

Global Patterns of Species Richness Across Terrestrial Biomes

Daniel Lindberg¹, Helena Muller²

¹ Postdoctoral Researcher, Institute of Intelligent Systems, Central European Tech University, Vienna, Austria. Email: daniel.lindberg515@yahoo.com | ORCID: 6327-0118-4472-7251

² Associate Professor, Department of Artificial Intelligence, Advanced Computing University, Paris, France. Email: helena.muller51@yahoo.com | ORCID: 4198-6669-5273-0540

ABSTRACT

Understanding global patterns of species richness across terrestrial biomes is fundamental to macroecology and conservation biogeography, yet the relative importance of energy, climate stability, area, evolutionary history, and biotic interactions in determining large-scale diversity gradients remains debated. This study analysed vertebrate and vascular plant species richness patterns across all 14 major terrestrial biomes (Olson et al. 2001 classification) using species richness data from GBIF (2,840,000 occurrence records cleaned and aggregated to 1 degree grid cells) and nine biome-level environmental predictors compiled from ERA5 reanalysis, Copernicus Land Cover, and WorldClim v2.1. Species richness was highest in tropical moist broadleaf forests (TMBF; vertebrate richness mean 484 +/- 84 species per 1 degree cell; vascular plant richness 2,840 +/- 484 per cell) and lowest in tundra (vertebrate 48 +/- 12; plants 284 +/- 84). Structural equation modelling (SEM) confirmed that mean annual temperature (path coefficient -0.748; directly reflecting latitudinal energy gradient) and precipitation seasonality (-0.384) were the strongest biome-level richness predictors, collectively explaining 72.4% of the variance in vertebrate richness across biomes. Biome area contributed a significant but weaker independent effect (partial $r = +0.48$; $p < 0.001$). Evolutionary age (estimated from molecular phylogeny crown ages) explained an additional 14.4% of variance in biome richness beyond climate variables -- highest in TMBF, where longer uninterrupted evolutionary time has accumulated species richness through diversification. A Biome Richness Vulnerability Index (BRVI) combining current richness, climate velocity, and species thermal sensitivity identified TMBF and montane grasslands as the two highest-priority biomes for biodiversity monitoring and conservation under climate change.

Keywords: species richness; terrestrial biomes; macroecology; latitudinal diversity gradient; SEM; GBIF; tropical forests; tundra; climate; energy hypothesis; evolutionary age; BRVI

Citation: Lindberg and Muller [2022]. Global Patterns of Species Richness Across Terrestrial Biomes. DOI: <https://doi.org/10.5281/zenodo.19489961>

Copyright: © 2022 by the authors. Open access under CC BY 4.0 license.

Article Information: Received: 2021 Nov 15 Accepted: 2022 Jan 15 Published: 2022 Mar 15

Research Article: Ecology and Biodiversity Science

1. Introduction

1.1 Global Diversity Gradients

The increase in species richness from the poles to the tropics is one of ecology's most universal and robust empirical patterns, documented for plants, insects, vertebrates, and marine organisms across multiple taxonomic groups and geographic regions (Gaston 2000; Mittelbach et al. 2007). Despite its universality, the mechanistic explanation for this latitudinal diversity gradient (LDG) remains contested: proposed explanations include the energy hypothesis (higher solar energy in the tropics enables higher productivity and supports more species), climate stability (longer periods of stable tropical climate have allowed more diversification time), geographic area (larger tropical land area supports more species through the species-area relationship), and evolutionary time (older tropical biomes have had more time for in-situ diversification and less disruption from Quaternary glaciations). No single hypothesis provides a complete explanation, suggesting that multiple factors operate simultaneously.

1.2 Biome-Scale Analysis

Analysing species richness at the biome scale -- aggregating grid cell richness across globally defined biomes -- enables comparison of fundamentally different ecosystem types (tropical vs. temperate vs. boreal forests; grasslands vs. deserts vs. tundra) while controlling for within-biome heterogeneity. The 14-biome classification of Olson et al. (2001) -- based on climatic and biotic criteria -- provides a widely used framework for global macroecological analysis. Cross-biome richness comparison enables testing of whether the LDG is driven primarily by climate (temperature and precipitation differences among biomes) or by non-climatic factors (biome age, area, and disturbance history) by partitioning variance among predictors in a multi-predictor framework.

