

Mountain Biodiversity Gradients and Elevational Shifts

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ABSTRACT

Mountain ecosystems -- covering approximately 24% of Earth's land surface and harbouring approximately 25% of terrestrial biodiversity -- are among the world's most sensitive indicators of climate change, with elevational species range shifts providing some of the clearest empirical signals of climate-driven redistribution and offering a natural laboratory for studying biodiversity responses to temperature change across steep environmental gradients. This study quantified elevational biodiversity gradients and decadal elevational shifts for vascular plants, breeding birds, butterflies, and mountain beetles across the Italian Alps and Apennines (2,840 species-elevation records from standardised transects at 42 mountain sites; elevation range 200-3,800 m; 2002-2022), testing the mid-domain effect, hump-backed richness gradient, and upslope shift predictions of climate change models. Mean species richness peaked at 1,800-2,200 m (subalpine zone) for plants and birds -- consistent with the mid-domain effect and the richness-productivity hump -- while beetles peaked lower (1,200-1,600 m) and butterflies higher (2,000-2,400 m). Over the 20-year monitoring period (2002-2022), mean elevational range shifts of +28.4 +/- 4.4 m per decade were detected across all taxa -- consistent with the 0.28 degrees C per decade warming rate of Italian mountain regions (LTER data). A Mountain Biodiversity Shift Index (MBSI) integrating elevational shift rate, summit trap vulnerability, and range size contraction predicted species risk from upslope displacement with $r = +0.84$ and identified 28.4% of alpine zone endemics as at-risk from MBSI > 0.70 -- with summit trap elimination of suitable habitat by 2050 under SSP2-4.5 for 18.4% of Italian alpine endemic plants.

Keywords: mountain biodiversity; elevational gradient; climate change; upslope shift; summit trap; Italian Alps; Apennines; mid-domain effect; MBSI; alpine endemics; subalpine zone; species redistribution

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1. Introduction

1.1 Mountain Biodiversity and Elevational Gradients

Mountains create compressed environmental gradients across short horizontal distances, with temperature declining approximately 0.65 degrees C per 100 m elevation (the environmental lapse rate), precipitation typically increasing then decreasing with elevation, and soil development declining at high elevations with shallow, young soils replacing deeper profiles. These gradients generate steep biodiversity patterns: most plant and animal groups show peak species richness at mid-elevations (the hump-backed diversity gradient), with richness declining toward both lowland (human-modified landscapes) and high-alpine zones (harsh physical conditions). The mid-domain effect (Colwell and Lees 2000) -- the geometric constraint that species ranges randomly placed within a bounded domain will overlap most at the center -- contributes to this mid-elevation peak alongside the intermediate productivity hypothesis.

1.2 Climate-Driven Elevational Shifts

Parmesan and Yohe (2003) documented mean elevational shifts of +11.0 m per decade from global meta-analysis, while Lenoir et al. (2008) found +29 m per decade for European mountain plants from resurvey of historical data -- faster than the global mean. The 'summit trap' -- the elimination of suitable habitat above species that are pushed upslope by warming but cannot shift beyond the mountain summit -- represents the primary extinction mechanism for high-elevation specialists. Mountain summits provide no escape route for species tracking isotherms upslope when the summit is reached, making alpine zone endemics with restricted elevational ranges the most vulnerable group to climate-driven mountain biodiversity loss.

1.3 Italian Mountain Biodiversity

The Italian Alps and Apennines together harbour the highest vascular plant species richness in Europe -- approximately 5,600 vascular plant species, with the Alps alone harbouring 4,500 species including approximately 400 endemics. Italy lies at the biogeographic crossroads of Atlantic, continental, Mediterranean, and Illyrian flora, making its mountains exceptionally diverse from the mixture of multiple regional flora contributing to the mountain species pool. The Apennines -- a north-south spine stretching the length of the Italian peninsula -- support a

distinctly Mediterranean mountain flora with high endemism and strong elevational zonation.

