MASTERARBEIT | MASTER'S THESIS

Titel | Title

Interaction, distribution, and modelling of mountain plant vegetation as a response to soil properties in the study area of Schrankogel Mountain, Austria

verfasst von | submitted by

Vanja Matijević univ. bacc.

angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2024

Studienkennzahl lt. Studienblatt | Degree programme code as it appears on the student record sheet:	UA 066 299
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Environmental Systems: Processes - Pollution - Solutions
Betreut von | Supervisor:	Univ.-Prof. Mag. Dr. Stefan Dullinger

Acknowledgements

Warmest thanks to everyone at the Department of Botany and Biodiversity Research, especially my supervisor, Univ.-Prof. Mag. Dr. Stefan Dullinger, for the trust and opportunity to do my thesis with his group and to gain knowledge, support and experience.

Thank you to everyone from the field season 2022: Norbert, Krystof, Marianna, Moritz, Moritz, Erich, and Johannes W. You made it an unforgettable experience and contributed to my sample size greatly.

Special thanks to Mathias Mayer for his insightful support with sampling and soil models.

Constructive, structured and especially patient guidance and support from Johannes Hausharter helped me navigate the project from very start to very finish; I appreciate it greatly.

My friends in Vienna and Zagreb were close physically and emotionally to follow the path that my studies and thesis production were, thank you immensely. Anđela, Evy, Fabio, Isabella, Susi, Uliana; Beno, Ines, Josip, Lana, Laura, Nela, Sebastijan; Anja, Bari, Ivana, Mihaela, Tea, and dearest Dr sc. nat. - Saumil Shah, you helped when I almost gave up.

Finally, nothing would be possible without my family - Tena, Dora, Domi, Tomi, Baby B., and above all, my amazing parents. I owe the majority of what I am and what I have achieved in life - to you and your unwavering trust in my choices and processes. Thank you from the bottom of my heart.

I also thank me and congratulate myself, for never giving up.

Abstract

This study aimed to evaluate the influence of soil water holding capacity on the predictive power of species distribution models (SDMs) for alpine plants, while utilizing a novel approach to calculate soil water holding capacity. The relationship between plants and their substrate, specifically in terms of water holding capacity was explored by fitting species distribution models with snow cover duration in May, mean June temperature and water holding capacity as predictors. Furthermore, the significance of a larger set of environmental variables in shaping local plant communities was explored through canonical correspondence analysis (CCA). Finally, the study examined the relationship between soil water holding capacity and physiological plant traits related to drought-resistance. In the SDMs, water holding capacity emerged as a valuable predictor of plant occurrences, explaining more of the variation in the data than either snow or temperature variables; and the CCA revealed a significant effect of all considered variables on species composition. Relationships between soil water holding capacity and the plant's drought-resistance were significant but the emerging patterns were partly unexpected. I conclude that for predicting the current and future distribution of plants in alpine environment, soil conditions need to be taken into account more routinely as this is commonly done.

Keywords: Species distribution modelling, alpine plants, soil, water holding capacity, plant drought traits

Kurzfassung

Ziel dieser Studie war es, pedologisches und ökologisches Wissen miteinander zu verknüpfen und den Einfluss der Wasserkapazität auf die Vorhersagekraft von Artverbreitungsmodelle (Species Distribution Models; SDMs) für alpine Pflanzengesellschaften zu demonstrieren, wobei ein neuer Ansatz zur Berechnung der Wasserkapazität verwendet wurde. Die Beziehung zwischen Pflanzen und ihrem Substrat, insbesondere in Bezug auf die Wasserkapazität, wurde mit passenden SDMs untersucht, wobei Dauer der Schneebedeckung im Mai, mittlere Temperatur im Juni und Wasserkapazität als Prädiktoren angewandt wurden. Darüber hinaus wurden im Rahmen der Studie die Bedeutung einer größeren Anzahl von Umweltvariablen für die Bildung lokaler Pflanzengesellschaften mittels kanonischer Korrespondenzanalyse (KKA), sowie die Beziehungen zwischen der Wasserkapazität und physiologischen Pflanzenmerkmalen im Zusammenhang mit der Trockenresistenz untersucht. In den SDMs erwies sich die Wasserkapazität als wertvoller Prädiktor für Pflanzenvorkommen, da sie mehr Datenvariationen erklärte als die Schnee- oder Temperaturvariablen. Die KKA demonstrierte den signifikanten Einfluss aller betrachteten Variablen auf die Artenzusammensetzung. Des Weiteren waren auch die Beziehungen zwischen der Wasserkapazität und der Trockenresistenz der Pflanzen signifikant, die gefundenen Muster jedoch teilweise unerwartet. Als allgemeine Schlussfolgerung ergibt sich, dass anders als bislang üblich, Bodenvariablen in Modellen der aktuellen und zukünftigen Verbreitung von Pflanzenarten regelmäßig berücksichtigt werden sollten.

Schlüsselwörter: Artverbreitungsmodelle, alpine Pflanzen, Boden, Wasserkapazität, Trockenheitsmerkmale der Pflanzen

Table of Contents

Acknowledgements ..... - 1 -

Abstract ..... - 2 -

Kurzfassung ..... - 3 -

Frame opening 1

Introduction 2

Methods 5

Study site 5

Soil sampling 5

Laboratory analyses 6

Data analysis 7

Results 9

SDMs 10

CCA 13

Plant drought traits 15

Discussion 17

SDMs 17

CCA 19

Plant drought traits 20

Conclusion 22

Frame closing 23

Literature 24

Appendix I

List of Figures II

List of Tables II

Data processing script III

Frame opening

The only worldwide distributed biome, the alpine biome, covers approximately 21.5% of the global mountain areas and is characterized by a vegetation dominated by graminoids, herbs, dwarf shrubs and cushion plants (Körner, 2020). These plants take up mineral resources and water from soils which are very different from those at lower altitudes. Over short distances, a large variety of alpine soil types can occur, from alpine sand dunes to peat bogs, from shallow soils typical of steep alpine slopes to the much deeper soils of some alpine meadows and dwarf shrub heaths. Plant communities are required to follow these below-ground patterns, meaning that soils and plant distributions are in close link (Elias, 2020). Much like alpine biota, soils of the alpine biome have evolved under extremely cold conditions. Snow is the vital element of ecology of this area, but the relationships between the factors are often more complex than we currently understand, especially in regions as remote and difficult to study as the tops of high mountains (Elias, 2020).

The fact that they are very reliant on a thermally insulating snow cover for the majority of the year makes alpine ecosystems particularly vulnerable to changes of snow cover (Edwards et al., 2007) as a consequence of climatic change which may result in dramatic loss of habitat for many organisms across the world's mountain areas (Thuiller et al. 2005, Engler et al. 2011, Rixen et al., 2014, Mountain Research Initiative EDW Working Group, 2015).

Recent assessments of the impact of climate change are reporting that these vulnerable areas should experience unparalleled warming rates in the current century, possibly even two to three times greater than observed in the 20th century (Nogués-Bravo et al., 2007). Apart from the increasing temperatures, changes to the water balance may additionally affect alpine species, at least in areas characterized by dry seasons already today (Pauli et al. 2012, Crimmins et al. 2011).

This study incorporates soil's water holding capacity, a relatively under-ulitized factor, to enhance the modelling of alpine plant species occurrences, and to ultimately increase the overall quality of species distribution models.

Introduction

Mountain ecosystems are rich in biodiversity, with aggregations of endemic species within narrow elevational belts (Rahbek et al., 2019). Since plant communities in high altitude regions are predominantly composed of cold-adapted species, it is presumed and observed (e.g. Pauli et al., 2006; Lamprecht et al., 2018) that they are highly susceptible to the impacts of global climate change. Consequently, these ecosystems provide a valuable setting for investigating global change and its environmental implications (Chersich et al., 2015).

Research conducted throughout the 20th century indicates a consistent rise in temperatures across alpine systems, with an average increase of approximately 2 °C since the early 1900. This temperature increase coincides with a general decrease in precipitation, although the probability of extreme precipitation events is increasing (Beniston et al., 1997; Wanner et al., 1997 as cited in Winkler et al., 2019). Notably, evidence suggests that temperatures in high-altitude regions are rising at a faster pace than in the lowlands and coastal areas (Mountain Research Initiative EDW Working Group, 2015). Therefore, alpine plant communities are expected to be substantially altered in response to global climate change, prompting increased interest in investigating changes in the distributions of single species as well as the composition of functional groups or entire communities (e.g. Kullman, 2010b; Johnson et al., 2011., as cited in Winkler et al., 2019).

In addition to climatic conditions, other environmental factors contribute to species richness and composition of alpine plant assemblages and the distribution of individual species, notably the soil. Soil characteristics in alpine landscapes are shaped by multiple factors, among which snowpack, snow duration and water runoff have particularly significant roles. These factors are, however, not isolated or independent, but rather influenced by each other as well as by their topographic, geological, climatic and biotic context (Seastedt, 2001). Due to global climatic changes, Alpine soils may experience more frequent intense rainfalls (>30 mm/day), leading to increased soil moisture levels and increased water saturation throughout the year, but, conversely, also to more intense surface run-off in the steep terrain and longer periods with no precipitation in between heavy rains, and hence intermittently higher drought stress (Körner, 2021). These changes in rainfall patterns and soil moisture are likely to also exacerbate erosion processes, increasing the landslide and flooding susceptibility (Chersich et al, 2015). This will inevitably impact plant species and communities inhabiting these soils.

Affecting all environmental factors of high elevation landscapes, climate change will also affect soil microbial communities and consequently, biogeochemical cycles (Broadbent et al., 2021). Cold soils

prevalent in alpine environments play a critical role in carbon storage and nutrient cycling, and their capacity for storage will strongly decline with the rise of mean annual temperatures (Hartley et al., 2021). Soils in these areas also have slower rates of organic matter decomposition and humification. They therefore act as carbon sinks as they store more carbon than they release into the atmosphere through decomposition processes. However, a study conducted by Na et al., (2011), manipulated near-surface temperatures with open-top chambers and found that a warming climate could potentially turn alpine meadows into global sources of atmospheric carbon due to changes in respiration rates. At the same time, it was shown that soil water content significantly decreased at sites with open-top chambers, due to an increase in above surface temperatures. Furthermore, such a temperature increase will also lead to alterations in plant-growing-season length and changes in organic matter decomposition rates.

Species distribution models (SDMs) are the prevalent tool for predicting likely effects of climate change on biodiversity including mountain floras (e.g. Randin et al. 2009, Engler et al. 2011, Chauvier-Mendes et al. 2024). These models relate environmental conditions to the occurrence of species to predict their distribution or even the composition of whole communities under different or changing environmental conditions (Winkler et al., 2019). Most commonly, the environmental variables included in these models are restricted to macroclimatic and topographic variables (Mod et al. 2016). Despite the well-known tight relationships between climate, soils and plants, soil properties are hence usually disregarded. Several studies have already indicated that this practice is flawed (Buri et al., 2019; Chauvier et al. 2021, Dubuis et al., 2012), and, as argued above, including water-related soil properties appears particularly timely and adequate into SDM-based scenarios of mountain plant diversity. However, accounting for soils in these models is still far from being standard.

A soil property of relevance in this context is soil water holding capacity (WHC) which indicates the soil's ability to retain water for plants. It is determined by the soil's texture, structure, and organic matter content. This capacity is crucial as it affects the soil's ability to supply water to plants, consisting usually of two main components – field capacity and permanent wilting point. Field capacity is the amount of soil moisture or water content held in the soil after excess water has drained away and the rate of downward movement has decreased to a constant value for a particular depth (Kirkham, 2005), representing the upper limit of water that soil can hold. Permanent wilting point is the minimum soil moisture level beyond which plants cannot extract water anymore (Kirkham, 2005). Below that point, plants wilt and cannot recover their turgidity even if water is added. The difference between these two terms is known as the soil water availability, the portion of water in the soil that can be readily absorbed by plant roots. This concept is crucial for understanding

how much water is actually available to plants for uptake and reflects the dynamic change of soil characteristics under the combined atmospheric conditions, plant requirements and soil properties (Zhang et al., 2021). Furthermore, soil's WHC can select for certain functional plant traits and thereby affect plant-soil feedbacks (Pugnaire et al., 2019). These plant functional traits are measurable features (morphological, physiological or phenological) and represent adaptive strategies to cope with the environment, ultimately determining a plant's fitness (Violle et al., 2007). However, whether plants assemblages above the treeline in temperate mountains show an imprint of water-related soil properties such as WHC on the trait profiles has not yet been assessed.

One main reason why soil-water related features as WHC are still rarely included in SDMs is the relative difficulty of obtaining the relevant data. However, so-called pedotransfer functions (PTF) offer a way forward here. The most frequently used PTFs are those relating soil organic matter (SOC) to water-related characteristics of the soil. They allow the estimation of unmeasured soil variables by using measured proxy variables such as particle size, bulk density and organic carbon (Wösten et al., 2001, as cited in Bagnall et al., 2022). PTFs are thus used to predict soil characteristics which are biologically more meaningful than the initially measured variables, such as the soil water holding capacity (WHC) that is influenced by the quantity of organic matter in the soil as well as soil texture (Li et al., 2007, as cited in Winkler et al., 2019).

