# Faster growing and more functionally diverse: global change alters functional trait composition of mountain plant communities in the European Alps

Running title: mountain plant community shifts

Sergey Rosbakh[1,*], Sabine B. Rumpf[2] and Stefan Dullinger[3]

[1] Department of Plant and Environmental Sciences, University of Copenhagen, Denmark, rosbakh@plen.ku.dk

[2] Department of Environmental Sciences, University of Basel, Switzerland, sabine.rumpf@unibas.ch

3 Biodiversity Dynamics and Conservation, University of Vienna, Austria, stefan.dullinger@univie.ac.at

ORCIDs

Sergey Rosbakh: 0000-0002-4599-6943

Sabine Rumpf: 0000-0001-5909-9568

Stefan Dullinger: 0000-0003-3919-0887

* Corresponding author: rosbakh@plen.ku.dk, + 45 60 59 75 50

## Summary

Understanding how global change reshapes mountain plant communities is essential for predicting biodiversity and ecosystem function in a warming world. Using resurvey data from over 1,400 alpine and subalpine vegetation plots across the European Alps, we show that community-weighted means of key functional traits – specific leaf area, leaf nitrogen, and seed mass – have increased significantly over recent decades, reflecting a widespread shift toward more resource-acquisitive strategies. Yet trait–environment relationships along the elevational gradient have remained remarkably stable, pointing to persistent abiotic filtering. Contrary to expectations, plant height declined slightly, and increases in seed mass were confined to lowland communities mainly, likely due to edaphic constraints and reduced uphill dispersal by large herbivores, respectively. These findings indicate that global change is reshaping the functional structure of montane plant communities by shifting baseline trait composition while leaving the underlying elevational filters largely intact.



Key words: European Alps, diversity, elevation, eutrophication, global change, grassland, montane, trait, warming

## Introduction

Mountains are globally important for their remarkable biodiversity (Testolin, Attorre, et al., 2021) and the critical ecosystem services they provide (Körner, 2004). These ecosystems play an essential role in regulating hydrological cycles, sequestering carbon and supporting unique flora and fauna adapted to steep environmental gradients (Grêt-Regamey & Weibel, 2020). Mountains also provide essential resources and livelihoods for millions of people. Furthermore, they serve as natural laboratories for understanding ecological and evolutionary processes, including species interactions, adaptation, and resilience, particularly relevant in the context of global environmental change (Körner, 2007).

Plant communities are shaped by the interplay of three fundamental processes: environmental filtering, biotic interactions, and dispersal limitations (Kraft et al., 2015; Weiher & Keddy, 2001). Environmental filtering acts on the regional species pool, favouring local establishment of species whose traits are suited to prevailing abiotic conditions, such as temperature, moisture and soil fertility (Bello et al., 2013). Biotic interactions, including competition, facilitation, and herbivory, further influence plant community composition and structure by mediating the coexistence of species (Choler et al., 2001; Maestre et al., 2009). Dispersal limitations constrain the pool of species that can colonize and persist in a given area (Myers & Harms, 2009; Poschlod et al., 2013).

In mountain ecosystems, elevational gradients strongly influence alter the relative influence of these abiotic factors on plant communities. Harsher environmental conditions at higher elevations, such as shorter growing seasons, lower temperatures and soil fertility, and stronger UV radiation, intensify environmental filtering, favouring stress-tolerant species adapted by specific traits (Bello et al., 2013; Pellissier et al., 2010). In contrast, negative biotic interactions like competition often diminish in importance but the role of facilitation increases due to lower resource availability and reduced species richness (Choler et al., 2001). Due to rough terrain and slow soil formation, vegetation becomes more fragmented at higher elevations, thereby reducing habitat connectivity (Körner, 2007) which leads to an increasing impact of dispersal limitations (Helm et al., 2024; Rosbakh et al., 2022).

The complex interactions between these three fundamental processes result in distinct community assembly patterns along elevational gradients. A typical alpine plant community is composed of short-statured, slow-growing, long-lived species with conservative resource-use strategies and small, light-weighted seeds that facilitate dispersal in the steep, fragmented terrain (Körner, 2021; Rosbakh et al., 2022; Testolin, Carmona, et al., 2021). In contrast, lowland communities are shaped predominantly by biotic interactions such as competition, with reduced influence of environmental filtering due to more favourable abiotic conditions and fewer dispersal limitations facilitated by a greater abundance and

diversity of dispersal vectors. (Pellissier et al., 2010; Rosbakh et al., 2022). As a result, typical lowland species are taller, faster-growing, shorter-lived plants with acquisitive resource-use strategies and larger, heavier seeds.

