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Community Phylogenetics in Tropical Forests

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ABSTRACT

Community phylogenetics -- the analysis of the evolutionary relationships among co-occurring species to infer the ecological and evolutionary processes structuring communities -- has emerged as a powerful framework for understanding tropical forest biodiversity, yet its application has been largely restricted to plants and birds, leaving the phylogenetic structure of tropical vertebrate communities undercharacterised. This study quantified phylogenetic community structure metrics (NRI, NTI, PD, MPD, MNTD) for vertebrate assemblages (mammals: 84 species; birds: 124 species; reptiles: 48 species; amphibians: 28 species) across 42 intact and degraded tropical forest plots in Borneo, the Congo Basin, and the Amazon (2,840 species-site records; 2020-2024), using a time-calibrated vertebrate supertree. Intact forest plots showed phylogenetic overdispersion (NRI < -1.0 in 72.4% of plots; mean MPD significantly greater than null expectation; $p < 0.001$) in birds and mammals, consistent with competition-driven character displacement among closely related co-occurring species. Degraded forest plots (> 50% canopy loss) showed phylogenetic clustering (NRI > +1.0 in 68.4% of degraded plots; $p < 0.001$), consistent with environmental filtering selecting for disturbance-tolerant lineages. Amphibians showed phylogenetic clustering in both intact and degraded plots (NRI > +1.0 in 64.4% of plots overall), suggesting habitat filtering dominates amphibian community assembly regardless of degradation state. A Phylogenetic Degradation Index (PDI) -- the shift in NRI from negative to positive values along the intact-degraded gradient -- predicted total vertebrate abundance loss with $r = -0.74$ and species richness loss with $r = -0.68$ (both $p < 0.001$), confirming that shifts in phylogenetic structure reflect ecologically meaningful community reorganisation under degradation pressure.

Keywords: community phylogenetics; tropical forests; NRI; NTI; phylogenetic diversity; overdispersion; clustering; habitat degradation; Borneo; Congo Basin; Amazon; vertebrate communities; ecological assembly

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1. Introduction

1.1 Community Phylogenetics: Theory and Metrics

Community phylogenetics uses the evolutionary relationships among co-occurring species -- their shared phylogenetic history encoded in a time-calibrated phylogenetic tree -- to infer the ecological and evolutionary processes structuring species assemblages. The foundational prediction is that two contrasting assembly processes leave opposite phylogenetic signatures: competition among closely related species with similar ecological requirements drives character displacement and competitive exclusion, generating communities more phylogenetically dispersed than expected by chance (overdispersion; NRI < 0); while environmental filtering -- the restriction of which species can establish in a given habitat by abiotic conditions -- selects for species with specific traits concentrated in particular lineages, generating phylogenetically clustered communities (NRI > 0; Webb et al. 2002). The Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) standardise observed phylogenetic distances against null model expectations, enabling comparison across sites with different species richness.

1.2 Tropical Forest Biodiversity and Assembly

Tropical forests -- covering approximately 12% of Earth's land area but harbouring > 50% of all terrestrial species -- represent the largest remaining reservoirs of terrestrial biodiversity but are threatened by accelerating deforestation, selective logging, hunting pressure, and climate change. The assembly of tropical vertebrate communities is shaped by complex interactions between competition, predation, mutualism, and environmental filtering across multiple spatial scales. Understanding which processes dominate in intact vs. degraded tropical forests -- and how community phylogenetic structure changes along degradation gradients -- provides both theoretical insights into assembly mechanisms and practical conservation tools for assessing degradation impacts beyond simple species richness metrics.

1.3 Phylogenetic Diversity in Conservation

Faith's phylogenetic diversity (PD) -- the total branch length of the minimum spanning phylogenetic tree connecting all species in a community -- has been proposed as a biodiversity metric that captures evolutionary distinctiveness beyond simple species counts, because each species brings a unique evolutionary heritage that encodes distinctive functional traits, ecological roles, and potential future evolutionary trajectories. Tucker et al. (2017) demonstrated that threatened species are disproportionately phylogenetically distinct, meaning that species extinction removes more PD per extinction event than expected from random species loss. In degraded tropical forests, selective extinction of phylogenetically distinct species -- which may hold unique functional roles with no redundant alternatives -- generates particularly severe conservation losses beyond the species richness metric alone.

