

RESEARCH ARTICLE

Community assembly on inland cliffs is context-dependent

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Handling Editor: Kechang Niu**Abstract**

1. Under harsh environmental conditions, community assembly processes are expected to drive pronounced functional convergence, with communities dominated by stress-tolerant species. Integrating local communities with their regional species pools enables evaluating environmental filtering and disentangling habitat-specific assembly processes. To assess whether the strength and direction of environmental filtering in extreme habitats depends on regional climate and topography, we adopted a trait-based approach on a relatively underexplored habitat such as inland limestone cliffs.
2. To test whether limestone inland cliffs function as extreme habitats that filter regional species pools towards stress-tolerant trait syndromes or alternative habitat-specific assembly processes, we sampled vegetation on inland limestone cliffs along an aridity gradient in three study areas spanning different European biogeographic regions, namely Alpine, Continental and Mediterranean. We compiled regional species pools from the Global Biodiversity Information Facility and integrated them into trait-based null models to compare observed community structure against expectations under stochastic assembly, using a combination of functional traits compiled from field measurements and from databases. Additionally, to assess whether community assembly rules are shared across regions or shaped by regional context and topography, we quantify trait-based non-random assembly and functional convergence across biogeographic regions and different cliff aspects.
3. The results show that in inland limestone cliffs, extremeness is context-dependent. It varies with the selected traits, intensifies in humid regions and weakens on pole-facing slopes in dry regions. Cliff plants showed reduced plant height across all regions and aspects, whereas leaf dry matter content was higher and seed mass was lower under specific conditions.

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4. These patterns indicate non-random trait distributions towards conservative leaf strategies and reduced plant size, while the prevalence of small propagules may facilitate colonization of suitable microsites for establishment, often scarce and spatially scattered. Functional convergence occurred in the Alpine region and on equator-facing cliffs in the Mediterranean region, with slope and microtopographic heterogeneity showing limited effects. Overall, inland limestone cliffs showed evidence of non-random trait assembly and localized abiotic filtering, suggesting that these patterns are context-dependent.

KEYWORDS

environmental filtering, extreme habitats, functional convergence, functional diversity, functional traits, non-random assembly, stress tolerance, vegetation

1 | INTRODUCTION

Cliff ecosystems impose strong abiotic stress and strict habitat discontinuity, making them suitable systems for studying how species from a regional species-pool assemble into isolated communities (Cornell & Harrison, 2014; Larson et al., 2000). Species pools, typically defined at broad spatial scales, are shaped by regional environmental factors such as climate and geodiversity and by evolutionary and historical processes such as speciation and biogeographic history (Hewitt, 1999, 2000; Hjort et al., 2015; Pärtel, 2002; Ricklefs, 1987; Svenning & Skov, 2004). On the contrary, community assembly processes operate at finer spatial scales and involve stochasticity, dispersal limitations, and biotic and abiotic selection mechanisms (Vellend, 2010). Under harsh environmental conditions, abiotic filtering is expected to drive the selection process towards stress-tolerant species, leading to strong functional convergence (Weiher & Keddy, 1995). In contrast, in less stressful conditions, limited similarity between co-existing species in a community promotes niche partitioning, leading to greater functional divergence and a broader spectrum of successful strategies (HilleRisLambers et al., 2012). However, these expectations are rarely evaluated in geomorphologically extreme and spatially scattered systems such as cliff ecosystems, where steep environmental gradients and strong spatial constraints may alter the expression of classical assembly rules. As such, cliff habitats provide a natural laboratory to test the context dependence and robustness of widely established functional trait-based predictions.

Testing the role of regional species pools strengthens inference on environmental filtering in habitat-specific assembly processes (Fløjgaard et al., 2020), because it allows accounting for species absent from local communities that could potentially occur under given environmental conditions (Pärtel et al., 2011). Habitats characterized by extreme and regionally uncommon environmental conditions, particularly inland cliffs, provide excellent opportunities to test functional assembly processes (Smrithy et al., 2025). However, comparative assessments of how extreme habitats filter available regional species pools through trait-based assembly processes remain scarce (de Bello et al., 2012; Le Bagousse-Pinguet et al., 2017), particularly for inland cliff vegetation. The appearance of extremophilic organisms, such

as vegetative desiccation-tolerant vascular plants capable of coping with severe water limitation, indicates the existence of extremely dry habitats (Marks et al., 2021; Rothschild & Mancinelli, 2001). However, cliffs are not inherently arid (Booth & Larson, 1998; Aho et al., 2014). Although steep slopes limit soil to scattered microsites such as ledges and crevices where vascular plants typically establish (Ursic et al., 1997), gentler slopes allow for localized soil accumulation, enhancing both moisture and nutrient levels (Kuntz & Larson, 2006; Oosting & Anderson, 1937). In addition, because rocky substrates have low water-storage capacity and drain rapidly, cliffs should represent a stronger xeric environment in comparison to the surrounding landscape as the macroclimate becomes wetter (Larson et al., 2000). This contrast may be further modulated by biogeographic context, which has shaped regional species pools through evolutionary and historical processes (Hewitt, 1999, 2000; Ricklefs, 1987). In relatively arid regions, however, this filtering effect may be weakened on pole-facing slopes, where reduced solar radiation lowers evaporative demand and allows greater persistence of moisture in sheltered microtopographic features (Zohary, 1973). Despite these documented constraints and mitigating factors, biogeographic-scale studies testing whether cliffs act as extreme habitats and filter the regional species pool are almost lacking (March-Salas et al., 2025; Vojtkó et al., 2017). In this context, functional traits provide a framework to assess how environmental constraints influence community structure. Among the multiple dimensions of plant functional variation, leaf dry matter content, seed mass and plant height represent key ecological axes related to resource-use strategies, dispersal–establishment trade-offs and plant size variation (Díaz et al., 2016; Wright et al., 2004). These traits are therefore expected to capture contrasting functional responses to the environmental constraints characterizing cliff habitats, including limited resources, environmental stress and restricted establishment opportunities.

Based on these functional dimensions, this study aims to test whether inland limestone cliffs act as filters that favour stress-tolerant strategies. We predicted that cliff communities show shifts in functional trait composition and greater functional convergence relative to their regional species pools, consistent with environmental filtering. We further tested whether these patterns are context-dependent

by comparing cliff communities with their respective regional species pools across three European biogeographic regions (Alpine, Continental and Mediterranean). Specifically, we hypothesise that the strength and direction of environmental filtering on inland cliffs are context-dependent, varying along a macroclimatic gradient in water availability rather than being uniformly strong across all cliff habitats.

Predictions:

P1 (trait direction, stress tolerance predictions): Inland cliffs are stressful habitats. Following the general expectations of environmental filtering theory, we predict that cliff communities will preferentially assemble species with stress-tolerant strategies, including resource-conservative leaves, larger seeds and shorter sizes. This pattern is expected to be stronger in wetter regions and weaker on pole-facing slopes in drier regions.

P1bis (trait direction, cliff-specific alternative predictions): Because functional strategies can be habitat-dependent and are not necessarily represented by a single trait combination, we also tested alternative predictions for leaf dry matter content and seed mass. Lower leaf dry matter content may reflect drought strategies based on greater tissue water storage capacity (Lamont & Lamont, 2025), whereas lower seed mass may reflect a regeneration strategy favouring colonization through greater propagule production (Moles & Westoby, 2004) and, potentially, enhanced dispersal ability among spatially scattered microsites.

