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Intraspecific variation of CSR-strategies across the elevational gradient on
Mt. Schrankogel, Austria

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Abstract

Given that alpine regions are suffering a temperature increase twice the global average, the interrelation of elevation, temperature, and water availability renders intraspecific trait variation (ITV) central to predicting species distribution and community assembly under ongoing climate change. Utilizing a trait-based approach, this study investigated leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) in order to assess the relative importance of competition (C), stress tolerance (S), and ruderal (R) strategies within four alpine plant species across elevation, climatic and morphometric gradients on Mt. Schrankogel (3497 m a.s.l.), Tyrol, Austria. The main finding revealed a predominance of stress tolerance (S) with increasing elevation and a less prominent role for ruderal (R) and a minor role for competitive (C) strategies, as the latter two diminish towards the mountain summit. Across environmental gradients, significant intraspecific variation in traits and strategies was identified, highlighting that within-species variability is a crucial component of alpine plant responses and may be key in adapting to fast-changing temperature- and precipitation regimes in the alpine realm. In order to enhance our understanding of alpine plants under global change, greater consideration of intraspecific trait variation is proposed in order to refine predictions of plant responses and improve conservation efforts under ongoing climate change.

Zusammenfassung

In Anbetracht der Tatsache, dass sich alpine Regionen im Vergleich zum globalen Durchschnitt etwa doppelt so stark erwärmen, wird die intraspezifische Merkmalsvariation aufgrund des engen Zusammenspiels von Höhe, Temperatur und Wasserverfügbarkeit zu einem zentralen Baustein für Prognosen der Artenverbreitung und der Zusammensetzung von Pflanzengemeinschaften im Klimawandel. Im Rahmen dieser Studie wurden am Schrankogel (3497 m ü. M.) in Tirol, Österreich, entlang von Höhen-, Temperatur- und morphometrischen Gradienten die Blattfläche (LA), die spezifische Blattfläche (SLA) und der Blatt-Trockenmassegehalt (LDMC) von vier alpinen Pflanzenarten erhoben, um die relative Bedeutung der CSR-Strategien Konkurrenz (C), Stresstoleranz (S) und Ruderalität (R) auf intraspezifischer Ebene zu quantifizieren. Die Ergebnisse zeigen, dass mit zunehmender Höhe die Dominanz von Stresstoleranz (S) stetig wächst, während Ruderalität (R) und insbesondere Konkurrenz (C) an Bedeutung verlieren und zum Gipfel hin abnehmen. Über alle Umweltgradienten hinweg konnte eine ausgeprägte intraspezifische Variation sowohl der Blattmerkmale als auch der abgeleiteten Strategien nachgewiesen werden. Dies unterstreicht die Bedeutung der innerartlichen Variabilität als wesentlicher Bestandteil der Anpassungsfähigkeit alpiner Pflanzen und betont ihre Schlüsselrolle bei der Anpassung an sich rasch verändernde Temperatur- und Niederschlagsregime. Um das Verständnis alpiner Pflanzengesellschaften unter dem globalen Wandel zu vertiefen, wird daher eine stärkere Berücksichtigung der intraspezifischen Merkmalsvariation empfohlen. Dies kann zu präziseren Vorhersagen der Anpassung von Pflanzen und verbesserten Naturschutz- und Managementmaßnahmen in alpinen Lebensräumen führen.

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1. Introduction

Anthropogenic climate change is increasing alpine temperatures at roughly twice the global average (Calvin et al., 2023; Rumpf et al., 2018), driving upslope shifts of cold-adapted plant species via local extirpation at lower distributional margins and facilitating upslope expansion of warm-adapted species for both elevational and geographical distributions (Steinbauer et al., 2018). The former leads to increases in species richness on European mountain summits altering community composition as competitive species are favoured, threatening the persistence of cryophilic specialists (Steinbauer et al., 2022, 2018). Moreover, climate projections predict seasonal shifts in precipitation expected to transform water availability in alpine regions (Buchner et al., 2017; Steinbauer et al., 2022). In particular, longer dry periods as projected for the European Alps (Beniston et al., 2018), coupled with rising temperatures, will increase evapotranspiration (Sherwood and Fu, 2014; Steinbauer et al., 2022) and impose additional pressure on alpine plants (Rosbakh et al., 2017).

In order to understand how alpine plants respond to environmental properties such as temperature, water availability and snow cover along elevational gradients we focus on morpho-functional traits that affect growth, reproduction as well as survival and, hence, overall fitness. Morphological traits refer to physical characteristics such as the size and shape of both vegetative and reproductive organs, providing structural integrity and are linked to resource acquisition (Wright et al., 2004).

The prevailing strategy scheme to classify plant species according to their functional traits is the Competitive, Stress-tolerator and Ruderal (CSR) framework, introduced by Grime in 1974. It classifies plant strategies as viable trait combinations of competitive ability, abiotic stress tolerance and disturbance response (Pierce et al., 2017a). Here, a core premise is the trade-off between resource acquisition and -conservation that shapes competitive advantages across environments (Reich, 2014).

The mentioned compromise is reflected by the CSR framework's focal leaf traits: Leaf Area (LA), Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC). For that matter, alpine environments are associated with high LDMC and low SLA and LA (durable, dense leaves), whereas high-resource settings favour low LDMC but high SLA and LA (thin, fast-growing leaves) (Henn and Damschen, 2021; Körner, 2021; Pérez-Harguindeguy et al., 2013). A combination of these traits classifies a species as competitor (C) competing with its neighbours through rapid vegetative growth and size; as stress-tolerator (S) retaining resources and repair dense, persistent tissues and as: ruderal (R) allocating resources mainly to propagules in order to recover quickly

after disturbance. Intermediate strategies (SR, CS, CR, CSR, ...) represent more central positions along these axes (Pierce et al., 2017a).

Nowadays, such trait-based approaches are widely used in ecological and evolutionary research highlighting the differentiation between species or communities, although often times neglecting the impact of intraspecific variation (ITV). On the other hand, studies incorporating ITV are typically conducted with trait values provided by online repositories - often lacking additional abiotic information (Violle et al., 2007; Violle and Jiang, 2009). A meta-analysis demonstrated that ITV accounts for an average of 25 % of observed trait variability within communities and 32 % among communities (Siefert et al., 2015) underlining its ecological importance and lack of research thereby.

Here, the macro-ecological, interspecific approach of the CSR framework will be extended to the intraspecific level, considering a multitude of environmental gradients as existing literature has shown that the expression of these functional traits demonstrates a high degree of variability across a range of different resource and environmental regimes (Keddy, 1992). Along the elevational gradient an ever-increasing role of stress tolerators (S) at the cost of competition (C) and the ruderal (R) strategy can be expected, as documented by research on species- and community level (Li et al., 2026; Rafiee et al., 2024). This is in line with the stress gradient hypothesis, stating the alpine belt is governed by abiotic, mainly climatic factors (Cannone and Pignatti, 2014; Lamprecht et al., 2018; Rumpf et al., 2019) whilst competition with neighbouring species decreases towards the summit (Kulonen et al., 2018).

In order to address ITV in alpine environments, we assess three functional traits of four alpine plant species based on individuals at their low- and high elevational margin as well as their distributional optima. The focal traits - Leaf Area (LA), Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC) - were selected as they are the foundation in order to calculate the CSR strategy of individuals of multiple species (see Chapter 2.4).

Specifically, the following questions are posed:

- 1) How does the expression of functional traits (LA, SLA and LDMC) and strategies (C, S and R) at the species optima compare to its high- and low-elevational margin?
- 2) What function of functional traits (LA, SLA and LDMC) and strategies (C, S and R) can be detected along the elevational gradient?
- 3) How does the expression of functional traits (LA, SLA and LDMC) and strategies (C, S and R) across climatic and morphological gradients compare to that of the elevational gradient?

