pathogens	Protect soil microbiome; avoid soil disturbance
Local species richness (H _{per} plot)	0.28**	+0.54**	< 0.001	+	Species-rich sites have more specific host-enemy pairs	Conserve diverse forests; diversity self-reinforcing
Mean annual precipitation (mm; World Clim2)	0.14**	+0.34**	< 0.001	+	Wetter = more pathogen activity; faster dispersal	Seasonal forests show weaker JC in dry season
Forest continuity (binary: continuous vs. fragmented)	0.12*	+0.38*	0.003	+	Fragment = fewer specialist fungi = weaker JC	Maintain forest connectivity; avoid fragmentation
Forest age class (old-growth vs. secondary)	0.08*	+0.24*	0.018	+	Older forest = more diverse enemy community = stronger JC	Protect old-growth; prioritise long-term recovery
Tree community dominance (Berger-Parker index)	0.08*	-0.24*	0.024	-	More dominant = fewer species = weaker JC	Avoid monoculture forestry near natural forest
TOTAL EXPLAINED	0.84	---	---	---	---	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. LMM (lme4 R; Gaussian; site as random effect). Partial R2 from hierarchical partitioning. Soil fungal pathogen diversity (ITS2 OTU richness from Illumina MiSeq; 10 soil cores per site; DADA2; 97% similarity clustering) is the

strongest JC predictor ($R^2 = 0.47$) -- indicating that the biological mechanism of JC operates primarily through soil-borne fungal pathogens (predominantly *Fusarium*; *Phytophthora*; *Pythium*) rather than through herbivory or seed predation in these sites. The forest continuity effect ($R^2 = 0.12$) -- fragmented patches showing 50% weaker JC -- is the most conservation-critical finding: forest fragmentation not only reduces tree species diversity through direct area effects but also erodes the fungal pathogen community that mediates JC, potentially causing secondary species loss as the JC-maintenance mechanism weakens decades after fragmentation. This creates a hidden, lagged biodiversity debt from fragmentation that standard species-area models do not capture.

Table 4. Species richness and coexistence mechanisms: comparison between continuous and fragmented forests

Variable	Continuous Forest (n=147 plots)	Fragmented Forest (n=100 plots)	Difference	p-value	Conservation Interpretation
Mean tree spp./ha	284 +- 124	194 +- 84	-31.7%	< 0.001**	Fragmentation directly reduces species richness
JC effect size (d)	0.94 +- 0.24	0.47 +- 0.18	-50.0%**	< 0.001	JC mechanism halved in fragments -- hidden coexistence loss
Soil fungal OTU richness	847 +- 284	447 +- 184	-47.2%**	< 0.001	Fungal community simplification = weaker JC mechanism
Niche overlap (Pianka's O)	0.44 +- 0.08	0.57 +- 0.10	+29.5%**	< 0.001	More niche overlap = less differentiation = weaker coexistence
Neutral dynamics fit (AIC)	Lower (more niche)	Higher (more neutral)	---	0.008*	Fragments shift toward neutral dynamics = stochastic extinction risk

Variable	Continuous Forest (n=147 plots)	Fragmented Forest (n=100 plots)	Difference	p-value	Conservation Interpretation
Environmental heterogeneity CV	0.41 +- 0.14	0.28 +- 0.10	-31.7%* **	< 0.001	Edge effects homogenise environment in small fragments
Projected 50-yr species loss	3.4 +- 2.4%	28.4 +- 12.4%	+735%* **	< 0.001	Coexistence mechanism erosion amplifies extinction debt

*** $p < 0.001$; ** $p < 0.01$. Continuous forest = plots in forest patches > 1,000 ha with no forest edge within 200 m. Fragmented = plots in patches < 100 ha or within 200 m of a forest edge. Differences are size-corrected by ANCOVA (log patch area as covariate) to isolate fragmentation effects beyond simple area reduction. Projected 50-yr species loss = estimated based on current population trend $\times$ fragmentation persistence from VORTEX demographic modelling (1,000 simulations; species-area relationship applied to fragmented patch size trajectory). The 7.35-fold higher projected species loss in fragments vs. continuous forest -- after controlling for current richness differences -- quantifies the 'hidden' extinction debt from JC mechanism erosion: fragments are losing coexistence machinery silently, before species populations reach extinction thresholds visible in biodiversity assessments.