Global change fundamentally alters the processes that govern community assembly. Mountain ecosystems, where environmental filtering driven by specific temperature and snow conditions shapes community structure, are thought to be particularly vulnerable to accelerating climate change (Schmeller et al., 2022). Warming can relax environmental filtering by reducing climatic constraints, thereby enabling the establishment of species with traits favouring rapid growth and high resource acquisition previously restricted to lower elevations (Lamprecht et al., 2018a; Steinbauer et al., 2022; Vitasse et al., 2021). Additionally, warmer and longer summers can accelerate microbial decomposition and nitrogen mineralization, thereby enriching soil nutrient pools (Rustad et al., 2001). Together with spatially heterogeneous atmospheric nitrogen deposition, particularly pronounced on the fringes of some mountain ridges (e.g. the Northern Alps; (Kirchner *et al.* 2014), this process can further accelerate community shifts toward species with acquisitive resource-use strategies (Zhu et al., 2020). Simultaneously, biotic interactions such as competition may be intensified by climate warming and nutrient enrichment as previously excluded species establish, potentially favouring competitive dominants over stress-tolerant species (Alexander et al., 2015). Further, recent land-use changes in

mountainous regions – such as intensification at lower elevations, and tourism expansion and grazing cessation at higher elevations – may have contributed to shifts in plant community composition by favouring species with traits adapted to these altered land-use regimes (Midolo et al., 2021). Dispersal processes are also likely disrupted by changes in landscape connectivity due to land-use intensification (e.g. using seed mixtures to improve grassland productivity at low and middle elevations) or changes in the population size and activity patterns of dispersal agents (e.g. wild ungulates and domestic cattle; (Primi et al., 2024)). Collectively, these alternations to assembly processes are expected to drive profound changes in montane species composition, leading to the emergence of novel communities with possible implications for biodiversity (Chauvier-Mendes et al., 2024).

Here, we use >1,400 resurveyed vegetation plots in the European Alps and an extensive, original dataset of four plant functional traits – plant height, specific leaf area (SLA), leaf nitrogen content (LeafN), and seed mass – to analyse long-term changes in the functional composition of mountain plant communities. These traits were selected because they represent major ecological axes of plant specialization (Díaz et al. 2016; Westoby 1998), making them particularly relevant for understanding the mechanisms that shape plant community structure and composition across environmental gradients (e.g., Bello et al. 2013; Choler 2005; Rosbakh et al. 2022; Spasojevic & Suding 2012). Changes in their

community-weighted means (CWMs) and community-level variances (i.e. functional diversity; FD), are widely used in plant ecology to infer how plant communities are shaped by environmental filtering, biotic interactions, and dispersal limitations (Ricotta & Moretti 2011). Higher CWMs of mean height, SLA, LeafN and seed mass are commonly interpreted as indicative of a higher impact of competition, and a lower impact of environmental filtering on community assembly. Similarly, higher FD is often correlated with weak environmental filtering, stronger competitive interactions among plant community members and lower environmental constraints on colonization (Bello et al., 2013; Götzenberger et al., 2012; Rosbakh et al., 2022).

Accordingly, we tested the overarching hypothesis (*H*) that global change has altered community assembly processes in mountain plant communities towards a reduced impact of environmental constraints, an increased importance of competition and altered dispersal processes. Specifically, we predicted: (*H1*) that alleviating cold stress and nutrient limitation would favour fast-growing, resource-acquisitive species, resulting in higher CWMs of all four traits;

(*H2*) that upslope migration of acquisitive species (Rumpf et al., 2018a) and/or increases in their local abundance (Lamprecht et al., 2018a) that would be also reflected in higher FD values in the recent communities (i.e. increased functional trait diversity);

(*H3*) that weakened abiotic constraints along the elevational gradient would attenuate trait–environment coupling, producing significantly shallower slopes in the CWM–elevation regressions in recent surveys compared to historical baselines.

## Materials and methods

*Mountain plant community data*

To analyse the temporal changes in the functional composition of mountain plant communities in the European Alps, we used previously collected historical and recent vegetation data (Rumpf et al., 2018b, 2019). The initial historical dataset comprised 1,576 relevés (hereafter referred to as 'plots'; Figure 1) of non-forest vegetation, recorded before 1970, digitized from published sources. These data included detailed site descriptions, such as elevation (m a.s.l.), slope inclination (degrees), aspect (16 compass directions), plot size ($m^2$), total vascular plant cover (%), plant community type, bedrock type, and survey date. Where survey years were unspecified, they were estimated as publication year minus two.

Historical plots lacked precise geographical coordinates. Therefore, a standardized approach was used to approximate their locations based on metadata. Each described locality was represented as a polygon within which the plot might be situated. This polygon was intersected with a 25 × 25 m resolution digital elevation model, matching the metadata for elevation (±50 m), slope

(±20°), and aspect (±40°). Bedrock information was reclassified as calcareous, siliceous, or intermediate based on either the original description or phytosociological classification. These areas were further filtered by proximity (≤200 m) to trails identified using aerial imagery from Google Earth, reflecting accessibility assumptions of the original studies. Final coordinates were assigned to the centroid of the largest contiguous area that satisfied all these criteria.

