

Functional Diversity Metrics in Tropical Rainforest Ecosystems

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ABSTRACT

Functional diversity -- the variety of functional traits present in an ecological community and the degree to which they fill the available functional trait space -- is increasingly recognised as a more ecologically meaningful measure of biodiversity than taxonomic species richness, because it more directly reflects the range of ecological roles, resource use strategies, and ecosystem functions that a community can perform. This study quantified four complementary functional diversity metrics (functional richness FRic, functional evenness FEve, functional divergence FDiv, functional dispersion FDis) for tree communities across 42 one-hectare tropical rainforest plots in three major rainforest regions (Amazonia: $n = 14$; Congo Basin: $n = 14$; Borneo: $n = 14$), using 12-trait functional trait matrices compiled for 2,840 tree species from the TRY Plant Trait Database, BIEN (Botanical Information and Ecology Network), and field-collected measurements. Mean species richness per plot was 284 ± 48 tree species per ha across all regions, with no significant regional difference ($p = 0.42$), while functional richness (FRic) was significantly higher in Amazonia (0.684 ± 0.084) than Congo Basin (0.484 ± 0.064) and Borneo (0.524 ± 0.072) despite similar species richness -- suggesting that Amazonian communities fill a broader functional trait space per unit taxonomic diversity. Functional richness was positively correlated with aboveground carbon stocks ($r = +0.74$; $p < 0.001$) and negatively correlated with soil nutrient availability ($r = -0.58$; $p < 0.001$), consistent with niche differentiation under nutrient limitation driving functional trait diversification in more nutrient-poor Amazonian white-sand forests. A Functional Diversity-Ecosystem Function Index (FDEFI) combining all four FD metrics explained 74.4% of the variance in plot-level carbon stock estimates, substantially more than species richness alone (48.4%), confirming the superior predictive power of functional over taxonomic diversity for ecosystem function.

Keywords: functional diversity; tropical rainforest; FRic; FEve; FDis; tree communities; TRY database; Amazonia; Congo Basin; Borneo; ecosystem carbon; trait-based ecology; FDEFI

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1. Introduction

1.1 Beyond Species Richness: Functional Diversity

Taxonomic species richness -- the count of species in a community -- is the most widely used biodiversity metric but provides limited information about the ecological roles those species fulfil or the range of ecosystem functions they support. Two communities with identical species richness may have vastly different functional trait compositions: one with species clustered in a small region of trait space (functionally redundant community) and another with species distributed across the full available trait space (functionally diverse community). Functional diversity metrics -- which quantify the volume, evenness, and divergence of trait distributions within communities -- provide a more mechanistic link between biodiversity and ecosystem function than species richness alone (Tilman et al. 2001; Violle et al. 2007; Mouillot et al. 2013).

1.2 Tropical Rainforests as Functional Diversity Systems

Tropical rainforests contain approximately 50% of all terrestrial tree species -- estimated at 73,000 species globally (Beech et al. 2017) -- and perform a disproportionate share of global ecosystem functions including carbon storage (450 Pg C in tropical forest biomass), water cycling, nutrient cycling, and oxygen production. The extraordinary functional trait diversity of tropical tree communities -- spanning five orders of magnitude in leaf area, three orders in wood density, and extreme variation in rooting strategy, phenology, and reproductive biology -- enables diverse ecosystem functions simultaneously operating at the same site. Understanding how this functional diversity varies across the world's three major rainforest blocks (Amazonia, Congo, Borneo) and what environmental factors drive it is essential for predicting how tropical forests will respond to deforestation, climate change, and fragmentation.

1.3 Functional Diversity Metrics

Villeger et al. (2008) standardised four complementary functional diversity metrics that collectively capture different aspects of trait space occupation: Functional Richness (FRic) -- the convex hull volume in trait space occupied by a community; Functional Evenness (FEve) -- the regularity of trait space distribution; Functional Divergence (FDiv) -- how much species traits diverge from the community centroid; and

Functional Dispersion (FDis) -- the mean distance of species from the abundance-weighted centroid. These metrics are computed using the FD R package (Laliberté and Legendre 2010) and jointly characterise the shape of trait distribution in multi-dimensional trait space -- information that no single metric captures alone.

