universität wien

MASTERARBEIT | MASTER'S THESIS

Titel | Title

The importance of soil properties in plant species distribution models on the alpine landscape of Mount Schrankogel (Tyrol, Austria)

verfasst von | submitted by

William John Eden

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 066 832
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Botanik
Betreut von | Supervisor:	Univ.-Prof. Mag. Dr. Stefan Dullinger

Acknowledgements

A huge thank you to Stefan Dullinger for allowing me the opportunity to pursue this thesis and for offering his expertise and feedback throughout the project. A huge thank you also to Kryštof Chytrý for his careful guidance and feedback in the processing and analysis of the data.

A special thanks to Ruth Falkenhahn with whom I shared the field and lab work, I could not have wished for someone nicer to work with, we made a great team!

Thank you to the Microclim research group for assembling this dataset on the plant species of Mt Schrankogel which I put to use in this thesis, and to those who helped in the collection and sieving of the soil samples, I'm hugely grateful for your efforts.

A special thanks to Mathias Mayer, for his guidance on the field and lab methodology, and to BOKU's Department of Forest and Soil Sciences for use of their soil laboratory. Many thanks also to Vanja Matijević for her contribution to the soil dataset.

Thank you to my family and friends for all the support and encouragement during this project and during my time in Vienna.

Abstract

Selecting environmental variables for accurate prediction of species distributions is a challenge for understanding how at-risk communities such as alpine plants are responding to climate change. This study aimed to quantify the most meaningful soil variables to incorporate in species distribution models (SDMs) for plant species occurring in an alpine environment. It also aimed to find patterns in the effectiveness of soil variables used in alpine plant SDMs, based on variations in functional traits and Ecological Indicator Values across the modelled species. A dataset of seven different soil variables and a temperature variable (mean annual minimum temperature), and the distribution of 79 species occurring in an above-treeline environment in the Alps, was assembled to fit SDMs using an ensemble modelling method.

Total carbon content was the most important soil variable, and across all species only had a slightly lower predictive power than the temperature variable, with a mean TSS score of 0.448 compared to 0.498. Overall, the inclusion of any of the four soil variables – total carbon content, total nitrogen content, water holding capacity, or pH – significantly improved the performance of SDMs that initially used temperature as the single predictor. There were statistically significant relationships between the improvement in predictive power by these four soil variables and two functional traits: LT_{50} (lethal temperature at which species loses 50% of photosynthetic activity) and leaf nitrogen content. These relationships showed an increase in the importance of soil variables for species with lower LT_{50} and lower leaf nitrogen values; traits which confer tolerance to stressful conditions. The improvement in predictive power by the four soil variables were also highly correlated. These results are indicative of a gradient in the importance of soil conditions for species distributions, being more important for species occurring in less-developed soils and high elevation soil patches where adaptation to stress is vital for survival. For a non-negligible number of species occurring above the treeline, soil conditions are particularly important for their distribution, and therefore soil variables or their proxies should not be neglected in SDMs projecting the responses of the alpine flora to climate change.

Key words: species distribution modelling, soil predictors, alpine plants, above-treeline, soil gradient, functional traits, stress.

Kurzfassung

Die Auswahl von Umweltvariablen für eine genaue Vorhersage der Artenverbreitung ist eine Herausforderung, um zu verstehen, wie gefährdete Gemeinschaften wie alpine Pflanzen auf den Klimawandel reagieren. Diese Studie zielte darauf ab, die aussagekräftigsten Bodenvariablen zu quantifizieren, die in Artenverbreitungsmodelle (SDMs) für Pflanzenarten, die in einer alpinen Umgebung vorkommen, einbezogen werden sollten. Sie zielte auch darauf ab, Muster in der Effektivität von Bodenvariablen zu finden, die in SDMs für alpine Pflanzen verwendet werden, basierend auf Variationen in funktionalen Merkmalen und ökologischen Indikatorwerten bei den modellierten Arten. Ein Datensatz mit sieben verschiedenen Bodenvariablen und einer Temperaturvariable (mittlere jährliche Mindesttemperatur) sowie die Verteilung von 79 Arten, die in einer oberirdischen Umgebung in den Alpen vorkommen, wurde zusammengestellt, um SDMs mit einer Ensemble-Modellierungsmethode anzupassen.

Der Gesamtkohlenstoffgehalt war die wichtigste Bodenvariable und hatte über alle Arten hinweg nur eine etwas geringere Vorhersagekraft als die Temperaturvariable, mit einem mittleren TSS-Wert von 0,448 im Vergleich zu 0,498. Insgesamt verbesserte die Einbeziehung einer der vier Bodenvariablen - Gesamtkohlenstoffgehalt, Gesamtstickstoffgehalt, Wasserhaltevermögen oder pH-Wert – die Leistung der SDMs, die ursprünglich die Temperatur als einzigen Prädiktor verwendeten, erheblich. Es gab statistisch signifikante Beziehungen zwischen der Verbesserung der Vorhersagekraft durch diese vier Bodenvariablen und zwei funktionalen Merkmalen: LT_{50} (tödliche Temperatur, bei der die Art 50 % ihrer photosynthetischen Aktivität verliert) und Blattstickstoffgehalt. Diese Beziehungen zeigten, dass die Bedeutung der Bodenvariablen für Arten mit niedrigeren LT_{50} und niedrigeren Blattstickstoffwerten zunahm; Eigenschaften, die Toleranz gegenüber stressigen Bedingungen verleihen. Die Verbesserung der Vorhersagekraft durch die vier Bodenvariablen war ebenfalls hoch korreliert. Diese Ergebnisse deuten auf ein Gefälle in der Bedeutung der Bodenbedingungen für die Verteilung der Arten hin, wobei die Bedeutung für Arten, die auf weniger entwickelten Böden und in hoch gelegenen Bodenflecken vorkommen, wo die Anpassung an Stress für das Überleben entscheidend ist, größer ist. Für eine nicht zu vernachlässigende Anzahl von Arten, die oberhalb der Baumgrenze vorkommen, sind die Bodenbedingungen besonders wichtig für ihre Verbreitung, und daher sollten Bodenvariablen oder ihre Ersatzwerte in SDMs, die die Reaktionen der Alpenflora auf den Klimawandel projizieren, nicht vernachlässigt werden.

