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Does the performance of alpine plant species depend on the composition of their neighbors in terms of CSR strategy types?

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Abstract

Steep elevational gradients in alpine environments create strong variation in abiotic stress and biotic interactions among plants. These variations structure communities over short distances and contribute to the high diversity of vascular plant species in the alpine regions. To understand how such diversity is maintained, functional trait-based approaches have become widely used, as they link species traits to ecological strategies and environmental responses. The CSR framework offers a way to classify plant species into three strategy types: competitors (C), stress tolerators (S) and ruderals (R). With the implementation proposed by Pierce et al. (2017), CSR strategies can be quantified using three commonly measured functional traits: leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC).

This thesis investigates the relationship between the performance of alpine plants and the functional composition of their neighbors in relation to their CSR strategies. It evaluates if these compositions influence individual plant growth, interannual variability in plant growth or flower production and how they change across an elevational gradient. Using a stratified random sampling approach, 1,658 plots were established on Mount Schrankogel (3,497m) in Tyrol, Austria, and performance data was collected over multiple seasons (2021-2024). Additional data for LA, SLA and LDMC was acquired from the TRY database and the StrateFy tool was used to calculate the CSR strategy scores of the species. Different mixed effects models were then fitted for each response variable to assess the influence of CSR strategy deviations between the target plants and their neighbors.

The results showed that regression models indicated no significant effect of the average CSR strategies of neighbors on individual plant performance. For the interannual variability in plant growth on the other hand, results were statistically significant, but the variance explained by it was marginal. CSR variations of the plant communities along the elevational gradient were consistent with previous findings by Pierce et al. (2017).

Overall, the results indicate that in this alpine system, other environmental conditions play a far bigger role in influencing plant performance than the functional composition of their neighbors. This is enhanced by the fact that LA, SLA and LDMC do not seem to fully capture a plant´s ecological strategy type, which limits CSR based approaches in explaining plant performances. These results can be seen as an addition to understanding community assembly processes in alpine ecosystems and an evaluation of the applicability of the StrateFy tool on the species level of alpine plants. A morpho-physiological model that integrates additional traits related to growth and resource acquisition may be better suited to correctly determine a plant's life strategy and should be considered in future work focused on the species level CSR strategies.

Zusammenfassung

Die hohe Reliefenergie in alpinen Lebensräumen führt zu einer starken Variation abiotischer Stressfaktoren und biotischer Interaktionen zwischen Pflanzen. Diese Unterschiede bewirken bereits über kurze Distanzen eine Differenzierung der Pflanzengesellschaften und tragen zu der hohen Diversität von Gefäßpflanzenarten in alpinen Regionen bei. Um zu verstehen, wie diese Vielfalt aufrechterhalten wird, werden zunehmend funktionelle, trait-basierte Ansätze eingesetzt, da sie Artmerkmale mit ökologischen Strategien und Reaktionen auf die Umwelt verknüpfen. Das CSR-Konzept bietet eine Möglichkeit Pflanzenarten in drei Strategietypen einzuteilen: Konkurrenz (C), Stresstoleranz (S) und Ruderalität (R). Mit der von Pierce et al. (2017) vorgeschlagenen Implementierung lassen sich CSR-Strategien anhand von drei häufig gemessenen funktionellen Merkmalen quantifizieren: Blattfläche (LA), spezifische Blattfläche (SLA) und Trockensubstanzgehalt der Blätter (LDMC).

Diese Arbeit untersucht den Zusammenhang zwischen der Leistung alpiner Pflanzen und der funktionellen Zusammensetzung ihrer Nachbarn in Bezug auf deren CSR-Strategien. Analysiert wird, ob die gemeinschaftliche CSR-Zusammensetzung das individuelle Pflanzenwachstum, die interannuelle Variabilität des Pflanzenwachstums sowie die Blütenproduktion beeinflusst und wie sich diese Zusammensetzung entlang eines Höhengradienten verändert. Unter Verwendung eines geschichteten Zufallsstichprobenverfahrens wurden 1.658 Versuchsflächen auf dem Schrankogel (3.497 m) in Tirol, Österreich, eingerichtet und Leistungsdaten über mehrere Vegetationsperioden (2021-2024) erhoben. Ergänzende Daten zu LA, SLA und LDMC wurden aus der TRY-Datenbank bezogen und die CSR-Strategietypen der Arten wurden mithilfe des StrateFy-Tools berechnet. Anschließend wurden gemischte Effektmodelle angepasst, um so den Einfluss von CSR-Strategieabweichungen zwischen Zielpflanzen und ihrer Nachbarschaft zu analysieren.

Die Ergebnisse zeigen, dass die durchschnittlichen CSR-Strategiewerte der Nachbarpflanzen keinen signifikanten Einfluss auf die Leistung einzelner Pflanzen hatten. Für die interannuelle Variabilität des Pflanzenwachstums wurden hingegen statistisch signifikante Effekte festgestellt, deren erklärte Varianz war allerdings marginal. Die CSR-Variationen der Pflanzengemeinschaften entlang des Höhengradienten stimmten mit früheren Ergebnissen von Pierce et al. (2017) überein.

Insgesamt deuten die Ergebnisse darauf hin, dass in diesem alpinen System andere Umweltbedingungen eine weitaus größere Rolle für die Pflanzenleistung spielen als die funktionelle Zusammensetzung ihrer Nachbarn. Zudem scheint es, als würden LA, SLA und LDMC die ökologische Strategie einer Pflanzenart nicht vollständig erfassen, was CSR-basierte Ansätze zur Erklärung der Pflanzenleistung einschränkt. Die Ergebnisse tragen zum Verständnis der Gemeinschaftsbildungsprozesse in alpinen Ökosystemen bei und bewerten die Anwendbarkeit des StrateFy-Tools auf Artniveau. Für zukünftige Studien auf Artenebene könnten morpho-physiologische Modelle, die zusätzliche Merkmale des Wachstums und der Ressourcenaneignung verwenden, besser geeignet sein, um pflanzliche Lebensstrategien adäquat abzubilden.

Introduction

Alpine environments

The alpine life zone, located above the climatic tree line of mountainous regions, is typically seen as a challenging environment to live in (Körner, 2021). It is characterized by rugged landscapes and extreme weather, which accounts for low temperatures, high UV radiation, strong winds and short growing seasons. Although these conditions can strongly constrain plant life, they have led to the development of diverse and specialized alpine communities. In Europe, alpine environments might only cover 3% of the continent´s area, but they are home to approximately 20% of the continent´s native vascular plant species (Nagy et al., 2003). Species living there have evolved remarkable adaptations that enable them to withstand these extreme conditions (Billings & Mooney, 1968). Commonly found are low stature, long lived plant species, which include graminoids, herbs, dwarf shrubs, cushion plants, mosses and lichens (Körner, 2021; Testolin et al., 2021). To understand how this diversity is possible, it requires examining the functional traits and ecological strategies that allow plants to persist in this ecosystem.

Plant functional traits and communities

According to Rabotnov (1975, as cited in Onipchenko et al., 2021), a species' life strategy refers to the set of adaptations that allow it to coexist with other organisms and occupy a specific niche within its ecosystem. These adaptations are often expressed through functional traits, which are seen as any physical, phenological or morphological features that are measurable and influence an individual plant´s fitness (Violle et al., 2007). In recent decades, trait-based approaches have become increasingly important for understanding the ecological strategies that shape plant community assembly and patterns of species dominance (Lebrija-Trejos et al., 2010; Reich, 2014). In alpine environments, numerous factors influence the combination of favorable traits in plants.

There are abiotic stressors like low temperature, high radiation, strong winds, short growing seasons and limited soil nutrients (Sati et al., 2024). Temperature is generally seen as the primary environmental factor shaping species distribution along elevational gradients, as it strongly influences plant physiology, growth and fitness (Moser et al., 2005; Pauli et al., 2012). Especially in the mountain regions temperature changes can vary a lot due to microtopographic differences in features like slope, aspect or exposure of the surfaces (Löffler et al., 2006; Graae et al., 2018). Together with other local stressors, this results in a complex environmental mosaic that favors different adaptive strategies within a small area.

The other strong influence on alpine plant performance is made by biotic interactions within their community. This includes competition, facilitation, herbivory or mutualistic relationships, which all influence the local plant composition. Competing interactions for example, where plants try to outsource the environment in a more efficient way than others, add a new stressor to an environment to which local species must adapt. This is often seen

with resources such as nutrients, light or water (Craine & Dybzinski, 2013). Facilitative interactions on the other hand, where a species increases the performance of another species, allows plants to grow in environments for which they are less adapted (Callaway, 2007). In alpine ecosystems, cushion plants for example may act as a “nursing place” for other species during primary succession (Cavieres et al., 2002). According to the stress gradient hypothesis (Bertness & Callaway, 1994), the influence of competitive biotic interactions tends to decline with increasing elevation as abiotic stress intensifies.

Overall, alpine plant communities are shaped by an interplay of biotic and abiotic stressors which together influence the development of species-specific functional traits. In mountain regions, these shifts occur within remarkably small geographical distances and make alpine habitats an ideal place to study trait-based community compositions.

The CSR Model

The CSR model, originally introduced by Grime (1974), is a prominent framework in plant ecology. It provides a mechanical explanation for plant community patterns and allows for the prediction, quantification and comparison of community structures and ecosystem processes (Cerabolini et al., 2010). The model considers how plants balance survival, competition and reproduction depending on levels of stress and disturbance in their environment. According to Grime (2001), stress refers to environmental conditions that limit a plant’s photosynthetic activity, such as insufficient light, water, nutrients or suboptimal temperatures. Disturbance by contrast is associated with a partial or complete destruction of plant biomass due to herbivores, pathogens, human actions or environmental conditions. Depending on the combination of these factors, plants can be classified into three primary categories.

Competitors (C): These kinds of plants are best suited to environments where resources are abundant and disturbance is minimal. Under such conditions, they can rapidly monopolize resources and outcompete other species. Their strategy prioritizes fast, continued vegetative growth and high reproductive output.

Stress-tolerators (S): S selected species on the contrary are plants adapted to harsh and resource poor environments. These conditions may involve extreme temperatures, droughts, or nutrient deficient soils. They often grow slower and their main energy investment goes into their resource holding capacity for surviving extreme environmental conditions.

Ruderals (R): Ruderals thrive in habitats characterized by frequent disturbances. A large proportion of their resources are invested in their propagules (e.g. seeds or spores) instead of long-term survival structures. In case of repeated disruptions, these opportunistic species will be the first to populate newly available habitats.

Grime’s triangular CSR model (1974) not only outlines the three primary plant strategies mentioned before but also allows for combinations between them. These intermediate strategies fall into four categories; (1) Competitive ruderals (CR) thrive in environments with

low stress and moderate disturbance, such as nutrient rich meadows or grazed pastures; (2) stress tolerant competitors (CS) are found in undisturbed yet moderately stressed conditions, like nutrient poor forests or shrubland; (3) stress tolerant ruderals (SR) are adapted to low nutrient, lightly disturbed areas such as rocky outcrops or crevices in cliff sand walls; and (4) CSR intermediates, which occur in habitats where stress and disturbance restrict competition to a moderate level, like unfertilized pastures and meadows (J. P. Grime, 1977).

To apply the CSR model in a practical and standardized way, this study will follow the approach developed by Pierce et al. (2017). Instead of using Grime's original framework of classifying plants based on their ecological behavior and habitat characteristics, this method relies on directly measured functional traits, specifically leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC), to assign each species their relative proportions of each strategy. These three leaf traits are used, because they reflect key tradeoffs in plant resource management. LA reflects a plant´s ability to capture sunlight, LDMC is linked to how efficiently a plant retains nutrients and SLA indicates the potential for resource acquisition and growth speed (Garnier et al., 2017; Ricotta et al., 2023). For instance, high SLA and low LDMC are typically associated with ruderal strategies (fast growth, low lifespan), while low SLA and high LDMC indicate adaptations from stress tolerators (slow growth, persistent). Competitive species often display a high SLA and an intermediate LDMC (fast growth, moderate persistence).

