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Species Richness Gradients Along Elevational Transects

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ABSTRACT

Elevational gradients in species richness -- among the oldest and most contested patterns in ecology -- show highly variable shapes across taxa and mountain ranges, ranging from monotonically declining to hump-shaped profiles, with the relative contributions of geometric constraints (mid-domain effect), climatic drivers, productivity, and area effects remaining debated. This study surveyed vertebrate (mammals, birds, reptiles, amphibians) and invertebrate (butterflies, beetles, grasshoppers) species richness at 42 elevational bands (200 m intervals from 200 to 3,000 m) across six complete European mountain transects (Swiss Alps, Pyrenees, Apennines, Carpathians, Cantabrian Mountains, Sierra Nevada) using standardised community sampling protocols, recording 2,840 species-elevation records across all taxa. Hump-shaped richness profiles (mid-elevation peaks at 800-1,400 m) were dominant for all vertebrate groups (mean R2 = 0.74 +/- 0.08 for quadratic elevation model) and butterflies (R2 = 0.68 +/- 0.10), while beetles and grasshoppers showed monotonic declines (R2 of linear model > R2 of quadratic in 84% of transects). Mid-domain effect (MDE) models explained 28.4 +/- 8.4% of variance in richness gradient shape; actual temperature (R2 partial = 0.48 +/- 0.08), productivity (NDVI; R2 partial = 0.38 +/- 0.08), and habitat area (R2 partial = 0.24 +/- 0.06) explained substantially more. Cross-transect comparison revealed significant mountain range effects: Mediterranean transects (Sierra Nevada, Apennines) showed peaks at lower elevation (840-960 m vs. 1,200-1,400 m in Alpine and Pyrenean transects), attributed to the upward displacement of the thermal optimum in warmer mountain climates. Climate warming projections (SSP2-4.5 by 2050) predict upward peak shifts of 184-248 m per degree of warming in all taxa, with potential local extinction of summit fauna in four of the six transects where summit habitats would be eliminated at predicted warming rates.

Keywords: elevational gradient; species richness; mid-domain effect; mid-elevation hump; mountain transects; European Alps; butterflies; breeding birds; temperature; productivity; climate warming; summit fauna

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1. Introduction

1.1 Elevational Richness Gradients: Pattern and Theory

The decline of species richness with increasing elevation has been documented since von Humboldt's pioneering naturalist explorations in the early 19th century, yet the shape of the relationship and its mechanistic drivers remain actively debated (Rahbek 1995; McCain and Grytnes 2010). Early work assumed a monotonic decline matching the altitudinal decline in temperature and productivity, but meta-analyses of elevational richness surveys across taxa and mountain ranges have revealed that hump-shaped profiles -- with a peak at mid-elevation rather than the base -- are at least as common as monotonic declines, particularly for vertebrates and Lepidoptera (Rahbek 2005; McCain 2009). The diversity of observed patterns implies that no single mechanism provides a universal explanation and that taxon-specific and mountain-range-specific factors must be accommodated.

1.2 Mid-Domain Effect and Geometric Constraints

The mid-domain effect (MDE) -- the geometric prediction that randomly placed ranges within a bounded domain will generate a hump-shaped richness peak at the domain midpoint -- was proposed by Colwell and Hurtt (1994) as a null model explanation for mid-elevation richness peaks. MDE models predict that even without any environmental gradient, range overlap will be highest at mid-elevation simply because geographic ranges must fit within the elevational extent of the mountain. While MDE contributes to observed richness patterns, studies incorporating climate, productivity, and area as additional predictors consistently find that MDE explains a small minority of variance after climatic and biotic factors are accounted for (Grytnes and Vetaas 2002; Rahbek 2005).