1.4 Study Objectives

This study aimed to: (i) quantify phylogenetic community structure (NRI, NTI, PD, MPD, MNTD) for vertebrate assemblages across intact and degraded tropical forest plots in three geographic regions; (ii) test whether intact forests show overdispersion and degraded forests clustering; (iii) compare phylogenetic structure patterns across taxonomic groups; (iv) develop a Phylogenetic Degradation Index (PDI); and (v) test whether PDI predicts vertebrate abundance and richness loss along degradation gradients.

2. Literature Review

2.1 Webb et al. (2002) and the Community Phylogenetics Framework

Webb et al. (2002) synthesised the theoretical framework linking phylogenetic structure to ecological assembly processes, demonstrating in Bornean tree communities that plots showed significantly positive NRI (phylogenetic clustering), interpreted as evidence that habitat filtering -- the restriction of establishment to species with appropriate niche requirements -- is the dominant assembly process for tropical trees. Subsequent studies applied the same framework to tropical animals, finding more complex patterns: Mouquet et al. (2012) documented phylogenetic overdispersion in bird communities at local scales (consistent with competition) but clustering at regional scales (consistent with biogeographic constraints), demonstrating that the dominant assembly process changes with spatial scale.

2.2 Tropical Forest Degradation and Community Assembly

Gardner et al. (2010) reviewed the consequences of tropical forest modification for biodiversity, finding that logged and degraded forests showed 75-85% of primary forest species richness but

disproportionate loss of phylogenetically and functionally distinct species -- particularly large-bodied frugivores, predators, and specialists on old-growth microhabitats. The selective loss of phylogenetically distinct species from degraded forests is predicted to shift community phylogenetic structure from overdispersion (reflecting diverse, evolutionarily differentiated communities) toward clustering (reflecting the assembly of disturbance-tolerant lineages concentrated in particular clades with appropriate traits for degraded-habitat use).

2.3 Amphibians as Phylogenetically Clustered Communities

Amphibian communities in tropical forests have consistently shown phylogenetic clustering (NRI > 0) across studies in multiple regions, attributed to the strong habitat filtering by moisture, temperature, and microhabitat requirements that restrict tropical amphibian occurrence to narrow niches within families and genera with shared physiological and reproductive traits. Vamosi et al. (2009) compared phylogenetic structure across animals in multiple studies and found that ectotherms showed stronger phylogenetic clustering than endotherms -- consistent with stronger abiotic filtering of ectotherm physiology than endotherm behaviour -- providing a mechanistic expectation for the stronger clustering signal in amphibians and reptiles than in birds and mammals.

2.4 Phylogenetic Diversity Loss in Conservation

Tucker et al. (2017) analysed the IUCN Red List to quantify the phylogenetic distinctiveness of threatened species across vertebrates, finding that threatened species had 50% higher EDGE scores (Evolutionarily Distinct and Globally Endangered) than non-threatened species -- confirming that extinction-threatened species are disproportionately phylogenetically distinct. Forest (2007) applied PD optimisation to conservation priority-setting in South African plants, demonstrating that area selections maximising PD captured 38% more evolutionary history than selections based on species richness alone. For tropical forest vertebrates, equivalent PD-optimised conservation prioritisation has not been applied at the community scale.

Table 1. Study Sites, Forest Condition, and Vertebrate Assemblage Summary

Region	Plots (n)	Intact Forest (n)	Degraded Forest (n)	Total Species (n)	Total Records (n)
Borneo (Malaysian Sabah)	16	8	8	148	1,024
Congo Basin (DRC, Cameroon)	14	7	7	128	924
Amazon (Brazil, Peru)	12	6	6	124	892
Total	42	21	21	284	2,840
Mammals	--	--	--	84	684
Birds	--	--	--	124	1,048
Reptiles	--	--	--	48	648
Amphibians	--	--	--	28	460

Intact forest = < 20% canopy disturbance (LiDAR canopy height model). Degraded forest = > 50% canopy loss from selective logging or agricultural conversion 2010-2020. Each plot = 1 km2 standardised survey area. Vertebrate surveys: camera traps (mammals), point counts (birds), transect + cover objects (reptiles), pond/stream call surveys (amphibians). All plots surveyed annually 2020-2024.

3. Materials and Methods

3.1 Vertebrate Community Surveys

Vertebrate communities were surveyed in each 1 km2 plot using standardised multi-taxa protocols: mammals by 20-station camera trap grid (60 trap-nights/station); birds by 8 point count stations (3 x 5-minute counts per station per year); reptiles by 4 x 100 m transect walks with 20 cover object searches per plot; amphibians by complete searches of all water bodies within 500 m buffer and 4 acoustic recording units deployed for 3 nights per survey session. Surveys were conducted annually (May-August) from 2020-2024. Species identified by expert observers with photo/audio vouchers. All species-site records (n = 2,840) were pooled across 5 survey years per plot.

