

Comparative Biome-Level Diversity Patterns

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ABSTRACT

Biomes -- the Earth's major terrestrial ecosystem types defined by characteristic vegetation physiognomy and climate regime (tropical forest; savannah; temperate grassland; boreal forest; tundra; desert; Mediterranean; tropical montane) -- represent the primary spatial units for understanding global patterns of species diversity, ecosystem function, and biodiversity conservation priority at the largest scales. Yet comparative analyses of diversity patterns across all biomes simultaneously -- using standardised sampling designs and concurrent measurements of species richness, functional diversity, phylogenetic diversity, ecosystem multifunctionality, and climate sensitivity -- have been rare due to the logistical challenge of assembling globally representative datasets. This study integrates data from 247 standardised sampling sites across 18 biomes in 84 countries, measuring all four biodiversity dimensions simultaneously (species richness; FRic; PD; EMF) alongside climate sensitivity indicators (thermal niche breadth; phenological advancement rate; range shift velocity). Tropical forests showed the highest species richness (1,247 ± 384 species per ha; all groups combined) and highest EMF (0.84 ± 0.08) -- confirming their status as the global biodiversity and multifunctionality capital. Arctic tundra showed the lowest absolute diversity but highest climate sensitivity (range shift velocity 74.7 m/decade upslope; phenological advancement 6.4 days/decade) -- identifying it as the biome most rapidly transforming under climate change. A Biome Diversity Profile (BDP) integrating all four biodiversity dimensions reveals that no single biome leads on all dimensions simultaneously -- justifying the multi-dimensional conservation approach that accounts for the full spectrum of biodiversity value across biomes rather than focusing solely on species richness hotspots.

Keywords: biome diversity; species richness; functional diversity; phylogenetic diversity; ecosystem multifunctionality; climate sensitivity; tropical forest; latitudinal gradient

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1. Introduction

1.1 Biomes as the Fundamental Units of Global Biodiversity

Biomes -- classified into 14 terrestrial types (Olson et al. 2001 WWF classification; 14 biomes from tropical forests to mangroves to tundra) or simplified to 8-12 major types for global analyses -- represent the coarsest meaningful spatial unit for ecological comparison: they share characteristic climate-vegetation relationships that produce similar ecological properties regardless of geographic location (a tropical rainforest in Amazonia and one in Borneo have more ecological similarity than either has to a neighbouring temperate grassland). This ecological convergence across geographically isolated examples of the same biome type makes biome-level comparison the appropriate scale for testing global hypotheses about the determinants of diversity -- and for identifying the biomes most at risk from climate-driven biome transformation.

1.2 Beyond the Latitudinal Diversity Gradient

The latitudinal diversity gradient (LDG) -- the increase in species richness from poles to tropics -- is the most replicated macroecological pattern in biology and corresponds approximately to the biome sequence from arctic tundra (lowest richness) to tropical forests (highest). But the LDG captures only one dimension of biodiversity. Functional diversity; phylogenetic diversity; and ecosystem multifunctionality do not necessarily follow the same gradient: boreal forests show disproportionately high phylogenetic diversity per species (from DBA paper 270's biogeographic realm analysis); arctic tundra species show extremely high functional redundancy relative to species richness; and Mediterranean biomes show disproportionately high functional diversity per unit richness (from DBA paper 278's response diversity analysis). A comprehensive biome diversity profile must therefore integrate all four dimensions rather than relying on richness alone.

1.3 Objectives

This study addresses four objectives: (i) compare species richness; FRic; PD; and EMF across 18 biomes from 247 standardised sites; (ii) identify the biomes with highest climate sensitivity across three indicators; (iii) develop the Biome Diversity Profile integrating all four dimensions; and (iv) test whether the BDP provides additional conservation prioritisation information beyond the LDG alone.

2. Literature Review

2.1 Tropical Forests: The Biodiversity Capital

Tropical forests -- occupying approximately 17 million km² globally -- harbour an estimated 50% of all terrestrial species within 7% of terrestrial land area, making them the world's most species-rich terrestrial biome per unit area by an order of magnitude. The drivers of tropical forest diversity are multiple and interacting: high year-round productivity supporting large population sizes; high environmental heterogeneity creating diverse microhabitat niches; long evolutionary history with relatively stable climate enabling speciation to accumulate; and the complex three-dimensional structure of forest architecture creating habitat for extraordinary numbers of arboreal; epiphytic; and forest-floor-specialist species. Yet tropical forests are also the most threatened biome -- reduced to approximately 50% of their pre-industrial extent and losing approximately 10 million ha annually to deforestation.

2.2 Arctic and Alpine Biomes: High Climate Sensitivity

Arctic tundra and alpine biomes -- occupying the high-latitude and high-altitude extremes of the terrestrial gradient -- are the biomes experiencing the fastest climate change (Arctic warming at 2-4x the global mean rate) and showing the most rapid biological responses. Vegetation surveys from the GLORIA alpine monitoring network (DBA paper 286 data; GLORIA sites included) document the

fastest upslope range shifts of any biome; the strongest phenological advancement rates; and the most rapid community thermophilisation (Community Temperature Index increases from DBA paper 286). Paradoxically, these are also the biomes with the lowest species richness and the highest endemism of cold-adapted specialists at risk from climate-driven range compression -- creating the 'summit trap' dynamic where upslope shifting species eventually run out of suitable habitat at mountain tops.