P2 (functional structure): Inland cliff plant communities exhibit functional convergence (reduced functional diversity relative to null expectations), consistent with strong abiotic filtering. This pattern is expected to be stronger in wetter regions and weaker on pole-facing slopes in drier regions.

P3 (scale of control): If convergence occurs, local topographic factors that affect soil availability (slope, microtopographic complexity) will explain more variance in functional diversity than regional bioclimatic variation.

2 | MATERIALS AND METHODS

2.1 | Study area

We selected three study areas of comparable spatial extent across different European biogeographic regions and identified suitable limestone cliff habitats within each area. These sites are distributed along a gradient of water availability, which approximately halves from the Alpine to the Continental region and again from the Continental to the Mediterranean region, as quantified by the aridity index (Figure 1; Zomer et al., 2022). The alpine site (Northern Alps, Germany; Figure 1a) experiences an alpine climate. Here, limestone cliffs are common landscape features, formed by massive limestone successions that sustain specialized calcareous flora adapted to severe conditions, including snow-free winters (Chytrý et al., 2020). The surrounding vegetation varies along the elevational gradient, ranging from beech and mixed conifer forests through subalpine

krummholz to alpine meadows. The mid-gradient Continental site (Frankenjura, Germany; Figure 1b) experiences a temperate climate and sits on Jurassic limestones. Here, limestone cliffs are common landscape features formed by the erosion of Jurassic limestone formations. The calcicolous plant communities harbour relict alpine populations that have persisted on inland calcareous cliffs throughout Holocene forest expansion and postglacial warming (Birks & Willis, 2008). The surrounding vegetation is composed of woodlands, calcareous grasslands and juniper thickets. At the driest extreme, the Mediterranean site (southern Tuscany, Italy; Figure 1c) experiences a Mediterranean climate. Here, limestone cliffs are rare landscape features, formed by limestone successions, which generate cliffs that host highly specialized perennial chasmophytic plant communities (Chytrý et al., 2020). The surrounding vegetation is dominated by oak forests mixed with thermophilic shrubs. We provide a detailed description of each study area, including its climate and characteristic vegetation, in Appendix A.

2.2 | Sampling design and data collection

To sample inland cliff vegetation, we identified suitable cliff sites based on occurrences of characteristic and widespread species of sun-exposed and shaded cliff communities for each biogeographic region (Leuschner & Ellenberg, 2017). These species served as habitat indicators to guide site selection within each region and avoid plots devoid of vascular vegetation (details in Appendix B). We minimized environmental variability by using a stratified random sampling design (Le et al., 2025), ensuring that plots were distributed across the available cliff habitat within each study site, according to the following criteria: (i) each plot had to be located on a limestone cliff face (a rock face at least 4 m high and with a slope exceeding 45°; Larson et al., 2000); (ii) the target species of the sun-exposed community had to occur on equator-facing cliff faces, whereas those of the shaded community had to occur on pole-facing cliff faces; (iii) plots were established at least 2 m above the cliff base to avoid vegetation potential disturbance by grazing or browsing; (iv) to minimize anthropogenic disturbances, sampling sites were chosen at least 5 m away from climbing routes (March-Salas et al., 2023); (v) plots were not established in caves or beneath overhangs; and (vi) a target minimum distance of 100 m between plots within the same aspect category to reduce potential spatial dependency, where permitted by the availability of suitable cliff habitat. For each study site, representative of a given biogeographical region, we then randomly selected eight occurrences per target species in a GIS environment. Due to the very limited availability of suitable limestone cliffs in the Mediterranean study area, the minimum target distance could not be achieved for all replicates (see Appendix C for effective plot distances). This resulted in a total of 48 plots (16 plots per study area, equally distributed between pole- and equator-facing cliffs). Field surveys were timed to match the phenological peak of the target species in each region. The plot size was 3 m × 3 m (Giusso del Galdo et al., 2016). Because

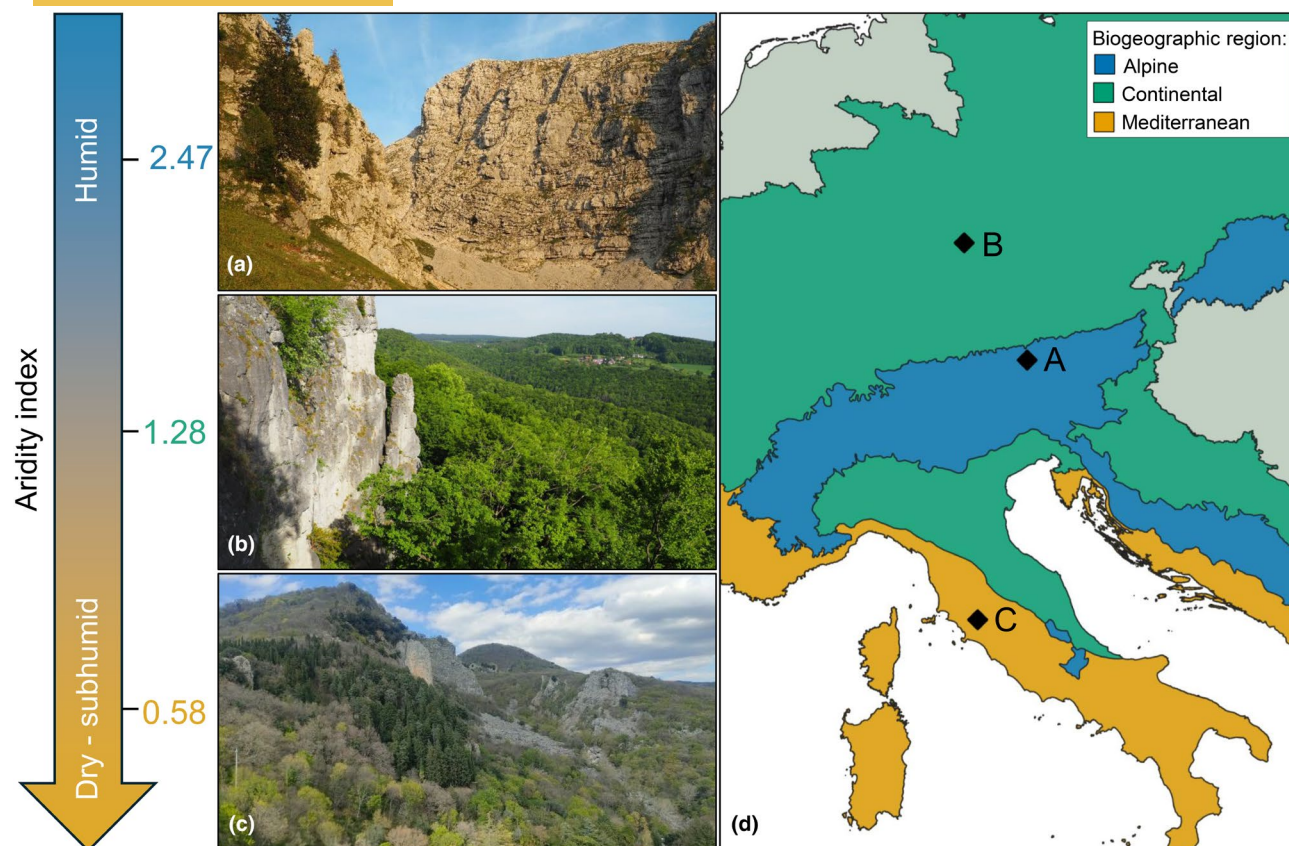


FIGURE 1 The three study areas (panels a, b: Germany; panel c: Italy) in relation to the aridity index (i.e. the ratio of mean annual precipitation to mean annual potential evapotranspiration; means have been calculated across plots) overlaid on European biogeographical regions (panel d). Surveyed cliffs ranged from 1167 to 2211 m.a.s.l. in the Alpine region, 398 to 518 m.a.s.l. in the Continental region, and 330 to 706 m.a.s.l. in the Mediterranean region. Photo credits: Deola T. (a, b) and Bonari G. (c), 2024–2025. Data sources: European Environment Agency (2016); Zomer et al. (2022).