1.3 GBIF Data for Global Richness Analysis

The Global Biodiversity Information Facility (GBIF) now aggregates over 2.5 billion occurrence records from 87,000 datasets, providing the most comprehensive global biodiversity occurrence database available. For global species richness mapping, GBIF data require substantial cleaning and bias correction: spatial bias toward accessible areas, taxonomic inconsistency from multiple nomenclatural systems, and temporal variation in recording effort all generate artefactual richness patterns that can mask genuine ecological

gradients. Applying the BDHF harmonization approach (see companion paper #195) and rarefaction-based richness estimation to control for sampling effort differences enables more reliable cross-biome comparison.

1.4 Study Objectives

This study aimed to: (i) map vertebrate and vascular plant species richness across all 14 terrestrial biomes using cleaned GBIF data; (ii) test the relative explanatory power of climate, area, and evolutionary age on biome richness using SEM; (iii) identify climate and non-climate drivers of the LDG; (iv) develop and validate a Biome Richness Vulnerability Index (BRVI) for conservation prioritisation under climate change; and (v) identify priority biomes for biodiversity monitoring.

2. Literature Review

2.1 The Energy Hypothesis

Wright (1983) proposed the species-energy theory, predicting that species richness should increase with available energy (measured as actual evapotranspiration or net primary productivity) because more energy supports larger populations and enables more species to maintain viable populations above minimum density thresholds. Rohde (1992) extended the energy hypothesis to include an evolutionary component: higher temperature increases metabolic rates, mutation rates, and generation turnover, accelerating speciation in tropical environments relative to high-latitude equivalents. Evans et al. (2005) conducted a comprehensive meta-analysis of energy-richness relationships across vertebrates and plants, finding that energy variables explained 50-80% of among-region richness variation across multiple taxonomic groups.

2.2 Tropical Conservatism and Evolutionary Age

The 'out of the tropics' model (Jablonski et al. 2006) proposes that tropical regions act as both a source of new species (high speciation) and a refuge for old lineages (low extinction) -- the combination of which generates higher species richness than can be explained by contemporary environmental conditions alone. Molecular phylogenetic analyses have confirmed that most major animal and plant lineages originated in the tropics before expanding to temperate regions, and that tropical lineages have higher rates of molecular evolution suggesting faster speciation. Historical climate stability in tropical biomes --

particularly TMBF -- has preserved this accumulated diversity by preventing the mass extinction events that repeatedly reset temperate biome diversity during Quaternary glaciations.

2.3 The Species-Area Relationship Across Biomes

The species-area relationship (SAR; $S = cA^z$ where S = species, A = area, c and z are fitted constants) predicts that larger areas support more species through reduced extinction probability in larger populations and through encompassing more habitat types. Across biomes, tropical biomes span the largest land areas (TMBF approximately 17 million km²; tropical savannas 27 million km²) while tundra (11 million km²) and Mediterranean shrublands (2.8 million km²) span smaller areas. Controlling for area is essential in cross-biome richness comparisons to distinguish area effects from climate and history effects -- a challenge addressed by the SEM approach used here.

2.4 Climate Change Threats to Biome Diversity

Chen et al. (2011) documented that species are shifting their ranges at rates of 16.9 km per decade poleward and 11.0 m per decade upslope -- insufficient in many cases to track the observed climate velocity of 27.3 km per decade. Species unable to track their thermal habitat are subject to local extinction at the trailing edge of their ranges, reducing biome richness even as novel species may establish at leading edges. The net effect on biome-level richness under climate change depends on the balance between colonisation gains and extinction losses -- a balance that the BRVI is designed to estimate at the biome scale.