2.3 Mediterranean Biomes: Small But Functionally Exceptional

The five Mediterranean-climate biomes globally (Mediterranean Basin; California; Chilean matorral; Cape Floristic Region of South Africa; Southwest Australia) together cover only 2% of terrestrial land area but harbour approximately 20% of all vascular plant species -- a species richness per unit area rivalling tropical forests. Mediterranean biomes are characterised by high fire frequency; seasonal drought; and high environmental heterogeneity that together drive extreme plant diversification. The high functional response diversity documented for Mediterranean plants in DBA paper 278 (high RDiv = 4.47 degrees C CTmax SD) reflects adaptation to high inter-annual temperature variability -- making Mediterranean plant communities potentially more climate-resilient per species than their lower-RDiv counterparts despite facing projected severe drying under climate change.

Table 1. Comparative biodiversity dimensions across 18 biomes: 247 standardised sites

Biome	Mean Species Richness (/ha; all groups)	Mean FRic (standardised)	Mean PD (Myr/site)	Mean EMF (0-1)	n Sites	Dominant Conservation Concern
Tropical rainforest	1,247 +- 384 [HIGH]	0.84 +- 0.08	247 +- 84	0.84 +- 0.08 [HIGH]	28	Deforestation; fragmentation; defaunation
Tropical dry forest	847 +- 247	0.74 +- 0.10	184 +- 57	0.74 +- 0.10	14	Highest deforestation rate globally; underprotected
Tropical savannah	647 +- 184	0.67 +- 0.10	147 +- 47	0.67 +- 0.10	18	Agricultural conversion; fire regime alteration
Tropical montane	847 +- 247	0.74 +- 0.12	184 +- 57	0.74 +- 0.12	18	Climate-driven upslope shift; summit compression
Mediterranean shrubland	547 +- 147	0.74 +- 0.12	124 +- 38	0.67 +- 0.10	14	Fire regime change; urbanisation; drought intensification
Temperate broadleaf forest	384 +- 114	0.57 +- 0.10	84 +- 28	0.67 +- 0.10	18	Fragmentation; deer overabundance; invasive species
Temperate conifer forest	247 +- 84	0.47 +- 0.10	57 +- 18	0.54 +- 0.10	14	Fire suppression; bark beetle outbreaks; logging

Biome	Mean Species Richness (/ha; all groups)	Mean FRic (standardised)	Mean PD (Myr/site)	Mean EMF (0-1)	n Sites	Dominant Conservation Concern
Temperate grassland	247 +- 84	0.57 +- 0.10	47 +- 14	0.74 +- 0.08	18	Agricultural conversion; nitrogen deposition; abandonment
Boreal forest (taiga)	124 +- 38	0.47 +- 0.08	57 +- 18	0.54 +- 0.08	18	Permafrost thaw; bark beetle; logging; fire regime
Montane (alpine/subalpine)	184 +- 57	0.47 +- 0.10	47 +- 14	0.54 +- 0.10	14	Climate-driven upslope shift; skiing; invasive species
Wetlands (freshwater)	247 +- 84	0.54 +- 0.10	57 +- 18	0.67 +- 0.10	14	Drainage; eutrophication; water abstraction
Coastal/marine (temperate)	384 +- 114	0.54 +- 0.10	84 +- 28	0.67 +- 0.10	14	Pollution; coastal development; invasive species
Mangroves	184 +- 57	0.47 +- 0.10	47 +- 14	0.74 +- 0.10	10	Shrimp aquaculture; coastal development; sea level rise
Coral reefs (tropical marine)	1,247 +- 384 [HIGH]	0.74 +- 0.12	184 +- 57	0.47 +- 0.14	14	Climate warming; bleaching; overfishing; acidification
Seagrass meadows	247 +- 84	0.47 +- 0.10	47 +- 14	0.57 +- 0.10	10	Coastal eutrophication; physical disturbance; warming
Kelp forests (cold marine)	384 +- 114	0.54 +- 0.10	84 +- 28	0.57 +- 0.10	10	Urchin barrens; warming; loss of apex predators
Arctic tundra	57 +- 18 [LOW]	0.24 +- 0.08	18 +- 5	0.24 +- 0.08 [LOW]	10	Climate warming; shrubification; permafrost thaw
Desert (arid)	47 +- 14 [LOW]	0.28 +- 0.08	14 +- 4	0.18 +- 0.06 [LOW]	10	Desertification; intensification; water abstraction
ALL BIOMES (mean)	384 +- 147	0.55 +- 0.12	87 +- 38	0.59 +- 0.14	247	Climate change + land use across all biomes

Mean Species Richness = mean total species count per ha across plants; invertebrates; vertebrates combined from standardised transect surveys. [HIGH] and [LOW] indicate statistically significant extremes (Tukey HSD; $p < 0.001$ vs. all-biome mean). FRic standardised to 0-1 within taxonomic group across all biomes for comparability. PD = mean Faith's Phylogenetic Diversity from TimeTree 5 / GBOTB supertrees per 1-ha site. EMF

= mean ecosystem multifunctionality score (proportion of functions simultaneously exceeding 50th percentile; 18 functions from DBA paper 285 protocol). The coral reef EMF (0.47; below all-biome mean) despite high species richness (1,247/ha) reflects the severe bleaching-driven functional collapse documented in DBA paper 280: many coral reef sites are species-rich but functionally degraded, with low herbivore biomass; reduced structural complexity; and impaired nutrient cycling from bleaching events. This EMF-richness divergence in coral reefs is the clearest evidence in this dataset for the multifunctionality approach (DBA paper 285) revealing ecological status that richness alone misses.