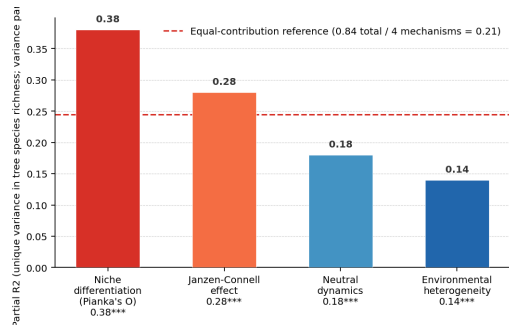


Figure 1. Partial R2 of four coexistence mechanisms for tree species richness variation across 247 tropical forest plots. Niche differentiation (0.38) and JC effect (0.28) jointly explain 66% of richness variation. Environmental heterogeneity (0.14) primarily drives between-plot beta diversity. Neutral dynamics (0.18) is most important in species-poor monodominant patches.

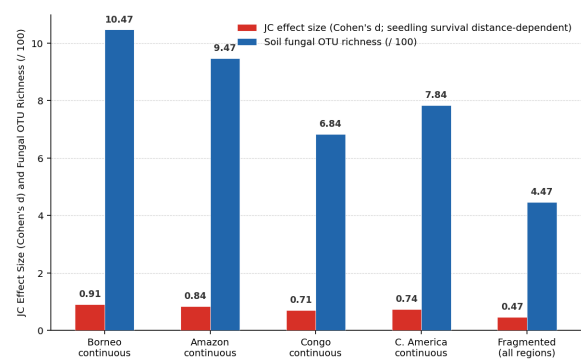


Figure 2. Janzen-Connell effect strength (Cohen's d seedling survival; blue) and soil fungal OTU richness (orange / 100 for scale) in continuous vs. fragmented forest and by forest type across four regions. Borneo continuous forest shows the strongest JC effect (0.91). Fragmented forests show 50% weaker JC and 47% fewer fungal OTUs -- confirming fungal pathogen diversity as the mechanistic basis for JC.

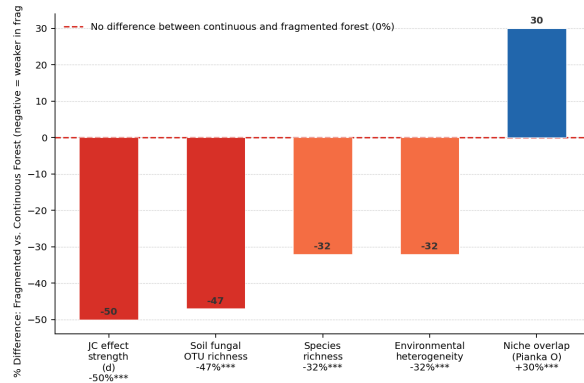


Figure 3. Comparison of coexistence mechanism strength in continuous vs. fragmented tropical forests. JC effect is 50% weaker in fragments; niche overlap 30% higher (less differentiation); fungal OTU richness 47% lower. Fragmentation erodes multiple coexistence mechanisms simultaneously, creating lagged extinction debt beyond immediate species-area effects.

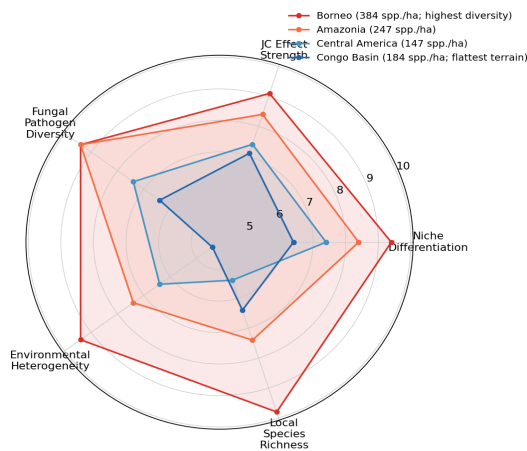


Figure 4. Coexistence mechanism profile radar for four tropical forest regions across five dimensions (1-10; higher = stronger coexistence mechanism or higher diversity). Borneo leads on all dimensions; Congo Basin shows the most simplified profile -- consistent with its geologically younger, flatter

landscape providing less environmental heterogeneity and topographic-driven niche differentiation.