Schlüsselwörter: Modellierung der Artenverteilung, Bodenprädiktoren, alpine Pflanzen, oberhalb der Baumgrenze, Bodengradient, funktionelle Merkmale, Stress

Contents

Introduction

Improvement in the accuracy of plant species distribution models (SDMs) is crucial to the task of predicting distributional changes of at-risk plant species under climate change (Austin and Van Niel, 2011; Mod et al., 2016), such as species occurring in the alpine zone (Engler et al., 2011). Climatic variables have seen the major focus and been considered the most important predictors in plant SDMs (Mod et al., 2016; Coudun et al., 2006). It has long been thought that both climatic and soil factors are crucial in species composition and community structure (Whittaker, 1975), and yet climate predictors have commonly been used in SDMs without soil predictors. Inaccuracies that result from this neglect of soil properties, and from the assumption that climate predictors alone are sufficient in plant SDMs (Austin and Van Niel, 2011), have hardly been assessed so far.

Substrates are particularly important in directly influencing plant physiology, in terms of the nutrient and water availability for plants (Alvarez at al., 2009; Matias et al., 2011). For example, it has been shown that arctic-alpine plant fitness is dependent on variations in soil moisture conditions and the availability of nutrients, due to effects on traits which enable photosynthesis and the ability for vegetative growth (e.g. Wookey et al., 1995; Wookey et al., 1994; Little et al., 2016). Nutrient availability in soils is also a key factor in the ability of plants to colonise new sites (Sardans and Peñuelas, 2012). While the ability of soils to retain water has direct effects on vegetation (Jasper et al., 2006), it is also linked to nutrient availability by affecting processes such as soil mineralisation rates (Sardans and Peñuelas, 2012). Soil pH is another property that directly affects plant growth given its influence on the availability of ions and therefore for the uptake of nutrients (Austin, 1980). The composition of plant species in alpine habitats is often correlated with pH, where many species have an optimum range of pH conditions in which they occur (Vonlanthan et al., 2006; Gégout et al., 2003).

Variables that describe soil properties such as soil nutrient status or water availability, are critical in explaining plant distributions in heterogeneous landscapes, such as mountains (Cianfrani et al., 2019; Dubuis et al., 2013). Where soil predictors have been included in species distribution studies across multiple vegetational zones in the Alps, this has been shown to significantly improve plant SDMs (Buri et al., 2020). Buri et al. (2020) incorporated a swathe of soil properties into SDMs of alpine plant species in a temperate mountain environment and found significant improvements in predictions, via geochemical indicators like pH and inorganic carbon and an indicator of soil drainage. Another indicator of soil water availability for plants, the soil water holding capacity, was found to be an important predictor for plants in the same region of the western Swiss Alps. On a larger scale, a study

into climate change predictions of poleward shifts of plants revealed soil variables to play an important role in determining plant distributions, and importantly constrained by c. 40% the predicted northwards movement of plants under climate change (Ni and Vellend, 2024); whether soil conditions limit the ability for plants to move, is highly relevant in alpine environments, too, for the necessity of cold-adapted plants to migrate to higher elevations under warming (Rumpf et al., 2018).

Above the treeline, the role of soil properties in determining plant distributions has received even less attention, even though soils have long been known to be particularly important in determining ecotypic differentiation among alpine species due to the abundance of calcium, giving contrasting floral compositions between soils on calcareous bedrock and siliceous bedrock (Körner, 2003; e.g. Michalet et al., 2002). In addition, over smaller scales in above-treeline landscapes, topographical complexity forms microhabitats with sharp contrasts not only in temperature but also in soil type, caused by geo-morphological processes that occur both along and within elevations (Scherrer and Körner, 2011; Randin et al., 2009). These processes shape soil conditions by controlling erosion and accumulation of water and substrate across alpine landscapes, especially in forest-free areas. For example, the rugged terrain of alpine landscapes encounters recurrent erosion of soil by small avalanches and snowmelt which can be beneficial for the maintenance of rare plant species by preventing mature soil development (Doležal and Šrůtek, 2002). Accordingly, these processes create sharp contrasts that occur between well-developed soils, which take many hundreds of years to form, and less-developed 'raw' soils over short distances (Körner and Hiltbrunner, 2021). With the associated variations in nutrient availability between well-developed and raw soil, and their major influence on plant growth (e.g. Little et al., 2016), it is likely that soil conditions are important predictors for the distributions of many plant species above the treeline. Nevertheless, very few published studies have focused on the importance of soil conditions in plant SDMs - beyond the calcareous-siliceous dichotomy - explicitly in above-treeline habitats in the alpine zone.