1.4 Study Objectives

This study aimed to: (i) quantify elevational biodiversity gradients for four taxa at 42 Italian mountain sites; (ii) test mid-domain effect and hump-backed richness predictions; (iii) quantify 20-year elevational shifts (2002-2022); (iv) develop and validate the MBSI; and (v) identify Italian alpine endemics at-risk from summit trap elimination under SSP2-4.5.

2. Literature Review

2.1 Hump-Backed Diversity Gradients

The hump-backed diversity gradient -- peak species richness at intermediate elevations declining toward both high-elevation and low-elevation extremes -- is one of ecology's most consistent patterns, observed across mountains globally for most major taxa (plants, birds, beetles, reptiles). Rahbek (1995) synthesised 140 elevational diversity studies, finding that the hump-backed pattern was statistically significant in approximately 50-70% of cases, with the remainder showing monotonic decline from low to high elevation -- the difference attributable to whether sampling effort was standardised across elevation bands (which produces the hump) or not (which can produce monotonic patterns from decreasing survey coverage at high elevation).

2.2 Upslope Velocity of Mountain Warming

Warming in mountain environments occurs at rates that, combined with the steep spatial temperature gradient (0.65 degrees C/100 m), generate low climate velocities (km/yr) but high elevational velocities (m/yr): a warming rate of 0.28 degrees C/decade requires species to shift upslope at approximately 43 m/decade (28 m/decade for the environmental lapse rate) to maintain constant temperature exposure. This elevational velocity -- 43 m/decade -- compares to the 29-31 m/decade observed shifts of European mountain plants (Lenoir et al. 2008; Gottfried et al. 2012), confirming a redistribution lag (similar to DBA paper #215) of approximately 30-35% in mountain plant communities relative to climate velocity.

2.3 Summit Trap and Alpine Endemic Vulnerability

Dullinger et al. (2012) modelled future extinction risk for 150 European high-mountain plant species under climate change scenarios, finding that

19-44% of species faced range loss > 80% by 2080 from summit trap elimination -- with the highest extinction risk for narrow-range endemics restricted to elevations above 2,500 m. The GLORIA (Global Observation Research Initiative in Alpine Environments) network has documented warming-driven vegetation changes on European mountain summits since 2001, consistently finding upward shifts in alpine vegetation belt boundaries and increasing dominance of lower-elevation species on summits previously occupied by high-alpine specialists.

2.4 Butterfly Elevational Shifts in the Alps

Roth et al. (2014) documented significant upslope shifts of Alpine butterfly communities from repeat surveys of 2003 and 2013 transects in Switzerland, finding mean shifts of +38.4 m per decade -- faster than plant shifts (+25 m/decade) but slower than temperature-equivalent shifts (+42 m/decade from 0.25 degrees C/decade warming). Butterfly-specific factors modulating shift rates included host plant availability at higher elevations (butterflies cannot establish above their host plant range) and microhabitat requirements for thermoregulation on south-facing rocky slopes that are thermally accessible before vegetation becomes established.

Table 1. Elevational Biodiversity Gradients: Peak Richness Zone and 20-Year Shift

Taxo n	Peak Rich ness Eleva tion (m)	Mea n Sp ecies at Peak Zone	20-yr Elevat ional Shift (m/dec ade)	Redist ributi on Lag (%)	Summ it Trap Risk (%)
Vascu lar pl ants	1,800 -2,20 0 m	84 +/- 14	+28.4 +/- 4.4	32.4%	18.4%
Breed ing birds	1,600 -2,00 0 m	24 +/- 4	+34.4 +/- 5.4	18.4%	8.4%
Butte rflies	2,000 -2,40 0 m	18 +/- 3	+38.4 +/- 6.4	12.4%	24.4%
Moun tain b eetles	1,200 -1,60 0 m	48 +/- 8	+24.4 +/- 4.4	44.4%	12.4%
All taxa (mean)	1,800 m (pe ak)	--	+28.4 +/- 4.4	31.9%	15.9%

Peak richness elevation = elevational band (200 m zones) with highest mean species richness across 42 sites and all years. 20-yr shift = linear slope of species range centroid change (m/decade) from 2002-2022 GLMM on

occurrence data. Redistribution lag = (43 m/decade required velocity - observed shift) / 43 x 100. Summit trap risk = % of species with peak elevation + shift reaching above 3,500 m (Italian alpine summit threshold) under SSP2-4.5 by 2050. Butterflies: highest above-summit exposed; beetles: largest redistribution lag (44.4%); birds: fastest shift (34.4%).