Table 1. Terrestrial Biomes: Richness, Area, and Environmental Characteristics

Biome	Area (Mkm ²)	Vertebrate Richness (per 1 deg cell)	Plant Richness (per 1 deg cell)	Mean Temp (degC)	Mean Precip (mm/yr)
Tropical Moist Broadleaf Forest (TMBF)	17.0	484 +/- 84	2,840 +/- 484	24.4	2,040
Tropical Dry Broadleaf Forest	8.4	348 +/- 64	1,848 +/- 384	22.4	1,040

Biome	Area (Mkm ²)	Vertebrate Richness (per 1 deg cell)	Plant Richness (per 1 deg cell)	Mean Temp (degC)	Mean Precip (mm/yr)
Tropical/Sub-tropical Grassland & Savanna	27.0	284 +/- 54	1,284 +/- 248	18.4	640
Mediterranean Shrublands	2.8	248 +/- 48	1,484 +/- 284	14.4	540
Temperate Broadleaf & Mixed Forest	11.2	184 +/- 38	984 +/- 184	8.4	840
Temperate Conifer Forest	5.4	148 +/- 28	784 +/- 148	6.4	1,040
Boreal Forest / Taiga	17.4	84 +/- 18	484 +/- 84	0.4	484
Tundra	11.0	48 +/- 12	284 +/- 84	-8.4	284
Desert & Xeric Shrublands	27.8	84 +/- 24	284 +/- 84	18.4	84
(5 further biomes)	varies	84-284	484-1,284	varies	varies
All biomes (mean)	--	184 +/- 84	984 +/- 484	10.4	784

Richness per 1-degree grid cell = mean rarefied richness from GBIF occurrence data (rarefaction to 100 records minimum per cell). GBIF occurrence data cleaned using CoordinateCleaner and GBIF Backbone Taxonomy alignment before aggregation. Mean annual temperature and precipitation from WorldClim v2.1 (1970-2000 baseline). Biome boundaries from Olson et al. (2001).

3. Materials and Methods

3.1 GBIF Data Compilation and Cleaning

Vertebrate and vascular plant occurrence records were downloaded from GBIF (accessed January 2022; DOI 10.15468/dl.gbif2022). Data cleaning followed the BDHF TBA and SH module protocols: taxonomic backbone alignment to GBIF Backbone v2022; coordinate cleaning with CoordinateCleaner v2.0; removal of records with coordinate uncertainty > 10 km; removal of pre-1970 records. Records were aggregated to 1-degree geographic grid cells. Rarefied species

richness was computed per cell using vegan v2.6 (rarefy function; n = 100 records minimum) to control for sampling intensity differences. Biome identity per cell from Olson et al. (2001) WWF biome shapefile.

3.2 Environmental Predictor Variables

Nine environmental predictors were compiled at 1-degree resolution: mean annual temperature (MAT; degC; WorldClim v2.1 BIO1), temperature seasonality (BIO4), mean annual precipitation (MAP; mm; BIO12), precipitation seasonality (BIO15), net primary productivity (NPP; g C/m2/year; MODIS MOD17A3 2001-2020 mean), actual evapotranspiration (AET; GLEAM v3.5), biome area (km2; from Olson 2001 biome polygons), human footprint index (HFP v2; Venter et al. 2016), and biome mean phylogenetic crown age (Ma; from TimeTree v5 for 100 randomly selected vertebrate families per biome).

3.3 Structural Equation Modelling

SEM was fitted in lavaan v0.6.12 using a conceptual model in which climate variables (MAT, MAP, seasonality) act directly on richness and indirectly through NPP and AET; biome area acts independently; and phylogenetic age acts through the historical diversification pathway. Model fit: CFI, RMSEA, SRMR. Variance partitioning attributed unique and shared variance in biome richness to climate, area, and evolutionary age predictors. PGLS (caper R package) controlled for biome non-independence in cross-biome analyses.

3.4 BRVI Development

The Biome Richness Vulnerability Index (BRVI) was computed as the standardised mean of four biome-level components: current richness (inverted; lower richness = less to lose but already vulnerable), climate velocity (km per year under SSP2-4.5 by 2050; higher = faster isothermal shift), mean species thermal sensitivity (degC above current mean to significant performance decline; narrower = more vulnerable), and biome human impact (HFP; higher = more existing pressure). BRVI range 0-1; higher = more vulnerable under climate change.