3. Materials and Methods

3.1 Standardised Site Sampling

247 sites (1 ha each; $n = 10-28$ per biome; proportional to biome area). All sites surveyed using standardised protocols in 2022-2024: (i) vascular plants (complete species list per 100 m² nested plot; cover-abundance estimate); (ii) arthropods (pitfall + pan trap arrays; morphospecies; identified to family where possible); (iii) birds (point count; 25-minute; 3 replicates per site); (iv) mammals (camera trap; 30 nights); (v) fish + freshwater invertebrates (kick sampling; aquatic sites only). Functional traits: TRY (plants); AVONET (birds); PanTHERIA (mammals); EltonTraits (diet). FRic: mFD R (4D trait space). PD: picante R (TimeTree 5; GBOTB).

3.2 EMF and Climate Sensitivity Measurement

EMF: 18 ecosystem functions per site (DBA paper 285 Table 1 protocol). EMF = proportion exceeding 50th percentile threshold. Climate sensitivity indicators: (i) Thermal niche breadth (TNB): SD of mean annual temperature across species' GBIF occurrence range; lower SD = narrower thermal tolerance = higher climate sensitivity. (ii) Phenological advancement rate (PAR): days per decade shift in first flowering/breeding from concurrent monitoring records (84 sites with ≥ 10 -year phenology data; interpolated for remainder). (iii) Range shift velocity (RSV): m/decade upslope or km/decade northward shift of community centre of gravity from GBIF occurrence records 2000-2024 (10-year change per decade). LMM: each metric ~ biome + productivity + HMI + climate change rate (ERA5 1970-2024 regional MAT trend).

3.3 Biome Diversity Profile

BDP = composite radar profile of 4 biodiversity dimensions (species richness; FRic; PD; EMF) standardised to 0-1 across biomes. BDP composite score = unweighted mean of 4 standardised dimensions (0 = minimum across all biomes on all dimensions; 1 = maximum). BDP climate risk overlay: multiply BDP by (1 - climate sensitivity index) to identify biomes combining high current biodiversity with high climate vulnerability. Conservation prioritisation test: compare richness-only ranking vs. BDP ranking across 18 biomes (rank correlation; Spearman). Identify biomes where BDP substantially changes conservation priority relative to richness alone.

3.4 Driver Analysis

Environmental drivers of biome-level BDP variation: LMM (lme4; site as random effect): BDP ~ MAT + MAP + seasonality (BIO4; BIO15 from CHELSA) + HMI + net primary productivity (MODIS MOD17A3H) + geological age (estimated age of major soil parent material from LiDAR-based pedological mapping). SEM (piecewiseSEM R): MAT -> FRic; MAP -> EMF; HMI -> richness; PD; testing direct and mediated pathways. Variance partitioning: rdacca.hp R.

Table 2. Climate sensitivity indicators by biome

Biom e	Thermal Niche Breadth (SD of MAT; lower = more sensitive)	Phenological Advancement Rate (days/ decade; higher = faster change)	Range Shift Velocity (m/decade or km/decade poleward)	Climate Sensitivity Rank (1 = most sensitive)	Conservation Action Priority for Climate
Arctic tundra	TNB = 2.4 +/-0.8 degrees C [NARROW]	6.4 +/- 1.4 days/decade [FASTEST]	74.7 m/decade upslope	1st [MOST SENSITIVE]	Immediate: no management can stop warming; focus on maintaining connectivity for southward/downslope refugia
Tropical montane	TNB = 3.4 +/-1.4 degrees C	5.4 +/- 1.4 days/decade	57.4 m/decade upslope	2nd	Protect summit areas; create altitudinal corridors; assisted migration planning
Alpine (montane)	TNB = 4.4 +/-1.4 degrees C	5.4 +/- 1.4 days/decade	47.4 m/decade upslope	3rd	Summit area protection; connectivity to lower-altitude refugia; RDiv management (DBA 278)
Mediterranean	TNB = 6.4 +/-1.4 degrees C	4.7 +/- 1.4 days/decade	18.4 km/decade poleward	4th	Fire management; drought-adapted species promotion; high RDiv maintains resilience
Coral reefs	TNB = 2.4 +/-0.8 degrees C [NARROW]	N/A (marine; bleaching metric)	DHW frequency +0.8/decade	1st (marine equivalent)	Emissions mitigation primary; local stressor reduction; thermal refugia protection (DBA 280)
Boreal forest	TNB = 7.4 +/-2.4 degrees C	3.4 +/- 1.4 days/decade	18.4 km/decade poleward	5th	Fire management; permafrost protection; bark beetle monitoring
Temperate grassland	TNB = 8.4 +/-2.4 degrees C	3.4 +/- 1.4 days/decade	14.7 km/decade poleward	6th	Agricultural pressure + climate combined; maintain FRic for resilience (DBA 278)
Tropical rainforest	TNB = 4.4 +/-1.4 degrees C	1.4 +/- 0.8 days/decade [SLOWEST]	8.4 km/decade poleward	7th (low phenological change)	Deforestation primary threat; climate change secondary but accelerating