This trait-based innovation has greatly expanded the practical applicability of the CSR theory, facilitating its broader use in the analysis of plant community structure and composition (Peng et al., 2024). Good et al. (2019) for example implied this framework to evaluate the filtering effect of snowmelt timing on species composition across alpine ecosystems. Similarly, Ricotta et al. (2023) used the CSR strategy-based approach to assess the degree of functional specialization of alpine plant species and communities.

Research objective

The CSR model has been applied to characterize species strategies across different ecosystems (Li & Shipley, 2017; Liu et al., 2025a) and several studies have shown that it can be used at the community level to predict the responses of plants to stress and disturbances (Bricca et al., 2021; Guerra et al., 2021; Zanzottera et al., 2020). However, studies like these are still scarce and the applicability of the CSR model on the species level is less understood. To address this gap, this study aims to investigate how the community level C, S and R values relate to the performance of individual alpine plants. I will test whether deviations in neighboring CSR compositions influence the vegetative growth (magnitude and variability) and flower production of the target plants and how the CSR community values change along the elevational gradient. The results should provide insight into the ecological mechanisms shaping alpine plant communities. Furthermore, it is also an evaluation of the applicability of the CSR classification method proposed by Pierce et al. (2017) in a high elevation alpine

environment, where steep environmental gradients and varying disturbances may influence species interactions.

The following three research questions and hypotheses will be discussed:

1) Does the performance of alpine plant species depend on the composition of their neighbors in terms of CSR strategy types?

   Previous work suggests that species are more likely to occur in communities where their trait values are closer to the community weighted mean (Muscarella & Uriarte, 2016). This pattern was strongest for multivariate trait combinations. I therefore assume that species closer to the CWM will perform better than species further away from the CWM.

2) Does the community CSR composition affect the interannual variability in plant growth of alpine plant species?

   In addition to assessing mean growth responses, this study further explores the influence that CSR strategy deviations between the target plant and its neighbors might have on the interannual variability of plant growth. Interannual variability reflects the temporal stability of plant performance and indicates the consistency of growth responses across years (Tilman et al., 2006). This can provide complementary information to mean growth rate, especially over a short observation period.

3) How does the composition of CSR strategies in alpine communities change with elevation?

   Based on the CSR theory, increasing elevation is often expected to favor stress tolerant strategies due to higher abiotic stress (J. P. Grime, 1977; Körner, 2021). However, empirical studies along elevational gradients have reported contrasting patterns depending on the mountain systems. I will therefore examine if the community CSR compositions follow the trajectory described by Pierce et al. (2017), which suggests that we will see a gradual shift with elevation away from C strategies towards S strategies and then for the nival zone a shift from S strategies to R strategies.

Materials and Methods

Study Framework

Schrankogel is a comprehensive long-term monitoring location for high altitude vegetation in the Alps. It includes approximately 1,000 permanent 1x1m plots established in 1994, covering elevations from 2,911 to 3,457m (Gottfried et al., 1998). The GLORIA program monitors the long-term impacts of climate change on alpine and nival ecosystems by tracking changes in plant species composition on mountain summits worldwide (GLORIA, n.d.). A resurvey of 362 of these plots was conducted in 2004, with a second resurvey of 661 plots carried out in 2014 (Pauli et al., 2007; Lamprecht et al., 2018). In addition to long-term monitoring, various other research approaches have been or are currently being conducted at the Schrankogel test site (Gottfried et al., 1998; Hülber et al., 2005; Huber et al., 2007; Grabherr et al., 2010; Hofmann et al., 2016; Steinbauer et al., 2020; Chytrý et al., 2024; Helm et al., 2024)

My master thesis study was conducted in the context of the MICROCLIM project (MicroClim, n.d.), which started in 2021. The main aim of the project is to investigate how microscale environmental variations and plant-plant interactions influence alpine plant communities, particularly in response to ongoing climate change. It focuses on the buffering effects of small-scale climatic differences, which may help mitigate the predicted biodiversity loss in high altitude ecosystems. Another point is the accurate prediction of future species distributions in the area. This is achieved through a combination of long-term monitoring, species distribution modelling and experimental studies.

For my study, I am using the vegetation and environmental data collected in the framework of the MICROCLIM project. I contributed to its field campaign in July and August 2024.

Study site

The study was carried out on Schrankogel (3,497m a.s.l., 47°02’39.1” N, 11°05’56.0” E), a prominent peak typical for the Eastern Central Alps and located in Tyrol, Austria (Fig. 1). The mountain is part of the “Stubaier Alpen”, one of Austria´s highest alpine regions and lies within the upper Sulztal valley, a side valley of the Ötztal. The area is characterized by siliceous bedrock, consisting mainly of amphibolites and gneiss (Hoinkes et al., 2021). Typical soil types are leptosols and cambisols (Hofmann et al., 2016).

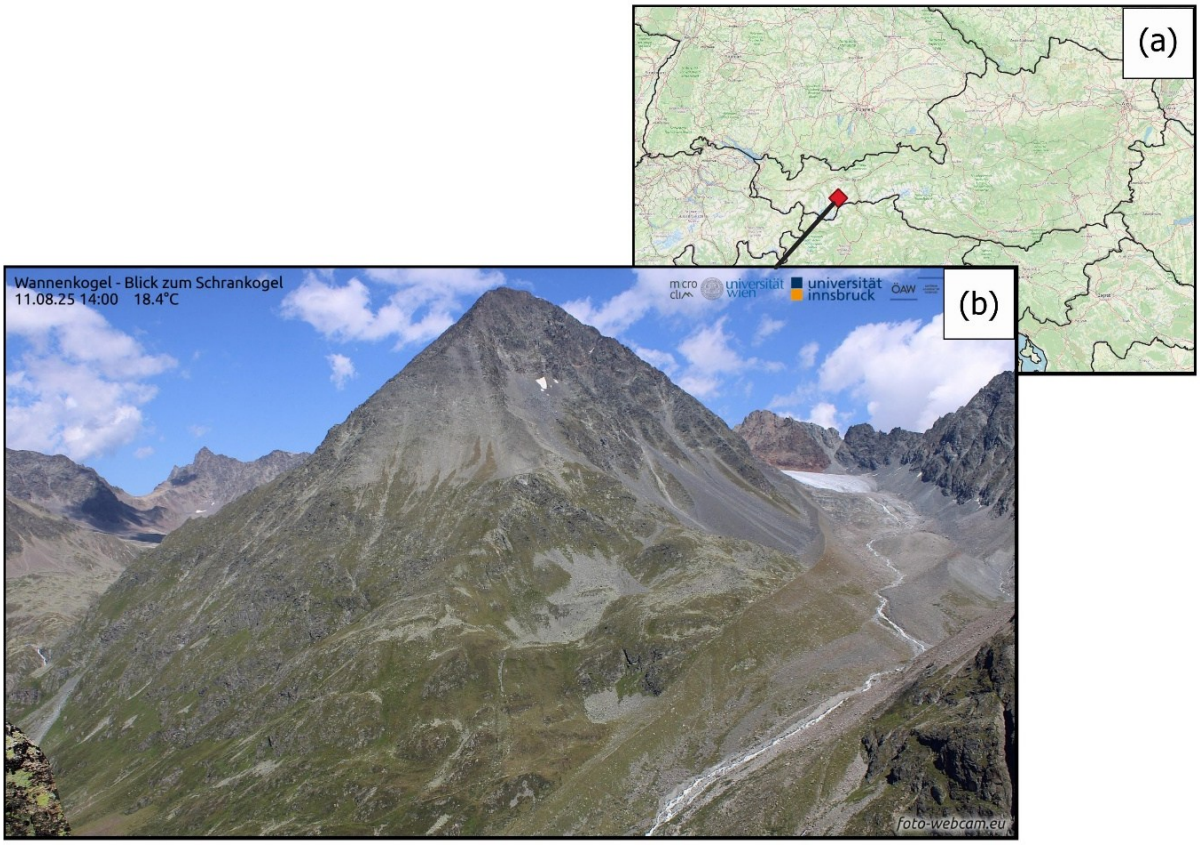

Figure 1. *(a) The location of Mount Schrankogel within Austria. (b) Mount Schrankogel as seen from Wannenkogel (8 August 2025 at 14:00 CET). Source: Basemap.at for the background layer (a) and Foto-Webcam.eu for the picture (b).*

There is no continuous weather data available directly from Mount Schrankogel. The nearest weather station can be found in Obergurgl (1,930m a.s.l.), which is located approximately 20 km south from the study site. Long term climate data shows a mean annual air temperature of 2.5 °C and annual precipitation of 889 mm (Chytrý et al., 2024). The seasonal variety can be seen in Figure 2. Using a standard lapse rate of 0.6 °C per 100m, the mean annual temperature at our study site can be estimated to range between -6.8°C and 3.4°C.

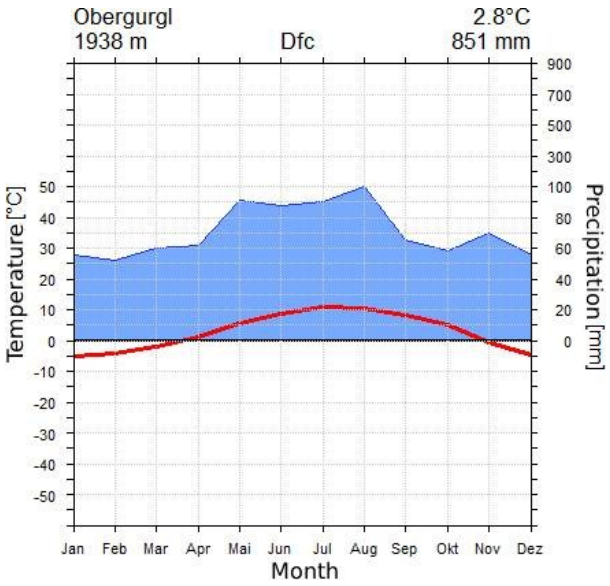

Figure 2. *Monthly temperature and precipitation profile for Obergurgl. Mean annual values in the figure (2.8 °C, 851 mm) differ slightly from reports in the paper due to measurement differences. Source: Klimadiagramme.de*

Schrankogel can be seen as a valuable "model mountain" for ecological research in the central Alps. It has a continuous and largely accessible altitudinal gradient from alpine grasslands up to the true nival zone. The mountain has all typical elements found in alpine to nival environments, including rocky ridgelines, enduring snowfields, scree covered slopes and isolated patches of cold adapted nival plants. The mountain´s northern and eastern side is surrounded by glaciers and glacier forelands, while its southern and western sides are glacier free (Gottfried et al., 1998). The study site is also part of the protected area of the "Naturpark Stubaier Alpen", which corresponds to an IUCN Category IV habitat/species management area (UNEP-WCMC, 2025).

The vegetation across the elevational gradient of the Schrankogel region reflects a diverse array of alpine communities, drawing on descriptions by Pauli et al. (2014) and Lamprecht (2012).

