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Community-weighted C, S and R values vary along the main environmental gradients in an alpine landscape (Mt. Schrankogel): temperature, snow melt-out, soil carbon and water holding capacity

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Abstract

Alpine vegetation is generally considered to be adapted to stressful conditions. However, environmental differences are pronounced within alpine landscapes and microscale conditions can be much more favourable to plant life than air temperature suggests. However, whether and to which degree this variability shapes the distribution of plant life-history strategies in an alpine landscape has hardly been explored so far. In my thesis, I used the CSR (competitor, stress-tolerator, ruderal) ecological strategy model of plant species as a framework to explore the possible relationship between environmental variability and predominant life-history strategies in the alpine landscape of Mt. Schrankogel in Tyrol, Austria. I especially tested which of the strategy types dominates in the study area, how strong the variation of strategy types is and whether this variation is related to gradients of temperature, snow melt and soil conditions. I therefore collated data on three leaf traits for 235 species found to grow across 885 vegetation plots in the forest-free subalpine to nival belts of this mountain. From these traits I computed C, S and R values for each species as well as community-weighted C, S and R values for each plot and correlated these values to gradients of mean annual temperature, length of snow cover, soil carbon content as well as soil water holding capacity. I found a clear dominance of the stress tolerator strategy across species and even more across community-weighted plot values. However, there was still considerable variation in these community-weighted values, and this variation was significantly correlated with environmental gradients. A strong significance was shown between each predictor (environmental variables) and the community-weighted mean of CSR composition. The results show that stress is the predominant filter of the alpine plant metacommunity and the most important driver of alpine plant community assembly. However, there was some variation along the main environmental gradients. In particular, the contribution of S-values increased with increasing temperature, shorter snow cover duration, higher carbon content and higher water holding capacity. The contribution of R-values increased with decreasing temperature, longer snow cover duration, lower carbon content and lower water holding capacity. The contribution of C-values increased with warmer temperature, shorter snow cover duration, higher carbon content and higher water holding capacity. My results hence suggest that considerable, environmentally driven variation in life-history strategies and associated plant traits is already realized in current alpine landscapes. As a corollary, changes of mean trait values and resulting ecosystem properties and functions could become realized relatively quickly when climate change proceeds as predicted.

Zusammenfassung

Alpine Vegetation gilt generell als an stressreiche Umweltbedingungen angepasst. Allerdings sind die Umweltbedingungen innerhalb alpiner Landschaften stark heterogen und mikroklimatische Bedingungen können für Pflanzen mehr von Vorteil sein, als die Lufttemperatur vermuten lässt. Ob und zu welchem Grad diese Variabilität die Verteilung pflanzlicher Lebensstrategien in alpinen Landschaften beeinflusst, wurde bisher jedoch kaum erforscht. In meiner Arbeit verwende ich das CSR–Modell (Konkurrenz (C), Stresstoleranz (S) und Ruderalität (R)) ökologischer Strategien von Pflanzenarten als konzeptionellen Rahmen, um mögliche Zusammenhänge zwischen Umweltvariabilität und dominierenden Lebensstrategien in der alpinen Landschaft des Schrankogels in Tirol, Österreich, zu untersuchen. Ich untersuchte insbesondere, welcher der Strategietypen im Untersuchungsgebiet dominiert, wie stark die Variation der Strategietypen ist und ob diese Variation mit den Umweltgradienten von Temperatur, Schneeschmelze und Bodenbedingungen zusammenhängt. Dafür wurden Blattmerkmale von 235 Arten, die auf 885 Versuchsflächen innerhalb der waldfreien subalpinen bis nivalen Zone dieses Berges vorkommen erworben. Aus diesen Merkmalen berechnete ich die C, S und R Werte für jede Art sowie gemeinschaftsgewichtete C, S und R Werte für jede Versuchsfläche und korrelierte diese Werte mit Gradienten der mittleren Jahrestemperatur, der Dauer der Schneebedeckung, des Kohlenstoffgehalt der Böden sowie deren Wasserhaltekapazität. Es ließ sich eine klare Dominanz des stresstoleranten Strategietyps über alle Arten hinweg und noch stärker innerhalb der Werte der gemeinschaftsgewichteten Versuchsflächen erkennen. Dennoch zeigte sich eine erhebliche Variation innerhalb der gewichteten Werte, und diese Variation korrelierte signifikant mit den Umweltgradienten. Zwischen jedem Prädiktor (Umweltvariable) und den gemeinschaftsgewichteten Mitteln der CSR-Zusammensetzung bestand ein hochsignifikanter Zusammenhang. Die Ergebnisse zeigen, dass Stress der vorherrschende Filter der alpinen Pflanzen-Metagemeinschaft und der wichtigste Treiber der Zusammensetzung alpiner Pflanzengemeinschaften ist. Es besteht jedoch eine gewisse Variation entlang der Umweltgradienten. Insbesondere nahm der Anteil an S-Werten mit zunehmender Temperatur, kürzerer Schneebedeckung, höherem Kohlenstoffgehalt und höherer Wasserhaltekapazität zu. Der Anteil an R-Werten nahm mit abnehmender Temperatur, längerer Schneebedeckung, niedrigem Kohlenstoffgehalt und niedriger Wasserhaltekapazität zu. Der Anteil der C-Werte stieg mit zunehmender Temperatur, kürzerer Schneebedeckung, höherem Kohlenstoffgehalt und höherer Wasserhaltekapazität. Meine Ergebnisse legen nahe, dass eine beträchtliche

umweltgetriebene Variation von Lebensstrategien und den damit verbundenen Pflanzenmerkmalen bereits in derzeitigen alpinen Landschaften realisiert ist. Daraus folgt, dass Veränderungen der mittleren Merkmalswerte und resultierenden Ökosystemeigenschaften und -funktionen relativ schnell eintreten können, wenn der Klimawandel wie prognostiziert voranschreitet.

Introduction

As climatic conditions above the treeline are characterized by cold temperatures and short growing seasons the ability to cope with climatic stress is often assumed to be key for plants in order to colonize these ecosystems (Körner, 2021; Pauli et al., 2014). However, the alpine landscape is characterized by a particularly rugged terrain, and this topographic heterogeneity, together with the lack of a forest cover, drives strong variation in local microclimates (Scherrer & Körner, 2010). In particular, the decoupling of air temperature from the thermal conditions near the ground can result in climatic conditions much more favourable than elevation-dependent free-air temperature would suggest (Geiger et al., 2009; Lembrechts et al., 2020). The rugged terrain also affects other processes relevant to vegetation in alpine landscapes such as (1) the ablation or accumulation of snow in convex and concave parts of the relief, which drive huge variation in growing season length as well as protection of meristems from winter frost (Good et al., 2019); and, (2) the intensity and frequency of disturbance, the ablation, accumulation and mobility of erosion material such as scree, and thus the formation of soils as well as their capacity to store and provide nutrients and water to plants (Randin et al., 2009; Yu et al., 2022). As a consequence, the above-treeline habitat may be called stressful when compared to nearby lowland environments on a coarse scale, but its internal variability is pronounced, possibly allowing species with very different adaptations to coexist within one alpine landscape.

The CSR model of plant strategies is a widely known theory that summarizes different major ways in which plant species can adapt to selection pressures in different environments and which co-determine the structure and dynamics of vascular plant communities and ecosystems (Grime, 1988; Pierce et al., 2017). The model suggests three main types of ecological strategies: competitors (C), stress tolerators (S) and ruderals (R) (Araujo Da Costa et al., 2020; Grime, 1988; Pierce et al., 2017). Competitors include species that successfully thrive in productive environments with abundant resources, where stress and disturbance play a minor role (Grime, 2001; Ricotta et al., 2023). They invest in the rapid growth of their biomass, allowing them to outcompete their neighbouring plants (Grime, 2001). Stress tolerators persist in stable habitats that are characterised by environmental stress and resource limitation by producing long-lived tissue (Araujo Da Costa et al., 2020; Grime, 2001). Ruderals have a short live cycle and are able to colonize areas that experience frequent disturbance (biomass destruction and removal

e.g. by erosion or herbivory) by investing in their reproductive organs and regeneration (Grime, 2001; Pierce et al., 2017).