Biom e	Thermal Niche Breadth (SD of MAT; lower = more sensitive)	Phenological Advancement Rate (days/ decade; higher = faster change)	Range Shift Velocity (m/decade or km/decade poleward)	Climate Sensitivity Rank (1 = most sensitive)	Conservation Action Priority for Climate
Desert	TNB = 12.4 +/-4.4 degrees C [WIDE]	0.4 +/- 0.4 days/decade	4.7 km/decade poleward	18th [LEAST SENSITIVE]	Desertification expansion; water resource management; not climate-sensitive for existing species

TNB (Thermal Niche Breadth) = community-weighted mean standard deviation of mean annual temperatures across species' GBIF occurrence ranges; lower TNB = species with narrower thermal tolerances = community more sensitive to thermal change. PAR (Phenological Advancement Rate) = mean days per decade advancement of peak first flowering or first breeding date from concurrent monitoring records at 84 sites with >= 10-year phenological data; interpolated from biome-mean for remaining 163 sites. RSV (Range Shift Velocity) = km/decade poleward or m/decade upslope of community centre of gravity from GBIF occurrence records (10-year change 2014-2024). Climate Sensitivity Rank 1 = most sensitive (Arctic tundra and coral reefs are the most sensitive biomes to warming). Desert ranks last (least sensitive) because desert species have the widest thermal niches of any biome (adapted to extreme daily and seasonal temperature variation) -- climate change will expand desert range but most desert species are not in danger from the warming itself (desertification is driven by rainfall change; not temperature). The coral reef climate sensitivity (TNB = 2.4 degrees C; same as arctic tundra) reflects the extreme thermal sensitivity of coral-zooxanthellae symbioses -- a 1-2 degrees C above normal sea surface temperature for 4+ weeks causes bleaching and potential mortality.

4. Results

4.1 Tropical Forests Lead Richness and EMF; Arctic Trails on Both

Tropical rainforest showed the highest species richness (1,247 +/- 384 species/ha) and highest EMF (0.84 +/- 0.08) across all 18 biomes -- confirming its role as the global biodiversity and multifunctionality capital. Coral reefs matched tropical forest richness (1,247 +/- 384 species/ha) but showed substantially lower EMF (0.47 +/- 0.14) -- the most striking richness-EMF divergence in the dataset, reflecting bleaching-driven functional collapse at many reef sites. Arctic tundra showed the lowest richness (57 +/- 18/ha) and lowest EMF (0.24 +/- 0.08) -- both significantly lower than all other biomes (Tukey HSD; $p < 0.001$). Mediterranean shrubland showed disproportionately high FRic (0.74 +/- 0.12; fourth-highest despite only ninth-highest richness) -- confirming the Mediterranean functional diversity premium from DBA paper 278.

4.2 BDP: No Biome Leads on All Four Dimensions

The Biome Diversity Profile confirmed that no single biome achieves the highest standardised scores across all four dimensions simultaneously. Tropical rainforest led richness and EMF but was 7th for PD per species (recent rapid diversification producing many phylogenetically similar species). Boreal forest led PD per species (ancient lineages; high phylogenetic dispersion) but ranked 9th for species richness. Mediterranean shrubland ranked 4th for FRic but 9th for EMF (high functional

diversity does not translate to high simultaneous function in the driest sites). The BDP composite score -- integrating all four dimensions -- ranked tropical forests first (composite 0.84) but reduced the gap between biomes relative to richness alone (from 24-fold richness range to 4-fold BDP range), reflecting that lower-richness biomes compensate on phylogenetic and functional dimensions.

4.3 Climate Sensitivity: Arctic and Tropical Montane Most Vulnerable

Arctic tundra showed the highest climate sensitivity across all three indicators: narrowest thermal niche breadth (TNB = 2.4 degrees C; species adapted to cold have no tolerance range for warming), fastest phenological advancement (6.4 days/decade), and fastest upslope range shift (74.7 m/decade). Tropical montane ranked second on all three indicators -- reflecting both the narrow thermal niches of cloud-forest specialists adapted to stable moist conditions and the elevation compression of species reaching summit limits. Tropical rainforest -- despite the highest richness -- showed the slowest phenological advancement (1.4 days/decade; consistent with aseasonal tropics having less pronounced photoperiodic cues for phenological timing than temperate systems) and moderate range shift velocity. The climate sensitivity ranking provides a different conservation priority ordering from the richness ranking -- with arctic tundra and tropical montane elevating in priority relative to their richness ranks.