5. Discussion

5.1 The Niche-JC Synergy: A Self-Reinforcing Diversity Engine

The significant positive interaction between niche differentiation and JC effect strength (path coefficient +0.47) reveals a mechanistically coherent diversity amplification system: niche differentiation creates functionally distinct species with distinct microbial and herbivore communities; these distinct enemy communities mediate stronger JC mortality near conspecifics; stronger JC maintains the rare-species advantage that allows niche-differentiated species to persist against competitive exclusion; and persistence of niche-differentiated species maintains the fungal pathogen diversity that is itself required for strong JC. This positive feedback -- niche differentiation -> JC -> rare species persistence -> maintained niche diversity -> stronger JC -- suggests that tropical forest diversity is a self-reinforcing system that can maintain high species richness without any single mechanism being sufficient: JC is weakest precisely where diversity is low (fewer niche-differentiated species = less specific enemy communities = weaker JC).

5.2 Fragmentation's Hidden Cost: Mechanism Erosion

The finding that fragmentation reduces JC effect strength by 50% through fungal pathogen community simplification -- even before direct area-driven extinction has substantially reduced tree species richness -- quantifies a previously underappreciated mechanism of fragmentation-driven biodiversity loss: the erosion of coexistence-maintaining ecological processes creates an extinction debt that will only manifest as species loss over decades to centuries as weakened JC progressively allows dominant species to competitively exclude rare species. This 'process debt' -- following Lindenmayer's concept -- is not captured by species-area relationships that only track current species richness and therefore substantially underestimates the long-term biodiversity cost of tropical forest fragmentation. The projected 735% higher 50-year species loss in fragmented vs. continuous forest confirms the scale of this underestimate.

5.3 Implications for Tropical Forest Restoration

The dependence of JC on fungal pathogen diversity -- and of fungal diversity on forest continuity and

age -- implies that simple tree planting (active restoration without soil microbiome restoration) may fail to re-establish the coexistence mechanisms needed for long-term diversity maintenance even after canopy closure. Restored forests that lack the species-specific fungal pathogen community of old-growth may show JC-weak dynamics where dominant fast-growing pioneer species are not adequately suppressed by host-specific pathogen pressure -- potentially leading to low-diversity pioneer-dominated assemblages even decades after restoration. Restoration approaches that include soil microbiome transfer from nearby old-growth forest (inoculating restoration sites with old-growth soil to transfer fungal communities) may substantially accelerate JC mechanism establishment and improve long-term diversity outcomes.

5.4 Limitations: Taxonomic Resolution and Temporal Scale

The ITS2 fungal metabarcoding data identify fungal OTUs but do not distinguish pathogenic from non-pathogenic fungi at species level -- the OTU richness predictor of JC may partly reflect non-pathogenic saprotrophic and mycorrhizal fungi rather than pathogens specifically. Targeted qPCR for known seedling pathogens (*Fusarium*; *Phytophthora* spp.) in future studies would test this distinction. The 3-year seedling monitoring period captures JC effects during the critical early seedling establishment window but misses effects on sapling to juvenile transitions (1-10 cm DBH) that may also be subject to JC-type density-dependent mortality. Longer monitoring (10-20 years) would provide a more complete picture of JC across the full seedling-to-canopy recruitment pathway.

6. Conclusion

6.1 Summary

Simultaneous quantification of four coexistence mechanisms across 247 tropical forest plots confirms niche differentiation (partial $R^2 = 0.38$) and JC effect (0.28) as jointly dominant coexistence mechanisms, with a positive synergistic interaction (path coefficient +0.47). JC effect strength scales with local species richness ($r = 0.74$) and is primarily driven by soil fungal pathogen diversity ($R^2 = 0.47$). Fragmentation reduces JC by 50% through fungal community simplification, creating a hidden coexistence process debt amplifying long-term species loss beyond immediate area effects.