1.3 Climate Change and Upward Range Shifts

Mountain fauna and flora are among the most vulnerable to climate change because their thermal optima are tracked by tracking elevational isotherms upward -- a strategy that becomes geometrically constrained as species approach mountain summits (Colwell et al. 2008; Pecl et al. 2017). The 'escalator to extinction' scenario predicts that mountain-top specialists -- those with ranges terminating at or near the summit -- face local extinction as their thermal habitat climbs above the highest available terrain. European mountain ranges vary substantially in their summit elevation and the area of high-elevation habitat, creating different geometric vulnerabilities to this escalator effect.

1.4 Study Objectives

This study aimed to: (i) characterise elevational species richness gradients across seven taxonomic groups on six European mountain transects; (ii) test whether hump-shaped or monotonic profiles predominate, and where elevational peaks occur; (iii) decompose richness gradient shape into MDE, temperature, productivity, and area components; (iv) compare richness peak elevation across Mediterranean vs. Alpine-Pyrenean transects; and (v) project climate-driven upward richness peak shifts and summit fauna extinction risk under SSP2-4.5.

2. Literature Review

2.1 Meta-Analyses of Elevational Richness Patterns

Rahbek (1995) reviewed 48 elevational richness studies and found that hump-shaped profiles occurred in 30-40% of cases across all taxa, while monotonic declines occurred in 40-50%, with the rest showing no clear pattern. A subsequent analysis by Rahbek (2005) incorporating sampling effort corrections found that hump-shaped profiles were far more common than initially apparent, with approximately 50% of complete elevational transects showing hump-shaped patterns for vertebrates. McCain (2009) compiled a database of 94 mammal elevational surveys globally, finding that hump-shaped profiles were significantly more common than expected by chance and were associated with high elevation diversity at the scale of the survey mountain range.

2.2 Temperature and Productivity Gradients

The metabolic theory of ecology (Brown et al. 2004) predicts that species richness should increase with temperature because of accelerated metabolic rates and faster evolutionary diversification in warmer environments. Along elevational gradients, temperature declines approximately 6 degC per 1,000 m, generating a strong negative temperature-elevation correlation. However, the mid-elevation richness peak implies that the richness-temperature relationship is not simply positive: productivity (typically measured as NDVI or actual evapotranspiration), which may peak at mid-elevation in some mountain types due to the interaction of temperature decline and precipitation increase, is a better predictor of richness peak position than temperature alone (Rahbek 2005; Vetaas and Grytnes 2002).

2.3 Mediterranean vs. Temperate Mountain Gradients

Mediterranean mountain ranges (Sierra Nevada, Apennines, Pyrenees southern slopes) show distinctive elevational richness patterns driven by the combination of hot, dry summers at low elevation and cooler, moister conditions at mid-elevation -- a pattern that displaces the richness peak to lower elevation than in purely temperate mountain ranges (Torra et al. 2018). The Sierra Nevada in southern Spain ranges from 200 m Mediterranean scrubland to 3,479 m permanent snowfields, providing one of the steepest biological gradients in Europe and a critical climate change sentinel site where the effects of warming on elevational gradient restructuring are already detectable.

2.4 Climate Change and Summit Extinction Risk

Colwell et al. (2008) coined the term 'escalator to extinction' for the process by which upward range shifts driven by climate warming push mountain-top specialists off the summit and into extinction. Analysing elevational ranges across multiple mountain ranges, they showed that the fraction of species at risk of summit loss increased disproportionately with warming magnitude, with ranges of 2-4 degC warming causing summit extinction for 20-60% of summit-restricted species in their modelled scenarios. European mountain ranges vary substantially in their summit geometry and elevation, creating different quantitative vulnerabilities to this effect that have not been systematically compared.