2. Materials and Methods

2.1 Study Area

The fieldwork was conducted in July and August 2025 at Mount Schrankogel (3497 m a.s.l., N 47° 2'39.135", E 11° 5'56.018") in the Stubaier Alps, Tyrol, Austria. The chosen area is highly suitable for the intended research as the distribution of plant species is well known due to the long-term ecological monitoring program GLORIA (gloria.ac.at) and the ongoing "MICROCLIM" project (<https://www.mountainresearch.at/microclim/>). For the latter, 900 1x1 m² plots of non-forest vegetation, including temperature loggers, were established across elevations of 1794 to 3497 m a.s.l.. Representative of the Eastern Central Alps, Mt. Schrankogel signifies a high elevation siliceous mountain, dominated mainly by amphibolite and gneiss (Hoinkes et al., 2021), offering a diverse mosaic of ridges, glaciers and steep slopes with differing aspects and resulting snow cover phenomena (Gottfried et al., 1998). The macroclimate of the study area is subcontinental. The meteorological station Obergurgl (1938 m, 11°01,5'E, 46°52'N), 20 kilometres from the study area, detects an average temperature of 2.5°C for the years of 1980-2021, and a mean annual precipitation sum of 889 mm ("Wetterprognose Österreich," 2024).



Figure 1: View of Mt. Schrankogel from Wannenkogel (www.foto-webcam.eu, n.d.), last accessed on 23.01.2026

2.2 Target Species and Sampling

In order to address intraspecific differences of traits and consequently of CSR strategies, only frequently abundant species with an elevational range of at least 700 m at Mount Schrankogel were considered. Secondly, a balanced share of high- and low-alpine species shall allow for further differentiation and enhanced results. Lastly, to minimize impact and act in alignment with conservation law, protected species were not considered. A set of four alpine species fulfilling these criteria were selected, shown in Table 1.

Table 1: Overview of the five target species and relevant information

Species	ID	Family	Species optima (m)	Min- & Max Elevation (m)	Sampled plots
<i>Campanula barbata</i>	CB	Campanulaceae	2216	1940 - 2830	8
<i>Campanula scheuchzeri</i>	CS	Campanulaceae	2211	1794 - 3012	8
<i>Trifolium pallescens</i>	TP	Fabaceae	2522	1963 - 2862	6
<i>Veronica alpina</i>	VA	Plantaginaceae	2618	2138 - 3080	8

Sampling was conducted in July and August 2025. To facilitate successful sampling, we had access to MICROCLIM's data of established 900 1x1 m² plots across Mt. Schrankogel, ranging between 1800 and 3450 m above sea level. The data provided the foundation for sampling of the target species at three distinct elevational levels, the low- and high-elevational margin as well as the species optima based on weighted densities of their distribution. For each elevational zone, 20 individuals of each taxon were sampled from at least two different plots to cover distinctive microclimates at similar elevations.

Upon arrival at the plots, 10 different individuals within the distance of up to 15 m of the MICROCLIM plots, occurring within similar communities and micro-habitats, were sampled. Individuals were sampled at least 1 m from one another to minimise the risk of sampling the same genotype. Only mature, non-senescent leaves that reached their full size on flowering adult specimens were collected. As this study aims to compare an individual's competitive ability, the largest leaf of each plant was sampled as its contribution to photosynthesis is the greatest (Anten, 2004). Individuals with clear signs of pathogens or herbivory were mostly excluded, though minor damage could not always be avoided. On site, leaf samples were placed between wet tissue, then

sealed in a breath-inflated zip lock bag to enhance CO₂ concentration and air humidity whilst minimising transpirational water loss. Until the completion of analyses the following day, leaves were kept cool and dark at around 5 °C (Pérez-Harguindeguy et al., 2013), before being dried at room temperature for 14 days to remove all moisture. In total, leaf samples of 240 individuals were collected.

2.3 Climatological- and Morphometric variables

Temperature variables such as mean annual temperature, minimal temperatures for both summer and winter as well as annual temperature range refer to soil temperature at 10 cm depth as measurements are taken from temperature loggers buried within the studied MICROCLIM plots. Measurements are provided in an hourly interval. In addition, morphometric variables were also included. Hill shade represents the illumination intensity over a surface according to the position of the sun (Chytrý et al., 2024; Horn, 1981). Therefore, it can be used as a proxy of solar radiation. TWI, the Total Wetness Index is a measure of relative soil moisture. The resolution of the morphometric variables was chosen at 151 m pixel size as the presence of most species is better explained by topographic variation at coarser scales (Chytrý et al., 2024). Snow cover duration was monitored by webcams set up on neighbouring mountains delivering images of the studied plots in 10- and 30 min intervals. A subset of 50 images per webcam was used to train a random-forest model for snow classification (Breiman, 2001; Kollert et al., 2026). For more detailed information browse the literature cited above.

2.4 Trait Measurements

In order to calculate the CSR strategy as proposed by Pierce et al. 2017 for each individual specimen, three functional traits were analyzed according to the “New handbook for standardised measurement of plant functional traits worldwide” (Pérez -Harguindeguy et al., 2013).

2.4.1 Leaf Area (LA)

The following day of sampling, each individual leaf was removed from the refrigerator before obtaining the fresh weight (fw) and consecutively scanned using a portable scanner (Canon CanoScan LiDE 400) at a resolution of 600 dpi. In order to determine the leaf area (LA) in mm², leaf scans were analyzed using ImageJ (“ImageJ Wiki,” n.d.).

2.4.2 Specific Leaf Area (SLA)

Specific Leaf Area was calculated as the ratio of leaf area to its dry weight. Weight measurements were obtained using a portable scale (INF digital fine scale) with an accuracy of 0.001 g. Low SLA values represent adaptations common in alpine habitats as leaf tissue is dense and leaf area small, able to deal with environmental stress (Körner, 2023, 2021; Pérez-Harguindeguy et al., 2013).

$$SLA = \frac{LA (cm^2)}{dry\ weight(g)}$$

2.4.3 Leaf Dry Matter Content (LDMC)

Leaf Dry Matter Content was calculated by the ratio of dry weight (dw) to saturated fresh weight (fw). Leaves expressing high values of LDMC are considered to be more rigid and consequently better equipped to withstand physical hazards, compared to those exhibiting low LDMC (Körner, 2023, 2021; Pérez-Harguindeguy et al., 2013).

$$LDMC = \frac{dry\ weight\ (dw)}{saturated\ fresh\ weight\ (fw)}$$

2.5 CSR calculation

Until the present time, several approaches on the basis of the CSR theory have been developed in order to characterize the functional space of vegetation (Grime et al., 1988; Hodgson et al., 1999). Whilst past methods emerged based on local flora assemblages, Pierce et al. 2017 created a tool based on global data and therefore applicable worldwide to calculate a plant's CSR strategy. Existing research has implemented this tool in a variety of spatial and ecological contexts based on trait data (LA, SLA & LDMC) extracted from online repositories such as the "TRY plant functional trait database" (Kattge et al., 2011). In recent years, studies conducted field work gathering trait measurements to further explore CSR strategies along environmental gradients (Bricca et al., 2022; Hasigerili et al., 2023).

Similarly, following the sampling of leaves along an elevational gradient, the interspecific application of the CSR calculation tool will be extended to test for possible intraspecific variation. Here, for each individual plant, trait measurements (LA, SLA and LDMC) of the sampled leaf will be inserted into the StrateFy - CSR strategy calculator (Pierce et al., 2017a) to classify the individual's strategy. Here, it is important to note that C, S and R values are not calculated directly from LA, SLA and LDMC. Instead, CSR values are derived from the trade-off between these traits, which is then compared against the global spectrum (position along multivariate axes based on the global ranges of trait values) (Pierce et al., 2017b). CSR strategies are expressed as percentages C:S:R, ranging from 0-100% in total or as a categorical factor (e.g. C, S, R, S/R, ...).

Once calculated, both numeric and categorical strategies of each individual will be exported and transferred to the R-Studio environment (R Core Team, 2024), thus enabling further data analysis.