plant establishment and survival are more constrained on steeper slopes and in areas with less microtopographic complexity (Kuntz & Larson, 2006), for each plot, we measured slope at the centre and visually estimated surface heterogeneity by qualitatively scoring microtopographic feature abundance. Specifically, we assigned a score ranging from one (low heterogeneity, smooth rock surface), and 10 (high heterogeneity, with abundant cracks, pockets or pits), following Boggess et al. (2017). We quantified species cover from scaled orthogonal cliff photographs by measuring the projected area of vascular plants in ImageJ software and expressing it as percent cover per plot (March-Salas et al., 2023). Fieldwork was conducted with the required permits where required (Berchtesgaden National Park, no. 2024_EXT_FVV_18, Regierung von Oberfranken and Oasi WWF Bosco Rocconi). Species were identified in the field, and samples or digital photographs were taken for taxonomic confirmation when needed (according to site permits). The plant nomenclature follows World Flora Online (WFO, 2024). For seven inaccessible Mediterranean plots, we used unmanned aerial systems, which are increasingly employed to map and characterize vegetation communities (Tavilla et al., 2026), to collect photographs and generate 3D models through post-processing, from which slope was estimated (de Simone, 2020; Sturzenegger & Stead, 2009). We

excluded records identified only to family and derived species' relative cover frequencies per plot from vascular plant percent cover.

2.3 | Regional species pools

Following Marteinsdóttir and Eriksson (2014), we defined the regional species pool as all species occurring within a buffer area around each plot, encompassing both cliff and surrounding non-cliff vegetation. This approach captures species theoretically able to colonize cliff habitats from the regional pool. Instead of field surveys, we retrieved occurrence data from the Global Biodiversity Information Facility (GBIF) within a 2 km × 2 km square centred on each plot; we removed taxa with unsuitable ecology and filtered records for data quality (filtering details in Appendix D; area-size effects in Appendix E).

2.4 | Plant traits

We selected leaf dry matter content (LDMC), seed mass (SM) and plant height (H) because they represent complementary and broadly

independent dimensions of plant functional variation (Díaz et al., 2016; Wright et al., 2004) while being available for a large proportion of vascular plant species (Kattge et al., 2020). LDMC represents variation along the leaf economics spectrum, ranging from acquisitive to conservative resource-use strategies (Wright et al., 2004). However, LDMC does not capture all drought-response strategies, as some taxa may rely on alternative mechanisms such as tissue water storage and succulence (Lamont & Lamont, 2025). SM represents an important dimension of plant regeneration strategies, reflecting a trade-off between investment in individual seeds and propagule production. Larger seeds generally provide greater seedling reserves and establishment advantages under stressful conditions but are associated with lower propagule number (Jakobsson & Eriksson, 2000; Moles & Westoby, 2004). Seed mass may also influence dispersal potential, although the strength and direction can vary among dispersal modes (Heleno & Vargas, 2015; Thomson et al., 2011; Xiao et al., 2005). Given the limited and spatially isolated establishment microsites available on cliffs, both higher and lower SM may therefore represent plausible functional responses depending on the relative importance of establishment advantage, propagule production and dispersal constraints. H describes variation along the plant size spectrum, from small stress-tolerant species to larger competitive species (Díaz et al., 2016). To evaluate the functional structure of inland cliff vegetation relative to null models derived from the regional species pool, we compiled functional trait data separately for the regional species pools used to generate null expectations and for the local cliff communities used to calculate observed functional indices. We then calculated a single mean value for each trait and species in both datasets before computing the functional indices. For regional species pools, we compiled trait values from the TRY Plant Trait Database (Kattge et al., 2020). We preliminarily filtered trait data to reduce the impact of outliers and unreliable records, based on observation error risk (Kemppinen et al., 2022; details in Appendix F). For local communities, considering that traits of more abundant species exert a key effect on ecosystem functioning (Grime, 1998), we aimed to measure or retrieve plant traits to represent approximately 80% of the total relative cover in each plot (Pakeman & Queded, 2007). Because plant height exhibits substantial intraspecific variation across environmental gradients (Albert et al., 2010; Jung et al., 2010), we obtained cliff-specific H values through direct field measurements. To do so, we measured and estimated values from scaled orthogonal photographs of cliff-growing individuals analysed with ImageJ software, focusing on the most abundant species across all plots. Because of field-sampling limitations, it was not possible to obtain systematic cliff-specific measurements of LDMC and SM. For LDMC, we initially compiled available values from TRY. To enhance LDMC coverage within plots, we measured missing key trait values following standardized protocols (Perez-Harguindeguy et al., 2016). Because part of the LDMC dataset was still based on non-cliff-specific values, we further evaluated the robustness of LDMC patterns in Mediterranean cliff communities by comparing CWM-LDMC calculated using (i) mixed datasets combining field measurements and TRY-derived values and (ii) field measurements only. These alternative approaches yielded comparable results (Appendix G). For SM, we relied exclusively on TRY records, including

some records with higher uncertainty. For fern species lacking SM data in TRY or with unrealistic values (>10 mg), we assigned 0.001 mg based on TRY-derived estimates for *Asplenium* species included in our regional species pools, although this value is slightly higher than reported values for ferns (Gómez-Noguez et al., 2016).

2.5 | Functional indices

From logarithmic transformed values of LDMC, SM and H, we calculated observed values of community weighted means (CWM) and functional diversity (FD; quantified as Rao's quadratic entropy) for each plot (Ricotta & Moretti, 2011). By incorporating regional species pools, null models provide a baseline to assess deviations of observed trait distributions and functional convergence from stochastic expectations (de Bello et al., 2021). To quantify these patterns, we first generated null distributions by randomizing trait values across the regional species pool and reassigning them to the observed species abundance vector in each plot (9999 randomizations for CWM; 999 randomizations for FD). We then calculated standardized effect sizes for trait-specific CWMs (SES-CWM) and functional diversity (SES-FD) by comparing observed values against their null distributions (de Bello et al., 2021). Sampling from regional species pools allowed us to account for species absent from local communities (Pärtel et al., 2011).