The purpose of this thesis is on enhancing our understanding of the role of soil-water-related variables, and especially soil's WHC, on the distribution of individual plants and the trait profiles of plant assemblages in the central Austrian Alps. Using a dense data sampling campaign at a model mountain in the Austrian Alps, I therefore evaluated the value of including WHC of soil into distribution models of a number of species, on the one hand; and, on the other hand, I correlated the soil's WHC with the community-weighted means of several traits assumed to reflect species' adaptations to drought. In particular, I focused on the following questions:

1. How accurately can the soil's WHC predict the occurrences of alpine plant species and how well does it perform in this respect as compared to other, more commonly considered gradients such as those of temperature and snow cover?

2. What is the relative impact of WHC and other soil properties on the assemblage composition as compared to other descriptors of the environment such as temperature, snow cover and terrain properties?

3. Do drought-resistance trait means of alpine plant assemblages correlate with the WHC of the sites where they are growing?

Methods

Study site

The fieldwork was conducted from July to August 2022 at Mount Schrankogel, part of the Stubaier Alps in Tyrol, Austria (47°02' 41" N, 11°05' 58" E) with the summit at 3497 m a.s.l. The siliceous bedrock mostly consists of gneiss (Hammer et al., 1929; Purtscheller, 1978, as cited in Lamprecht et al., 2018), while the most common soil types are leptosols and cambisols (Hofmann et al., 2016, as cited in Lamprecht et al., 2018). The vegetation in the lower alpine zone just above the treeline consist of dwarf-shrub communities and grasslands. The upper alpine zone is dominated by *Carex curvula* and *Oreochloa disticha* grasslands, while only scattered vegetation is found on the siliceous screes of the subnival and nival zones (Grabherr, 1993; Abrate, 1998; Dullinger, 1998.; as cited in Lamprecht et al., 2018).

Soil sampling

Throughout the field season, 300 soil samples were taken from locations distributed across the mountain. These locations were chosen from a total of 900 1 m² plots for which the vegetation had been surveyed as part of the MICROCLIM project (Mountainresearch.at, 2020). From these 900 plots, the subset of 300 plots for soil sampling was chosen to be as heterogenous as possible – i.e. to include elevations and terrain types (including the ridge, river valley, the moraine, etc.) as broadly as possible. At each of these plots, a temperature logger (hereafter just termed "logger") had been placed in one of the corners of the plot in July 2021. Within each plot all plant species had been recorded, and their covers estimated. Soil samples were taken in the immediate vicinity of each plot, but at least one meter away from the logger (as to not disturb the surveyed vegetation). These samples consisted of three haphazardly selected subsamples taken in available depth up to 20 cm (topsoil), using a shovel. If the immediate surrounding at the logger position was very heterogenous in respect to its terrain and plant community, the subsamples were taken at spots representing all the present terrain types.

The three subsamples of one plot were combined into one composite sample. The organic layer was removed before sampling the mineral soil. However, the depth of the organic layer was measured by means of a ruler. Soil samples were passed through a 2 mm mesh sieve to remove stones and roots. Sieved samples were air-dried in paper bags at 40°C. Prior to further analysis in the laboratory, samples were milled to achieve uniform particle size and subsequently dried again for one hour at 40 °C to ensure consistent dryness.

Laboratory analyses

For nutrient measurements, a microgram sized subsample was weighed into a tin capsule for each soil sample. The first measurement was conducted using the calibration standard (to establish a linear calibration curve). An additional calibration standard was repeated after every 15 samples to verify the measuring variables. The chosen method was oxygen stream combustion at a high temperature (950 °C) upon which the C is converted into CO_2 and N into N_2. Using a CN analyser (LECO Truspec CN, LECO Europe, NL, eu.leco.com) the percentage of carbon and nitrogen in the subsamples was measured via infrared detection (carbon) and thermal conductivity detection (nitrogen). This method is known as the Dumas dry combustion method (Wright & Bailey, 2001).

In soil science, the pH is usually measured by diluting the sample in either deionized water or 1 M solution of KCl or 0.01 M $CaCl_2$. However, some authors (e.g. Minasny et al., 2011) suggest that measuring in salt solutions should be a preferred method due to electrolyte exchanges between solution and surfaces. The differences in pH measured in solutions of deionized water and calcium chloride is related to the exchange of calcium (Ca^{2+}), hydrogen (H^{+}) and aluminium (Al^{3+}) ions on solid (soil) surfaces (Miller & Kissel, 2010; as cited in Minasny et al., 2011). Thus, the pH values measured in both solutions will be linearly related to each other and the one measured in deionized water will always be higher. For this study, the previously air-dried soil samples were mixed with a 0.01 M $CaCl_2$ solution in a 1:5 ratio using a vortex mixer for ~30 seconds. After the samples were left to rest for 24 hours, they were once again mixed with the vortex mixer before their pH was measured using an electrode. The results were expressed as pH ($CaCl_2$). The same procedure was repeated in parallel by diluting the samples in deionized water instead of $CaCl_2$ (same ratio of soil and liquid as above). The results were expressed as pH (H_2O) and are the ones used for all the following analyses. All was measured at room temperature. As previously elaborated – water holding capacity (hereafter WHC) is an indicator of water that can be absorbed and stored in the soil, for the purpose of e.g. supporting plant growth (Adams et al., 2020).

To avoid the time-consuming and costly task of determining WHC of the soil directly in the field, WHC was calculated by means of linear regression, using a model of water holding capacity (Equation 1) parametrized by Mathias Mayer,

$$WHC = 3.7863 * APD + 4.6054 * OLD + 3.0265 * C \quad (1)$$

where water holding capacity (l m^{-2}) is determined by three factors: carbon content in the mineral soil (C; in %), organic layer depth (OLD; in mm), and average penetration depth (APD; in mm). The

APD was derived from nine penetration depth measurements that were conducted at each of the 900 plots in 2021. Water holding capacity was determined for a maximum soil depth of 0-20 cm.

Data analysis

To investigate how accurately soil's WHC can predict plant species occurrences, species distribution models (SDMs) were fitted to the plant species' occurrence (presence/absence) data. Therefore, univariate generalised linear models (GLMs) with binomial error structures were calculated for each individual plant species, using the species' occurrence as response variable and either WHC, the days of snow cover in May (Snow5) or the mean temperature in June (MT6) – as predictor variables. Snow in May was chosen as a predictor as this month exhibits the largest variation in melt-out times between the logger positions, i.e. valleys are often still covered with snow whereas exposed ridges are already snow-free. Hence, it is a good indicator of the variation of the beginning of the growing season. The mean temperature in June was read out from loggers and used since it is the month when growing season starts at most sites of the study area.

For each predictor a model for a unimodal relationship was calculated, thus three GLMs were calculated per species. As measurement of soil WHC was only available for 279 of the plots, these 279 plots were included in these models. Furthermore, only species with at least twenty presences among these 279 plots were considered for modelling to avoid biased coefficient estimates (Peduzzi et al., 1996). The model's goodness of fit (performance) was assessed by calculating the pseudo-R^2 proposed by Tjur (2008; hereafter referred to as R^2).

To further explore the association between environmental (soil, climatic and topographic) variables and the occurrence of the 56 target species, a Canonical Correspondence Analysis (CCA) was performed. The target species were chosen out of all occurring plants in the area on the basis of representing the characteristic species and growth types of different habitat types while maximizing trait variation. The following environmental variables were considered for this analysis: the topographic position index (TP5_15), slope (SLP_51) and topographic wetness index (TWI_3) for characterising topography; days of snow cover in May (Snow5) and mean June temperature (MT6) as indicators for the local climate; and pH, soil WHC and the C:N ratio for describing soil qualities potentially crucial for nutrient availability, organic matter formation and nutrient cycling. The CCA was calculated based on a species-site matrix containing the individual species' occurrences as the response variable and a matrix containing the environmental properties of all sites as the explanatory variable. This analysis considered the 273 logger plots for which all environmental variables were available, and which included the presence of 56 target species.

An analysis of variance (ANOVA) was conducted to evaluate the overall significance of the CCA result as well as the significance of the individual predictors in the CCA by means of a permutation test with 999 permutations. To quantify the amount of variance in the species distribution data (i.e. the species-site matrix) explained by the environmental variables, an adjusted R^2 value was calculated using the 'RsquareAdj' function.

All analyses were performed using the R software environment (R Core Team, 2023) as well as the 'vegan' (Oksanen et al., 2022) package. The results were visualized using the "ggplot2" package (Wickham, 2016).

Finally, to assess to what extent drought-resistance-related traits of the plant species within these communities are related to the WHC of the soil, I used a total of five such traits. These traits had been measured at 5 five individuals of each of 56 plant species by Marianna Paetzolt in August 2021 (Paetzolt 2022). The five individuals had been sampled in larger populations close to the elevational optimum of each species on Mt. Schrankogel. The five measured traits and their assumed relationship to drought stress were: (1) leaf carbon isotope signature ($\delta^{13}C$), which when high, indicates a physiological adaptation for efficient water use. Hence, if the plant is frequently exposed to drought, as on soils with low WHC, $\delta^{13}C$ should be higher, i.e. we assumed it should be negatively associated with WHC. This has been demonstrated by Ma et al. (2012), showing that an increase in water availability (from precipitation) leads to a decrease in values of $\delta^{13}C$; (2), minimum conductance (Gmin), the measured rate of water loss after the stomata are closed during water stress, i.e. a trait important for estimating water fluxes in plant canopies during heat waves and in models of plant drought response (Duursma et al., 2018). We hypothesized that the minimum conductance would correlate positively with the soil's WHC. If a plant inhabits soils that have little water retention (and low water holding capacity values), minimal leaf conductance (Gmin) could be expected to be low as well, allowing the plants to lose water more slowly and avoid drought stress; (3) osmotic concentration (OC) of solutes - e.g. ions and sugars in plant cells and tissues, measured with an osmometer. A higher osmotic concentration is generally helpful under conditions of water limitation, i.e. drought, since it allows water retention, prevents water loss from the cell, maintains turgor pressure and contributes to overall metabolic stability. Due to this, we hypothesized that the osmotic concentration would show a negative correlation with WHC; (4) R600, which is the maximum photosynthetic rate, i.e. water content at which fluorescence/fluorescence max* declines to 0.6, calculated mathematically. The trait measures the rate of photosynthesis per unit of leaf mass, measured under favourable conditions of light, moisture, and temperature (Chapin & Eviner (2007)). Species that have a low photosynthetic capacity conserve water well because of low stomatal

conductance. Plants that are adapted to low water availability will thus likely have low stomatal conductance and a low photosynthetic capacity. We hence assumed that soil WHC of a site and R600 will correlate positively. Finally, we modelled (5) succulence (Suc), which represents the amount of water that is stored in the leaf, calculated as wet to dry leaf mass divided by the leaf area. We expected that succulence will negatively correlate with WHC, as higher succulence values indicate greater drought resistance, which should be associated with low soil WHC values, as well as the idea that succulent leaves can tolerate more water loss.

To analyse the association between these traits and the soil's WHC on a community level, the species-specific trait values were averaged across all species occurring within one vegetation plot and for which these values were available (i.e. the 56 target species), and these averages were unweighted by abundance. Only those logger plots were considered, where the 56 target species together covered at least 70% of the plant-covered area, to ensure that the calculated trait means were representative for the respective plots. These community trait means were then related to the soil's WHC using OLS (ordinary least square) regressions. Of the 279 plots for which the WHC was available, the target species covered the required percentage area at 187. Hence, OLS regressions were calculated on the data of these 187 plots.

Results

Laboratory analyses showed that the collected (n = 279) soil samples were highly variable in all features (carbon and nitrogen content, pH, and consequently, WHC; Table 1). The observed pH values ranged from 4.2 to 6.9.

The percentage of carbon present in the probes varied from 0.03% to 28.65%, demonstrating a substantial variability across the tested sites. Both the nitrogen content and the water holding capacity also varied markedly ranging from 0.02% to 2.7% and 0.7 to 164.8 l/m^2 respectively.

Table 1: Maximal, minimal, and mean values of measured soil variables

Soil variable	mean	min	max
pH	5.05	4.20	6.96
N percentage	0.47	0.02	2.17
C percentage	7.18	0.03	28.65
WHC [l/m^2]	56.47	0.70	164.80

SDMs

In the context of species distribution models, soil's WHC stood out as the most important predictor (Figure 1). Across all 56 species, WHC explained a median of 10% of the variability in species distributions, (10.2%; range 0.4% – 30.1%).
In contrast, both snow cover duration in May and the mean temperature in June exhibited weaker predictive power, with snow cover duration accounting for a median of 5.8% (0.2% – 25.6%), and mean June temperature a median of 7.3% (0.1% – 35.1%) for unimodal relationships.

On the level of individual species, the performance of the three different predictors varied substantially. WHC of the soil emerged as the most important predictor for explaining the occurrence of a number of species characteristic of lower elevation and relatively warm/dry conditions, such as *Carex sempervirens, Calluna vulgaris, Vaccinium spp.*, but also of some species that preferably grow on very shallow soils or rocks such as *Saxifraga bryoides*. This variable (WHC) explained more than 20% of the variation in the distributions of these species (Figure 2). In contrast, the mean temperature in June proved to be the best predictor for most species occurring in the uppermost areas of the study area such as *Poa laxa* and *Ranunculus glacialis*, exhibiting an explanatory power of around 35%, but also for some species of intermediate elevational peaks such as *Anthoxanthum alpinum* and *Ranunculus villarsii*, for which it explained 28% and 20% of the variation, respectively. Snow cover in May had generally weaker explanatory power (Figure 2), but well predicted the distribution of some species adapted to long-lasting snow cover (*Veronica alpine, Gnaphalium supinum, Oxyria digyna*) or particularly short snowpack (*Avenula versicolor*).

