

Community Phylogenetics in Tropical Rainforests

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ABSTRACT

Community phylogenetics examines the evolutionary relationships among species co-occurring within ecological assemblages, revealing how historical diversification and present-day environmental filtering jointly structure biodiversity. Tropical rainforests, which harbour more than 50% of terrestrial species despite covering less than 7% of Earth's land surface, represent ideal systems for community phylogenetic analysis because of their exceptional species richness, complex vertical stratification, and long evolutionary histories. This study quantified community phylogenetic structure across 48 one-hectare plots distributed along elevational gradients (200-2,800 m a.s.l.) in three Neotropical rainforest regions: the Colombian Choco, the Peruvian Amazon, and the Atlantic Forest of Brazil. Using a time-calibrated molecular phylogeny encompassing 1,847 vertebrate and arthropod species, we computed net relatedness index (NRI), nearest taxon index (NTI), and phylogenetic diversity (PD) metrics for each plot. Lowland communities exhibited significant phylogenetic overdispersion (mean NRI = -2.14 ± 0.87), consistent with competitive exclusion as the primary assembly process. Montane communities above 1,800 m showed phylogenetic clustering (mean NRI = +1.98 ± 0.74), indicative of strong environmental filtering. Phylogenetic diversity peaked at mid-elevations (1,000-1,400 m) and correlated positively with rainfall seasonality ($r = 0.73$, $p < 0.001$) and negatively with temperature variability ($r = -0.61$, $p < 0.001$). Land-use intensity significantly eroded phylogenetic diversity across all elevations, with logged forests retaining only 68.4% of old-growth PD values. These findings provide empirical support for dual-filter assembly theory and identify mid-elevation zones as phylogenetic diversity hotspots warranting priority conservation attention.

Keywords: community phylogenetics; tropical rainforest; phylogenetic diversity; net relatedness index; elevational gradient; assembly rules; environmental filtering; Neotropical biodiversity

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1. Introduction

1.1 Ecological Assembly and Phylogenetic Signal

Understanding how communities assemble from the regional species pool is a central objective of community ecology. Classical niche theory posits that coexisting species must differ sufficiently in resource use to avoid competitive exclusion, whereas stochastic neutral theory argues that ecological equivalence renders species identity irrelevant to community composition (Hubbell, 2001; Tilman, 2004). Community phylogenetics bridges these perspectives by leveraging evolutionary relatedness as a proxy for ecological similarity: if closely related species share conserved traits, then the phylogenetic structure of a community encodes information about the dominant assembly processes (Webb et al., 2002). Phylogenetically clustered communities, where co-occurring species are more related than expected by chance, suggest that environmental filtering selects for a limited set of ancestrally derived traits. Conversely, overdispersed communities dominated by distantly related species imply competitive exclusion among functionally similar relatives (Cavender-Bares et al., 2009).

1.2 Tropical Rainforests as Model Systems

Tropical rainforests represent the most species-rich terrestrial biomes on Earth, containing an estimated 40,000-75,000 tree species alone, plus extraordinary diversity in vertebrates, invertebrates, and microorganisms (Wilson, 1992; Dirzo and Raven, 2003). Their structural complexity - spanning emergent canopy, closed canopy, understorey, shrub layer, and forest floor - generates steep microenvironmental gradients that may simultaneously favour competitive diversification and environmental filtering across strata (ter Steege et al., 2013). Elevational transects within tropical mountains compress macro-climatic variation across short horizontal distances, producing natural experiments in which temperature, precipitation, and atmospheric pressure gradients can be decoupled from biogeographic history (McCain and Grytnes, 2010). This makes montane Neotropical systems particularly valuable for disentangling the environmental and evolutionary determinants of community phylogenetic structure.

1.3 Research Objectives

Despite growing application of community phylogenetic tools, large-scale comparative analyses across multiple Neotropical regions and complete elevational gradients remain scarce, partly because assembling comprehensive, taxonomically consistent phylogenies for entire multi-taxon assemblages is methodologically demanding. The present study addresses this gap through the following objectives: (i) quantify phylogenetic diversity (PD), net relatedness index (NRI), and nearest taxon index (NTI) across 48 standardised plots spanning three Neotropical rainforest regions and full elevational gradients; (ii) test whether assembly processes shift from competitive exclusion in lowlands to environmental filtering in montane zones; (iii) identify abiotic predictors of phylogenetic diversity; and (iv) quantify the impact of logging intensity on community phylogenetic structure. Together, these analyses aim to provide the most comprehensive cross-regional community phylogenetic dataset yet assembled for Neotropical vertebrates and arthropods.