2.6 | Statistical analysis

To test whether inland cliffs select vegetation dominated by stress-tolerant plants (P1) or alternative habitat-specific trait strategies (P1bis), and whether cliff communities show functional convergence consistent with abiotic filtering (P2), we performed aggregate analyses by fitting linear models to functional indices ($SES-CWM_{LDMC}$, $SES-CWM_{SM}$, $SES-CWM_H$ and $SES-FD$) with predictors biogeographic region (Alpine, Continental, Mediterranean), aspect (S =equator-facing, N =pole-facing), slope (51° – 140°) and microtopography (index 1–10, from low to high microtopographic complexity). The hierarchical replication structure of our sampling design is summarized in Table 1. To test whether the strength of stress tolerance filtering and functional convergence is weaker on pole-facing cliffs in drier biogeographic regions, we compared the additive model (no interaction) to a model including the aspect $\times$ biogeographic region interaction using an F-test for nested ANOVA models (Crawley, 2013). We estimated marginal means (EMMs) and pairwise contrasts (Lenth, 2016). Higher frequency of stress-tolerant plants relative to the regional species pool (stress tolerance predictions) was expected to be expressed as positive values of intercepts or EMMs of $SES-CWM_{LDMC}$ and $SES-CWM_{SM}$ and negative values of $SES-CWM_H$. Conversely, support for alternative hypotheses (cliff-specific alternative predictions) was expected to be expressed as negative values of intercepts or EMMs of $SES-CWM_{LDMC}$ and $SES-CWM_{SM}$, indicating, respectively, a drought-avoidance strategy based on greater water storage capacity and a shift towards smaller seeds associated with enhanced dispersal ability among isolated microsites.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Regional species pools	Study areas representing contrasting biogeographic regions	3 study areas
Cliff orientation	Plots classified as equator- or pole-facing	2 aspects per study area (8 plots per aspect)
Local topographic variation	Slope and microtopographic heterogeneity measured for each plot (continuous covariates)	48 plots
Local plant communities	Vegetation plots (3 m × 3 m) distributed across multiple limestone cliff systems within each study area	48 plots (16 per study area)

TABLE 1 Replication statement describing the hierarchical structure of the study design, the scale of inference for each factor considered in the study and the number of replicates at each sampling level.

Functional convergence was expected to be expressed as negative values of SES-FD. Because aggregate analyses can mask spatial heterogeneity, we also tested P1, P2 and P1bis on the plot scale to identify which individual plots show significant deviations from null expectations (for P1 stress tolerance predictions: right-tailed for LDMC and SM, left-tailed for H; for P1bis cliff-specific alternative predictions: left-tailed for LDMC and SM; for P2 functional convergence: left-tailed for FD). To rank the contribution of each predictor to functional convergence (P3), we quantified the independent contribution of each term in the linear model of SES(FD) using Type III sums of squares. Predictor importance was expressed as partial R^2 , representing the unique variance explained by each predictor after accounting for all other model terms. Details of the inferential procedures and diagnostic tests are provided in [Appendix H](#). To corroborate the aggregate analyses, we made permutation tests grouping plots at three levels: across the entire dataset, by biogeographic region and by aspect for CWM, and by the observed aspect × biogeographic region combinations for FD. To do so, for each group at each level, we performed one-tailed tests comparing the observed group mean of CWM for each trait and of FD with null distributions generated by permuting CWM and FD and computing the group mean for each permutation. Furthermore, we calculated 95% bias-corrected and accelerated bootstrap confidence intervals (BCa) for linear model coefficients, their relative importance, EMM and pairwise factor comparisons. We performed all analyses in R version 4.5.1 (R Core Team, 2025).

3 | RESULTS

3.1 | Species pools, species coverage and trait data

The three regional species pools comprised 966 species in total (Alpine: 531; Continental: 409; Mediterranean: 287; partially overlapping among regions). Across all inland cliff plots, we recorded 233 taxa (Alpine: 89; Continental: 97; Mediterranean: 69; partially overlapping among regions). We recorded species exhibiting vegetative desiccation tolerance sensu Marks et al. (2021) in 30 of the 48 plots (plots per biogeographic region: Alpine=5, Continental=16, Mediterranean=9; aspect: S=13; N=17). Succulents were absent in the Alpine region plots, frequent in Continental cliffs (all S facing

TABLE 2 *F*-test results comparing additive models with models including Aspect × Biogeographic region interaction for standardized effect size of community weighted mean (SES-CWM) traits and standardized effect size of functional diversity (SES-FD).

	Δ RSS	<i>p</i>
SES-CWM leaf dry matter content	0.366	0.878
SES-CWM seed mass	3.384	0.597
SES-CWM plant height	3.398	0.303
SES-FD	8.595	0.003

Note: Δ RSS is the change in residual sum of squares. The interactions significantly improved model fit only for SES-FD ($p < 0.05$). Bold values indicate statistically significant results ($p < 0.05$).

plots; mean relative frequency $8.4 \pm 13.1\%$; only two N facing plots), and very rare in the Mediterranean (two plots, $<1\%$ relative frequency 1%). Trait coverage in both regional species pools and across inland cliff plots was generally high ([Appendix I](#)).

3.2 | Functional trait shifts in inland cliff communities (P1 - P1bis)

The effect of inland cliffs on stress-tolerant trait values did not vary with aspect among biogeographic regions, as including aspect × biogeographic region interactions did not improve SES-CWM model fit ([Table 2](#)). Aggregate analyses indicate that cliff communities showed significant deviations in trait composition from regional species-pool null models, with higher leaf dry matter content (LDMC) than expected from regional species-pool null models, supporting P1 stress tolerance predictions ([Table 3](#), [Figure 2a](#)). The community weighted means of LDMC (CWM_{LDMC}) was higher than expected under null models in the Alpine ($EMM = 1.312$, $p < 0.001$, [Appendix J](#)) and Continental ($EMM = 1.074$, $p = 0.006$) regions, but not in the Mediterranean region ($EMM = 0.327$, $p = 0.102$, [Figure 2b](#)). The CWM_{LDMC} was higher than expected in the null models in communities exposed to the equator ($EMM = 0.935$, $p < 0.001$) and to the pole ($EMM = 0.874$, $p = 0.003$, [Figure 2c](#)). This is supported by a positive and significant intercept of the corresponding additive HC3 model for SES. The community weighted means of seed mass

TABLE 3 HC3-adjusted coefficients from linear models of standardized effect size of community weighted mean (SES-CWM) for three functional traits (leaf dry matter content, seed mass, plant height) and standardized effect size of functional diversity (SES-FD).

	Estimate	<i>p</i>	BCa CI
<i>SES-CWM leaf dry matter content</i>			
(Intercept)	1.282	0.002	[0.455, 1.821]
BGR Continental	-0.239	0.639	[-1.078, 0.767]
BGR Mediterranean	-0.985	0.025	[-1.702, -0.252]
Aspect	0.061	0.883	[-0.694, 0.788]
Slope	0.014	0.949	[-0.348, 0.486]
Microtopography	0.421	0.073	[0.013, 0.835]
<i>SES-CWM seed mass</i>			
(Intercept)	-1.053	0.048	[-2.112, -0.123]
BGR Continental	-0.145	0.849	[-1.477, 1.457]
BGR Mediterranean	0.015	0.973	[-0.808, 0.957]
Aspect	0.901	0.128	[-0.274, 2.006]
Slope	-0.337	0.323	[-0.800, 0.322]
Microtopography	0.445	0.135	[-0.189, 0.946]
<i>SES-CWM plant height</i>			
(Intercept)	-1.507	<0.001	[-2.027, -0.895]
BGR Continental	0.319	0.526	[-0.613, 1.288]
BGR Mediterranean	1.041	0.017	[0.230, 1.825]
Aspect	-0.193	0.589	[-0.859, 0.481]
Slope	0.112	0.579	[-0.204, 0.605]
Microtopography	0.156	0.414	[-0.202, 0.511]
<i>SES-FD</i>			
(Intercept)	-0.777	0.004	[-1.290, -0.264]
BGR Continental	1.867	<0.001	[0.911, 2.824]
BGR Mediterranean	1.804	0.001	[0.748, 2.860]
Aspect	0.020	0.951	[-0.619, 0.658]
Aspect:BGR Continental	-1.041	0.087	[-2.239, 0.158]
Aspect:BGR Mediterranean	-2.249	0.002	[-3.604, -0.895]
Slope	0.043	0.770	[-0.252, 0.338]
Microtopography	-0.092	0.595	[-0.439, 0.255]

Note: SES-CWM was analysed using additive models, whereas the SES-FD model included the Aspect $\times$ biogeographic region (BGR) interaction. For each trait and model term (Intercept; Aspect S vs. N; biogeographic region (BGR) contrasts vs. reference level alpine; Aspect $\times$ BGR interaction for SES-FD; slope; microtopography) the table reports the point estimate (Estimate), *p*-value (coeftest with HC3) and 95% BCa intervals. Covariates (slope, microtopography) are standardized. Bold values indicate statistically significant results ($p < 0.05$) for *F*-tests, or 95% bootstrap confidence intervals that do not include zero.