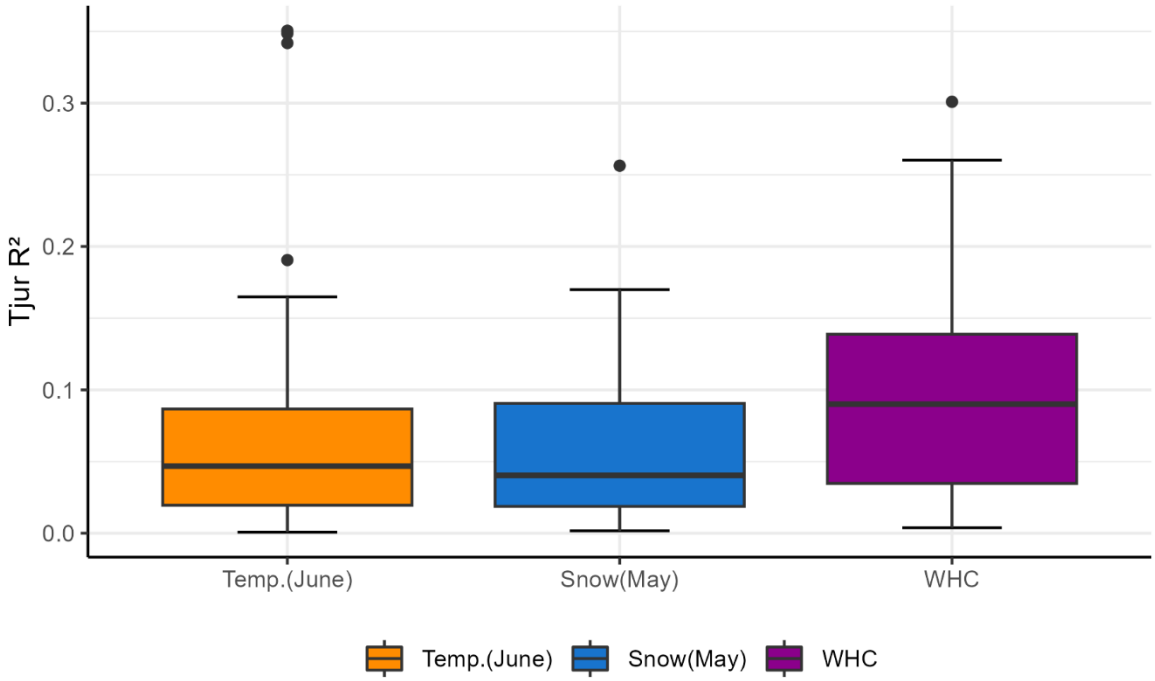

Figure 1: Amount of variation in species distributions explained by the three predictors (expressed as R^2).

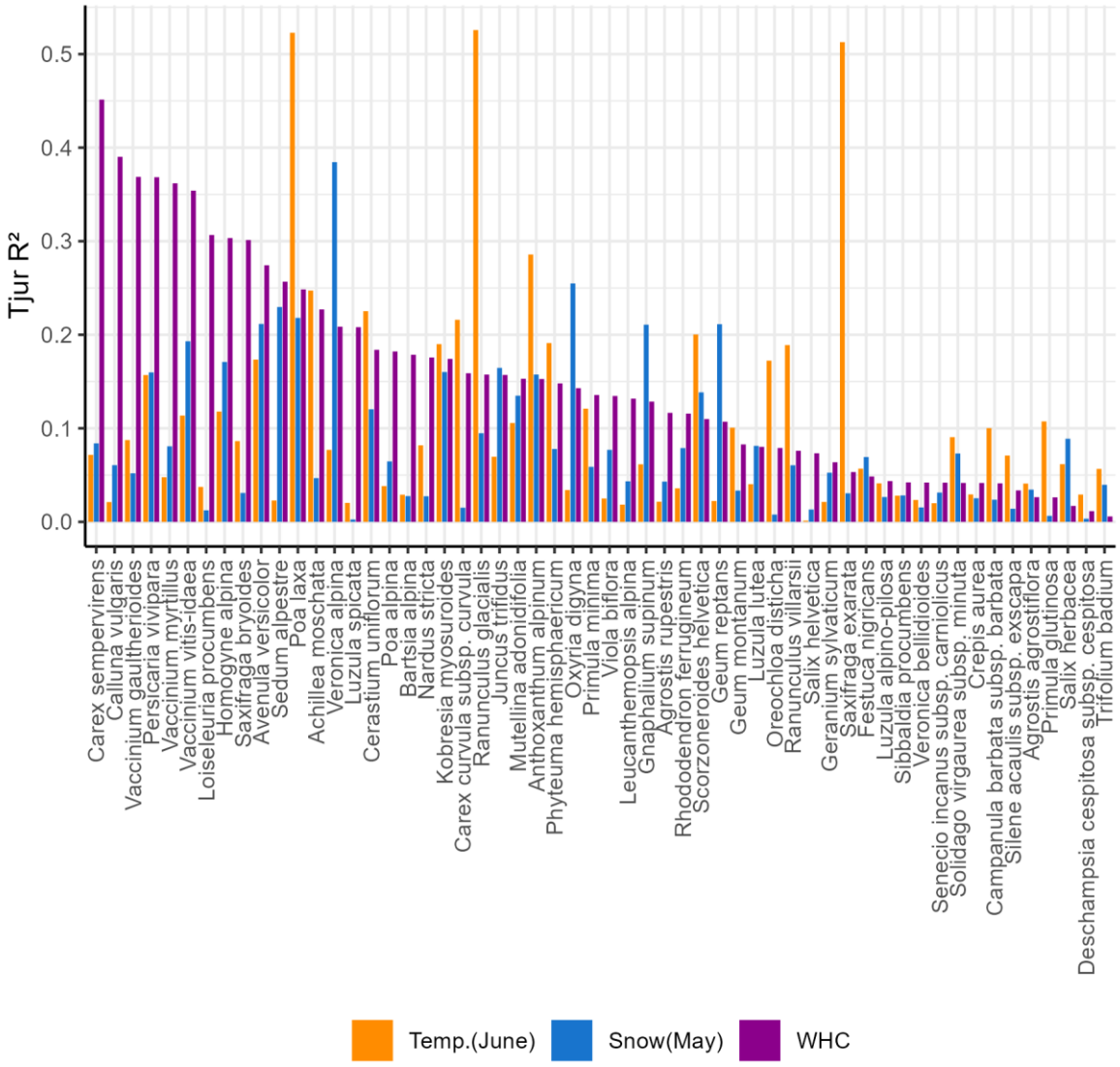

Figure 2: Explanatory power of the individual predictors in explaining distributions of individual species. Bars (y-axis) represent R^2 values grouped by species (x-axis) for each predictor.

CCA

The first two axes collectively explained 6% (1st: 4%, 2nd: 2%) of the overall variance in the distribution of the 56 target species, whereas the cumulative contribution of all eight restricted axes accounted for 11% of the variance.

The first CCA axis was strongly positively related to soil pH and snow, while it was negatively related to TWI_3, SLP_51, temperature, C:N ratio and WHC. The second axis was most strongly and positively correlated with TP, SLP, C:N ratio and WHC and negatively correlated to other 4 predictors (Table 3).

Permutation tests revealed that the Canonical Correspondence Analysis overall was significant ($F = 4.26$, $p = 0.001$, $Df = 1$). They further revealed that each of the considered environmental variables significantly (all: $p < 0.001$) influenced the species composition of the studied plant assemblages. Based on the values of the F-statistic the most important variable was WHC, followed by MT6 and snow. These results are consistent with those of the SDMs. The remaining soil variables were still more important than those related to topography.

The plants clustered in the lower right portion of the ordination space, correlated with a long snow cover such as *Geum reptans*, *Gnaphalium supinum*, *Oxyria digyna* and *Luzula alpino-pilosa*. The lower left ordination space mainly contains species from lower elevations which perfer higher temperatures such as *Nardus stricta*, *Crepis aurea* or *Campanula barbata.* Towards the upper left, species of windblown ridges tended to accumulate, such as *Kobresia myosuroides, Loiseleuria procumbens* or *Vaccinium gaultheriodes.* Finally, the upper right mainly contained species of raw soils with low C:N ratio, such as *Ranunculus glacialis, Saxifraga exarata* or *Poa laxa.* The WHC gradient mainly ran along the first axis and separates species from well-developed humus-rich soils such as *Rhododendron ferrugineum, Vaccinium myrtillus* or *Solidago virgaurea* from those of shallow and stony raw soils such as *Cerastium uniflorum* or *Saxifraga bryoides.*

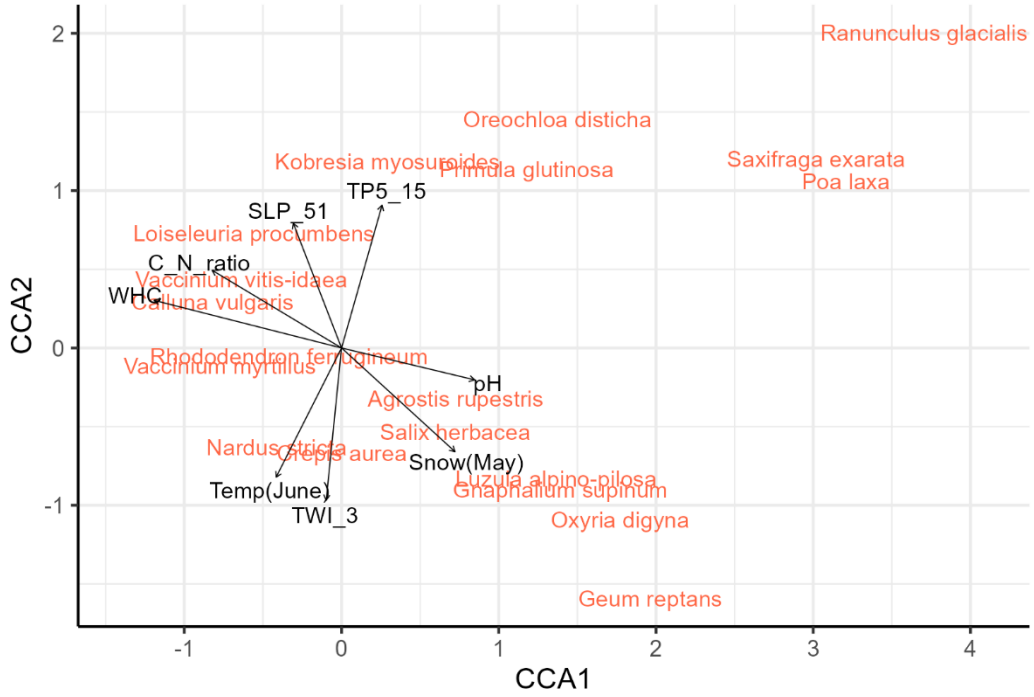

Figure 3: CCA ordination plot; indicating how selected target species (red) are distributed along environmental gradients (black arrows). The direction and length of the arrows indicate the strength of the influence of each predictor variable on the composition of species. To interpret the plot, one should examine the position of species points and their relationship to the predictor variable arrows. Species close together in the plot tend to have similar response to the predictor variables and are also more strongly influenced by that predictor variable. Opposingly, species that are far away from the arrows are less affected by that variable. Variables that have longer arrows or are positioned closer to the species points are more important in shaping the species composition. Additionally, the distance between species points indicates their similarity or dissimilarity in response to the predictor variables.

Table 2: Correlation of predictor variables with the first two constrained axes of the CCA.

Predictor	CCA1	CCA2
pH	0,54	-0.13
Snow (May)	0.46	-0.42
TP5_15	0.17	0.58
TWI_3	-0.06	-0.62
SLP_51	-0.20	0.51
Temp (June)	-0.27	-0.53
C:N ratio	-0.53	0.32
WHC	-0.77	0.19

Table 3: Results of a permutation test analysing the importance of the individual predictor.

Predictor	F	Pr(>F)
WHC	5.0938	< 0.001
Temp (June)	3.4317	< 0.001
Snow (May)	3.26	< 0.001
pH	3.08	< 0.001
C:N ratio	2.94	< 0.001
SLP_51	2.85	< 0.001
TWI_3	1.92	< 0.001
TP5_15	1.81	0.014

Plant drought traits

In the models relating plant community trait means to WHC, significant associations were observed between the WHC and all considered drought-resistance-related traits (Fig. 4). The explanatory power of WHC differed notably between the individual traits. Specifically, WHC accounted for 19%, 23% and 27% of the variation in carbon isotope ($\delta^{13}C$), osmotic concentration (OC) and maximum photosynthetic rate (R600) respectively. In contrast, its explanatory power was relatively low for minimum conductance (Gmin, 8%) and succulence (Suc, 9%). Surprisingly, however, regarding the direction of correlations, our hypotheses were only met in case of $\delta^{13}C$, Suc, and R600, but not in case of Gmin and OC.