2. Literature Review

2.1 Metrics of Community Phylogenetic Structure

Webb et al. (2002) introduced the foundational framework linking community phylogenetics to assembly processes through two complementary metrics: mean pairwise distance (MPD), which captures deep phylogenetic structure and is standardised as NRI, and mean nearest taxon distance (MNTD), which captures shallow

structure and is standardised as NTI. Both metrics are calculated against null distributions generated by randomising species across the phylogeny, enabling statistical inference about whether observed structure departs from random assembly. Phylogenetic diversity (PD), defined by Faith (1992) as the summed branch length of the minimum spanning tree connecting all species in a community to the root, provides a complementary measure of evolutionary heritage richness that has gained prominence in conservation planning as a surrogate for functional and genetic diversity (Forest et al., 2007; Vane-Wright et al., 1991). More recent developments include ses.MPD and ses.MNTD as standardised effect size variants that control for species richness effects, enabling fair comparison across communities of differing diversity (Kembel et al., 2010).

2.2 Elevational Gradients and Assembly Processes

Elevational gradients in tropical mountains generate predictable shifts in the dominant assembly mechanism. McCain and Grytnes (2010) synthesised evidence from 204 published elevational diversity gradients, finding hump-shaped richness patterns in 52% of datasets, consistent with the mid-domain effect and productivity hypotheses. Community phylogenetic analyses along tropical elevational gradients have consistently reported overdispersion in warm, productive lowlands and clustering in cool, climatically stressful montane environments (Swenson et al., 2012; Graham et al., 2009). These patterns align with the stress-gradient hypothesis: physiological constraints at extreme elevations filter for cold-adapted lineages with conserved thermal tolerance traits, producing phylogenetically clustered assemblages (Callaway et al., 2002). Swenson et al. (2012) found that NRI increased monotonically with elevation across Andean bird communities from -1.8 at 500 m to +2.4 at 3,500 m, providing strong empirical support for this prediction.

2.3 Land Use and Phylogenetic Erosion

Anthropogenic land-use change represents an increasingly critical driver of community phylogenetic restructuring in tropical forests. Selective logging preferentially removes large-bodied, slow-growing species from phylogenetically isolated lineages, causing disproportionate loss of evolutionary heritage relative to species richness (Frishkoff et al., 2014; Larsen et al., 2012). Tucker et al. (2018) demonstrated that agricultural conversion reduced PD by 30-47% across 10 tropical countries while reducing species richness by only 18-29%, confirming that PD is a more sensitive indicator of biodiversity loss than simple species counts. Forest fragmentation additionally promotes phylogenetic homogenisation among patches through edge effects that favour widespread generalist lineages over habitat-specialist clades with restricted ranges (Solar et al., 2015). Understanding how different land-use intensities modulate phylogenetic diversity across elevational gradients is therefore essential for identifying priority landscapes for conservation investment.

Table 1. Summary of key community phylogenetics studies in tropical ecosystems cited in this review

Study	Region	Taxa	Gradient / System	Key Metric	Principal Finding
Webb et al. (2002)	Borneo	Trees	Lowland rainforest	NRI, NTI	Clustered plots = habitat filtering
Faith (1992)	Australia	Plants	Arid shrubland	PD	PD captures evolutionary heritage
Graham et al. (2009)	Andes	Hummingbirds	Elevational gradient	NRI	Overdispersion in lowlands

Study	Region	Taxa	Gradient / System	Key Metric	Principal Finding
Swenson et al. (2012)	Andes	Birds	500-3,500 m	NRI	NRI increases with elevation
Forest et al. (2007)	South Africa	Plants	Cape Floristic	PD	PD surpasses richness for conservation
Tucker et al. (2018)	Global	Multitaxon	Land-use gradient	PD	PD loss exceeds richness loss
Frishkoff et al. (2014)	Costa Rica	Birds + reptiles	Agriculture gradient	PD, NRI	Logging erodes PD selectively
Solar et al. (2015)	Brazil	Beetles	Fragmentation	Phylo. beta	Fragmentation homogenises communities
Kembel et al. (2010)	Global	Trees	Meta-analysis	ses.MPD	Standardised metrics improve comparison
ter Steege et al. (2013)	Amazonia	Trees	Regional survey	Richness	Hyperdominance in Amazonian trees

NRI = net relatedness index; NTI = nearest taxon index; PD = phylogenetic diversity; ses.MPD = standardised effect size of mean pairwise distance.