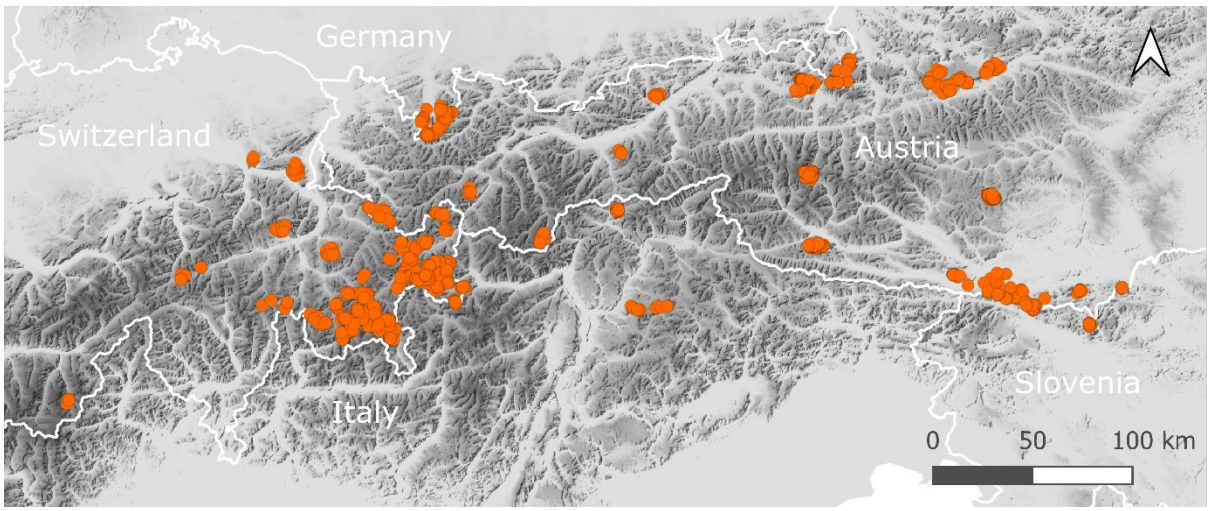


Figure 1. Location of the study sites across the European Alps. The map lines delineate study areas and do not necessarily depict accepted national boundaries.

In the vegetation periods of 2014 and 2015, the historical plots were re-surveyed following the same methodology as in the original studies. These plots span an elevational range from 485 to 3,226 m a.s.l. and cover time intervals from 45 to 104 years. The resolution of the digital elevation model (25 × 25 m) was coarser than the largest historical plot size (100 m²). Therefore, final resurvey locations

were fine-tuned in the field based on additional metadata to optimize accuracy using habitat characteristics (e.g., meadow, tall herbs, bog), micro-topographical features (e.g., snow beds, ridges), and observers avoided distinct vegetation boundaries to ensure homogeneity and consistency with historical sampling. Blind resurveys ensured unbiased comparisons between past and present plant communities.

Species were identified to the most precise taxonomic level, including subspecies where applicable. Unidentified specimens were collected for laboratory identification. Species cover-abundance was recorded using the Braun-Blanquet scale (levels: +, 1, 2, 3, 4, and 5), and total vascular plant cover was estimated in percent. Taxonomic adjustments were made post-fieldwork to address species aggregates, particularly in genera prone to revision (e.g., *Festuca*, *Alchemilla*, *Taraxacum*).

*Trait data*

We focused exclusively on vascular flowering plants; trees were excluded from the analysis. Because it was not feasible to collect trait data for all the species occurring in the focal plots, we restricted our analysis to the most frequent and/abundant species. Specifically, we excluded species occurring at fewer than 100 plots and with a maximum abundance of less than 3% across all sites in both historic and recent surveys. We measured trait data for 396 species, ensuring that

in every sampled plot, species with available trait data represented at least 80% of the total abundance. Plots for which trait coverage fell below this threshold were excluded, resulting in a final dataset of 1,442 plots. This approach ensured a robust estimation of plant community functional diversity and composition (Bello et al., 2013; Pakeman & Quested, 2007). Due to the laborious nature of measuring traits across multiple populations per species, we did not account for intraspecific trait variability. Instead, we treated trait values as species-specific means.

Most trait data were collected *in situ* under species' optimal ecological conditions between 2009 and 2022 following standardized protocols (Pérez-Harguindeguy et al., 2016) as part of projects on alpine plant ecology in the Northern Alps (e.g. (Rosbakh et al., 2022; Rumpf et al., 2018b; Zettlemoyer et al., 2024). In addition, we incorporated several unpublished functional trait datasets from the Karawanks and Nock Mountains (S. Rosbakh, unpublished) and the Stubaier Alps (S. Dullinger, unpublished). For the remaining trait data, we supplemented our dataset with values extracted from public databases, including the Tundra Trait Team (Bjorkman et al., 2018), TRY (Kattge et al., 2020), LEDA (Kleyer et al., 2008), and the Seed Information Database (SER, INSR, RBGK, 2023).