2.6 Data Analysis

The StrateFy- CSR strategy calculator (Pierce et al., 2017a) computed CSR strategies both numerically and categorically, enabling further analysis using R-Studio (R Core Team, 2024). Within the R-Studio environment traits and strategies have been standardized for each species in order to facilitate a direct comparison of species and the impact of environmental variables.

ANOVAs comparing each focal trait and CSR strategies across the sampled elevational level (low, optima and high) was conducted. Furthermore, linear mixed-effects models (*lmer* package) were conducted for each focal trait (LA, SLA and LDMC) and strategy (C, S and R), for all species combined, as well as individually. The trait or strategy in question represents the response variable while environmental gradients act as the predictor variable - species are considered as a random-effect.

3. Results

A comparison of strategies of all individuals, across species in a numerical manner is shown in Figure 2, whilst categorical strategies are shown in Table 2 for each species individually.

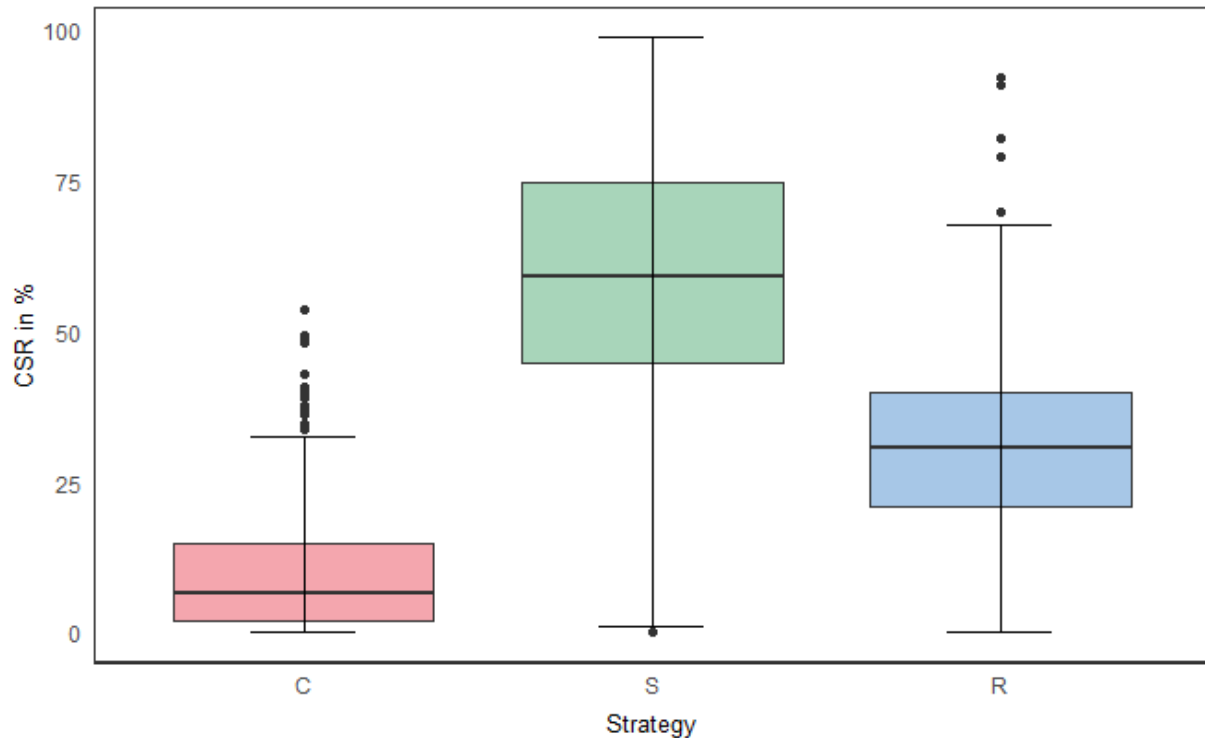


Figure 2: C, S and R strategies of individuals ($n=240$) of four alpine plant species across their elevational distribution, ranging from 0 to 100 %. The lower and upper hinges are represented by the 25% and 75% percentiles; the whiskers capture values within the range of $1.5 \times$ Interquartile Range, the remaining represent outliers of that range.

The mentioned results depict low values for competition (mean: 11 %, median: 7 %). In contrast, stress tolerance exhibits the highest values (mean: 57 %, median= 59 %). Investment towards ruderal properties is common among the species studied (mean: 32 %, median: 31 %).

A majority of categorical strategies (Table 2) accounts for stress tolerance, followed by the ruderal strategy. *Campanula barbata* subsp. *barbata* is the only species with individuals that can be classified as competitor, expressing the strategy of CR. It generally exhibits the highest investment towards competition, expressing strategies of SR/CSR, CSR, S/CSR, R/CSR, CR/CSR, CR, R/CR and S/CS. In contrast, *Veronica alpina* expresses a combination of stress- and ruderal related strategies such as SR, S/SR and only rarely S, R/SR and R. A more pronounced stress tolerance can be observed for *Campanula scheuchzeri* which most often exhibits the strategy of S/SR, followed by S and SR. Not much different is the strategy of *Trifolium pallescens* which predominantly exhibits the strategy S/SR, followed by SR, S/CSR, SR/CSR - expressing minor investment towards competition.

Comparing individuals across the elevational gradient a decreasing role of competition and ruderal strategies can be identified as well as an increase of stress tolerance towards higher elevations.

Table 2: Number of individuals per species and elevational level (low, optima and high) classified as C, S and R strategies and their intermediate stages (n= 240).

Species	CR	CR/ CSR	CS/ CSR	CSR	R	R/ CR	R/ CSR	R/ SR	S	S/ CS	S/ CSR	S/ SR	SR	SR/ CSR
<i>Campanula</i>														
<i>barbata</i>	5	6	5	12	0	1	6	0	0	1	11	0	0	13
<i>subsp.</i>														
<i>barbata</i>														
<i>Campanula</i>	0	0	0	0	0	0	0	0	20	0	0	33	7	0
<i>scheuchzeri</i>														
<i>Trifolium</i>	0	0	0	0	0	0	1	1	2	0	8	26	14	8
<i>pallenscens</i>														
<i>Veronica</i>	0	0	0	0	3	0	0	4	6	0	0	26	21	0
<i>alpina</i>														
Elevational level														
low	2	3	3	6	3	0	1	3	4	1	10	24	14	7
optima	2	2	2	1	0	1	5	2	8	0	4	30	16	7
high	1	1	0	5	0	0	1	0	16	0	5	31	12	7

3.1 Differences in traits and strategies of alpine plants across the elevational gradient

ANOVA revealed significant differences between elevational levels for each trait: LA ($F= 13.91$, $p < 0.001$), SLA ($F= 5.90$, $p= 0.003$) and LDMC ($F= 4.29$, $p= 0.02$), see Figure 3. The individuals at the high-elevational level consistently exhibit smaller values of LA than low-elevational individuals, while those at the distributional optima and low elevations were not significantly different (high-low: $\text{diff}= -0.71$, $p < 0.001$; high-optima: $\text{diff}= -0.65$, $p < 0.001$; optima-low: $\text{diff}= -0.06$, $p= 0.91$). The same pattern can also be observed for SLA (high-low: $\text{difference}= -0.52$, $p= 0.002$; high-optima: $\text{difference}= -0.35$, $p= 0.06$; optima-low: $\text{difference}= -0.16$, $p= 0.53$). An inverse pattern, with increasing values along the elevational gradient can be identified for LDMC, with only individuals from high- and low elevations able to be differentiated based on LDMC: (high-low: $\text{difference}= 0.45$, $p= 0.01$; high-optima: $\text{difference}= 0.27$, $p= 0.19$; optima-low: $\text{difference}= 0.18$, $p= 0.46$).