Variation in the sensitivities of plant SDMs have been identified when different environmental predictors are used. For example, Buri et al. (2019) found "large heterogeneity" in the response of SDMs to different soil predictors. Since plant functional traits represent adaptations to particular environmental conditions (Blonder et al., 2018; Soudzilovskaia et al., 2013), this heterogeneity might have a trait-related structure. For example, Dubuis et al. (2013) found that for plants with low specific leaf area (SLA) accounting for nitrogen and pH in SDMs improved accuracy most. More generally, one may hypothesise that species with traits increasing tolerance to stressors such as frost or drought might occur with a higher likelihood at sites where such stress more frequently occurs, e.g. on shallow

soils with low water holding capacity which also predominate at more frost-prone high elevations. For the same reasons, the sensitivity of plant SDMs to including soil properties may depend on their Ecological Indicator Values (EIVs) (Landolt, 2010) which are expert-based rankings of species' optima along environmental gradients and hence, as with functional traits, inform about their ecological adaptations. For example, the water holding capacity – a potentially important predictor in SDMs (Cianfrani, 2019) – may be important for species where the maintenance of a specific range of soil water content is vital, and therefore could be correlated to the EIV of moisture. Similarly, it has been found that SDMs of species from different elevations are differentially sensitive to soil conditions (Chauvier et al. 2021) which might result in a relationship with the EIV of temperature. However, except for Dubuis et al. (2013) assessments of whether traits or EIVs are systematically linked to the importance of soil for plant distribution have not yet been conducted.

The overall ambition of my thesis is to therefore quantify this importance and, in particular, to identify the most meaningful soil variables that help predict plant species distributions above the treeline. I also explore whether the variation in the response of species to these predictors is related to a set of functional traits assumed to be important for the adaptation of these plants to their environment. To this end, I have built alpine plant SDMs after the collection of a large dataset of several soil variables from nearly 900 plots on an exemplary mountain in the Austrian Alps, where the distributions of around 250 plant species are known and traits of about 50 of them have been measured. Based on this data I focus on two research questions:

- Question 1: What is the relative importance of various soil properties in explaining the above-treeline distribution of alpine plant species, in relation to a climate predictor?

- Question 2: Are there patterns in the relative sensitivity of SDMs to soil variables?

Methods

Data collection

Microclim Schrankogel dataset

The area of study was Mt Schrankogel in the Austrian Alps (3,497 m a.s.l., Tyrol, N47°02'39.1", E11°05'56.0"). A total of 900 1m^2 plots are located from the upper subalpine belt to the alpine and

nival zones, spanning an elevation of 1,677 m (Chytrý et al., 2023). Plots were selected based on a stratified random sampling design considering various topographical features and the NDVI from Sentinel 2 images. In the years 2021 and 2022, an inventory of all vascular plant species growing within each 1 m² plot was accomplished. Therefore, presence/absence data for a total of 252 species has been collected across all plots. Each plot has temperature loggers buried at 10 cm depth which have been taking temperature measurements from 1st September 2021 to 31st August 2023. The temperature variables available for use in this thesis were: daily temperature (mean, maximum, minimum, range, SD), monthly/seasonal/annual minimum and maximum temperature, hours above/below temperature thresholds, days above/below temperature thresholds, growing/freezing degree hours above/below temperature thresholds, and growing/freezing degree days above/below temperature thresholds. In 2021 and 2022, soil penetration depth was also measured by a borer stick into the soil at 9 points within the 1 m² plot.

Soil sampling

During July and August 2023, a fellow Master's student and myself, along with members of the Microclim team, collected soil samples from 580 plots, following the collection of samples from 276 plots by Vanja Matijević in summer 2022 (Matijević, 2024), meaning 856 plots have been sampled. 44 plots were excluded due to a combination of labelling errors during sample collection and laboratory analysis, double-sampling of plots, and inaccessibility i.e. high elevation or steep plots during adverse weather conditions. Each sample was taken from within a maximum 3 m distance from the 1 m^2 plot. The plot itself was avoided to prevent impacting the vegetation, but soil was taken from beneath vegetation which closely matched the vegetation found within the plot. After vegetation had been removed from an approximate area of 10 x 15 cm, a vertical hole was dug by trowel, and the depth of the top organic layer of the soil was measured. At each plot a judgement was made to distinguish the boundary between the organic layer and mineral layer of the soil, by assessing the colour, texture, and presence of mineral particles in the material. The upper 10 cm of mineral soil was taken and bagged, taking care to ensure an even distribution of soil across the 0-10 cm depth.

Within two to three days following sample collection, each soil sample was homogenised by sieving through a 2 mm mesh sieve. Through this process, stones and roots larger than 2 mm were removed. Samples were transferred to paper bags and stored in a drying room on location until being transported to the laboratory (BOKU, Wilhelm-Exner Haus, Vienna, Austria), where they were further

stored in a drying room at 40 °C. For all samples, subsamples were also placed in plastic bags and frozen, for the possibility of microbial analysis on a potential future project.

Soil parameters, temperature variables and species data

We gathered data for pH, total carbon content and total nitrogen content for each soil sample. For pH, measurements were made in both distilled water and calcium chloride, providing two values for each sample. As the two values correlated very strongly (Pearson's correlation coefficient, r = 0.958), only the H_2O pH measurements were used in the analysis, henceforth referred to as pH. For the carbon and nitrogen measurements, samples were oven dried overnight at 105 °C, then 200 mg of each was weighed into a foil 'packet', combusted, and analysed using the LECO TrueSpec Micro CHN providing carbon and nitrogen determination in parts per million/%. Minimum limits were set for nitrogen of 0.01% and carbon of 0.1% according to the TrueSpec's capabilities.

For 856 plots, along with H_2O/CaCl pH, total carbon content (Carbon), and total nitrogen content (Nitrogen), data for the soil predictors: soil penetration depth (Soil Depth) and organic layer thickness (Organic Layer Depth), were available for use in this study. The Carbon/Nitrogen ratio (C/N Ratio) was also determined. We modelled the Water Holding Capacity (WHC) in each plot based on the following formula provided by M. Mayer (BOKU; Matijević, 2024):

$$\text{WHC } (l/m^2) = 3.786 * \text{Soil Depth (cm)} + 4.605 * \text{Organic Layer Depth (cm)} + 3.0265 * \text{Carbon (\%)}$$

Due to difficulty in distinguishing mineral and organic soil during soil sampling, the organic layer was sometimes overrepresented in the samples. This resulted in 19 plots containing a carbon content of above 20%. According to IUSS Working Group WRB (2022), mineral soil must have carbon content lower than 20%. Therefore, all plots with carbon content >=20%, were coerced to 19%, becoming the upper carbon content limit.