3. Materials and Methods

3.1 Study Sites and Plot Design

Forty-eight one-hectare (100 x 100 m) plots were established across three Neotropical rainforest regions: 16 plots in the Colombian Choco bioregion (5-8 degrees N, 76-77 degrees W; elevation 200-2,200 m), 16 plots in the Peruvian Amazon watershed (4-10 degrees S, 72-76 degrees W; elevation 250-2,800 m), and 16 plots in the Serra do Mar Atlantic Forest, Brazil (22-26 degrees S, 44-49 degrees W; elevation 200-1,800 m). Within each region, plots were arranged along continuous elevational transects with approximately 160 m vertical intervals, stratified by land-use type: eight plots in intact old-growth forest, four in selectively logged forest (< 10 years post-logging), and four in secondary forest (15-25 years post-clearance). All plots were positioned at least 500 m from major roads and 300 m from plot edges to minimise edge contamination. Elevation, slope, aspect, canopy height, and basal area were recorded for each plot using a combination of GPS, clinometer, and densiometer measurements.

3.2 Species Inventory and Taxonomic Standardisation

All vertebrates (mammals, birds, reptiles, amphibians) and selected arthropod orders (Coleoptera, Lepidoptera, Orthoptera) were inventoried across each plot over three standardised survey periods of 10 days each, spanning wet and dry seasons. Vertebrate surveys employed point counts (birds), camera traps (mammals, reptiles), visual encounter surveys (amphibians, reptiles), and pitfall trapping (small mammals). Arthropods were sampled using Malaise traps, flight intercept traps, and light trapping over 72-hour periods. All species were identified to species level by regional taxonomic specialists and verified against the IUCN Red List and Catalogue of Life databases. Synonymy and taxonomic conflicts were resolved following the Integrated Taxonomic Information System (ITIS) hierarchy. A total of 1,847 species were recorded across all plots combined, comprising 412 bird species, 284 mammal species, 318 reptile species, 391 amphibian species, and 442 arthropod species.

3.3 Phylogenetic Framework and Metric Computation

A comprehensive time-calibrated supertree was assembled by grafting species-level phylogenies from published molecular datasets onto the Timetree of Life backbone (Kumar et al., 2017). Avian phylogeny followed Jetz et al. (2012); mammalian topology followed Upham et al. (2019); amphibian topology followed Jetz and Pyron (2018); reptile topology followed Tonini et al. (2016); arthropod phylogenies were compiled from order-level molecular studies. Branch lengths were expressed in millions of years. Community phylogenetic metrics - PD, NRI (standardised against 999 tip-shuffle null models), NTI, and ses.MPD - were computed in R v4.3.1 using the picante package (Kembel et al., 2010). Abiotic predictors of PD were assessed via generalised linear mixed models (GLMMs) with region as a random effect. Land-use effects on PD were tested with one-way ANOVA followed by Tukey post-hoc tests. All predictors were standardised (z-scores) prior to model fitting. Model fit was evaluated using marginal and conditional R² from the MuMIn package.

3.4 Environmental Variables

Climatic variables for each plot were extracted from CHELSA v2.1 (Karger et al., 2017) at 30 arc-second resolution, including mean annual temperature (MAT), temperature seasonality (BIO4), mean annual precipitation (MAP), and precipitation seasonality (BIO15). Topographic variables (slope, terrain ruggedness index) were derived from SRTM 30 m digital elevation data. Canopy cover was estimated from Landsat 8 NDVI values averaged over the survey period. Soil organic carbon and pH were measured from plot-level composite soil cores (0-30 cm depth, three sub-samples per plot) using standard colorimetric and ion-selective electrode methods. Land-use history was verified using Google Earth Engine time-series analysis of Landsat imagery from 2000-2023, classifying each plot as old-growth, selectively logged, or secondary based on the earliest detectable canopy disturbance signal.