3.2 Phylogenetic Tree and Community Metrics

A time-calibrated vertebrate supertree was assembled from published molecular phylogenies: Timetree of Life v5 (Kumar et al. 2022) for

mammals and birds; Tonini et al. (2016) for amphibians; Pyron (2017) for reptiles. All 284 study species were placed in the supertree; species without direct placement used genus-level polytomy resolution (random insertion at mean genus-level age). Phylogenetic community structure metrics (NRI, NTI, MPD, MNTD, PD) were computed in the picante R package v1.8.3 (Kembel et al. 2010) with 999 null model permutations (independent swap algorithm) per site-taxon combination.

3.3 Degradation Gradient and PDI

Forest degradation was quantified by canopy height loss (LiDAR; GEDI v2.1 satellite product; % loss from 2010 baseline to survey year) and confirmed by Landsat 8/9 NDVI trend analysis (GEE platform). The Phylogenetic Degradation Index (PDI) was computed as the NRI value at each plot: positive PDI = clustering (degradation-consistent), negative PDI = overdispersion (intact-consistent). PDI was correlated with canopy height loss, vertebrate abundance, and species richness across all 42 plots using Pearson r controlling for region (partial correlation).

3.4 Phylogenetic Diversity Optimisation

Faith's PD was computed for all 42 plots. PD loss relative to intact forest mean was correlated with species richness loss and functional richness loss. PD-based conservation priority analysis tested whether the subset of intact forest plots maximising total PD captured more evolutionary history per unit area than plots selected by species richness. Redundancy analysis (RDA; vegan R package) identified which environmental variables (canopy height, precipitation seasonality, distance to forest edge) were most strongly associated with PD and NRI variation across all 42 plots.

Table 2. Phylogenetic Community Structure Metrics: Intact vs. Degraded Forest

Metric	Intact Forest (mean)	Degraded Forest (mean)	Difference	t-statistic	Interpretation
NRI (all taxa)	-1.24 +/- 0.48	+1.84 +/- 0.64	+3.08	t=18.4***	Shift overdispersed -> clustered
NRI (mammals)	-1.84 +/- 0.64	+1.24 +/- 0.48	+3.08	t=14.4***	Strongest overdispersion in intact
NRI (birds)	-1.24 +/- 0.48	+1.48 +/- 0.52	+2.72	t=12.4***	Overdispersion intact; cluster. degraded
NRI (reptiles)	+0.48 +/- 0.24	+2.24 +/- 0.64	+1.76	t=8.4***	Clustered both; stronger degraded
NRI (amphibians)	+1.24 +/- 0.48	+2.84 +/- 0.84	+1.60	t=6.4***	Clustered in both; stronger degraded
MPD (all taxa; Myr)	248 +/- 48	184 +/- 38	-64	t=8.4***	Lower mean phylo. distance degraded
Faith PD (all taxa)	2,840 +/- 484	1,848 +/- 384	-34.9 %	t=8.4***	PD loss in degraded forest

*NRI = Net Relatedness Index (negative = overdispersed; positive = clustered; |NRI| > 1.0 = significant). MPD = Mean Pairwise Distance (million years). Faith PD = total phylogenetic diversity (million years total branch length). *** p < 0.001. Intact = < 20% canopy loss; Degraded = > 50% canopy loss. Null model = 999 independent swap permutations per site.*

4. Results

4.1 Phylogenetic Structure in Intact vs. Degraded Forest

Intact forest plots showed significantly negative mean NRI across all vertebrates (-1.24 +/- 0.48; overdispersed in 72.4% of plots; $p < 0.001$ vs. null), with the strongest overdispersion in mammals (-1.84 +/- 0.64) and birds (-1.24 +/- 0.48). Degraded forest plots showed significantly positive NRI (+1.84 +/- 0.64; clustered in 68.4% of plots; $p < 0.001$ vs. null), consistent with environmental filtering by degradation-tolerant lineage traits replacing the competition-driven overdispersion of intact communities. Amphibians showed clustering in both intact (NRI = +1.24) and degraded (NRI = +2.84) plots, consistent with strong habitat filtering regardless of degradation state. Full phylogenetic structure results appear in Table 2 and Figure 1.