As the purpose of this study was to compare the relative effects of soil and temperature variables on alpine plant distribution, I finally included a metric of temperature conditions, taken from soil temperature loggers, into the analysis. I selected the mean annual daily minimum temperature (henceforth referred to as Temperature), because preliminary tests by Chytrý et al. (2024, submitted) had suggested this to be the best microclimate predictor of species distributions in the study area.

Models were run on the 79 species that occurred in 50 or more plots where soil data was collected. Since one plot did not have data for the selected temperature predictor, the total number of plots used in the analysis was 855.

Data analysis

For all species, I modelled the predicted presence/absence using models consisting of each soil variable with and without Temperature, and with single-predictor Temperature models as the reference model. Prior to modelling, I applied a log10 transformation to each predictor variable except Soil Depth, Organic Layer Depth and Temperature to mitigate the influence of outliers. Three modelling methods were chosen: (1) Generalised Linear Models (GLM), (2) Generalised Additive Models (GAM), (3) Random Forest (RF) to build an ensemble of models. The models were evaluated using the True Skill Statistic (TSS) based on several 80%/20% training/testing data splits.

GLMs were performed in the R core package with second order polynomial functions applied to every predictor variable. GAMs were performed in the R mgcv package (version 1.9-1) using penalised regression splines for smooth terms applied to every predictor variable, where the degree of smoothness was estimated during model fitting. RFs were performed in the R tidymodels package (version 1.2.0). RF models for each predictor/predictor combination were specified by tuning the min_n hyperparameter (the number of observations required to keep splitting nodes), keeping m_try (the number of predictors sampled at each split) as 1 for single-predictor models and 2 for Temperature + soil predictor models, and the number of trees kept as 100 throughout. A 10-fold cross-validation resampling was applied to determine the most appropriate model specification.

Models were trained on an 80% random sample of the data for each species, with predictions made on the remaining 20%. By employing the v-fold cross-validation technique in R, each model was trained and predicted on five different 80%/20% random folds, with each fold ensuring a similar proportion of presences/absences for each species. After running the predictions, each model had five sets of predicted suitability scores. To convert suitability scores to binary predictions of presences/absences (1 or 0 score) in each plot, a standard threshold selection method was utilised to maximise the sum of sensitivity and specificity (Liu et al., 2013). The R pROC package (version 1.18.5) was used to generate ROC curve data, for Youden's Index (sensitivity + specificity - 1) to be calculated at each threshold on the ROC curve and maximised to find the "best" optimal threshold for

determining whether a predicted suitability score should equal a 1 (above threshold = predicted presence) or a 0 (below threshold = predicted absence).

TSS, a threshold dependent metric calculated by comparing the presence/absence observations to binary predictions (Allouche et al., 2006), was employed as the metric for assessing the predictive power of the models. The resulting TSS value for each model is a number between -1; the worst possible performance, where all presences are predicted as absences and all absences predicted as presences i.e. worse than random, and 1; the best possible performance where predictions align perfectly with observations. A score of 0 indicates the model has no predictive power i.e. no better than random guessing (Allouche et al., 2006). Any negative TSS values (<5% of the models) were coerced to 0 to ensure these had no undue influence in the ensemble.

Following calculation of predicted suitability scores and TSS values for GLMs, GAMs and RFs, ensemble predicted suitability scores were calculated. These were weighted by the TSS values of each model type to ensure the model type with the highest predictive power for a specific species was given greater weight in the ensemble. The following weighted average formula was used:

(GLM predicted suitability * GLM TSS
+ GAM predicted suitability * GAM TSS
+ RF predicted suitability * RF TSS)
/ (GLM TSS + GAM TSS + RF TSS)

The same method as described above was applied to find the “best” optimal threshold to determine the ensemble predicted presences and absences, to then calculate the ensemble TSS. This entire process was carried out across the five cross-validation folds, so that the ensemble models were not reliant on a single 80%/20% data split. The mean ensemble TSS value across the five folds was calculated for each model i.e. every species x predictor(s) combination.

A total of 1200 ensemble models were built, encompassing 79 species and 15 predictors/predictor combinations. I compared the overall predictive performances of the soil predictors with and without Temperature, and in relation to the single-predictor Temperature models. I also compared the improvement in the overall predictive performance of the models; firstly after including soil predictors in the Temperature models, by calculating for each species the absolute difference in TSS between the Temperature model and the TSS of each Temperature + soil predictor model. This metric is referred

to as “ΔTSSsoil”. Secondly, the converse relationship of the improvement after addition of Temperature to each single-predictor soil model, by calculating for each species the absolute difference in TSS between each soil predictor model and the TSS of each Temperature + soil predictor model. This metric is referred to as “ΔTSStemp”. Therefore; TSS values, ΔTSSsoil values, and ΔTSStemp values, were the metrics used for assessing model performance. Comparisons were made statistically by ANOVA performed with Tukey’s HSD tests to assess significant differences in means of TSS and ΔTSS values of the ensemble models, comparing the predictor(s) used across all species.

A descriptive per species analysis of the performance of all single-predictor models (eight models per species) and all Temperature + soil predictor models (seven models per species), was achieved by calculating the percentage of species for which each predictor/predictor combination yielded the highest TSS value, i.e. a description of the “best” model for each species. For each species, the single-predictor soil model with the highest TSS value, i.e. the “best” model excluding Temperature, was also calculated. A comparison was then made for each species; the improvement in TSS from the single-predictor Temperature model, to the best Temperature + soil predictor model.