The different strategies manifest themselves in syndromes of functional traits which are themselves linked to resource-use strategies (Escobedo et al., 2023), such as those associated to the 'plant-economic spectrum', a concept that describes the trade-off between resource acquisition and conservation (Díaz et al., 2016; Guo et al., 2018; Wright et al., 2004). It is hence possible to assign species to the different strategy types on the basis of syndromes of trait values. The most elaborate linkage of this kind has been provided by Pierce et al. (2017), who quantitatively assign species to CSR strategy types based on their values of three leaf traits: leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA). LA is linked to plant size and light interception (Díaz et al., 2016) which positively correlates with biomass production (Portes & Melo, 2014). LDMC, calculated by the ratio of leaf dry mass and leaf fresh mass, is a measure of the density of a leaf. High LDMC refers to tough leaves that can withstand environmental stressors and herbivory. SLA, a trait that positively correlates to relative growth rate (Pierce et al., 2013), is calculated by the ratio of leaf area and leaf dry mass and captures the trade off between rapid resource acquisition (high SLA) and conservative investment (low SLA) (Cornelissen et al., 2003). These traits are among those available for the largest number of plant species in the global plant functional trait data base TRY (Kattge et al., 2020). Although, they do not represent the CSR-strategy types directly they provide a way to estimate the values of individual species with respect to the three strategy types (Zanzottera et al., 2020). In general, species that score highly with respect to C have a higher SLA and large LA, whereas those scoring high with respect to S show conservative trait syndromes characterised by lower SLA and a higher LDMC (Yu et al., 2022). Ruderals, finally, i.e. those which score high for the R type tend to have, similar to C strategists, a high SLA and an intermediate to low LDMC, yet their LA tends to be low (Pierce et al., 2017).

Given that alpine habitats are considered stressful for plant species on account of their low temperatures and short growing season the expectation would hence be that these species generally score high for the S strategy, i.e. generally have low SLA and a high LDMC. However, the above-described gradients of microclimate, snow cover and disturbance may drive a species turn-over within alpine ecosystems that is also associated with a change in prevailing plant strategies. Put differently, while the average alpine species may exhibit a typical S strategy profile, there might nevertheless be considerable variation in predominant strategies among species, with repercussions on the distribution of them within the alpine habitat mosaic. This

has broader implications for ecosystems under climate change as shifts along these gradients, e.g. by warming or decreased snow cover duration, may consequently lead to shifts in strategy types with consequences for ecosystem functions and properties (Yu et al., 2022). However, to which degree such a turn-over actually exists, and how prevalent plant strategies are actually distributed across an alpine landscape has rarely been assessed so far. One of the few attempts recently found considerable variation of plant strategies in alpine grasslands of the large Tibetean plateau (Yu et al., 2022), but whether this variability is also detectable at much smaller scales within the micro-environmental mosaic of a single mountain landscape remains unexplored.

The aim of this thesis is to assess how environmental gradients affect the distribution of CSR-strategies on Mt. Schrankogel, a ca. 3.5 km²-alpine landscape in Tyrol, Austria. CSR values were calculated with the "StrateFy" calibration tool (Pierce et al., 2017) using the leaf traits LA, SLA and LDMC of ca. 250 species that grow across 900 sampling plots in this landscape. I moreover computed community-weighted mean (CWM) values of C, S and R for these 900 plots and analysed if and how these CWM values vary along gradients of soil temperature, snow cover and soil conditions. Based on the assumption that alpine regions are generally stressful environments for plants (Grime, 2001; Körner, 2021; Liu et al., 2025), I assumed that S strategies dominate on both the species and community level on Mt. Schrankogel. However, following the above considerations, I hypothesized that there will be considerable variation within species and communities, and that this variation will not be randomly distributed in the landscape. In particular I expected (1) to see S values declining and C values increasing with increasing temperature, either along the elevational or along microclimatic gradients (Scherrer & Körner, 2010); however, as the subnival and nival parts of the study site on Mt. Schrankogel are characterised by large scree fields which, at least in part, are a highly disturbed environments, I also expected (2) that the contribution of R strategists will also increase at higher elevations. Furthermore, (3) I hypothesized that a prolonged snow cover duration will lead to an increasing share of R selected species because of a shortened vegetation period which requires a rapid life cycle typical for ruderal species. Finally, temperature is not the only constraint on alpine plant life. Individual microsites might also be strongly exposed to solar radiation while shallow soils constrain water storage, and nutrient availability is often also very low on such shallow sites. Indeed, both nitrogen content and soil water holding capacity have been shown to be significant predictors of alpine plant distribution (Buri et al., 2020; Cianfrani et al., 2019; Dubuis et al., 2013). I therefore also expected (4) to see a shift towards S strategies along the gradient of decreasing soil nutrient and water availability.

Material and Methods

Sampling site and vegetation data

The study was carried out in the Austrian Alps on Mt. Schrankogel (3,497 m a.s.l., N47°02’39.1”, E11°05’56.0”) in the western part of the Stubaier Alps, Tyrol. The geological substrate is mainly composed of silicate rocks such as amphibolite and gneiss (Hoinkes et al., 2021). With its easily accessible elevational zones due to no glacier barriers, Mt. Schrankogel is an ideal mountain for botanical field work (Pauli et al., 2014). Therefore, it is the study site for the Microclim project (https://www.mountainresearch.at/microclim/), which provided the data used in this thesis. The study area covers approximately 3.5 km², within which 900 plots (1 × 1 m) were established during the summers of 2021 and 2022. The plots are located across the non-forest subalpine, alpine, and nival zones of Mt. Schrankogel, ranging in elevation from 1.794 m a.s.l. to 3.497 m a.s.l. (Chytrý et al., 2024). Plot locations were selected using a stratified random sampling design that accounted for major environmental gradients, including elevation, slope, topographic position index, potential incoming solar radiation, and normalized difference vegetation index (NDVI) derived from high-resolution Digital Terrain Model (DTM) and Sentinel-2 data (Chytrý et al., 2024; Helm et al., 2024). Within each plot, species composition of all vascular plants and their cover were recorded using a modified Braun-Blanquet cover-abundance scheme (r:0.1%, +:0.5%, 1:3%, 2a:10%, 2b:20%, 3:37.5%, 4:62.5%, 5:87.5%) (Braun-Blanquet, J, 1964). In addition, at each plot a temperature logger was installed at a soil depth of 10 cm, recording soil temperature hourly over a three-year period (2021–2024). Furthermore, snow melt-out was determined using webcam photos taken of Mt. Schrankogel every half hour and the number of snow-free days per year was derived therefrom (c.f. Kollert et al., 2026).

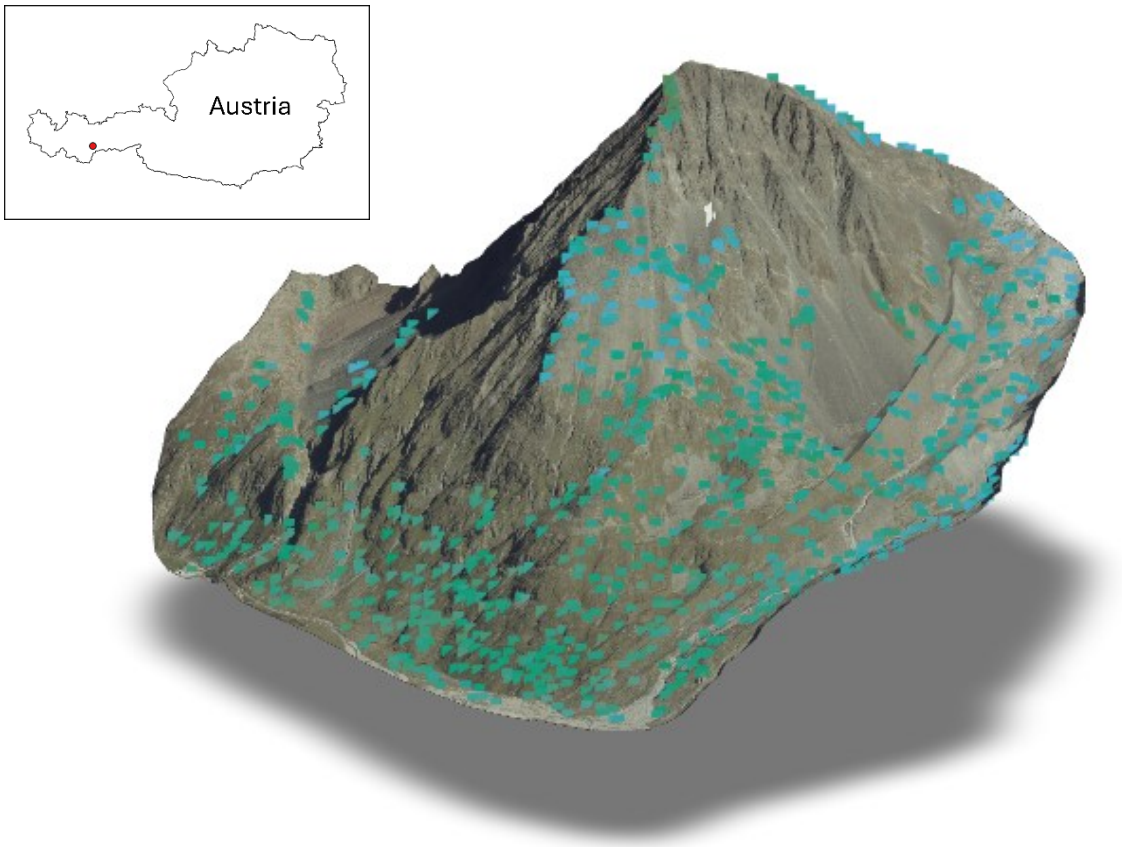

Fig. 1: Locations of the sampling plots across the study site Mt. Schrankogel. The figure shows a single perspective of the 3D model of the the mountain, therefore only plots visible from this viewing angle are depicted.