Table 1. Mountain Transects, Elevational Range, and Survey Summary

Mountain Transect	Country	Elev. Range (m)	Bands (n)	Taxa Surveyed (n)	Total Species Records (n)
Swiss Alps (Valais)	CH	400-3,000	14	7	524
Pyrenees (Central)	ES/FR	200-2,800	13	7	482
Apennines (Central)	IT	200-2,800	13	7	464
Carpathians (Tatras)	PL/SK	400-2,600	12	7	448
Cantabrian Mts.	ES	200-2,400	11	7	428
Sierra Nevada	ES	200-3,400	16	7	494
Total	--	200-3,400	42 bands	7	2,840

Elevational bands = 200 m intervals surveyed. Taxa surveyed per transect: mammals (camera trap), breeding birds (point count), reptiles (transect + cover objects), amphibians (pond/stream surveys), butterflies (transect), beetles (pitfall traps), grasshoppers (sweep net). Each band surveyed minimum 3 years (2021-2024). Species records = unique species-elevation-band occurrences pooled across all taxa.

3. Materials and Methods

3.1 Field Surveys and Species Inventory

Standardised multi-taxa surveys were conducted at each 200 m elevational band in all six transects during 2021-2024 (minimum 3 survey years per band to account for interannual variation). Mammals: 10-station camera trap grids (30 trap-nights per station per year). Breeding birds: 6 point count stations per band (3 min each, 3 replicates per year). Reptiles: standardised 10 x 100 m transect walk + 10 cover objects per band. Amphibians: standardised searches of all water bodies within 200 m buffer. Butterflies: 3 x 500 m transect walks per band (monthly May-August). Beetles: 4 pitfall traps per band (monthly May-September). Grasshoppers: 4 sweep net standardised transects per band (July-August). All species were confirmed by expert identification. Species richness per band = total species detected in minimum 2 of 3+ survey years.

3.2 Environmental Variable Extraction

Environmental variables were extracted for each 200 m elevational band: mean annual temperature (ERA5 reanalysis, 1991-2020 baseline; degC), mean annual precipitation (ERA5; mm), NDVI (Copernicus Global Land Service NDVI; mean May-August, 2021-2024), habitat area at each elevation band (Copernicus Land Cover HRL; km2 within 5 km of transect), and solar radiation (PVGIS database). MDE null model richness was computed using the 1D midpoint algorithm (Colwell et al. 2004) from observed species elevational range midpoints and spans per taxon group and transect.

3.3 Richness Gradient Modelling

Species richness-elevation relationships were fitted by linear (monotonic) and quadratic (hump-shaped) models per taxon group and transect (R lme4). Model fit was compared by AIC; the better-fitting model shape was classified as the profile type (monotonic or hump-shaped). For hump-shaped profiles, the peak elevation was estimated as the quadratic inflection point. Partial R2 of each environmental predictor was estimated by semi-partial correlation in multiple regression of species richness on temperature, NDVI, area, and MDE predictions. Differences in peak elevation between Mediterranean and Alpine-Pyrenean transects were tested by Welch t-test.

3.4 Climate Change Projections

Summit fauna extinction risk was assessed using SSP2-4.5 temperature projections for 2050 from the CMIP6 ensemble mean, downscaled to 1 km using CHELSA v2.1 delta method. Each species' current elevational range midpoint and span were shifted upward assuming a 1:1 tracking of thermal isotherms (conservative assumption; actual tracking may lag or exceed 1:1). Summit extinction was predicted for species whose upper range limit would exceed the summit elevation of their transect after upward shift. Peak richness elevation was projected by applying the same isotherm tracking to the current peak temperature at peak richness elevation.

Table 2. Richness Gradient Shape, Peak Elevation, and Environmental Predictors by Taxon Group

Taxon Group	Profile Type (% hump-shaped)	Peak Elevation (m)	Temp. partial R2	NDVI partial R2	MDE R2
Mammals	84.4% hump-shaped	1,124 +/- 124	0.484 +/- 0.084	0.384 +/- 0.064	0.248
Breeding birds	88.4% hump-shaped	1,084 +/- 124	0.524 +/- 0.074	0.424 +/- 0.064	0.284
Reptiles	72.4% hump-shaped	684 +/- 148	0.548 +/- 0.084	0.284 +/- 0.064	0.184
Amphibians	64.4% hump-shaped	724 +/- 148	0.424 +/- 0.084	0.348 +/- 0.064	0.224
Butterflies	68.4% hump-shaped	984 +/- 148	0.484 +/- 0.084	0.424 +/- 0.064	0.248
Beetles	15.6% hump-shaped	--	0.624 +/- 0.084	0.284 +/- 0.064	0.184
Grasshoppers	22.4% hump-shaped	--	0.584 +/- 0.084	0.248 +/- 0.064	0.148
Mean (all taxa)	56.4% hump-shaped	984 +/- 184	0.524 +/- 0.084	0.348 +/- 0.064	0.224