For Question 2, eight species functional traits were selected to perform linear regressions against the metric of ΔTSSsoil for soil predictors selected according to the results of Question 1. The functional traits were: vegetative height, chlorophyll content, leaf dry matter content (LDMC), osmotic potential (osmot_potential), specific leaf area (SLA), leaf carbon content per leaf dry mass (leaf_carbon), leaf nitrogen content per leaf dry mass (leaf_nitrogen), succulence, and LT_{50} – the lethal temperature at which Fv/Fm declines by 50% (LT_50). The variation in ΔTSSsoil was also evaluated against Ecological Indicator Values (EIVs) (Landolt, 2010), using linear regressions, and presented in the form of boxplots to capture the distribution of species within the categories of each EIV. The Landolt EIVs used were: Temperature, Reaction, Moisture and Nutrients.

Data for the functional traits had been collected by the Microclim team for 51 species which occurred in 50 or more plots i.e. the species that were modelled in this thesis. Each trait had been measured at five individuals per species collected at sites near their elevational optimum. The values of the five individuals had subsequently been averaged. To understand relationships between functional traits or EIVs and the predictive power of soil variables, linear regressions were built. Functional traits / EIVs were set as predictor variables, and the ΔTSSsoil metric as the response variables. 76 modelled species, for which each species had complete EIV data, were used in the evaluation with EIVs. Based on the results of the linear regressions, Pearson’s correlation analysis was performed to check the

extent to which the species functional traits / EIVs were correlated, and the extent to which ΔTSSsoil values were correlated.

All modelling and data analysis was carried out in R version 4.4.0 (R Core Team, 2024). The R Tidyverse package (version 2.0.0, Wickham et al., 2019) was utilised throughout the analysis.

Results

Comparison of the predictive performance of the three model types, and the ensemble

There were differences in the predictive performance of GLMs, GAMs, and RF models across all species and predictors/predictor combinations. Although a very similar comparison between predictors/predictor combinations occurred across the three model types, RFs overall yielded lower TSS values, as shown in Fig. 1 for single-predictor models. The ensemble models were most representative of GLMs and GAMs, due to weighting favouring the model types which yielded greater predictive power.

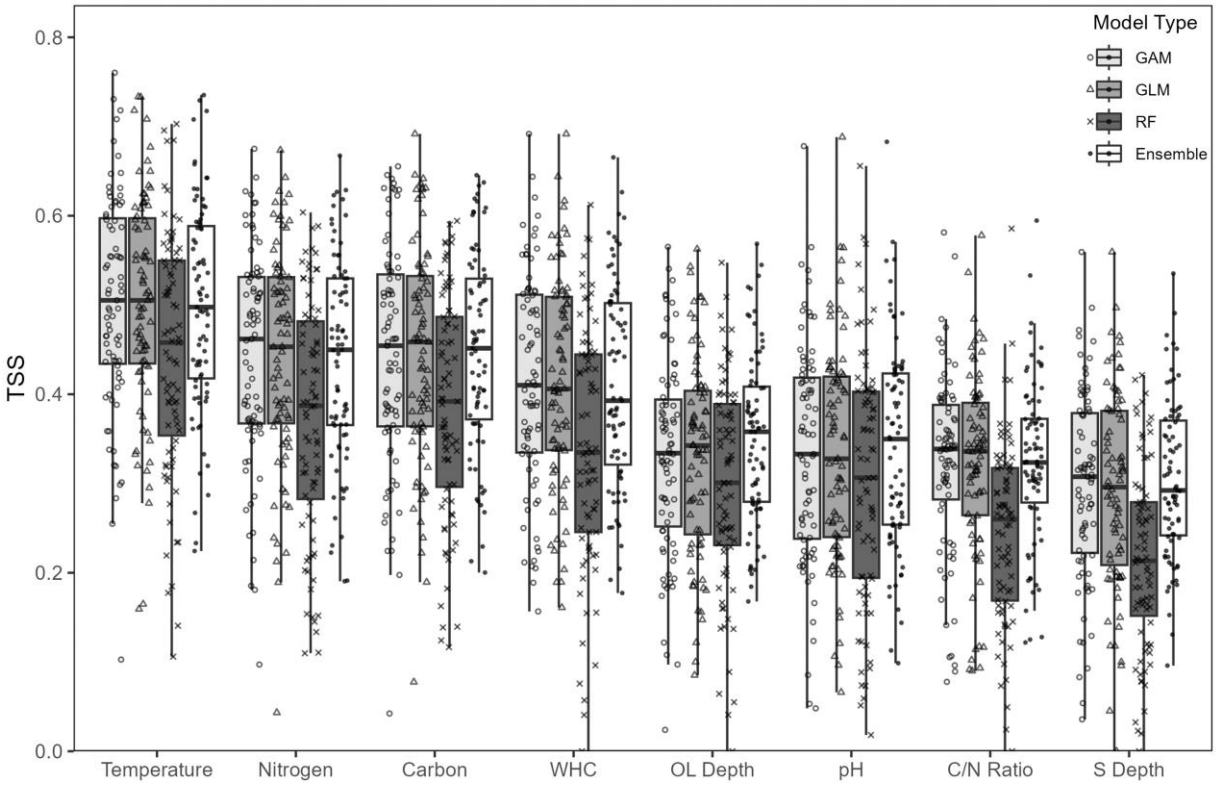

Figure 1. Single predictor models comparison between GAMs, GLMs and RFs, and the weighted Ensemble of the three model types. Symbols within boxplots represent the TSS values of individual species' models, where: circles = GAMs, triangles = GLMs, crosses = RFs, dots = Ensemble. Organic Layer Depth = OL Depth, Soil Depth = S Depth.