Trait data were available for most species included in the analysis: plant height (376 out of 396 species), specific leaf area (331 out of 396 species), leaf nitrogen content (286 out of 396 species), and seed mass (359 out of 396 species). Missing

trait values were imputed using the *missForest* package (Stekhoven & Bühlmann, 2012). To enhance imputation quality, we incorporated data on species phylogenetic relatedness (Durka & Michalski, 2012) as well as their ecological characteristics. For the latter, we used Landolt indicator values for temperature, continentality, light requirements, soil moisture, nutrients, pH, humus content, and dispersity (Landolt et al., 2010)). These indicators were selected because they correlate strongly with species' habitat requirements, such as air temperature, soil phosphorus content, and soil depth (e.g. (Rosbakh & Poschlod, 2021)) and are widely available for the flora of the European Alps. For a few species lacking Landolt indicator values, we assigned mean values calculated from all congeneric species present in the dataset. Given that missing trait values accounted for less than 20% of the dataset, we assumed that imputed values had minimal influence on the ecological signal in our analysis (Penone et al., 2014).

*Statistical analysis*

To assess long-term changes in the functional structure of mountain plant communities, we calculated community-weighted means (CWMs) and functional diversity (FD) – two measures explaining community assembly processes and ecosystem functioning (Ricotta & Moretti, 2011). CWMs represent the average trait value of a community, weighted by species relative abundance. This metric primarily reflects the traits of dominant species, providing insight into the

community's main adaptation strategies to local environmental conditions (De Bello et al., 2021). Functional diversity (FD) quantifies the variation in functional traits among species in a community and incorporates both species relative abundances and trait dissimilarities. FD reflects the balance between trait convergence, driven by environmental filtering, and trait divergence, associated with niche partitioning and resource complementarity. A low FD indicates functional similarity among species, suggesting strong environmental filtering, while a high FD represents greater trait differentiation, promoting species coexistence (Cadotte, 2017; Kraft et al., 2015). The FD was computed as Rao's quadratic entropy (Rao, 1982); both CWMs and FD were calculated for each of the 1,442 plots in both the original survey and the re-survey, based on species abundance data and available trait values using the *FD* package in R (Laliberté et al., 2014).

The change in CWM and FD values over time were estimated with linear mixed-effect models with year and plot included as fixed and random factor, respectively. We included plot elevation as an interaction term (i.e. CWM/FD ~ Year*Elevation + (1|Plot)) to test whether changes CWM and FD were elevation-specific. The differences in regression lines (both intercepts [i.e. average CWM/FD value] and slopes [i.e. the strength of trait-elevation relationship]) between the historic and recent data were estimated with the help of posthoc

Tukey test. Model assumptions were met in all cases. All statistical analyses were conducted in the statistical environment R (R Core Development Team, 2025).

We used ChatGPT to improve the language of the originally written text.

## Results

*Changes in individual traits*

We observed significant changes in the community-weighted means (CWMs) of all studied traits over the observation period (Figure 2; Table 1). Average plant height slightly but significantly decreased from 0.15 m in historical surveys to 0.14 m in recent surveys ($p < 0.001$, Figure 2A). In contrast, specific leaf area (SLA) significantly increased from 15.7 $mm^2/mg$ historically to 18.7 $mm^2/mg$ recently ($p < 0.001$, Figure 2B). Leaf nitrogen content (LeafN) also increased significantly from 2.10% to 2.34% ($p < 0.001$, Figure 2C), and seed mass increased from 0.77 mg historically to 0.85 mg in recent communities ($p < 0.001$, Figure 2D). In ecological terms, these trait changes indicate a shift towards plant communities composed of relatively shorter species characterized by faster growth rates, higher nutrient demands, and greater reproductive investment.

Table 1. Summary of linear mixed-effects model results for plant height, specific leaf area, leaf nitrogen content and functional diversity (estimated as Rao's Q) in historical and recent vegetation surveys across an elevational gradient. For each trait, the table shows the estimated intercepts (mean predicted value at the average elevation) and slopes (change per meter elevation). Estimates are shown as mean ± standard error. Asterisks (*) indicate statistically significant differences ($p < 0.05$) either between time periods (intercepts) or difference from zero within a time period (slopes). Models include survey period (Historical vs. Recent), elevation, and their interaction as fixed effects, and Site as a random effect.

| Model | Survey | Intercept | Slopes |
|---|---|---|---|
| **Canopy height** | Historical | 0.15 ± 0.01 | -0.01 ± 0.001 * |
| | Recent | 0.14 ± 0.01 * | -0.01 ± 0.001 * |
| **Specific leaf area** | Historical | 15.7 ± 0.09 | -0.49 ± 0.03 * |
| | Recent | 18.7 ± 0.09 * | -0.36 ± 0.03 * |
| **Leaf nitrogen content** | Historical | 2.10 ± 0.01 | -0.03 ± 0.01 * |
| | Recent | 2.34 ± 0.01 * | -0.02 ± 0.01 * |
| **Seed mass** | Historical | 0.77 ± 0.01 | -0.01 ± 0.01 n.s. |
| | Recent | 0.85 ± 0.01 * | -0.04 ± 0.01 * |
| | Historical | 1.68 ± 0.02 | -0.10 ± 0.01 * |

| | | | |
|---|---|---|---|
| **Functional trait diversity (Rao's Q)** | Recent | 2.60 ± 0.02 * | -0.12 ± 0.01 * |