(CWM_{SM}) was never higher than expected under null models, neither for the overall dataset (Figure 2d), nor in any bioclimatic region (Figure 2e) or aspect (Figure 2f), providing no support for P1 stress tolerance predictions. However, CWM_{SM} was significantly lower than expected under null models for the overall dataset (negative and significant intercept of the corresponding additive HC3 model for SES), in the Alpine (EMM = -0.603, $p = 0.047$) and Mediterranean (EMM = -0.588, $p = 0.029$) regions, and in communities exposed to N aspects (EMM = -1.096, $p = 0.016$), supporting P1bis cliff-specific alternative predictions. Community weighted means of plant height (CWM_H) was lower than expected in null models for the overall dataset (Figure 2g), providing support for P1 stress tolerance predictions.

CWM_H was lower than expected in null models in the Alpine (EMM = -1.603, $p < 0.001$; Figure 2h), Continental (EMM = -1.284, $p = 0.001$) and Mediterranean (EMM = -0.562, $p = 0.024$) regions, on the equator-facing (EMM = -1.246, $p < 0.001$, Figure 2i), and pole-facing plots (EMM = -1.053, $p < 0.001$). The only significant contrast occurs exclusively between the Alpine and Mediterranean regions ($\Delta = -1.041$, $p = 0.044$; Appendix K). Plot scale analyses show that in a subset of plots, the frequency of stress-tolerant species deviated significantly from null expectations, supporting P1 stress tolerance predictions: the CWM_{LDMC} was significantly higher than the null expectation in 31.3% of the plots, CWM_{SM} in 6% of the plots, and CWM_H was significantly lower than the null expectation in 50.0% of

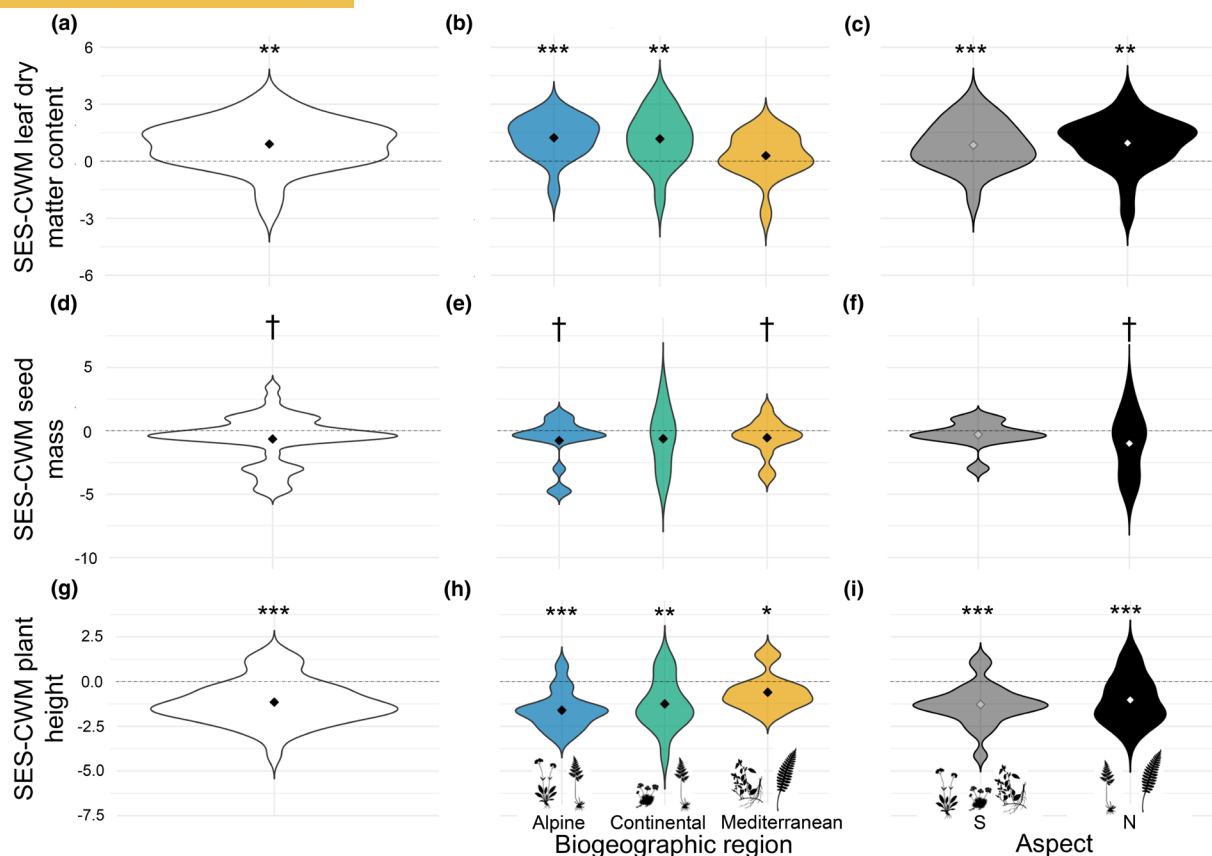


FIGURE 2 Distribution of standardized effect sizes for community weighted means (SES-CWM) of three traits proxy of stress tolerance: Leaf dry matter content (top row), seed mass (middle row) and plant height (bottom row). Panels are arranged in a 3 × 3 grid: Columns denote the type of comparison and rows correspond to traits. Column 1 (a, d, g) shows the overall distribution of SES-CWM across all plots ($n = 48$); Column 2 (b, e, h) shows within-biogeographic-region variation (Alpine, Continental, Mediterranean); Column 3 (c, f, i) shows the effect of aspect (Pole- vs. Equator-facing). Diamonds indicate sample means. For each panel, the significance of mean values different from zero was assessed with linear models using HC3 robust standard errors. The model intercept (for overall distributions) and the estimated marginal means (for biogeographic regions and aspects) were tested against zero. Significance is shown according to directional predictions: Asterisks indicate support for P1 stress tolerance predictions, with SES-CWM leaf dry matter content and SES-CWM seed mass greater than zero assessed using right-tailed tests, and SES-CWM plant height lower than zero assessed using left-tailed tests; daggers indicate support for P1bis cliff-specific alternative predictions, with SES-CWM leaf dry matter content and SES-CWM seed mass lower than zero assessed using left-tailed tests. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

the plots (one-tailed $p < 0.05$; $N = 48$; [Appendix L](#)). Conversely, supporting P1bis cliff-specific alternative predictions, CWM_{LDMC} and CWM_{SM} showed significantly lower values than null expectations in 4.2% and 20.8% of plots, respectively (one-tailed $p < 0.05$; $N = 48$).

