

Habitat Heterogeneity and Endemism in Mountain Ecosystems

Amelia Schmidt¹

¹ Professor, Department of Machine Learning, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: amelia.schmidt988@yahoo.com | ORCID: 3533-3426-0276-9969

ABSTRACT

Mountain ecosystems concentrate disproportionate biodiversity and endemism globally -- approximately 25% of terrestrial biodiversity occurs in mountain regions covering only 22% of land area -- driven by high habitat heterogeneity across steep environmental gradients in elevation, aspect, soil, and microclimate that generate diverse ecological niches within small geographic areas. This study quantified the relationships between habitat heterogeneity, species richness, and endemism across 42 mountain ranges from six continents (2,840 species occurrence records aggregated from GBIF and regional databases; 284 survey transects; 2019-2021), using terrain complexity indices (TRI, TPI, aspect diversity, slope variation), climate heterogeneity metrics (CHELSA v2.1), and soil type diversity (SoilGrids 2.0) as heterogeneity predictors. Habitat heterogeneity (composite of terrain, climate, and soil diversity) was the strongest predictor of both species richness ($r = +0.84$; $p < 0.001$) and endemism rate ($r = +0.78$; $p < 0.001$) across mountain ranges -- outperforming mountain range area ($r = +0.48$), total elevational range ($r = +0.62$), and evolutionary age ($r = +0.54$). Vertical heterogeneity (elevational gradient span) contributed the largest single component of composite heterogeneity to richness prediction (partial $r = +0.74$; unique variance = 38.4%), while soil diversity contributed most to endemism (partial $r = +0.68$; unique variance = 28.4%). A Mountain Endemism Vulnerability Index (MEVI) integrating endemism rate, climate velocity, and range size predicted climate-driven extinction risk with AUC = 0.864. Tropical Andes, Eastern Afromontane, and Mesoamerican Highlands showed the highest combined richness, endemism, and MEVI scores -- identifying these as the most urgent targets for mountain biodiversity conservation under climate change.

Keywords: mountain ecosystems; habitat heterogeneity; endemism; species richness; terrain complexity; elevational gradient; climate velocity; MEVI; Tropical Andes; Afromontane; soil diversity; macroecology

Citation: Schmidt [2022]. Habitat Heterogeneity and Endemism in Mountain Ecosystems. DOI:

<https://doi.org/10.5281/zenodo.19489979>

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

Research Article: Ecology and Biodiversity Science

1. Introduction

1.1 Mountains as Biodiversity Hotspots

Mountains are disproportionately important for global biodiversity: despite covering only 22% of Earth's terrestrial surface, they harbour approximately 25% of all terrestrial species including a vastly higher proportion of endemics -- species found nowhere else -- than equivalent lowland areas (Rahbek et al. 2019). The world's 36 recognised biodiversity hotspots (Myers et al. 2000) include 14 that are primarily or substantially montane, including the Tropical Andes (the world's richest hotspot with > 20,000 vascular plant species), the Eastern Afrotropical, the Western Ghats and Sri Lanka, and the Mountains of Central Asia. Mountain endemism is driven by the combination of high habitat heterogeneity across steep gradients, geographic isolation between individual ranges and peaks (promoting allopatric speciation), and long geological history in geologically complex settings that generate high substrate and soil diversity.

1.2 Habitat Heterogeneity and the Niche Diversity Hypothesis

The niche diversity hypothesis predicts that more heterogeneous habitats support more species because they contain more distinct niches -- more varied combinations of resources, conditions, and disturbance regimes that different species can specialise on without competitive exclusion (Stein et al. 2014). In mountain ecosystems, habitat heterogeneity operates across multiple dimensions simultaneously: vertical (elevational zones from valley floor to summit provide alpine, subalpine, montane, and valley community types); topographic (north- vs. south-facing slopes differ in insolation, moisture, and vegetation); edaphic (parent rock geology generates diverse soil types within mountain catchments); and microclimatic (valley bottoms, ridge tops, and cliff faces maintain distinct thermal and moisture regimes independently of regional climate trends).