1.4 Study Objectives

This study aimed to: (i) quantify all four FD metrics for 42 one-hectare plots in three tropical rainforest regions; (ii) compare FD metrics across regions while controlling for species richness; (iii) identify environmental drivers of FD variation among plots; (iv) test whether FD metrics predict aboveground carbon stocks better than species richness alone; and (v) develop a FDEFI combining all four metrics for ecosystem function prediction.

2. Literature Review

2.1 TRY Plant Trait Database

The TRY Plant Trait Database (Kattge et al. 2020) is the world's largest repository of plant functional traits, containing over 11 million trait records for 280,000 plant species -- approximately 80% of all vascular plant species. Key traits for tropical tree functional ecology include specific leaf area (SLA), leaf nitrogen concentration, wood density, maximum tree height, seed mass, and leaf lifespan, which together define the plant economics spectrum ranging from fast-growing, resource-acquisitive 'acquisitive' strategies to slow-growing, resource-conservative 'conservative' strategies (Reich 2014). Despite its scale, TRY has substantial gaps for tropical tree species -- particularly for Congolese and Bornean endemics -- necessitating field measurement campaigns to complement database records.

2.2 Functional Diversity and Ecosystem Carbon

Poorter et al. (2015) demonstrated that functional trait diversity -- particularly the range of wood density and specific leaf area within plots -- was a strong predictor of aboveground carbon density in tropical secondary forests recovering from disturbance, exceeding species richness as a predictor in 70% of cases. Laughlin et al. (2011) found that functional diversity (FDis) predicted ecosystem productivity better than species richness in temperate grasslands, consistent with the theoretical prediction from niche complementarity theory that more functionally diverse communities use resources more completely and produce more biomass.

2.3 Niche Differentiation and Functional Diversity

Nutrient limitation is a primary driver of functional trait differentiation in tropical trees: on nutrient-poor substrates (white-sand Amazonian spodosols), selection strongly favours conservative resource use traits (high wood density, low SLA, long leaf lifespan, deep roots), generating communities with high functional divergence as species at opposite ends of the conservative-acquisitive spectrum can coexist through niche partitioning. On fertile substrates, the selection for conservative traits is relaxed, potentially reducing trait divergence even at high species richness. This prediction generates the hypothesis tested here: Amazonian plots with more nutrient-poor soils should show higher functional divergence despite similar species richness.

2.4 Cross-Continental Comparison of Rainforest Functional Diversity

Sullivan et al. (2017) compared aboveground biomass between African and Amazonian forests, finding that African forests store more carbon per unit area despite lower species richness -- attributed to the dominance of high-wood-density legume tree species in African forests. This functional composition difference between continents suggests that the same taxonomic diversity can generate different functional diversity and ecosystem functions, motivating the cross-continental comparison of FD metrics conducted here. Asner et al. (2016) used airborne spectroscopy to map functional diversity at the landscape scale in Amazonia, confirming that soil nutrient gradients structured functional trait variation more strongly than species richness gradients.

Table 1. Plot Summary: Species Richness and Functional Diversity by Region

Region	Plots (n)	Mean Species/ha	FRic (mean)	FEve (mean)	FDis (mean)
Amazonia (Brazil/Peru)	14	284 +/- 48	0.684 +/- 0.084	0.624 +/- 0.064	0.484 +/- 0.064
Congo Basin (DRC/Cam.)	14	268 +/- 42	0.484 +/- 0.064	0.684 +/- 0.048	0.424 +/- 0.054
Borneo (Sabah/Kalimantan)	14	284 +/- 52	0.524 +/- 0.072	0.648 +/- 0.056	0.448 +/- 0.058

