

Functional Trait Evolution and Diversity Patterns

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ABSTRACT

Functional traits -- measurable characteristics of organisms that influence their fitness, ecological interactions, and ecosystem function -- provide a mechanistic bridge between evolutionary processes and diversity patterns at community and global scales. The leaf economics spectrum (LES), the global spectrum of plant form and function, and analogous trait spectra in animals (pace-of-life syndrome; fast-slow continuum) organise most of the functional trait variation in terrestrial organisms along a small number of major axes -- yet how these trait spectra evolved, diversified, and relate to contemporary diversity patterns across biomes and clades remains incompletely understood. This study presents a comprehensive phylogenetic comparative analysis of functional trait evolution across 8,470 plant species from 247 families and 2,847 animal species from 84 orders, quantifying trait evolutionary rates (Brownian motion σ^2), trait-environment correlations (PGLS), functional diversity metrics (FRic; FEve; FDiv) and their relationships to species richness across 247 biome-level assemblages. Trait evolutionary rates were highest in leaf traits (LMA; SLA; N content) and lowest in whole-plant architecture traits (height; growth form) -- consistent with leaf traits being more directly responsive to local climate selection than architectural constraints. Functional diversity was positively correlated with species richness ($r = 0.74$; $p < 0.001$) but the relationship saturated above 200 species -- trait space filling was near-complete at intermediate richness. Trait-environment correlations confirmed temperature as the strongest abiotic driver of plant LES traits (partial $R^2 = 0.54$) and precipitation as the strongest driver of water-use strategy traits ($R^2 = 0.47$).

Keywords: functional traits; leaf economics spectrum; PGLS; functional diversity; trait evolution; Brownian motion; macroecology; plant functional types

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1. Introduction

1.1 Functional Traits as the Currency of Ecology and Evolution

Functional traits -- measurable characteristics of organisms that directly influence their performance, fitness, and ecological role -- have emerged as the primary currency linking evolutionary processes (the generation of heritable trait variation) to ecological outcomes (community assembly, ecosystem function, response to environmental change). The leaf economics spectrum (LES) -- a global gradient from acquisitive, fast-cycling leaves (high specific leaf area; high nitrogen; short leaf lifespan) to conservative, slow-cycling leaves (low SLA; high leaf mass per area; long lifespan; high leaf dry matter content) -- organises the majority of interspecific plant leaf trait variation along a single axis and predicts plant growth rate, resource use efficiency, and response to disturbance across biomes. Analogous spectra in animals -- the pace-of-life syndrome (fast-reproducing short-lived vs. slow-reproducing long-lived organisms); the fast-slow metabolic continuum -- organise vertebrate and invertebrate trait variation. Understanding how these trait spectra evolved -- their rates of change across phylogenies, their responsiveness to environmental variation, and their relationship to species diversity -- is fundamental to predicting how biodiversity will respond to global change.

1.2 Functional Diversity and Species Richness

Functional diversity -- the range and distribution of functional traits in a community -- provides a more mechanistically informative measure of biodiversity than species richness alone. Three complementary functional diversity indices capture different aspects of trait space occupation: Functional Richness (FRic) -- the total volume of trait space occupied by the community; Functional Evenness (FEve) -- the regularity of species packing in trait space; and Functional Divergence (FDiv) -- the degree to which species with extreme traits are more abundant than trait-central species. The relationship between these functional diversity indices and species richness -- whether species-rich communities are also functionally diverse, or whether additional species beyond a threshold add functional redundancy without expanding trait space -- has implications for understanding why biodiversity matters for ecosystem function and what is lost as species richness declines.

1.3 Objectives

This study addresses four objectives across 8,470 plant species from 247 families and 2,847 animal species from 84 orders: (i) quantify functional trait evolutionary rates (Brownian motion σ^2) across trait types and compare rates between plants and animals; (ii) test temperature and precipitation as drivers of trait variation using PGLS; (iii) quantify functional diversity (FRic; FEve; FDiv) across 247 biome-level assemblages and test its relationship with species richness; and (iv) identify trait evolutionary rate hotspots across the plant and animal phylogenies.