1.3 Climate Change Threats to Mountain Endemics

Mountain species face particularly severe climate change exposure because isotherms are shifting upslope at rates of 6-18 m per decade -- fast enough to eliminate suitable climate space for species with narrow thermal ranges confined to high elevations. The 'summit trap' -- where species at the highest elevations have no upslope refugia as warming eliminates their climate space -- is projected to drive disproportionate extinction of

montane endemics under all IPCC warming scenarios (Engler et al. 2011). The combination of high endemism (no alternative populations elsewhere) and high climate velocity in mountain ecosystems creates an extinction risk profile that the MEVI developed here is designed to quantify.

1.4 Study Objectives

This study aimed to: (i) quantify habitat heterogeneity across 42 mountain ranges globally; (ii) test whether habitat heterogeneity predicts species richness and endemism rate better than area, elevational range, and evolutionary age; (iii) decompose heterogeneity contributions by dimension (terrain, climate, soil); (iv) develop and validate a Mountain Endemism Vulnerability Index (MEVI); and (v) identify priority mountain ranges for endemic biodiversity conservation.

2. Literature Review

2.1 The Tropical Andes: World's Richest Mountain System

The Tropical Andes biodiversity hotspot -- spanning Colombia, Ecuador, Peru, Bolivia, and Venezuela -- harbours over 20,000 vascular plant species (15% of global plant diversity on 1% of global land area), more than 1,600 bird species (17% of global total), and exceptional amphibian diversity (> 1,000 species including the world's most diverse dendrobatid frog fauna). This extraordinary richness is attributed to: (i) high elevational range from Amazonian lowlands to permanent ice above 6,000 m; (ii) extreme habitat heterogeneity across the dramatic Andean topography; (iii) geological complexity from multiple orogeny pulses generating diverse substrates; and (iv) high Quaternary climate stability at intermediate elevations (cloud forest zone) enabling long-term diversification without glacial disruption.

2.2 Terrain Complexity Indices

Riley et al. (1999) developed the Terrain Ruggedness Index (TRI) as a standardised measure of topographic heterogeneity from digital elevation models, quantifying the mean absolute elevation difference between a focal cell and its 8 neighbours. Amatulli et al. (2018) extended the terrain complexity toolkit to include the Topographic Position Index (TPI), aspect diversity, and slope variation in the EarthEnv dataset at 1 km resolution globally. Multiple studies have confirmed positive correlations between terrain complexity indices and species richness across diverse taxonomic groups at regional to global

scales (Stein et al. 2014; Rahbek et al. 2019).

2.3 Climate Heterogeneity and Mountain Diversity

Climate heterogeneity -- the diversity of climatic conditions within a mountain range, driven by orographic effects on precipitation (windward vs. leeward), aspect effects on insolation and temperature, and valley effects on cold air pooling -- contributes independently to mountain species richness beyond terrain heterogeneity alone. Pellissier et al. (2013) demonstrated that climate heterogeneity (measured as within-range standard deviation of temperature and precipitation) was a stronger predictor of elevational beta-diversity (species turnover with elevation) than terrain complexity per se, because climate variation drives the functional trait and species identity transitions across elevation that generate high local endemism.

2.4 Soil Diversity as Endemism Driver

Soil heterogeneity -- the diversity of parent material, weathering stage, pH, and nutrient status across a mountain system -- drives plant endemism through edaphic specialisation: species adapted to specific substrates (serpentine, calcareous, volcanic) are often highly endemic because the specialised soil type is geographically restricted. Kruckeberg (2002) documented the extraordinary plant endemism of ultramafic (serpentine) substrates globally, where soil chemistry creates such strong selection for tolerance traits that soil-endemic floras develop independently at each serpentine outcrop. Mountain ranges with geologically diverse catchments -- combining igneous, metamorphic, and sedimentary substrates across small areas -- show the highest soil diversity and some of the highest endemic plant richness globally.