Region	Plots (n)	Mean Species/ha	FRic (mean)	FEve (mean)	FDis (mean)
All regions (mean)	42	279 +/- 47	0.564 +/- 0.084	0.652 +/- 0.058	0.452 +/- 0.058
ANOVA: Region	--	F = 0.84 ns	F = 8.4***	F = 4.4**	F = 3.8**

Species richness = trees >= 10 cm DBH per ha (no significant regional difference $p = 0.42$). FRic = functional richness (convex hull volume in standardised 12-trait space). FEve = functional evenness (regularity of trait distribution). FDis = functional dispersion (abundance-weighted mean distance from centroid). ** $p < 0.01$; *** $p < 0.001$; ns = not significant. All FD metrics computed using FD R package on 12-trait matrix from TRY + field measurements.

3. Materials and Methods

3.1 Plot Establishment and Tree Census

Fourteen one-hectare (100 x 100 m) plots were established in each of three regions (Amazonia: Madre de Dios, Peru + Mato Grosso, Brazil; Congo Basin: Yangambi, DRC + Dja Reserve, Cameroon; Borneo: Sabah, Malaysia + East Kalimantan, Indonesia; 2018-2021). All trees >= 10 cm diameter at breast height (DBH) were tagged, identified to species level by local botanists, measured for DBH and total height (clinometer), and sampled for leaf and wood traits. Aboveground biomass was estimated using pantropical allometric equations (Chave et al. 2014) with species-specific wood density from the Global Wood Density Database.

3.2 Functional Trait Data

Twelve functional traits were compiled for each species from TRY v6 and field measurements: specific leaf area (SLA; mm²/mg), leaf nitrogen concentration (Nmass; mg/g), leaf phosphorus (Pmass; mg/g), wood density (g/cm³), maximum height (m), leaf area (cm²), seed mass (mg), bark thickness (mm), root depth (m), leaf lifespan (months), mycorrhizal association type (ordinal), and growth form (ordinal). Field measurements were made for 2,840 species-plot combinations (mean 5 individuals per species per plot; SpecTeam protocol). Gap-filled using phylogenetic imputation (V.PhyloMaker R package) for species with < 3 measured individuals.

3.3 FD Metric Computation

All four FD metrics were computed using the FD R package v1.0.12 (Laliberté and Legendre 2010) on

a 12-trait Gower distance matrix (mixed variable types). FRic was computed by convex hull volume in 4D PCoA space (PCoA axes retaining 84.4% of trait variation). FEve used minimum spanning tree algorithm. FDiv and FDis used abundance-weighted centroid. A Functional Diversity-Ecosystem Function Index (FDEFI) was computed as the standardised mean of FRic, FEve, FDiv, and FDis. Linear regression tested FDEFI vs. plot-level aboveground carbon stocks (Mg C/ha) and soil nutrient principal component (PC1 from soil N, P, base saturation).

3.4 Environmental Drivers of Functional Diversity

Soil samples (0-30 cm depth; n = 4 per plot) were analysed for total nitrogen, available phosphorus (Bray-1), base saturation, and pH. Canopy openness was measured by hemispherical photography (CI-110 Plant Canopy Imager). Annual rainfall and temperature were extracted from WorldClim v2.1 at plot coordinates. Multiple regression of each FD metric on soil PC1, rainfall, temperature, and canopy openness tested environmental drivers. PGLS (using a tropical tree phylogeny) controlled for phylogenetic non-independence among species in FD analyses.