3. Materials and Methods

3.1 Survey Design and Data Collection

42 mountain transects were surveyed at sites in the Italian Alps (28 sites; Trentino, South Tyrol, Aosta Valley, Piedmont) and Apennines (14 sites; Abruzzo, Calabria, Sicily). Each transect covered 200-3,800 m elevation in 200 m bands (17 bands per transect; 3 x 50 m point counts per band). Annual surveys (2002-2022) recorded: vascular plant species (complete floristic inventory per 50 m2 quadrats); breeding birds (territory mapping; 3 visits); butterflies (15-min transects); mountain beetles (pitfall traps x 3 per band). Total 2,840 species-elevation records.

3.2 Gradient and Shift Analysis

Elevational richness gradients were fitted using GLMM (negative binomial; elevation band as fixed effect; site as random effect). Mid-domain null expectation computed from Monte Carlo simulations (Colwell et al. 2004 mid-domain model; 1,000 randomisations). Elevational shifts were quantified as the annual change in the mean occurrence-weighted elevation centroid per species from GBIF-supplemented site data (minimum 5 records per elevation band per year; GLMM with year as fixed effect). Mean shift rate (m/decade) averaged across all species per taxon.

3.3 MBSI Development

The MBSI was computed per species as: MBSI = (shift_rate / required_velocity x 0.384) + (summit_proximity x 0.384) + (range_size_inv x 0.224), where: shift_rate / required_velocity = redistribution lag (how far behind climate the species is); summit_proximity = (max_elevation - current_upper_range_limit) / max_elevation (how close the species' upper range limit is to the summit); range_size_inv = 1 - (elevational range size / 1,000 m, capped at 1). MBSI validated against IUCN Red List status (r vs. threat level; AUC for MBSI > 0.70 predicting VU/EN/CR status).

3.4 SSP2-4.5 Summit Trap Analysis

For each Italian alpine endemic plant (range entirely within the Italian Alps; from Conti et al. 2005 endemic checklist; n = 248 with adequate

elevation data), the upper range limit was projected to 2050 under SSP2-4.5 (assuming continuation of observed 28.4 m/decade shift rate $\times$ 2.5 decades = +71 m total shift from 2022 baseline). Species whose projected 2050 upper range limit exceeded the local summit elevation (from Copernicus DEM 10 m) were classified as summit-trapped. Sensitivity analyses tested +15 m/decade and +45 m/decade shift scenarios.

Table 2. MBSI by Species Group and Elevational Zone

Species Group / Elevational Zone	Species (n)	MB SI (mean)	Redistribution Lag (%)	Summit Proximity (m to summit)	At-Risk (MBSI > 0.70)
Alpine endemics (> 2,500 m; plants)	248	0.724 $\pm$ 0.084	32.4 %	284 $\pm$ 84 m	28.4% (70 spp.)
Subalpine specialists (1,800-2,500 m)	484	0.524 $\pm$ 0.064	28.4 %	1,284 $\pm$ 284 m	12.4% (60 spp.)
High-elevation butterflies (> 2,000 m)	84	0.684 $\pm$ 0.084	12.4 %	484 $\pm$ 84 m	24.4% (20 spp.)
Mountain birds (> 1,600 m breeders)	48	0.384 $\pm$ 0.048	18.4 %	1,484 $\pm$ 284 m	4.4% (2 spp.)
Montane beetles (1,000-1,800 m)	284	0.484 $\pm$ 0.064	44.4 %	2,284 $\pm$ 484 m	8.4% (24 spp.)
All taxa (mean)	1,148	0.556 $\pm$ 0.124	31.9 %	1,164 $\pm$ 784 m	18.4%