Furthermore, testing for differences in C, S and R across individuals at different elevational levels revealed that all strategies demonstrate statistically significant differentiation. S allows for a

differentiation of individuals ($F= 8.14$, $p < 0.001$) although significantly solely between high- and low elevational levels (high-low: difference= 0.62, $p < 0.001$; high-optima: difference= 0.30, $p= 0.13$; optima-low: difference= 0.32, $p= 0.09$), see Figure 3. Furthermore, C allows for the prediction of individuals across the elevational gradient ($F= 12.50$, $p < 0.001$) although not significantly so for those at the distributional optima and low elevations (high-low: difference= -0.8, $p < 0.001$; high-optima: difference= -0.43, $p= 0.004$; optima-low: difference= -0.37, $p= 0.01$). Individuals across the elevational gradient can also be predicted based on their ruderal strategy, R ($F= 3.57$, $p= 0.03$), although only significantly so for high- and low elevational levels (high-low: difference= -0.41, $p= 0.02$; high-optima: difference= -0.18, $p= 0.50$; optima-low: difference= -0.24, $p= 0.28$).

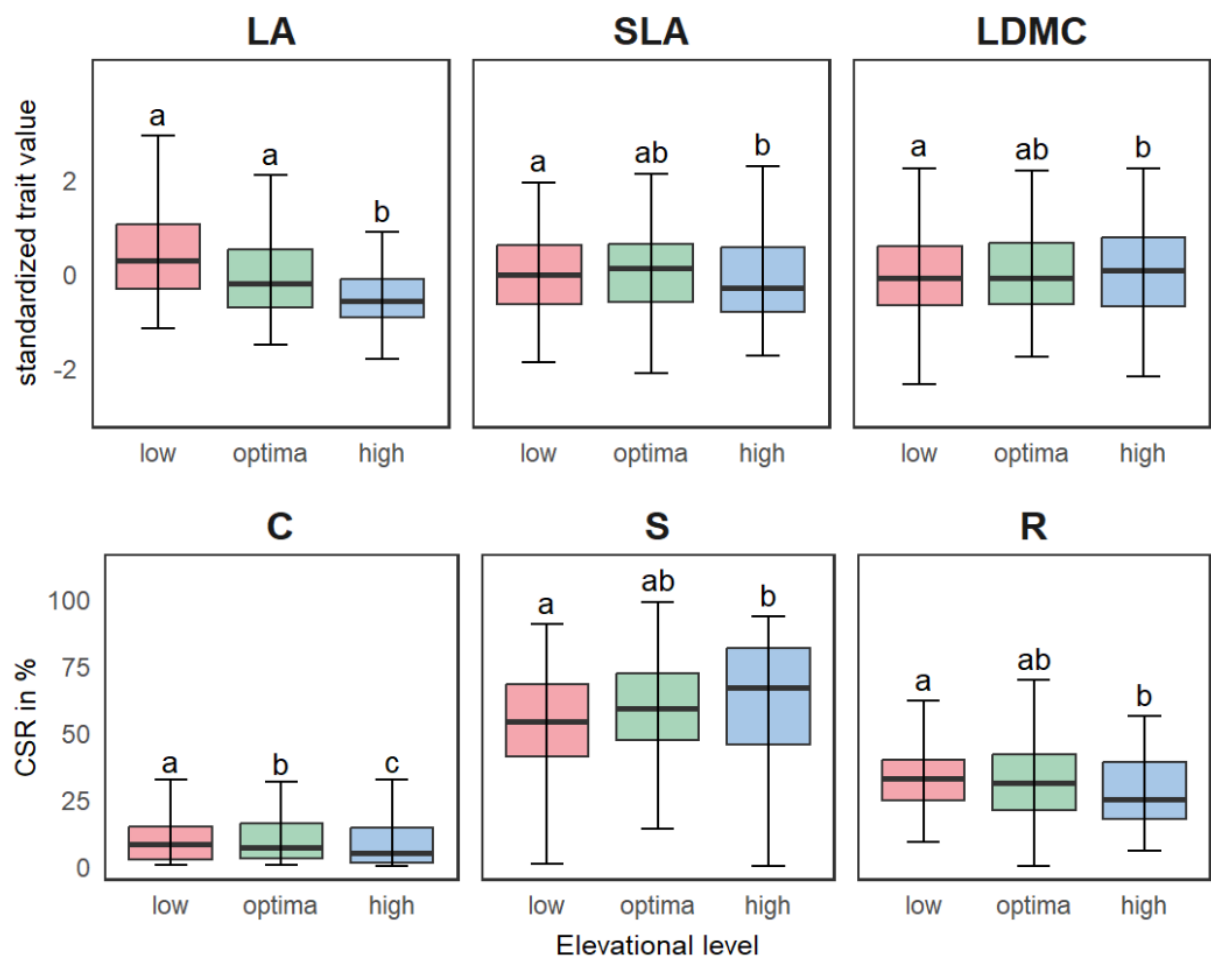


Figure 3: Distribution of standardized values of LA (Leaf Area), SLA (Specific Leaf Area) and LDMC (Leaf Dry Matter Content) as well as strategies (C, S and R) of all focal species across elevational levels (low, optima and high) on Mt. Schrankogel. The bold horizontal line represents the median trait size of each trait for each level. The lower and upper hinges are represented by the 25% and 75% percentiles. The whiskers capture values within the range of 1.5 x Interquartile Range, the remaining represent outliers of the mentioned range.

3.2 Function of traits and strategies of alpine plants across the elevational gradient

LA and SLA exhibit a highly significant negative linear relationship with elevation, LA: (Estimate= -0.0008, $t = -4.51$, $p < 0.001$) and SLA: (Estimate= -0.0006, $t = -3.38$, $p < 0.001$), see Figure 4. In contrast, LDMC exhibits a positive linear relationship with elevation (LDMC: Estimate= 0.0004, $t = 2.49$, $p = 0.01$). Regarding the strategies of C, S and R, each one exhibits a linear relationship with elevation. Both C and R exhibit a negative relationship with elevation, C: (Estimate= -0.0007, $t = -4.36$, $p < 0.001$) and R: (Estimate= -0.0004, $t = -2.56$, $p = 0.01$) while S exhibits a positive relationship with elevation (Estimate= 0.0007, $t = 3.78$, $p < 0.001$).