Soil analysis

Soil samples of every plot were collected over the time span of two years (2022, 2023). The samples were analysed in the laboratory, where soil carbon and soil nitrogen were determined. The oven dried soil was run through the LECO TrueSpec Micro CHN (LECO, 2022). There soil carbon and soil nitrogen were measured, both quantified in parts per million and percentage. The water holding capacity (WHC) for each plot was modelled using Soil Depth (cm), Organic Layer Depth (cm) and Carbon (%). This work was carried out in 2023 (Eden, 2024).

Trait Data

For a total of 252 species the functional leaf traits leaf area (LA; mm^2), specific leaf area (SLA; mm2 mg-1) and leaf dry matter content (LDMC; %) were requested from the TRY global trait data base (https://www.try-db.org; (Kattge et al., 2011)). As stated in Pierce et al. (2017), using three traits is sufficient for the calculation of the survival strategy type of species. Taking more functional traits into consideration does not substantially change the CSR values that are

derived through them. Collectively 47964 values were obtained, 16845 for LA, 12571 for SLA, and 18563 for LDMC. The names of the individual plant species were checked and adjusted to the Euro+Med database nomenclature (emplantbase.org). In order to obtain a single value for each trait of each species, the mean of available measurements was calculated. For species with a coefficient of variation (CV) above 0.9, trait values outside species specific plausible ranges were excluded from analysis to remove extreme outliers and non plausible measurements. To complement these data, for 3 species additional trait measurements (LA, SLA and LDMC) that were measured on five individuals at Schrankogel, as described by Paetzolt (2022), were also included.

The C, S, and R values of the selected species were determined using the "StrateFy" strategy calculator (Pierce et al., 2017), implemented as a Microsoft Excel tool. Ultimately, CSR values were obtained for 235 species. The values are expressed as percentages so the sum of CSR values of a species always equals 100%. Data for 17 species were unavailable. However, as this represents only ~7% of all species, it is unlikely to significantly affect the outcomes of this thesis.

For each plot the total vegetation cover and the cover of species with available CSR data were calculated. Only the plots where at least 75% of the total cover was represented by species where the CSR values were known, were retained for further analysis. Based on this criterion, only one plot was removed from the analysis due to insufficient CSR coverage. Since some plots had no vegetation data 885 plots finally remained for further analyses. Using the *weighted.mean* function in R a weighted-mean CSR value for the selected plots was computed by weighting species CSR values of a plot by their respective cover , thereby obtaining community-weighted CSR values.

Statistical analysis

All analyses were conducted with R version 4.5.1 (R Core Team 2025). Boxplots were computed to show the overall distribution of C, S and R strategy types at both the species and the community-weighted level. Ternary diagrams for species CSR values and for community-weighed CSR values of each plot were made with the ggtern package (version 3.0.5) (Hamilton & Ferry, 2018). For both the CSR values of species and the community-weighted CSR values of the plots Friedman tests and Pairwise Wilcoxon signed-rank tests with Bonferroni correction were conducted to test for significant differences among the CSR strategies. To analyse how environmental variables influence the relative dominance of CSR strategies, multinomial regression models were conducted using the multinom function of the nnet package (version

7.3-20) (Ripley, 2025) to model the relationship between a predictor variable and the community-weighted strategy proportions. Each model was conducted with one of the following predictor variables: mean annual temperature (MAT), elevation, snow cover, carbon, nitrogen, and water holding capacity (WHC). To facilitate comparison across models, each predictor was scaled to a mean of 0 and a standard deviation of 1. This does not interfere with the models predictions but improves interpretability and comparability of coefficients (Schielzeth, 2010). Overall model significance was assessed using a Chi^2-test and p-values were adjusted using a Bonferroni correction across the performed tests (n = 6). After fitting the models, response plots were generated via the ggpredict function of the ggeffects package (version 2.3.1) (Lüdecke, 2018) to visualize the predicted effects of each predictor on the community-weighted CSR proportions. The effects of environmental predictors (covariates) on the community-weighted CSR composition were visualized using ternary diagrams, generated with the plot3logit package (Santi et al., 2022). The plot3logit ternary diagrams were also based on the multinomial regression models that were conducted beforehand.

Since soil carbon and soil nitrogen as well as MAT and elevation were highly correlated and hence produced very similar model results (Pearson $r = 0.97$, $p < 0.001$, and $r = -0.81$, $p < 0.001$, respectively; Table A2), only models for soil carbon and MAT are shown.

Results

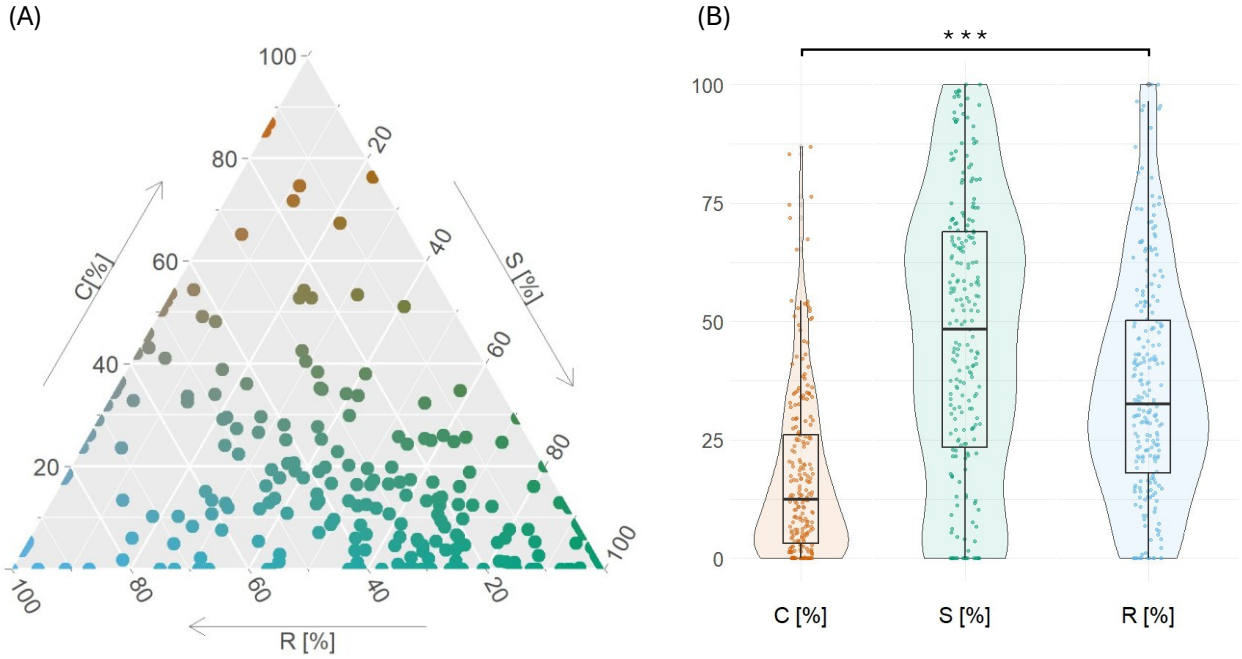

Fig. 2: Competitor (C), ruderal (R) and stress-tolerant (S) strategy values (%) of 235 species occurring in the non-forest subalpine to nival habitats of Mt. Schrankogel. In panel (A) each point represents a species and their combination of CSR strategy values. The top corner corresponds to 100% C-strategists, the right corner to 100% S-strategists, and the left corner to 100% R-strategists. Points located between the corners indicate species with mixed strategies, reflecting varying contributions of C, S, and R values. The colours orange (C), green (S) and blue (R) each represent one of the three strategy types, with pure colours at the corners and proportionally mixed colours for species with traits that indicate mixed strategies located between them. Panel (B) shows the distribution of C, S and R values across all 235 species, with colours as in (A). *** refers to the highly significant difference ($p < 0.001$) in mean ranks between the three values according to a Friedman test.