In the upper subalpine zone, acidic soils support *Rhododendretum ferruginei* heaths and stands dominated by *Salix helvetica*. The lower alpine belt hosts a variety of plant communities, including siliceous scree vegetation such as *Caricetum sempervirentis* (Rübel, 1911), as well as nutrient poor grasslands like *Sieversio-Nardetum strictae* (Lüdi, 1948) and *Agrostio schraderanae-Festucetum nigricantis* (Grabherr, 1993). In the upper alpine zone, *Caricetum curvulae* (Rübel, 1911) forms the dominant grassland type, shaped largely by the sedge *Carex curvula*. These grasslands are interspersed with pioneer species including *Oreochloa disticha*, *Festuca intercedens* and cushion plants such as *Silene exscapa* and *Minuartia sedoides.* As the elevation increases into the subnival and nival zones, vegetation becomes increasingly sparse. These regions are composed of highly specialized and cryophilic species typical of siliceous scree communities. That would include *Androsace alpina*, *Cerastium uniflorum*, *Poa laxa*, *Ranunculus glacialis* and *Saxifraga bryoides*.

Experimental setup

The MICROCLIM project structure was laid out into different Tasks. The first step and part of Task 5 was to establish 900 one square meter sampling plots, covering approximately 5 km^2 of the mountain. These plots were originally established in July 2021 and August 2022 by the MICROCLIM project team, whose plot design and sampling methodology are described in (Chytrý et al., 2024; Helm et al., 2024).

Plot locations were selected using a stratified random sampling approach that incorporated a range of environmental variables. This included elevation, both micro- and macro-slope, as well as fine- and coarse-scale Topographic Position Index (TPI) (Conrad et al., 2015; Wilson & Gallant, 2000). Additional criteria included potential incoming solar radiation (Bremer et al., 2016) and the Normalized Difference Vegetation Index (NDVI), representing peak vegetation activity during the 2020 growing season. Each plot was also geo-referenced using a high precision GPS device (~0.2m accuracy), which assigns it to a cell in a 1m-digital terrain model (DTM). A temperature logger (Geoprecision M-log 5W) was installed at the lower left corner of each plot, with its sensor tip positioned at a soil depth of 10 cm. The loggers recorded the temperature at hourly intervals with an accuracy of 0.1 °C.

The plots are distributed along an elevational gradient from 1,794 to 3,497 m.a.s.l., capturing the full range of subalpine, alpine and nival zones. They cover the entire non-forested accessible area of Mount Schrankogel and the adjacent south facing slope of the Sulztal valley. Very steep and hazardous areas had to be excluded from the sampling sites.

When the sampling campaign of 2021 ended, 767 T5 plots were available. From these, a subset of 57 plant species (Appendix, Table A1), referred to as target species, was selected to represent the overall flora of the area in terms of growth form, phylogenetic diversity and habitat preferences. This would lay the base for Task 7, which was centered around the monitoring of plant vital rates on Mount Schrankogel and will be the focus of this study. A total of 460 T5 plots were needed to ensure that each target species was represented by 24 to 34 occurrences, with no more than five species selected around any single plot.

The 1,658 T7 plots were established as follows (Fig. 3). 1-5 individuals of different target species were selected in close proximity to the T5 plots, usually within less than 2 meters. Each target individual was marked using bamboo sticks to ensure clear relocation and its distance from the logger was recorded to the nearest centimeter. A 20 x 20 cm frame was temporarily centered on each target individual, defining the neighborhood that would be used for further measurements. Each vascular plant species within the frame was recorded and its cover estimated independently by two observers. A nine-degree Braun-Blanquet type scale was used (r:0.1%, +:0.5%, 1a:2%, 1b:4%, 2a:10%, 2b:20%, 3:37.5%, 4:62.5%, 5:87.5%), following the approach described by Westhoff & Van Der Maarel (1978). In total, 232 vascular plant species (Appendix, Table A2) were recorded across all T7 plots combined. Furthermore, photographs were taken of the framed areas to assist with relocation and document changes over the years.

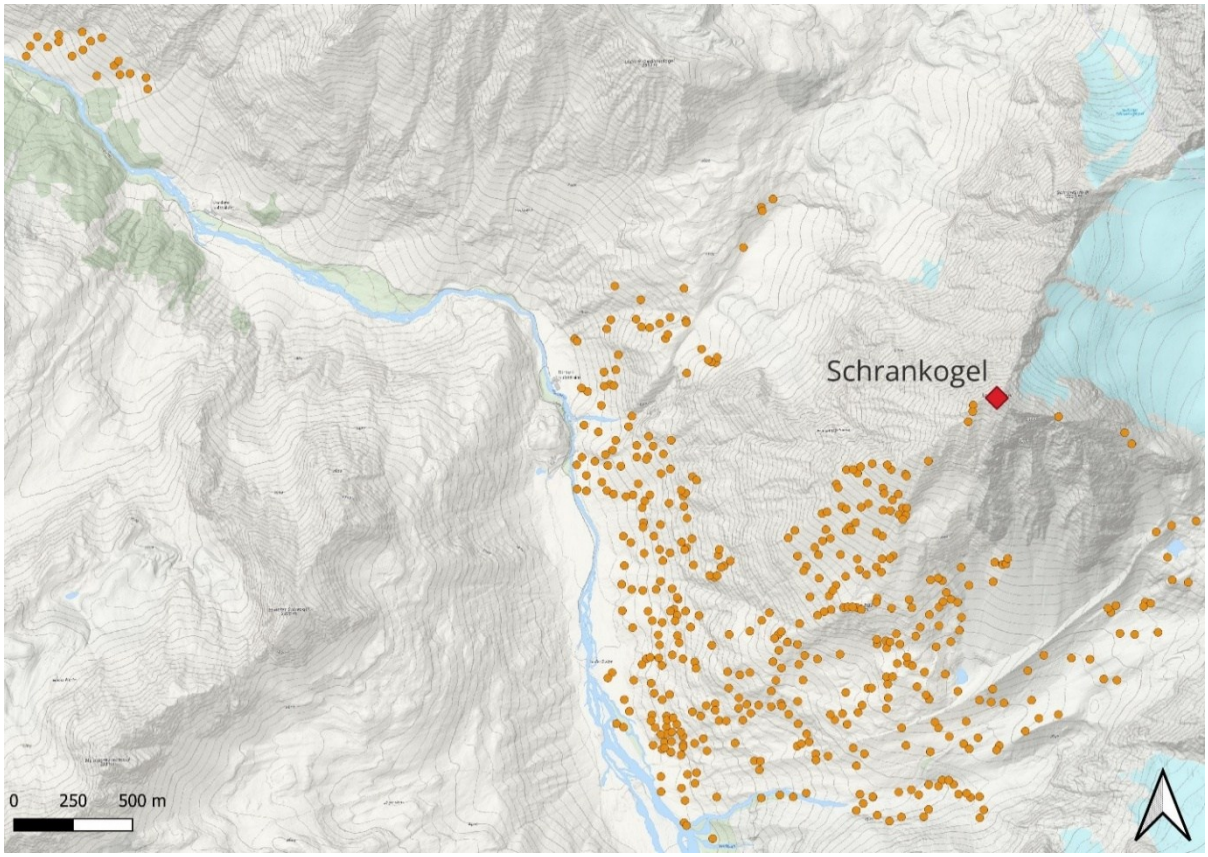

***Figure 3**. Location of the T7 plots (orange markers) on Schrankogel, with the summit indicated by a red diamond. Source: basemap.at for the background layer*

Field Measurements

The T7 plots were revisited each summer between 2022 and 2024 to perform various measurements. To minimize interannual phenological variations of the target plants, visitations were always done from late July to early August, which corresponded to the peak growing season of most alpine plants.

During fieldwork, plots were located using a QGIS extension mobile app called “QField”, which ran on mobile phones (Samsung Xcover 4S) exclusively used for the fieldwork. The App displayed the approximate location of each plot on a topographic map of the mountain and the exact location was identified with the help of reference photographs from previous years, as well as the wooden markers left behind. Once the plots were found, they were marked with a flagged stake labeled with their designated letter as seen in Figure 4.

Figure 4*. Overview picture of one of the T7 plots with five target individuals marked using flagged stakes.*

For each target individual, the following tasks were performed. A 20 x 20 cm frame was placed on the ground, with the target individual located in the center. A picture was taken with a DSLR camera, showing the whole frame, the plot number and its designated letter (Fig. 5). Several fitness parameters were then measured for each target individual.

- Vital status: It was assessed if the target individual was still alive or dead. If it was not visible or had only dry aboveground biomass, it was marked as dead, but the plot was still revisited the following year, as it might have regrown from underground organs.
- Cover: The cover of the target individual was estimated as the horizontal projection of its aboveground organs on the soil´s surface, rounded to the nearest percent and assessed annually by two observers.
- Reproductive output: Reproductive output was recorded as the number of reproductive units, such as flowers, inflorescences or entire stalks, depending on what was practical to count for each species.

Measurements were excluded from further analysis if target individuals could not be reliably identified or had been significantly impacted by external disturbances, including trampling, massive grazing or unintentional mowing.

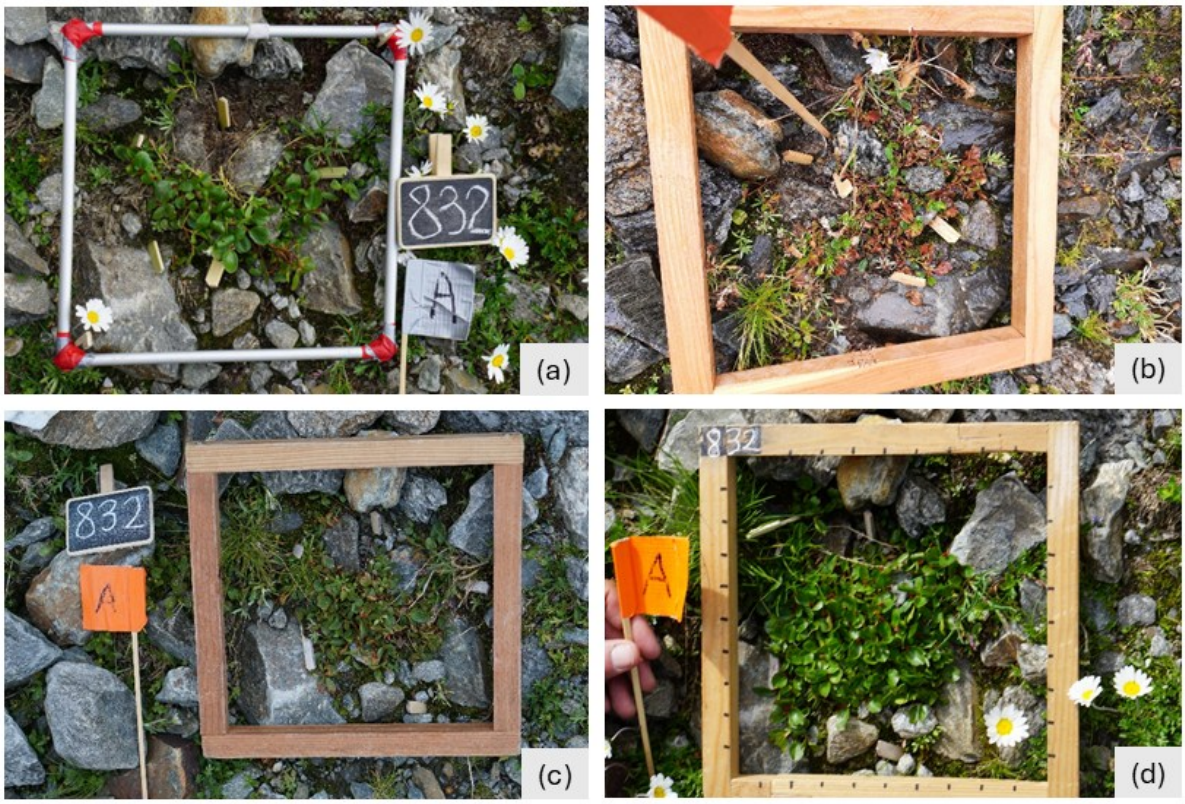

***Figure 5**. Annual photographs of plot 832A (2573 m a.s.l.) taken between 2021 and 2024. (a) 2021, (b) 2022, (c) 2023, (d) 2024.*

Figure 5, which represents the annual photographs of an exemplary plot, demonstrates interannual variation in the vegetation cover of alpine plants. The cover was 13.5 cm^2 in 2021, decreased to 11.5 cm^2 in 2022 and then increased to 18.5 cm^2 in 2023 and 23.5 cm^2 in 2024. In 2022, brown leaves are visible among the plant's foliage, suggesting exposure to some form of stress.