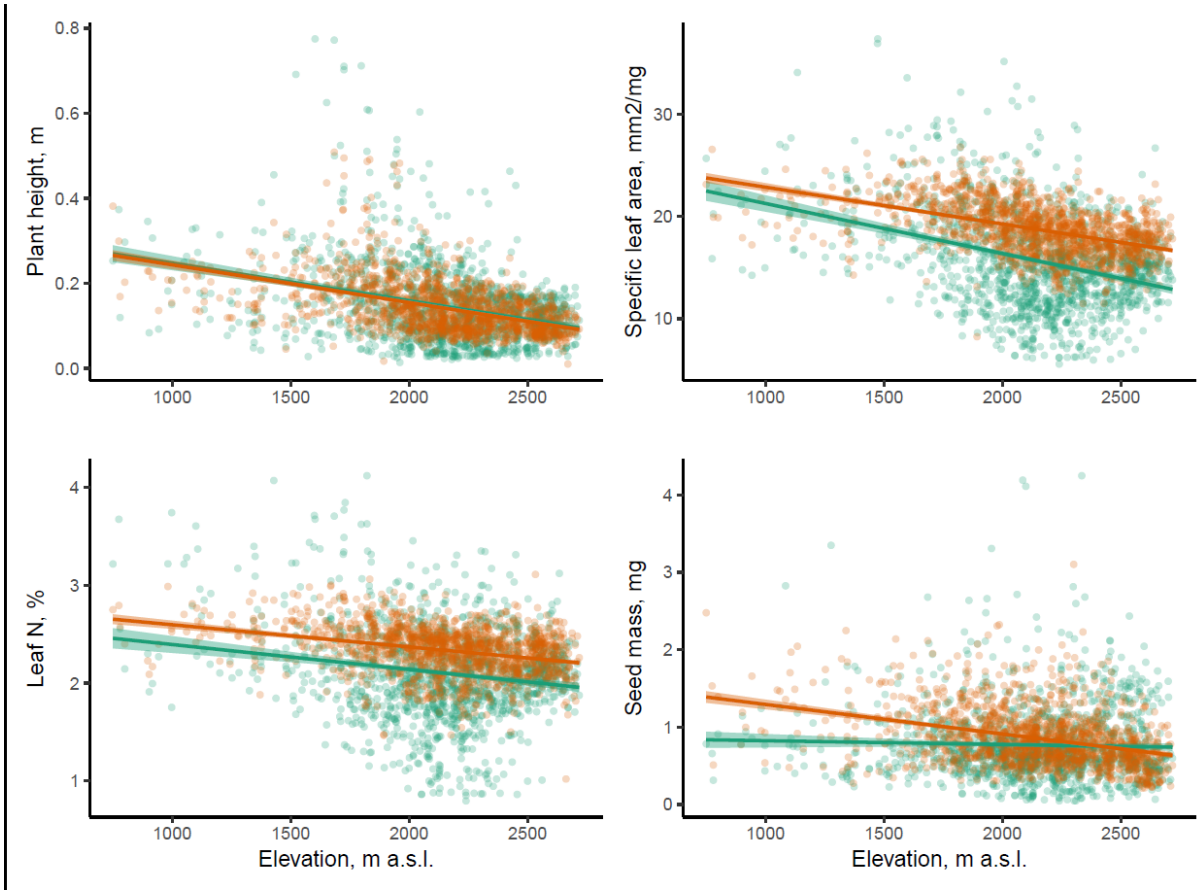


Figure 2. Changes in community-weighted means of A) plant height, B) specific leaf area, C) leaf nitrogen content and D) seed mass with elevation in 1,442 historic (green) and recent (orange) European mountain plant communities as estimated by linear mixed-effect models. Solid lines indicate significant relationships ($p < 0.05$), the shaded areas denote the 95% confidence interval. See Table 1 for specific model intercepts and slopes.

301

302 *Changes in functional diversity*

303 The observed change in all trait means corresponded to a significant increase in
304 functional diversity (FD) from historical (average FD = 1.7) to recent plant
305 communities (average FD = 2.6; $p < 0.001$; Figure 3, Table 1). Ecologically, this
306 increase indicates that recent communities host species with a broader range of
307 ecological strategies compared to historical communities. FD exhibited a
308 consistent negative relationship with elevation in both historical and recent
309 datasets, with similar slopes (-0.10 historically vs. -0.12 recently) that did not
310 differ statistically, demonstrating that the overall elevational pattern remained
311 stable over time (Figure 3, Table 1).