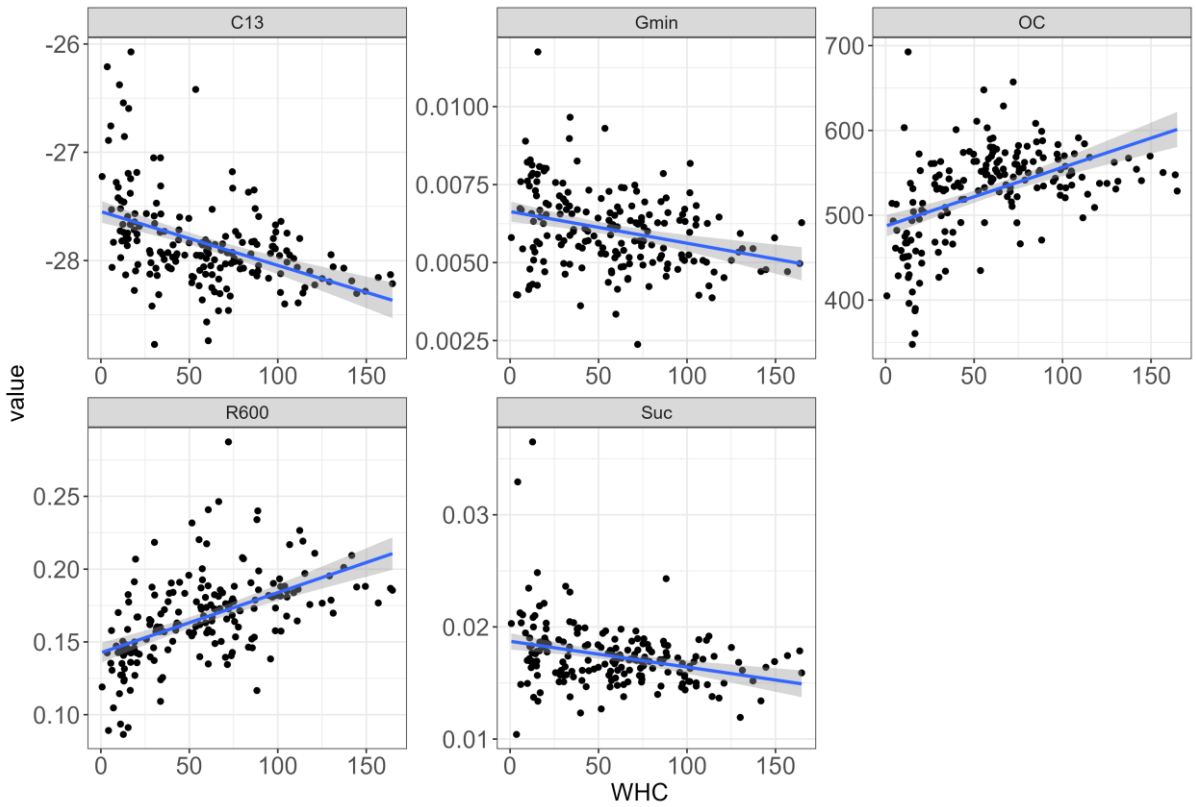

Figure 4: Relationships between drought-resistance-related trait means and WHC. The blue lines and shaded areas represent the regression lines and 95% confidence intervals of an OLS regression respectively.

Discussion

The analysis showed that the soil's WHC successfully and accurately performs when built into an SDM for alpine species prediction. Compared to the variables of snow and temperature, it achieved a median R^2 value of 0.1, while snow had 0.058, and temperature 0.073. This suggests that the soil's WHC indeed is a more effective predictor of plant distributions than these commonly considered gradients.

Regarding the impact on the assemblage composition, the individual predictor WHC had the highest F value of all environmental descriptors tested (Table 3). This again emphasizes the impact of the soils' WHC on alpine plant assemblages compared to other environmental descriptors, including the soil variables of pH, and C:N ratio.

Lastly, the interaction and correlation of soil's WHC and drought-resistance plant traits was displayed strongly, although with some ambiguity in the direction of this relationship. However, the correlations found contribute to our understanding of why the impact of WHC on plant distribution and assemblage composition is significant.

SDMs

Water holding capacity emerged as the predictor of highest importance, on average across species, in SDMs. That edaphic variables are very valuable for accurate SDMs of mountain plants has already been shown by others, but often with a focus on pH or mineral content related to bedrock chemistry (e.g. Dubuis et al., 2012, Buri et al., 2017). In our study, conducted in an area of relatively homogeneous bedrock and with an exclusive focus on the landscape above the treeline, WHC turned out to be the attribute of the soil most important for plant distribution. This was especially true for species typically growing on either well developed (e.g. *Carex sempervirens, Calluna vulgaris, Vaccinium spp.*) or hardly developed soils (e.g. *Saxifraga bryoides*), i.e. for species on soils where the WHC is either unusually high or low. The strong impact of WHC echoes results of Cianfrani et al. (2019). These authors pointed out, however, that other environmental variables such as snow and temperature are often measured across shorter time intervals than WHC and could increase in relevance if averaged across longer time spans, reducing the effect of outlier measurements and short-term weather peculiarities. This consideration is also worth in our case as WHC mirrors conditions that have hardly changed over the last decades, at least, while temperature and snow variables mirror conditions of the last two years only. Despite these caveats, the importance of WHC appears clear and the main reason for being neglected in most SDM applications likely is the costly and time-consuming work needed to collect the relevant data.

The connection for well-developed soils and WHC could be in the fact that with an increase in storage capacity (if well-developed soils hold more organic C), evaporation rises, and runoff reduces. Additionally, WHC explained 50% of the variation in the occurrence of *Saxifraga exarate*, as *Poa laxa* and *Ranunculus glacialis*. Moreover, while the influence of WHC was pivotal in determining the distribution of certain species, it is noteworthy that snow and temperature also exerted considerable influence in determining the distribution of some species.

Seasonal climate and temperature variability are key characteristics of temperate mountains, resulting in limitations in plant growth and reproduction. However, snowmelt date and mean soil temperature above 4.9 °C are the main limiting factors of the growing season (Bürli et al., 2021). Nevertheless, the results of our SDMs showed that snow was less important for explaining species distributions than expected and previously reported (e. g. Panchard et al., 2023).
While this is true on average across species, some of them still were highly responsive to snow cover, and these species were often those known to be specialists of late-melting sites in the alpine landscape, such as *Veronica alpina* (R^2 = 0.4), *Oxyria digyna* (R^2 = 0.25), *Gnaphalium supinum* and *Geum reptans* (R^2 = 0.2). We conclude that snow cover can well distinguish the sites were snowbed specialists grow but has limited discriminatory power for species occurring at 'average' alpine sites.

Temperature is commonly found to be the most important predictor of mountain plant distribution, because of the steep elevational and hence thermal gradient in these landscapes (Buri et al., 2017, Maharjan et al., 2021). It is noteworthy, however, that most of these studies use mean annual temperature as predictor, which could introduce a bias. As demonstrated by Mod et al., (2016), annual means of temperature may not accurately represent the conditions during both the growing season or winter, which are often crucial for the survival and distribution of species. Especially in plant communities of alpine environments characterised by the high seasonal variability of their climate, special care must be taken when it comes to the choice of predictors to accurately depict this climatic variability. As seen above in the result section, nival species, i.e. those occurring in the uppermost areas of the study area such as *Poa laxa* and *Ranunculus glacialis*, were predicted best by the mean temperature in June, with an explanatory power of around 35% (Figure 2). This contradicts some of the previously published research, e.g. Gottfried et al., 2002 (as cited in Pauli et al., 2006), in which the authors suggest that summer snow cover is the main limiting factor for these species.

Overall, the approach taken enabled us to quantify the importance of environmental predictors, and ultimately provide valuable insights into the factors influencing the occurrence of species. Furthermore, the success of an edaphic variable such as the soil's WHC as an SDM predictor is in accordance with improvements in the quality of SDMs of plant species demonstrated for other

edaphic variables in various studies such as those of Buri et al. (2017; 2019), Dubuis et al. (2012), Roe et al., 2022. In these papers however, the considered soil variables were CaO, pH, total N, and C:N ratio, instead of the WHC.

Another reason why the SDM results in this paper are challenging to compare to other researchers' work is the difficulty in comparing studies that quantify model performance differently, such as Tjur R^2 in this study, as well as the widely used AUC (e.g. Dubuis et al. 2019, Randin et al. 2009), and Kappa values (e.g. Roe et al., 2022). Moreover, in a comparable study from 2010, Austin & Van Niel pointed out that no two studies have identical predictors for temperature or water, let alone soil predictors or soil water holding capacity, with an additional recognition that accurate soil moisture data over large areas are rarely available (Mod et al., 2016).

Finally, we add that the relatively small sample size forced us to use univariate SDMs. A problem with this approach is that the different variables used, WHC, snow and temperature, correlate to a certain extent (see Figure 5 in the Appendix). The amount of variation explained in univariate models hence includes an unknown amount shared between any two or even all three of them. It might hence be that WHC has superior explanatory power because it covers relevant parts of the elevational, and hence temperature gradient, plus information of the soil. As a consequence, its superiority as a predictor of plant distribution might appear exaggerated to a certain extent.

CCA

Regarding the impact of the WHC and other soil properties on the assemblage composition as compared to other descriptors of the environment, in a permutation test analysing the importance of the individual predictor WHC had the highest F value of 5.1 (Table 3), making it the most important individual predictor.

As shown by the CCA plot (Figure 3), the occurrence of some species appears to be strongly related to soil's WHC, such as *Calluna vulgaris*, *Vaccinium vitis-idaea* and *Vaccinium gaultherioides.* This might be due to their similar in moisture requirements, root depth, or life strategies, being stress tolerant competitors (Landolt et al., 2010). It is, however, important to note that plant species do not exhibit an exclusive relationship with soil WHC, as they thrive because of an interplay between biotic and abiotic factors (González-Salazar, Stephens and Marquet, 2013). Furthermore, WHC of the soil has a perpendicular relationship to slope and the topographic position index (both variables reflecting the morphology of the surrounding terrain), indicating that these factors influence species composition independently from each other. That is reasonable since an increase in slope generally leads to better drainage, affecting the availability of water. While WHC is intrinsically determined by

the soil's physical properties, the slope still influences the soil's WHC by affecting runoff rates and water infiltration. Steeper slopes usually lead to quicker drainage, while gentle ones may retain water longer, allowing for water saturation of the soils. Similarly, it is most likely that the pH itself does not affect plants, but rather change the mobilization and availability of nutrients, and limits the amount of micro- as well as macronutrients, such as phosphorous (Larcher, 1995. and Scheffer and Schachtschabel, 1998; as cited in Vonlanthen et al. 2006).

With respect to temperature and snow cover, the position of most species in the ordination space largely mirrors SDM results and known species preferences (e.g. Vonlanthen et al. 2006, Fischer et al. 2008). For example, *Crepis aurea* prefers warmer conditions while *Gnaphalium supinum, Oxyria digyna* and *Luzula alpino-pilosa* are most likely to be found at late-melting sites, and *Kobresia myosuroides*, *Loiseleuria procumbens* or *Vaccinium gaultheriodes* at exposed and often early-melting sites such as rocky outcrops, ridge tops.

More generally, the outcome of the CCA shows that while some species show a strong relationship with one or a few dominating variables, most of the 56 analysed species are accumulated in the centre of the ordination space, indicating that average conditions are present at most of the observed habitats. This also goes in hand with the work published by Vonlanthen et al. (2006), where it was revealed that most plant communities were occupying roughly similar ecological niches.

Plant drought traits

There are no publications that observe plant drought traits on such a small geographical scale and straightforwardly combine it with pedological measurements of WHC. As seen in the results section, all models relating WHC to plant community traits showed significant associations between them (Table 1). Some expectations of ours came out as true and visible in the models, and some have not.

Our model revealed the expected relationship between the soil's WHC and the carbon isotope, with low values of $\delta^{13}C$ associated with higher WHC values. However, as noted by Seibt et al. (2008), observing these trends in $\delta^{13}C$ only, is not a reliable indicator of changes in a plant's water use efficiency. One should rather also independently estimate gas exchanges and environmental conditions. We didn't have the data necessary to include these factors, but overall, our model of $\delta^{13}C$ values showed to be increasing on soils with low WHC, i.e. under higher likelihood of dry conditions, which is consistent with findings of previous studies (Seibt et al., 2008, Yang et al., 2021).

We assumed that the minimum conductance (Gmin) would positively correlate with the soil's WHC. However, this expectation was not confirmed by our results (negative correlation), with 8% of explanatory power, which is relatively low. The study most closely related to our approach was conducted by Blackman et al., (2016) on cuticular conductance, and concluded that plant roots also provide water storage capacity which should be incorporated into models that integrate traits influencing the plants' capabilities to withstand increasing levels of drought stress.

As elaborated by Chen and Jiang (2010) in Ahmed et al., (2020), osmotic regulation is a method for plants to cope with water deficient conditions, maintaining the turgor pressure in cells and avoiding dehydration. Nevertheless, we found that higher osmotic potential correlates with higher WHC in our data, i.e. with presumably lower drought stress. One possible explanation is that higher accumulation of osmotically effective substances also protects species against frost because it lowers the freezing temperature of protoplasm. Tissue adaptations to both frost and drought and might hence interfere. One could speculate that species from lower elevations are more in need of frost protection because their sites melt out earlier and are hence more exposed to occasional deep (night-time) temperature early in the growth period than those of higher and later melting elevations. Moreover, osmotic regulation is mostly a direct result of the nitrogen concentrations of the ecosystem, and N concentration tends to be low and carbon-poor sites with low WHC. In combination, these two facts might explain why we found osmotic concentration to be 'inversely' related to WHC.