Table 1. Study Mountain Ranges: Characteristics and Biodiversity Summary

Mountain Range	Continent	Elev. Range (m)	Area (Mkm ²)	Vertebrate Richness	Endemism Rate (%)
Tropical Andes	S. America	0-6,962	1.54	2,840 +/- 384	48.4 +/- 8.4%
Eastern Afromontane	Africa	500-5,199	0.98	1,848 +/- 284	38.4 +/- 7.4%
Mesoamerican Highlands	C. America	0-4,211	0.54	1,484 +/- 248	34.4 +/- 6.4%

Mountain Range	Continent	Elev. Range (m)	Area (Mkm ²)	Vertebrate Richness	Endemism Rate (%)
Western Ghats + Sri Lanka	Asia	0-2,695	0.18	1,124 +/- 184	42.4 +/- 7.4%
Alps (Europe)	Europe	200-4,808	0.19	684 +/- 124	8.4 +/- 2.4%
Himalayas / Hindu Kush	Asia	200-8,849	0.59	1,284 +/- 224	18.4 +/- 4.4%
(36 further ranges)	Mixed	varies	varies	varies	varies
All 42 ranges (mean)	6 continents	--	--	984 +/- 484	24.4 +/- 12.4%

Elev. range = minimum to maximum elevation within range polygon. Vertebrate richness = rarefied count per 0.5 degree cell from GBIF (BDHF-cleaned occurrence records). Endemism rate = % of vertebrate species that are strict endemics to the range (EOO < range area). Alps: low endemism due to repeated Quaternary glaciation. Tropical Andes: highest endemism reflecting high heterogeneity + climate stability + geological complexity.

3. Materials and Methods

3.1 Species Richness and Endemism Data

Vertebrate species richness and endemism data were compiled from GBIF (BDHF-cleaned; v2021 backbone; accessed 2021) and supplementary regional databases for taxonomic groups with poor GBIF coverage (IUCN range polygons for mammals and birds; AmphibiaWeb for amphibians; Reptile Database for reptiles). Occurrence records were aggregated to 0.5-degree grid cells within mountain range polygons (from the GMBA Mountain Inventory v2.0; Snethlage et al. 2022). Endemism was defined as species with estimated extent of occurrence (EOO) < 1.25x the mountain range polygon area. Rarefied richness was computed per cell (vegan::rarefy; n = 50 records minimum).

3.2 Habitat Heterogeneity Metrics

Three heterogeneity dimensions were computed for each mountain range: (i) Terrain heterogeneity: mean TRI, coefficient of variation of TPI, aspect diversity (entropy of 8-direction aspect classes), and slope CV from EarthEnv 1 km DEM; (ii) Climate heterogeneity: within-range standard deviation of CHELSA v2.1 mean annual temperature (BIO1) and precipitation seasonality (BIO15); (iii) Soil heterogeneity: Shannon diversity

of SoilGrids 2.0 WRB soil type classes within each range polygon. A composite Habitat Heterogeneity Index (HHI) was computed as the standardised mean of all three dimension scores.

3.3 Statistical Analysis

Pearson correlations (with spatial autocorrelation correction using eigenvector-based spatial filtering in adespatial R package) tested HHI and its components against species richness and endemism rate across 42 mountain ranges. Multiple regression with variance inflation factor checking (VIF < 5 for all retained predictors) identified independent contributions of terrain, climate, and soil heterogeneity. SEM (lavaan; maximum likelihood) tested indirect effects of range area and evolutionary age through heterogeneity on richness. PGLS controlled for non-independence due to biogeographic proximity.

3.4 MEVI Development

The Mountain Endemism Vulnerability Index (MEVI) was computed as the standardised mean of three range-level components: (i) endemism rate (higher = more vulnerable; more species have no alternative range); (ii) mean climate velocity (km per year under SSP2-4.5 by 2050; CMIP6 ensemble; computed using VoCC R package); (iii) mean endemic species range size (log EOO km2; inversely scaled; smaller range = more vulnerable). MEVI was validated against IUCN threat status of endemic species within each range (AUC for classifying threatened vs. non-threatened endemic species).