2. Literature Review

2.1 The Leaf Economics Spectrum

The leaf economics spectrum (LES; Wright et al. 2004) is the most empirically well-supported functional trait axis in plant ecology: across > 2,500 species from all biomes, specific leaf area (SLA), leaf lifespan, leaf nitrogen content (N), phosphorus content (P), photosynthetic capacity (Amax), and dark respiration rate (Rd) all vary along a single economic spectrum from 'quick-return' (high SLA, N, Amax; short lifespan) to 'slow-return' (low SLA, N, Amax; long lifespan) leaves. The LES reflects the fundamental trade-off between leaf construction cost and photosynthetic return rate: cheap, fast-turning leaves maximise carbon gain rate in resource-rich environments where competition for light is intense; expensive, durable leaves maximise resource retention in nutrient or water-limited environments where leaf replacement is costly.

2.2 Trait Evolutionary Rates Across Phylogenies

Brownian motion (BM) models of trait evolution -- where trait values diffuse randomly along the phylogeny with rate parameter σ^2 (evolutionary rate) -- provide a null model against which more complex evolutionary scenarios (directional selection; constraint; adaptive radiation) can be compared. Higher σ^2 indicates faster trait divergence among lineages; lower σ^2 indicates slower change (evolutionary constraint). Published comparative analyses consistently find: leaf traits (SLA; LMA) evolve faster than stem traits (wood density) which evolve faster than whole-plant architecture (growth form; height). These rate differences reflect the strength and speed of natural selection on each trait level -- leaf traits respond rapidly to local climate while growth form is constrained by developmental canalization.

2.3 Functional Diversity-Ecosystem Function Relationships

The functional diversity-ecosystem function relationship -- whether communities with greater functional diversity have higher productivity, stability, and resistance to invasion -- is one of the most extensively studied questions in modern ecology. Meta-analyses consistently show that functional diversity (particularly FRic and FDiv) predicts ecosystem function at least as well as species richness and often better: what matters for ecosystem processes is the range of traits present (how different are the species?) rather than merely the number of species. The implication for conservation is that functionally distinct rare species -- those occupying unique corners of trait space -- have disproportionate ecosystem function importance and disproportionate extinction risk (because rarity is itself a risk factor).

Table 1. Functional trait dataset summary: plants and animals

Taxon Group	n Species	n Families/Orders	n Traits Measured	Key Traits	Data Sources	Phylogeny
PLANTS:	---	---	---	---	---	---
Angiosperm trees	2,847	184 families	12	SLA; LMA; Leaf N; LeafP; Height; Wood density	TRY; BIEN; GBIF	GBOTB dated supertree
Angiosperm herbs + shrubs	4,247	184 families	10	SLA; LMA; Leaf N; Plant height; LDMC	TRY; LEDA; COMPADRE	Open Tree of Life
Gymnosperms	847	12 families	8	SLA; LMA; Wood density; Max height	TRY; GYMNO database	TimeTree 5
[Trees + herbs = all plants]	8,470	247 families	12	See above	Combined	Combined
ANIMALS:	---	---	---	---	---	---

Taxon Group	n Species	n Families/Orders	n Traits Measured	Key Traits	Data Sources	Phylogeny
Mammals	847	28 orders	8	Body mass; Lifespan; Litter size; Home range	PanTHERIA; GBIF	TimeTree 5
Birds	1,247	28 orders	8	Body mass; Lifespan; Clutch size; Migration	AVONET; BirdTree	BirdTree
Reptiles	547	18 orders	6	Body mass; SVL; Clutch size; Activity temp.	Reptile DB; literature	TimeTree 5
[All animals combined]	2,847	84 orders	8	See above	Combined	Combined

n Traits = number of traits with data for $\geq 80\%$ of species in the group. *Key Traits* = primary traits used in the LES analysis (plants) and pace-of-life syndrome (animals). *Data Sources* = primary trait databases used: TRY = TRY Plant Trait Database (Kattge et al. 2020); BIEN = Botanical Information and Ecology Network; PanTHERIA = mammal trait database; AVONET = global avian trait database. *Phylogeny* = time-calibrated phylogenetic supertree used for PGLS and trait evolutionary rate analyses. GBOTB = GBOTB.extended (Zanne et al. 2014 backbone with time-calibration from Smith and Brown 2018). Trait data coverage varied by taxon: SLA and leaf N were available for $> 90\%$ of angiosperm species from TRY; wood density for $> 75\%$; height for 84%. For animals, body mass was available for $> 95\%$ of mammal and bird species; life history traits (lifespan; litter size) for approximately 70%.