3.3 | Functional convergence in inland cliff communities and its drivers (P2 - P3)

The effect of inland cliffs on functional convergence varied with aspect among biogeographic regions, as adding Aspect × biogeographic region interactions improved SES-FD model fit. Aggregate analyses based on the selected functional traits and partially accounting for intraspecific trait variability indicate that there is overall functional convergence of the cliff communities beyond that expected in the regional-pool null models ([Figure 3a](#)). Functional diversity (FD) was lower than expected under null models in the Alpine region on both

equator- and pole-exposed cliff faces (S: $EMM = -0.757$, $p < 0.001$; N: $EMM = -0.777$, $p = 0.002$; [Figure 3b](#)) and in the Mediterranean region on equator-exposed cliff faces only ($EMM = -1.203$, $p < 0.001$; $\Delta(S - N) = -2.23$, $p < 0.001$). Plot scale analyses show that 12.5% of the plots exhibited significant functional convergence (one-tailed $p < 0.05$; $N = 48$; [Appendix M](#)).

The predictors selected in the SES-FD linear model represented a substantial fraction of the variance (adjusted $R^2 = 0.51$). Local topographic factors only negligibly contributed to R^2 ([Table 4](#)).

The permutation test ([Appendix N](#)) generally corroborates the results obtained from the EMM and the linear models. The only exception was the observed FD across the entire dataset, for which the permutation test indicated that it did not differ significantly from the null expectation ($p = 0.643$). Sensitivity analyses conducted after excluding influential observations ([Appendix O](#)) corroborate the conclusions from the inferential models fitted to the full dataset ([Appendix P](#)).

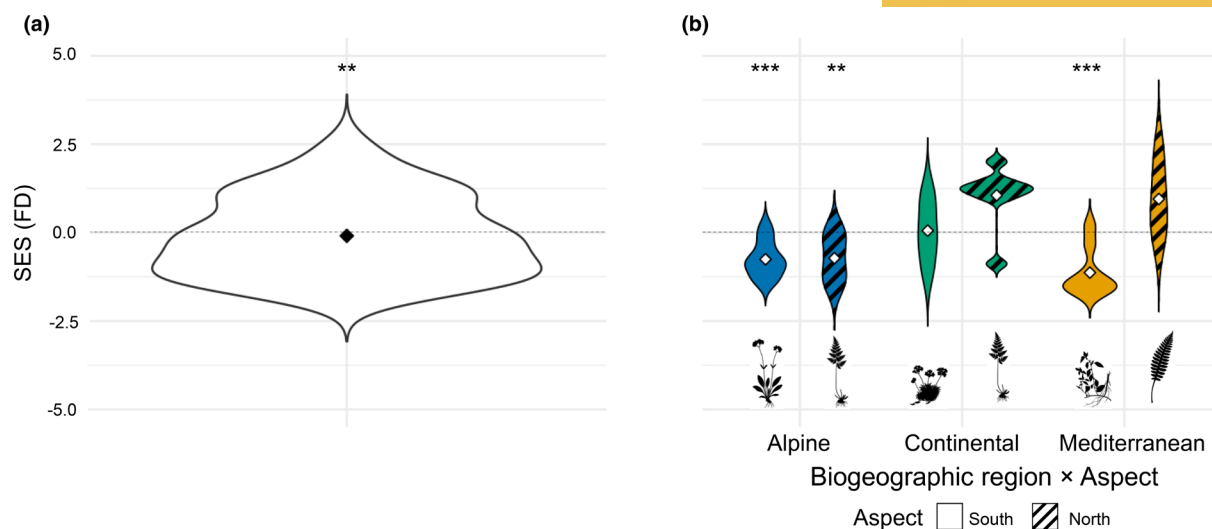


FIGURE 3 Distribution of standardized effect sizes (SES) for functional diversity quantified as Rao's quadratic entropy. Panel (a) shows the overall distribution of SES-functional diversity across all plots ($n=48$). Panel (b) shows the effect of aspect (Pole- vs. Equator-facing) within each biogeographic region (Alpine, Continental, Mediterranean). Diamonds indicate sample means. For each panel, the significance of mean values different from zero was assessed with linear models using HC3 robust standard errors. The model intercept (for overall distributions) and the estimated marginal means (for biogeographic regions and aspects) were tested against zero. Significance is shown only when the intercept or the one-tailed tests indicate functional convergence: that is SES-functional diversity significantly less than zero (left-tailed tests). Significance levels: *** $p < 0.001$, ** $p < 0.01$.

TABLE 4 Relative importance of predictors in the linear model of standardized effect size for functional diversity.

Predictor	F	Partial R^2
Biogeographic region	11.142	0.358
Aspect	21.086	0.345
Aspect $\times$ Biogeographic region	6.894	0.256
Slope	0.110	0.003
Microtopography	0.427	0.011

Note: Type III sums of squares were used to estimate the independent contribution of each predictor after accounting for all other terms in the model. Predictor importance is expressed as partial R^2 , representing the proportion of variance uniquely explained by each term after controlling for the remaining predictors.

4 | DISCUSSION

Our results suggest that inland limestone cliffs preferentially support stress-tolerant species compared to their regional species pools, but the magnitude and direction of these patterns vary by trait and biogeographic region considered. Functional convergence was most evident in the Alpine region and on equator-facing (likely drier) cliffs of the Mediterranean region. These patterns may reflect a combination of factors, including environmental filtering, macroclimatic differences among biogeographic regions that may modulate the contrast between the microclimatic conditions experienced on cliffs and those prevailing in surrounding habitats and biogeographic legacy. Notably, variation in FD was not explained by variation in local topographic factors.

4.1 | Functional trait shifts in inland cliff communities (P1 - P1bis)

Assuming that LDMC and H are indicative of stress-tolerant strategies, inland limestone cliffs tend to select more stress-tolerant plants relative to the regional species pool, although the strength and direction of this pattern vary between regions and traits. LDMC is significantly higher on cliffs in the Alpine and Continental regions, regardless of the aspect. The LDMC signal in the Continental region is likely attenuated by locally abundant succulents (e.g. *Sedum* spp.), which have low LDMC despite being stress-tolerant. In the Mediterranean area, the LDMC pattern did not consistently deviate from null expectations, regardless of aspect. H is consistently lower than null expectations across all biogeographic regions and in both pole- and equator-facing communities, with the strongest deviation observed in the Alpine region, as reflected by the significant Alpine–Mediterranean contrast. The patterns observed in the Mediterranean region are consistent with Lavergne et al. (2003), who found no significant differences in specific leaf area (SLA), a leaf economic trait generally inversely related to LDMC (Wilson et al., 1999), but significant differences in H between rock endemics and widespread congeners. These findings indicate that the inland cliffs constitute drier and more stressful microhabitats than the surrounding landscape, primarily where the regional climate is relatively humid. Contrary to expectation, community weighted SM was lower than expected by the null models in the Alpine and Mediterranean regions and in pole-facing communities, suggesting a potential role of dispersal-related processes in community assembly. Safe sites for establishment on vertical cliffs are extremely scarce, discontinuous

and often vertically separated (Larson et al., 2000). A colonization strategy based on producing many small, wind-dispersed propagules may be more effective than producing fewer large ones that favour establishment (Jakobsson & Eriksson, 2000). Although we standardized sampling through the selection of characteristic cliff plant species within each study area and aspect, analyses at the plot level revealed marked heterogeneity in functional trait composition. Within these standardized cliff communities, individual plots showed significant deviations from null expectations in both directions for LDMC and SM, indicating that local assemblages may be shifted towards plants representing contrasting positions along functional trait axes. For LDMC, opposite deviations may reflect the coexistence of conservative leaf strategies and drought responses based on tissue water storage. Similarly, opposite deviations in seed mass suggest that local cliff communities may accommodate contrasting regeneration and dispersal strategies. Positive deviations were associated with plots dominated by woody species producing relatively large propagules and, in several cases, relying on animal-mediated dispersal (e.g. *Corylus avellana*, *Sambucus nigra* and *Taxus baccata* in Continental pole-facing cliffs), whereas negative deviations were associated with spore-dispersing ferns, which, although requiring liquid water for fertilization, have modest growth requirements (Woodhouse & Nobel, 1982). We found no evidence that pole-facing Mediterranean cliffs uniquely lack selective drivers; therefore, unlike in drier regions (e.g. subdeserts) reported by Zohary (1973), they do not seem to provide microrefugia for relatively hygrophilous species. The observed patterns were robust across statistical approaches, showing close agreement between methods.