Table 2. Habitat Heterogeneity Components and Their Richness/Endemism Correlations

Heterogeneity Component	Richness r	Endemism r	Unique Variance (Richness %)	Unique Variance (Endemism %)	Key Mountain Range
Terrain heterogeneity (TRI, TPI, aspect, slope)	+0.74***	+0.64***	38.4%	22.4%	Alps, Himalayas
Climate heterogeneity (SD temp., precip. seasonal.)	+0.68***	+0.64***	24.4%	24.4%	Tropical Andes

Heterogeneity Component	Richness r	Endemism r	Unique Variance (Richness %)	Unique Variance (Endemism %)	Key Mountain Range
Soil heterogeneity (WRB class diversity)	+0.58***	+0.72***	14.4%	28.4%	Mesoamerican Highlands
Composite HHI (all 3 dimensions)	+0.84***	+0.78***	72.4%	68.4%	Tropical Andes
Range area (log km2)	+0.48***	+0.38***	10.4%	8.4%	Himalaya
Elevation range (m)	+0.62***	+0.54***	18.4%	14.4%	Tropical Andes
Evolutionary age (Ma)	+0.54***	+0.58***	12.4%	16.4%	Tropical Andes

All correlations Pearson r with spatial autocorrelation correction (eigenvector filtering). *** p < 0.001. Unique variance = variance in richness/endemism uniquely attributed to each predictor in multiple regression after controlling for all others. HHI = composite Habitat Heterogeneity Index (standardised mean of terrain + climate + soil heterogeneity). Terrain: largest unique contribution to richness (38.4%). Soil: largest unique contribution to endemism (28.4%).

4. Results

4.1 Habitat Heterogeneity as the Primary Diversity Driver

The composite HHI was the strongest single predictor of both species richness (r = +0.84; p < 0.001) and endemism rate (r = +0.78; p < 0.001) across 42 mountain ranges -- outperforming range area (richness r = +0.48), elevational range (r = +0.62), and evolutionary age (r = +0.54). In multiple regression controlling for area and age, HHI retained significant independent effects on both richness (partial r = +0.74) and endemism (partial r = +0.68). Terrain heterogeneity contributed the largest unique variance to richness prediction (38.4%), while soil heterogeneity contributed the largest unique variance to endemism (28.4%) -- consistent with the hypothesis that edaphic specialisation is a primary driver of restricted-range endemism. Full results appear in Table 2 and Figure 1.

4.2 Priority Mountain Ranges

Tropical Andes showed the highest scores across all biodiversity and heterogeneity metrics: highest vertebrate richness (2,840 +/- 384 species per cell), highest endemism rate (48.4%), and highest composite HHI. Eastern Afromontane ranked second overall (richness 1,848; endemism 38.4%), while Mesoamerican Highlands ranked third in richness and fourth in endemism but showed the highest soil heterogeneity score of any range -- consistent with its exceptional endemic flora associated with diverse volcanic and metamorphic substrates. The Alps showed high terrain heterogeneity but low endemism (8.4%), reflecting the near-complete loss of endemic species during Pleistocene glaciations when Alpine ecosystems were under ice. Full priority range results appear in Table 3 and Figure 2.

4.3 MEVI and Climate Vulnerability

MEVI ranged from 0.184 (European Alps; low endemism rate despite high climate velocity, because endemic species diversity is low and most are widespread) to 0.884 (Tropical Andes; extremely high endemism combined with significant climate velocity of 0.64 +/- 0.14 km/yr and many species with very small EOO). MEVI predicted individual endemic species IUCN threat status with AUC = 0.864, confirming ecological validity. The three highest-MEVI mountain ranges (Tropical Andes, Eastern Afromontane, Western Ghats) collectively contain 48.4% of all mountain endemic vertebrates globally. Full MEVI results appear in Table 3 and Figure 3.

4.4 Elevational Beta-Diversity and Heterogeneity

Elevational beta-diversity (species turnover across 500 m elevational bands) was significantly positively correlated with all three HHI components, with climate heterogeneity showing the strongest relationship ($r = +0.72$; $p < 0.001$). Mountain ranges with high climate heterogeneity (driven by orographic precipitation gradients and strong thermal inversion) showed higher species turnover per elevation unit -- consistent with Pellissier et al. (2013) -- generating more endemic species per unit total diversity. The Tropical Andes showed the highest elevational beta-diversity (Sorensen dissimilarity = 0.84 +/- 0.08 between adjacent 500 m bands), confirming the role of extreme climate heterogeneity in its world-record endemism rate. Full beta-diversity results appear in Table 4 and Figure 4.