As shown by Terashima et al. (2006), photosynthetic rate is strongly correlated with leaf structural traits such as leaf mass per area and leaf thickness, which is an important determinant in CO_2 diffusion and transport. In our data, the WHC of soil explained 27% of the community-averaged value of this trait, thus being the variable most closely related to WHC. As a corollary, water availability seems to be a crucial factor of this trait, too. Vice versa, (occasional) drought stress appears to be an efficient selective filter with respect to this trait in an alpine flora, a finding that has not been published so far.

Lastly, as stated by Delf (1912), succulence is the water content per unit area of leaf surface, as well as percentage of water content of a plant, a commonly used definition. Another possibility is that the succulence increases with water availability, so the relationship with WHC should be positive, which was not the case in our models. However, succulence appears to be related to many other environmental factors. For example, in the work of Chapman (1931), succulence was shown to directly result from lack of iron, insufficient nitrogen supply, or excessive supply of potassium salts. Other authors have reported it to be a result of NaCl ion quantities in the cell, changes in the ATP metabolism, the ratio of absorbed and free ions in plant cells, and finally, a consequence of

metabolic pathways influenced by many factors (Schulze et al. 2005; Jennings, 1968; Arnold, 1955; as cited in Grigore & Toma, 2017). All these potentially confounding factors are likely responsible for the weak correlation we found between WHC and the average community value of this trait in our data.

Conclusion

In the study, the importance of water holding capacity of the soil was examined in relation to the distribution of alpine plants, and the species composition of alpine plant communities was assessed via three different approaches. The results highlight the importance of soil factors, which are often overlooked in such environmental research, for alpine vegetation. The combined findings suggest that understanding water-related soil properties might be, contrary to what is often and formerly thought, crucial for predicting plant distributions and assessing their responses to inevitable changes in climate. Observed correlations and model successes point to WHC as almost accidentally (due to lack of previous such work), but maybe understandingly, avoided predictor, though further research is needed to refine these models.

The significant success of species distribution models using the WHC of soil represents an enrichment in methodology for predicting species' occurrences. By explaining a median of 8% and 10% variability, models highlight the strength of WHC as a predictor, albeit space for enhancement.

Sample size and sampling year limitations, as well as a small pool of literature that has already explored similar topics, leave results inconclusive and open further questions. Regarding the soil's WHC in general, it remains more of a measure of the potential to hold water and less of the realized water availability of the soil. As stressed by Pritchard (2011), less than 3% of articles published in ecological journals are dealing with belowground processes and addressing environmental changes. This study once more shows how soil-plant biology is inherently difficult to study, and moreover, difficult to make comparable.

To have an even better prediction on the impacts of climate change on alpine flora, a convenient sequel to this study would be to expand the climatological data with additional years and/or months measured and to expand the soil data by sampling and analysing the rest of the logger plots at the study site. More generally, our results indicate that alterations in precipitation, and consequently, water availability for plants, will further alter plant growth, physiology, structure and distribution, and the effect of rising temperatures.

Frame closing

The study has highlighted the often overlooked, but significant role of the soil's WHC in predicting the distribution of alpine plant species and species composition. By incorporating WHC of the soil into SDMs, I demonstrated its predictive power, surpassing traditionally considered factors like temperature and snow cover. Regardless of sample size and climatological scope limitations, the findings underline the potential of soil's WHC as a valuable predictor in ecological modelling.

Moreover, through CCA I explored and presented the complex interplay between predictors and individual species, while the analysis of plant traits connected to drought has shown that we do not know all the variables of plant physiognomy.

Furthermore, my results emphasize the need to include belowground processes, a variable seldom neglected in ecological research, except when the focal point is on microbial communities. Future studies should expand the dataset, incorporate more extensive temporal and spatial measurements, and additionally explore the interaction between WHC and other environmental variables. As climate change accelerates and alters precipitation patterns, understanding soil-water dynamics becomes even more important for predicting alterations in alpine vegetation.

Finally, this study serves as a tool in the direction of greater comprehensive understanding of the role the soil performs in ecological systems, advocating for its inclusion in plant distribution models. The results invite for an incorporated approach to studying plant ecology, in which soil properties are recognized as key elements in shaping the future of alpine biodiversity.

Literature

Adams, M.B., Archer, V.A., Bailey, S., McGuire, K., Miniat, C.F., Neary, D.G., O'Geen, T., Robichaud, P.R. and Strobel, M. (2020). Soils and Water. Forest and Rangeland Soils of the United States Under Changing Conditions, pp.33–49. doi:https://doi.org/10.1007/978-3-030-45216-2_3.

Ahmed, K., Shabbir, G., Ahmed, M. and Shah, K.N. (2020). Phenotyping for drought resistance in bread wheat using physiological and biochemical traits. Science of The Total Environment, 729, p.139082. doi:https://doi.org/10.1016/j.scitotenv.2020.139082.

Austin, M.P. and Van Niel, K.P. (2010) 'Improving species distribution models for Climate Change Studies: Variable selection and scale', Journal of Biogeography, 38(1), pp. 1–8. doi:10.1111/j.1365-2699.2010.02416.x.

Bagnall, D.K., Cristine L.S. Morgan, Cope, M., G. Mac Bean, Cappellazzi, S.B., Kelsey L.H. Greub, Liptzin, D., Norris, C.L., Rieke, E.L., Tracy, P.W., Aberle, E., Ashworth, A.J., Oscar Bañuelos Tavarez, Bary, A.I., R. Louis Baumhardt, Alberto Borbón Gracia, Brainard, D.C., Brennan, J.R., Dolores Briones Reyes and Bruhjell, D. (2022). Carbon-sensitive pedotransfer functions for plant available water. Soil Science Society of America Journal, 86(3), pp.612–629. doi:https://doi.org/10.1002/saj2.20395.

Blackman, C.J., Pfautsch, S., Choat, B., Delzon, S., Gleason, S.M. and Duursma, R.A. (2016). Toward an index of desiccation time to tree mortality under drought. Plant, Cell & Environment, 39(10), pp.2342–2345. doi:https://doi.org/10.1111/pce.12758.

Broadbent, A.A.D., Snell, H.S.K., Michas, A., Pritchard, W.J., Newbold, L., Cordero, I., Goodall, T., Schallhart, N., Kaufmann, R., Griffiths, R.I., Schloter, M., Bahn, M. and Bardgett, R.D. (2021). Climate change alters temporal dynamics of alpine soil microbial functioning and biogeochemical cycling via earlier snowmelt. The ISME Journal, [online] 15, pp.1–12. doi:https://doi.org/10.1038/s41396-021-00922-0.

Buri, A., Cianfrani, C., Pinto-Figueroa, E., Yashiro, E., Spangenberg, J.E., Adatte, T., Verrecchia, E., Guisan, A. and Pradervand, J.-N. (2017). Soil factors improve predictions of plant species distribution in a mountain environment. Progress in Physical Geography: Earth and Environment, 41(6), pp.703–722. doi:https://doi.org/10.1177/0309133317738162.

Buri, A., Grand, S., Yashiro, E., Adatte, T., Spangenberg, J.E., Pinto-Figueroa, E., Verrecchia, E. and Guisan, A. (2019). What are the most crucial soil variables for predicting the distribution of mountain

PLANT SPECIES? A COMPREHENSIVE STUDY IN THE SWISS ALPS. JOURNAL OF BIOGEOGRAPHY, 47(5), PP.1143–1153. DOI:HTTPS://DOI.ORG/10.1111/JBI.13803.

BÜRLI, S., THEURILLAT, J.-P., WINKLER, M., LAMPRECHT, A., PAULI, H., RIXEN, C., STEINBAUER, K., WIPF, S., ABDALADZE, O., ANDREWS, C., BARANČOK, P., BENITO-ALONSO, J.L., FERNÁNDEZ CALZADO, M.R., CARRANZA, M.L., DICK, J., ERSCHBAMER, B., GHOSN, D., GIGAURI, K., KAZAKIS, G. AND MALLAUN, M. (2021). A COMMON SOIL TEMPERATURE THRESHOLD FOR THE UPPER LIMIT OF ALPINE GRASSLANDS IN EUROPEAN MOUNTAINS. ALPINE BOTANY, 131(1), PP.41–52. DOI:HTTPS://DOI.ORG/10.1007/S00035-021-00250-1.

CHAPMAN, G.W. (1931). THE CAUSE OF SUCCULENCE IN PLANTS. NEW PHYTOLOGIST, 30(2), PP.119–127. DOI:HTTPS://DOI.ORG/10.1111/J.1469-8137.1931.TB07411.X.

CHAUVIER, Y., THUILLER, W., BRUN, P., LAVERGNE, S., DESCOMBES, P., KARGER, D.N., RENAUD, J. AND ZIMMERMANN, N.E. (2021). INFLUENCE OF CLIMATE, SOIL, AND LAND COVER ON PLANT SPECIES DISTRIBUTION IN THE EUROPEAN ALPS. ECOLOGICAL MONOGRAPHS, 91(2). DOI:HTTPS://DOI.ORG/10.1002/ECM.1433.

CHAUVIER-MENDES, Y., POLLOCK, L.J., VERBURG, P.H., KARGER, D.N., PELLISSIER, L., LAVERGNE, S., ZIMMERMANN, N.E. AND THUILLER, W. (2024). TRANSNATIONAL CONSERVATION TO ANTICIPATE FUTURE PLANT SHIFTS IN EUROPE. NATURE ECOLOGY & EVOLUTION, [ONLINE] 8(3), PP.454–466. DOI:HTTPS://DOI.ORG/10.1038/S41559-023-02287-3.

CHERSICH, S., REJŠEK, K., VRANOVÁ, V., BORDONI, M., MEISINA, C. (2015) 'CLIMATE CHANGE IMPACTS ON THE ALPINE ECOSYSTEM: AN OVERVIEW WITH FOCUS ON THE SOIL', JOURNAL OF FOREST SCIENCE, 61(11), PP. 496–514. DOI:10.17221/47/2015-JFS.

CIANFRANI, C., BURI, A., VITTOZ, P., GRAND, S., ZINGG, B., VERRECCHIA, E. AND GUISAN, A. (2019). SPATIAL MODELLING OF SOIL WATER HOLDING CAPACITY IMPROVES MODELS OF PLANT DISTRIBUTIONS IN MOUNTAIN LANDSCAPES. PLANT AND SOIL, 438(1-2), PP.57–70. DOI:HTTPS://DOI.ORG/10.1007/S11104-019-04016-X.

CHAPIN, F.S. AND EVINER, V.T. (2007) 'BIOGEOCHEMISTRY OF TERRESTRIAL NET PRIMARY PRODUCTION', TREATISE ON GEOCHEMISTRY, PP. 1–35. DOI:10.1016/B0-08-043751-6/08130-5.

CRIMMINS, S.M., DOBROWSKI, S.Z., GREENBERG, J.A., ABATZOGLOU, J.T. AND MYNSBERGE, A.R. (2011). CHANGES IN CLIMATIC WATER BALANCE DRIVE DOWNHILL SHIFTS IN PLANT SPECIES' OPTIMUM ELEVATIONS. SCIENCE, 331(6015), PP.324–327. DOI:HTTPS://DOI.ORG/10.1126/SCIENCE.1199040.

DELF, E.M. (1912) 'TRANSPIRATION IN SUCCULENT PLANTS', ANNALS OF BOTANY, OS-26(2), PP. 409–442. DOI:10.1093/OXFORDJOURNALS.AOB.A089398.

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Pascal Vittoz and Guisan, A. (2012). Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. Journal of Vegetation Science, 24(4), pp.593–606. doi:https://doi.org/10.1111/jvs.12002.

Duursma, R.A., Blackman, C.J., Lopéz, R., Martin-StPaul, N.K., Cochard, H. and Medlyn, B.E. (2018). On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls. New Phytologist, 221(2), pp.693–705. doi:https://doi.org/10.1111/nph.15395.

Edwards, A.C., Scalenghe, R. and Freppaz, M. (2007). Changes in the seasonal snow cover of alpine regions and its effect on soil processes: A review. Quaternary International, 162-163, pp.172–181. doi:https://doi.org/10.1016/j.quaint.2006.10.027.

Elias, S.A. (2020). Nature of Alpine Soils. Elsevier eBooks, pp.409–417. doi:https://doi.org/10.1016/b978-0-12-409548-9.12398-x.

ENGLER, R., RANDIN, C.F., THUILLER, W., DULLINGER, S., ZIMMERMANN, N.E., ARAÚJO, M.B., PEARMAN, P.B., LE LAY, G., PIEDALLU, C., ALBERT, C.H., CHOLER, P., COLDEA, G., De LAMO, X., DIRNBÖCK, T., GÉGOUT, J.-C., GÓMEZ-GARCÍA, D., GRYTNES, J.-A., HEEGAARD, E., HØISTAD, F. and NOGUÉS-BRAVO, D. (2011). 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology, 17(7), pp.2330–2341. doi:https://doi.org/10.1111/j.1365-2486.2010.02393.x.

Fischer, Manfred & Oswald, K. & Adler, W.. (2008). Exkursionsflora für Österreich, Liechtenstein und Südtirol. 3. Auflage. Biologiezentrum der Oberösterreichischen Landesmuseen, Linz

González-Salazar, C., Stephens, C.R. and Marquet, P.A. (2013). Comparing the relative contributions of biotic and abiotic factors as mediators of species' distributions. Ecological Modelling, 248, pp.57–70. doi:https://doi.org/10.1016/j.ecolmodel.2012.10.007.