4.2 | Functional convergence in inland cliff communities and its drivers (P2 - P3)

Functional convergence was observed, but not consistently across limestone inland cliffs. It occurred in the Alpine biogeographic region, the most humid and coldest along our gradient, and in equator-facing communities within the Mediterranean region, the most arid along our gradient. No evidence of functional convergence was detected in the Continental region. This context dependency may explain why different statistical approaches provided contrasting evidence for functional convergence when considering the entire dataset. We suggest that this pattern may arise because limestone cliffs, owing to their distinctive geomorphological properties, generate environmental conditions that differ markedly from the surrounding landscape, particularly where the regional climate provides sufficient moisture. Additionally, alpine cliffs may also have amplified typical high-elevation stressors in our plots, for example, increased frost exposure when snow cover is absent and strong winds (Körner, 2021). However, such factors should primarily strengthen environmental filtering on colder, pole-facing walls, which we did not find. The absence of detected functional convergence in the Continental region could be due to the coexistence of different stress tolerance and dispersal strategies that imply contrasting values of measured traits

(Volaire, 2018). These strategies may become locally dominant, as suggested by the heterogeneous CWM patterns observed among plots. In the driest region, the absence of functional convergence on pole-facing cliffs may be related to the presence of shaded crevices that can retain more favourable moisture conditions (Zohary, 1973), allowing the persistence of diverse functional strategies and growth forms. In contrast, on equator-facing cliffs, where such microsites are expected to be less frequent due to higher solar radiation and evaporation, we detected significant functional convergence.

In our linear model of FD, the largest independent contributions were associated with aspect and biogeographic region, which showed comparable effect sizes, followed by their interaction. Contrary to expectations, local topographic parameters (slope, microtopographic complexity) contribute little. While higher microtopographic heterogeneity increases colonization and vegetation cover by increasing the number of available establishment sites (Kuntz & Larson, 2006), it may not substantially alter the range of functional strategies present in the community. Similarly, the limited effect of slope may reflect the strong environmental constraints already associated with cliff habitats, where conditions may exceed thresholds beyond which additional variation in steepness has limited marginal influence on community assembly patterns. One possible explanation is that, once the pool of viable functional strategies has already been constrained by strong environmental filtering, historical contingency and priority effects may determine which species occupy available microsites (Fukami, 2015), as early colonists in cliff crevices may persist and influence subsequent establishment trajectories ('cork in a bottle'; Davis, 1951). Competition is unlikely to be the primary driver structuring communities on steep cliff faces, as interaction neighbourhoods are often limited to a few individuals within the same microtopographic feature (Gao et al., 2024).

5 | LIMITATIONS

Several limitations should be considered when interpreting the patterns we found. The study areas were selected to represent contrasting biogeographic regions but do not encompass the full variability within each region. Nevertheless, the inclusion of Mediterranean, Continental and Alpine regions captures a broad climatic and biogeographic gradient across Europe (European Environment Agency, 2016). The use of two target species with contrasting ecologies on equator- and pole-facing cliffs may have heightened aspect-related contrasts in functional responses. Although we incorporated cliff-specific measurements for selected traits and species and performed a sensitivity analysis, most trait values, particularly those for regional species pools and seed mass, and partially for leaf dry matter content, were derived from databases. Consequently, local phenotypic and intraspecific variation may be only partially captured. However, trait variation among species generally exceeds that observed within species (Jung et al., 2010). Moreover, our inference was based on a limited set of functional traits, representing only a subset of the functional dimensions

relevant to persistence in cliff environments. Nevertheless, the selected traits capture major axes of plant functional variation, encompassing leaf economics, regeneration strategies and plant size (Díaz et al., 2016) and therefore represent a substantial component of the functional variation potentially relevant to community assembly. Finally, the characterization of local environmental conditions was simplified. The use of a single slope value per plot and simplified measures of microtopographic complexity may not fully capture the fine-scale heterogeneity experienced by cliff plants, potentially contributing to the lack of detected topographic effects. In addition, a slightly different protocol was used to quantify slope in a subset of equator-facing Mediterranean plots, introducing additional uncertainty. Local water availability was also not quantified directly, limiting our ability to relate functional patterns to the hydrological conditions experienced by cliff plants. Nevertheless, direct quantification of water availability on limestone rock surfaces is challenging because of pronounced fine-scale heterogeneity in moisture conditions (Sass et al., 2026).

6 | CONCLUSIONS

Incorporating regional species pools into functional analyses broadens inference on non-random assembly patterns in extreme habitats by incorporating absences driven by deterministic and stochastic processes (e.g. environmental filtering and dispersal limitation). The signature of abiotic filtering in vascular plant communities occurring on limestone inland cliffs seems trait-contingent, meaning that non-random trait patterns depend on the specific trait axes considered (e.g. leaf economics, dispersal-establishment and the plant size spectrum). Functional convergence was spatially heterogeneous across limestone inland cliffs, indicating that environmental filtering varies with regional context and cliff aspect, with stronger convergence under conditions expected to impose greater environmental constraints. Topographic factors that affect soil availability contribute little to local functional convergence; microtopographic heterogeneity may increase total cover without imposing strong trait filtering, while the high overall steepness of inland cliffs may limit the availability of suitable microsites for vascular plant establishment, suggesting priority effects. Together, these findings re-frame 'extreme' habitats as context-dependent systems that can be compared and predicted using trait filters and integrating regional species pools.

AUTHOR CONTRIBUTIONS

Thomas Deola, Gianmaria Bonari, Alessandro Bricca and Juan Lorite conceived the idea and designed the methodology; Claudia Angiolini, Manuel J. Steinbauer and Anke Jentsch contributed critically to the idea; Thomas Deola, Gianmaria Bonari, Leopoldo de Simone, Sofie Paulus and Francesco Candini collected the data; Thomas Deola analysed the data; Thomas Deola, Gianmaria Bonari and Alessandro Bricca led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest, financial or otherwise, that could be perceived as influencing the work reported in this manuscript.

DATA AVAILABILITY STATEMENT

The data and R script supporting the findings of this study are available in the Zenodo repository Deola et al. (2026) at <https://doi.org/10.5281/zenodo.18621112>.

STATEMENT ON INCLUSION

Our study brings together authors from different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. Study areas.

Appendix B. Target species occurrences.

Table B1. Target species of sun-exposed and shaded cliff communities in each biogeographic region.

Appendix C. Effective nearest-neighbour plot distances.