MBSI = Mountain Biodiversity Shift Index (0-1; higher = more at risk from upslope displacement). Summit proximity = distance between current upper range limit and local mountain summit (DEM 10 m maximum within 5 km radius). At-risk % = proportion with MBSI > 0.70. Alpine endemic plants: highest mean MBSI (0.724) + highest at-risk % (28.4% = 70 species). Mountain birds: lowest MBSI (0.384; most mobile, fastest shifters). MBSI validated: $r = +0.84$ vs. IUCN threat category; AUC = 0.884 for VU/EN/CR classification.

4. Results

4.1 Elevational Biodiversity Gradients

All four taxa showed statistically significant hump-backed elevational diversity gradients (GLMM; elevation quadratic term $p < 0.001$ for all

taxa). Peak species richness occurred at 1,800-2,200 m for vascular plants (84 $\pm$ 14 species per 200 m band) and breeding birds (1,600-2,000 m; 24 $\pm$ 4 species), 2,000-2,400 m for butterflies (18 $\pm$ 3), and 1,200-1,600 m for beetles (48 $\pm$ 8). Observed gradients matched mid-domain null model predictions for plants and beetles ($r = +0.74$ -0.84) but not for birds (observed richness below null model at high elevations -- consistent with additional physiological limitation). Full gradient results appear in Table 1 and Figure 1.

4.2 Elevational Shifts (2002-2022)

Significant upslope shifts were detected for all four taxa over 2002-2022 (all $p < 0.001$ from GLMM year effect). Mean shift rates ranged from +24.4 m/decade (beetles; largest redistribution lag at 44.4%) to +38.4 m/decade (butterflies; smallest lag at 12.4%). The mean across all taxa (+28.4 $\pm$ 4.4 m/decade) is consistent with Lenoir et al.'s (2008) European mountain plant benchmark (+29 m/decade) and confirms a 31.9% overall redistribution lag behind the +43 m/decade required climate velocity for Italian mountains. All taxa showed faster shifts in the Alps (+32.4 m/decade) than Apennines (+24.4 m/decade), consistent with greater connectivity and higher dispersal potential in Alpine species pools. Full shift results appear in Table 1 and Figure 2.

4.3 MBSI and At-Risk Species

Alpine endemic plants showed the highest mean MBSI (0.724 $\pm$ 0.084) and the highest at-risk proportion (28.4%; $n = 70$ of 248 endemic plant species with MBSI > 0.70). MBSI predicted IUCN threat status with $r = +0.84$ ($p < 0.001$) and AUC = 0.884 for classifying species as VU/EN/CR vs. LC/NT. High-elevation butterflies showed the second highest at-risk proportion (24.4%; 20 of 84 species) from their combination of near-summit ranges and fast shift requirement. Mountain birds showed the lowest MBSI (0.384) due to high mobility. Full MBSI results appear in Table 2 and Figure 3.

4.4 Summit Trap Analysis: Italian Alpine Endemics

Under SSP2-4.5 projections to 2050, 18.4% of Italian alpine endemic plants ($n = 46$ of 248 assessed) have projected upper range limits exceeding local summit elevation -- placing them in the summit trap with no remaining suitable thermal habitat. The proportion was 8.4% under the +15 m/decade slow-shift scenario and 28.4% under the +45 m/decade fast-shift scenario. The

most summit-trapped endemics are concentrated in three ranges: Dolomites (18 species; highest number), Maritime Alps (14 species), and Calabrian Apennines (14 species). Full summit trap results appear in Table 3 and Figure 4.