Grigore, M.-N. and Toma, C. (2017) 'Succulence', Anatomical Adaptations of Halophytes, pp. 41–124. doi:10.1007/978-3-319-66480-4_3.

Hartley, I.P., Hill, T.C., Chadburn, S.E. and Hugelius, G. (2021). Temperature effects on carbon storage are controlled by soil stabilisation capacities. Nature Communications, 12(1). doi:https://doi.org/10.1038/s41467-021-27101-1.

KIRKHAM, M.B. (2005). FIELD CAPACITY, WILTING POINT, AVAILABLE WATER, AND THE NON-LIMITING WATER RANGE. PRINCIPLES OF SOIL AND PLANT WATER RELATIONS, PP.101–115. DOI:HTTPS://DOI.ORG/10.1016/B978-012409751-3/50008-6.

KÖRNER, C. (2020). PLANT ADAPTATIONS TO ALPINE ENVIRONMENTS. ELSEVIER EBOOKS, PP.355–361. DOI:HTTPS://DOI.ORG/10.1016/B978-0-12-409548-9.11793-2.

KÖRNER, C. (2021): ALPINE PLANT LIFE. 3RD EDITION. SPRINGER, BERLIN – HEIDELBERG.

LANDOLT, E., BÄUMLER, B., ERHARDT, A., HEGG, O., KLÖTZLI, F., LÄMMLER, W., NOBIS, M., RUDMANN-MAURER, K., SCHWEINGRUBER, F. H., THEURILLAT, J.-P., URMI, E., VUST, M. AND WOHLGEMUTH, T. 2010. FLORA INDICATIVA: ÖKOLOGISCHE ZEIGERWERTE UND BIOLOGISCHE KENNZEICHEN ZUR FLORA DER SCHWEIZ UND DER ALPEN [ECOLOGICAL INDICATORS VALUES AND BIOLOGICAL ATTRIBUTES OF THE FLORA OF SWITZERLAND AND THE ALPS (IN GERMAN)]. – HAUPT, P. 376.

LAMPRECHT, A., SEMENCHUK, P.R., STEINBAUER, K., WINKLER, M. AND PAULI, H. (2018). CLIMATE CHANGE LEADS TO ACCELERATED TRANSFORMATION OF HIGH-ELEVATION VEGETATION IN THE CENTRAL ALPS. NEW PHYTOLOGIST, [ONLINE] 220(2), PP.447–459. DOI:HTTPS://DOI.ORG/10.1111/NPH.15290.

"LECO." LECO CORPORATION, 12 SEPT. 2024, WWW.LECO.COM/. ACCESSED 19 SEPT. 2024.

MA, J.-Y., SUN, W., LIU, X.-N. AND CHEN, F.-H. (2012). VARIATION IN THE STABLE CARBON AND NITROGEN ISOTOPE COMPOSITION OF PLANTS AND SOIL ALONG A PRECIPITATION GRADIENT IN NORTHERN CHINA. PLOS ONE, 7(12), P. DOI:HTTPS://DOI.ORG/10.1371/JOURNAL.PONE.0051894.

MAHARJAN, S.K., STERCK, F.J., RAES, N. AND POORTER, L. (2021). TEMPERATURE AND SOILS PREDICT THE DISTRIBUTION OF PLANT SPECIES ALONG THE HIMALAYAN ELEVATIONAL GRADIENT. JOURNAL OF TROPICAL ECOLOGY, 38(2), PP.58–70. DOI:HTTPS://DOI.ORG/10.1017/S026646742100050X.

MINASNY, B., MCBRATNEY, A.B., BROUGH, D.M. AND JACQUIER, D. (2011). MODELS RELATING SOIL PH MEASUREMENTS IN WATER AND CALCIUM CHLORIDE THAT INCORPORATE ELECTROLYTE CONCENTRATION. EUROPEAN JOURNAL OF SOIL SCIENCE, 62(5), PP.728–732. DOI:HTTPS://DOI.ORG/10.1111/J.1365-2389.2011.01386.X.

MOUNTAIN RESEARCH INITIATIVE EDW WORKING GROUP (2015) 'ELEVATION-DEPENDENT WARMING IN MOUNTAIN REGIONS OF THE WORLD', NATURE CLIMATE CHANGE, 5(5), PP. 424–430. DOI:10.1038/NCLIMATE2563.

MOUNTAINRESEARCH.AT. (2020). MICROCLIM. [ONLINE] AVAILABLE AT: HTTPS://WWW.MOUNTAINRESEARCH.AT/MICROCLIM/ [ACCESSED 24 OCT. 2024].

Mod, H.K., Scherrer, D., Luoto, M. and Guisan, A. (2016). What we use is not what we know: environmental predictors in plant distribution models. Journal of Vegetation Science, 27(6), pp.1308–1322. doi:https://doi.org/10.1111/jvs.12444.

Na, L., Genxu, W., Yan, Y., Yongheng, G. and Guangsheng, L. (2011). Plant production, and carbon and nitrogen source pools, are strongly intensified by experimental warming in alpine ecosystems in the Qinghai-Tibet Plateau. Soil Biology and Biochemistry, 43(5), pp.942–953. doi:https://doi.org/10.1016/j.soilbio.2011.01.009.

Nogués-Bravo, D., Araújo, M.B., Errea, M.P. and Martínez-Rica, J.P. (2007). Exposure of global mountain systems to climate warming during the 21st Century. Global Environmental Change, 17(3-4), pp.420–428. doi:https://doi.org/10.1016/j.gloenvcha.2006.11.007.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). _vegan: Community Ecology Package_. R package version 2.6-4, https://CRAN.R-project.org/package=vegan

Paetzolt, M. 2022: Functional traits of alpine plants along an elevational gradient on Schrankogel, Tyrol. Master thesis, Friedrich Schiller Universität Jena.

Panchard, T., Olivier Broennimann, Mathieu Gravey, Grégoire Mariethoz and Guisan, A. (2023). Snow cover persistence as a useful predictor of alpine plant distributions. Journal of Biogeography, 50(10), pp.1789–1802. doi:https://doi.org/10.1111/jbi.14689.

PAULI, H., GOTTFRIED, M., REITER, K., KLETTNER, C. and GRABHERR, G. (2006). Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA* master site Schrankogel, Tyrol, Austria. Global Change Biology, 13(1), pp.147–156. doi:https://doi.org/10.1111/j.1365-2486.2006.01282.x.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R.F., Ghosn, D., Holten, J.I., Kanka, R., Kazakis, G., Kollar, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U. and Mesa, J.M. (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. Science, [online] 336(6079), pp.353–355. doi:https://doi.org/10.1126/science.1219033.

PEDUZZI, P., CONCATO, J., KEMPER, E., HOLFORD, T.R. AND FEINSTEIN, A.R. (1996). A SIMULATION STUDY OF THE NUMBER OF EVENTS PER VARIABLE IN LOGISTIC REGRESSION ANALYSIS. JOURNAL OF CLINICAL EPIDEMIOLOGY, 49(12), PP.1373–1379. DOI:HTTPS://DOI.ORG/10.1016/S0895-4356(96)00236-3.

PRITCHARD, S.G. (2011). SOIL ORGANISMS AND GLOBAL CLIMATE CHANGE. PLANT PATHOLOGY, 60(1), PP.82–99. DOI:HTTPS://DOI.ORG/10.1111/J.1365-3059.2010.02405.X.

PUGNAIRE, F.I., MORILLO, J.A., PEÑUELAS, J., REICH, P.B., BARDGETT, R.D., GAXIOLA, A., WARDLE, D.A. AND VAN DER PUTTEN, W.H. (2019). CLIMATE CHANGE EFFECTS ON PLANT-SOIL FEEDBACKS AND CONSEQUENCES FOR BIODIVERSITY AND FUNCTIONING OF TERRESTRIAL ECOSYSTEMS. SCIENCE ADVANCES, [ONLINE] 5(11), P.EAAZ1834. DOI:HTTPS://DOI.ORG/10.1126/SCIADV.AAZ1834.

R CORE TEAM (2023). _R: A LANGUAGE AND ENVIRONMENT FOR STATISTICAL COMPUTING_. R FOUNDATION FOR STATISTICAL COMPUTING, VIENNA, AUSTRIA. HTTPS://WWW.R-PROJECT.ORG/

RAHBEK, C., BORREGAARD, M.K., ANTONELLI, A., COLWELL, R.K., HOLT, B.G., NOGUES-BRAVO, D., RASMUSSEN, C.M.Ø., RICHARDSON, K., ROSING, M.T., WHITTAKER, R.J. AND FJELDSÅ, J. (2019). BUILDING MOUNTAIN BIODIVERSITY: GEOLOGICAL AND EVOLUTIONARY PROCESSES. SCIENCE, 365(6458), PP.1114–1119. DOI:HTTPS://DOI.ORG/10.1126/SCIENCE.AAX0151.

RANDIN, C.F., ENGLER, R., NORMAND, S., ZAPPA, M., ZIMMERMANN, N.E., PEARMAN, P.B., VITTOZ, P., THUILLER, W. AND GUISAN, A. (2009). CLIMATE CHANGE AND PLANT DISTRIBUTION: LOCAL MODELS PREDICT HIGH-ELEVATION PERSISTENCE. GLOBAL CHANGE BIOLOGY, 15(6), PP.1557–1569. DOI:HTTPS://DOI.ORG/10.1111/J.1365-2486.2008.01766.X.

RIXEN, C., WIPF, S., FREI, E. AND STÖCKLI, V. (2014). FASTER, HIGHER, MORE? PAST, PRESENT AND FUTURE DYNAMICS OF ALPINE AND ARCTIC FLORA UNDER CLIMATE CHANGE. ALPINE BOTANY, 124(2), PP.77–79. DOI:HTTPS://DOI.ORG/10.1007/S00035-014-0141-Z.

ROE, N.A., DUCEY, M.J., LEE, T.D., FRASER, O.L., COLTER, R.A. AND HALLETT, R.A. (2022). SOIL CHEMICAL VARIABLES IMPROVE MODELS OF UNDERSTOREY PLANT SPECIES DISTRIBUTIONS. JOURNAL OF BIOGEOGRAPHY, 49(4), PP.753–766. DOI:HTTPS://DOI.ORG/10.1111/JBI.14344.

SEASTEDT, T. R. (2001). 'SOILS' IN STRUCTURE AND FUNCTION OF AN ALPINE ECOSYSTEM NIWOT RIDGE, COLORADO, EDITED BY BOWMAN, W. D. & SEASTEDT, T. R., PP. 157-173. NEW YORK: OXFORD UNIVERSITY PRESS.

SEIBT, U., RAJABI, A., GRIFFITHS, H. AND BERRY, J.A. (2008). CARBON ISOTOPES AND WATER USE EFFICIENCY: SENSE AND SENSITIVITY. OECOLOGIA, 155(3), PP.441–454. DOI:HTTPS://DOI.ORG/10.1007/S00442-007-0932-7.

TERASHIMA, I., HANBA, Y.T., TAZOE, Y., VYAS, P. AND YANO, S. (2005). IRRADIANCE AND PHENOTYPE: COMPARATIVE ECO-DEVELOPMENT OF SUN AND SHADE LEAVES IN RELATION TO PHOTOSYNTHETIC CO2 DIFFUSION. JOURNAL OF EXPERIMENTAL BOTANY, 57(2), PP.343–354. DOI:HTTPS://DOI.ORG/10.1093/JXB/ERJ014.

TJUR, T. (2009) 'COEFFICIENTS OF DETERMINATION IN LOGISTIC REGRESSION MODELS—A NEW PROPOSAL: THE COEFFICIENT OF DISCRIMINATION', THE AMERICAN STATISTICIAN, 63(4), PP. 366–372. DOI:10.1198/TAST.2009.08210.

VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. AND GARNIER, E. (2007). LET THE CONCEPT OF TRAIT BE FUNCTIONAL! OIKOS, 116(5), PP.882–892. DOI:HTTPS://DOI.ORG/10.1111/J.0030-1299.2007.15559.X.

VONLANTHEN, C.M., BÜHLER, A., VEIT, H., KAMMER, P.M. AND EUGSTER, W. (2006). ALPINE PLANT COMMUNITIES: A STATISTICAL ASSESSMENT OF THEIR RELATION TO MICROCLIMATOLOGICAL, PEDOLOGICAL, GEOMORPHOLOGICAL, AND OTHER FACTORS. PHYSICAL GEOGRAPHY, 27(2), PP.137–154. DOI:HTTPS://DOI.ORG/10.2747/0272-3646.27.2.137.

WICKHAM H (2016). GGPLOT2: ELEGANT GRAPHICS FOR DATA ANALYSIS. SPRINGER-VERLAG NEW YORK. ISBN 978-3-319-24277-4, HTTPS://GGPLOT2.TIDYVERSE.ORG.

WINKLER, D.E., LUBETKIN, K.C., CARRELL, A.A., JABIS, M.D., YANG, Y. AND KUEPPERS, L.M. (2019). RESPONSES OF ALPINE PLANT COMMUNITIES TO CLIMATE WARMING. ECOSYSTEM CONSEQUENCES OF SOIL WARMING, PP.297–346. DOI:HTTPS://DOI.ORG/10.1016/B978-0-12-813493-1.00013-2.