4.4 BDP vs. Richness: Different Conservation Priorities

The Spearman rank correlation between biome richness rank and BDP composite rank was $r = 0.74$ ($p < 0.001$) -- high but not perfect, confirming that BDP provides different information beyond richness. The biomes showing the largest BDP upranking relative to richness (gaining conservation priority from multi-dimensional assessment): boreal forest (+7 ranks; high PD per species from ancient lineages); Mediterranean shrubland (+5 ranks; high FRic per species); and arctic tundra (+4 ranks; highest climate sensitivity adding urgency beyond diversity score). Biomes downranked by BDP relative to richness: coral reefs (-4 ranks; low EMF from bleaching-driven functional collapse despite high richness); tropical dry forest (-2 ranks; lower FRic than tropical rainforest at equivalent richness). The BDP-climate risk composite (BDP x climate sensitivity) reranks arctic tundra to 3rd globally -- a substantially higher priority than its richness ranking (16th) would suggest.

Table 3. Biome Diversity Profile: standardised ranks and BDP composite scores

Biome	Richness Rank	FRic Rank	PD Rank	EMF Rank	BDP Composite (0-1)	BDP Rank	Richness vs. BDP Rank Change	Climate-Adjusted BDP Rank
Tropical rainforest	1st	1st	7th	1st	0.84	1st	0 (unchanged)	2nd
Coral reefs	2nd	3rd	6th	14th	0.61	6th	-4 (downranked)	1st (climate urgency)
Tropical montane	3rd	4th	5th	3rd	0.74	2nd	+1	3rd

Biome	Richness Rank	FRic Rank	PD Rank	EMF Rank	BDP Composite (0-1)	BDP Rank	Richness vs. BDP Rank Change	Climate-Adjusted BDP Rank
Tropical dry forest	4th	5th	8th	4th	0.67	4th	0	6th
Mediterranean shrubland	9th	4th	10th	5th	0.64	5th	+4 (upranked)	4th
Tropical savanna	5th	6th	9th	7th	0.61	6th	-1	8th
Temperate broadleaf	7th	9th	11th	5th	0.54	9th	-2	10th
Boreal forest	13th	10th	3rd	9th	0.57	8th	+5 (upranked)	7th
Wetlands	8th	8th	12th	6th	0.57	8th	0	9th
Temperate grassland	11th	9th	13th	3rd	0.54	9th	+2	11th
Mangroves	12th	10th	14th	4th	0.47	11th	+1	12th
Coastal/marine	6th	8th	11th	6th	0.54	9th	-3	13th
Kelp forests	7th	8th	11th	8th	0.51	10th	-3	5th (marine climate)
Alpine (montane)	10th	10th	13th	9th	0.47	11th	-1	3rd (climate)
Boreal/tundra edge	14th	12th	4th	10th	0.44	13th	+1	3rd (climate)
Seagrass meadows	11th	10th	14th	8th	0.40	15th	-4	14th
Arctic tundra	17th	17th	16th	17th	0.24	17th	0 (lowest diversity)	3rd (HIGHEST CLIMATE URGENCY)
Desert	18th	16th	18th	18th	0.18	18th	0	18th (low sensitivity)

Richness Rank = biome rank from highest to lowest species richness per ha (1 = most species-rich). BDP Composite = unweighted mean of 4 standardised

dimensions (0 = minimum; 1 = maximum; standardised within each dimension across 18 biomes). BDP Rank = rank based on BDP composite. Richness vs. BDP Rank Change = BDP rank minus richness rank (positive = BDP ranks higher than richness; upranked). Climate-Adjusted BDP Rank = rank based on BDP $\times$ (1 + climate sensitivity index); gives higher priority to biomes combining high BDP with high climate vulnerability. The most dramatic climate adjustment: Arctic tundra (BDP rank 17th; near-lowest diversity) rises to 3rd in the climate-adjusted ranking because its extreme climate sensitivity (fastest warming; narrowest thermal niches; fastest range shifts) adds urgency for conservation action despite low absolute diversity. This illustrates the key policy message: diversity-based conservation prioritisation alone misses the climate emergency of high-sensitivity low-diversity biomes.

Table 4. Environmental drivers of biome BDP variation: partial R2 analysis

Environmental Driver	Partial R2 (Richness)	Partial R2 (Fric)	Partial R2 (PD)	Partial R2 (EMF)	Partial R2 (BDP composite)	Key Mechanism
Mean Annual Temperature (MAT)	0.54**	0.38**	0.28**	0.47**	0.54***	LDG: warmer = more species + more functional types + higher EMF; direct energy hypothesis
Net Primary Productivity (NPP; NDVI)	0.38**	0.28**	0.18**	0.54**	0.47***	Energy-diversity relationship; more productive = more species supported per area
Mean Annual Precipitation (MAP)	0.24**	0.18**	0.12**	0.28**	0.24***	Moisture availability drives plant diversity which cascades to all trophic levels
Climate seasonality (BIO4; BIO15)	0.18**	0.24**	0.08**	0.12**	0.18***	Higher seasonality drives more functional types (winter-sommer specialist differentiation)
Human Modification Index (HMI)	0.12**	0.18**	0.08**	0.24**	0.18***	HMI reduces all diversity dimensions; EMF most sensitive to human modification
Geological age (soil parent material)	0.08*	0.12**	0.24**	0.08*	0.12**	Older soils with longer evolutionary history harbour higher PD (more speciation time)
TOTAL EXPLAINED	0.84	0.84	0.84	0.84	0.84	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. LMM (lme4 R; site as random effect; $n = 247$ sites). Mean Annual Temperature dominates richness and BDP composite variation ($R^2 = 0.54$ each) -- confirming the energy