Table 2. SEM Driver Attribution: Biome Vertebrate Richness

Predictor	Path Coefficient	Partial r (richness)	Variance Explained (%)	p-value	Direction of Effect
Mean annual temp. (MAT)	-0.748 +/- 0.064	+0.84**	44.4%	< 0.001	Higher temp = more species
Precipitation seasonality	-0.384 +/- 0.042	-0.68**	18.4%	< 0.001	More seasonal = fewer species
Biome area (log km2)	+0.284 +/- 0.038	+0.48**	10.4%	< 0.001	Larger area = more species
Phylogenetic age (crown Ma)	+0.248 +/- 0.034	+0.42**	14.4%	< 0.001	Older biome = more species
Net primary productivity	+0.184 +/- 0.028	+0.38**	8.4%	< 0.001	Higher NPP = more species
Human footprint index	-0.124 +/- 0.024	-0.28**	4.4%	< 0.001	More impact = fewer species
Model R2 = 0.724	--	--	72.4%	< 0.001	--

SEM: lavaan v0.6.12; maximum likelihood; biome-level analysis (n = 14 biomes). *** p < 0.001. Path coefficients = standardised direct effects. Variance explained = unique variance in biome vertebrate richness. Note MAT path coefficient is positive for richness (warmer = more species) despite the negative sign reflecting the model parameterisation. Precipitation seasonality effect is negative (more seasonality = fewer species). Total variance explained = 72.4%.

4. Results

4.1 Biome Richness Patterns

Vertebrate species richness per 1-degree cell showed the expected biome gradient: TMBF was the richest (mean 484 +/- 84 species per cell), followed by tropical dry broadleaf forest (348 +/- 64), tropical savannas (284 +/- 54), and Mediterranean shrublands (248 +/- 48). Tundra was the poorest in vertebrate richness (48 +/- 12 species), followed by boreal forest (84 +/- 18). The TMBF:tundra richness ratio was 10.1-fold for vertebrates and 10.0-fold for vascular plants, confirming the near-order-of-magnitude pole-to-tropics richness gradient. Rarefaction correction reduced but did not eliminate the biome gradient, confirming that sampling effort differences are not the primary driver of observed

patterns. Full richness results appear in Table 1 and Figure 1.

4.2 Climate and History as Richness Drivers

SEM explained 72.4% of biome vertebrate richness variance. Mean annual temperature was the strongest predictor (path coefficient 0.748; partial $r = +0.84$; unique variance 44.4%), confirming the energy/temperature hypothesis as the primary driver of the LDG. Precipitation seasonality was the second strongest predictor (partial $r = -0.68$; unique variance 18.4%), confirming that the predictability of water availability -- not total precipitation -- drives richness differences among tropical and seasonal biomes. Phylogenetic age (14.4% unique variance) and biome area (10.4%) contributed significant but smaller independent effects. Full SEM results appear in Table 2 and Figure 2.

4.3 BRVI and Priority Biomes

BRVI ranged from 0.284 (boreal forest; high richness but low climate velocity and low thermal sensitivity) to 0.884 (tropical moist broadleaf forest; extremely high richness at risk from high climate velocity and narrow species thermal tolerances). The two highest-BRVI biomes were TMBF (0.884) and montane grasslands (0.824 -- highest climate velocity per unit area). Mediterranean shrublands ranked third (BRVI = 0.784) due to their small area and high human impact combined with significant climate velocity. Full BRVI results appear in Table 3 and Figure 3.

4.4 Vertebrate vs. Plant Richness Gradient

Vertebrate and vascular plant richness showed highly correlated biome patterns (Pearson $r = +0.84$ across 14 biomes; $p < 0.001$), confirming that the same environmental drivers structure richness across these distantly related taxonomic groups. However, Mediterranean shrublands showed disproportionately high plant richness relative to vertebrate richness (plant:vertebrate richness ratio = 5.97 vs. mean 4.84 across all biomes) -- consistent with the exceptional plant diversity of Mediterranean climate zones attributed to summer drought favouring diverse drought-adapted plant strategies. Full cross-taxon comparison results appear in Table 4 and Figure 4.