Data analysis

As we didn´t measure the leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) for the full set of the species in the plots, the trait data had to be requested from external sources. Two datasets (Request IDs: 37405 and 39214) were obtained from the TRY global trait data base (www.try-db.org; Kattge et al., 2020). A total of 62520 functional trait records were used, containing 17820 individual measurements of LA (mm^2), 26152 measurements of SLA (mm^2/mg) and 18548 of LDMC (%). Extreme outliers were disregarded, as these disproportionally skewed species means and likely reflected measuring or reporting errors. From this dataset, we calculated the mean values for each plant species to obtain representative trait estimates that could be used for further analysis.

To calculate the CSR strategies, we used the StrateFy tool developed by Pierce et al. (2017, Supplementary Table S2). The mean values of LA, SLA and LDMC were imported into the Excel worksheet, which was provided by the authors of the paper. The tool uses regression equations that were previously calibrated from a PCA of the mentioned three leaf traits in a global dataset. These equations were then used to calculate the relative proportions of the C, S and R parameters for each plant species, scaled so that their combined contribution equals 100%. While these three leaf traits do not capture all aspects of plant functioning, they are strongly associated with a wider range of physiological, morphological and reproductive characteristics, which should allow them to serve as effective indicators of ecological strategies. The same publication also provided a list of calculated CSR strategies for numerous plant species (Pierce et al., 2017, Supplementary Table S1), which we incorporated for species without data in our TRY dataset. Overall, CSR strategy data for 18 species out of 232 were missing, which were therefore excluded from further calculations. Given the small proportion of missing data (7.76%), it is unlikely to affect our results.

Community weighted means

A commonly used approach for quantifying the functional composition of plant communities is to use the community weighted means (CWM). CWMs represent the average trait value within a community, weighted by the relative abundance of each species (Ricotta & Moretti, 2011). This reflects more accurately which dominant ecological strategies are present and links the species level traits to a community level functional structure. I calculated them for the CSR strategies of each plot as:

$$Mean_{CSR} = \frac{\sum_{i=1}^{n}(cover_i \times CSR_i)}{\sum_{i=1}^{n} cover_i}$$

Where $cover_i$ is the percentage cover of species *i* in a given plot, CSR_i is the respective C, S, or R value of species *i*, and n is the total number of species in the plot.

To visualize distribution patterns at the species and community level, two ternary plots were generated using the plotly R package (Sievert, 2020). These plots display the relative proportion of the three strategy types for each species or community in a triangular

coordinate system, with values expressed as percentages. In addition, boxplots were created using the ggplot2 R package (Wickham, 2011) to summarize the overall distribution of the C, S and R components across the target species and the plots.

Cover change over time

To analyze changes in cover over time of our target species, both the absolute cover change and the relative cover change were calculated. I used both methods because they provide complementary perspectives on species' performance. The calculations were performed for consecutive yearly intervals from 2021 to 2024, using the following formulas:

Absolute change in cover:

$$\Delta C_{absolute} = C_t - C_{t-1}$$

Relative change in cover:

$$\Delta C_{relative} = ln(\frac{C_t}{C_{t-1}})$$

where C_t is the cover value in years t for a given species in a given plot and C_{t-1} is the cover value in the previous year.

Flower counts over time

The second measure for plant performance was flower count. There was data available for the number of flowers (F1), number of inflorescences (F2) and number of stalks (F3) produced by the target individuals each year. What exactly got counted differed from species to species due to their varying reproductive structures. To ensure comparability between them, all variables were combined into a single standardized metric, which is hereafter still referred to as "flowers" for simplicity. When more than one reproductive structure was counted for a species, priority was given in the order of F1 > F2 > F3. For each target individual, the number of flowers was calculated as the mean across all four years. The average measure provided a more reliable estimate of overall performance, as many individuals produced no flowers in some years.

Correlation tests

To check if there were strong relationships between the CSR strategies that could affect the analysis, a correlation test was conducted between the CWM values of C, S and R. Normality of the data was assessed using a Shapiro-Wilk test and through visual inspection of Q-Q plots. Because the data was not normally distributed, a Spearman rank correlation was used.

The results showed a moderate negative correlation between CWM-C and CWM-S ($\rho = -0.39$, $p < 0.001$), a weak positive correlation between CWM-C and CWM-R ($\rho = 0.06$, $p < 0.020$) and a strong negative correlation between CWM-S and CWM-R ($\rho = -0.89$, $p < 0.001$). Due to the high correlation between CWM-S and CWM-R, which could affect model interpretation, I decided to construct separate models including only one CSR strategy as a predictor at a time.

Effects of Elevation on Community CSR Strategies

Together with the community ternary plot I wanted to assess how community level CSR strategies vary along the elevational gradient. To do this, separate linear regression models were constructed for each CSR strategy, with CWM values as the response variable and elevation as the predictor.

Formula

CWM-CSR ~ elevation

Scatterplot graphs with regression lines were produced using the ggplot2 package in R.

Modelling species cover change

To assess whether species performance is influenced by the CSR strategies of their neighboring plant community, linear mixed effects models were fitted using the *lmer* function from the lme4 R package (Bates et al., 2015). The models either used absolute or relative change in cover as the response variable and the target species´ strategy deviation from the neighbors (CSR_diff), as well as its cover from the previous year (C_{t-1}) as the predictors. The strategy deviation for each target individual was calculated as the difference between its C, S or R strategy and the CWM of the same value of its plot (excluding the target species itself). Separate models were fitted for deviations in C, S and R strategy types (C_diff, S_diff and R_diff) but will be referred to as CSR_diff. To account for repeated measurements and hence potential dependencies in the data, random intercepts were included for year nested within species and for plot.

Formula

absolute_cover_change ~ CSR_diff + C_{t-1} + (1|species/year) + (1|plot)

relative_cover_change ~ CSR_diff + C_{t-1} + (1|species/year) + (1|plot)

Because the three axes of CSR strategies are inherently correlated, I also tested an integrated measure of CSR dissimilarity, called Euclidean distance. This measures the distance between the CSR coordinates of each target species and its surrounding community.

Modelling species flower count

To see whether the species reproductive output is influenced by the CSR strategies of their neighbors, generalized mixed effects models were fitted using the lme4 package in R. I initially fitted Poisson mixed models but overdispersion was detected each time. Models were therefore refitted using negative binomial mixed models from the same package. The mean number of flowers across years for each individual (mean_flowers) was used as the response variable and CSR_diff as well as the initial cover from the year 2021 (cover_T0) were used as the predictors. Due to variations in flower production across taxa, I added species as a random intercept.

Formula

mean_flowers ~ CSR_diff + cover_T0 + (1 | species)

Modelling species growth variability

Another hypothesis was centered around the growth variability of our target plants due to strategy deviations from the surrounding plant communities. To quantify interannual variability in plant growth, I calculated the standard deviation of relative annual cover change for each target plant (cover_SD). I fitted again linear mixed effects models with cover_SD as the response value and CSR_diff and cover_T0 as the predictors. Based on the interpretation of previous graphs, where I plotted CSR_diff against the relative cover changes of the plants, I expected a unimodal relationship. I therefore included the quadratic polynomial term for CSR_diff. Species and plot were used as random intercepts.

Formula

Cover_SD ~ CSR_diff + cover_T0 + (1 | species) + (1 | plot)

General statistical procedures

Prior to the analysis, all predictor variables were standardized to have a mean of 0 and a standard deviation of 1. This scaling ensures that the resulting model estimates represent the effect of a one standard deviation change in the predictor, which facilitates the later interpretation of the results. I also calculated the model fits, which were assessed using the marginal and conditional R^2 values, which represent the variance explained by the fixed effects (R^2m) and by both fixed and random effects (R^2c) (Nakagawa et al., 2017). To account for multiple testing across models, the Holm-Benferroni correction was applied (p.adjust function in R) whenever separate models were fitted for the same response variable, with the intention of reducing false positives (Holm, 1979).

All calculations and analyses in this thesis were conducted via Microsoft Excel and the statistical program R, version 4.2.0 (R Core Team, 2025), interfaced with Rstudio (RStudio Team, 2024). Overview maps were created using QGIS (QGIS Team, 2023). A map from Basemap.at was used to display topography and terrain context.

Results

Ternary plots of species and community level CSR compositions

Figure 6. displays the position of each species from our plots in the CSR triangle based on their unique strategy combination. A total of 232 species are represented. While a lot of species tend to cluster towards the S strategy type, some can also be seen to line up on the opposite side, which indicates an S score of 0%. Detailed CSR strategy scores for each species are available in the Appendix (Table A2).

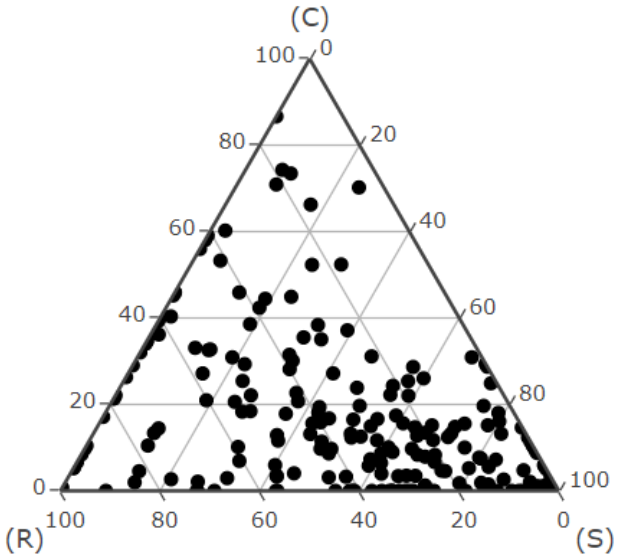

***Figure 6**. CSR strategy composition of the studied species. Each point represents one species and is positioned according to its relative proportion of competitive (C), stress tolerant (S) and ruderal (R) strategies.*

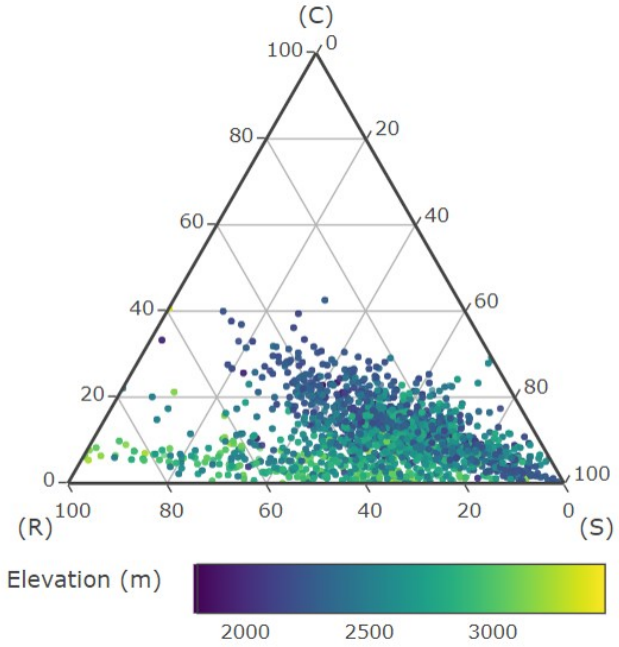

***Figure 7**. CWM-CSR strategy composition of each plot. Each point represents one community and is positioned according to its relative proportion of competitive (C), stress tolerant (S) and ruderal (R) strategies. Points are color coded by elevation (in meters).*

Figure 7. displays the position of each studied plot in the CSR triangle based on their CWM strategy combination. Overall, 1,658 plots are represented. Points are also colored by elevation, ranging from 1,794m to 3,456m. The community level ternary plot displays a similar pattern as seen before. In general, communities have a clear tendency for a high S score and a low C score. Notably, the highest C score observed is only 41.05%, while S and R reach scores of nearly 100%. Additionally, a clear elevational trend is visible. Plots on higher elevations show a downwards shift, which indicates a decrease of the C score. Shifting patterns for S and R are less intuitive to see and will be further examined in the following section.