The 235 species were widely distributed across the CSR-triangle, with all of stress tolerators, ruderals and competitive species represented in the entire flora observed. Species scoring high on these three different strategy types were, for example *Tussilago farfara* (C:S:R = 87:0:13%), *Adenostyles alliariae* (C:S:R = 85:0:15%), *Loiseleuria procumbens* (C:S:R = 0:100:0%), *Juniperus communis subsp. nana* (C:S:R = 0:100:0%), *Saxifraga androsacea* (C:S:R = 0:0:100%) and *Gentiana nivalis* (C:S:R = 0:0:100%). However, on average there was a clear trend towards higher stress-tolerator than ruderal and in particular C values (Fig. 2). Across all species, the median S-values was nearly 50%, while the median R and C-values were 33 and 12%, respectively; and the maximum S and R-values reached 100%, while the maximum C-value was only 87%. A Friedman test showed significant differences among the mean C, S and R values of the 235 species ($\chi^2 = 89.11$, $p < 0.001$). All pairwise comparisons were highly significant ($p < 0.001$).

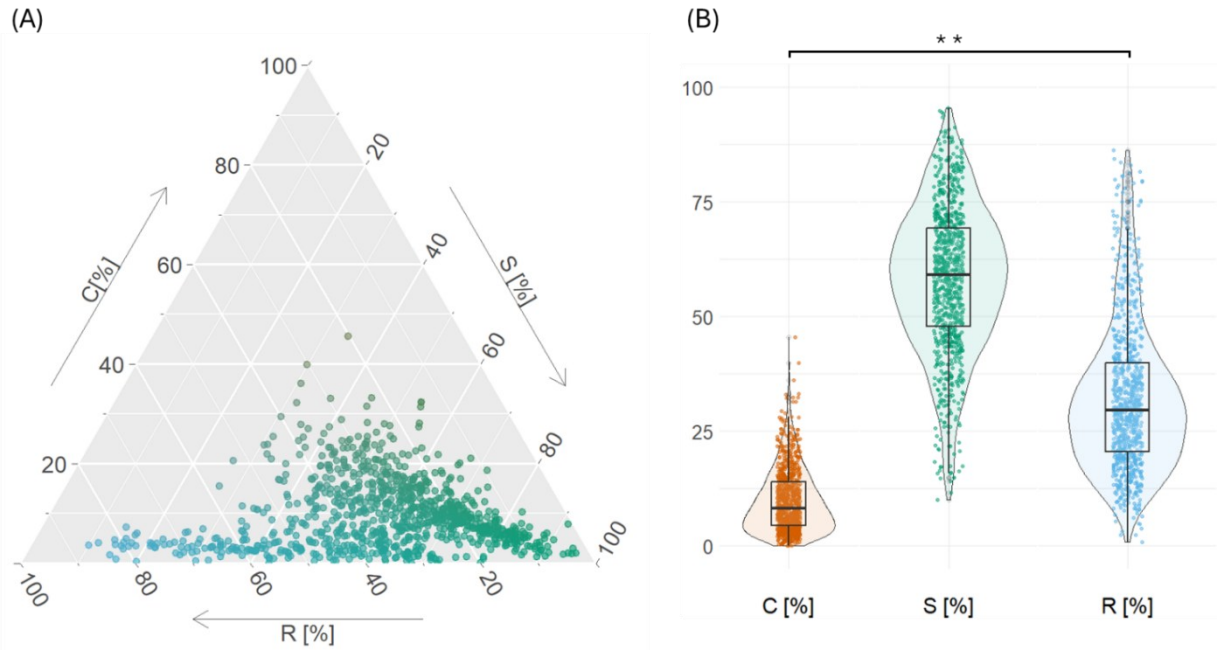

Fig. 3: Community-weighted competitor (C), ruderal (R) and stress-tolerant (S) strategy values of 885 plant communities on Mt. Schrankogel. In panel (A) each point represents one community. The colours orange (C), green (S) and blue (R) each represent one of the three strategy types, with pure colours at the corners and proportionally mixed colours for points located between them. Panel (B) shows the distribution of community-weighted C, S and R strategy values (%)across the 885 plots. Colour codes are as in (A). ** refers to the highly significant difference ($p < 0.01$) in mean ranks between the three values according to a Friedman test.

The predominance of S over R and C strategies became even more clear when community-weighted means were computed from the values of individual species (Fig. 3). Accordingly, the distribution of communities was much more clustered within the CSR triangle than the distribution of individual species. In particular, CWM values concentrated towards the lower right corner of the triangle, i.e., at high S, low to intermediate R and low C-values. The median CWM S-value was almost 60%, as compared to 29 and 8% for R and C-strategy values. Maxima reached 95 and 85% in case of S and R, but only 46% in case of CWMs of C. A Friedman test showed significant differences among all community-weighted CSR values ($\chi^2 = 1416.4$, $p < 0.001$). In addition, all pairwise comparisons were highly significant ($p < 0.01$ throughout). Plots with the highest community-weighted C values are characterised by productive alpine grassland communities, that also include small perennial herbs. Several plots with high community-weighted S values are represented by dwarf shrub heaths, dominated by Loiseleuria procumbens, as well as cushion forming species. In addition also graminoids typical of alpine grassland are also represented in plots with high S values. Plots with the highest R values are correspond to subnival communities, that include pioneer species and plants with short growing season that are typically growing in snowbeds or scree vegetation (Körner, 2021).

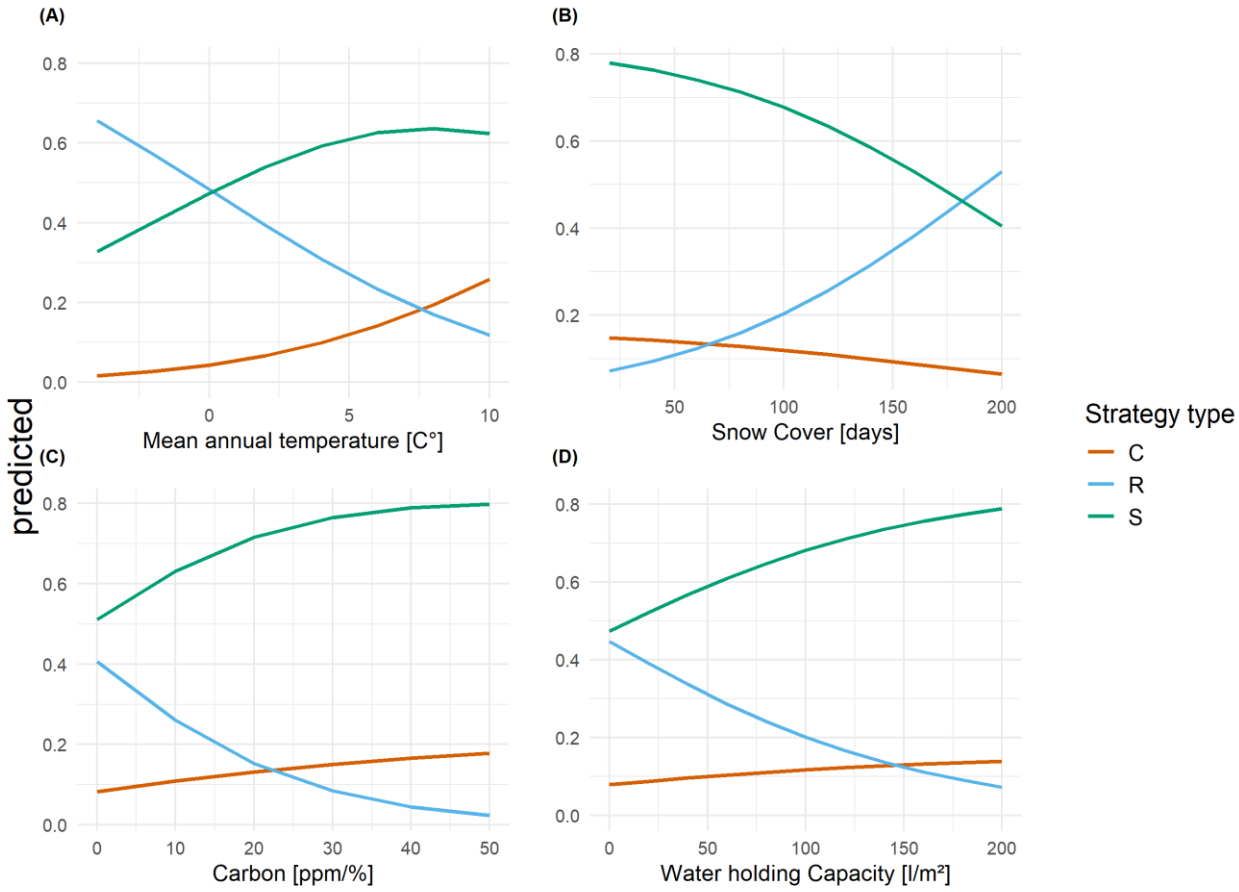

Fig. 4: Multinomial regression response curves for the relationship between community-weighted competitive (C), ruderal (R) and stress-tolerant (S) strategy values of 885 plant communities on Mt. Schrankogel and four environmental gradients.