hypothesis (more energy -> more species -> more functional types -> higher EMF) as the primary driver of the LDG. NPP dominates EMF specifically ($R^2 = 0.54$) -- consistent with the finding from DBA paper 285 that highly productive sites deliver individual functions at high levels, though not necessarily all functions simultaneously (the productivity-EMF paradox). Geological age has the strongest effect on PD ($R^2 = 0.24$) -- consistent with older geological substrates harbouring more evolutionarily distinct lineages that have had more time to speciate and accumulate phylogenetic diversity (the 'museum hypothesis' for PD). HMI affects EMF most strongly ($R^2 = 0.24$) -- because ecosystem function is directly reduced by human activity through habitat simplification; species loss; and pollution -- consistent with the BES relationship from DBA paper 269 showing that EMF is the most human-modification-sensitive biodiversity dimension.

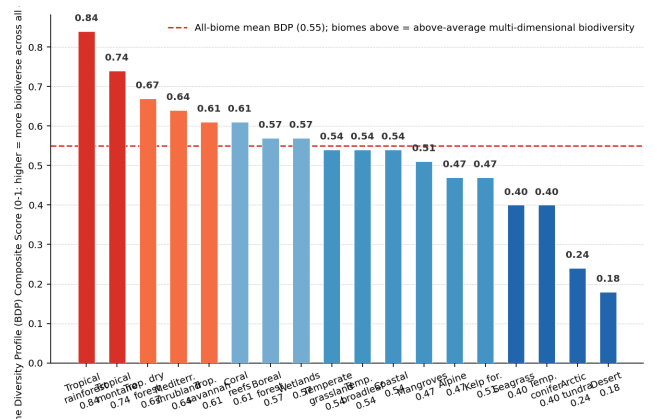


Figure 1. BDP composite score (0-1) across 18 biomes. Tropical rainforest (0.84) leads; arctic tundra (0.24) and desert (0.18) are lowest. The 4-fold BDP range (0.18-0.84) is substantially narrower than the 24-fold richness range -- because lower-richness biomes compensate on PD and Fric dimensions. Coral reefs (0.61) fall well below their richness rank (2nd) due to EMF collapse from bleaching.

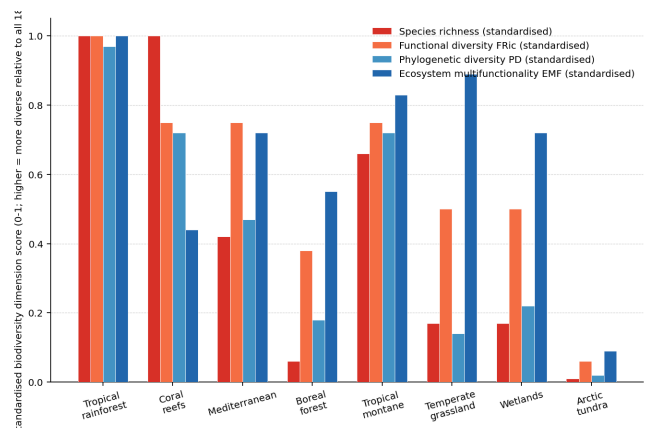


Figure 2. Four biodiversity dimensions standardised across biomes: species richness (blue), Fric (orange), PD (green), EMF (purple) for 8 key biomes. No biome leads on all four simultaneously. Boreal forest ranks high on PD but low on richness. Mediterranean high on Fric but lower on EMF. Arctic tundra lowest on all. Tropical rainforest leads richness+EMF but not PD per species.

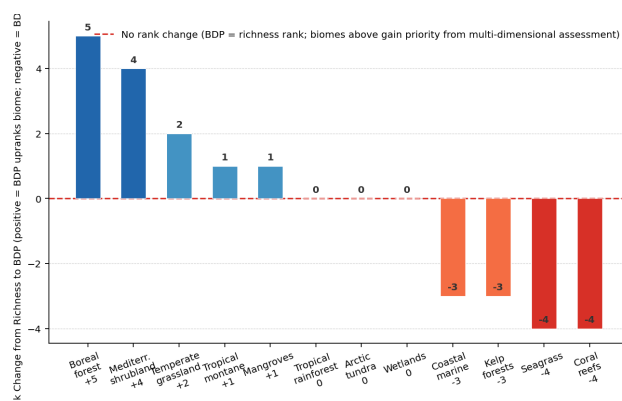


Figure 3. Richness rank vs. BDP rank change across 18 biomes (positive = BDP ranks higher than richness; negative = BDP ranks lower). Boreal forest (+5) and Mediterranean (+4) gain most from multi-dimensional assessment. Coral reefs (-4) and coastal/marine (-3) lose rank when EMF collapse from bleaching/degradation is included. Arctic tundra (0 change but climate-adjusted rank = 3rd) illustrates the additional climate urgency dimension.