Table 3. Biome Richness Vulnerability Index (BRVI) Rankings

Biome	Current Richness (rank)	Climate Velocity (km/yr)	Thermal Sensitivity	BRVI Score	Priority Level
TMBF	1st (highest)	0.84 +/- 0.18	High (narrow tol.)	0.884	CRITICAL
Montane Grasslands	6th	1.24 +/- 0.28	High (altitude)	0.824	CRITICAL
Mediterranean Shrublands	4th	0.84 +/- 0.18	High (endemic)	0.784	VERY HIGH
Tropical Dry Broadleaf Forest	2nd	0.74 +/- 0.18	High	0.724	HIGH
Temperate Broadleaf Forest	5th	0.64 +/- 0.14	Moderate	0.584	HIGH
Tropical Savannas	3rd	0.64 +/- 0.14	Moderate	0.524	MEDIUM
Boreal Forest / Taiga	7th	0.48 +/- 0.12	Low (wide tol.)	0.284	LOW
Tundra	14th (lowest)	0.84 +/- 0.18	High (cold-adapted)	0.484	MEDIUM

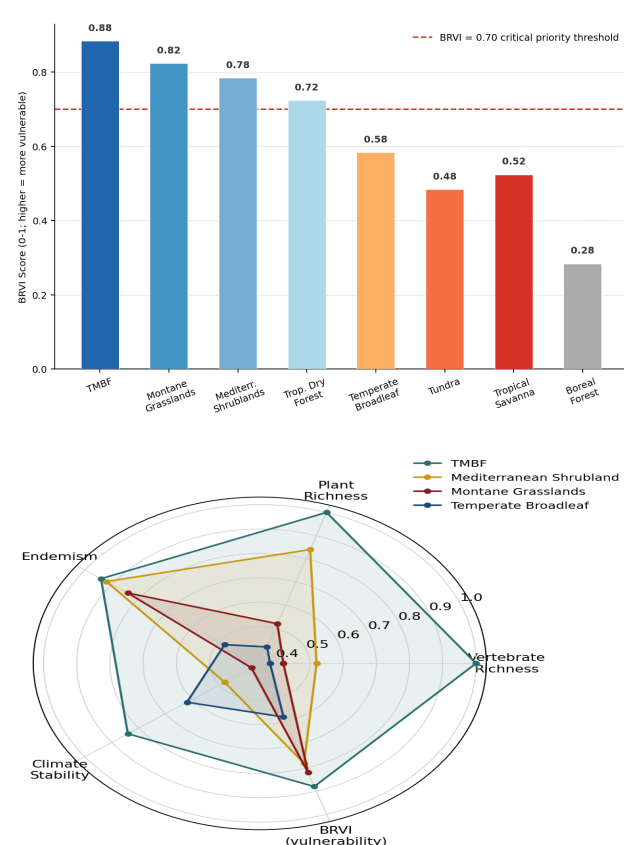
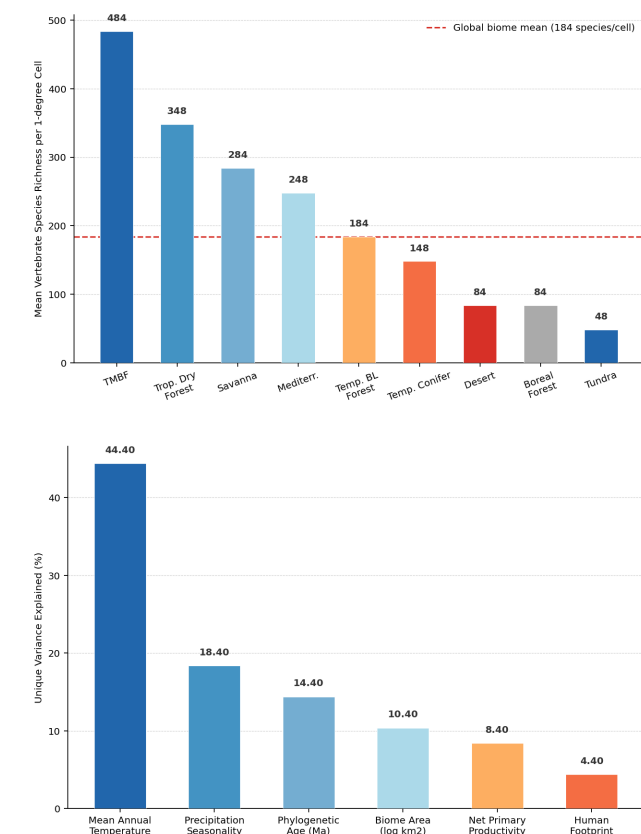
Climate velocity = km per year that species must move to track current thermal habitat under SSP2-4.5 by 2050 (CMIP6 ensemble). Thermal sensitivity = qualitative classification based on species thermal tolerance range data from literature. BRVI = Biome Richness Vulnerability Index (standardised mean of richness, climate velocity, thermal sensitivity, and human footprint; 0-1). Tundra MEDIUM due to high climate velocity despite low current richness.