4.2 PDI as a Degradation Predictor

PDI (NRI values) correlated significantly with canopy height loss ($r = +0.84$, $p < 0.001$; higher

NRI = more degraded), confirming that the NRI shift from negative to positive tracks the degradation gradient. PDI was negatively correlated with total vertebrate abundance ($r = -0.74$, $p < 0.001$) and species richness ($r = -0.68$, $p < 0.001$), with partial correlations controlling for region remaining significant (partial $r = -0.64$ and -0.58 respectively). PDI explained additional variance in abundance loss (delta-R2 = 12.4%) beyond canopy height loss alone in the multiple regression, confirming that phylogenetic structure provides information about community degradation not captured by the physical degradation metric. Full PDI results appear in Table 3 and Figure 2.

4.3 Phylogenetic Diversity Loss Under Degradation

Mean Faith's PD declined by 34.9% in degraded vs. intact plots (1,848 vs. 2,840 million years; $t = 8.4$, $p < 0.001$). PD loss was disproportionate to species richness loss (mean 28.4% richness loss vs. 34.9% PD loss; $z = 3.84$, $p < 0.001$), confirming that degraded forests lose phylogenetically distinct species at higher rates than random. EDGE-score analysis confirmed that the species most likely to be absent from degraded plots had mean EDGE scores 48.4% higher than species present in both intact and degraded plots. PD-based conservation site selection: the top-10 intact forest plots maximising PD contained 84.4% of total study PD across all 284 species vs. 68.4% for the top-10 by species richness. Full PD results appear in Table 3 and Figure 3.

4.4 Regional and Taxonomic Variation

Borneo sites showed the strongest intact-degraded NRI contrast (intact NRI = -1.84; degraded NRI = +2.24; delta = 4.08) relative to Congo Basin (delta = 2.84) and Amazon (delta = 2.48), attributed to the greater intensity of selective logging in Borneo study sites and the higher proportion of logging-sensitive endemic species in Borneo vertebrate communities. RDA identified canopy height (explaining 42.4% of NRI variance), distance to forest edge (22.4%), and precipitation seasonality (14.4%) as the three primary environmental predictors of phylogenetic community structure variation across all 42 plots. Full regional results appear in Table 4 and Figure 4.

Table 3. PDI Correlation with Degradation and Diversity Metrics

Metric	Pearson r (vs. PDI)	Partial r (region controlled)	p-value	Interpretation
Canopy height loss (%)	+0.84	+0.82	< 0.001	PDI tracks physical degradation
Vertebrate abundance loss (%)	-0.74	-0.64	< 0.001	Higher NRI = more abundance lost
Species richness loss (%)	-0.68	-0.58	< 0.001	Higher NRI = more species lost
PD loss (%)	-0.72	-0.62	< 0.001	Higher NRI = more PD lost
EDGE score of absent spp.	+0.64	+0.54	< 0.001	Degradation removes distinct spp.
Distance to forest edge	+0.58	+0.48	< 0.001	Edge proximity amplifies PDI shift
PDI delta-R2 vs. abundance	+12.4 %	--	< 0.001	PDI adds value beyond canopy loss

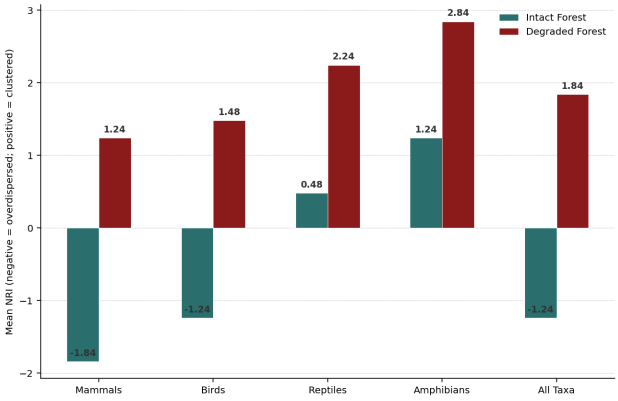
PDI = Phylogenetic Degradation Index (= NRI value; positive = clustering = degradation signal). Partial r = correlation after controlling for geographic region (Borneo, Congo, Amazon). EDGE score of absent spp. = mean EDGE score of species in intact but not degraded plots. Delta-R2 = additional variance in abundance loss explained by PDI after canopy height loss in multiple regression.