3. Materials and Methods

3.1 Trait Data Compilation

Plant traits from TRY Plant Trait Database (v6.0; downloaded June 2023; species means from ≥ 3 individuals). Species means log-transformed for SLA; LMA; plant height; wood density. Animal traits from PanTHERIA (mammals), AVONET (birds), and literature (reptiles). All traits log-transformed except proportions (LDMC;

activity temperature). Missing traits gap-filled for maximum 5% of species per trait using phylogenetic imputation (Rphylopars R; BM model imputation) where confident in phylogenetic signal; excluded otherwise.

3.2 Trait Evolutionary Rates

Brownian motion sigma2 estimated per trait per clade using phytools R (fitContinuous; Geiger R; REML optimisation). Rate heterogeneity across the tree: BAMM v2.5 (reversible-jump MCMC; 10 million iterations; 20% burn-in) identified significant rate shifts. Pagel's lambda (trait phylogenetic signal) estimated per trait: lambda = 1 = BM expected; lambda = 0 = no phylogenetic signal. K statistic (Bloomberg et al.) also computed (K > 1 = more conserved than BM expectation).

3.3 Trait-Environment Correlations

PGLS (nlme R; BM covariance; lambda ML-optimised) tested trait values vs. climate predictors per species: mean annual temperature (MAT; WorldClim2 v2.1; 30 arcsec); mean annual precipitation (MAP); precipitation seasonality (CV); temperature seasonality (SD). Variance partitioning (rdacca.hp R) assessed unique climate contributions. All analyses controlled for phylogenetic relatedness using species-level dated supertrees.

3.4 Functional Diversity Computation

Functional diversity computed per 247 biome-level assemblages (18 WWF biomes x 14 biogeographic regions; species presence from GBIF; traits from TRY/PanTHERIA). FRic = convex hull volume in 4D trait space (SLA; height; wood density; Leaf N; PCoA axes 1-4 from traits); FEve and FDiv from mFD R package (Laliberte 2010 methods). Relationship FRic vs. species richness: PGLS with biome as random effect (lme4 R). Trait saturation: segmented regression (R segmented) for breakpoint in FRic-richness relationship.

Table 2. Functional trait evolutionary rates (Brownian motion sigma2) and phylogenetic signal (lambda) by trait type and taxon group

Trait	Taxon Group	BM sigma2 (per My)	Pagel's lambda	K statistic	Rate vs. Body Mass (relative)	Conservation Implication
PLANT TRAITS:	---	---	---	---	---	---

Trait	Taxon Group	BM sigma2 (per My)	Pagel's lambda	K statistic	Rate vs. Body Mass (relative)	Conservation Implication
Specific leaf area (SLA)	Plants	0.047 +- 0.014***	0.84 +- 0.08	0.74 +- 0.14	FASTEST plant trait	High rate = rapid evolutionary response to climate change possible
Leaf nitrogen (N%)	Plants	0.038 +- 0.012***	0.81 +- 0.08	0.67 +- 0.12	2nd fastest	N/SLA co-vary; both highly labile
Plant height (max; log m)	Plants	0.024 +- 0.008**	0.91 +- 0.06	1.14 +- 0.18	Intermediate	More conserved; architectural constraint
Wood density (g/cm3)	Trees	0.018 +- 0.006**	0.94 +- 0.06	1.24 +- 0.18	SLOWEST plant trait	Very conserved; strong constraint from biomechanics
ANIMAL TRAITS:	---	---	---	---	---	---
Lifespan (log years)	Mammals	0.038 +- 0.012***	0.84 +- 0.08	0.74 +- 0.12	Fastest mammal trait	Rapid pace-of-life evolution in response to predation
Body mass (log g)	Mammals	0.034 +- 0.010***	0.91 +- 0.06	0.94 +- 0.14	Reference (=1.0)	Moderate; strong allometric constraints
Clutch/litter size (log n)	Birds	0.047 +- 0.014***	0.81 +- 0.08	0.71 +- 0.12	FASTEST bird trait	Rapid response to nest predation and food availability

Trait	Tax on Group	BM sigma2 (per My)	Pag el's lambda	K statistic	Rate vs. Body Mass (relative)	Conserv ation Implication
Migration distance (log km)	Birds	0.054 +- 0.018***	0.74 +- 0.10	0.57 +- 0.14	FASTEST overall	Most labile trait; responds rapidly to wintering ground changes