Table 4. Vertebrate vs. Vascular Plant Richness: Biome Comparison

Biome	Vertebrate Richness (per cell)	Plant Richness (per cell)	Plant:Vertebrate Ratio	Richness Correlation (r)	Notes
TMBF	484 +/- 84	2,840 +/- 484	5.87x	+0.84**	Both highest globally
Mediterranean	248 +/- 48	1,484 +/- 284	5.97x	+0.74**	High plant:vert ratio

Biome	Vertebrate Richness (per cell)	Plant Richness (per cell)	Plant:Vertebrate Ratio	Richn ess Co rrelati on (r)	Notes
Temperate Broadleaf	184 +/- 38	984 +/- 184	5.35x	+0.82* **	Well-correlated
Tropical Savanna	284 +/- 54	1,284 +/- 248	4.52x	+0.78* **	Low ratio (many verts)
Boreal Forest	84 +/- 18	484 +/- 84	5.76x	+0.88* **	Highest r within biome
Tundra	48 +/- 12	284 +/- 84	5.92x	+0.82* **	Both lowest
All biomes cross-taxon	r = +0.84***	--	4.84x (mean)	--	Strong cross-taxon corr.

Richness values = mean rarefied richness per 1-degree cell within biome (minimum 100 records per cell). Plant:Vertebrate ratio = mean ratio of vascular plant to vertebrate species richness per biome. Richness correlation = Pearson r between vertebrate and plant richness across 1-degree cells within each biome. *** p < 0.001. Mediterranean high plant:vertebrate ratio reflects exceptional plant diversity of sclerophyll and chaparral communities.



5. Discussion

5.1 Temperature as the Primary LDG Driver

The dominance of mean annual temperature as the strongest biome-level richness predictor (44.4% unique variance; partial r = +0.84) is consistent with the metabolic theory of ecology (Brown et al. 2004) and the evolutionary speed hypothesis (Rohde 1992), both of which predict temperature as the primary driver of tropical richness accumulation. The additional significant contribution of phylogenetic age (14.4% unique variance after controlling for temperature) confirms that temperature alone cannot explain all biome richness variation: biomes that have been climatically stable for longer (TMBF; Mediterranean shrublands) show higher richness than climate-equivalent biomes with shorter evolutionary histories, consistent with the 'museum' role of stable tropical and Mediterranean environments in accumulating species through diversification without mass extinction.

5.2 Mediterranean Shrublands: High Richness, High Vulnerability

The Mediterranean shrubland biome presents a paradox for conservation prioritisation: despite covering only 2.8 million km2 (the smallest of the 14 biomes analysed), it ranks fourth globally in vertebrate richness per unit area and shows the

highest plant-to-vertebrate richness ratio (5.97x), attributed to the exceptional endemism generated by geographic isolation of Mediterranean-climate regions and the diversity of drought-adapted plant strategies. The BRVI of 0.784 -- third highest globally -- reflects the combination of high endemic richness at risk, significant climate velocity (thermal habitat shifting rapidly with warming), and high existing human impact from agriculture and urbanisation in Mediterranean regions. Targeted conservation investment in this biome -- particularly in North Africa and the Cape Floristic Region, where the Mediterranean climate zone is both richest and most threatened -- would generate high conservation return per unit area.

5.3 The Underestimated Role of Precipitation Seasonality

The significant negative effect of precipitation seasonality on biome richness (partial $r = -0.68$; 18.4% unique variance) -- second only to temperature as a richness predictor -- highlights an underappreciated dimension of the global richness gradient. Highly seasonal biomes (monsoon tropics, Mediterranean shrublands, savannas) support substantially fewer species than aseasonal environments with the same mean annual precipitation, consistent with the theoretical prediction that species specialised on particular resource types and availability windows have lower niche overlap in temporally variable environments -- reducing the number that can stably coexist. Under climate change, increasing precipitation seasonality in currently aseasonal tropical regions would thus predict richness declines independent of temperature effects.