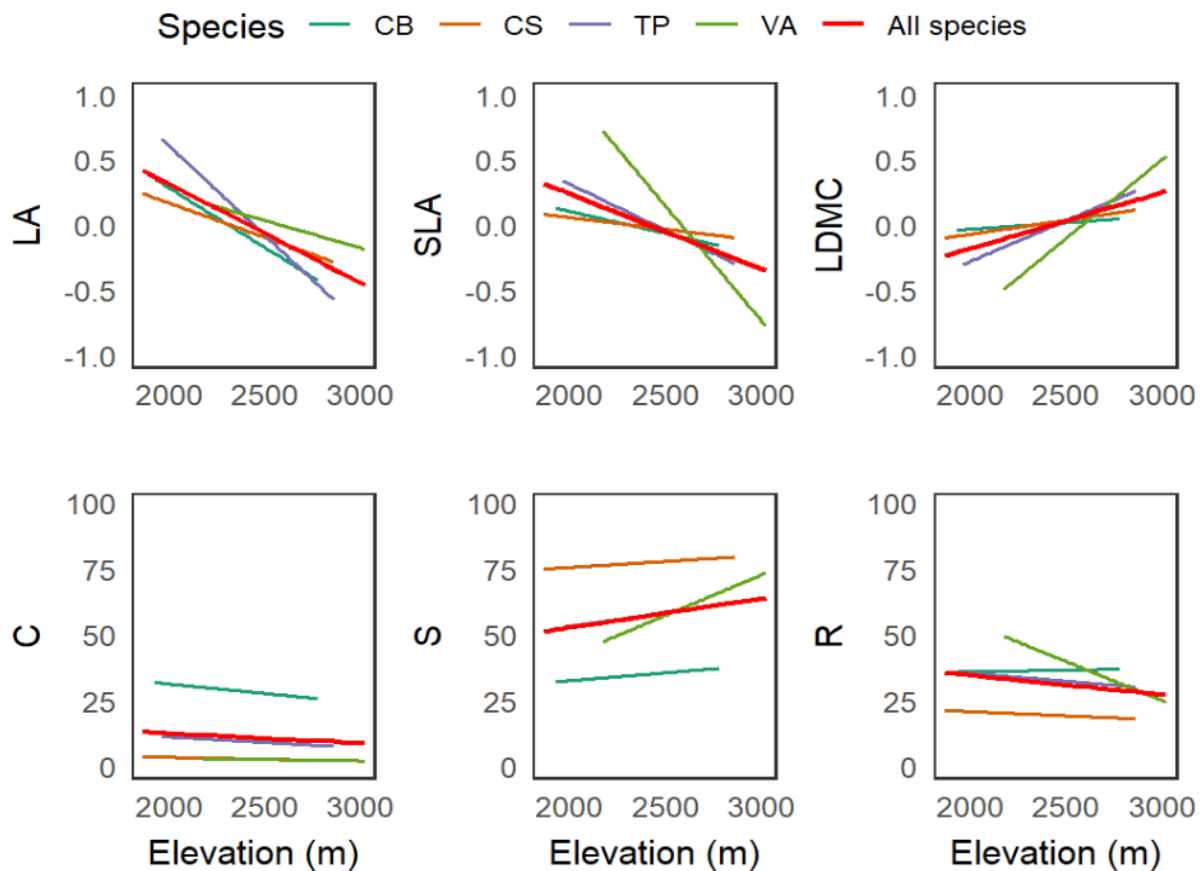


Figure 4: Dependence of focal traits (upper row) and strategies (lower row) on elevation. Here, shown in the first row of graphs are linear functions for the focal traits LA, SLA and LDMC (standardized) of each species (CB= *Campanula barbata* subsp. *barbata*; CS= *Campanula scheuchzeri*; TP= *Trifolium pallescens*; VA= *Veronica alpina*), as well as for all species (red line) across the elevational gradient. Below, the same be can be seen for the focal strategies of C, S and R, although here numeric values ranging from 0-100 have been used in order to enhance understanding.

Table 3 shows the effect sizes of traits and strategies across the elevational gradient for each species.

Table 3: T-values of linear regressions relating traits and strategies of individuals with elevation. Traits and strategies were standardized for each species individually, to compare effect sizes among species. Significant relationships (i.e. |values| > 1.96) are given in bold.

Elevational gradient	LA	SLA	LDMC	C	S	R
<i>Campanula barbata</i> subsp. <i>barbata</i>	-2.56	-0.90	0.27	-2.04	1.00	0.27
<i>Campanula scheuchzeri</i>	-1.61	-0.59	0.65	-1.66	1.19	-0.91
<i>Trifolium pallescens</i>	-4.46	-2.05	1.80	-4.37	2.66	-1.66
<i>Veronica alpina</i>	-0.95	-4.61	2.90	-1.20	3.56	-3.74

3.3 Intraspecific variation of traits and strategies of alpine plants across climatic- and morphometric gradients

T-values of linear regressions relating traits and strategies with additional environmental gradients were extracted and are shown in Table 4. As mean annual temperature increases, C and LA increase. A similar pattern can be observed for the minimum summer temperature - with increasing temperatures, competition and leaf area increase while S decreases significantly, although only borderline. In contrast, with increasing minimum winter temperatures SLA and R decrease while LDMC increases. Instead, focusing on the mean annual temperature range an increase of SLA and R at the cost of LDMC and S can be observed. As snow cover duration increases both leaf area and competition decrease. A clear stress gradient is expressed by Hill Shade (HSD), a proxy for solar radiation. As radiation increases stress tolerance rises, while competition and the ruderal strategy diminish, alongside SLA and LA.

Table 4: T-values of linear mixed effects models for traits and strategies across environmental gradients. Values > 1.96 represent a statistically significant positive relationship ($p > 0.05$) between the trait/strategy and its environmental predictor (bold) whereas statistically significant negative relationships are represented by values < - 1.96 (bold). Remaining values do not exhibit any statistical significance.

	LA	SLA	LDMC	C	S	R
Mean annual temperature	3.60	-1.62	0.86	3.81	-0.58	-0.84
Min. temperature winter	1.12	-4.08	3.04	1.66	1.48	-2.37
Min. temperature summer	4.12	-0.17	0.21	4.12	-1.72	0.46
Annual temperature range	0.61	4.18	-3.78	0.33	-2.57	2.83
Snow cover duration	-4.57	-0.47	1.23	-4.36	1.65	0.01
HSD (Hill Shade)	-3.21	-2.67	0.90	-3.10	3.14	-2.51
TWI (Total Wetness Index)	4.21	-1.34	1.05	4.03	-0.62	-0.79

4. Discussion

The present study examined the intraspecific variation of morphological traits used to calculate Grime's CSR strategies (Pierce et al., 2017a) of four alpine plant species along the elevational gradient on Mt. Schrankogel in Austria. The intraspecific pattern was found to be in line with previous research, which suggests that stress tolerance is the predominant strategy for plants in the alpine realm (Bricca et al., 2022; Grime, 2001; Hasigerili et al., 2023). This was followed by resource investment towards the ruderal strategy, while the competitive strategy played only a negligible role (Callaway et al., 2002), as illustrated in Figure 2. *Veronica alpina* which inhabits snowbeds on siliceous bedrock primarily expresses a combination of stress- and ruderal-related strategies (S/SR, SR), exhibiting increasing stress tolerance and diminishing investment towards the ruderal strategy with rising elevation. A more pronounced stress tolerance can be observed for *Campanula scheuchzeri* and *Trifolium pallescens*, again followed by the ruderal strategy, and lastly competition. Across all study species, competition is most prominent for *Campanula barbata* subsp. *barbata*, although still expressing rather generalist-strategies (SR/CSR, CSR, ...). This highlights the comparatively minor role of competition for the observed alpine plants.

In accordance with the findings of studies conducted on species and community level, the intraspecific adaptations observed across the elevational gradient are evidently consistent with the stress gradient hypothesis (Callaway et al., 2002). This is proven by decreasing investment in competition and the ruderal strategy, alongside leaf area (LA) and specific leaf area (SLA) as elevation rises (Qi et al., 2014; Zhong et al., 2014), while stress tolerance and leaf dry matter content (LDMC) exhibit an increase (Li et al., 2026; Rafiee et al., 2024).

A majority of existing literature documents SLA to be highest at the elevational optima (Maccagni and Willi, 2022; Qi et al., 2014; Rosbakh et al., 2014), commonly associated with high resource assimilation and growth (Pérez-Harguindeguy et al., 2013). This phenomenon aligns with the abundant centre hypothesis, which posits that species exhibit optimal fitness levels at the core of their geographical distribution (Wulff, 1943). Here, values of SLA at the elevational optima, are indifferent to those at high- and low elevations, therefore not indicating increased fitness. SLA at high elevations is the lowest and statistically different solely to individuals at the low-elevational level. Conversely, progressively higher LDMC at high elevations is indicative of thick and dense leaves, which are well-adapted to physical hazards and harsh conditions corresponding to increased stress tolerance at high elevations (Körner, 2021).

Across the gradient of mean annual temperature, the opposite to the elevational gradient can be observed as LA and competition increase while stress tolerance tends to decrease. In context, a more robust pattern for stress tolerance was identified at the community level for 107 alpine plant

species using large-scale temperature variables, which demonstrates a decline in stress tolerance with rising temperatures (Rafiee et al., 2024). Yet again, with rising summer minimum temperatures, plants increasingly invest in large leaf sizes and their competitive strategy while stress tolerance tends to decrease. The former phenomenon can be attributed to the inhibitory effect of low temperatures on meristematic activity and, consequently, plant growth (Li et al., 2026).