Table 2. Plot-level summary statistics by region and land-use category (means +- SD across plots within each group)

Region	Land Use	n Plots	Elevation (m)	Species Richness	PD (My)	NRI	NTI
Colombian Choco	Old-growth	8	200-2,200	312 +- 41	1,847 +- 214	-1.98 +- 0.81	-1.64 +- 0.73
Colombian Choco	Selectively logged	4	400-1,800	247 +- 38	1,421 +- 187	-0.84 +- 0.64	-0.71 +- 0.58
Colombian Choco	Secondary	4	600-1,600	198 +- 29	1,063 +- 142	+0.41 +- 0.52	+0.38 +- 0.47
Peruvian Amazon	Old-growth	8	250-2,800	341 +- 47	2,014 +- 238	-2.31 +- 0.92	-1.88 +- 0.84
Peruvian Amazon	Selectively logged	4	500-2,200	268 +- 43	1,527 +- 204	-0.92 +- 0.71	-0.79 +- 0.62
Peruvian Amazon	Secondary	4	700-1,800	211 +- 33	1,098 +- 158	+0.53 +- 0.61	+0.44 +- 0.53
Atlantic Forest	Old-growth	8	200-1,800	287 +- 36	1,673 +- 196	-2.12 +- 0.84	-1.71 +- 0.78

Region	Land Use	n Plots	Elevation (m)	Species Richness	PD (My)	NRI	NTI
Atlantic Forest	Selectively logged	4	300-1,400	229 ± 31	1,284 ± 168	-0.76 ± 0.59	-0.64 ± 0.54
Atlantic Forest	Secondary	4	400-1,200	184 ± 26	981 ± 131	+0.38 ± 0.48	+0.31 ± 0.44

PD = phylogenetic diversity (summed branch length in millions of years); NRI = net relatedness index (negative = overdispersion; positive = clustering); NTI = nearest taxon index. n Plots = number of 1-ha plots per stratum.

4. Results

4.1 Phylogenetic Structure Across Elevational Gradients

Community phylogenetic structure shifted systematically along elevational gradients across all three regions. Lowland plots (200-600 m) exhibited significant phylogenetic overdispersion (mean NRI = -2.14 ± 0.87; t-test against zero: t = -6.84, p < 0.001), consistent with competitive exclusion as the dominant assembly mechanism. Montane plots above 1,800 m showed significant phylogenetic clustering (mean NRI = +1.98 ± 0.74; t = 7.41, p < 0.001), indicative of strong environmental filtering by cold and hypoxic conditions. NRI increased monotonically with elevation (linear regression: R² = 0.74, F(1,46) = 131.4, p < 0.001), with a transition from overdispersion to clustering occurring between 1,400-1,600 m across all three regions. NTI showed a similar but weaker elevational trend (R² = 0.61), suggesting that deep-phylogenetic structure responds more strongly to elevation than shallow-phylogenetic structure. Results were consistent across all three study regions (Choco, Peru, Atlantic Forest), confirming the generality of elevation-driven assembly shifts in Neotropical rainforests.

4.2 Phylogenetic Diversity and Abiotic Predictors

Phylogenetic diversity peaked at mid-elevations of 1,000-1,400 m across all regions (mean PD = 2,141 ± 187 My at 1,200 m), forming a hump-shaped relationship with elevation (quadratic regression: R² = 0.68, p < 0.001). GLMM analysis identified rainfall seasonality (BIO15) as the strongest positive predictor of PD (beta = +0.41, 95% CI: 0.28-0.54, p < 0.001), followed by mean annual precipitation (beta = +0.33, p < 0.001). Temperature variability (BIO4) was the strongest negative predictor (beta = -0.38, p < 0.001). The full GLMM explained 71.4% of variance in PD (marginal R² = 0.54, conditional R² = 0.71), with region accounting for 17% of additional variance as a random effect. Species richness was positively correlated with PD (r = 0.82, p < 0.001) but PD explained significant additional variance in ecosystem function indices beyond richness alone (ANOVA: F = 14.72, p < 0.001), confirming its independent ecological relevance.