Elevational patterns in community CSR strategies

The linear regression models revealed that as elevation increases, communities tend to shift further from a C and S strategy and more towards the R strategy type (Figure 8). C values decrease by approximately 0.92% per 100m ($p < 0.001$, $R^2m = 0.112$, $R^2c = 0.711$), S values decrease by about 0.77% per 100m ($p < 0.001$, $R^2m = 0.01$, $R^2c = 0.637$), while R values increase by roughly 1.75% per 100m ($p < 0.001$, $R^2m = 0.076$, $R^2c = 0.637$).

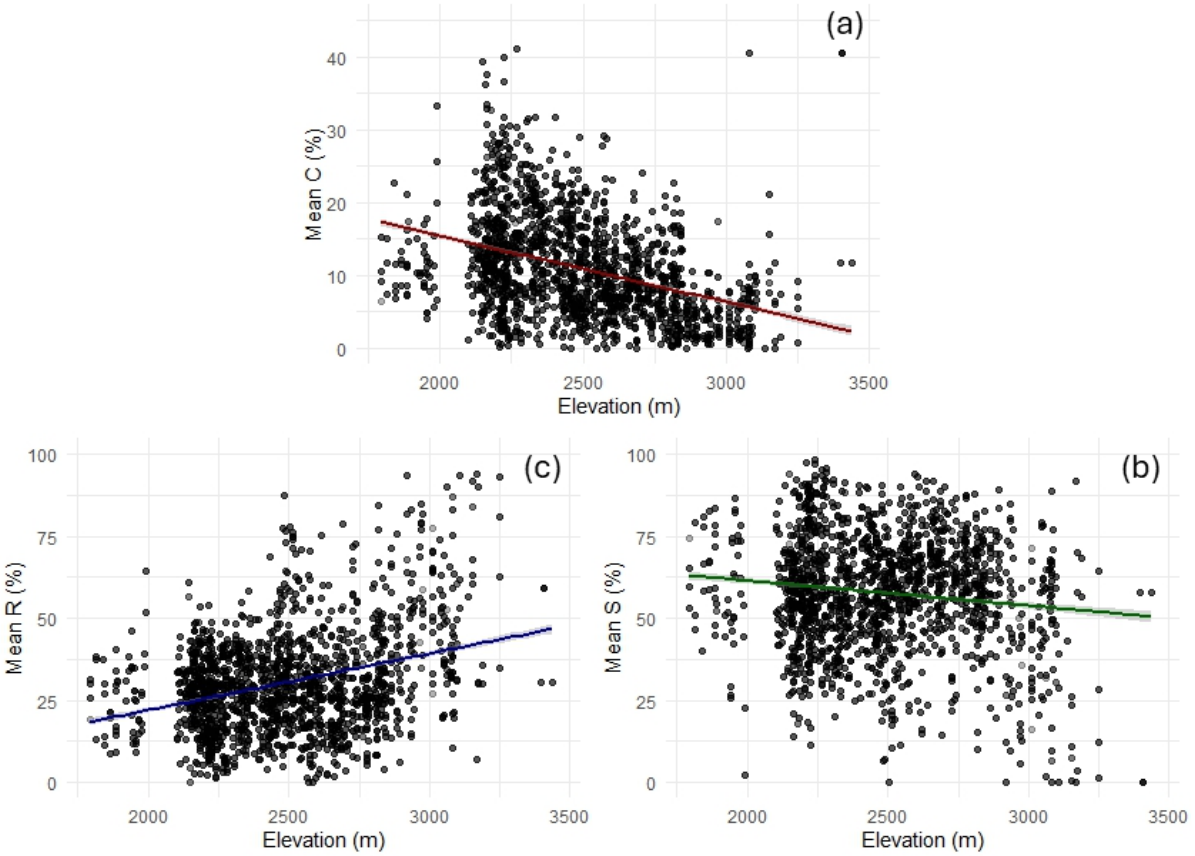

***Figure 8**. Scatterplots showing community level mean C (a), S (b) and R (c) scores in relation to elevation. Each dot represents a plot. The colored lines indicate linear trends fitted for each variable. Y axes are scaled individually due to differences in variable ranges (S and R: 0-100%, C: 0-45%).*

Distribution of CSR strategy scores

To further illustrate the patterns observed in the ternary plots, boxplots were created for the C, S and R components at both the species and community level.

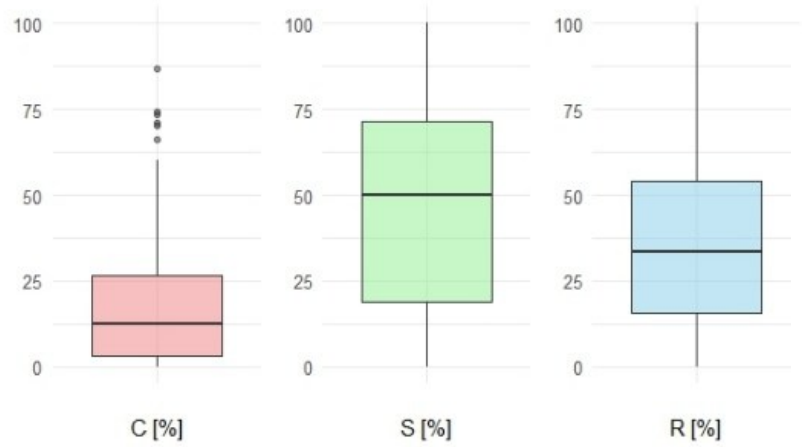

***Figure 9**. Boxplot showing the distribution of average CSR strategy scores calculated across all studied species, expressed as percentages (%). Colors represent the strategy types: competitive (red), stress tolerant (green) and ruderal (blue).*

The species level boxplot (Fig. 9) illustrates the observed trend of species clustering toward the stress tolerant strategy, with a median S value of 49.86%. In comparison, ruderal (R) strategies account for a median of 33.43%, while competitive strategies (C) are notably lower, with a median of 12.36%. While most species exhibit an overall low C score, a few species show exceptionally high competitive values, reaching up to 86.65%. The wide interquartile ranges for the S and R strategy types indicate that species vary widely in their degree of stress tolerance and ruderal strategies. Moreover, the whiskers for S and R extend across the full possible range, indicating that some species specialize almost exclusively in either the stress tolerance or ruderal strategy type.

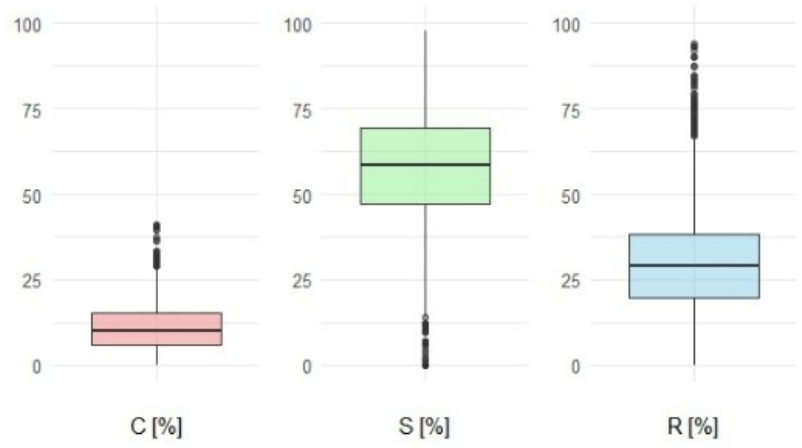

***Figure 10**. Boxplot showing the distribution of CWM-CSR strategy scores calculated across all plots, expressed as percentages (%). Colors represent the strategy types: competitive (red), stress tolerant (green) and ruderal (blue).*

The same pattern is even more pronounced at the community level, as shown in Figure 10. Here the median S score is 58.36%, while the R score is 28.91% and the C score is 10.00%. Competitive strategies are generally low, with some outliers reaching C scores of up to 40%. The relatively long whiskers and many outliers in the boxplots further indicate considerable variability among communities, especially for the S and R strategies.

Effects of CSR strategy deviations on species cover change

To investigate if changes in species cover over time are influenced by the deviation of the species´ CSR strategy from the community means, I modeled both absolute and relative cover change in relation to CSR strategy deviations between each species and its surrounding vegetation. I used linear mixed effects models including lagged cover (C_{t-1}) and one of the CSR strategy deviations (C_diff, S_diff or R_diff) as fixed effects, with plot and year nested in species as random intercepts. In total six models were fitted, three accounting for absolute cover change (Table 1) and three for relative cover change (Table 2).

Table 1. *Linear mixed effects model results for absolute cover change predicted by initial cover and CSR strategy deviations*

Predictors	*Estimate*	*Std.-error*	*P-value*
Model AC			
R^2m= 0.073, R^2c= 0.109			
absolute cover change ~ C_diff + C_{t-1} *+ random intercepts: plot, year nested in species*			
C_{t-1}	-1.370	0.081	< 0.001
C-diff	-0.099	0.096	0.621
Model AS			
R^2m= 0.074, R^2c= 0.111			
absolute cover change ~ S_diff + C_{t-1} *+ random intercepts: plot, year nested in species*			
C_{t-1}	-1.378	0.081	< 0.001
S-diff	0.124	0.098	0.621
Model AR			
R^2m= 0.073, R^2c= 0.109			
absolute cover change ~ R_diff + C_{t-1} *+ random intercepts: plot, year nested in species*			
C_{t-1}	-1.370	0.081	< 0.001
R-diff	-0.052	0.100	0.621

Table 2. *Linear mixed effects model results for relative cover change predicted by initial cover and CSR strategy deviations*

Predictors	*Estimate*	*Std.-error*	*P-value*
Model RC			
R^2m= 0.025, R^2c= 0.081			
relative cover change ~ C_diff + C_{t-1} *+ random intercepts: plot, year nested in species*			
C_{t-1}	-0.001	0.012	< 0.001
C-diff	-0.008	0.014	0.789
Model RS			
R^2m= 0.025, R^2c= 0.082			
relative cover change ~ S_diff + C_{t-1} *+ random intercepts: plot, year nested in species*			
C_{t-1}	-0.113	0.012	< 0.001
S-diff	0.015	0.014	0.789
Model RR			
R^2m= 0.025, R^2c= 0.082			
relative cover change ~ R_diff + C_{t-1} *+ random intercepts: plot, year nested in species*			
C_{t-1}	-0.112	0.012	< 0.001
R-diff	-0.015	0.014	0.789

Both absolute and relative cover change models showed a consistently strong negative effect of lagged cover (C_{t-1}) on subsequent cover changes ($p < 0.001$). In contrast, CSR strategy deviations between the target species and their neighbors (C_diff, S_diff, R_diff) did not significantly explain variation in cover change in either model.