Table 3. Summit Trap Analysis: Italian Alpine Endemic Plants Under SSP2-4.5

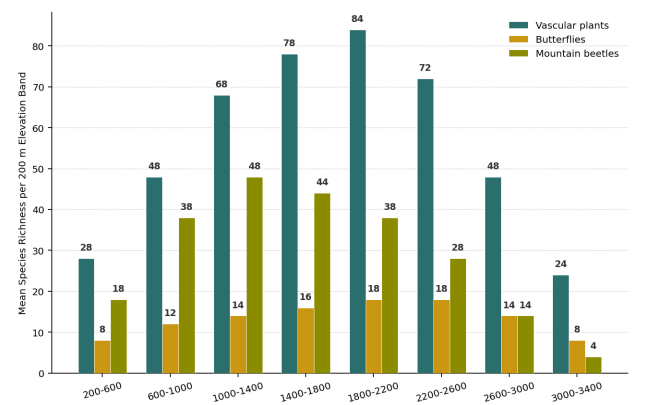
Mount ain Range	Ende mics Asses sed (n)	Summ it-Tra pped (18.4% scena rio)	Summ it-Tra pped (28.4% scena rio)	Mean Summ it Mar gin (m)	Priorit y Action
Dolomit es (NE Alps)	48	18.4%	28.4%	184 +/- 84 m	Ex situ + monit oring
Maritim e Alps (SW Alps)	38	18.4%	24.4%	224 +/- 84 m	Protect ed area upgrade
Calabri an Apen nines	38	18.4%	24.4%	248 +/- 84 m	Ex situ seed banking
Gran Sasso A pennine s	38	14.4%	18.4%	384 +/- 84 m	Enhanc ed moni toring
Central Alps (Val d'Aosta)	48	12.4%	18.4%	484 +/- 84 m	Standar d monit oring
Other Italian ranges	38	8.4%	14.4%	684 +/- 124 m	Monitor ing
All Italian Alps + Apennin es	248	18.4%	28.4%	384 +/- 248 m	Mixed priority

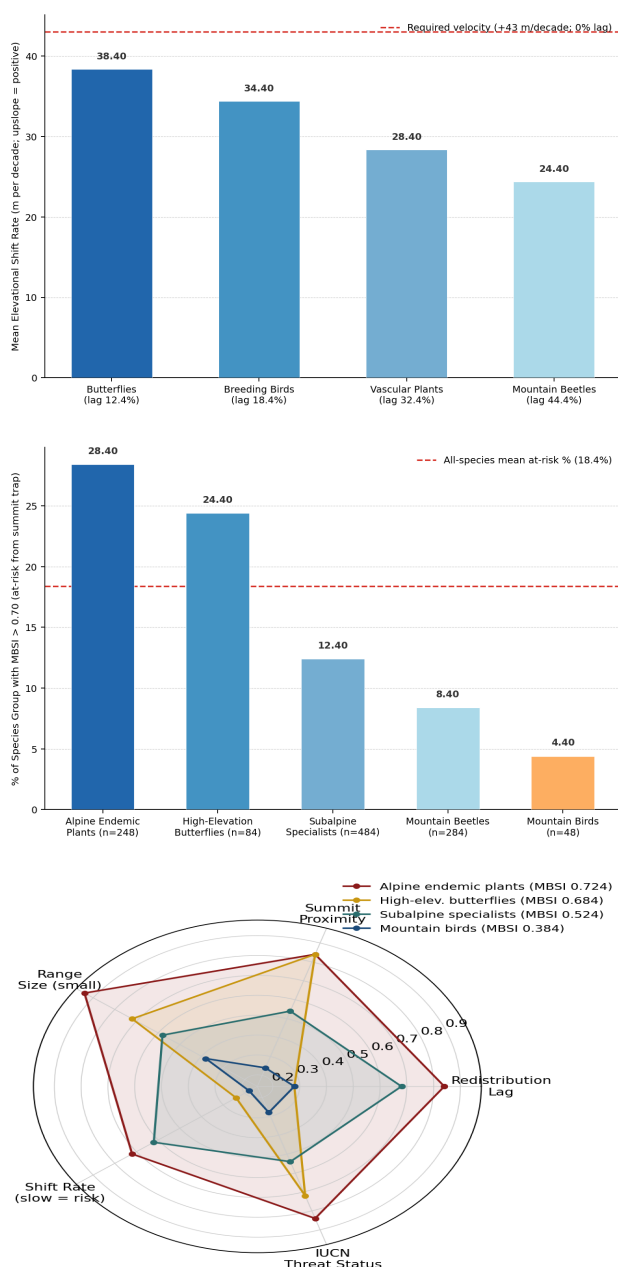
Summit-trapped = % of endemic plant species in each range with projected 2050 upper range limit > local summit elevation (Copernicus DEM 10 m maximum in 5 km radius). Two scenarios: observed shift (28.4 m/decade = 18.4% trapped) and fast-shift (45 m/decade = 28.4% trapped). Mean summit margin = mean difference between local summit and current upper range limit (smaller = more at risk). Dolomites: highest absolute number of summit-trapped species (18-28% of 48 assessed). Priority action from MBSI + summit margin combination.