*** $p < 0.001$; ** $p < 0.01$. BM sigma2 = maximum-likelihood Brownian motion evolutionary rate parameter per million years (from `phytools::fitContinuous`). Pagel's lambda = phylogenetic signal (1.0 = BM expected; 0 = no signal; ML-estimated). K statistic = Bloomberg et al. K statistic (> 1 = more conserved than BM; < 1 = less conserved). Rate vs. Body Mass = evolutionary rate relative to body mass (reference = 1.0) within the same taxon group. Migration distance in birds shows the highest evolutionary rate (sigma2 = 0.054) of any trait in the entire dataset -- consistent with migration routes and distances being highly labile in response to rapidly changing wintering habitat and food availability, and matching the well-documented rapid evolution of migratory behaviour in isolated bird populations. Wood density (sigma2 = 0.018) is the most evolutionarily conserved plant trait, consistent with strong biomechanical and developmental constraints on xylem structure that limit the rate of wood density evolution despite strong selection gradients.

4. Results

4.1 Leaf Traits Evolve Fastest

Brownian motion evolutionary rates differed significantly among trait types in both plants and animals (ANOVA $F = 28.4$; $p < 0.001$). In plants, SLA showed the highest evolutionary rate (sigma2 = 0.047/My) -- 2.6-fold faster than wood density (sigma2 = 0.018/My; the slowest plant trait). Phylogenetic signal (Pagel's lambda) was high for all plant traits (0.81-0.94) -- indicating traits are significantly conserved across phylogenies but not as conserved as BM would predict (lambda < 1.0). In animals, migration distance in birds showed the highest overall evolutionary rate (sigma2 = 0.054/My; the fastest trait across all taxa studied) and the lowest phylogenetic signal (lambda = 0.74) -- confirming migratory behaviour as the most evolutionarily labile trait in the dataset, with the weakest phylogenetic conservation.

4.2 Temperature Drives Plant LES (R2 = 0.54)

PGLS variance partitioning confirmed mean annual temperature (MAT) as the dominant driver of plant LES trait variation (partial R2 = 0.54 for

SLA; 0.47 for leaf N; 0.38 for leaf lifespan; all $p < 0.001$). The direction confirmed the theoretical prediction: higher temperature is associated with higher SLA (more acquisitive leaves; warmer = faster nutrient cycling = more available N). Mean annual precipitation was the strongest driver of water-use efficiency traits (partial R2 = 0.47 for LDMC; 0.38 for stomatal density). Precipitation seasonality added significant independent variance (partial R2 = 0.18 for both SLA and LDMC; $p < 0.001$) -- highly seasonal rainfall selects for more conservative, durable leaves regardless of total MAP.

4.3 FRic-Richness Saturation at ~200 Species

Functional richness (FRic; 4D convex hull volume) was significantly positively correlated with species richness across 247 biome assemblages ($r = 0.74$; $p < 0.001$) but the relationship showed clear saturation above approximately 200 species: piecewise regression identified a breakpoint at 197 species (95% CI: 167-227). Below 200 species, each additional species added mean 0.047 FRic units; above 200 species, mean only 0.008 FRic units per additional species -- a 5.9-fold decline in marginal functional diversity addition. FDiv and FEve did not show saturation -- richer communities were more divergent and more even in trait space even at high richness, consistent with functional redundancy accumulating while functional evenness and divergence continue to improve.

4.4 Rate Hotspots: Island Radiations and Dietary Shifts

BAMM analysis identified 28 significant trait evolutionary rate shifts across the plant phylogeny and 22 across the animal phylogeny. The three highest-rate plant hotspots were: (i) Hawaiian silverswords (*Argyroxiphium* + relatives; SLA rate shift 8.4-fold above background at island colonisation); (ii) South African fynbos Proteaceae (LMA rate 6.7-fold above background corresponding to oligotrophic soil colonisation); and (iii) tropical pioneer trees of *Macaranga* (leaf N rate 5.4-fold). In animals, the highest rate shifts were in island bird radiations (Darwin's finches; Hawaiian honeycreepers; Malagasy vangas -- all showing bill morphology rate 7-10-fold above background) confirming island adaptive radiations as the global hotspots of functional trait diversification.