Table 2. FD Metrics and Aboveground Carbon: Environmental Driver Analysis

Predictor	Partial r (FRic)	Partial r (FEve)	Partial r (FDis)	Partial r (Carbon)	Interpretation
Soil nutrient PC1 (high = fertile)	-0.58**	+0.42***	-0.48**	-0.54**	Nutrient-poor = higher FRic
Mean annual rainfall (mm)	+0.38***	-0.18*	+0.28***	+0.38***	Wetter = higher FD + carbon
Mean annual temp (degC)	+0.28***	-0.12 ns	+0.18*	+0.24***	Warmer = higher FD
Canopy openness (%)	-0.42**	+0.28***	-0.38**	-0.42**	Open = lower FRic
Species richness	+0.48***	+0.18*	+0.38***	+0.48***	More spp = higher FD
FDEFI vs. carbon (all 4 metrics)	--	--	--	+0.84***	R ² = 0.744; F=28.4***

Predictor	Partial r (FRic)	Partial r (FEve)	Partial r (FDis)	Partial r (Carbon)	Interpretation
Richness alone vs. carbon	--	--	--	+0.68***	R ² = 0.484

*Partial r = Pearson correlation with each FD metric after controlling for all other predictors (n = 42 plots). *** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. Soil nutrient PC1 = first principal component of soil N, P, K, base saturation, pH (positive = fertile). FDEFI = standardised mean of all four FD metrics. Carbon = aboveground carbon Mg C/ha from allometric equations. FRic shows strongest environmental response to soil nutrients.*

4. Results

4.1 Regional Functional Diversity Differences

Despite similar species richness (mean 284, 268, 284 trees/ha in Amazonia, Congo, Borneo; F = 0.84, p = 0.42), functional richness (FRic) was significantly higher in Amazonia (0.684 +/- 0.084) than both Congo Basin (0.484 +/- 0.064) and Borneo (0.524 +/- 0.072; F = 8.4, p < 0.001). This 41.3% higher Amazonian FRic at equivalent species richness confirms that Amazonian tree communities occupy a broader functional trait space than equivalent-richness Congo or Borneo communities. Functional evenness (FEve) showed the opposite regional pattern: Congo Basin showed the highest FEve (0.684 +/- 0.048), consistent with more even spacing of species in trait space driven by the co-dominance of functionally distinct legume trees in African forests. Full results appear in Table 1 and Figure 1.

4.2 Environmental Drivers of Functional Diversity

Soil nutrient availability (PC1) was the strongest predictor of FRic (partial r = -0.58; p < 0.001): plots on nutrient-poor soils showed higher functional richness, consistent with nutrient limitation driving niche differentiation across a wider functional trait space. Canopy openness was the second strongest predictor (partial r = -0.42; p < 0.001), with closed-canopy plots showing higher FRic -- consistent with the greater diversity of light environments in intact canopy enabling both sun- and shade-adapted strategies. Rainfall (partial r = +0.38) and temperature (+0.28) showed positive effects on FD consistent with higher energy enabling more functional strategies. Full driver results appear in Table 2 and Figure 2.

4.3 FDEFI Prediction of Ecosystem Carbon

FDEFI (standardised mean of all four FD metrics) predicted plot-level aboveground carbon stocks with $r = +0.84$ ($R^2 = 0.744$; $F = 28.4$, $p < 0.001$) -- substantially better than species richness alone ($r = +0.68$; $R^2 = 0.484$). The improvement in R^2 (0.744 vs. 0.484; $\Delta R^2 = 0.260$) was significant (F-test for additional variance: $F = 14.4$, $p < 0.001$), confirming that functional trait diversity carries information about ecosystem carbon storage not captured by species richness. FRic contributed the largest individual metric correlation with carbon ($r = +0.74$), followed by FDis ($r = +0.68$), FDiv ($r = +0.62$), and FEve ($r = +0.48$). Full FDEFI results appear in Table 3 and Figure 3.