Overall, model fit was relatively low. For absolute cover change, marginal R^2 values were approximately 0.073, with slightly higher conditional R^2 values around 0.110. For relative cover change, marginal R^2 values were lower at 0.025, while conditional R^2 values reached around 0.082.

All models showed singular fit, indicating that the variance associated with some random effects (plot, year or species) was estimated to be effectively zero. However, due to the sampling design, the random effects were retained.

Additional models that included elevation as a predictor were tested but elevation did not meaningfully improve model fit or change the interpretation of the results (Appendix Table A3 and A4). The models that used the Euclidian distance also showed no significant effect (Appendix Table A5). To explore if effects might be masked in the combined analysis, I also examined the results for each target species individually, but no significant effects were found either.

So, while the mixed effects models for cover change did not show any significance for CSR deviations, the graphs did show patterns for differences in growth variability (Appendix Figure A1). Results are presented in the matching chapter.

Effects of CSR strategy deviations on species flower production

To see if species strategy deviations influence flower production, negative binomial mixed effects models were fitted. The response variable was the mean flower count (mean_flowers), with CSR_diff and initial cover from the year 2021 (cover_T0) as fixed effects. Species was added as a random intercept. In total, three models were fitted (Table 3).

Table 3. *Negative binomial mixed effects model results for mean flower count predicted by initial cover and CSR strategy deviations*

Predictors	*Estimate*	*Std.-error*	*P-value*
Model FC			
R^2m= 0.101, R^2c= 0.109			
mean_flowers ~ C_diff + cover_T0 + random intercept: species			
Cover_T0	0.312	0.045	< 0.001
C-diff	-0.024	0.026	0.954
Model FS			
R^2m= 0.102, R^2c= 0.112			
mean_flowers ~ S_diff + cover_T0 + random intercept: species			
Cover_T0	0.313	0.044	< 0.001
S-diff	0.022	0.026	0.954
Model FR			
R^2m= 0.104, R^2c= 0.115			
mean_flowers ~ R_diff + cover_T0 + random intercept: species			
Cover_T0	0.317	0.044	< 0.001
R-diff	-0.027	0.027	0.954

The models for mean flower count (Table 3) revealed a consistently strong positive effect of initial cover (cover_T0) on flower production across all three models ($p < 0.001$). In contrast, deviations in CSR strategy scores (C_diff, S_diff, R_diff) had also no significant effects on flower production ($p = 0.954$). Marginal R^2 values ranged from 0.101 to 0.104 and conditional R^2 values ranged from 0.109 to 0.115.

Effects of CSR strategy deviations on species growth variability

For the analysis of the interannual variability in plant growth, I fitted linear mixed effect models with cover_SD as the response value and CSR_diff and cover_T0 as the predictors (Table 4). For CSR_diff I included the quadratic polynomial term. Species and plot were added as random intercepts.

Table 4. *Linear mixed effects model results for growth variability predicted by initial cover and CSR strategy deviations*

Predictors	*Estimate*	*Std.-error*	*P-value*
Model			
R^2m= 0.002, R^2c= 0.153			
Cover_SD ~ C_diff + cover_T0 + random intercept: species, plot			
Cover_T0	-0.003	0.018	0.870
C-diff (linear)	-0.022	0.021	0.299
C-diff (quadratic)	-0.001	0.011	0.902
Model			
R^2m= 0.008, R^2c= 0.148			
Cover_SD ~ S_diff + cover_T0 + random intercept: species, plot			
Cover_T0	-0.003	0.018	0.877
S-diff (linear)	0.021	0.021	0.311
S-diff (quadratic)	-0.043	0.014	0.002
Model			
R^2m= 0.005, R^2c= 0.142			
Cover_SD ~ R_diff + cover_T0 + random intercept: species, plot			
Cover_T0	-0.001	0.018	0.942
R-diff (linear)	0.029	0.021	0.176
R-diff (quadratic)	-0.029	0.013	0.022

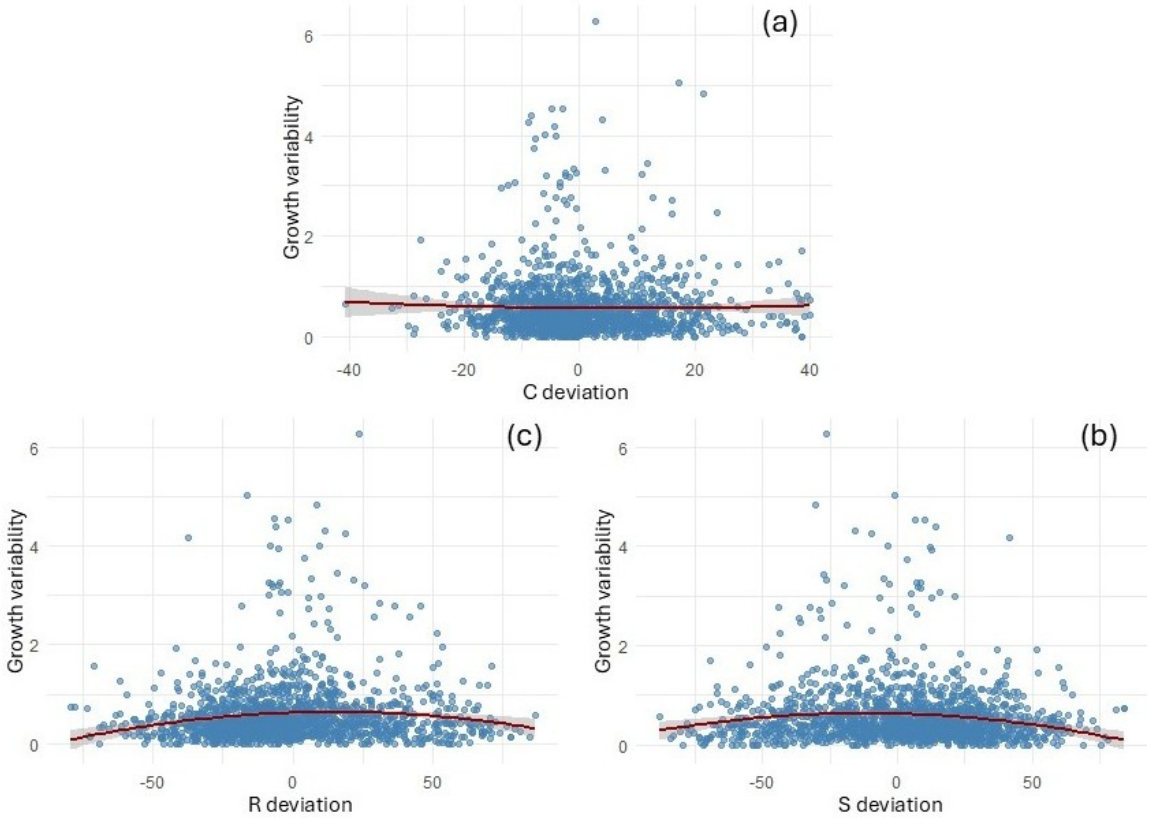

Figure 11. *Scatterplots showing the relationship between growth variability (standard deviation of relative cover change) and C_diff (a), S_diff (b) and R_diff (c), expressed in percentage (%). Each dot represents a target Individuum and the red curves show the quadratic regression fits with a 95% confidence interval. The x-axis vary in scaling due to differences in the min/max variables.*

Across all three models, growth variability showed no linear relationship with the strategy deviations (C_diff, S_diff, R_diff). However, when tested for nonlinear effects using the quadratic term, S_diff and R_diff had a significantly negative relationship, indicating a unimodal shape. C_diff still didn´t show any significance. This can also be seen in Figure 11, as S and R growth variability is highest in intermediate levels of trait deviation and declines towards the extremes. Overall, the fixed effects however explained only a small proportion of variance in all three models (R^2m <0.01). Conditional R^2 values (0.14-0.15) indicate that the majority of the explained variances in growth variability got attributed to the random intercepts of species and plot.

Discussion

Weak effects of CSR strategy deviations on plant performance

The main aim of this study was to test whether the performance of alpine plant species depends on the functional composition of their neighboring community, expressed in terms of CSR strategy types. Contrary to expectations, deviations in CSR strategy scores of neighbors did not significantly affect changes in the target species´ performance. These results suggest that the performance of alpine plant species is only weakly related to the CSR composition of the plant community they live in. There are a few factors that might influence the weak relationships observed in this study.

There has been quite some research done on the CWM trait values in different habitats and how plants grow where their traits align most with their surrounding community. One study on tropical tree seedlings for example found that widespread species were generally closer to the CWM trait values and exhibited lower overall trait variation (Umaña et al., 2015). Muscarella & Uriarte (2016), on which findings I based my hypothesis on, also concluded that most of their analyzed species had a higher occurrence where their trait value aligned more closely to the CWM. However, Mitchell et al. (2018) expanded on this study and concluded that plant species do not converge toward the trait optima of their habitats. They did not find any consistent patterns that would demonstrate that species were nearer the CWM in habitats where they occurred more frequently, compared to where they were less abundant.

I looked at the traits that got used in these studies to see if there was any pattern. Mitchell et al. assessed SLA and LDMC and found no significant effect. Umaña et al. (2015) analyzed LA, SLA, leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF), leaf area ratio (LAR), stem specific length (SSL) and leaf thickness (LT). In their findings, LT, LA and SLA from abundant species did not align closely with median community values. Muscarella & Uriarte tested wood density (WD) and leaf mass per area (LMA) and found about 70% of species supported the CWM optimality hypothesis for at least one trait, while about 25% of species significantly opposed the hypothesis for at least one trait. It seems that the traits used by the StrateFy tool might not be adequate for placing alpine plants at their optimal CSR strategy. StrateFy is a broad tool that is built to be used on all global biomes. This makes it able to place plants reliably at their general ecological strategies (Li & Shipley, 2017) but it thereby sacrifices accuracy, which might make it struggle to capture fine scale differences. Umaña et al. (2015) also points out that traits like LAR and LMF are related to photosynthetic and respiration rates, which are expected to be closer related to growth than others (Poorter et al., 2012). LT, LA and SLA are organ level traits and can be difficult to interpret without broader information about the whole plant allocation (Marks, 2007).

Mitchell et al. (2018) also added that CWM might be a poor measure for the environmental trait optimum. They argue that Evolutionary constraints can limit trait expression and dominant species with unique trait expressions can disproportionately influence the CWM.

Rosado & De Mattos (2017) examined the limitations of the StrateFy tool itself. They used the CSR analysis to see if in a highly stressful environment, dominant plant species would show a greater proportion of the S strategy than subordinate species. While the tool reliably classified all species as having a S/CS strategy, the most dominant species had neither similar values nor the highest S scores. They found this to be specifically true for extreme environments where CSR strategies occur in a narrower range, to which mountain ecosystems also belong. Another study found similar problems, where the StrateFy tool gave two different plants the same strategy type (S/CSR), even though one was a typical stress tolerant species and the other a very competitive species (Novakovskiy et al., 2021). They seemed very similar based on their LA, SLA and LDMC values but varied strongly in their height. Novakovskiy et al. (2021) concluded that a morpho-physiological model using additional plant traits is therefore more precise but also requires much more experimental data.

For this study, the hypothesis was based on the fact that CWMs would filter for the best strategy type of the local environment. If the target species´ strategy type was closer to the matching CWM, it should therefore perform better. These findings however support the idea that LA, SLA and LDMC are not enough to reliably explain a plant species´ optimum strategy type in this environment. As the models rely on this assumption, this would explain the continuous weak and insignificant findings. While this seems to be the most prominent argument of why my results oppose the hypothesis, there are some other ideas that I want to discuss.