Despite the predominance of high S values there was still considerable variation across CWM values across local communities, and this variation was not randomly distributed. By contrast, the multinomial regression model suggested highly significant correlations with the environmental gradients considered (Fig. 4, Table 1). In particular, the contribution of S-values increased with increasing temperature, shorter snow cover, higher carbon content and higher water holding capacity. The contribution of R-values increased with decreasing temperature, increasing snow cover, lower carbon content and lower water holding capacity. The contribution of C-values increased with warmer temperature, decreasing snow cover, higher carbon content and higher water holding capacity.

Figure 5 illustrates how these effects on individual C, S and R values combine into shifts of a community within the CSR space upon a standardized increase of the four predictor variables. The main direction of shift in response to increasing temperature is a shift towards C-values,

which is particularly pronounced in communities characterized by high R, and less intense for those characterized by high S-values. Hence, in addition to the trend towards higher C-values there is a weaker additional trend from high R towards higher S values. An increase of snow cover drives a community towards higher R-values, largely independent of whether they score high or low on C and S, respectively. Vice, versa, higher carbon, nitrogen and water holding capacity mainly result in lower R-values, in favour of either higher C or higher S values. Concernig effect sizes, the impact of snow cover is somewhat weaker than the one of temperature and soil conditions.

Table 1: The results from multinomial models, using mean annual temperature (MAT), elevation, snow cover, carbon nitrogen and water holding capacity (WHC) as predictors. The table includes the estimates and the standard errors for each model. P-values were extracted from an overall Chi square test and adjusted to the Bonferroni correction. Significant ($p < 0.05$) p-values are in bold.

Predictor	Strategy Type	Estimates	Standard Errors	Chi ²	p-Value
MAT	C	0.537	0.139	22.11	**< 0.001**
	S	0.282	0.076		
Elevation	C	-0.498	0.133	22.89	**< 0.001**
	S	-0.287	0.077		
Snow Cover	C	-0.353	0.127	18.41	**< 0.001**
	S	-0.331	0.082		
Carbon	C	0.482	0.129	28.30	**< 0.001**
	S	0.438	0.092		
Nitrogen	C	0.501	0.126	25.41	**< 0.001**
	S	0.393	0.090		
WHC	C	0.432	0.128	28.24	**< 0.001**
	S	0.422	0.085		

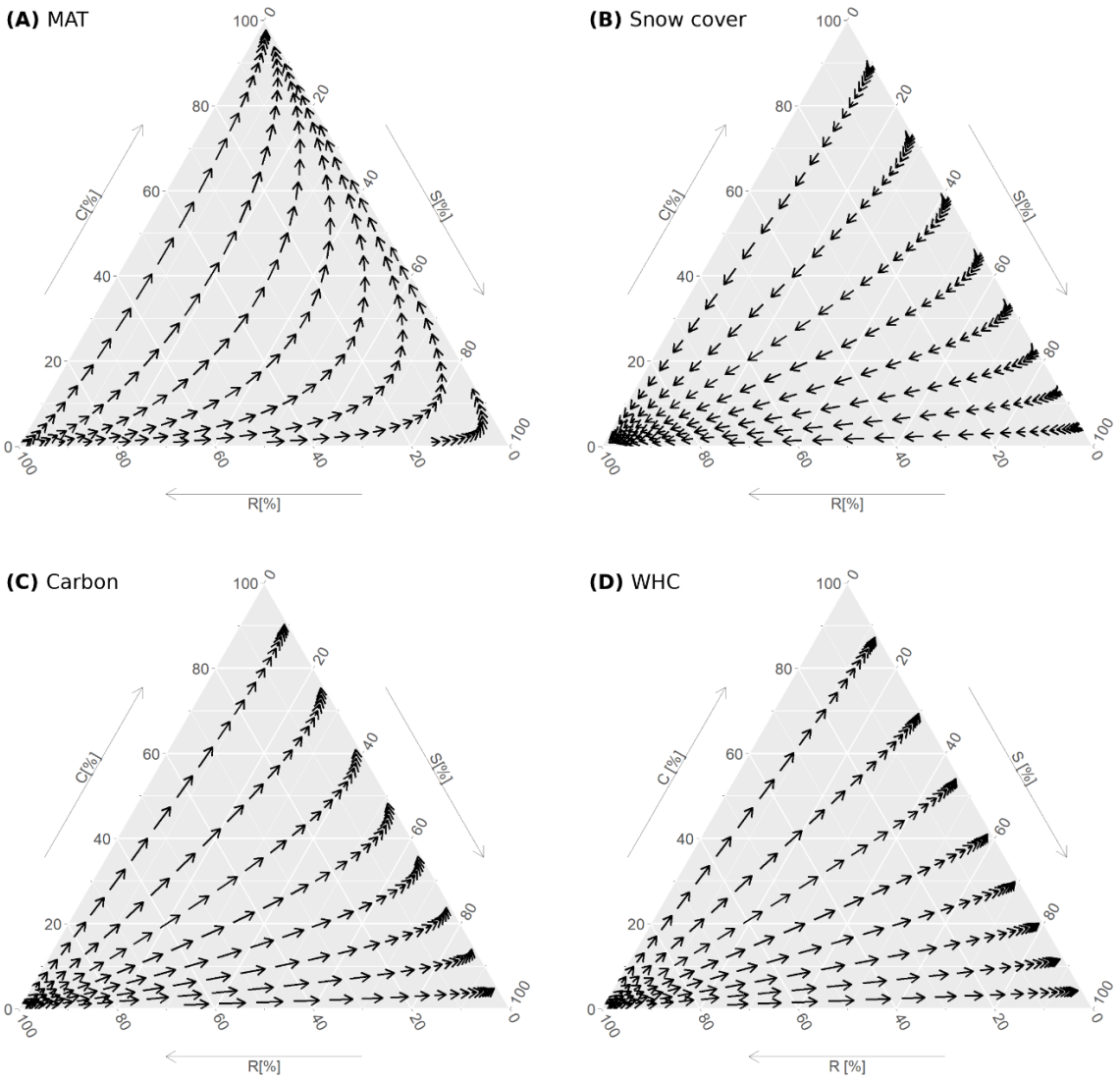

Fig. 5: Vector fields illustrating how increasing values along four environmental gradients affect the expected position of community-weighted mean CSR values within the CSR triangle. Arrows represent vector fields that indicate how species composition, in terms of CWMs of C, S and R values would shift within the triangle if scaled environmental predictors would be increased by 0.5 standard deviations.

Discussion

As expected, the results of this study suggest that overall, both on the species and community level the life-history strategies of plants on Mt. Schrankogel are primarily characterised by stress tolerance and, secondly, by ruderal strategies. This indicates that tolerance of abiotic stress via cold temperature and short periods of favourable conditions, and, secondarily, adaptation to disturbance rather than competitive ability act as main filters of community assembly in this typical alpine landscape. However, and also in line with my expectations, there was considerable variation, both among species and communities, in positions within the CSR triangle, and this variation was not random, but significantly linked to the main environmental gradients that determine plant life in alpine ecosystems (Körner 2021).

In general, plant communities on plots with extreme CSR values appear to be representative of the respective life strategy types. Communities on plots with high S values were characterised by species exhibiting growth forms adapted to harsh environmental conditions, such as cushion plants and dwarf shrubs. These life forms create a microhabitat close to the ground that help plants withstand environmental stress such as strong winds and low temperatures (Cavieres et al., 2016; Körner, 2021). Plots with high R values are characterised by species adapted to scree habitats with short growing seasons. Some species, such as *Cerastium uniflorum*, exhibit opportunistic flowering behaviour, as they flower very shortly after dormancy (Körner, 2021). In the plots with the highest community-weighted C values, species typical of alpine grasslands prevailed. Interestingly, some plots with relatively high community-weighted C values were not necessarily associated with communities dominated by strongly competitive species. Instead, they were often driven by the presence of *Ranunculus glacialis* (C:S:R = 32:54:14 %), which is, despite a relatively high C value due to high LA, considered a stress tolerant plant with a conservative growth strategy (Wagner et al., 2010). The highest plot in the dataset (3,456 m a.s.l.) displays a C value of 32% as it only includes *Ranunculus glacialis*. These results suggest that CSR values, while being well correlated with life-history strategies along large sets of species, may not always reflect these strategies well in individual species.