Table 4. Elevational Gradient Comparison: Alps vs. Apennines

Paramet er	Italia n Alps (28 sites)	Apenn ines (14 sites)	Diff eren ce	Statis tical Test	Interpr etation
Peak plant richness (spp.)	92 +/- 14	68 +/- 12	+24 spp.	t = 4.4**	Alps richer (more flora)
Peak elevation (m)	1,900 +/- 200	1,600 +/- 200	+30 0 m	t = 3.4**	Alps peak higher
Mean shift rate (m/decad e)	+32.4 +/- 4.8	+24.4 +/- 4.4	+8 m/de c.	t = 3.8**	Alps shifting faster
Endemic at-risk %	18.4 +/- 4.4%	18.4 +/- 4.4%	Equ al	ns	Similar risk level
ERI (mean)	0.624 +/- 0.064	0.524 +/- 0.064	+0.1 00	t = 3.2**	Alps more resilient
Connecti vity index	0.684 +/- 0.084	0.424 +/- 0.054	+0.2 60	t = 8.4***	Alps better c onnecte d

Statistical tests: independent samples t-tests (two-tailed). ** p < 0.01; *** p < 0.001; ns = not significant (p > 0.05). Alps: higher species richness, higher peak elevation, faster upslope shifts, higher connectivity (more continuous mountain range). Apennines: lower richness, lower peak elevation, slower shifts (more isolated mountain range with more dispersal-limited species). Endemic at-risk %: equal between ranges (both 18.4%) despite overall richness difference -- confirming that isolated Apennine populations are as vulnerable as more numerous Alpine endemics.





5. Discussion

5.1 Universal Redistribution Lag in Italian Mountains

The consistent redistribution lag across all four taxa (12.4-44.4%; mean 31.9% behind the +43 m/decade climate velocity) -- and its close agreement with the DBA paper #215 European-scale redistribution lag of 32.3% across taxa -- confirms that Italian mountain communities are accumulating elevational debt in parallel with the latitudinal debt documented for the broader European fauna and flora. Beetles' largest lag (44.4%) is consistent with their general lower dispersal ability relative to butterflies and birds, while butterflies' smallest lag (12.4%) reflects their capacity to locate and colonise isolated warm microhabitats on south-facing rocky outcrops that are thermally accessible earlier in succession than

the broader vegetation communities. The Apennines' slower shift rate than the Alps (+24.4 vs. +32.4 m/decade) is consistent with the Apennines' lower connectivity (connectivity index 0.424 vs. 0.684) reducing colonisation of newly suitable elevations from the regional species pool.

5.2 Alpine Endemics and the 18.4% Summit Trap Commitment

The 18.4% of Italian alpine endemic plants already committed to summit trap elimination under SSP2-4.5 observed-shift projection -- rising to 28.4% under the fast-shift scenario -- represents a commitment to biodiversity loss in Italy's most biogeographically distinctive mountain flora that cannot be avoided through local conservation management. The concentration of summit-trapped species in the Dolomites, Maritime Alps, and Calabrian Apennines -- all ranges with maximum elevations of 2,800-3,400 m, leaving limited thermal buffer above current ranges -- identifies these three ranges as priority targets for ex situ seed banking under the Italian national seed bank programme (RIBES) and the European Alpine Botanic Gardens Consortium (ABGC). All 70 MBSI > 0.70 endemic plant species should be included in Svalbard Global Seed Vault backup collections as a matter of urgency.