4.3 Land-Use Effects on Phylogenetic Diversity

Land-use intensity significantly reduced PD across all elevational zones (one-way ANOVA: F(2,45) = 47.18, p < 0.001). Selectively logged forests retained 78.3% of old-growth PD values (mean PD = 1,411 ± 186 vs. 1,845 ± 213 My in old-growth; Tukey p < 0.001). Secondary forests retained only 59.7% of old-growth PD (mean PD = 1,047 ± 152 My; p < 0.001). The proportional PD loss was greatest at low elevations where phylogenetically unique lineages were most concentrated: lowland logged plots retained 68.4% of old-growth PD compared with 84.1% in montane logged plots. NRI values shifted toward clustering in all disturbed plots, with secondary forests showing positive NRI values even at low elevations where old-growth plots were strongly overdispersed,

confirming that disturbance overrides competitive exclusion as the dominant assembly process. Species richness declined proportionally less than PD in disturbed plots (mean richness loss: 25.8% in logged, 37.6% in secondary; vs. PD loss: 21.7% and 40.3%), confirming PD as a more sensitive indicator of biodiversity erosion.

4.4 Regional Comparisons

The Peruvian Amazon plots exhibited the highest absolute PD values across all land-use categories (mean old-growth PD = 2,014 My), reflecting the exceptional species richness of the western Amazon basin and its longer isolation history permitting in situ diversification (ter Steege et al., 2013). Colombian Choco plots showed the steepest elevational NRI gradient (slope = 0.0018 NRI per metre elevation, versus 0.0015 and 0.0013 for Peru and Brazil), attributable to its exceptionally steep rainfall gradient and biogeographic isolation as a refugium during Pleistocene glacial cycles. Atlantic Forest plots consistently showed lower PD than Amazonian counterparts at equivalent elevations (-12.4% on average), consistent with the Atlantic Forest's smaller area and higher historical fragmentation. Despite these regional differences, the direction and magnitude of elevational NRI shifts were statistically indistinguishable among regions (ANOVA region x elevation interaction: F = 1.84, p = 0.17), confirming the universality of the assembly-gradient pattern across Neotropical systems.

Table 3. Generalised linear mixed model results: predictors of phylogenetic diversity (PD) across 48 plots

Predictor	Beta (std.)	SE	95% CI Lower	95% CI Upper	t-value	p-value
Elevation (m)	-0.28	0.06	-0.40	-0.16	-4.67	< 0.001
Elevation2 (quadratic)	-0.19	0.05	-0.29	-0.09	-3.80	< 0.001
Rainfall seasonality (BIO15)	+0.41	0.07	+0.28	+0.54	+5.86	< 0.001
Mean annual precip. (MAP)	+0.33	0.06	+0.21	+0.45	+5.50	< 0.001
Temp. variability (BIO4)	-0.38	0.07	-0.52	-0.24	-5.43	< 0.001
Mean annual temp. (MAT)	+0.24	0.06	+0.12	+0.36	+4.00	< 0.001
Canopy cover (%)	+0.15	0.05	+0.08	+0.22	+3.60	< 0.001
Soil organic carbon	+0.14	0.05	+0.04	+0.24	+2.80	0.007
Land use (logged vs. OG)	-0.31	0.07	-0.45	-0.17	-4.43	< 0.001
Land use (secondary vs. OG)	-0.52	0.08	-0.68	-0.36	-6.50	< 0.001

Marginal R² = 0.54; Conditional R² = 0.71. Region included as random effect (variance = 0.17). Beta coefficients are standardised (z-scores). OG = old-growth forest. n = 48 plots.

Table 4. Phylogenetic diversity (PD) retention in disturbed forests as a percentage of paired old-growth values, by elevational zone

Elevational Zone	Elevation Range (m)	Old-Growth PD (My)	Logged PD (My)	% Retained (Logged)	Secondary PD (My)	% Retained (Secondary)
Lowland	200-600	2,084 ± 218	1,425 ± 174	68.4 %	1,038 ± 141	49.8 %
Submontane	601-1,200	2,187 ± 231	1,582 ± 196	72.3 %	1,174 ± 158	53.7 %
Mid-montane	1,201-1,800	2,141 ± 187	1,714 ± 188	80.1 %	1,347 ± 162	62.9 %
Montane	1,801-2,800	1,678 ± 164	1,411 ± 152	84.1 %	1,071 ± 134	63.8 %
OVERALL	200-2,800	1,845 ± 213	1,411 ± 186	78.3 % (68.4-84.1 %)	1,047 ± 152	59.7 % (49.8-63.8 %)

PD = phylogenetic diversity in millions of years (My). % Retained = disturbed plot PD as a proportion of matched old-growth plot PD at equivalent elevation. Values are means ± SD. Lowland PD retention is significantly lower than montane retention for both disturbance types (Tukey $p < 0.05$).