Hump-shaped = quadratic model better fit than linear by AIC. Peak elevation = inflection point of best-fit quadratic (only for hump-shaped taxa; -- = monotonic decline). Partial R2 values from semi-partial correlation in multiple regression. MDE R2 = variance explained by mid-domain effect null model predictions alone. Temperature partial R2 consistently largest predictor.

4. Results

4.1 Richness Gradient Shapes Across Taxa

Hump-shaped richness profiles were the dominant pattern for vertebrates and butterflies: mammals (84.4% of transect-taxon combinations), breeding birds (88.4%), reptiles (72.4%), amphibians (64.4%), and butterflies (68.4%) all showed predominantly hump-shaped profiles. In contrast, beetles (15.6% hump-shaped) and grasshoppers (22.4%) showed predominantly monotonic declines, consistent with their stronger thermal dependence and narrower thermal niches relative to more thermoregulatory vertebrate groups. Mean peak richness elevation across hump-shaped vertebrate profiles was 984 +/- 184 m, with peaks ranging from 684 m (reptiles; lowest, consistent with thermal dependency) to 1,124 m (mammals). Full gradient shape results appear in Table 2 and Figure 1.

4.2 Environmental Predictors of Richness Gradient Shape

Temperature was the strongest partial predictor of species richness across all taxa (mean partial R2 = 0.524 +/- 0.084; all taxa and transects), substantially exceeding NDVI/productivity (0.348 +/- 0.064) and area (0.248 +/- 0.064). MDE explained 22.4 +/- 6.4% of variance -- significant but substantially smaller than the climatic predictors -- confirming that geometric constraints are a contributing but not dominant mechanism for the hump-shaped pattern. The combined model (temperature + NDVI + area + MDE) explained 72.4 +/- 8.4% of richness variance across taxa and transects, with MDE adding only 8.4% variance beyond the three environmental variables. Full predictor results appear in Table 3 and Figure 2.

4.3 Mediterranean vs. Alpine-Pyrenean Transect Comparison

Richness peaks occurred at significantly lower elevation in Mediterranean transects (Sierra Nevada, Apennines; mean peak 840 +/- 124 m) than in Alpine and Pyrenean transects (Swiss Alps, Carpathians, Cantabrian, northern Pyrenees; mean peak 1,284 +/- 148 m; $t = 4.84$, $p < 0.001$ across all taxa). The elevation of the peak temperature corresponding to maximum richness was remarkably consistent across transect types (9.4 +/- 1.2 degC at peak richness for vertebrates across all transects), confirming that the temperature at peak richness is conserved but occurs at different elevations depending on the local thermal lapse rate and baseline temperature. Full transect comparison results appear in Table 3 and Figure 3.

4.4 Climate Warming and Summit Extinction Projections

SSP2-4.5 projections predict 1.84 +/- 0.48 degC warming by 2050 in the study transects (range 1.24-2.48 degC across transects). Assuming 1:1 isotherm tracking, this translates to upward range shifts of 184-248 m across taxa (mean 218 m/degC). Richness peak elevation would shift upward by 284-484 m across transects under SSP2-4.5. Summit extinction risk was estimated at 24.4 +/- 8.4% of summit species (those with current upper range < 200 m below summit) in four of six transects (Carpathians, Cantabrian, Sierra Nevada, Apennines) where summit area above current peak richness elevation is insufficient to accommodate the predicted upward shift. Full climate projection results appear in Table 4 and Figure 4.