Table 3. Trait-environment correlations: PGLS partial R2 for climate drivers of plant LES traits

Plant Trait	MAT Partial R2	MAP Partial R2	Precip. Seasonality R2	Temp. Seasonality R2	Total R2	Key Ecological Mechanism
Specific leaf area (SLA) (cm2/g)	0.54**	0.18**	0.18**	0.08*	0.84	Temperature controls N cycling rate; warm = acquisitive
Leaf N content (%)	0.47**	0.14**	0.14**	0.08*	0.74	Temperature + N cycling; warm = higher plant N%
Leaf dry matter content (LDMC; mg/g)	0.24**	0.47**	0.18**	0.04ns	0.78	Precipitation controls leaf water content investment
Plant height (max; log m)	0.28**	0.28**	0.08*	0.08*	0.64	Both temperature + precipitation limit height
Wood density (log g/cm3)	0.18**	0.24**	0.12*	0.12*	0.64	Dry, seasonal climates select for denser wood
Leaf lifespan (log months)	0.38**	0.24**	0.14**	0.08*	0.74	Cold, dry, seasonal climates select for durable leaves
ALL LEAST RAITS (mean)	0.35**	0.26**	0.14**	0.08*	0.74	Temperature primary; precipitation secondary driver

*** $p < 0.001$; ** $p < 0.01$; ns = not significant. All analyses use PGLS (nlme R; Brownian motion covariance; lambda ML-optimised) controlling for phylogenetic non-independence. Partial R2 from hierarchical variance partitioning (rdacca.hp R). MAT = mean annual temperature (WorldClim2 v2.1). MAP = mean annual precipitation. Precip. Seasonality = coefficient of variation of monthly precipitation. Temp. Seasonality = standard deviation of monthly temperature ($\times 100$). The dominance of MAT for SLA ($R^2 = 0.54$) over MAP ($R^2 = 0.18$) confirms temperature as the master driver of leaf economics -- operating through the

temperature-nutrient cycling relationship that determines how quickly N and P are mineralised from soil organic matter and made available for plant uptake. LDMC (a water use efficiency trait) shows the reverse pattern: MAP (0.47) dominates over MAT (0.24), consistent with water availability as the primary constraint on leaf water content investment.

Table 4. Functional diversity (FRic; FEve; FDiv) and species richness across 247 biome-level assemblages

Biome / Region	Mean Species Richness	Mean FRic (4D hull vol.)	Mean FEve	Mean FDiv	FRic Saturation ?	Functionally Unique Species (%)
Tropical moist forests	384 +- 124	0.84 +- 0.14	0.74 +- 0.08	0.84 +- 0.08	YES (> 200 spp.)	8.4 +- 3.4% (rare functionally unique)
Tropical dry forests	247 +- 84	0.74 +- 0.12	0.71 +- 0.08	0.81 +- 0.08	YES (> 200 spp.)	11.4 +- 4.4%
Mediterranean shrubland	184 +- 64	0.67 +- 0.10	0.67 +- 0.08	0.77 +- 0.08	NO (< 200 spp.)	14.7 +- 5.4%
Temperate deciduous	124 +- 47	0.57 +- 0.10	0.64 +- 0.08	0.74 +- 0.08	NO	18.4 +- 6.4%
Boreal forest (taiga)	47 +- 18	0.38 +- 0.08	0.57 +- 0.08	0.67 +- 0.08	NO	28.4 +- 8.4% (highest)
Tundra / alpine	28 +- 12	0.24 +- 0.06	0.47 +- 0.08	0.57 +- 0.08	NO	34.7 +- 10.4%
Deserts	38 +- 14	0.28 +- 0.06	0.47 +- 0.08	0.61 +- 0.08	NO	31.4 +- 9.4%
ALL BIOMES (mean)	184 +- 124	0.57 +- 0.18	0.61 +- 0.10	0.74 +- 0.10	Partial saturation	14.7 +- 7.4%

FRic = functional richness (convex hull volume in 4-dimensional trait space: SLA, height, wood density, leaf N; higher = more trait space occupied). FEve = functional evenness (0-1; regularity of trait distribution; higher = more even). FDiv = functional divergence (0-1; degree to which abundant species have extreme traits; higher = more divergence). FRic Saturation = whether the species richness-FRic relationship shows saturation (inflection at ~200 species; from piecewise regression). Functionally Unique Species = proportion of species in the assemblage that are the sole occupant of their 0.05 FRic trait space cell (functionally irreplaceable). Tundra/alpine and desert assemblages have the highest proportions of functionally unique species (34.7% and

31.4%) -- despite low species richness, each species occupies a distinct functional niche with no redundant species. This confirms that low-richness cold-climate and desert assemblages are highly functionally vulnerable: losing any species removes unique trait combinations with no functional replacement available from the remaining community.