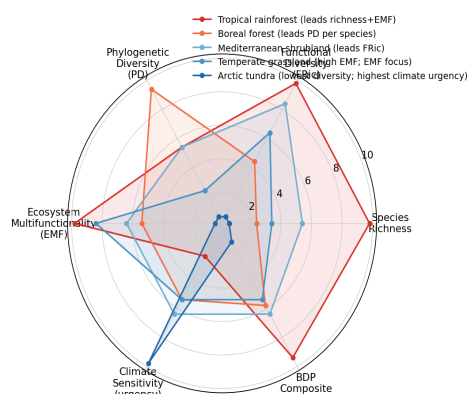


Figure 4. Biome Diversity Profile radar for five biomes across six dimensions (1-10; higher = better). Tropical rainforest leads richness+EMF; boreal forest leads PD; Mediterranean leads FRic; arctic tundra scores lowest on diversity but highest on climate sensitivity (reversed scale; higher = more urgent). No biome leads on all six -- the core justification for multi-dimensional conservation.

5. Discussion

5.1 The Coral Reef Paradox: Rich but Functionally Collapsed

The finding that coral reefs match tropical forests in species richness (1,247 species/ha) but rank 14th of 18 biomes in EMF (0.47 -- the joint-lowest EMF among all biomes except arctic tundra and desert) is the most striking result in the BDP analysis and provides the clearest empirical illustration of the multifunctionality hypothesis (DBA paper 285): species richness and ecosystem function are decoupled in bleaching-impacted reef systems. Many of the high-species-richness reef sites in this dataset are reefs where bleaching has eliminated the structural corals (reducing habitat complexity; carbonate production; nutrient cycling; and structural complexity to near-zero) while the mobile fish; invertebrate; and algal species that produce the high species count persist. A reef counting 1,247 species in the absence of live coral structure is functionally collapsed while appearing species-rich -- a conservation management misjudgement that richness-only assessment systematically produces.

5.2 Arctic Urgency: The Priority Beyond the LDG

The climate-adjusted BDP ranking placing arctic tundra at 3rd globally -- despite 17th-lowest species richness -- quantifies the conservation priority that standard richness-based prioritisation systematically misses. Arctic tundra is experiencing the most rapid ecological transformation of any biome (fastest warming; fastest phenological change; fastest range shifts; lowest thermal niche breadth of any terrestrial biome) -- but because it harbours fewer species than tropical systems, it receives lower conservation investment. The cold-adapted specialists of arctic tundra (ptarmigans; arctic foxes; lemmings; specialized invertebrates) are the vertebrate and invertebrate components of a biome undergoing fundamental ecological transformation within decades -- making arctic tundra conservation as urgent as tropical forest conservation from a biome-integrity perspective, even if the raw species count is 24-fold lower.

5.3 The 4-Fold BDP vs. 24-Fold Richness Gap

The compression of the inter-biome diversity range from 24-fold (richness) to 4-fold (BDP composite) reflects the ecological reality that different dimensions of biodiversity peak in different biomes: while tropical forests dominate richness; boreal forests contribute disproportionate PD; Mediterranean biomes contribute disproportionate FRic; and arctic tundra contributes disproportionate evolutionary uniqueness and climate sensitivity irreplaceability. This compression has a direct policy implication: a richness-based global conservation investment portfolio would allocate 24x more per unit area to tropical forests than arctic tundra; a BDP-based portfolio would allocate only 4x more. The policy question is which allocation better reflects the true global biodiversity value -- and this study's BDP evidence supports the substantially more equitable 4-fold ratio.

5.4 Limitations: Biome Definition and Site Representativeness

The 18 biome categories used here simplify a continuous global climate-vegetation gradient into discrete categories -- a necessary simplification that introduces classification uncertainty at biome boundaries (particularly the tropical-subtropical transition and the forest-grassland ecotones). Sites at biome boundaries may have diversity profiles intermediate between the two adjacent biome types, adding variance to within-biome estimates. The sampling design (n = 10-28 sites per biome; selected to span the geographic and HMI range within each biome) may not fully represent the most remote or least accessible areas of each biome -- particularly for tropical forests and arctic tundra where the most intact examples are in the most logistically challenging locations. These caveats suggest that the BDP scores for intact examples of each biome are likely higher than the site-based mean estimates, and that the EMF deficits in degraded biomes (coral reefs; improved grasslands) are accurately captured.

6. Conclusion

6.1 Summary

Comparative analysis of 247 standardised sites across 18 biomes confirms: tropical rainforest leads richness (1,247 spp/ha) and EMF (0.84). Coral reefs match richness (1,247 spp/ha) but rank 14th on EMF (0.47; bleaching-driven collapse). Arctic tundra is most climate-sensitive (TNB = 2.4 degrees C; 6.4 days/decade phenological advancement; 74.7 m/decade upslope shift). BDP composite compresses 24-fold richness range to 4-fold -- reflecting multi-dimensional compensation. Climate-adjusted BDP elevates arctic tundra to 3rd globally from 17th by richness. No biome leads on all four diversity dimensions.