One other reason might be that the temporal scale of the experiment is just too short to see any significant changes in the overall growth rate tendency, especially given the alpine environment, where plants typically already have a slow growth rate due to temperature constraints (Nagelmüller et al., 2017; Körner, 2021). Additionally, the study period coincided with unusually warm years and may therefore not reflect the long-term climatic conditions under which the local vegetation developed.

Our leaf traits were taken from the TRY database and we calculated the species average values. This leaves out any plasticity and intraspecific variation that might happen in response to environmental conditions. As shown by Henn et al. (2018), trait expression can shift considerably across temperature gradients. Target species might therefore express different CSR strategy scores than the ones we assigned to them, which would weaken the relationship between CSR_diff and the target plant´s performance. Furthermore, the cover of the neighboring plants was taken from the first year (2021) and not remeasured afterwards. Temporal changes of their abundance were therefore not captured and as a result their influence might have been misrepresented.

Weak effects of CSR strategy deviations on growth variability

This hypothesis was motivated by patterns observed in the relationships between growth rate and CSR deviations (Appendix Figure A1). The interpretation was that plants that differ less in their CSR strategies compared to their neighbors would show more growth variability. In the results the growth variability models showed significance for the S and R deviations but not

for the C deviations (Figure 11). However, considering how low the estimated coefficients are and that the model only explains a negligible proportion of the variances, the results are of limited ecological importance. There are multiple reasons why this might be the case.

For once, it is possible that the ecological effect of CSR strategy deviations on the growth variability is by itself very small. The significance in the findings is then potentially related to the larger sample size (n = 1,562), which enables us to detect a consistent effect, even though it is very weak. The model was also run with other environmental factors, like elevation, temperature or snow cover but they added little explanatory benefits. Most of the explained growth variability that the models capture relates back to the random effects of species identity and local site conditions. What the models do not capture are then other species- or site-specific factors and episodic disturbance events.

Additionally, this relates back to the same problems encountered with the previous models, concerning cover change and flower production. The CSR strategy scores are taken from the StrateFy tool, weakening the ability of the models to detect any meaningful relationships.

Community assembly and CSR strategy shifts with elevation

Looking at the scatterplots (Figure 8) and the CWM ternary plot (Figure 7) in relation to the elevational gradient, we see that it mostly follows the successional trajectory of plant communities in the central Alps as described by Pierce et al. (2017, Fig.4). Pierce and colleagues describe a transition from ruderal strategies, typical for highly disturbed alpine scree slopes (*Thlasietea rotundifolii* Br.-Bl. et al. 1947), towards more stress tolerant alpine snow bed vegetations (*Salicetea herbaceae* Br.-Bl. Et al. 1947) and siliceous alpine grasslands (*Caricion curvule* Br.-Bl. 1925), to then more competitive strategies in the siliceous alpine pastures (*Nardion strictae* Br.-Bl. in Br.-Bl.& Jenny 1926). The Pierce et al. community assembly matches the description of the Schrankogel as previously described by Lamprecht (2012) and Pauli et al. (2014).

Findings seem to be consistent with recent studies. Competition is typically stronger at lower elevations and in environments with low abiotic stress but tends to decline with altitude and augmenting environmental stress (Choler et al., 2001; Callaway et al., 2002; Zanzottera et al., 2020). Ruderals on the other hand increase continually with elevational gain. From ~2,500m onwards, habitats affected or even dominated by mobile scree become frequent at Schrankogel and are primarily inhabited by species that are adapted to severe and frequent disturbances (Liu et al., 2025b). This can also explain why S goes down in Figure 8b. While stress tolerance is expected to increase with elevation due to increasing environmental stress (Gobbi et al., 2010), the upper part of the mountain seems to favor ruderal strategies. Because CSR components are constrained to sum up to 100% and S scores are already high in the low to mid elevations, a strong increase in R reduces the contribution of other S selective strategy components. The observed decline in S should therefore not be interpreted as a decline in environmental stress but is rather a shift in the community strategy composition towards more disturbance adapted species.

Conclusion

Overall, the results indicate that neither plant growth, flower production nor growth variability of individual mountain plants seem to be influenced by the CSR strategy deviations between them and their surrounding community. While some statistically significant relationships were detected, the explained variance by CSR deviations was consistently small. Most of the explained variances were instead attributed to the species identities and local site conditions. The findings also suggest that CSR based approaches that only use a limited set of leaf traits (LA, SLA and LMC) may not sufficiently capture the complexity of a plants strategy allocation that is needed to reflect its performance. So, while the CSR framework provides a valuable conceptual basis for the comparison of plant strategies, the StrateFy tool appears to be limited in its ability to capture more fine scale variations of alpine plants. However, when tested on a broader scale, the findings align with previous work. The Stratefy´s ability in placing plants or communities at their generally right CSR strategy thereby seems to be consistent.

I conclude that the results brought new evidence to an ongoing discussion on the applicability of trait-based strategy frameworks and how many traits are needed to reliably capture a plants strategy allocation. Future research around community assembly patterns and plant performances that use such a strategy framework would benefit from incorporating other integrative traits (e.g. plant height or leaf dry weight) if they rely on accuracy. It would be interesting to repeat the experiment with a morpho-physiological model to see if more detailed trait information would improve the ability of the CSR framework to answer my hypotheses.

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Appendix

Table A1 - *List of the T7 target species*

Target species	
Achillea moschata	Mutellina adonidifolia
Agrostis agrostiflora	Nardus stricta
Agrostis alpina	Oreochloa disticha
Agrostis rupestris	Oxyria digyna
Androsace alpina	Persicaria vivipara
Anthoxanthum alpinum	Phyteuma hemisphaericum
Avenula versicolor	Poa alpina
Bartsia alpina	Poa laxa
Calluna vulgaris	Primula glutinosa
Campanula barbata	Primula minima
Carex curvula	Ranunculus glacialis
Carex sempervirens	Ranunculus villarsii
Cerastium uniflorum	Salix herbacea
Crepis aurea	Saxifraga bryoides
Deschampsia cespitosa	Saxifraga exarata
Festuca nigrescens	Scorzoneroides helvetica
Festuca nigricans	Sedum alpestre
Geranium sylvaticum	Senecio incanus
Geum montanum	Sibbaldia procumbens
Geum reptans	Silene acaulis
Gnaphalium supinum	Solidago virgaurea
Homogyne alpina	Trifolium badium
Juncus trifidus	Vaccinium gaultherioides
Kobresia myosuroides	Vaccinium myrtillus
Leucanthemopsis alpina	Vaccinium vitis-idaea
Loiseleuria procumbens	Veronica alpina
Luzula alpino-pilosa	Veronica bellidioides
Luzula lutea	Viola biflora
Luzula spicata	

Table A2 - *List of the 232 observed plant species in the T7 plots on mount Schrankogel and their calculated CSR values*

ID	Species	C%	S%	R%
1.	Achillea millefolium	22	58.8	19.2
2.	Achillea moschata	5.8	58.9	35.3
3.	Acinos alpinus	4.7	74.1	21.2
4.	Adenostyles alliariae	86.7	0	13.3
5.	Agrostis agrostiflora	9.7	49.5	40.8
6.	Agrostis alpina	1.1	95.2	3.7
7.	Agrostis rupestris	1.9	83.5	14.7
8.	Agrostis stolonifera	11.4	46.7	41.9
9.	Ajuga pyramidalis	27.2	41.1	31.7
10.	Alchemilla alpina	15.2	66.9	17.9
11.	Alchemilla vulgaris	37.2	39	23.9
12.	Allium lusitanicum	NA	NA	NA
13.	Androsace alpina	0	43.2	56.8
14.	Androsace obtusifolia	0	27.5	72.5
15.	Antennaria carpatica	10	76.1	13.9
16.	Antennaria dioica	1.8	79.1	19.1
17.	Anthoxanthum alpinum	8.7	60	31.3
18.	Anthoxanthum odoratum	8.4	67.4	24.2
19.	Anthyllis vulneraria	32	0	68
20.	Arabis alpina	9.7	0	90.3
21.	Arctostaphylos uva-ursi	11.3	88.7	0
22.	Arenaria biflora	0	43.5	56.5
23.	Arenaria ciliata	1.4	98.6	0
24.	Arnica montana	59.1	0	40.9
25.	Aster alpinus	10.1	60.8	29.2
26.	Astragalus frigidus	32.7	13.7	53.5
27.	Avenella flexuosa	3.5	67.7	28.8
28.	Avenula versicolor	14.6	85.2	0.1
29.	Bartsia alpina	7.3	58.5	34.2
30.	Bellidiastrum michelii	34.4	0	65.6
31.	Botrychium lunaria	25.4	23.8	50.7
32.	Briza media	22.1	27.2	50.7
33.	Calamagrostis villosa	19.4	42.3	38.3
34.	Calluna vulgaris	0	92	8
35.	Campanula barbata	18.4	28.9	52.7
36.	Campanula scheuchzeri	3.1	52.3	44.6
37.	Cardamine alpina	NA	NA	NA
38.	Cardamine resedifolia	4	62.4	33.6
39.	Carex aterrima	17.4	58.6	24
40.	Carex capillaris	0.8	85.4	13.8
41.	Carex curvula	6	94	0
42.	Carex echinata	5.6	83.1	11.3

43.	Carex ferruginea	15.6	73.3	11.1
44.	Carex frigida	23.8	47.6	28.6
45.	Carex nigra	15.6	60.9	23.4
46.	Carex ornithopoda	8.3	71	20.7
47.	Carex sempervirens	14.8	71.7	13.4
48.	Carlina acaulis	44.4	18.9	36.7
49.	Cerastium alpinum	2.1	26.5	71.4
50.	Cerastium arvense	3.5	41.6	54.9
51.	Cerastium cerastoides	0	30.9	69.1
52.	Cerastium fontanum	10.5	12.3	77.2
53.	Cerastium uniflorum	6.6	0	93.4
54.	Chaerophyllum villarsii	NA	NA	NA
55.	Chamorchis alpina	21.4	0	78.6
56.	Cirsium acaule	74.3	7.4	18.3
57.	Cirsium spinosissimum	29.4	70.6	0
58.	Clematis alpina	44.9	23.9	31.2
59.	Coeloglossum viride	34.6	0	65.4
60.	Crepis aurea	18.3	27.3	54.4
61.	Crocus albiflorus	16.6	55.3	28.1
62.	Cystopteris alpina	NA	NA	NA
63.	Deschampsia cespitosa	13.5	66.5	20.1
64.	Diphasiastrum alpinum	7.2	83.7	9
65.	Doronicum clusii	36.5	0	63.5
66.	Doronicum grandiflorum	39.3	0	60.7
67.	Draba dubia	0	85	15
68.	Draba fladnizensis	NA	NA	NA
69.	Dryas octopetala	7.5	80.6	11.9
70.	Dryopteris carthusiana	73.4	9.5	17.1
71.	Dryopteris dilatata	42.4	18.7	38.9
72.	Dryopteris filix-mas	70.9	7.9	21.2
73.	Empetrum hermaphroditum	0	93.9	6.1
74.	Epilobium anagallidifolium	0	59	41
75.	Epilobium collinum	NA	NA	NA
76.	Epilobium nutans	10.2	30.5	59.3
77.	Equisetum arvense	14.7	63.8	21.5
78.	Erigeron alpinus	16.7	43.4	39.9
79.	Erigeron uniflorus	2.7	20.9	76.4
80.	Euphorbia cyparissias	0	55.2	44.8
81.	Euphrasia minima	2	13.9	84.1
82.	Euphrasia officinalis	3.3	55.6	41.1
83.	Festuca halleri	2.1	93.2	4.8
84.	Festuca nigrescens	6.7	71.7	21.6
85.	Festuca nigricans	NA	NA	NA
86.	Fragaria vesca	38.6	18.8	42.7
87.	Galium anisophyllon	0	74.9	25.1
88.	Gentiana acaulis	13.2	81.8	5