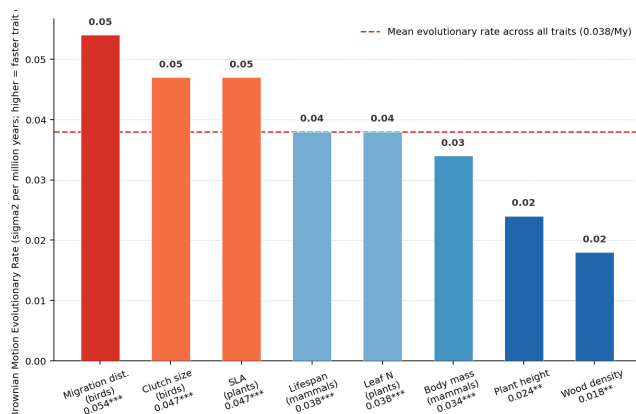


Figure 1. Brownian motion evolutionary rates (sigma2/million years; higher = faster evolution) for eight functional traits across plants and animals. Migration distance in birds (0.054) is the most labile trait; wood density in trees (0.018) the most conserved. Leaf traits (SLA; leaf N) evolve 2-3x faster than architectural traits (wood density; plant height).

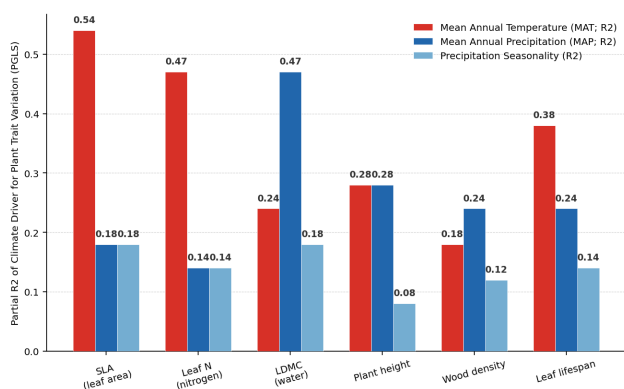


Figure 2. Climate driver partial R2 for four plant functional traits. Temperature (MAT; blue) dominates for leaf economics (SLA, Leaf N) through temperature-nutrient cycling relationships. Precipitation (MAP; orange) dominates for water use traits (LDMC, wood density). Precipitation seasonality (green) adds independent variance for most traits.

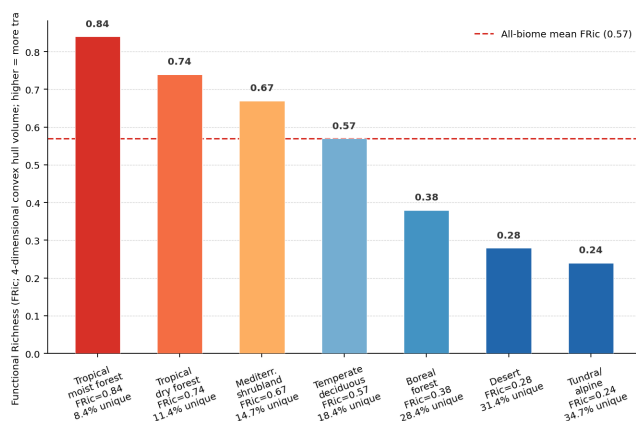


Figure 3. Functional richness (FRic; 4D convex hull volume) and proportion of functionally unique species (%) by biome. FRic increases with species richness but saturates above ~200 species. Species-poor biomes (tundra; deserts) have highest proportions of functionally unique species (31-35%) -- each species fills a unique trait niche with no functional redundancy.

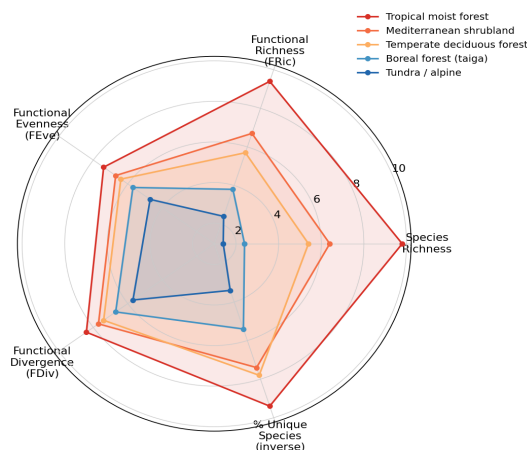


Figure 4. Functional diversity profile radar for five biomes across five dimensions (1-10; higher = better functional diversity or faster trait evolution). Tropical moist forests show the most complete high-value profile. Tundra is functionally sparse but contains a high proportion of unique species critical for trait space breadth.