312

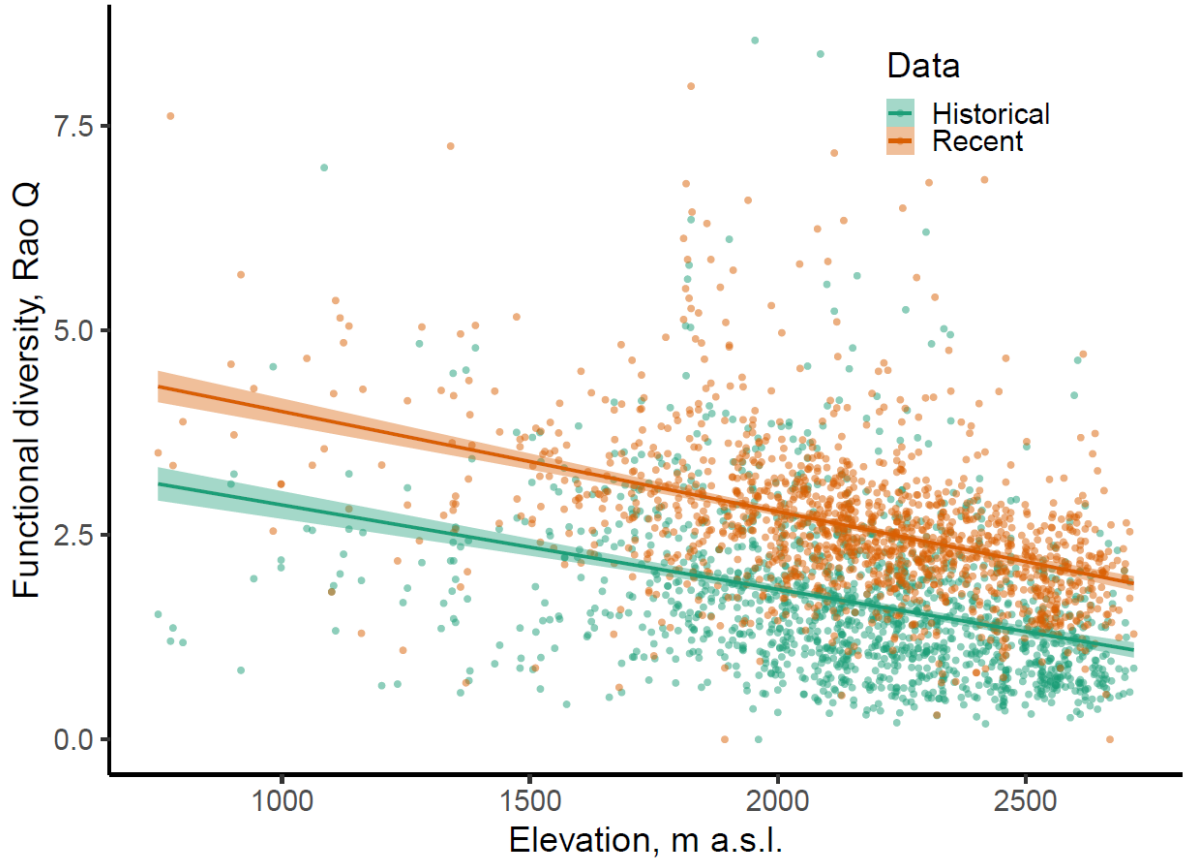


Figure 3. Changes in functional diversity of the four traits with elevation in 1,442 historic (green) and recent (orange) European alpine plant communities as estimated by linear mixed-effect models. Solid lines indicate significant relationships ($p < 0.05$), the shaded areas denote the 95% confidence intervals.

*Role of elevation in structuring mountain plant communities*

Elevation consistently structured mountain plant communities, influencing both trait variation and functional diversity (FD) in the historical as well as in the recent data. Plant height had a stable negative relationship with elevation, with slopes unchanged between historical and recent surveys (Figure 2A; Table 1).

Specific leaf area (SLA) also displayed a significant negative relationship with elevation in both datasets, though this relationship weakened slightly in recent surveys (-0.49 historically vs. -0.36 recently, both statistically different from zero; Figure 2B; Table 1). Leaf nitrogen content (LeafN) similarly exhibited a consistent negative relationship with elevation, with minimal differences between historical and recent slopes (-0.03 historically vs. -0.02 recently, both statistically different from zero; Table 1; Figure 2C). In contrast, seed mass, which had historically no significant elevational trend, developed a significant negative relationship with elevation recently (Table 1; Figure 2D). Functional diversity also had a consistent negative relationship with elevation, with slopes remaining similar over time (-0.10 historically vs. -0.12 recently; Figure 3, Table 1), further highlighting the stable influence of elevation on mountain plant community structure.

## Discussion

Our resurvey of 1,442 mountain vegetation plots across the European Alps revealed clear shifts in functional trait composition and diversity over the past decades. Consistent with our expectations, recent communities are dominated by species with higher specific leaf area (SLA), larger leaf nitrogen content (LeafN) and increased seed mass, indicated by the significantly larger community-weighted means (CWMs). The shift in CWMs coincides with higher functional diversity at all elevations, as novel trait combinations become more common. Despite this trait turnover, the classic signature of trait variation along the elevational gradient remains largely intact; slopes for plant height, SLA and LeafN differed little from historical values, suggesting that global change has weakened but not erased the mountains' abiotic filters. This suite of patterns points to a mountain ecosystem in transition, where relaxed environmental constraints are opening colonization opportunities for new species without fundamentally redrawing the elevational template.