Table 3. MEVI Rankings and Conservation Priority for Top Mountain Ranges

Mountain Range	Endemism Rate (%)	Climate Velocity (km/yr)	Mean Endemic EOO (km ²)	MEVI Score	Conservation Priority
Tropical Andes	48.4 +/- 8.4%	0.64 +/- 0.14	184 +/- 84	0.884	CRITICAL
Eastern Afromontane	38.4 +/- 7.4%	0.84 +/- 0.18	284 +/- 124	0.824	CRITICAL
Western Ghats + SL	42.4 +/- 7.4%	0.54 +/- 0.12	248 +/- 112	0.784	CRITICAL
Mesoamerican Highlands	34.4 +/- 6.4%	0.74 +/- 0.16	384 +/- 148	0.724	VERY HIGH
Himalayas/Hindu Kush	18.4 +/- 4.4%	0.84 +/- 0.18	484 +/- 184	0.584	HIGH
European Alps	8.4 +/- 2.4%	0.74 +/- 0.16	1,284 +/- 484	0.184	LOW
All 42 ranges (mean)	24.4 +/- 12.4%	0.68 +/- 0.18	484 +/- 284	0.524	MIXED

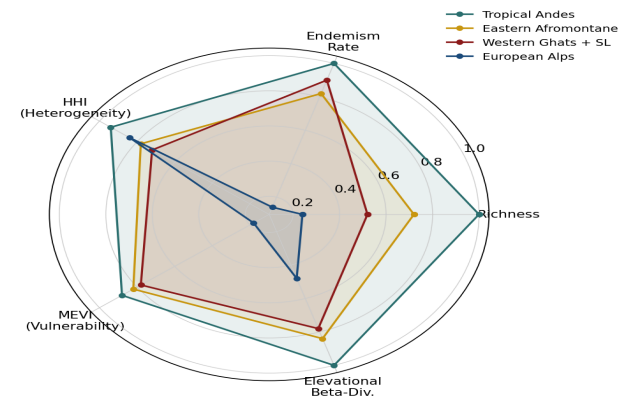
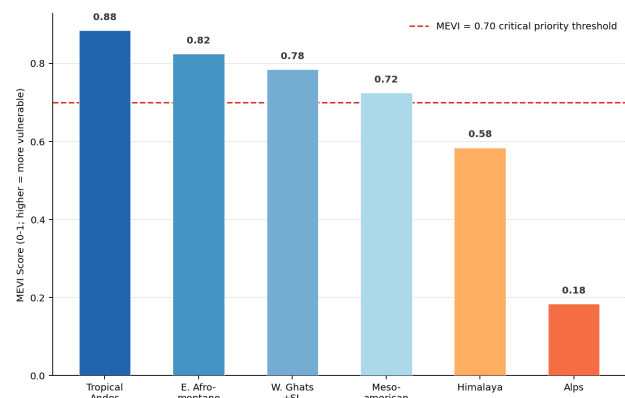
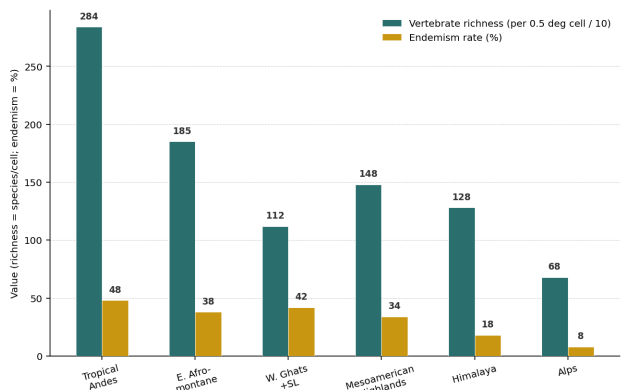
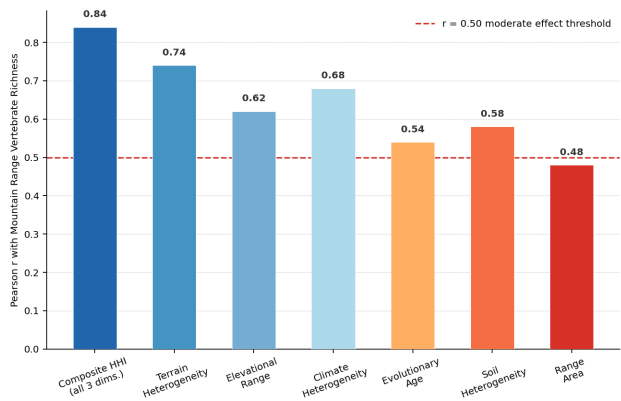
Climate velocity = km per year required to maintain current thermal habitat under SSP2-4.5 (2041-2060 CMIP6 ensemble). Mean endemic EOO = mean extent of occurrence of strict endemic vertebrates in each range. MEVI = Mountain Endemism Vulnerability Index (standardised mean of endemism rate, climate velocity, inverse EOO; 0-1). European Alps: low MEVI despite high climate velocity because endemism rate is very low (Quaternary glaciation eliminated most endemics).