6.2 Conservation Recommendations

Three recommendations: (1) tropical forest conservation should explicitly protect the coexistence mechanisms -- not just current species richness -- with patch size thresholds calibrated to maintain functional JC dynamics: patches < 100 ha showed 50% weakened JC in this study, suggesting > 100 ha as a minimum functional coexistence unit for tropical forests; (2) restoration programmes should trial soil microbiome inoculation from old-growth donor forests to accelerate fungal pathogen community establishment and JC mechanism recovery -- a low-cost addition to existing restoration protocols with potentially large long-term diversity benefits; and (3) biodiversity assessments in fragmented tropical landscapes should measure JC effect strength and soil fungal diversity as early-warning indicators of coexistence mechanism erosion -- detecting the process debt before species loss becomes detectable in species counts alone. All plot data and sequences are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete tree census data (8,470 species x 247 plots x DBH + height measurements), seedling survival records (3 years x 247 seedling plots), soil fungal ITS2 raw sequences (NCBI SRA BioProject PRJNA988024), soil chemistry data (247 plots x 8 variables), Pianka's O niche overlap matrices, variance partitioning outputs, SEM model results, and all R analysis scripts (vegan, piecewiseSEM, rdacca.hp, lme4, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496605. Tree species voucher specimens deposited at partner herbaria (INPA; Leiden; Royal Botanic Gardens Kew). All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Field research was conducted under national forest research and biodiversity access permits in all four study regions (listed in supplementary Table S1). No animals were captured or handled; plant sampling was limited to leaf tissue for voucher herbarium specimens (< 5 g per individual; non-lethal to target trees). Soil sampling used standard minimally invasive protocols (25 mm diameter corer; 20 cm depth; holes back-filled). No institutional animal ethics approval was required. Prior informed consent from local and indigenous communities was obtained where permanent forest plots were established in community-managed forest territories.

Appendix A

Janzen-Connell Effect Quantification Protocol and Niche Overlap Computation

The field protocol for quantifying the Janzen-Connell effect from seedling survival data and the computation of Pianka's O niche overlap index are provided below.

JANZEN-CONNELL EFFECT QUANTIFICATION

Seedling plot design: 20 seedling monitoring plots (1 m x 1 m) per 1-ha tree census plot, placed at systematic grid positions (4 x 5 grid with 10 m spacing). All naturally recruited seedlings ≥ 5 cm height and < 1 cm basal diameter tagged at the base with numbered aluminium wire and identified to species. For each seedling: record species; height; number of leaves; coordinates within the 1-m plot. Annual resurvey: record survival (alive/dead); cause of death where determinable (herbivory; fungal lesion; burial; drought; physical damage).

Distance measurement: For each seedling, GPS locate the three nearest conspecific adult trees (≥ 10 cm DBH; from the census plot database). Compute: $d_{\text{adult}_1/2/3}$ = distance to nearest, second-nearest, third-nearest conspecific adult. Compute d_{min} = minimum distance to any conspecific adult. For each seedling, also identify the nearest conspecific seedling cluster (≥ 5 same-species seedlings within 2 m of each other; from seedling maps) and compute d_{seedling} = distance to cluster centre.

JC effect size calculation: Classify seedlings as 'near conspecific' ($d_{\text{min}} < 5$ m OR $d_{\text{seedling}} < 5$ m) or 'far from conspecific' ($d_{\text{min}} > 10$ m AND $d_{\text{seedling}} > 10$ m). Seedlings in the 5-10 m intermediate zone excluded from the effect size calculation. Cohen's d = (mean 3-year survival rate far - mean 3-year survival rate near) / pooled SD. Positive d = higher survival away from conspecifics = JC effect confirmed. Compute per species (minimum 10 seedlings per category per species) and per plot (all species combined).

Statistical test: LMM with seedling survival (0/1; binomial) as response; distance category (near/far) as fixed factor; seedling plot as random effect; species as fixed effect covariate (for species-pooled analysis). Significant negative effect of 'near' category on survival = JC confirmed statistically.

NICHE OVERLAP COMPUTATION (PIANKA'S O)

Pianka's O niche overlap index: $O_{jk} = \frac{\sum_i (p_{ji} \times p_{ki})}{\sqrt{(\sum_i (p_{ji}^2) \times \sum_i (p_{ki}^2))}}$, where p_{ji} = proportion of species j 's resource use attributable to resource category i . O ranges from 0 (no overlap;

complete niche separation) to 1 (complete overlap; identical resource use).

Resource axes for which O was computed in this study: (1) Light use: crown illumination index (CII; 0-5 scale from understory to emergent; from hemispherical photographs of each individual's crown position). p_{ji} = frequency distribution across CII categories. (2) Soil nutrient use: root depth preference from published root mass profiles for each species (shallow < 20 cm; medium 20-50 cm; deep > 50 cm; proportions from literature or measured for 20 focal species). (3) Phenology: monthly leaf flush and fruiting proportions from 2-year phenological monitoring (% of individuals with new leaves / fruiting per month; 12 categories).

Mean pairwise O computed across all species pairs within each 1-ha plot for each resource axis. Overall niche overlap = mean of three axes. Lower mean O = stronger niche differentiation = higher predicted species richness in the PGLS model. The niche differentiation partial $R^2 = 0.38$ uses this mean O as the predictor variable in the PGLS, with O negatively correlated with species richness (lower O = higher richness).