WRIGHT, A.F. AND BAILEY, J.S. (2001) 'ORGANIC CARBON, TOTAL CARBON, AND TOTAL NITROGEN DETERMINATIONS IN SOILS OF VARIABLE CALCIUM CARBONATE CONTENTS USING A LECO CN-2000 DRY COMBUSTION ANALYZER', COMMUNICATIONS IN SOIL SCIENCE AND PLANT ANALYSIS, 32(19–20), PP. 3243–3258. DOI:10.1081/CSS-120001118.

YANG, Y., GOU, R., ZHAO, J., QI, N., WEN, Z., JALAL KASSOUT, LI, R., LIN, G. AND ZHENG, H. (2021). VARIATION IN CARBON ISOTOPE COMPOSITION OF PLANTS ACROSS AN ARIDITY GRADIENT ON THE LOESS PLATEAU, CHINA. GLOBAL ECOLOGY AND CONSERVATION, 33, PP.E01948–E01948. DOI:HTTPS://DOI.ORG/10.1016/J.GECCO.2021.E01948.

ZHANG, Y., WANG, K., WANG, J., LIU, C. AND SHANGGUAN, Z. (2021). CHANGES IN SOIL WATER HOLDING CAPACITY AND WATER AVAILABILITY FOLLOWING VEGETATION RESTORATION ON THE CHINESE LOESS PLATEAU. SCIENTIFIC REPORTS, 11(1). DOI:HTTPS://DOI.ORG/10.1038/S41598-021-88914-0.

Appendix

Table 4: Observed plant species in the statistical analyses - "Target species" (above70% of presence on the logger plots).

1.	*Achillea moschata*	29.	*Oreochloa disticha*
2.	*Agrostis agrostiflora*	30.	*Oxyria digyna*
3.	*Agrostis rupestris*	31.	*Persicaria vivipara*
4.	*Anthoxanthum alpinum*	32.	*Phyteuma hemisphaericum*
5.	*Avenula versicolor*	33.	*Poa alpina*
6.	*Bartsia alpina*	34.	*Poa laxa*
7.	*Calluna vulgaris*	35.	*Primula glutinosa*
8.	*Campanula barbata subsp. barbata*	36.	*Primula minima*
9.	*Carex curvula subsp. curvula*	37.	*Ranunculus glacialis*
10.	*Carex sempervirens*	38.	*Ranunculus villarsii*
11.	*Cerastium uniflorum*	39.	*Rhododendron ferrugineum*
12.	*Crepis aurea*	40.	*Salix helvetica*
13.	*Deschampsia cespitosa subsp. cespitosa*	41.	*Salix herbacea*
14.	*Festuca nigricans*	42.	*Saxifraga bryoides*
15.	*Geranium sylvaticum*	43.	*Saxifraga exarata*
16.	*Geum montanum*	44.	*Scorzoneroides helvetica*
17.	*Geum reptans*	45.	*Sedum alpestre*
18.	*Gnaphalium supinum*	46.	*Senecio incanus subsp. carniolicus*
19.	*Homogyne alpina*	47.	*Sibbaldia procumbens*
20.	*Juncus trifidus*	48.	*Silene acaulis subsp. exscapa*
21.	*Kobresia myosuroides*	49.	*Solidago virgaurea subsp. minuta*
22.	*Leucanthemopsis alpina*	50.	*Trifolium badium*
23.	*Loiseleuria procumbens*	51.	*Vaccinium gaultherioides*
24.	*Luzula alpino-pilosa*	52.	*Vaccinium myrtillus*
25.	*Luzula lutea*	53.	*Vaccinium vitis-idaea*
26.	*Luzula spicata*	54.	*Veronica alpina*
27.	*Mutellina adonidifolia*	55.	*Veronica bellidioides*
28.	*Nardus stricta*	56.	*Viola biflora*

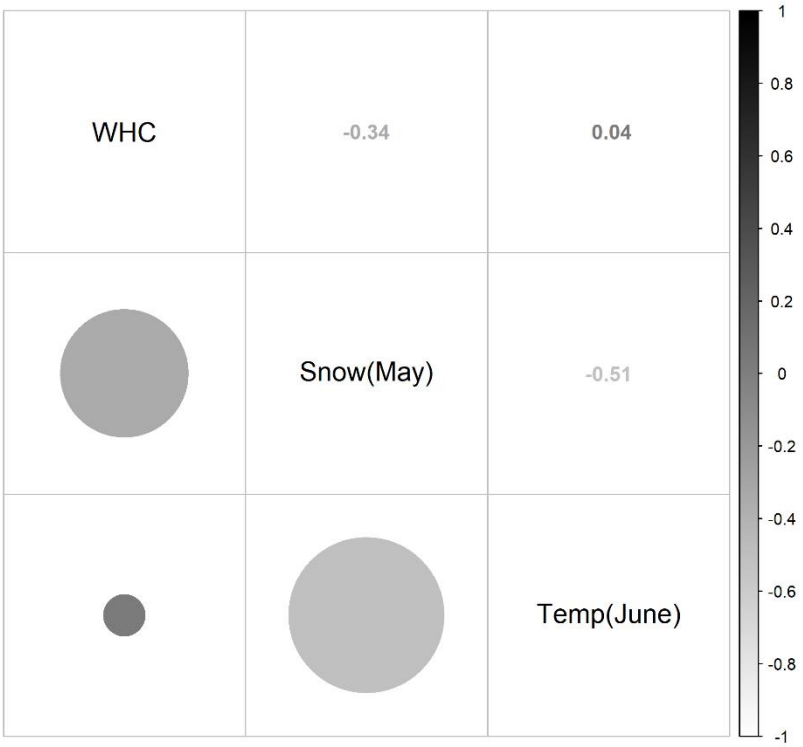

Figure 5: Correlation matrix of three SDM predictors: WHC, snow, and temperature.

List of Figures

Figure 1: Amount of variation in species distributions explained by the three predictors (expressed as R^2). 11
Figure 2: Explanatory power of the individual predictors in explaining distributions of individual species 12
Figure 3: CCA ordination plot 14
Figure 4: Relationships between drought-resistance-related trait means and WHC.. 16
Figure 5: Correlation matrix of three SDM predictors: WHC, snow, and temperature. II

List of Tables

Table 1: Maximal, minimal, and mean values of measured soil variables 9
Table 2: Correlation of predictor variables with the first two constrained axes of the CCA. 14
Table 3: Results of a permutation test analysing the importance of the individual predictor. 15
Table 4: Observed plant species in the statistical analyses – "Target species". I