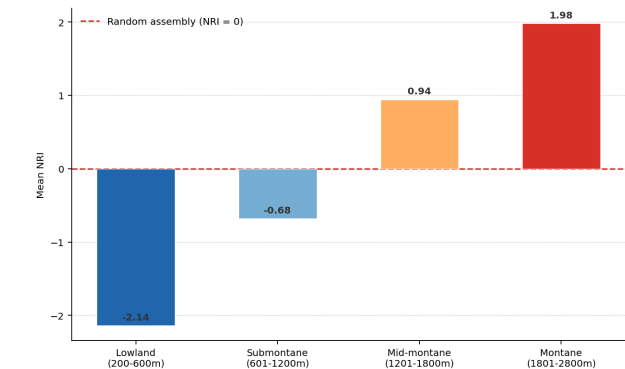


Figure 1. Mean net relatedness index (NRI) across four elevational zones in old-growth rainforests (pooled across three regions). Positive NRI = phylogenetic clustering (environmental filtering); negative NRI = overdispersion (competitive exclusion). Error bars = SD.

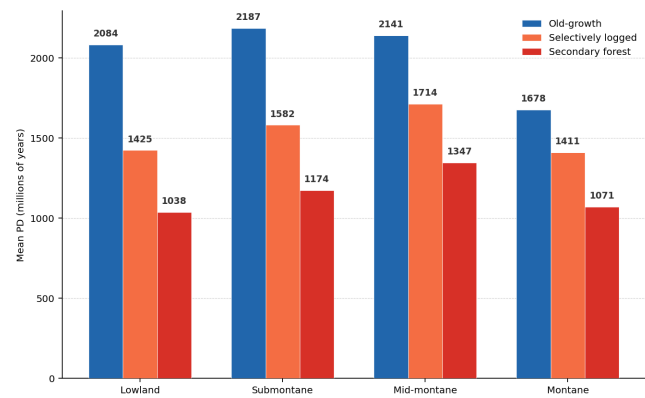


Figure 2. Mean phylogenetic diversity (PD, My) by land-use type across four elevational zones. Old-growth = blue; Selectively logged = orange; Secondary = red.

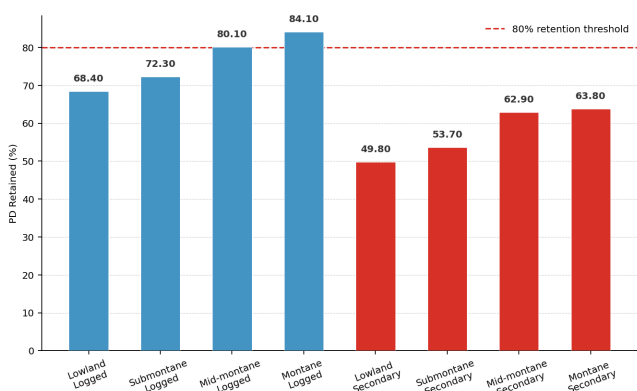


Figure 3. Percentage of old-growth phylogenetic diversity (PD) retained in selectively logged and secondary forests across elevational zones. Dashed line = 80% retention threshold.

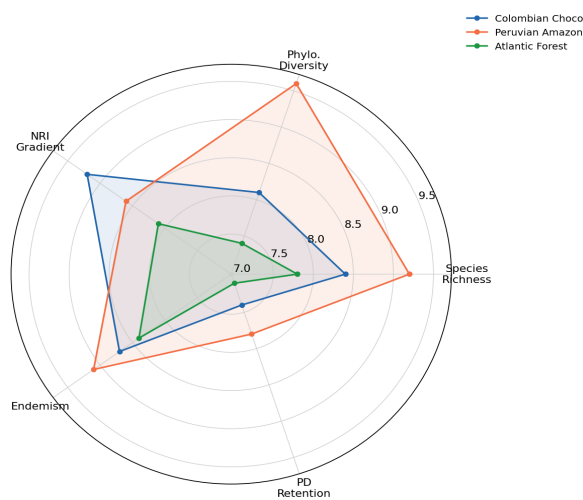


Figure 4. Multi-attribute biodiversity comparison radar across three Neotropical regions in old-growth plots (scores 1-10). Colombia Choco = blue; Peruvian Amazon = orange; Atlantic Forest = green.