As temperature increases, and hence elevation decreases, the dominance of community level S and C strategists rises. While the growing contribution of C-strategies with warmer temperature was expected from the reduction of cold stress and longer growing seasons, the parallel increase of S strategists was surprising. A possible reason for this unexpected pattern might be that at subnival to nival elevations the growing season is too short for the expression of stress-tolerance

traits such as high carbon content of leaves (low SLA, high LDMC), and only species with trait values typical of a ruderal strategy can survive under these conditions. In addition diurnal freeze-thaw cycles during snow free periods on high elevations can cause frost heave and cryoturbation, repeatedly disturbing the soil surface (Körner, 2021; Randin et al., 2009). Such physical disturbances create unstable substrates and may limit the establishment of stress tolerant species, which typically invest into long lived tissues for adaptation to stressful but stable conditions. Indeed, a similar pattern has been described by Caccianiga et al. (2006), showing that continued physical disturbance in alpine environments can maintain plant communities in a state of primary succession that is better suited for ruderal species. The increase of R-strategists with higher elevations was in line with our initial hypothesis, and the arguments just discussed, but not necessarily with common expectations. However, ruderals do occur under various kinds of stressful environments such as deserts or salt marshes (Grime, 2001; Pierce et al., 2017). In particular, the so-called stress-tolerant ruderals are characteristic of sites with short growth periods which offer suboptimal conditions for vegetative production and reproduction, though often with pronounced annual variability (Grime, 2001). Such conditions actually prevail in the upper alpine and subnival belts of Schrankogel and other temperate mountains (Körner, 2021). In addition, as mentioned above, the scarce vegetation cover, together with intense erosion, freeze-thaw cycles and steep slopes, destabilize the substrate on which the plants live and hence increase the frequency of disturbance events – conditions which likely also favour R over S strategies (Good et al., 2019; Grime & Pierce, 2012).

Plots with a longer snow cover duration also showed higher community level R values, suggesting that a longer snow cover favours ruderal strategists. Longer snow cover duration can be interpreted as a stress factor in alpine environments, as snow cover deprives plants of light and may hinder nutrient uptake in general (Good et al., 2019). However, with early snow melt plants will be exposed to deeper frost and higher temperature fluctuations, whereas snow cover acts as a buffer and protects plants by providing thermal insulation. In addition, snow cover enhances soil moisture availability, as snowmelt supplies plants with water during warmer periods when exposed soils may dry out (Good et al., 2019). Although snowmelt initially increases water availability, shorter snow cover duration may cause meltwater inputs to cease earlier, potentially leading to soil dryness later in the growing season (Björk & Molau, 2007). Our results indicate that stress from exposure to deep temperature is the more important factor for the distribution of strategy types as with snow cover duration shorter than 50 days

stress tolerators become predominant while the R strategy prevails with a snow cover duration > 200 days.

Increasing WHC, soil carbon and soil nitrogen levels in the alpine habitats of Mt. Schrankogel primarily disadvantage ruderal species in favour of both stress tolerators and competitive species. While benefits for C strategies were expected, the decline in R and increase in S strategies were surprising and different from the results of Yu et al. (2022) who reported shifts towards competitive and ruderal strategies with increasing soil nutrients and higher WHC. However, the alpine grasslands of the Tibetan Plateau, which Yu et al. (2022) studied, differ from our study area by the semi-arid climate and the exclusive focus on grasslands with well-developed soils. By contrast, the variation in soil properties in Schrankogel is pronounced and mirrors, primarily, the difference between grasslands and dwarf shrub heaths on the one hand, and open vegetation on scree and rock on the other hand. The decline of ruderals hence most likely mirrors the advantages of this strategy, in the latter, disturbed environments. By contrast, the more stable grassland and heathlands favour either C or S strategists, depending on additional factors, such as exposure to extreme temperature conditions or competitive intensity.

Caveats

Community-weighted means (CWM) of CSR values were used instead of mean values. By using the weighted mean values, the relative abundance (cover) of the plant species occupied on the respective plots was taken into consideration and therefore reflect dominant contributors to community biomass. However, a limitation of the CWM is that rare species that only take a small cover percentage in the plots contribute less to the community CSR score, even if they represent distinct strategies or microhabitats. Therefore, the community CSR value of plots is mainly derived from large, dominant plant species and may smooth over more subtle differences.

Although the CSR classification of plant species is widely used, it has limitations that are relevant for the interpretation of my results. Since plant traits were obtained form the TRY database that compiles plant data from multiple sources, there is a risk of methodological inconsistency and insufficient consideration of intra-specific variability. In fact, considering phenotypic plasticity and ecotypic variation (Escobedo et al., 2023; Pierce et al., 2017; Zhang & Wang, 2021) would perhaps result in even clearer relationships between strategy values and environmental gradients as those I found in my data as individuals of the same species can

express different phenotypes in response to different climate and soil properties (Whitman & Agrawal, 2009; Yu et al., 2022).. Put differently, since the CSR values for the plant species used in this thesis are based on mean values derived from measurements of multiple plant individuals sampled across different locations, these values may not fully represent the CSR-strategies of the species under the specific environmental conditions at Mt. Schrankogel. Consequently, true CSR values at this site may differ from those calculated with the obtained values from the TRY database, potentially weakening the ecological patterns observed.

Since the calculation of CSR values is based solely on plant leaf traits and does not take plant height or plant live forms into consideration, the results should be interpreted cautiously. Plant height often indicates a competitive advantage, as taller plants can outcompete others for light (Novakovskiy et al., 2021). For example, the evergreen shrub *Pinus mugo* (C:S:R = 3:97:0%) exibits a C value of 0% and is therefore, according to the "Stratefy" model, not considered a competitive species. However, when growing alongside shorter plants that are nonevergreen *Pinus mugo* could possibly outcompete them, due to its height advantage. Plant height was initially excluded from CSR calculations to allow the comparison of aquatic and terrestrial species on a global scale, as leaf traits are universally measurable (Pierce et al., 2017). Nonetheless, in some cases, to ensure a more realistic calculation of life-history strategies, it would certainly be useful to include other traits in addition (Novakovskiy et al., 2021).

Despite the growing body of research on CSR strategies in various ecosystems, it remains challenging to depict a habitat specific plant community accurately, particularly in environmental heterogenous alpine systems. While CSR values capture important tendencies in resource use and plant responses to abiotic stress or disturbance, they should not be taken as direct indicators of habitat preferences. Alpine habitats are instead shaped by multiple factors that jointly influence species distribution and community assembly, a complex issue that the three leaf traits used in this thesis can only partially address (Rosado & De Mattos, 2017). The "StrateFy" tool is useful for generalisation, but it can lack accuracy in fine-scale habitats (Novakovskiy et al., 2021).

Conclusion

Overall, this study illustrates that environmental stress is the dominant filter shaping life-history strategies of plants in the alpine habitat of Mt. Schrankogel. However, the contribution of other

strategies can be substantial, and this contribution varies predictably along gradients of temperature, snow cover duration and soil properties. These results indicate that alpine habitats are highly complex systems where plant community assembly can hardly be described by a single environmental predictor. In the context of ongoing climate change, shifts in temperature regimes are expected to further alter environmental conditions of alpine habitats. Such warming effects will lead to upwards shift of plant species and ultimately to changes in the functional composition of alpine communities. Therefore, understanding how environmental gradients shape plant strategies is essential for predicting the effects of environmental change on alpine vegetation.