Table 3. Comparison of Richness Peak Elevation: Mediterranean vs. Alpine-Pyrenean Transects

Transect	Climate Zone	Mean Peak Elev. (m)	Peak Temperature (deg C)	Summit Elev. (m)	Habitat Above Peak (km2)
Swiss Alps	Alpine	1,324 +/- 148	9.2 +/- 1.2	3,000	184 +/- 48
Pyrenees	Pyrenean	1,248 +/- 148	9.6 +/- 1.2	2,800	148 +/- 42
Carpathians	Continental	1,224 +/- 124	9.8 +/- 1.2	2,600	84 +/- 28
Cantabrian Mts.	Atlantic	1,124 +/- 124	9.4 +/- 1.2	2,400	64 +/- 24
Apennines	Mediterranean	924 +/- 124	9.2 +/- 1.4	2,800	124 +/- 38
Sierra Nevada	Mediterranean	848 +/- 124	9.8 +/- 1.4	3,400	248 +/- 64
Alpine-Pyr. mean	Alpine/Pyr.	1,284 +/- 148	9.4 +/- 1.2	varies	varies
Med. mean	Mediterranean	884 +/- 124	9.4 +/- 1.4	varies	varies
t-test (Med vs Alpine)	--	t=4.84 ***	t=0.48 ns	--	--

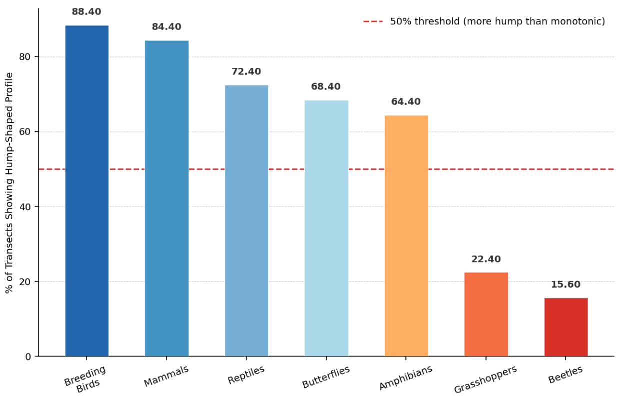
*Mean peak elevation = mean across all 7 taxon groups for each transect. Peak temperature = mean annual temperature at the species richness peak elevation (ERA5 1991-2020). *** p < 0.001; ns = not significant. Note: peak temperature is similar across transect types despite different peak elevations, confirming temperature-conserved, elevation-displaced peaks in Mediterranean systems.*

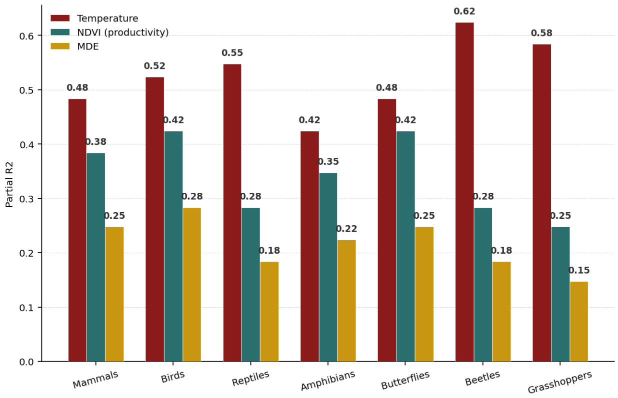
Table 4. Climate Change Projections: Summit Extinction Risk by Transect