Question 1: The relative importance of soil properties in relation to a climate predictor

Predictive performance of SDMs

Models built with the Temperature predictor alone yielded TSS values varying from 0.224 for *Kobresia myosuroides* to 0.735 for *Ranunculus glacialis*, with a median TSS value of 0.498 (Table 1A). All soil predictors alone had an overall lower predictive power than Temperature (Fig. 2A), where Temperature was the predictor which yielded the highest TSS value for 58% of species. For 42% of species, soil predictors had the greatest predictive power in single-predictor models, where either Carbon, Nitrogen or WHC were the best predictors for 38% of species (Table 1A). Among soil predictors, Carbon and Nitrogen had the highest predictive power with median TSS values of 0.452 and 0.450 respectively, and Carbon yielding a marginally higher mean TSS value than Nitrogen (0.448 compared to 0.439). Soil Depth was the poorest performing predictor with a median TSS value of 0.292. pH yielded the maximum TSS value for all single-predictor soil models, at 0.683 for *Geum reptans*.

Table 1. (A) Single-predictor ensemble model results, (B) Temperature + soil predictor ensemble model results. Including the median increase in TSS after the addition of each soil predictor to the Temperature model (ΔTSSsoil).

Predictor	*Median TSS*	*Max TSS*	*Min TSS*	*TSS range*	*% species with highest TSS*	*Median ΔTSSsoil*
(A)			**Single-predictor models**			
Temperature	0.498	0.735	0.224	0.511	58	-
Carbon	0.452	0.645	0.200	0.445	15	-
Nitrogen	0.450	0.667	0.190	0.477	14	-
WHC	0.393	0.665	0.177	0.488	9	-
Organic Layer Depth	0.358	0.569	0.168	0.401	0	-
pH	0.350	0.683	0.099	0.584	3	-
C/N ratio	0.324	0.595	0.122	0.473	0	-
Soil Depth	0.292	0.535	0.096	0.439	1	-
(B)			**Temperature + soil predictor models**			
Carbon	0.580	0.787	0.328	0.459	30	0.081
Nitrogen	0.577	0.762	0.273	0.489	15	0.080
WHC	0.565	0.773	0.275	0.498	22	0.066
C/N ratio	0.552	0.762	0.283	0.479	9	0.030
pH	0.542	0.813	0.237	0.576	15	0.041
Organic Layer Depth	0.534	0.753	0.299	0.454	5	0.027
Soil Depth	0.529	0.738	0.226	0.512	4	0.029

According to ANOVA ($F(7, 624) = 33.823$, P-value < 0.0001) with Tukey's HSD tests, Carbon and Nitrogen had significantly higher predictive power than Organic Layer Depth, pH, C/N Ratio, and Soil

Depth (P-values < 0.0001, mean diffs. > 0.089), and shared a group with WHC (Fig. 2). WHC also had significantly higher predictive power compared with Organic Layer Depth (P-value = 0.0083, mean diff. = 0.059), pH (P-value = 0.0016, mean diff. = 0.068), and both C/N Ratio and Soil Depth (P-values < 0.0001, mean diffs. > 0.086). Although Temperature had significantly higher predictive power than Nitrogen (P-value = 0.0117, mean diff. = 0.059) and the five lowest performing soil predictors (p-values = 0.0000, mean diffs. > 0.089), it was not significantly more predictive than Carbon (P-value = 0.0597, mean diff. = 0.050). Carbon therefore shared an HSD means group with Temperature. The four least predictive soil predictors were not significantly different from each other.