*Trait turnover towards more resource-acquisitive strategies*

Across the European Alps, specific leaf area (SLA) increased by nearly 20% (from 15.7 to 18.7 $mm^2\ mg^{-1}$), leaf nitrogen content by about 11% (from 2.10% to 2.34%), and seed mass by approximately 10% (from 0.77 mg to 0.85 mg), whereas mean plant height declined by 7% (from 0.15 m to 0.14 m). Although

364 our observational design cannot definitively isolate individual drivers, several
365 lines of evidence from both observational and manipulative studies conducted in
366 similar cold ecosystems support regional climate warming as a primary force. For
367 example, the increases in SLA and LeafN align with previously observed patterns
368 along elevational gradients, where reductions in low-temperature stress favour
369 species producing larger, thinner, and less dense leaves capable of higher
370 photosynthetic rates (Midolo et al., 2019). Likewise, a downslope translocation
371 experiment of intact plant-soil mesocosms demonstrated a comparable shift from
372 resource-conservative to resource-acquisitive leaf traits under warmer conditions,
373 marked by significant increases in SLA and leaf nitrogen (Schuchardt et al.,
374 2023). Concurrently, ongoing atmospheric nitrogen deposition at the Alps'
375 fringes (Kirchner et al., 2014) likely reinforce this community-level shift toward
376 acquisitive trait syndromes as supported by e.g. fertilization trials in montane
377 grasslands (Quétier et al., 2007; Rose et al., 2013). Additionally, the ongoing
378 abandonment of traditional grazing in many European mountain regions (e.g.
379 (Cernusca *et al.* 1999; Orlandi *et al.* 2016)) likely relaxed disturbance filters, thus
380 contributing to the observed shifts in community trait composition. This change
381 might have facilitated the (re)establishment of species characterized by higher
382 SLA values, higher leaf nitrogen content, and larger seeds – traits typically
383 selected against under grazing, as herbivores preferentially consume nutrient-
384 rich, high-SLA foliage (Díaz et al., 2001; Laliberté et al., 2012). Taken together,
385 these interacting global change drivers – regional warming, increased nutrient

availability, and decreased grazing pressure – appear to collectively drive the observed functional shifts towards resource-acquisitive species traits in montane grassland communities across the Alps.

*Decoupling of plant height from other acquisitive traits under global change*

Unlike SLA, leaf nitrogen content, and seed mass, community-weighted mean (CWM) plant height declined slightly but significantly over time, a finding that contradicted our expectations of a shift toward taller species under global change. In trait-based frameworks, plant height is often linked to competitive dominance, rapid growth, and light acquisition, and is expected to increase with warming, eutrophication, and grazing cessation (Díaz et al., 2016; Laliberté et al., 2012; Westoby, 1998). However, several ecological and methodological factors likely explain this unexpected result. First, our analysis excluded shrubs and trees to focus on herbaceous vegetation, thereby omitting one of the most visible signals of global change in alpine ecosystems: woody plant expansion (Cannone et al., 2022; Gehrig-Fasel et al., 2007). In this context, height increases occurring via the establishment or expansion of woody plants are simply not visible in our dataset. Second, our trait dataset relies on species-level means and does not account for the substantial intraspecific variation in plant height (Rixen et al., 2022): real trait responses to the changing montane environments may involve plastic or locally adapted shifts in height that are not captured in CWMs based on

fixed averages. Finally, and more importantly, many of our sites are situated on shallow, often skeletal soils, a common feature of montane landscapes. These edaphic conditions physically limit root development, imposing allometric constraints on aboveground biomass: plants cannot grow tall without sufficient rooting depth (Schenk & Jackson, 2002; Tumber-Dávila et al., 2022). As a result, even when climatic conditions relax, tall-statured lowland species may be unable to establish or persist due to edaphic limitations. In this context, the persistence or even slight decline in plant height may reflect ongoing filtering by substrate physical properties, which continue to limit vertical growth despite broader functional shifts in leaf and seed traits. Collectively, these observations suggest that global change has not uniformly driven all traits in the same direction, and that height may respond to a different or more constrained set of environmental drivers than SLA, nutrient content, or seed mass.