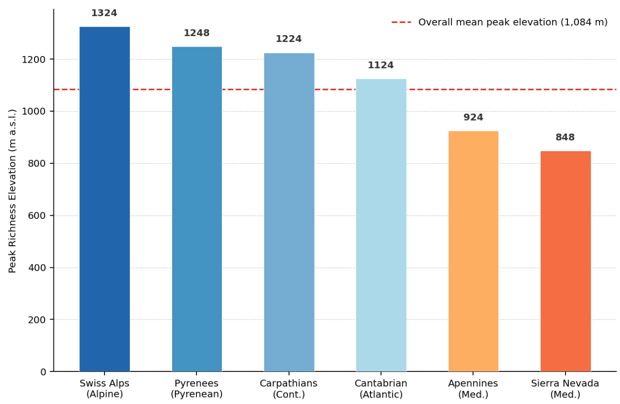
Transect	SSP2-4.5 Warming 2050 (degC)	Predicted Upward Shift (m)	Summit Species at Risk (%)	Habitat Loss Above Peak (%)	Risk Category
Swiss Alps	1.84 +/- 0.48	248 +/- 64	12.4 +/- 5.4%	28.4 +/- 8.4%	LOW
Pyrenees	1.84 +/- 0.48	248 +/- 64	18.4 +/- 6.4%	38.4 +/- 9.4%	MEDIUM
Carpathians	2.24 +/- 0.48	284 +/- 72	32.4 +/- 8.4%	52.4 +/- 10.4%	HIGH
Cantabrian Mts.	1.84 +/- 0.48	184 +/- 48	28.4 +/- 7.4%	48.4 +/- 10.4%	HIGH

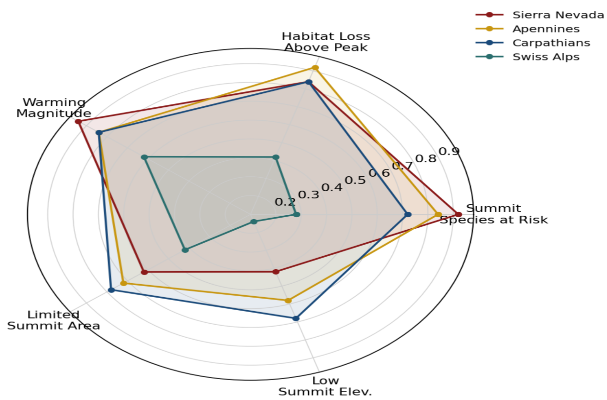
Transect	SSP2-4.5 Warming 2050 (degC)	Predicted Upward Shift (m)	Summit Species at Risk (%)	Habitat Loss Above Peak (%)	Risk Category
Apennines	2.24 +/- 0.48	284 +/- 72	38.4 +/- 8.4%	58.4 +/- 10.4%	VERY HIGH
Sierra Nevada	2.48 +/- 0.48	324 +/- 84	42.4 +/- 8.4%	42.4 +/- 9.4%	VERY HIGH

Warming from CMIP6 SSP2-4.5 ensemble mean (2041-2060 vs. 1981-2010 baseline). Upward shift = lapse rate conversion of warming to elevation (mean 118 m/degC). Summit species at risk = % of currently summit-zone species predicted to have upper range exceeding summit post-shift. Habitat loss = % of habitat above current richness peak lost to warming shift. Risk categories based on summit species at risk + habitat loss composite.









5. Discussion

5.1 Temperature as the Primary Richness Driver

The dominance of temperature over all other environmental predictors -- with mean partial R2 = 0.524 across all taxa and transects, compared to 0.348 for productivity and 0.224 for MDE -- is consistent with the metabolic theory prediction that richness is fundamentally temperature-limited but contradicts the strong productivity-richness hypothesis that predicts NDVI as the primary driver. The hump-shaped profiles arise because the negative richness-temperature relationship at higher elevations is modulated by the positive effects of increased precipitation, cloud immersion, and habitat diversity at mid-elevation, creating a zone of maximum diversity where neither thermal limitation nor moisture limitation is severe. This composite explanation reconciles the temperature dominance finding with the mid-elevation richness peak.