From temperature to temperature range - as the mean annual temperature range increases, a rise of SLA and the ruderal strategy, at the expense of LDMC and stress tolerance was observed. Therefore, under an increased degree of temperature variation in the alpine realm, representing repeated disturbance, ruderal individuals undergo a rapid life cycle in order to ensure survival before unfavourable conditions lead to biomass destruction (Pierce et al., 2007). Alternatively, the option of plants modifying their leaf structure towards higher stress tolerance, i.e., to produce structurally dense leaves, is likely to be less successful and therefore less prominent at sites where temperature range is particularly high (Pierce et al., 2017b, 2007).

It is interesting to note that, as the duration of snow cover increases, both leaf area and competition diminish, while stress tolerance tends to increase and the ruderal strategy remains stable. In accordance with rising minimum winter temperatures, likely facilitated by snow cover (Haeberli, 1973), a decrease of SLA and the ruderal strategy can be observed while LDMC increases, similarly to the tendency of S and C. A shift from the ruderal strategy towards stress tolerance through elevated LDMC aligns with previous research, which identified the dominance of low stature plant communities, as is common for stress-adapted specialists, on sites with a late snow melt-out (Jonas et al., 2008).

An additional gradient driving stress tolerance is expressed by Hill Shade (HSD), a proxy for solar radiation. Here, higher solar radiation is associated with elevated stress tolerance, while competition and the ruderal strategy, along with SLA and LA, diminish. This finding aligns with the conclusion of previous research, as Manuel et al. (1999) highlights the importance of stress tolerance for *Geum montanum* as solar radiation poses an increasing stressor towards the mountain summit.

In contrast, as relative soil moisture, in this case referred to as Total Wetness Index (TWI) rises, competitive abilities are favoured, as indicated by the promotion of large leaves and competition. A recent study (Erkelenz et al., 2025) highlighted the effect of elevated water availability, whereby plants exhibit an increased investment in leaf structures and elevated CO₂ assimilation, similar to the here documented increase in LA and the trend of increasing LDMC.

An increasing investment towards large, competitive leaves is in line with the establishment of plants with a higher stature and an increased growth rate within the alpine realm, as under ongoing climate change the above properties are promoted by rising temperatures, increased temperature variability as well as earlier snow melt-out (Buchner et al., 2017; Erkelenz et al., 2025; Jonas et al., 2008; Ohmura, 2012; Steinbauer et al., 2022, 2018). Here, the relation of traits and strategies on an intraspecific level across gradients, identifies the importance of stress tolerance in the alpine realm, although recognizes the environmental drivers of alternative strategies, such as the ruderal strategy and competition, that will likely be promoted under ongoing climate change.

Therefore, the ability of alpine plant specialists to adapt to a changing climate will be decisive in determining community composition and ecosystem dynamics in the future. In this context, research suggests that under cold and harsh conditions, environmental filtering reduces intraspecific trait variation, particularly among high-alpine specialists (Bricca et al., 2022; Kuppler et al., 2020). Conversely, as environmental severity diminishes, communities exhibit elevated intraspecific trait variation as a result of increasing importance of competitive processes (Bricca et al., 2022). In light of ongoing climate change, increased ITV of climatically favoured low-elevation species may be an indication of elevated competitive abilities of upslope shifting species, posing a threat to high-elevation specialists (Rixen et al., 2022), which are typically more stagnant (Rumpf et al., 2018). These findings suggest that species with a lower elevational preference likely possess a greater potential to respond flexibly to environmental changes and to increasing interspecific competition from upslope-shifting species (Alexander et al., 2015; Rixen et al., 2022; Rumpf et al., 2018; Steinbauer et al., 2018).

5. Conclusion

The present study examines the intraspecific variation in CSR strategies (Grime, 2001) of four alpine species along environmental gradients on Mt. Schrankogel, in Austria. The results support the predominance of the stress tolerance strategy (S) in the alpine environment and align with evidence at intra- and interspecific as well as community levels (Bricca et al., 2022; Li et al., 2026; Rafiee et al., 2024). The increasing relevance of stress tolerance towards the mountain summit as well as the less prominent role of the ruderal strategy (R) and competition (C) in the alpine realm, further diminishing with increasing elevation (Callaway et al., 2002) aligns with the stress-gradient hypothesis. Overall, high intraspecific variation of traits (LA, SLA, LDMC) and strategies of alpine plants across numerous gradients was identified, calling for greater consideration of intraspecific variation in ecological studies, since most of past research on plant functional traits has been conducted on an interspecific or community level, neglecting variation within species. In instances, where intraspecific variation was accounted for, oftentimes a mean value of trait-database entries has been utilized, disregarding the effect of a plants' biotic and abiotic environment on trait expression, similarly highlighted by other researchers (Bricca et al., 2022; Hasigerili et al., 2023; Keddy, 1992; Siefert et al., 2015). However, disregarding the impact of environmental factors on trait expression may obscure the role of intraspecific variation, which is crucial for understanding species distributions and community assembly under a changing climate, as high intraspecific trait variation enhances the ability to respond flexibly to environmental change (Rixen et al., 2022). Consequently, future research should explicitly account for intraspecific trait variation in order to refine predictions of plant responses and improve conservation efforts under ongoing climate change.

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References

- Alexander, J.M., Diez, J.M., Levine, J.M., 2015. Novel competitors shape species' responses to climate change. *Nature* 525, 515–518. <https://doi.org/10.1038/nature14952>
- Anten, N.P.R., 2004. Optimal Photosynthetic Characteristics of Individual Plants in Vegetation Stands and Implications for Species Coexistence. *Annals of Botany* 95, 495–506. <https://doi.org/10.1093/aob/mci048>
- Beniston, M., Farinotti, D., Stoffel, M., Andreassen, L.M., Coppola, E., Eckert, N., Fantini, A., Giacona, F., Hauck, C., Huss, M., Huwald, H., Lehning, M., López-Moreno, J.-I., Magnusson, J., Marty, C., Morán-Tejeda, E., Morin, S., Naaim, M., Provenzale, A., Rabatel, A., Six, D., Stötter, J., Strasser, U., Terzago, S., Vincent, C., 2018. The European mountain cryosphere: a review of its current state, trends, and future challenges. *The Cryosphere* 12, 759–794. <https://doi.org/10.5194/tc-12-759-2018>
- Breiman, L., 2001. Random Forests. *Machine Learning* 45, 5–32. <https://doi.org/10.1023/A:1010933404324>
- Bricca, A., Musciano, M.D., Ferrara, A., Theurillat, J.-P., Cutini, M., 2022. Community assembly along climatic gradient: Contrasting pattern between- and within- species. *Perspectives in Plant Ecology, Evolution and Systematics* 56, 125675. <https://doi.org/10.1016/j.ppees.2022.125675>
- Buchner, O., Roach, T., Gertzen, J., Schenk, S., Karadar, M., Stöggli, W., Miller, R., Bertel, C., Neuner, G., Kranner, I., 2017. Drought affects the heat-hardening capacity of alpine plants as indicated by changes in xanthophyll cycle pigments, singlet oxygen scavenging, α -tocopherol and plant hormones. *Environmental and Experimental Botany* 133, 159–175. <https://doi.org/10.1016/j.envexpbot.2016.10.010>
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848. <https://doi.org/10.1038/nature00812>
- Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P.W., Trisos, C., Romero, J., Aldunce, P., Barrett, K., Blanco, G., Cheung, W.W.L., Connors, S., Denton, F., Diongue-Niang, A., Dodman, D., Garschagen, M., Geden, O., Hayward, B., Jones, C., Jotzo, F., Krug, T., Lasco, R., Lee, Y.-Y., Masson-Delmotte, V., Meinshausen, M., Mintenbeck, K., Mokssit, A., Otto, F.E.L., Pathak, M., Pirani, A., Poloczanska, E., Pörtner, H.-O., Revi, A., Roberts, D.C., Roy, J., Ruane, A.C., Skea, J., Shukla, P.R., Slade, R., Slangen, A., Sokona, Y., Sörensson, A.A., Tignor, M., Van Vuuren, D., Wei, Y.-M., Winkler, H., Zhai, P., Zommers, Z., Hourcade, J.-C., Johnson, F.X., Pachauri, S., Simpson, N.P., Singh, C., Thomas, A., Totin, E., Arias, P., Bustamante, M., Elgizouli, I., Flato, G., Howden, M., Méndez-Vallejo, C., Pereira, J.J., Pichs-Madruga, R., Rose, S.K., Saheb, Y., Sánchez Rodríguez, R., Ürge-Vorsatz, D., Xiao, C., Yassaa, N., Alegría, A., Armour, K., Bednar-Friedl, B., Blok, K., Cissé, G., Dentener, F., Eriksen, S., Fischer, E., Garner, G., Guivarch, C., Haasnoot, M., Hansen, G., Hauser, M., Hawkins, E., Hermans, T., Kopp, R., Leprince-Ringuet, N., Lewis, J., Ley, D., Ludden, C., Niamir, L., Nicholls, Z., Some, S., Szopa, S., Trewin, B., Van Der Wijst, K.-I., Winter, G., Witting, M., Birt, A., Ha, M., Romero, J., Kim, J., Haites, E.F., Jung, Y., Stavins, R., Birt, A., Ha, M., Orendain, D.J.A., Ignon, L., Park, S., Park, Y., Reisinger, A., Cammaramo, D., Fischlin, A., Fuglestedt, J.S., Hansen, G., Ludden, C., Masson-Delmotte, V., Matthews, J.B.R., Mintenbeck, K., Pirani, A., Poloczanska, E., Leprince-Ringuet, N., Péan, C., 2023. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland. Intergovernmental Panel on Climate Change (IPCC). <https://doi.org/10.59327/IPCC/AR6-9789291691647>