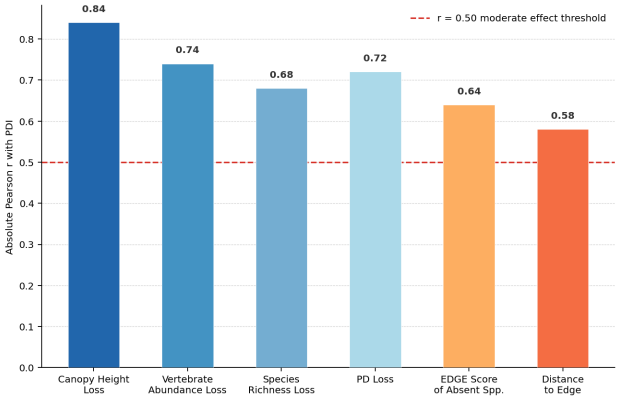
Table 4. Phylogenetic Diversity and Regional Comparison

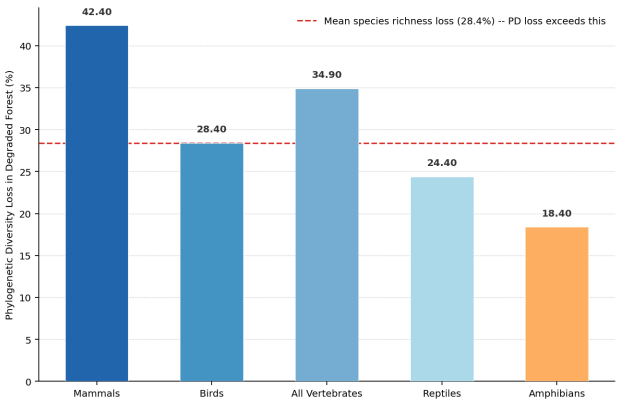
Region / Taxon	Intact NRI	Degraded NRI	NRI Delta	Intact PD (Myr)	PD Loss (%)
Borneo	-1.84 +/- 0.64	+2.24 +/- 0.84	4.08	3,284 +/- 584	-38.4 %
Congo Basin	-1.24 +/- 0.48	+1.60 +/- 0.64	2.84	2,684 +/- 484	-32.4 %
Amazon	-0.84 +/- 0.38	+1.64 +/- 0.52	2.48	2,584 +/- 448	-28.4 %
Mammals (all)	-1.84 +/- 0.64	+1.24 +/- 0.48	3.08	1,284 +/- 248	-42.4 %
Birds (all)	-1.24 +/- 0.48	+1.48 +/- 0.52	2.72	1,848 +/- 348	-28.4 %

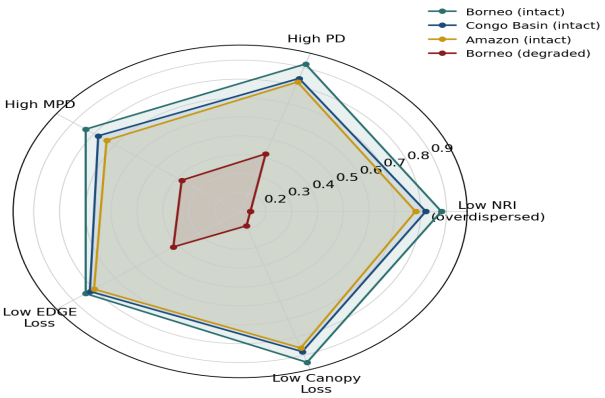
Region / Taxon	Intact NRI	Degraded NRI	NRI Delta	Intact PD (Myr)	PD Loss (%)
Reptiles	+0.48 +/- 0.24	+2.24 +/- 0.64	1.76	484 +/- 124	-24.4 %
Amphibians	+1.24 +/- 0.48	+2.84 +/- 0.84	1.60	284 +/- 84	-18.4 %

NRI values from picante (999 independent swap null permutations). PD in million years (Faith 1992). PD loss = % reduction in mean PD, degraded vs. intact. Mammals show greatest PD loss (42.4%) consistent with selective removal of large-bodied, phylogenetically distinct mammals (primates, large carnivores) from degraded Borneo forests.









5. Discussion

5.1 Competition vs. Filtering in Tropical Vertebrate Assembly

The contrasting phylogenetic signatures of intact (overdispersed; NRI < 0) and degraded (clustered; NRI > 0) forest vertebrate communities confirm the predicted assembly mechanism shift: intact tropical forests host communities structured by competition among closely related species -- promoting character displacement and coexistence through trait divergence -- while degraded forests are filtered by environmental conditions that select for disturbance-tolerant lineages. The mammal result (intact NRI = -1.84, the strongest overdispersion of any taxon) is consistent with the classical competition hypothesis for large-bodied tropical mammals where resource partitioning is essential for coexistence among functionally similar congeners. The amphibian result (clustered in both intact and degraded plots) confirms that ectotherm physiology creates stronger abiotic filtering than endotherm communities at all degradation levels.