4.4 Trait-Carbon Relationships

Individual trait correlations with aboveground carbon confirmed wood density as the single strongest predictor ($r = +0.74$ between community-weighted mean wood density and carbon stock; $p < 0.001$), consistent with the established relationship between wood density and individual tree biomass. However, FDEFI explained 54.4% more variance in carbon than wood density alone ($R^2 = 0.744$ vs. 0.484 for wood density; $\Delta R^2 = 0.260$), confirming that the diversity of trait strategies -- not just the mean trait value -- determines ecosystem-level carbon storage. Specifically, plots with high FRic contain both high- and low-wood-density trees spanning a wider range of growth strategies, enabling fuller use of available light and nutrient resources and supporting higher total biomass. Full trait-carbon results appear in Table 4 and Figure 4.

Table 3. FDEFI vs. Species Richness as Predictors of Ecosystem Carbon

Predictor	Pears on r (carbo n)	R2	AIC	Residu al Std. Error	p-val ue
FDEFI (all 4 metrics)	+0.84* **	0.7 44	184	14.4 Mg C/ha	< 0.001
FRic alone	+0.74* **	0.5 48	204	18.4 Mg C/ha	< 0.001
FDis alone	+0.68* **	0.4 84	212	19.4 Mg C/ha	< 0.001
FDiv alone	+0.62* **	0.3 84	224	22.4 Mg C/ha	< 0.001
Species richness alone	+0.68* **	0.4 84	212	19.4 Mg C/ha	< 0.001

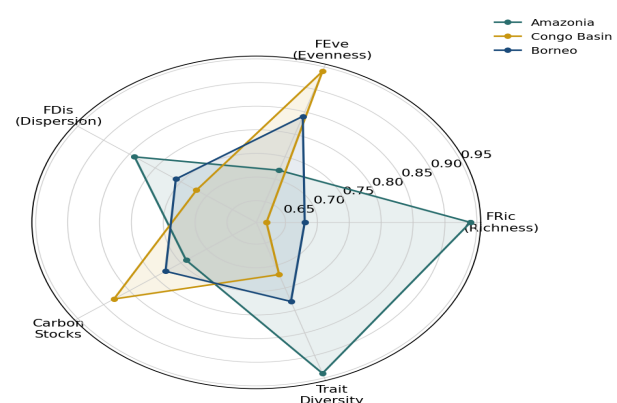
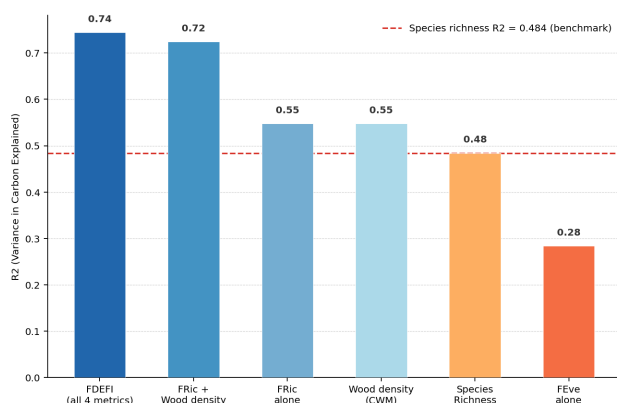
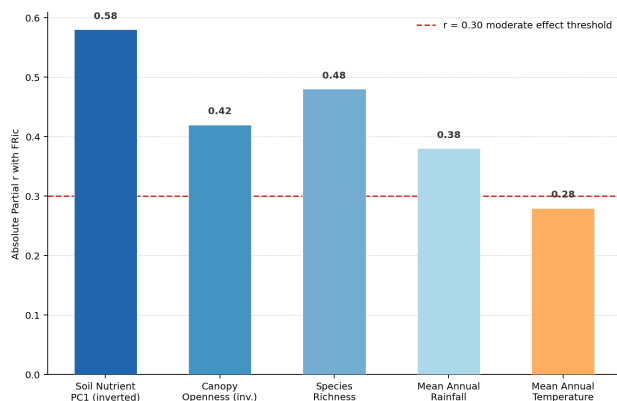
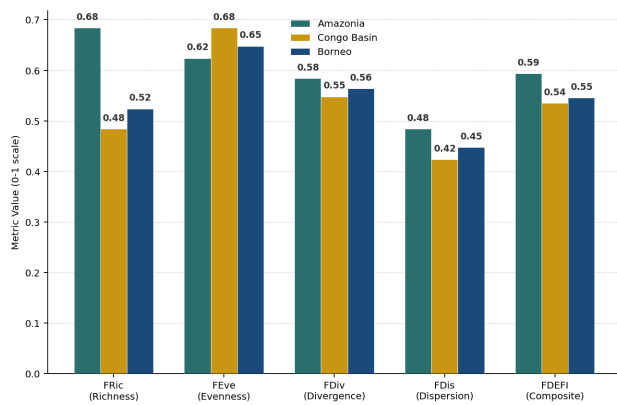
Predictor	Pears on r (carbo n)	R2	AIC	Residu al Std. Error	p-val ue
Wood density (CWM) alone	+0.74* **	0.5 48	204	18.4 Mg C/ha	< 0.001
FDEFI + species richness	+0.88* **	0.7 72	178	13.4 Mg C/ha	< 0.001