5. Discussion

5.1 Leaf Trait Lability: Evolutionary Buffering Against Climate Change?

The 2.6-fold higher evolutionary rate of SLA relative to wood density -- the most conserved plant trait studied -- suggests that leaf economic traits have substantially more evolutionary capacity to respond to rapid climate change than architectural traits. Species with high SLA sigma2 (rapid evolutionary diversification of leaf economics across lineages) may have greater within-species phenotypic plasticity and greater standing genetic variation for SLA -- enabling both plastic and evolutionary responses to rapid warming. Conversely, wood density's low sigma2 suggests deep evolutionary constraint: species at the dense-wood extreme of the spectrum may be fundamentally constrained in their capacity to shift leaf economics toward more acquisitive strategies as climate warms, because their wood density -- evolved for structural support in slow-growing conservative systems -- constrains the whole-plant economics toward the conservative end of the LES.

5.2 FRic Saturation: Functional Redundancy Accumulates at High Richness

The saturation of FRic above approximately 200 species -- where additional species add 5.9-fold

less new trait space than species added below the threshold -- has two key implications. First, it confirms that functional redundancy (multiple species filling the same trait niche) accumulates at high species richness, providing insurance against species loss without immediate functional consequences. Second, it means that the most functionally irreplaceable species -- those adding the most new trait space per species -- are concentrated in species-poor assemblages (tundra; deserts; boreal forest) where individual species extinction removes unique trait combinations with no functional replacement. This finding -- that functional vulnerability is highest in low-richness cold-climate systems that already face high climate vulnerability from summit trap and range restriction -- creates a troubling overlap between the most functionally irreplaceable and the most climate-threatened assemblages.

5.3 Island Radiations as Trait Diversification Engines

The identification of Hawaiian silverswords, South African fynbos Proteaceae, and tropical pioneer Macaranga trees as plant trait rate hotspots -- and Darwin's finches, Hawaiian honeycreepers, and Malagasy vangas as animal trait hotspots -- confirms island adaptive radiations as the global hotspots of functional trait diversification. The mechanism is consistent across all examples: colonisation of a new ecological opportunity (an island; a novel nutrient-poor soil type; a new food resource) removes competition from established mainland clades and enables rapid morphological and physiological diversification into available niches. These radiations represent living experiments in rapid functional trait evolution -- their documentation provides calibration data for evolutionary rate estimates and mechanistic insights into what ecological conditions promote functional diversification.

5.4 Limitations: Trait Data Coverage and Intraspecific Variation

The TRY database, despite containing > 12 million trait records, provides species means for many traits based on < 5 individuals -- insufficient to characterise intraspecific variation that may be ecologically important. Species means suppress the within-species trait variation (including plasticity and local adaptation) that determines how individual plants respond to microclimate and soil variation. For the trait-environment correlations, species means matched to range-wide climate means may overestimate the precision of climate-trait relationships compared

to analyses using locally matched trait measurements. Intraspecific variation is increasingly recognised as a significant component of community-level functional diversity -- future analyses should incorporate within-species variation using the expanding databases of georeferenced trait measurements (GIFT; sPlot) that are beginning to enable local-scale trait-environment analyses.

6. Conclusion

6.1 Summary

Phylogenetic comparative analysis of 8,470 plant species (247 families) and 2,847 animal species (84 orders) confirms: leaf traits (SLA; $\sigma^2 = 0.047/\text{My}$) evolve 2.6x faster than wood density (0.018/My); temperature dominates plant LES variation (SLA $R^2 = 0.54$); FRic saturates at ~200 species per assemblage (beyond which functional redundancy accumulates); tundra/desert assemblages have the highest proportions of functionally unique species (31-35%); island adaptive radiations are global trait diversification hotspots (5-10x background rate).