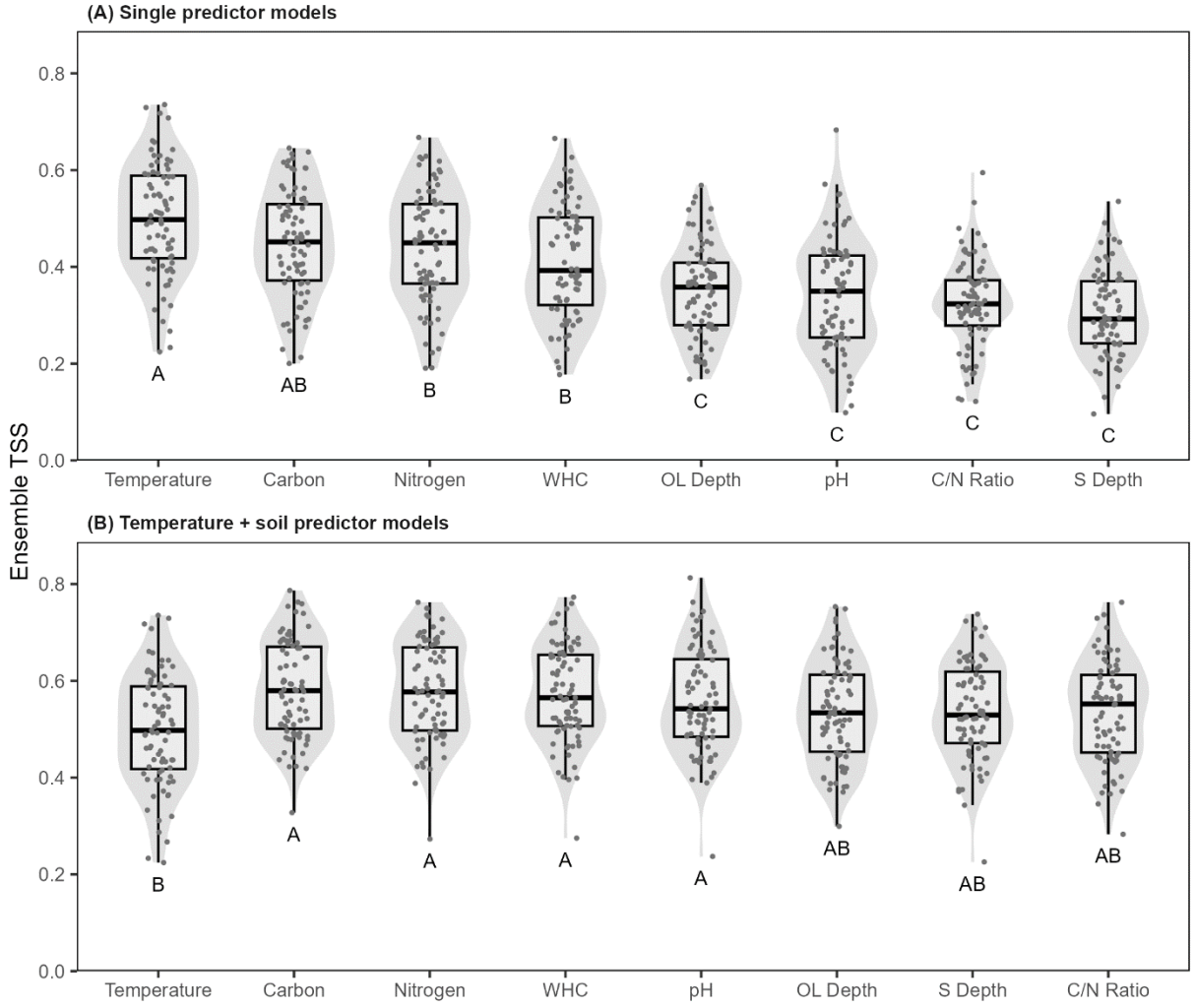

Figure 2. Ensemble TSS for (A) single-predictor models and (B) Temperature + soil predictor models, where each point represents a species. Letters represent groups with significant differences in mean TSS values. The single-predictor Temperature model is included in both panels for comparison. Organic Layer Depth = OL Depth, Soil Depth = S Depth.

Temperature + soil predictor combinations yielded median TSS values consistently higher than the single-predictor models (Table 1B). The most predictive model of all 1200 models was Temperature + pH for *Geum reptans* with a TSS value of 0.813. According to ANOVA ($F(7, 624) = 5.875$, P-value <

0.0001) with Tukey's HSD tests, Temperature + soil predictor models had far less variation in means compared with the single-predictor models, where no predictor combination had significantly higher means than any other (Fig. 2B). However, when comparing Temperature + soil predictor models to single-predictor Temperature models, Temperature had a significantly lower mean TSS value compared with: Temperature + Carbon (P-value < 0.0001, mean diff. = 0.083), Temperature + Nitrogen (p-value < 0.0001, mean diff. = 0.080), Temperature + WHC (P-value = .0002, mean diff. = 0.074) and Temperature + pH (P-value = 0.0087, mean diff. = 0.059). These Temperature + soil predictor combinations all shared an HSD group with means significantly higher than the single predictor Temperature models.

Therefore, Carbon, Nitrogen, WHC and pH were the variables which all significantly improved the predictive performance of the Temperature models, although to varying degrees (Table 1B). Across all Temperature + soil predictor combinations, Carbon was overall the best predictor, yielding the highest TSS score for 30% of species. When included in Temperature models, the predictive capacity of WHC and pH was relatively high in comparison with their use in single-predictor models, yielding the highest TSS scores for 22% and 15% of species respectively. After the addition of Nitrogen to Temperature models, this combination yielded the highest TSS score for 15% of species. Therefore, when included in Temperature models, Nitrogen did not become the best predictor for a greater number of species to the extent that Carbon, WHC, and pH did. C/N Ratio, Organic Layer Depth, and Soil Depth, when included in Temperature models, cumulatively yielded the highest TSS scores for 18% of species.

Improvements in TSS after the addition of soil predictors to Temperature models (ΔTSSsoil) and after the addition of Temperature to soil predictor models (ΔTSStemp):

The improvements in TSS after the addition of soil predictors to Temperature models can be seen in Fig. 3A. Carbon and Nitrogen were the predictors which most improved the models with respective 0.081 and 0.080 median ΔTSSsoil increases (Table 1B). Therefore, although Nitrogen performed less well than WHC in terms of the percentage of species for which it is the best predictor (in combination with Temperature), adding Nitrogen resulted in a slightly higher TSS than WHC on average across all species. However, according to ANOVA ($F(6, 546) = 10.543$, P-value < 0.0001) with Tukey's HSD tests, the means of Temperature + WHC and Temperature + pH were not significantly different from those of Temperature + Carbon and Temperature + Nitrogen (P-values > 0.1039, mean diffs. < 0.021); this is a similar pattern to Figure 1B, where these four variables shared the same HSD means group. Carbon, Nitrogen and WHC improved the models significantly more than C/N ratio, Soil Depth and Organic

Layer Depth (P-values < 0.0017, mean diffs. > 0.036), whereas the improvement by pH was not significantly different to any soil predictor.