Data processing script

```
##loading libraries
library(sf)
library(tidyverse)
library(ggplot2)
library(ggpubr)
library(corrplot)
library("performance")
library(ade4)
library(dplyr)
library(vegan)
library(pROC)
library("ggvegan")

# load working directory
setwd("D:/A/dipl/01_R_project/02_data/01_initial_input_data")
# Sets the working directory to the specified path.

# PLANT DROUGHT TRAITS VS. WHC #####
# read in soil
soil <- read.csv("D:/A/dipl/01_R_project/02_data/02_merged_data/soil_data_total_new.csv") %>%
  na.omit() # Reads the soil data from a CSV file and removes rows with NA values.

#filter(logger_ID != 538) # This logger is removed because mt6 is wrong (-36.8°C) #this was gotten by merging individual datasets (below)
soil <- soil %>% rename(WHC = whc_0_20)
# Renames the column 'whc_0_20' to 'WHC'.

# Calculate the mean values for pH, nitrogen (n), carbon (c), and WHC (water holding capacity) in the soil data.
soilmean <- soil %>%
  summarize(mean_ph_water = mean(ph_water, na.rm = TRUE),
            mean_n = mean(n, na.rm = TRUE),
            mean_c = mean(c, na.rm = TRUE),
            mean_WHC = mean(WHC, na.rm = TRUE))

# add plant traits
relevees_traits <- read.csv("D:/A/dipl/01_R_project/02_data/02_merged_data/relevees_traits.csv", sep = ";") # Reads plant trait data from a CSV file using ';' as the delimiter.

# add data with above 70% coverage of plants per logger
```

```
above70 <- read.csv("D:/A/dipl/01_R_project/02_data/02_merged_data/above70.csv") %>%
 na.omit() # Reads data with plant coverage above 70% from a CSV file and removes rows with NA values.

above70 <- above70 %>%
 rename(osmotic_concentration = osmot_potential) # Renames the column 'osmot_potential' to 'osmotic_concentration'.

# calculate unweighted means of plant traits
unweighted_soil <- above70 %>%
 group_by(logger_ID) %>%
 summarise(mC13 = mean(C13, na.rm = TRUE),
        mOC= mean(osmotic_concentration, na.rm = TRUE),
        mGmin = mean(Gmin, na.rm = TRUE),
        mR600 = mean(R600, na.rm = TRUE),
        mSUCC = mean(succ, na.rm = TRUE)) %>%
 left_join(soil, .) %>%
 select(-c(ph_water:c)) %>%
 na.omit()
# Calculates unweighted mean values for various plant traits, joins with the soil data, and removes columns not needed for further analysis.

# adapt for creating graphs
mean_of_traits_lm <- unweighted_soil %>%
 pivot_longer(cols = c(mC13, mOC, mGmin, mR600, mSUCC)) %>%  # elongating just plant traits
 nest_by(name) %>%
 mutate(model = list(lm(value ~ WHC, data = data)),
      r2 = summary(model)$adj.r.squared,
      p_value = unname(broom::glance(model)$p.value))
# Transforms the data into a long format, creates linear models for each plant trait against WHC, calculates R² and p-values for each model.

#create graph: unweighted mean of traits vs. soil WHC
mean_of_traits_lm %>%
 select(name, data) %>%
 unnest(data) %>%
 ggplot(aes(x = WHC, y = value)) +
 geom_point() +
 geom_smooth(method = lm, formula = y ~ x) +
 facet_wrap(~ name, scales = "free", labeller = labeller(name = c("mC13" = "C13", "mGmin" = "Gmin", "mOC" = "OC", "mR600" = "R600", "mSUCC" = "Suc"))) +
```

```
 labs(x = "WHC") +
 theme_bw() +
 theme(plot.title = element_text(size = 18),
       strip.text = element_text(size = 12),
       axis.text = element_text(size = 16),    # Increase axis text size
       axis.title.x = element_text(size = 16),  # Increase x-axis label size
       axis.title.y = element_text(size = 16))
# Plots the relationship between unweighted mean traits and soil WHC, with a linear regression line, and customizes the appearance of the graph.

# save graph
ggsave("D:/A/dipl/01_R_project/02_data/04_figures/final_plots/unweighted_means_ploottt.png", width = 280, height = 190, unit = "mm")
# Saves the generated plot to the specified path.

# extract r-values of unweighted trait means
p_unw_mean <- mean_of_traits_lm %>% select(r2, p_value)
write.csv(p_unw_mean, "D:/A/dipl/01_R_project/02_data/p_unw_mean.csv")
# Extracts R² and p-values from the model results and writes them to a CSV file.

# SDMs #####
# add topo-clim predictor variables
predictors <- read_delim("D:/A/dipl/01_R_project/02_data/02_merged_data/predictors_all.csv", delim = ",") %>% na.omit
# Reads predictor variables data from a CSV file and removes rows with NA values.

# combine predictor variables with plant traits
predictors_species <- relevees_traits %>%
 na.omit() %>%
 select(logger_ID, TAXON) %>%
 mutate(presence = 1) %>%
 pivot_wider(names_from = TAXON, values_from = presence, values_fill = 0) %>%
 pivot_longer(!logger_ID) %>%
 rename(taxon = name, presence = value) %>%
 left_join(predictors) %>%
# Transforms the plant trait data to wide format by species presence, joins with predictor data, and removes data from logger_ID 538.

# Filter species with at least 30 occurrences
predictors_occurence30 <- predictors_species %>%
 group_by(taxon) %>%
```

```
 summarise(presence = sum(presence)) %>%
 filter(presence >= 30)
# Filters species that have at least 30 occurrences for further modeling.

# load data
relevees_traits <-
read_csv2("D:/A/dipl/01_R_project/02_data/02_merged_data/relevees_traits.csv") %>% na.omit()
%>% mutate_at(vars(5:8), as.numeric)
# Reads and processes plant trait data with ';' as delimiter, removes NA values, and converts
specified columns to numeric.

# logger plots where species are present
predictors_species <- predictors_species %>%
 group_by(taxon) %>%
 filter(taxon %in% predictors_occurence30$taxon) %>%
 ungroup()
# Filters the predictors species data to include only those species with at least 30 occurrences.

# Then group the table by Taxon and use the nest() function and ungroup() to create the nested
dataframe and save it #again under nested_sdm_data e.g.
nested_sdm_data30 <- predictors_species %>%
 select(1:11) %>% #, 14, 15) %>%
 na.omit() %>%
 mutate(across(c(TP5_15:mt6), scale)) %>%  # this was scaled as mean of 0 and stand.dev of 1
 nest_by(taxon)
# Creates a nested data frame grouped by species taxon, scales predictor variables, and removes
rows with NA values.

# build model
clima_models20 <- nested_sdm_data30 %>%
 mutate(model_mt6_lin = list(glm(presence ~ mt6,
                        data = data, family="binomial")),
       model_mt6_poly = list(glm(presence ~ poly(mt6, 2),
                         data = data, family="binomial")),
       model_snow5_lin = list(glm(presence ~ snow5,
                         data = data, family="binomial")),
       model_snow5_poly = list(glm(presence ~ poly(snow5, 2),
                          data = data, family="binomial")),
       model_whc20_lin = list(glm(presence ~ whc_0_20,
                         data = data, family="binomial")),
       model_whc20_poly = list(glm(presence ~ poly(whc_0_20, 2),
```

```
                    data = data, family="binomial")),
    R2_mt6_lin = c(r2_tjur(model_mt6_lin)),
    R2_mt6_poly = c(r2_tjur(model_mt6_poly)),
    R2_snow5_lin = c(r2_tjur(model_snow5_lin)),
    R2_snow5_poly = c(r2_tjur(model_snow5_poly)),
    R2_whc20_lin = c(r2_tjur(model_whc20_lin)),
    R2_whc20_poly = c(r2_tjur(model_whc20_poly)))
# Fits generalized linear models with binomial family to the data for various predictors and
polynomial terms, calculates R² values.

# build graph
clima_models30 %>%
 ungroup() %>%
 select(R2_mt6_poly, R2_snow5_poly, R2_whc20_poly) %>%
 pivot_longer(everything(), names_to = "R2_type", values_to = "R2_value") %>%
 rowwise() %>%
 mutate(relationship = unlist(str_split(R2_type, "_"))[3],
     predictor = unlist(str_split(R2_type, "_"))[2]) %>%
 ggplot(aes(x = predictor, y = R2_value, fill = interaction(relationship, predictor))) +
 stat_boxplot(aes(group= interaction(relationship, predictor)), geom="errorbar", width = 0.3,
position = position_dodge(width = 0.8)) +
 geom_boxplot(position = position_dodge(width = 0.8)) +
 scale_fill_manual(values = c("darkorange", "dodgerblue3", "darkmagenta"),
           labels = c("Temp.(June)", "Snow(May)", "WHC"), name=NULL) +
 scale_x_discrete(labels = c("Temp.(June)", "Snow(May)", "WHC")) +
 labs(x = NULL, y = "Tjur R²") +
 theme_bw() + theme(legend.position = "bottom",
              axis.line = element_line(colour = "black"),
              panel.border = element_blank())
# Plots the Tjur R² values for polynomial models, showing the distribution of R² values for different
predictors.
ggsave("new_final_boxplot.png", height = 9.5, width = 15.5, unit = "cm", dpi = 300)
# Saves the generated boxplot to the specified path.

# build barplot:
clima_models30 %>%
 ungroup() %>%
 select(taxon, R2_mt6_lin:R2_whc20_poly) %>%
 mutate(plot_order = rank(-R2_whc20_poly)) %>%
 pivot_longer(!c(taxon, plot_order), names_to = "R2_type", values_to = "R2_value") %>%
 rowwise() %>%
```

```
 mutate(relationship = unlist(str_split(R2_type, "_"))[3],
      predictor = unlist(str_split(R2_type, "_"))[2]) %>%
 filter(relationship == 'poly') %>%
 mutate(R2_value = R2_value * 1.5) %>% # Corrected line
 ggplot(aes(x = reorder(taxon, plot_order), y = R2_value, fill = interaction(relationship, predictor))) +
 geom_bar(stat= "identity", position = position_dodge(width = 0.9), width = 0.8) + # Adjust the
width here
 scale_fill_manual(values = c("darkorange", "dodgerblue3", "darkmagenta"),
             labels = c("Temp.(June)", "Snow(May)", "WHC"), name=NULL) +
 labs(x = NULL, y = "Tjur R²") +
 theme_bw() + theme(axis.text.x = element_text(angle=90, hjust= 1, vjust=0.5),
              legend.position = "bottom",
              axis.line = element_line(colour = "black"),
              panel.border = element_blank())
# Creates a bar plot of Tjur R² values for polynomial models, showing the importance of different
predictors for species.

ggsave("new_finaltargetpoly.png", height = 15, width = 15.5, unit = "cm", dpi = 300)
# Saves the generated bar plot to the specified path.

# extract R values for each predictor
poly_species_summary <- clima_models20 %>%
 ungroup() %>%
 select(taxon, starts_with("R2_")) %>%
 filter(!is.na(R2_snow5_poly) & !is.na(R2_whc20_poly) & !is.na(R2_mt6_poly)) %>%
 summarise(mean_R2_snow = mean(R2_snow5_poly),
        min_R2_snow = min(R2_snow5_poly),
        max_R2_snow = max(R2_snow5_poly),
        mean_R2_whc = mean(R2_whc20_poly),
        min_R2_whc = min(R2_whc20_poly),
        max_R2_whc = max(R2_whc20_poly),
        mean_R2_temp = mean(R2_mt6_poly),
        min_R2_temp = min(R2_mt6_poly),
        max_R2_temp = max(R2_mt6_poly))
# Summarizes the R² values for each predictor by calculating mean, minimum, and maximum values.
write.csv(poly_species_summary, "polyvalues_summary.csv", row.names = FALSE)

# CCA ####
# Adapt data
ccapredictors <- predictors %>%
```

```
 na.omit() %>%  # Remove rows with any missing values
 arrange(logger_ID) %>%  # Sort data by 'logger_ID'
 rename(WHC = whc_0_20) %>% # Rename column 'whc_0_20' to 'WHC'
 rename(Snow(May)  = snow5) %>%
 rename (Temp(June) = mt6) %>%
 rename(pH = ph_water) %>% # Rename column 'ph_water' to 'pH'
 column_to_rownames("logger_ID")  # Set 'logger_ID' as row names

length(unique(predictors$logger_ID))  # Count the number of unique 'logger_ID' values

# Create site-species matrix for CCA
ccasite_species_matrix <- relevees_traits %>%
 select(logger_ID, TAXON, cover_percent) %>%  # Select relevant columns
 pivot_wider(names_from = TAXON, values_from = cover_percent, values_fill = 0) %>%  # Transform
data to wide format with 'TAXON' as columns
 filter(logger_ID %in% rownames(ccapredictors)) %>%  # Filter rows to include only those with
matching 'logger_ID' in 'ccapredictors'
 arrange(logger_ID) %>%  # Sort data by 'logger_ID'
 column_to_rownames("logger_ID")  # Set 'logger_ID' as row names

# Create target site-species matrix
targetsite_species_matrix <- relevees_traits %>%
 filter(TAXON %in% relevees_traits$TAXON) %>%  # Filter data to include only taxa present in the
dataset
 select(logger_ID, TAXON, cover_percent) %>%  # Select relevant columns
 pivot_wider(names_from = TAXON, values_from = cover_percent, values_fill = 0) %>%  # Transform
data to wide format with 'TAXON' as columns
 filter(logger_ID %in% rownames(ccapredictors)) %>%  # Filter rows to include only those with
matching 'logger_ID' in 'ccapredictors'
 arrange(logger_ID) %>%  # Sort data by 'logger_ID'
 column_to_rownames("logger_ID")  # Set 'logger_ID' as row names

# Subset predictors to match site-species matrices
ccapredictorstargspec <- ccapredictors[rownames(ccapredictors) %in%
rownames(targetsite_species_matrix), ] # Subset 'ccapredictors' to include only rows matching
'targetsite_species_matrix'
ccapredictors <- ccapredictors[rownames(ccapredictors) %in% rownames(ccasite_species_matrix), ]
# Subset 'ccapredictors' to include only rows matching 'ccasite_species_matrix'

# Check if row names match between matrices
all(rownames(ccasite_species_matrix) == rownames(ccapredictors))  # Check if row names in
'ccasite_species_matrix' match those in 'ccapredictors'
```

```
all(rownames(targetsite_species_matrix) == rownames(ccapredictorstargspec))  # Check if row names in 'targetsite_species_matrix' match those in 'ccapredictorstargspec'

# Perform Canonical Correspondence Analysis (CCA) on site species data
ccaall <- cca(ccasite_species_matrix ~ ., ccapredictors)  # Perform CCA with site species data and predictors

# Perform stepwise selection to identify significant predictors
finalccaall <- ordistep(ccaall, direction = "backward", permutations = how(nperm = 999))  # Perform backward stepwise selection with 999 permutations
print(finalccaall)  # Print the results of the stepwise selection

# Perform ANOVA to test overall significance of the CCA model
anova(finalccaall, permutations = how(nperm = 999))  # Perform ANOVA with 999 permutations

# Perform ANOVA to test significance of individual predictors
anova(finalccaall, permutations = how(nperm = 999), by = "terms")  # Perform ANOVA by terms to test significance of individual predictors

# Calculate adjusted R-squared for the final CCA model
RsquareAdj(finalccaall)  # Calculate and print adjusted R-squared value for the model

# Perform CCA on target site species data
ccatarget <- cca(targetsite_species_matrix ~ ., ccapredictorstargspec)  # Perform CCA with target site species data and predictors

# Perform stepwise selection on the target CCA model
finalccatarget <- ordistep(ccatarget, direction = "backward", permutations = how(nperm = 999))  # Perform backward stepwise selection with 999 permutations
summary(finalccatarget)  # Print summary of the final CCA model

# Perform ANOVA on the target CCA model
anova(finalccatarget, permutations = how(nperm = 999))  # Perform ANOVA with 999 permutations

# Perform ANOVA to test significance of individual predictors in the target CCA model
anova(finalccatarget, permutations = how(nperm = 999), by = "terms")  # Perform ANOVA by terms to test significance of individual predictors

# Calculate adjusted R-squared for the target CCA model
finalccatarget_r2 <- RsquareAdj(finalccatarget)  # Calculate and print adjusted R-squared value for the target model
```

```
# Prepare data for plotting
cca_data <- fortify(finalccatarget, axes = 1:2)  # Extract data for plotting CCA axes 1 and 2
take <- c('CCA1', 'CCA2')  # Specify the columns for CCA axes 1 and 2
arrows <- subset(cca_data, score == 'biplot')  # Extract biplot arrow scores
# Calculate multiplier for scaling arrows to plot range
mul <- ggvegan:::arrow_mul(arrows[, take],
                           subset(cca_data, select = take, score == 'species'))
arrows[, take] <- arrows[, take] * mul  # Scale biplot arrows

arrows <- arrows %>%
  mutate(across(label, ~ str_replace_all(., "`", "")))

# Define desired taxa for plotting
desired_taxa <- c("Geum reptans", "Crepis aurea", "Gnaphalium supinum", "Oxyria digyna",
                  "Luzula alpino-pilosa", "Nardus stricta",
                  "Campanula barbata", "Kobresia myosuroides",
                  "Loiseleuria procumbens", "Vaccinium gaultheriodes",
                  "Ranunculus glacialis", "Saxifraga exarata",
                  "Poa laxa", "Rhododendron ferrugineum",
                  "Vaccinium myrtillus", "Solidago virgaurea",
                  "Calluna vulgaris", "Vaccinium vitis-idaea",
                  "Salix herbacea", "Agrostis rupestris",
                  "Oreochloa disticha", "Silene acaulis", "Primula glutinosa")

# Filter CCA data for desired taxa
filtered_cca_data <- subset(cca_data, label %in% desired_taxa & score == 'species')  # Filter data for
specified taxa

# Plot CCA results
ggplot() +
  geom_text(data = filtered_cca_data,
            mapping = aes(x = CCA1, y = CCA2, label = label), size = 3, colour = "#FF6644") +  # Add text
labels for desired taxa
  geom_segment(data = arrows,
               mapping = aes(x = 0, y = 0, xend = CCA1, yend = CCA2),
               arrow = arrow(length = unit(0.01, "npc")),
               linewidth = 0.2) +  # Add arrows for biplot vectors
  geom_text(data = arrows, # Add text labels for arrows, offset from arrow heads
            mapping = aes(label = label, x = CCA1 * 1.1, y = CCA2 * 1.1), size = 3) +
  coord_fixed() +  # Fix aspect ratio of plot
```

```
 scale_x_continuous(limits = c(-1.4, 4.1), breaks = c(-1:4)) + # Set x-axis limits and breaks
 theme_bw() + theme(legend.position = "none",
              axis.line = element_line(colour = "black"),
              panel.border = element_blank())  # Customize plot appearance
# Save the plot to a file
ggsave("D:/A/dipl/01_R_project/02_data/04_figures/new_finalcca.png", height = 9.5, width = 15.5,
unit = "cm", dpi = 300) # Save the plot as a PNG file

# correlations #####
predictors_species <- predictors_species %>% rename(WHC = whc_0_20)
predictors_species <- predictors_species %>% rename("Snow(May)" = "snow5")
predictors_species <- predictors_species %>% rename("Temp(June)" = "mt6")

correlation_predictors <- predictors_species %>%
 select(-c(taxon:presence)) %>%
 distinct() %>%
 select(WHC, `Snow(May)`, `Temp(June)`) %>% # selecting the columns of interest
 drop_na(WHC, `Snow(May)`, `Temp(June)`) %>% # drop rows with NA in any of the specified
columns
 cor(method = "pearson")
# Set up the PNG device
png("D:/A/dipl/01_R_project/02_data/04_figures/correlation_plots/corr_final.png",
   width = 200, height = 200, units = "mm", res = 300)

# Create the correlation plot
corrplot.mixed(correlation_predictors,
          lower = "circle",
          upper = "number",
          upper.col = colorRampPalette(c("white", "black"))(200),  # Grayscale color ramp
          lower.col = colorRampPalette(c("white", "black"))(200),  # Grayscale color ramp
          tl.col = "black",
          tl.cex = 1.3)
dev.off()
```