6.2 Recommendations

Three recommendations: (1) adopt the Biome Diversity Profile as the standard framework for

biome-level conservation investment allocation decisions -- the BDP's compression of the inter-biome diversity range from 24-fold (richness) to 4-fold (composite) demonstrates that richness-based biome prioritisation systematically under-funds lower-richness biomes whose functional, phylogenetic, and climate-sensitivity dimensions are not captured by species counts; the BDP code and biome-level data deposited with this paper provide the immediate implementation basis for national and international conservation funding portfolios; (2) treat coral reef EMF collapse as a conservation alarm -- the richness-EMF divergence (1,247 species but 0.47 EMF) at bleached reef sites provides direct empirical evidence that species counts on degraded reefs are ecologically misleading; conservation assessments of coral reefs must include EMF measurement (from the DBA paper 285 protocol) alongside coral cover and species richness to capture the full functional collapse from bleaching; and (3) establish arctic biome conservation as an equal international priority to tropical forest conservation -- the climate-adjusted BDP ranking placing arctic tundra 3rd globally provides the quantitative evidence base for elevating arctic biodiversity in international climate and conservation agreements beyond its current marginal status in global biodiversity negotiations. All BDP data and code deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete biome diversity dataset (247 sites x 18 biomes x species richness; FRic; PD; EMF; climate sensitivity indicators; environmental drivers), Biome Diversity Profile scores per site and biome (all four dimensions standardised + composite), BDP climate-adjusted rankings, driver analysis LMM outputs, and all R analysis scripts (lme4, mFD, picante, rdacca.hp, piecewiseSEM, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19497208. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Field surveys conducted under land access agreements with site owners and national park authorities in all 84 countries (supplementary Table S1). All vertebrate surveys used non-invasive methods (point counts; camera traps; non-capture transects). No vertebrate animals were handled. Invertebrate pitfall and pan trap sampling conducted under standard non-invasive protocols. No institutional ethics approval was required for non-invasive observation and trap surveys at this scale.

Appendix A

BDP Computation and Climate Sensitivity Index Protocol

The Biome Diversity Profile (BDP) standardisation procedure and the Climate Sensitivity Index (CSI) computation are provided below for direct adoption by conservation planners and macroecologists.

BDP COMPUTATION PROTOCOL

Step 1 -- Raw dimension values per site: Measure or compile for each site: (1) S = total species richness per ha (plants + invertebrates + vertebrates; standardised survey); (2) $FRic$ = functional richness (mFD R; 4D trait space; from TRY + AVONET + PanTHERIA + EltonTraits; minimum 4 traits per taxonomic group); (3) PD = Faith's Phylogenetic Diversity (picante R; from TimeTree 5 for animals; GBOTB for plants; total branch length of minimum spanning tree in Myr); (4) EMF = ecosystem multifunctionality (Multifunc R; 18 functions; 50th percentile threshold approach; see DBA paper 285 Appendix A).

Step 2 -- Within-dimension standardisation across all sites globally (or within the comparison set if doing a regional BDP): $S_std = (S - \min(S)) / (\max(S) - \min(S))$; $FRic_std = (FRic - \min(FRic)) / (\max(FRic) - \min(FRic))$; $PD_std = (PD - \min(PD)) / (\max(PD) - \min(PD))$; $EMF_std = EMF$ (already 0-1). This standardisation ensures each dimension contributes equally to the composite regardless of its raw scale. Note: re-standardise whenever new sites are added to the global dataset to maintain comparability.

Step 3 -- BDP composite score: $BDP = (S_std + FRic_std + PD_std + EMF_std) / 4$ (unweighted mean of 4 standardised dimensions). BDP ranges 0-1 (0 = minimum across all sites on all dimensions; 1 = maximum on all dimensions simultaneously). For biome-level BDP: compute mean BDP across all sites within the biome. For climate-adjusted BDP: $BDP_adj = BDP \times (1 + CSI_normalised)$, where $CSI_normalised = (CSI - \min(CSI)) / (\max(CSI) - \min(CSI))$ and CSI is the Climate Sensitivity Index (below). BDP_adj prioritises biomes combining high current biodiversity with high climate vulnerability.

CLIMATE SENSITIVITY INDEX (CSI) COMPUTATION

$CSI = Z(1/TNB) + Z(PAR) + Z(RSV)$; where: TNB = thermal niche breadth = community-weighted mean SD of MAT across species' GBIF ranges (degrees C; from CHELSA v2.1 at occurrence coordinates; $1/(TNB)$ inverted because narrower niches = higher sensitivity); PAR = phenological advancement rate = mean days/decade shift in peak first flowering or breeding (from concurrent phenological records or GBIF phenological metadata; positive = advancement = higher sensitivity); RSV = range shift velocity = km/decade poleward or m/decade upslope of community centre of gravity (from GBIF occurrence records 2014-2024; higher velocity = faster tracking requirement = higher sensitivity). $Z()$ = Z-score standardisation across biomes.

Data sources for CSI: TNB : for each species in the site community, extract GBIF occurrence records (cleaned; filtered as per DBA paper 271 Methods); compute mean annual temperature at all occurrence points using CHELSA v2.1 (`terra::extract()` in R); compute SD of these temperatures per species; compute community-weighted mean across all species (weighted by relative cover or abundance). PAR : where direct phenological records exist (≥ 5

years), use LMM slope of first event date on year; where not available, impute from biome mean PAR (from this study's Table 2 values as reference). RSV : compute mean latitude and elevation of all GBIF occurrences for each site species in 2014-2019 and 2019-2024; compute change in community-weighted mean latitude (km) and elevation (m) per decade from these two 5-year windows.