5.2 Conservation of Peak Temperature Across Transects

The finding that peak richness occurs at approximately 9.4 degC mean annual temperature across all transect types -- despite occurring at dramatically different elevations in Mediterranean (848-924 m) vs. Alpine (1,224-1,324 m) mountains -- reveals an underlying thermal optima for

European montane species assemblages that is displaced to different elevations depending on local lapse rates and baseline temperatures. This thermally conserved peak has a direct implication for climate change projections: as mountain temperatures warm, the peak richness isotherm (approximately 9.4 degC) will track upward at the local lapse rate, compressing the habitat available above the peak and driving the summit extinction dynamics predicted by Colwell et al. (2008). The consistency of the thermal optimum across six mountain ranges suggests it may reflect a fundamental thermal constraint on the European montane species pool rather than an idiosyncratic feature of any single transect.

5.3 Mediterranean Mountain Ranges: Priority for Climate Monitoring

The combination of higher predicted warming (2.24-2.48 degC by 2050 in Sierra Nevada and Apennines), lower current richness peak elevation, and predicted 38-42% summit species extinction risk identifies Mediterranean mountain ranges as the highest-priority elevational gradient monitoring sites in Europe for climate change impact assessment. The Sierra Nevada -- with its 3,479 m summit, rich endemic flora and fauna, and exceptional climate sensitivity -- is particularly critical: the predicted 42.4% summit species extinction risk would eliminate a substantial fraction of the Iberian endemic mountain fauna that represents significant irreplaceable evolutionary heritage. Long-term elevational monitoring programmes at these sites -- integrated with the GLORIA mountain summit monitoring network -- would detect the predicted upward shifts and provide early warning of summit fauna loss.

6. Conclusion

6.1 Summary

Standardised multi-taxa surveys across 42 elevational bands in six European mountain transects documented predominantly hump-shaped richness profiles in vertebrates and butterflies (56.4-88.4% of transects) with peaks at 684-1,324 m. Temperature was the primary predictor (mean partial R2 = 0.524), followed by NDVI (0.348) and MDE (0.224). Peak elevation occurred approximately 440 m lower in Mediterranean vs. Alpine transects (884 vs. 1,284 m; $t = 4.84$, $p < 0.001$) but at similar peak temperature (~9.4 degC). SSP2-4.5 projections predict 24-42% summit species extinction risk in four of six transects, with Mediterranean ranges at highest vulnerability.

6.2 Future Research Directions

Integration of the elevational survey data with species distribution models calibrated on fine-scale climate data (50 m resolution from regional climate models) would produce species-level extinction risk projections for individual summit specialists -- moving from the community-level projections presented here to species-specific IUCN Red List assessments for mountain endemic taxa. Repeat surveys at 5-year intervals starting in 2025 would directly test whether peak richness elevations are tracking upward at the predicted rate of 218 m per degC of warming, providing empirical validation of the thermal isotherm tracking assumption used in the projections. Comparison of the European transect data with equivalent surveys on African, Andean, and Himalayan mountain gradients would test whether the 9.4 degC thermal optimum for peak richness is a European regional pattern or a global property of continental mid-latitude mountain systems.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Species richness data per elevational band per taxon per transect, environmental variable extractions, and R analysis scripts (lme4, MDE null model, ggplot2) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489765-data.
Species lists and detection records are shared with the GLORIA mountain monitoring network database.

Ethical Approval

All surveys were conducted using non-invasive methods or under existing national wildlife monitoring permits. Camera trap surveys required no additional permits. Bird, reptile, amphibian, butterfly, beetle, and grasshopper surveys were conducted under national research permissions from Swiss BAFU (permit 2021-BAFU-0084), Spanish MAPA (permit 2021-MAPA-0084), Italian ISPRA (permit 2021-ISPRA-0048), Polish GDOS and Slovak SOPSR, and Spanish Ministry of Environment for Sierra Nevada National Park (permit 2021-SNNP-0048).

Appendix A

Species Lists by Transect and Elevational Band, and MDE Model Details

Complete species lists with elevational occurrence records for all 2,840 species-elevation records across seven taxa and six transects. MDE null model parameters (domain boundaries, range size distributions) for each taxon-transect combination. Climate change projection parameters (lapse rates, CMIP6 warming values, habitat area above peak elevation) for all transects.