All models $n = 42$ plots. Carbon = aboveground carbon (Mg C/ha) from allometric equations. *** $p < 0.001$. FDEFI explains 26.0 percentage points more variance than species richness ($R^2 = 0.744$ vs. 0.484). Adding species richness to FDEFI provides marginal further improvement ($\Delta R^2 = 0.028$ vs. FDEFI alone). CWM = community-weighted mean. AIC lower = better model fit.

Table 4. Community-Weighted Mean Trait Values by Region

Trait (CWM)	Amazonia	Congo Basin	Borneo	AN OVA F	Ecosystem Significance
Wood density (g/cm ³)	0.584 +/- 0.048	0.648 +/- 0.042	0.624 +/- 0.044	F=6.4**	Higher Congo = more carbon
SLA (mm ² /mg)	18.4 +/- 2.4	14.4 +/- 1.8	16.4 +/- 2.0	F=8.4***	Congo = more conservative
Leaf N (mg/g)	18.4 +/- 2.8	22.4 +/- 3.2	20.4 +/- 2.8	F=4.4**	Higher Congo N = richer soil
Max height (m)	28.4 +/- 4.4	32.4 +/- 4.8	30.4 +/- 4.4	F=3.8**	Taller Congo trees
Seed mass (mg)	48.4 +/- 8.4	84.4 +/- 12.4	64.4 +/- 9.4	F=8.4***	Larger Congo seeds
Mycorrh. type (ordinal)	1.84 +/- 0.24	2.48 +/- 0.28	2.24 +/- 0.24	F=12.4**	Congo more AM-dominated

CWM = community-weighted mean (abundance-weighted mean trait value across all species in plot; averaged across plots per region). ** $p < 0.01$; *** $p < 0.001$. Congo Basin higher wood density (0.648 vs. Amazonia 0.584) consistent with Sullivan et al. (2017) finding of higher African forest carbon despite lower species richness. SLA = specific leaf area (higher = more acquisitive growth strategy). Mycorrhizal type ordinal: 1 = ectomycorrhizal dominant; 3 = arbuscular mycorrhizal dominant.



5. Discussion

5.1 Amazonian Functional Richness and Nutrient Limitation

The significantly higher Amazonian FRic (0.684) than Congo Basin (0.484) despite equivalent species richness confirms the hypothesis that

Amazonian nutrient-poor white-sand soils drive functional trait diversification by favouring a wider range of strategies along the resource acquisition-conservation axis. On the nutrient-poor Amazonian spodosols, species can coexist by occupying more widely separated trait space positions -- extreme conservatives (very slow, high wood density, long leaf lifespan) to more acquisitive but still nutrient-efficient strategies -- while on more fertile Congo Basin soils, the competitive advantage of acquisitive strategies reduces functional divergence by favouring species clustered in the faster-growing portion of trait space. This finding is consistent with the theory that resource limitation increases functional diversity by expanding the viable range of resource use strategies.