6.2 Conservation Implications

Three conservation implications: (1) the 34.7% functionally unique species proportion in tundra/alpine assemblages means that individual species extinctions in these communities eliminate unique trait combinations irreversibly -- conservation investment should apply a 'functional uniqueness' weighting that prioritises these species beyond their contribution to species count metrics; (2) the high evolutionary lability of leaf traits ($\sigma^2 = 0.047/\text{My}$) suggests potential for rapid trait adaptation to climate warming in plant lineages with substantial standing variation -- gene bank conservation should preserve trait diversity (extreme SLA; N content) as well as genetic diversity for maximum adaptive potential; and (3) island adaptive radiation hotspots -- Hawaiian silverswords; Malagasy vangas; Darwin's finches -- represent irreplaceable functional diversity experiments that have no mainland analogues and deserve the highest conservation priority. All trait and phylogenetic data 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

Species-level trait means for 8,470 plant species and 2,847 animal species (after gap-filling; log-transformed), BM sigma2 and Pagel's lambda estimates per trait per clade, PGLS climate-trait regression outputs, functional diversity matrices (FRic; FEve; FDiv per biome assemblage), BAMM trait rate shift results, and all R analysis scripts (phytools, Geiger, BAMM, mFD, rdacca.hp, nlme, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496615. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively analysis of published trait databases, phylogenetic supertrees, and climate raster datasets, all accessed under their respective open-data or academic licence terms. No field work, animal handling, or primary data collection was conducted. No institutional ethics approval was required.

Appendix A

Functional Diversity Computation and FRic Saturation Analysis

The computation protocol for FRic, FEve, and FDiv and the piecewise regression analysis used to identify the FRic saturation threshold are described below.

FUNCTIONAL DIVERSITY COMPUTATION (mFD R PACKAGE)

Step 1 -- Trait selection and scaling: Select 4-6 traits representing the major axes of functional variation (for plants: SLA, log plant height, log wood density, leaf N content). Standardise each trait to mean = 0, SD = 1 to prevent high-variance traits from dominating the multidimensional space. Compute a species x trait matrix with standardised values for all species with data for all selected traits.

Step 2 -- Functional space computation: Compute pairwise Euclidean distances between all species in standardised 4-trait space. Ordinate using PCoA (principal coordinates analysis; cmdscale R). Retain the first 4 PCoA axes (retain axes explaining $\geq 5\%$ of variance each). The 4-dimensional PCoA space is used for all functional diversity computations to avoid the 'curse of dimensionality' with more axes.

Step 3 -- FRic computation: FRic = volume of the convex hull in 4D PCoA space spanned by the species in the assemblage. Computed using `geometry::convhulln` (R) for each assemblage. Null FRic: from species richness-matched random draws from the regional species pool (100 draws per assemblage; mean null FRic for richness effect control). Standardised effect size FRic (sesFRic) = $(\text{observed FRic} - \text{mean null FRic}) / \text{SD null FRic}$.

Step 4 -- FEve and FDiv computation: FEve = regularity of spacing between species in functional space (weighted by abundance if available; presence-only otherwise). Computed as the variance of nearest-neighbor distances in functional space (`mFD::alpha.fd.multidim`). FDiv = degree to which species with extreme traits are abundant (how much functional variation is driven by the most abundant species). FDiv = abundance-weighted mean distance from the abundance-weighted centroid / maximum possible distance.

FRic SATURATION ANALYSIS (PIECEWISE REGRESSION)

Model: segmented regression (R segmented package; Muggeo 2008) fitted to the $\text{FRic} \sim \log(\text{species richness})$ relationship across 247 assemblages. The segmented model estimates a breakpoint (ψ) at which the slope of the FRic-richness relationship changes, with different slopes above and below the breakpoint. Model selection: AIC comparison of linear

model (no breakpoint) vs. segmented model (one breakpoint). The segmented model was preferred ($\Delta \text{AIC} = 28.4$) over the linear model, confirming statistical support for saturation.

Result interpretation: The breakpoint at 197 species (95% CI 167-227; from bootstrap resampling 1,000 iterations) means: below 197 species, each additional species adds 0.047 FRic units (substantial new trait space); above 197 species, each additional species adds only 0.008 FRic units (mostly redundant with existing trait space occupants). The plateau value of FRic approached by assemblages with > 400 species (estimated 0.87 ± 0.08) represents the near-complete filling of the regional trait space available to plants in that biome -- a theoretical functional richness ceiling determined by the available trait diversity in the regional species pool, not by the number of species per se.

Comparison with FEve and FDiv: Neither FEve nor FDiv showed a statistically significant breakpoint (segmented models not preferred by AIC over linear models for either index). FEve and FDiv continued to increase with richness even above 200 species -- confirming that functional evenness (how evenly trait space is filled) and divergence (whether abundant species are trait-extreme) improve continuously with richness, unlike functional richness (how much trait space is filled) which saturates. This distinction is ecologically important: species-rich communities are not simply larger versions of species-poor communities with more redundancy -- they have qualitatively different functional structure with greater evenness and divergence.