- Cannone, N., Pignatti, S., 2014. Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? *Climatic Change* 123, 201–214. <https://doi.org/10.1007/s10584-014-1065-8>
- Chytrý, K., Helm, N., Hülber, K., Moser, D., Wessely, J., Hausharter, J., Kollert, A., Mayr, A., Rutzinger, M., Winkler, M., Pauli, H., Saccone, P., Paetzolt, M., Hietz, P., Dullinger, S., 2024. Limited impact of microtopography on alpine plant distribution. *Ecography* 2024, e06744. <https://doi.org/10.1111/ecog.06744>
- Cutini, M., Flavio, M., Giuliana, B., Guido, R., Jean-Paul, T., 2021. Bioclimatic pattern in a Mediterranean mountain area: assessment from a classification approach on a regional scale. *Int J Biometeorol* 65, 1085–1097. <https://doi.org/10.1007/s00484-021-02089-x>
- Erkelenz, J., Geange, S.R., Atkinson, J., Anderson, E., Correia, M., Ahler, S.J., Bradler, P., Löwenstein, C.E., Elsy, A., Maré, C., Eshelman, S., Mauki, D., Guclu, C., Eckberg, J., Maitner, B., Gya, R., Töpfer, J., Klanderud, K., Enquist, B.J., Michaletz, S.T., Ray, C.A., Von Oppen, J., Cubino, J.P., Halbritter, A.H., Vandvik, V., 2025. Intraspecific Functional Trait Responses to Experimental Warming Vary With Precipitation and Growth Form. *J Vegetation Science* 36, e70098. <https://doi.org/10.1111/jvs.70098>
- Gottfried, M., Pauli, H., Grabherr, G., 1998. Prediction of Vegetation Patterns at the Limits of Plant Life: A New View of the Alpine-Nival Ecotone. *Arctic and Alpine Research* 30, 207. <https://doi.org/10.2307/1551968>
- Grime, J.P., 2001. Plant strategies, vegetation processes, and ecosystem properties, 2nd ed. ed. Wiley, Chichester, West sussex ; New York, NY.
- Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Data Sources for the Autecological Accounts, in: *Comparative Plant Ecology*. Springer Netherlands, Dordrecht, pp. 7–19. https://doi.org/10.1007/978-94-017-1094-7_2
- Haeberli, W., 1973. Die Basis-Temperatur der winterlichen Schneedecke als möglicher Indikator für die Verbreitung von Permafrost in den Alpen. *Zeitschrift für Gletscherkunde und Glazialgeologie* 9, 221–227.
- Hasigerili, Guo, K., Zheng, M.-M., Liu, R.-L., Wang, Y.-Y., Gao, Y., Shu, L., Wang, X.-R., Zhang, J., Guo, W.-Y., 2023. Intraspecific variations of adaptive strategies of native and invasive plant species along an elevational gradient. *Flora* 304, 152297. <https://doi.org/10.1016/j.flora.2023.152297>
- Henn, J.J., Damschen, E.I., 2021. Plant age affects intraspecific variation in functional traits. *Plant Ecol* 222, 669–680. <https://doi.org/10.1007/s11258-021-01136-2>
- Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P., Thompson, K., 1999. Allocating C-S-R Plant Functional Types: A Soft Approach to a Hard Problem. *Oikos* 85, 282. <https://doi.org/10.2307/3546494>
- Hoinkes, G., Krainer, K., Tropper, P., 2021. Ötztaler Alpen, Stubai Alpen und Texelgruppe, Sammlung geologischer Führer. Borntraeger, Stuttgart.
- Horn, B.K.P., 1981. Hill shading and the reflectance map. *Proc. IEEE* 69, 14–47. <https://doi.org/10.1109/PROC.1981.11918>
- ImageJ Wiki [WWW Document], n.d. . ImageJ Wiki. URL <https://imagej.github.io/> (accessed 1.23.26).
- Jonas, T., Rixen, C., Sturm, M., Stoeckli, V., 2008. How alpine plant growth is linked to snow cover and climate variability. *J. Geophys. Res.* 113, 2007JG000680. <https://doi.org/10.1029/2007JG000680>
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin lii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A.,

- Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J. -F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY – a global database of plant traits. *Global Change Biology* 17, 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. *J Vegetation Science* 3, 157–164. <https://doi.org/10.2307/3235676>
- Kollert, A., Chytrý, K., Helm, N., Hülber, K., Moser, D., Wessely, J., Lhermitte, S., Gascoin, S., Mayr, A., Saccone, P., Hausharter, J., Warscher, M., Strasser, U., Dullinger, S., Rutzinger, M., 2026. Does meter-scale snow data matter for modeling alpine plant distribution? A comparison of four data sources at two resolutions. *Ecological Modelling* 511, 111366. <https://doi.org/10.1016/j.ecolmodel.2025.111366>
- Körner, C., 2023. Concepts in Alpine Plant Ecology. *Plants* 12, 2666. <https://doi.org/10.3390/plants12142666>
- Körner, C., 2021. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer International Publishing, Cham. <https://doi.org/10.1007/978-3-030-59538-8>
- Kulonen, A., Imboden, R.A., Rixen, C., Maier, S.B., Wipf, S., 2018. Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Diversity and Distributions* 24, 252–261. <https://doi.org/10.1111/ddi.12673>
- Kuppler, J., Albert, C.H., Ames, G.M., Armbruster, W.S., Boenisch, G., Boucher, F.C., Campbell, D.R., Carneiro, L.T., Chacón-Madrigal, E., Enquist, B.J., Fonseca, C.R., Gómez, J.M., Guisan, A., Higuchi, P., Karger, D.N., Kattge, J., Kleyer, M., Kraft, N.J.B., Larue-Kontić, A.C., Lázaro, A., Lechleitner, M., Loughnan, D., Minden, V., Niinemets, Ü., Overbeck, G.E., Parachnowitsch, A.L., Perfectti, F., Pillar, V.D., Schellenberger Costa, D., Sletvold, N., Stang, M., Alves-dos-Santos, I., Streit, H., Wright, J., Zych, M., Junker, R.R., 2020. Global gradients in intraspecific variation in vegetative and floral traits are partially associated with climate and species richness. *Global Ecol Biogeogr* 29, 992–1007. <https://doi.org/10.1111/geb.13077>
- Lamprecht, A., Semenchuk, P.R., Steinbauer, K., Winkler, M., Pauli, H., 2018. Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytologist* 220, 447–459. <https://doi.org/10.1111/nph.15290>
- Li, J., Yang, J., Li, S., Xu, X., Li, X., 2026. Adaptive leaf functional traits and CSR strategies along an environmental gradient on the eastern slope of the Helan Mountains. *Plant Ecol* 227, 13. <https://doi.org/10.1007/s11258-025-01572-4>
- Maccagni, A., Willi, Y., 2022. Trait divergence and trade-offs among Brassicaceae species differing in elevational distribution. *Evolution* 76, 1986–2003. <https://doi.org/10.1111/evo.14554>
- Ohmura, A., 2012. Enhanced temperature variability in high-altitude climate change. *Theor Appl Climatol* 110, 499–508. <https://doi.org/10.1007/s00704-012-0687-x>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., De Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen,