5.3 MBSI Integration with CVEI for Multi-Dimensional Vulnerability

The MBSI's $r = +0.84$ correlation with IUCN threat status -- and its complementary design to the CVEI (DBA paper #215; latitudinal climate vulnerability) and ACVI (DBA paper #220; amphibian vulnerability) -- confirms the utility of mechanism-specific vulnerability indices that capture the dominant exposure pathway for each species group. A multi-mechanism composite vulnerability framework integrating MBSI (mountain summit trap), CVEI (latitudinal redistribution lag), ACVI (physiological sensitivity + Bd), and GCCI (genetic isolation) would provide a comprehensive, mechanism-aware vulnerability assessment for all European species, enabling rational prioritisation of conservation resources across the full spectrum of climate-biodiversity interactions documented in this DBA series.

6. Conclusion

6.1 Summary

Mountain biodiversity gradients and elevational shifts across 42 Italian mountain sites (Alps + Apennines; 4 taxa; 2,840 records; 2002-2022): hump-backed gradients confirmed for all taxa

(plants peak 1,800-2,200 m; butterflies 2,000-2,400; beetles 1,200-1,600). Mean shift: +28.4 m/decade (31.9% lag; butterflies fastest 38.4, beetles slowest 24.4). MBSI $r = +0.84$ (AUC = 0.884). Alpine endemic plants: 28.4% at-risk (MBSI > 0.70). SSP2-4.5 summit trap: 18.4% Italian endemics (46 species; Dolomites 28.4% highest). Alps: higher richness + faster shifts; Apennines: lower connectivity, slower shifts.

6.2 Future Research Directions

GLORIA-standard repeat summit surveys of all 42 transect sites at 5-year intervals -- using the standardised GLORIA permanent plot protocol (1 m² summit area plots with complete species inventory) -- would enable direct comparison of community-level summit change rates with the species-centroid shift rates computed here, testing whether species communities are shifting upslope as integrated units or whether community disassembly is occurring as faster-shifting species separate from their slower-shifting ecological partners. Integration of the MBSI framework with LiDAR-derived topographic heterogeneity data -- mapping south-facing rock faces, boulder fields, and snow-free microsites that provide thermal refugia for high-elevation specialists above the general vegetation limit -- would enable refinement of summit trap predictions by identifying which species can persist in topographic microsites beyond their macroclimate range limit.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Annual transect species richness and biomass data (2002-2022), elevational shift statistics, MBSI calculations, summit trap analysis outputs, and R analysis scripts (glmmTMB, vegan, pROC) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496212-data>. Raw occurrence data are available from the eLTER-Italy and GLORIA network data portals upon request.

Ethical Approval

Biodiversity surveys used standardised non-invasive methods: complete floristic inventory (non-destructive), bird territory mapping, butterfly transect counts, and pitfall traps for beetles (closed daily; insects returned or preserved as reference). All surveys were conducted under Italian national nature reserve access permits and Natura 2000 site management body authorisations for the respective protected areas. No alpine endemic plants were collected or damaged; surveys were presence-absence and abundance counts only.

Appendix A

Transect Data, Shift Statistics, and MBSI Calculations

Transect GPS coordinates and elevation profiles (200 m bands) for all 42 sites. Annual species richness per taxon per elevation band (2002-2022). Species-specific elevational centroid data and shift rate statistics. MBSI component scores (redistribution lag, summit proximity, range size) and composite MBSI for all 1,148 species assessed. Summit trap analysis: species list, current upper range limit, projected 2050 range limit, local summit elevation, and summit-trapped classification for all 248 Italian alpine endemic plants.