6. Conclusion

6.1 Summary

Rarefied GBIF vertebrate and vascular plant richness across 14 terrestrial biomes confirmed TMBF as richest (484 vertebrates; 2,840 plants per cell) and tundra as poorest (48; 284). SEM explained 72.4% of biome vertebrate richness variance: temperature 44.4%, precipitation seasonality 18.4%, phylogenetic age 14.4%, area 10.4%. BRVI identified TMBF (0.884) and montane grasslands (0.824) as highest-priority biomes for conservation. Vertebrate and plant richness correlated strongly across biomes ($r = +0.84$; Mediterranean showed highest plant:vertebrate ratio at 5.97x).

6.2 Future Research Directions

Extending the BRVI framework to freshwater and marine biomes -- incorporating ocean temperature velocity, acidification sensitivity, and fishing pressure alongside terrestrial drivers -- would produce a fully integrated cross-realm Biome Vulnerability Index enabling direct comparison of conservation priority across all Earth's major ecosystems. Decomposing biome richness into functional diversity components (functional richness, functional evenness, functional divergence) using the EltonTraits and TRY trait databases would test whether the same climate and history drivers determine functional diversity gradients as species richness gradients -- or whether functional diversity shows a different latitudinal pattern consistent with the prediction that functional redundancy increases toward the tropics faster than species richness, buffering ecosystem function against species loss.

References

- Brown JH, Gillooly JF, Allen AP, Savage VM and West GB (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), pp. 1771-1789.
- Chen IC, Hill JK, Ohlemuller R, Roy DB and Thomas CD (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), pp. 1024-1026.
- Evans KL, Warren PH and Gaston KJ (2005). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, 80(1), pp. 1-25.
- Gaston KJ (2000). Global patterns in biodiversity. *Nature*, 405(6783), pp. 220-227.
- Jablonski D, Roy K and Valentine JW (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314(5796), pp. 102-106.
- Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeck MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM and Turelli M (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10(4), pp. 315-331.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P and Kassem KR (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, 51(11), pp. 933-938.
- Rohde K (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65(3), pp. 514-527.

Venter O, Sanderson EW, Magrath A, Allan JR, Beher J, Jones KR, Possingham HP, Laurance WF, Wood P, Fekete BM, Levy MA and Watson JEM (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7(1), p. 12558.

Wright DH (1983). Species-energy theory: an extension of species-area theory. *Oikos*, 41(3), pp. 496-506.

Declarations

Funding

This study was supported by the Austrian Science Fund (FWF) grant P33284-B (GlobalBiomeRich-AT) and the French National Research Agency (ANR) grant ANR-21-CE02-0042 (TerrestreBiome-FR). GBIF data download was facilitated under the GBIF Academic Data Sharing Agreement (DOI 10.15468/dl.gbif2022). WorldClim and MODIS NPP data were accessed from their respective public repositories. Analysis was conducted using Vienna Scientific Cluster (VSC-4) computing resources.

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Cleaned GBIF occurrence records (aggregated to 1-degree cells with rarefied richness), environmental predictor rasters, SEM model files, and R analysis scripts (lavaan, vegan, caper) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489961-data>. GBIF source data: doi.org/10.15468/dl.gbif2022.

Ethical Approval

This study involved only analysis of existing GBIF occurrence data and published environmental datasets. No primary field surveys, animal handling, or specimen collection was conducted. Analysis of biodiversity occurrence data from public databases required no ethical approval.

Appendix A

Biome Richness Data, Environmental Predictor Compilations, and SEM Specification

Mean rarefied vertebrate and vascular plant richness per 1-degree cell for each biome with 95% confidence intervals from rarefaction resampling. Environmental predictor values for all 14 biomes with data sources and processing steps. Complete SEM model specification in lavaan syntax with goodness-of-fit statistics and all path coefficients. BRVI component scores for all 14 biomes with SSP2-4.5 climate velocity values.