89.	Gentiana bavarica	0	66	34
90.	Gentiana brachyphylla	0	66.6	33.4
91.	Gentiana nivalis	0	0	100
92.	Gentiana punctata	60.2	3	36.8
93.	Gentianella campestris	5.4	0	94.6
94.	Geranium sylvaticum	35.5	31	33.5
95.	Geum montanum	28.7	56.4	14.9
96.	Geum reptans	28.7	71.3	0
97.	Gnaphalium norvegicum	17.8	36.3	45.9
98.	Gnaphalium supinum	0	64.5	35.5
99.	Gnaphalium sylvaticum	12.3	52.2	35.5
100.	Gymnadenia conopsea	58	0	42
101.	Gymnocarpium dryopteris	33.1	10.5	56.4
102.	Helianthemum nummularium	11.8	68.9	19.3
103.	Hieracium alpinum	27.2	15	57.9
104.	Hieracium glanduliferum	26.3	0	73.7
105.	Hieracium hoppeanum	35.1	34.8	30.1
106.	Hieracium intybaceum	32.6	13.4	54
107.	hieracium piliferum	NA	NA	NA
108.	Hieracium pilosella	22.7	36	41.3
109.	Hieracium villosum	29.3	22.3	48.4
110.	Homogyne alpina	24.9	73.9	1.2
111.	Huperzia selago	0	81.3	18.7
112.	Hypochaeris uniflora	45.9	0	54.1
113.	Juncus jacquinii	12.4	87.6	0
114.	Juncus trifidus	5.8	94.2	0
115.	Juniperus communis	0	86.6	13.4
116.	Kobresia myosuroides	5.1	94.9	0
117.	Laserpitium halleri	70.2	24.8	5
118.	Leontodon hispidus	45.9	0	54.1
119.	Leucanthemopsis alpina	5.2	0	94.8
120.	Linaria alpina	0	9.1	90.9
121.	Lloydia serotina	34.7	0	65.3
122.	Loiseleuria procumbens	0	100	0
123.	Lotus corniculatus	4.1	44.8	51.1
124.	Luzula alpina	NA	NA	NA
125.	Luzula alpino-pilosa	16.8	45.5	37.7
126.	Luzula lutea	13.3	71.8	14.9
127.	Luzula luzuloides	20.7	37.3	42
128.	Luzula multiflora	9.7	47.3	42.9
129.	Luzula spicata	1.2	96.5	2.3
130.	Melampyrum sylvaticum	17.1	0	82.9
131.	Minuartia gerardii	0	62.5	37.5
132.	Minuartia recurva	0.3	85.8	13.9
133.	Minuartia sedoides	0	87.6	12.4
134.	Mutellina adonidifolia	NA	NA	NA

135.	Myosotis alpestris	20.6	24.7	54.7
136.	Nardus stricta	4.8	90.5	4.7
137.	Nigritella rhellicani	NA	NA	NA
138.	Oreochloa disticha	1.6	98.4	0
139.	Oxyria digyna	22.1	0	77.9
140.	Oxytropis campestris	31.5	30.2	38.3
141.	Parnassia palustris	21	18.8	60.2
142.	Pedicularis aspleniifolia	NA	NA	NA
143.	Pedicularis kerneri	19.7	75.1	5.3
144.	Pedicularis recutita	NA	NA	NA
145.	Pedicularis tuberosa	25.4	57.1	17.6
146.	Persicaria vivipara	19.7	50.2	30.1
147.	Peucedanum ostruthium	66.2	17.1	16.7
148.	Phleum alpinum	9.7	65.7	24.6
149.	Phyteuma betonicifolium	40.2	0	59.8
150.	Phyteuma globulariifolium	3.3	41.8	54.9
151.	Phyteuma hemisphaericum	2.9	32	65.1
152.	Phyteuma orbiculare	15	54.8	30.3
153.	Pimpinella saxifraga	38.4	32.5	29.1
154.	Pinguicula leptoceras	NA	NA	NA
155.	Poa alpina	15.2	78.2	6.7
156.	Poa laxa	11.7	57.7	30.6
157.	Poa nemoralis	6.9	32.4	60.6
158.	Potentilla aurea	15.6	42.7	41.6
159.	Potentilla crantzii	12.8	65.2	22.1
160.	Potentilla erecta	16.5	50.5	33
161.	Potentilla frigida	NA	NA	NA
162.	Potentilla grandiflora	26	59.8	14.1
163.	Primula glutinosa	21.4	0	78.6
164.	Primula hirsuta	29	0	71
165.	Primula minima	1.4	98.6	0
166.	Prunella vulgaris	12.5	54	33.5
167.	Pseudorchis albida	36.6	0	63.4
168.	Pulsatilla alpina	45.9	12.9	41.2
169.	Pulsatilla vernalis	30.9	67.1	2
170.	Pyrola minor	13.2	51.6	35.1
171.	Ranunculus acris	53.3	5.5	41.3
172.	Ranunculus glacialis	40.6	0	59.4
173.	Ranunculus kuepferi	22.2	55.1	22.7
174.	Ranunculus villarsii	28.2	31.9	39.9
175.	Rhinanthus glacialis	6	40.1	53.9
176.	Rhododendron ferrugineum	9.3	90.7	0
177.	Rubus idaeus	52.3	24.3	23.4
178.	Rumex alpestris	56	0	44
179.	Rumex scutatus	34	0	66
180.	Sagina saginoides	0	70.8	29.2

181.	Salix helvetica	18.1	42.7	39.2
182.	Salix herbacea	4.6	74.9	20.5
183.	Salix reticulata	10.5	89.5	0
184.	Salix retusa	1.3	72.5	26.2
185.	Salix serpyllifolia	2.6	87.6	9.8
186.	Saussurea alpina	30.1	31.5	38.4
187.	Saxifraga aizoides	0	66.6	33.4
188.	Saxifraga androsacea	0.7	0	99.3
189.	Saxifraga bryoides	0	68	32
190.	Saxifraga exarata	0	90.5	9.5
191.	Saxifraga oppositifolia	0	69.9	30.1
192.	Saxifraga paniculata	10.2	89.8	0
193.	Saxifraga seguieri	0	0	100
194.	Saxifraga stellaris	10.5	0	89.5
195.	Scabiosa lucida	NA	NA	NA
196.	Scorzoneroides helvetica	12.9	37	50.1
197.	Sedum acre	0	0	100
198.	Sedum alpestre	0	92.7	7.3
199.	Selaginella selaginoides	0	58	42
200.	Sempervivum montanum	0.2	95.8	4.1
201.	Senecio doronicum	16.1	80	3.9
202.	Senecio incanus	18	78.9	3.1
203.	Sibbaldia procumbens	7.9	69.2	22.9
204.	Silene acaulis	0	27.3	72.7
205.	Silene nutans	40.4	2	57.7
206.	Silene vulgaris	45.2	0	54.8
207.	Soldanella pusilla	6.4	61.1	32.4
208.	Solidago virgaurea	31.1	46.9	22
209.	Stellaria graminea	14.5	12.5	73.1
210.	Thesium alpinum	NA	NA	NA
211.	Thymus praecox	0	69.1	30.9
212.	Thymus pulegioides	1.5	85.1	13.4
213.	Tofieldia pusilla	3.4	66.1	30.5
214.	Trichophorum cespitosum	NA	NA	NA
215.	Trifolium alpinum	12.4	71.5	16
216.	Trifolium badium	15.9	44.3	39.9
217.	Trifolium pallescens	9	62.1	28.9
218.	Trifolium pratense	30.9	19	50.1
219.	Trifolium repens	36.2	1.6	62.2
220.	Trisetum spicatum	7.7	80.2	12.1
221.	Trollius europaeus	52.4	30.1	17.5
222.	Vaccinium gaultherioides	5.2	79.3	15.4
223.	Vaccinium myrtillus	13.2	43.6	43.3
224.	Vaccinium vitis-idaea	3.4	96.6	0
225.	Valeriana tripteris	34	0	66
226.	Veronica alpina	4.5	13.5	81.9

227.	Veronica bellidioides	8.8	91.2	0
228.	Veronica chamaedrys	11.6	37.9	50.5
229.	Veronica fruticans	0	58.7	41.3
230.	Veronica officinalis	3.5	69.5	27
231.	Veronica serpyllifolia	13.4	12.1	74.5
232.	Viola biflora	8.4	0	91.6

Table A3 - *Linear mixed effects model results for absolute cover change predicted by initial cover, CSR strategy deviations and elevation*

Predictors[1]	*Estimate (scaled)*	*Std.-error*	*P-value*
Model			
R^2m= 0.071, R^2c= 0.105			
absolute cover change ~ C_{t-1} + C_diff + elevation + random intercepts: plot, year nested in species			
C_{t-1}	-1.387	0.080	< 0.001
C-diff	-0.065	0.095	0.974
Elevation	-0.242	0.091	0.008
Model			
R^2m= 0.072, R^2c= 0.106			
absolute cover change ~ C_{t-1} + S_diff + elevation + random intercepts: plot, year nested in species			
C_{t-1}	-1.397	0.082	< 0.001
S-diff	0.114	0.095	0.699
Elevation	-0.248	0.090	0.006
Model			
R^2m= 0.071, R^2c= 0.105			
absolute cover change ~ C_{t-1} + R_diff + elevation + random intercepts: plot, year nested in species			
C_{t-1}	-1.390	0.082	< 0.001
R-diff	-0.068	0.098	0.974
Elevation	-0.255	0.090	0.005

Table A4 - *Linear mixed effects model results for relative cover change predicted by initial cover and CSR strategy deviations and elevation*

Predictors[1]	*Estimate (scaled)*	*Std.-error*	*P-value*
Model			
R^2m= 0.025, R^2c= 0.081			
relative cover change ~ C_{t-1} + C_diff + elevation + random intercepts: plot, year nested in species			
C_{t-1}	-0.012	0.012	< 0.001
C-diff	-0.014	0.014	0.798
Elevation	-0.013	0.013	0.344
Model			
R^2m= 0.025, R^2c= 0.081			
relative cover change ~ C_{t-1} + S_diff + elevation + random intercepts: plot, year nested in species			
C_{t-1}	-0.115	0.012	< 0.001
S-diff	0.015	0.014	0.798
Elevation	-0.013	0.013	0.318
Model			
R^2m= 0.025, R^2c= 0.081			
relative cover change ~ C_{t-1} + R_diff + elevation + random intercepts: plot, year nested in species			
C_{t-1}	-0.114	0.012	< 0.001
R-diff	-0.016	0.014	0.798
Elevation	-0.014	0.013	0.274

Table A5 - *Linear mixed effects model results for absolute and relative cover change predicted by initial cover and CSR dissimilarity*

Predictors[1]	*Estimate (scaled)*	*Std.-error*	*P-value*
Model			
R^2m= 0.031, R^2c= 0.042			
absolute cover change ~ C_{t-1} + CSR_dissimilarity + random intercepts: plot, year nested in species			
Cover_T0	-1.374	0.081	< 0.001
CSR_dissimilarity	0.043	0.086	0.615
Model			
R^2m= 0.028, R^2c= 0.104			
relative cover change ~ C_{t-1} + CSR_dissimilarity + random intercepts: plot, year nested in species			
Cover_T0	-0.112	0.012	< 0.001
CSR_dissimilarity	0.001	0.012	0.93

Figure A1 - *Graphs showing the absolute cover change (a-c) and relative cover change (d-f) in relation to the CSR strategy deviations. X axes are scaled individually due to different CSR strategy deviation ranges.*