Table C1. Summary of nearest-neighbour distances (m) among vegetation plots within each biogeographic region (BGR) and aspect category. The table reports the number of plots (n), minimum and mean nearest-neighbour distances, and the number of plots with a nearest-neighbour distance <100m. During field sampling, a target minimum distance of 100m between plots was adopted whenever permitted by the availability of suitable limestone cliff habitat. Distances were calculated from geographic coordinates and represent horizontal (planimetric) distances. Actual distances along the cliff surface are greater because of the steep topography of cliff habitats.

Appendix D. Methodology description of Global Biodiversity Information Facility (GBIF) data extraction and filtering for the definition of regional species pools.

Table D1. GBIF occurrences before and after filtering for the definition of the regional species pools in each biogeographic region.

Appendix E. Exploratory analysis to test the variations in area size for defining the regional species pool.

Table E1. Species of the local species pool in the alpine biogeographic region (n = 84) that have been included in the corresponding regional species pool at different dimensions of the side of the square.

Appendix F. TRY trait data filtering workflow for regional species pools.

Appendix G. Sensitivity analysis of LDMC estimates based on cliff-specific versus database-derived trait values.

Appendix H. Inferential procedure and diagnostics testing for additive linear models of standardized effect size.

Table H1. Diagnostics summary for additive linear models of standardized effect size (SES) of community weighted mean (CWM) computed for three functional traits: leaf dry matter content (LDMC), seed mass (SM), plant height (H), and of SES of functional diversity (FD). For each model, the table reports: residual standard error (Residual SE); model fit statistics (R squared, Adj R squared, F stat with numerator and denominator df and F p-value); normality test (Shapiro–Wilk W and p); heteroscedasticity tests (studentized Breusch–Pagan statistic and p; Non-constant Variance Score Test / ncvTest p; Levene's test F and p); influence diagnostics (maximum Cook's distance, Cook's cutoff used, and number of observations exceeding the cutoff); and the number of BCa bootstrap confidence intervals available for contrasts (N BCa available). Models are additive (SES ~ aspect + biogeographic region + slope + microtopography) and main inference uses HC3 heteroscedasticity-consistent standard errors. The sample size is equal to 48.

Appendix I. Trait coverage.

Table I1. Distribution of trait coverage across regional species pools for the traits leaf dry matter content (LDMC), seed mass (SM), and plant height (H).

Appendix J. Estimated marginal means (emmeans) for each biogeographic region and aspect.

Table J1. Estimated marginal means (EMMs) for each biogeographic region and aspect (equator-facing (S) and pole-facing (N)), with HC3 (heteroscedasticity-consistent, type HC3) standard errors and bootstrap BCa 95% confidence intervals (R=2000), for standardized effect size community weighted mean of leaf dry matter content (SES-CWM_{LDMC}), seed mass (SES-CWM_{SM}), and plant height (SES-CWM_H) and for standardized effect size functional diversity (SES-FD). For each SES and factor level the table reports: estimated marginal mean (Estimate), HC3 standard error (SE), t-ratio, one-tailed p-value for the test of the mean against 0 for P1 stress tolerance predictions: right-tailed for SES-CWMLDMC and SES-CWMSM, and left-tailed for SES-CWMH; for P1bis cliff-specific alternative predictions: left-tailed for SES-CWMLDMC and SES-CWMSM; for P2 functional convergence: left-tailed for SES-FD, and the BCa bootstrap 95% confidence limits. All estimates derive from linear models including aspect, biogeographic region, slope, and microtopography as predictors; SES-FD estimates were obtained from models including the aspect × biogeographic region interaction. HC3 standard errors were used to account for heteroscedasticity, and BCa intervals are provided as a robustness check. Degrees of freedom are equal to 42.

Appendix K. Pairwise estimated marginal mean (emmeans) contrasts for each biogeographic region and aspect.

Table K1. Pairwise estimated marginal mean (emmeans) contrasts with Tukey-adjusted p-values and bootstrap BCa 95% confidence intervals (R=2000) for standardized effect size community weighted mean of leaf dry matter content (SES-CWM_{LDMC}), seed mass (SES-CWM_{SM}), and plant height (SES-CWM_H) and for standardized effect size functional diversity (SES-FD). SES-CWM contrast estimates derive from additive models, whereas

SES-CWM contrast estimates derive from the SES-FD model including the aspect × biogeographic region (BGR) interaction. SES-CWM contrasts are reported for aspect and biogeographic region. SES-FD contrasts are reported for aspect within a biogeographic region. For each contrast we report: estimate of the contrast (Estimate), standard error (SE), t-ratio, Tukey-adjusted p-value, and BCa bootstrap intervals (BCa CI).

Appendix L. Plot scale analyses of stress tolerance.

Appendix M. Plot scale analyses of functional convergence.

Appendix N. Permutation tests.

Table N1. Permutation tests of community weighted means (CWMs) for leaf dry matter content (LDMC), seed mass (SM), plant height (H), and of functional diversity (FD). For CWM analyses, plots were grouped at three levels: across the entire dataset (ED), by biogeographic region (BGR, three groups), and by aspect (two groups). For FD analyses, plots were grouped at two levels: across the entire dataset (ED) and by the combination of aspect and biogeographic region (six groups). For each group at each level, we performed one-tailed tests of CWM and FD comparing the observed group mean (mean obs) of CWM for each trait and of FD to null distributions generated by permuting CWM and FD (N=9999 permutations for CWM, 999 permutations for FD) and computing the group mean for each permutation (mean perm). We performed right-tailed tests of CWM_{LDMC} and CWM_{SM} and left-tailed tests of CWM_H for P1 stress tolerance predictions; left-tailed tests of CWM_{LDMC} and CWM_{SM} for P1bis cliff-specific alternative predictions; and left-tailed tests of FD for P2 functional convergence.

Appendix O. Influential observations in the additive linear models of standardized effect size.

Table O1. Observations with elevated influence (Cook's distance) identified by the modelling pipeline for standardized effect size community weighted mean of leaf dry matter content (SES-CWM_{LDMC}), seed mass (SES-CWM_{SM}), and plant height (SES-CWM_H) and for standardized effect size functional diversity (SES-FD). For each flagged observation, the table reports: Trait; Plot number; Cook's distance (CookD); the observed values of the response (SES), and model predictors included in the fit (aspect, biogeographic region, slope, microtopography). The Cook's cutoff used to detect influential points is provided in Appendix I. Models were re-fitted without them as sensitivity checks (Appendix O).

Appendix P. Additive linear reduced models of standardized effect size.

Table P1. HC3-adjusted coefficients of reduced models refit after removing influential observations identified by Cook's distance for standardized effect size community weighted mean of leaf dry matter content (SES-CWM_{LDMC}), seed mass (SES-CWM_{SM}), and plant height (SES-CWM_H) and for standardized effect size functional diversity (SES-FD). SES-CWM was analysed using additive models, whereas the SES-FD model included the aspect × biogeographic region (BGR) interaction. For each trait and model term (Intercept; aspect S vs. N; biogeographic region (BGR) vs. reference level alpine; Aspect × BGR interaction for SES-FD;

slope; microtopography) the table reports the point estimate (Estimate), heteroscedasticity-consistent standard error (HC3_SE; $\text{vcov} = \text{HC3}$), t value, p-value (coef test with HC3) and 95% HC3 confidence interval (CI 95 Lower, CI 95 Upper). Reduced models exclude observations with Cook's distance above the pipeline cutoff (default 4/n).

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