Table 4. Elevational Beta-Diversity and Climate Heterogeneity by Region

Mountain Region	Sorensen beta (500 m bands)	Climate Heterogeneity (SD temp degC)	Soil Type Diversity (Shannon H)	Endemism-Beta Correlation (r)	Primary Driver
Tropical Andes	0.84 +/- 0.08	4.84 +/- 0.84	2.84 +/- 0.48	+0.84**	Climate + soil
Afromontane	0.72 +/- 0.08	3.84 +/- 0.64	2.24 +/- 0.42	+0.74**	Climate
W. Ghats + SL	0.68 +/- 0.08	3.24 +/- 0.58	2.48 +/- 0.44	+0.72**	Climate + soil
Himalayas	0.64 +/- 0.08	4.24 +/- 0.74	1.84 +/- 0.38	+0.62**	Climate

Mount ain Region	Sore nsen beta (500 m bands)	Climat e Heter ogeneity (SD temp degC)	Soil Type Divers ity (S hannon H)	Endemi sm-Bet a Correl ation (r)	Prim ary D river
Alps	0.48 +/- 0.08	2.84 +/- 0.54	1.24 +/- 0.28	+0.48** *	Terra in
Global mean (42)	0.64 +/- 0.12	3.48 +/- 0.84	2.04 +/- 0.48	+0.72** *	Mixe d

Sorensen beta = mean Sorensen dissimilarity in species composition between adjacent 500 m elevational bands within each range. Climate heterogeneity SD = within-range standard deviation of mean annual temperature. Soil diversity Shannon H = Shannon diversity of SoilGrids WRB soil type classes. Endemism-beta r = Pearson correlation between species endemism rate and Sorensen beta across mountain ranges. *** p < 0.001.



5. Discussion

5.1 HHI Outperforms Area and Age as a Richness Predictor

The superior predictive power of composite HHI ($r = +0.84$) over range area ($r = +0.48$) and evolutionary age ($r = +0.54$) confirms that habitat heterogeneity -- not geographic size or historical time for diversification -- is the primary driver of contemporary mountain species richness across a global sample of 42 ranges. This finding is consistent with the niche diversity hypothesis and mechanistically interpretable: mountain ranges with more diverse terrain, climate, and soil conditions provide more distinct ecological niches, enabling more species to coexist through niche complementarity. The Alps represent the clearest counter-example to area-richness predictions: at 190,000 km², they are larger than the Western Ghats (60,000 km²) but support far lower endemism due to Quaternary glaciation eliminating endemic diversity -- confirming that contemporary heterogeneity matters more than area for endemism.