*Shifts in functional trait diversity*

From a community-assembly perspective, the simultaneous shift in the community weighted means of specific leaf area, leaf nitrogen and seed size toward acquisitive strategies and the increase in functional diversity point to a weakening of abiotic filters under global change. These findings confirmed our second hypothesis. Warming has reduced frost frequency and lengthened growing seasons (Pepin et al., 2022), opening thermal niches (Gottfried et al.,

2012) that allow species with previously excluded trait combinations to establish and expand the trait space. As species with higher temperature requirements for growth increase their abundance in their existing populations (Lamprecht et al., 2018b) and/or shift upslope in response to warmer conditions (Rumpf et al., 2018a), they introduce new trait values into resident assemblages, driving large gains in functional diversity. Moreover, the intensified grassland management at lower elevations (Cernusca et al., 1999) and localized nitrogen deposition at the fringes of the Alps (Kirchner et al., 2014) might have increased soil fertility (Rumpf et al., 2025), further relaxing nutrient-based constraints. At the same time, the cessation of traditional grazing and the shrubification (Dullinger et al., 2004; Gehrig-Fasel et al., 2007) have created a mosaic of habitats that support both stress-tolerant and resource-acquisitive species, broadening the range of co-existing trait syndromes. Taken together, we assume that the relaxation of temperature, nutrient and, in part, grazing disturbance have made a larger proportion of local sites colonizable to a larger proportion of species from the regional metacommunity. Real colonization dynamics have probably been fostered by small-scale heterogeneity (variation in aspect, slope and soil depth) which tends to increase species turn-over and hence propagule input from species with diverse traits over small distances (Helm et al., 2024; Körner & Hiltbrunner, 2021; Scherrer & Körner, 2011). In fact, this short- to mid-term increase in functional diversity may, at least in part, be transitional and characterize non-equilibrium assemblages that follow environmental changes with a delay

(Svenning & Sandel, 2013). When approaching a new equilibrium, eventual trait change might become more clearly directional, with species with resource-conservative strategies replaced by species with resource-acquisitive strategies, and functional diversity might decrease again, as supposed for taxonomic diversity (Jackson & Sax, 2010). In summary, we suppose that global change has, in many local assemblages, unlocked portions of the trait space that were once inaccessible which led to functionally novel, but likely transitional plant communities.

*Elevation-driven abiotic filters continue to structure mountain plant communities*

Although trait means (i.e. community-weighted means; [CWM]) and overall functional diversity have increased considerably across the elevational gradient, the slopes of all CWM–elevation relationships remained consistently negative, indicating that environmental filtering continues to structure mountain plant communities. Plant height declined at an almost identical rate in both historical and recent surveys, reflecting persistent constraints imposed by low temperatures, increased wind exposure and shallow and nutrient-poorer soils (Bello et al., 2013; Pellissier et al., 2010; Rosbakh et al., 2022). Similarly, specific leaf area and leaf nitrogen content decline with elevation, indicating ongoing selection from the regional species pool for species with conservative growth strategies in increasingly harsh environments (Bello et al., 2013; Rosbakh et al., 2015).

Although the magnitude of some of these slopes has decreased slightly, their persistent negativity suggests that cold stress and nutrient limitation associated with elevation remain key environmental filters. Together with the concurrent increase in mean trait intercepts across all elevations, these persistent negative gradients suggest that global change has only partially relaxed environmental filtering, raising baseline trait values without eliminating the fundamental elevational sieve. Finally, dispersal limitation likely reinforces this pattern by constraining species turnover within each elevational band. Because most species cannot rapidly shift their ranges uphill in response to warming, community reassembly at a given elevation is primarily restricted to species already present in the historical meta-community of that zone. As a result, the enduring structure of elevational trait gradients may reflect not only persistent abiotic filters, but also the inertia imposed by limited species movement across elevation, a legacy of historical community composition that continues to shape present-day trait–environment relationships.

Notably, seed mass deviated from the otherwise stable trait–elevation relationships: while it was historically unrelated to elevation, it developed a significant negative slope in recent surveys. This shift complements the overall increase in seed mass community-weighted means, but suggests that this trend is primarily driven by lowland communities becoming increasingly dominated by species with heavier seeds. This likely reflects warmer conditions, elevated nutrient availability, and reduced grazing pressure, factors that favor species with

greater reproductive investment. In contrast, the contribution of heavy-seeded species appears to have declined in high-elevation plots, contributing to the emergence of the recent negative elevation trend. A likely explanation for this asymmetry lies in changing dispersal dynamics. Historically, transhumance (i.e. seasonal migration of large domestic animals such as cows and horses across elevations) facilitated the uphill transport of large seeds across elevation bands. The substantial decline of transhumance in the European Alps in recent decades (Cernusca et al., 1999; Gehrig-Fasel et al., 2007) might have weakened this mechanism, particularly above the treeline where such animals are now largely absent. As a result, seed arrival at higher elevations has likely become more limited, constraining the establishment of heavy-seeded species and reinforcing the filtering effects of harsh environmental conditions. Seed mass has thus emerged as a trait shaped both by the relaxation of ecological constraints in lowlands and the erosion of anthropogenic seed dispersal across elevation.

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## Author contributions

SRo conceived the study, collected plant-trait data, performed the statistical analyses and drafted the initial manuscript. SBR and SD re-surveyed the plots and collected complementary plant-trait data. All authors contributed to drafting and critically revising the manuscript and approved the final version.

## Data availability

All trait and vegetation resurvey data, along with R scripts used in the analysis, will be made publicly available in [e.g., Zenodo or Dryad] upon publication.

## Conflict of interest

The authors declare no competing interests.

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