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Appendix

Table A1 – List of species and their CSR values

Taxon	C (%)	S (%)	R (%)
Achillea millefolium	29.9	42.1	28.0
Achillea moschata	5.4	39.0	55.6
Acinos alpinus	4.7	74.1	21.2
Adenostyles alliariae	85.3	0.0	14.7
Agrostis agrostiflora	9.7	49.5	40.8
Agrostis alpina	0.0	100.0	0.0
Agrostis rupestris	0.9	64.8	34.3
Agrostis stolonifera	8.6	54.6	36.8
Ajuga pyramidalis	19.9	42.9	37.2
Alchemilla alpina	14.0	65.5	20.5
Alchemilla vulgaris agg.	33.9	41.5	24.6
Androsace alpina	0.0	43.2	56.8
Androsace obtusifolia	0.0	27.5	72.5
Antennaria carpatica	3.9	73.0	23.1
Antennaria dioica	6.1	55.0	38.9
Anthoxanthum alpinum	12.7	45.1	42.2
Anthyllis vulneraria	41.1	5.4	53.5
Arabis alpina	26.1	0.0	73.9
Arabis alpina subsp. alpina	1.8	17.8	80.3
Arctostaphylos uva-ursi	12.0	88.0	0.0
Arenaria biflora	0.0	43.5	56.5
Arenaria ciliata s. str.	1.4	98.6	0.0
Arnica montana	54.4	3.6	42.1
Asplenium viride	17.8	40.3	41.9
Aster alpinus	8.2	68.9	22.9
Astragalus frigidus	33.6	12.9	53.5
Atocion rupestre	2.8	43.9	53.3
Avenella flexuosa	3.5	67.7	28.8
Avenula versicolor	9.8	71.2	19.0
Bartsia alpina	10.8	58.3	30.9
Bellidiastrum michelii	34.4	0.0	65.6
Botrychium lunaria	29.7	27.2	43.1
Briza media	16.5	52.4	31.2
Calamagrostis villosa	22.8	43.5	33.6
Calluna vulgaris	0.0	88.6	11.4
Campanula barbata subsp. barbata	25.2	33.7	41.1
Campanula scheuchzeri	3.7	56.1	40.3
Cardamine resedifolia	3.7	57.8	38.5
Carex aterrima	17.4	58.6	24.0
Carex brunnescens	7.7	83.3	9.0
Carex capillaris	1.5	81.5	17.0
Carex curvula subsp. curvula	5.0	92.7	2.3
Carex echinata	10.7	66.6	22.8
Carex ferruginea	13.7	65.0	21.3
Carex frigida	15.2	25.1	59.7
Carex nigra	16.9	57.0	26.1
Carex ornithopoda	16.5	50.0	33.5
Carex sempervirens	12.2	74.9	12.8
Carlina acaulis subsp. acaulis	53.5	31.6	14.9
Cerastium alpinum s. str.	2.1	30.8	67.1
Cerastium arvense subsp. strictum	1.3	57.7	40.9

Cerastium cerastoides	0.0	13.0	87.0
Cerastium fontanum s. str.	7.6	31.6	60.8
Cerastium pedunculatum	3.6	0.0	96.4
Cerastium uniflorum	4.4	0.0	95.6
Cirsium acaule	67.4	21.7	10.9
Cirsium spinosissimum	29.4	70.6	0.0
Clematis alpina	49.2	7.6	43.1
Coeloglossum viride	35.9	0.0	64.1
Crepis aurea	26.7	28.3	45.1
Crocus albiflorus	16.6	55.3	28.1
Dactylis glomerata subsp. glomerata	27.8	37.7	34.5
Deschampsia cespitosa subsp. cespitosa	12.5	66.0	21.5
Diphasiastrum alpinum	2.8	97.2	0.0
Doronicum clusii subsp. clusii	36.5	0.0	63.5
Draba dubia	0.0	85.0	15.0
Dryas octopetala	1.3	84.2	14.5
Dryopteris carthusiana	52.8	22.2	25.0
Dryopteris dilatata	74.7	11.2	14.1
Dryopteris filix-mas s. str.	71.8	11.7	16.5
Empetrum hermaphroditum	0.0	93.9	6.1
Epilobium anagallidifolium	0.2	58.6	41.2
Epilobium nutans	10.8	28.4	60.8
Equisetum arvense	19.9	54.3	25.9
Erigeron alpinus	13.4	45.1	41.5
Erigeron uniflorus	10.3	23.0	66.7
Euphorbia cyparissias	4.6	62.3	33.1
Euphrasia minima	0.0	0.0	100.0
Euphrasia officinalis subsp. picta	1.5	44.3	54.2
Festuca halleri agg.	0.0	94.2	5.8
Festuca nigrescens	6.7	71.7	21.6
Festuca nigricans	8.7	49.5	41.8
Festuca norica	6.7	71.7	21.6
Fragaria vesca	25.3	39.6	35.1
Galium anisophyllon	0.0	74.9	25.1
Gentiana acaulis	16.1	67.6	16.3
Gentiana bavarica	0.0	67.1	32.9
Gentiana brachyphylla	0.0	66.6	33.4
Gentiana nivalis	0.0	0.0	100.0
Gentiana punctata	65.3	6.2	28.6
Gentianella campestris	5.4	0.0	94.6
Geranium sylvaticum	42.6	27.7	29.8
Geum montanum	34.7	58.3	6.9
Geum reptans	25.7	63.8	10.5
Gnaphalium norvegicum	17.8	36.3	45.9
Gnaphalium supinum	0.0	33.3	66.7
Gnaphalium sylvaticum	12.3	52.2	35.5
Gymnadenia conopsea	52.2	0.0	47.8
Gymnocarpium dryopteris	38.9	16.1	45.0
Helianthemum nummularium subsp. grandiflorum	11.9	30.5	57.6
Hieracium alpinum s. lat.	32.8	4.1	63.1
Hieracium glanduliferum	26.3	0.0	73.7
Hieracium hoppeanum subsp. hoppeanum	35.1	34.8	30.1
Hieracium intybaceum	32.6	13.4	54.0
Hieracium murorum	42.1	0.0	57.9
Hieracium pilosella agg.	35.3	34.4	30.3
Homogyne alpina	24.9	62.2	12.9

Huperzia selago	0.2	84.4	15.4
Hypericum maculatum s. str.	12.5	53.6	33.9
Hypochaeris uniflora	45.9	0.0	54.1
Juncus jacquinii	7.8	92.2	0.0
Juncus trifidus	6.0	80.3	13.8
Juniperus communis subsp. nana	0.0	100.0	0.0
Kobresia myosuroides	2.5	97.5	0.0
Laserpitium halleri	76.4	22.8	0.8
Leontodon hispidus	43.1	1.6	55.3
Leucanthemopsis alpina	6.0	17.4	76.6
Lilium martagon	50.5	0.0	49.5
Linaria alpina subsp. alpina	0.0	9.1	90.9
Lloydia serotina	34.7	0.0	65.3
Loiseleuria procumbens	0.0	100.0	0.0
Lotus corniculatus	16.3	34.8	49.0
Luzula alpino-pilosa	16.8	45.5	37.7
Luzula lutea	12.6	69.0	18.3
Luzula luzuloides	20.7	37.3	42.0
Luzula multiflora s. lat.	10.9	41.0	48.1
Luzula spicata	5.4	68.8	25.8
Luzula sudetica	12.8	29.7	57.5
Lycopodium annotinum	0.0	69.1	30.9
Maianthemum bifolium	27.4	24.2	48.3
Melampyrum sylvaticum	17.6	0.0	82.4
Minuartia gerardii	0.0	62.5	37.5
Minuartia recurva	0.0	79.6	20.4
Minuartia sedoides	0.0	87.6	12.4
Mutellina adonidifolia	24.3	54.5	21.1
Myosotis alpestris	11.7	36.0	52.3
Nardus stricta	5.3	85.6	9.1
Oreochloa disticha	1.9	98.1	0.0
Oxyria digyna	23.8	0.0	76.2
Oxytropis campestris	18.9	67.9	13.3
Parnassia palustris	23.6	6.7	69.7
Pedicularis asplenifolia	6.8	93.2	0.0
Pedicularis kerneri	14.6	44.2	41.2
Pedicularis tuberosa	25.4	57.1	17.6
Persicaria vivipara	19.7	50.2	30.1
Peucedanum ostruthium	52.9	24.1	22.9
Phleum alpinum agg.	11.8	55.5	32.6
Phyteuma betonicifolium	34.0	17.3	48.7
Phyteuma globulariifolium subsp. pedemontanum	1.5	74.2	24.3
Phyteuma hemisphaericum	3.8	71.4	24.8
Phyteuma orbiculare	24.1	23.9	51.9
Pimpinella saxifraga subsp. saxifraga	38.4	32.5	29.1
Pinus mugo	2.6	97.4	0.0
Platanthera bifolia	50.8	0.0	49.2
Poa alpina	6.2	62.4	31.4
Poa chaixii	14.4	59.3	26.3
Poa laxa	2.3	66.3	31.4
Poa nemoralis	19.2	38.3	42.6
Poa supina	10.2	18.7	71.1
Polystichum lonchitis	51.2	40.7	8.2
Potentilla aurea	17.4	52.4	30.2
Potentilla crantzii	16.9	62.6	20.5
Potentilla erecta	4.5	67.2	28.3