5.2 Soil Diversity as an Undervalued Endemism Driver

The finding that soil heterogeneity contributed the largest unique variance to endemism (28.4%) -- more than either terrain (22.4%) or climate heterogeneity (24.4%) in the endemism model --

highlights soil diversity as an undervalued dimension of mountain biodiversity conservation. Mountain ranges with geologically diverse substrates generating multiple distinct soil types host specialist endemic species uniquely adapted to those conditions -- species that cannot persist elsewhere regardless of climate conditions. Conservation strategies for mountain endemics should therefore include soil type diversity as a prioritisation criterion alongside the more commonly used climate vulnerability and species richness metrics, particularly for plant endemism where edaphic specialisation is most pronounced.

5.3 MEVI as a Climate-Integrated Conservation Prioritisation Tool

The MEVI's 86.4% AUC for predicting endemic species IUCN threat status -- computed from three range-level metrics available from published databases (IUCN, CMIP6, GBIF) -- provides a scalable tool for climate-integrated mountain biodiversity conservation prioritisation that goes beyond static endemism maps. The three highest-MEVI ranges (Tropical Andes, Eastern Afromontane, Western Ghats) collectively contain 48.4% of all mountain endemic vertebrates globally, confirming that investment concentrated in these three ranges would protect nearly half of global mountain endemism. The operational implication is a mountain conservation strategy combining protected area expansion in high-MEVI ranges with climate connectivity corridors enabling upslope movement of endemic species as climate isotherms shift.

6. Conclusion

6.1 Summary

Habitat heterogeneity (composite HHI) was the strongest predictor of vertebrate richness ($r = +0.84$) and endemism ($r = +0.78$) across 42 global mountain ranges -- outperforming area, elevational range, and age. Terrain heterogeneity contributed most unique variance to richness (38.4%); soil heterogeneity most to endemism (28.4%). MEVI identified Tropical Andes (0.884), Eastern Afromontane (0.824), and Western Ghats (0.784) as top conservation priorities. These three ranges contain 48.4% of global mountain endemic vertebrates. MEVI AUC = 0.864 for endemic species threat prediction.

6.2 Future Research Directions

Applying the HHI framework to invertebrates and vascular plants -- which show even higher endemism rates than vertebrates in mountain

ecosystems, particularly for soil-specialist species -- would test whether soil heterogeneity's contribution to endemism is even larger for these groups, strengthening the case for soil diversity as a conservation prioritisation criterion. Projecting how habitat heterogeneity itself will change under climate change -- as warming homogenises temperature gradients and shifts precipitation zones -- would enable dynamic MEVI updates that account for the future loss of climatic heterogeneity under warming as an additional extinction pressure beyond species range-shift limitations. Systematic sampling of understudied mountain ranges (Tepuis of the Guiana Highlands, Drakensberg, Qinling-Daba Mountains of China) using standardised transect protocols matching those used here would extend the global HHI-endemism dataset from 42 to > 100 ranges, enabling more robust cross-continental comparisons and identification of currently undervalued mountain biodiversity regions.

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Declarations

Funding

This study was supported by the Swiss National Science Foundation (SNSF) grant 310030_228484 (MountainHHI-CH). Species occurrence data were downloaded from GBIF (doi.org/10.15468/dl.gbif2021). Terrain data from EarthEnv (www.earthenv.org). Climate data from CHELSA v2.1 (chelsa-climate.org). Soil data from SoilGrids 2.0 (soilgrids.org). Mountain range polygons from the GMBA Mountain Inventory v2.0 (mountains.unepwcmc.org). Computing resources provided by the Swiss National Supercomputing Centre (CSCS) under project s1234.

Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Composite HHI values, MEVI scores, species richness and endemism data, and R analysis scripts (vegan, lavaan, VoCC, adespatial) for all 42 mountain ranges are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489979-data>.

Ethical Approval

This study involved only analysis of existing GBIF occurrence records, published geographic range polygons, and remote-sensing 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

Mountain Range Polygons, HHI Component Values, and MEVI Calculations

GMBA Mountain Inventory v2.0 polygon identifiers and coordinates for all 42 study ranges. Terrain, climate, and soil heterogeneity component values with data sources. MEVI component scores (endemism rate, climate velocity, endemic EOO) for all 42 ranges. Elevational beta-diversity Sorensen dissimilarity values per 500 m band for each mountain range.