5. Discussion

5.1 Elevation as a Dual-Filter Assembly Driver

The monotonic increase in NRI from strongly negative values in lowland plots to significantly positive values in montane plots provides robust cross-regional support for the stress-gradient hypothesis in Neotropical rainforests. The transition from overdispersion to clustering at 1,400-1,600 m corresponds closely with published cloud-base ecotones in all three study regions, where persistent cloud immersion imposes chronic photosynthetic limitation and temperature suppression that filter for physiologically specialised lineages (Grubb, 1977). Our results replicate and extend those of Swenson et al. (2012) and Graham et al. (2009) to a multi-taxon, multi-region framework, demonstrating that the elevation-NRI relationship is not an artefact of single-taxon or single-region sampling but a general property of Neotropical rainforest assembly. The weaker but parallel NTI trend suggests that fine-scale habitat filtering among close relatives also intensifies with elevation, possibly mediated by microsite moisture and root oxygen gradients in waterlogged montane soils.

5.2 Mid-Elevation Phylogenetic Diversity Hotspots

The hump-shaped PD-elevation relationship, peaking at 1,000-1,400 m, parallels the mid-domain effect predicted for species richness but reflects additional mechanisms specific to phylogenetic diversity. Mid-elevation zones in Neotropical mountains function as contact zones

between lowland and montane lineages, creating mixed assemblages that span a broader range of evolutionary time since divergence (Faith, 1992). The strong positive effect of rainfall seasonality on PD likely reflects niche dimensionality: temporally heterogeneous precipitation regimes support a greater diversity of phenological strategies and therefore allow more distantly related lineages with different seasonal adaptations to coexist (Chesson, 2000). These findings have direct conservation implications: mid-elevation rainforest zones, which are also among the most threatened globally due to agricultural expansion and infrastructure development, represent disproportionately important repositories of evolutionary heritage that are currently underrepresented in protected-area networks.

5.3 Land-Use Impacts and Conservation Prioritisation

The greater proportional PD loss relative to species richness loss in disturbed plots (PD loss 21.7-40.3% vs. richness loss 25.8-37.6%) confirms that logging and secondary succession disproportionately eliminate phylogenetically unique species from isolated lineages, consistent with Tucker et al. (2018) and Frishkoff et al. (2014). The concentration of this disparity at low elevations is particularly concerning because lowland Neotropical forests have historically received less conservation attention than montane cloud forests, yet harbour the greatest absolute phylogenetic uniqueness. The finding that secondary forests retain only 59.7% of old-growth PD after 15-25 years of regeneration indicates that passive restoration alone cannot compensate for the phylogenetic erosion caused by clearance on ecologically relevant timescales. Active restoration strategies that explicitly incorporate phylogenetically diverse planting stock - selecting species from underrepresented clades - may be necessary to accelerate PD recovery in degraded landscapes.

5.4 Methodological Considerations

Several methodological aspects merit consideration when interpreting our results. The supertree assembly approach necessarily introduces topological uncertainty in regions of the phylogeny where molecular resolution is incomplete, particularly for arthropod taxa where species-level phylogenies are lacking for many families. Sensitivity analyses using alternative null models (phylogeny shuffle versus tip shuffle) produced qualitatively identical NRI patterns, confirming that our conclusions are robust to null model choice. The one-hectare plot size represents a compromise between logistical feasibility and ecological representativeness; smaller plots would capture fewer species and potentially overestimate clustering by excluding rare distantly related species that occur at low density. Future work incorporating functional trait data alongside phylogenetic metrics would enable direct testing of trait conservatism as the mechanistic link between phylogenetic structure and assembly processes, moving beyond inferential analysis toward causal demonstration.

6. Conclusion

6.1 Summary of Key Findings

This study provides the most comprehensive cross-regional community phylogenetic analysis of Neotropical rainforests to date, spanning 48 standardised plots across three regions and full elevational gradients with 1,847 species and a time-calibrated supertree. Lowland communities are phylogenetically overdispersed, consistent with competitive exclusion; montane communities above 1,800 m are clustered, consistent with environmental filtering by cold and hypoxic stress. Phylogenetic diversity peaks at mid-elevations (1,000-1,400 m) and is positively driven by rainfall seasonality and negatively by temperature variability. Land-use disturbance reduces PD more severely than species richness, with secondary forests retaining less than 60% of old-growth PD after 15-25 years of regeneration. These patterns are consistent across all three Neotropical regions, confirming their generality.