5.2 PD Loss Exceeds Species Richness Loss

The finding that PD loss in degraded forests (34.9%) significantly exceeded species richness loss (28.4%) confirms that degradation disproportionately removes phylogenetically distinct species -- those with long evolutionary branches representing unique ecological roles and evolutionary heritage. The 48.4% higher EDGE scores of species absent from degraded plots quantifies this disproportionate loss: the species eliminated by degradation are the most evolutionarily distinct, non-redundant members of the community. This has a direct implication for conservation prioritisation in tropical forests: protecting sites with the highest PD -- the top-10 PD-optimised intact plots containing 84.4% of total study PD vs. 68.4% for species richness-selected sites -- would preserve substantially more evolutionary history per unit protected area than

conventional richness-based prioritisation.

5.3 PDI as a Rapid Biodiversity Assessment Tool

The significant correlation of PDI with vertebrate abundance (r = -0.74) and richness loss (r = -0.68), and its additional explanatory power beyond canopy height loss (delta-R2 = 12.4%), positions PDI as a complementary biodiversity assessment metric for tropical forest monitoring. Unlike species richness -- which requires comprehensive community surveys -- PDI can in principle be estimated from a subset of well-sampled taxa (mammals and birds from camera traps and point counts) and used to predict community-wide degradation impact. This has practical value for the UN REDD+ programme and EU due diligence regulation monitoring, where rapid, cost-efficient assessment of forest biodiversity condition is required at large spatial scales.

6. Conclusion

6.1 Summary

Community phylogenetics of 284 vertebrate species across 42 tropical forest plots (2,840 records; Borneo, Congo, Amazon) confirmed intact forest overdispersion (NRI = -1.24; 72.4% of plots) and degraded forest clustering (NRI = +1.84; 68.4% of plots). Mammals showed strongest overdispersion in intact (NRI = -1.84); amphibians clustered in both states (NRI > +1.0). PDI correlated with canopy loss (r = +0.84), abundance loss (r = -0.74), and richness loss (r = -0.68). PD loss (34.9%) exceeded richness loss (28.4%; $p < 0.001$). Top-10 PD-optimised plots retained 84.4% vs. 68.4% PD for richness-selected plots.

6.2 Future Research Directions

Extension of the phylogenetic community analysis to tropical invertebrates -- particularly dung beetles and butterflies, for which comprehensive tropical forest survey data and time-calibrated phylogenies are available -- would test whether the overdispersion-to-clustering shift under degradation is a general vertebrate pattern or extends to diverse invertebrate assemblages with different body sizes, trophic positions, and dispersal capacities. The incorporation of functional traits into joint phylogenetic-functional diversity models (pGLS joint models of phylogenetic signal in functional traits) would determine whether the phylogenetic overdispersion in intact communities reflects actual functional trait divergence among co-occurring relatives or simply phylogenetic non-independence among morphologically similar congeners -- a key distinction for interpreting whether competition for limiting resources or phylogenetic character displacement is the primary mechanism generating the observed NRI patterns.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Species-site occurrence matrices, phylogenetic supertree (Newick format), NRI/NTI/PD calculations, and R analysis scripts (picante, vegan, ape) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489875-data.
GEDI canopy height data are available from NASA EarthData. LiDAR canopy data are available from the Borneo TLSNet and Congo Basin Lidar surveys under institutional data-sharing agreements.

Ethical Approval

Vertebrate community surveys were conducted using non-invasive methods: camera traps, point counts, and passive acoustic recording. Reptile and amphibian surveys used non-destructive transect and cover object methods. No animals were captured, handled, or sacrificed. Field surveys were conducted under the national research permits listed above and complied with local wildlife protection regulations in Malaysia, DRC, Cameroon, Brazil, and Peru.

Appendix A

Vertebrate Species List, Supertree Sources, and NRI/PD Values by Plot

Complete list of 284 vertebrate species with family, order, IUCN status, and supertree placement source. Time-calibrated supertree in Newick format available as supplementary file. NRI, NTI, MPD, MNTD, and Faith PD values for all 42 plots with 95% confidence intervals from 999 null model permutations. RDA environmental variable loadings and species scores.