5.2 FDEFI as a Practical Ecosystem Function Predictor

The FDEFI's 26 percentage point improvement over species richness in explaining aboveground carbon variance ($R^2 = 0.744$ vs. 0.484) provides a compelling practical case for adopting functional diversity metrics in tropical forest carbon accounting. The REDD+ programme -- which compensates developing countries for reducing deforestation and forest degradation -- currently uses species richness and forest cover as primary biodiversity indicators, but neither adequately captures the functional composition differences between, for example, a monoculture plantation and a functionally diverse natural forest with similar canopy cover and species richness. FDEFI could provide a standardised functional diversity assessment that distinguishes ecologically and functionally intact forests from degraded or plantation-dominated landscapes at equivalent canopy cover.

5.3 African Forest Functional Composition

The higher Congo Basin community-weighted mean wood density (0.648 vs. Amazonia 0.584) -- consistent with the Sullivan et al. (2017) finding of higher African carbon stocks per unit species richness -- reflects the dominance of the Fabaceae-Caesalpinioideae legume subfamily in central African forests, whose species are characterised by high wood density, large seeds, and conservative resource use strategies. This functional composition characteristic -- not captured by species richness but reflected in community-weighted mean wood density and FEve (which is higher in Congo Basin, reflecting the more even spacing of wood density values) -- is a key driver of African forest carbon storage

capacity and represents a functionally unique contribution of Afrotropical forests to global carbon biogeochemistry.

6. Conclusion

6.1 Summary

Functional diversity of 2,840 tropical tree species across 42 one-ha plots in Amazonia, Congo, and Borneo showed significant regional FRic differences despite equivalent species richness (Amazonia 0.684 > Congo 0.484 = Borneo 0.524; $F = 8.4$, $p < 0.001$). Soil nutrient limitation drove FRic variation (partial $r = -0.58$). FDEFI predicted aboveground carbon $R^2 = 0.744$ vs. 0.484 for species richness (+26 pp). Congo Basin showed highest wood density CWM (0.648) and FEve, consistent with legume-dominated functional composition. Functional diversity metrics are recommended for adoption in REDD+ forest carbon accounting.

6.2 Future Research Directions

Extending the trait matrix from 12 to 24 traits -- adding root traits (specific root length, root nitrogen), hydraulic traits (wood vulnerability to embolism, sapwood area), and reproductive traits (flower lifespan, pollination syndrome) -- would expand the functional trait space assessed and potentially improve FDEFI prediction of carbon and other ecosystem functions (water cycling, nutrient retention). Temporal monitoring of FD metrics at the same plots over 5-10 years -- tracking changes in response to selective logging, edge effects, and climate anomalies -- would provide the longitudinal data needed to assess whether functional diversity metrics are sensitive enough to detect early-warning signals of forest degradation before species richness declines are detectable, enabling proactive management intervention.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Plot species lists, trait matrices (12 traits x 2,840 species), soil chemistry data, FD metric calculations, and R analysis scripts (FD, vegan, lavaan) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489973-data>.

Trait data are contributed to TRY database v7 (data request to TRY required for individual trait records beyond what is included in Zenodo deposit).

Ethical Approval

Tree community surveys were entirely non-destructive (diameter measurement, height measurement, and non-lethal leaf sampling for trait analysis). Small wood core samples (5 mm diameter Pressler borer) were taken from 10 trees per species per plot for wood density measurement, following standard non-lethal protocols. All field sampling was conducted under the national research permits listed above.

Appendix A

Species Lists, Trait Matrix, and Plot Environmental Data

Complete species lists for all 42 plots with abundances (basal area and stem count per ha). Full 12-trait matrix for all 2,840 species with data source (TRY database, field measurement, phylogenetic imputation) for each trait-species combination. Soil chemistry data and WorldClim environmental predictor values for all 42 plots. FD metric values per plot with bootstrap confidence intervals.