Potentilla grandiflora	26.0	59.8	14.1
Primula glutinosa	13.3	50.2	36.5
Primula hirsuta	29.0	0.0	71.0
Primula minima	1.4	98.6	0.0
Prunella vulgaris	22.5	27.1	50.5
Pseudorchis albida subsp. albida	34.9	0.0	65.1
Pulsatilla alpina subsp. apiifolia	34.1	39.3	26.5
Pulsatilla vernalis	24.7	70.4	5.0
Pyrola minor	20.3	46.8	32.9
Ranunculus acris subsp. acris	40.4	29.4	30.2
Ranunculus glacialis	32.3	53.5	14.1
Ranunculus villarsii	28.2	31.9	39.9
Rhinanthus glacialis	8.8	61.3	29.9
Rhododendron ferrugineum	7.9	92.1	0.0
Rubus idaeus	38.0	40.7	21.3
Rumex alpestris	53.7	0.0	46.3
Rumex scutatus	31.9	0.0	68.1
Sagina saginoides	0.0	70.8	29.2
Salix appendiculata	25.8	52.4	21.8
Salix helvetica	13.3	63.3	23.4
Salix herbacea	6.2	72.3	21.5
Salix reticulata	12.9	86.0	1.1
Salix retusa s. str.	1.5	82.6	15.9
Salix serpyllifolia	2.6	87.6	9.8
Saussurea alpina	36.2	21.5	42.3
Saxifraga aizoides	0.0	31.6	68.4
Saxifraga androsacea	0.0	0.0	100.0
Saxifraga bryoides	0.0	68.0	32.0
Saxifraga exarata	0.0	100.0	0.0
Saxifraga oppositifolia s. str.	0.0	69.9	30.1
Saxifraga paniculata	20.1	79.9	0.0
Saxifraga seguieri	0.0	25.1	74.9
Saxifraga stellaris subsp. robusta	5.1	0.0	94.9
Scorzoneroides helvetica	12.9	37.0	50.1
Sedum acre	0.0	0.0	100.0
Sedum alpestre	0.0	92.7	7.3
Selaginella selaginoides	0.0	56.9	43.1
Sempervivum montanum s. str.	0.2	95.8	4.1
Senecio doronicum s. str.	16.1	80.0	3.9
Senecio incanus subsp. carniolicus	25.0	58.3	16.7
Sibbaldia procumbens	9.5	67.7	22.8
Silene acaulis subsp. exscapa	0.0	4.5	95.5
Silene nutans subsp. nutans	29.5	21.6	48.9
Silene vulgaris	45.6	0.0	54.4
Soldanella pusilla	5.4	65.8	28.8
Solidago virgaurea subsp. minuta	29.2	21.1	49.7
Stellaria graminea	8.3	26.3	65.3
Thymus praecox subsp. polytrichus	0.0	74.0	26.0
Thymus pulegioides subsp. pulegioides	0.0	76.0	24.0
Tofieldia pusilla	2.0	69.3	28.7
Trichophorum cespitosum subsp. cespitosum	1.2	98.8	0.0
Trifolium alpinum	12.4	71.5	16.0
Trifolium badium	13.4	27.1	59.5
Trifolium pallescens	7.1	48.3	44.6
Trifolium pratense subsp. pratense	19.0	42.4	38.7
Trifolium repens	19.4	34.2	46.4

Trisetum spicatum	7.7	80.2	12.1
Trollius europaeus	54.2	22.2	23.5
Tussilago farfara	86.9	0.0	13.1
Vaccinium gaultherioides	5.2	79.3	15.4
Vaccinium myrtillus	5.8	65.5	28.7
Vaccinium vitis-idaea	4.2	95.8	0.0
Valeriana officinalis subsp. tenuifolia	48.2	10.2	41.5
Valeriana tripteris	35.1	0.0	64.9
Veronica alpina	4.9	24.9	70.2
Veronica bellidioides	8.8	91.2	0.0
Veronica chamaedrys subsp. micans	13.8	37.5	48.7
Veronica fruticans	0.0	58.8	41.2
Veronica officinalis	6.7	56.4	36.8
Veronica serpyllifolia subsp. humifusa	13.4	12.1	74.5
Viola biflora	18.6	0.0	81.4
Viola palustris	20.5	36.3	43.1

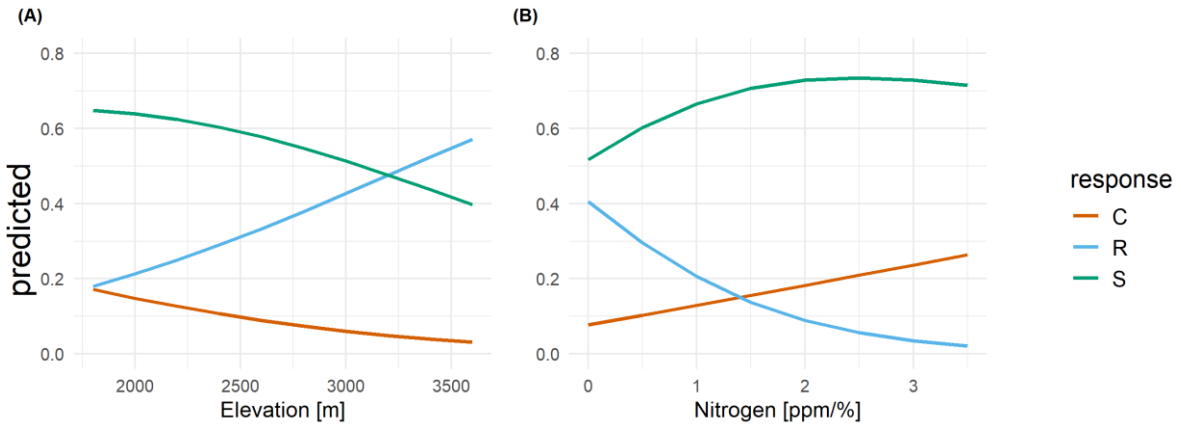

Fig. A1: Multinomial regression response curves for the environmental gradients: elevation (A) and nitrogen (B). The y-axis shows model predicted community-weighted proportions (0–1), which can be interpreted as percentages of CSR strategy type. The colours orange (C), green (S) and blue (R) each represent one of the three strategy types.

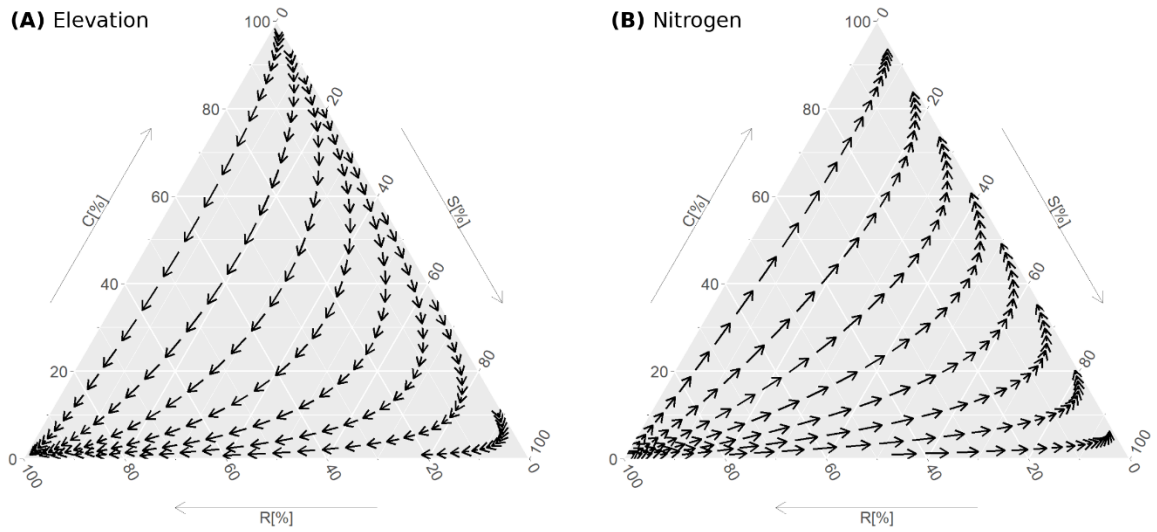

Fig. A2: Vector fields showing the effect of the changing predictor, elevation (A) and nitrogen (B), on the probability distribution of CSR values of a plant community. In each plot the top corner is representing C strategist, the bottom left corner representing R strategist and the bottom right corner representing S strategist The arrows of the ternary plots indicate both the direction and magnitude of change in the predicted distribution of survival strategies, in response to increasing values of the respective predictor

Table A2: Pearson's correlation matrix calculated for the environmental variables. All pairwise correlations were highly significant ($p < 0.05$).

	MAT	Elevation	Snow cover	Carbon	Nitrogen
MAT					
Elevation	-0.80				
Snow cover	-0.54	0.53			
Carbon	0.40	-0.48	-0.45		
Nitrogen	0.41	-0.47	-0.44	0.97	
WHC	0.41	-0.47	-0.45	0.84	0.80