- J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167. <https://doi.org/10.1071/BT12225>
- Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R.M., Cerabolini, B., 2007. Disturbance is the principal α -scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology* 95, 698–706. <https://doi.org/10.1111/j.1365-2745.2007.01242.x>
- Pierce, S., Negreiros, D., Cerabolini, B., Kattge, J., Diaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia, N., Onipchenko, V., Bodegom, P., Frenette Dussault, C., Weiher, E., Pinho, B., Cornelissen, J., Grime, J., Thompson, K., Hunt, R., Wilson, P., Tampucci, D., 2017a. StrateFy - The global vascular plant CSR strategy calculator - Pierce et al 2017 *Functional Ecology*.
- Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia, N.A., Onipchenko, V.G., Van Bodegom, P.M., Frenette-Dussault, C., Weiher, E., Pinho, B.X., Cornelissen, J.H.C., Grime, J.P., Thompson, K., Hunt, R., Wilson, P.J., Buffa, G., Nyakunga, O.C., Reich, P.B., Caccianiga, M., Mangili, F., Ceriani, R.M., Luzzaro, A., Brusa, G., Siefert, A., Barbosa, N.P.U., Chapin, F.S., Cornwell, W.K., Fang, J., Fernandes, G.W., Garnier, E., Le Stradic, S., Peñuelas, J., Melo, F.P.L., Slaviero, A., Tabarelli, M., Tampucci, D., 2017b. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* 31, 444–457. <https://doi.org/10.1111/1365-2435.12722>
- Qi, W., Bu, H., Liu, K., Li, Wenjin, Knops, J.M.H., Wang, J., Li, Wenlong, Du, G., 2014. Biological traits are correlated with elevational distribution range of eastern Tibetan herbaceous species. *Plant Ecol* 215, 1187–1198. <https://doi.org/10.1007/s11258-014-0377-0>
- R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rafiee, F., Ejtehadi, H., Farzam, M., Behroozian, M., 2024. Variation in CSR plant strategies along soil and climate gradients: A comparison between rocky outcrops and nearby rangelands. *J Vegetation Science* 35, e13311. <https://doi.org/10.1111/jvs.13311>
- Reich, P.B., 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102, 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Rixen, C., Wipf, S., Rumpf, S.B., Giejsztowt, J., Millen, J., Morgan, J.W., Nicotra, A.B., Venn, S., Zong, S., Dickinson, K.J.M., Freschet, G.T., Kurzböck, C., Li, J., Pan, H., Pfund, B., Quaglia, E., Su, X., Wang, W., Wang, X., Yin, H., Deslippe, J.R., 2022. Intraspecific trait variation in alpine plants relates to their elevational distribution. *Journal of Ecology* 110, 860–875. <https://doi.org/10.1111/1365-2745.13848>
- Rosbakh, S., Bernhardt-Römermann, M., Poschlod, P., 2014. Elevation matters: contrasting effects of climate change on the vegetation development at different elevations in the Bavarian Alps. *Alp Botany* 124, 143–154. <https://doi.org/10.1007/s00035-014-0139-6>
- Rosbakh, S., Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I., Poschlod, P., 2017. Contrasting Effects of Extreme Drought and Snowmelt Patterns on Mountain Plants along an Elevation Gradient. *Front. Plant Sci.* 8, 1478. <https://doi.org/10.3389/fpls.2017.01478>
- Rumpf, S.B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N.E., Dullinger, S., 2018. Range dynamics of mountain plants decrease with elevation. *Proc. Natl. Acad. Sci. U.S.A.* 115, 1848–1853. <https://doi.org/10.1073/pnas.1713936115>
- Rumpf, S.B., Hülber, K., Wessely, J., Willner, W., Moser, D., Gattringer, A., Klonner, G., Zimmermann, N.E., Dullinger, S., 2019. Extinction debts and colonization credits of non-forest plants in the European Alps. *Nat Commun* 10, 4293. <https://doi.org/10.1038/s41467-019-12343-x>
- Sherwood, S., Fu, Q., 2014. A Drier Future? *Science* 343, 737–739. <https://doi.org/10.1126/science.1247620>
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M.V., De L. Dantas, V., De Bello, F., Duarte,

- L.D.S., Fonseca, C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama, C., Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerström, A., Bagousse-Pinguet, Y.L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.McC., Peltzer, D.A., Pérez-Ramos, I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schöb, C., Shipley, B., Sundqvist, M., Sykes, M.T., Vandewalle, M., Wardle, D.A., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18, 1406–1419. <https://doi.org/10.1111/ele.12508>
- Steinbauer, K., Lamprecht, A., Winkler, M., Di Cecco, V., Fasching, V., Ghosn, D., Maringer, A., Remoundou, I., Suen, M., Stanisci, A., Venn, S., Pauli, H., 2022. Recent changes in high-mountain plant community functional composition in contrasting climate regimes. *Science of The Total Environment* 829, 154541. <https://doi.org/10.1016/j.scitotenv.2022.154541>
- Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A.D., Breiner, F.T., Burg, S., Czortek, P., Dawes, M.A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V.A., Fernández-Arberas, O., Fossheim, K.F., Gómez-García, D., Georges, D., Grindrud, E.T., Haider, S., Haugum, S.V., Henriksen, H., Herreros, M.J., Jaroszewicz, B., Jaroszynska, F., Kanka, R., Kapfer, J., Klanderud, K., Kühn, I., Lamprecht, A., Matteodo, M., Di Cella, U.M., Normand, S., Odland, A., Olsen, S.L., Palacio, S., Petey, M., Piscová, V., Sedlakova, B., Steinbauer, K., Stöckli, V., Svenning, J.-C., Teppa, G., Theurillat, J.-P., Vittoz, P., Woodin, S.J., Zimmermann, N.E., Wipf, S., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556, 231–234. <https://doi.org/10.1038/s41586-018-0005-6>
- Violle, C., Jiang, L., 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology* 2, 87–93. <https://doi.org/10.1093/jpe/rtp007>
- Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Wetterprognose Österreich, 2024. URL <https://www.geosphere.at/de> (accessed 1.25.26).
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827. <https://doi.org/10.1038/nature02403>
- Wulff, E.V., 1943. An introduction to historical plant geography. www.foto-webcam.eu, F.R./ G.K., n.d. Wannenkogel - Blick zum Schrankogel - Foto-Webcam.eu. URL <https://www.foto-webcam.eu/webcam/wannenkogel/2025/07/12/1230> (accessed 1.23.26).
- Zhong, M., Wang, J., Liu, K., Wu, R., Liu, Y., Wei, X., Pan, D., Shao, X., 2014. Leaf Morphology Shift of Three Dominant Species along Altitudinal Gradient in an Alpine Meadow of the Qinghai-Tibetan Plateau. *Polish Journal of Ecology* 62, 639–648. <https://doi.org/10.3161/104.062.0409>