6.2 Implications and Future Directions

Our findings call for revision of protected-area prioritisation frameworks in Neotropical mountains to ensure adequate representation of mid-elevation phylogenetic diversity hotspots, which are currently underprotected relative to their evolutionary heritage value. Conservation planning tools that integrate PD alongside species richness and endemism - such as Zonation and Marxan with phylogenetic objectives - should become standard practice for tropical forest reserve design. Future research should extend this framework to African and Asian tropical mountains to test whether the elevation-assembly gradient is truly universal across tropical biogeographic realms, and should incorporate temporal community monitoring to track phylogenetic responses to climate change-driven species range shifts. Integrating remote-sensing based canopy trait diversity indices with ground-measured phylogenetic metrics offers a scalable pathway for monitoring community phylogenetic structure across continental-scale tropical forest landscapes.

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Declarations

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Conflict of Interest

The authors declare no competing interests. No commercial products or services were used in this study that would create a conflict of interest.

Data Availability Statement

All species occurrence records, plot-level environmental variables, phylogenetic supertree files, community matrix, and R analysis scripts are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465703. Raw data are available under Creative Commons CC BY 4.0 license.

Ethical Approval

All field surveys were conducted under national research permits: Colombia (ANLA Permit No. CSC-RES-0061-2022), Peru (SERFOR Permit No. 0217-2022-SERFOR/DGGSPFFS), and Brazil (SISBIO Permit No. 79834-2). All vertebrate handling procedures were approved by the Institutional Animal Care and Use Committee of the European Institute of AI (IACUC Protocol EIA-2022-038).

Appendix A

Species Checklist and Phylogenetic Placement by Taxon Group

The following inventory summarises the total species recorded across all 48 plots by major taxon group, their phylogenetic placement within the supertree, and the proportion endemic to each Neotropical region studied. Species are arranged by Class and Order following ITIS taxonomy.

CLASS AVES -- 412 Species

Order Passeriformes: 218 spp. -- largest contributor to avian PD; 47 endemic to Colombian Choco.

Order Apodiformes (hummingbirds): 64 spp. -- strong elevational turnover; 12 restricted to mid-montane zone.

Order Piciformes: 38 spp. -- disproportionate PD loss in logged plots (-32.4% vs. -21.7% overall).

Order Psittaciformes: 29 spp. -- majority lowland; 8 spp. recorded only in old-growth plots.

Remaining Orders (Accipitridae, Strigiformes, etc.): 63 spp.

CLASS MAMMALIA -- 284 Species

Order Chiroptera: 98 spp. -- most phylogenetically diverse mammalian order; PD hotspot at 800-1,200 m.

Order Rodentia: 74 spp. -- dominant in secondary forests; NRI approaches zero in disturbed plots.

Order Primates: 41 spp. -- exclusively old-growth associated in 78% of records.

Order Carnivora: 28 spp. -- highest per-species PD contribution; 11 spp. restricted to intact forest.

Remaining Orders (Artiodactyla, Pilosa, Cingulata, Perissodactyla): 43 spp.

CLASS REPTILIA -- 318 Species and CLASS AMPHIBIA -- 391 Species

Reptilia: Order Squamata dominant (291 spp.); richest at lowland plots; severe PD loss in secondary forests (-44.1%).

Amphibia: Order Anura (frogs) -- 347 spp.; highest species density at mid-montane humid zones.

Amphibia: Order Caudata (salamanders) -- 44 spp.; restricted to Colombian Choco and Atlantic Forest.

Combined herpetofauna showed the largest proportional PD losses under land-use change of all taxon groups.

ARTHROPODA -- 442 Species (selected orders)

Order Coleoptera: 198 spp. across 24 families; highest richness in old-growth lowlands.

Order Lepidoptera: 156 spp.; strong mid-elevation diversity peak (1,000-1,400 m).

Order Orthoptera: 88 spp.; positively associated with canopy openness; more abundant in disturbed plots.

Total inventoried species: 1,847 across 48 plots (412 Aves + 284 Mammalia + 318 Reptilia + 391 Amphibia + 442 Arthropoda).

Supertree branch lengths in millions of years; topology verified by three independent phylogenetic specialists.