The results of the converse relationship, analysing the improvement in TSS of Temperature + soil predictor models compared to single-predictor soil models, are presented in Fig. 3B. This shows consistently higher ΔTSStemp values compared with ΔTSSsoil. Differences in ΔTSStemp between predictors were again analysed according to ANOVA ($F(6, 546) = 14.803$, P-value < 0.0001) with Tukey's HSD tests. There were no significant differences in the improvement of TSS by adding Temperature to WHC, Nitrogen and Carbon models; these are the three predictors where adding Temperature yielded the least improvement in comparison with the remaining soil predictors. The largest improvements in TSS were for the soil predictors which yielded the least predictive power in single-predictor models; pH, C/N Ratio, and Soil Depth. In general, the magnitude of ΔTSStemp was thus negatively correlated to the magnitude of ΔTSSsoil: soil variables with high ΔTSSsoil had low ΔTSStemp, and vice versa. The only exception to this was pH which shared an HSD means group with Carbon, Nitrogen and WHC meaning it was in the group of soil predictors which yielded the greatest TSS improvements after their addition to Temperature models (Fig. 3A). However, in Fig. 3B, pH models saw a significantly higher increase in TSS after the addition of Temperature compared with Carbon (P-value < 0.0001, mean diff. = 0.083), Nitrogen (P-value < 0.0001, mean diff. = 0.078) and WHC (P-value = 0.0041, mean diff. = 0.054).

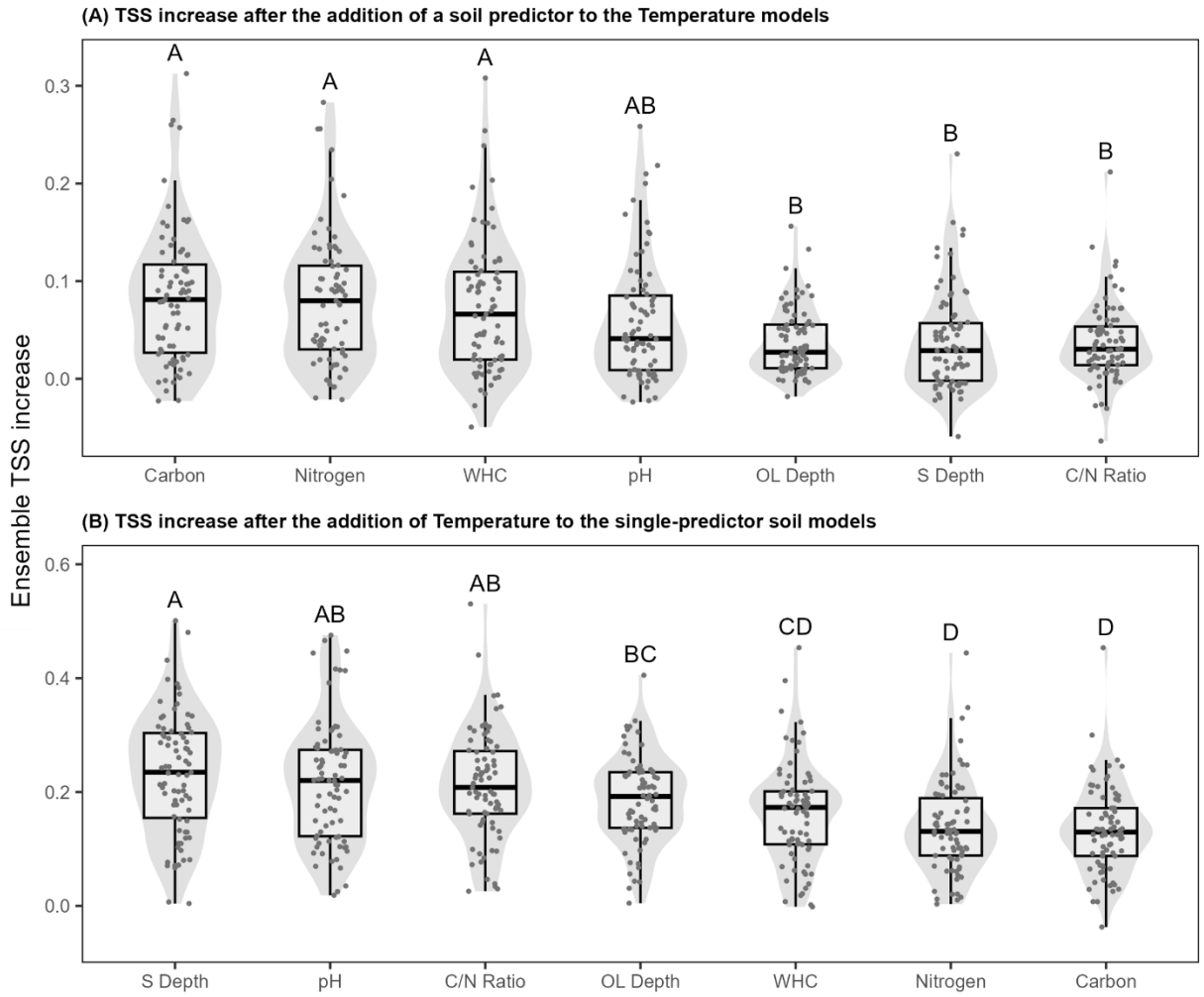

Figure 3. (A) ΔTSSsoil for each soil predictor, where each point represents a species. Letters represent groups with significant differences in mean ΔTSSsoil values. (B) ΔTSStemp for each soil predictor, where each circle represents a species. Letters represent groups with significant differences in mean ΔTSStemp values. Organic Layer Depth = OL Depth, Soil Depth = S Depth.

Fig. 4 shows for each species the increase in TSS from the single-predictor Temperature model to the Temperature + soil predictor model which yielded the highest TSS value. On average across all species, adding the one "best" soil variable hence increased the TSS of the Temperature models by 0.102 ± 0.065 (see Appendix 1 for each species best ΔTSSsoil value/predictor). High TSS improvements are apparent for species for which Temperature has relatively low TSS values, such as *Avenula versicolor*, *Korbresia myosuroides* and *Luzula spicata*. However, species like *Geum reptans*, *Calluna vulgaris* and *Oreochloa disticha*, with far higher TSS values for Temperature models of near 0.6, still see large gains in TSS following the addition of soil predictors.

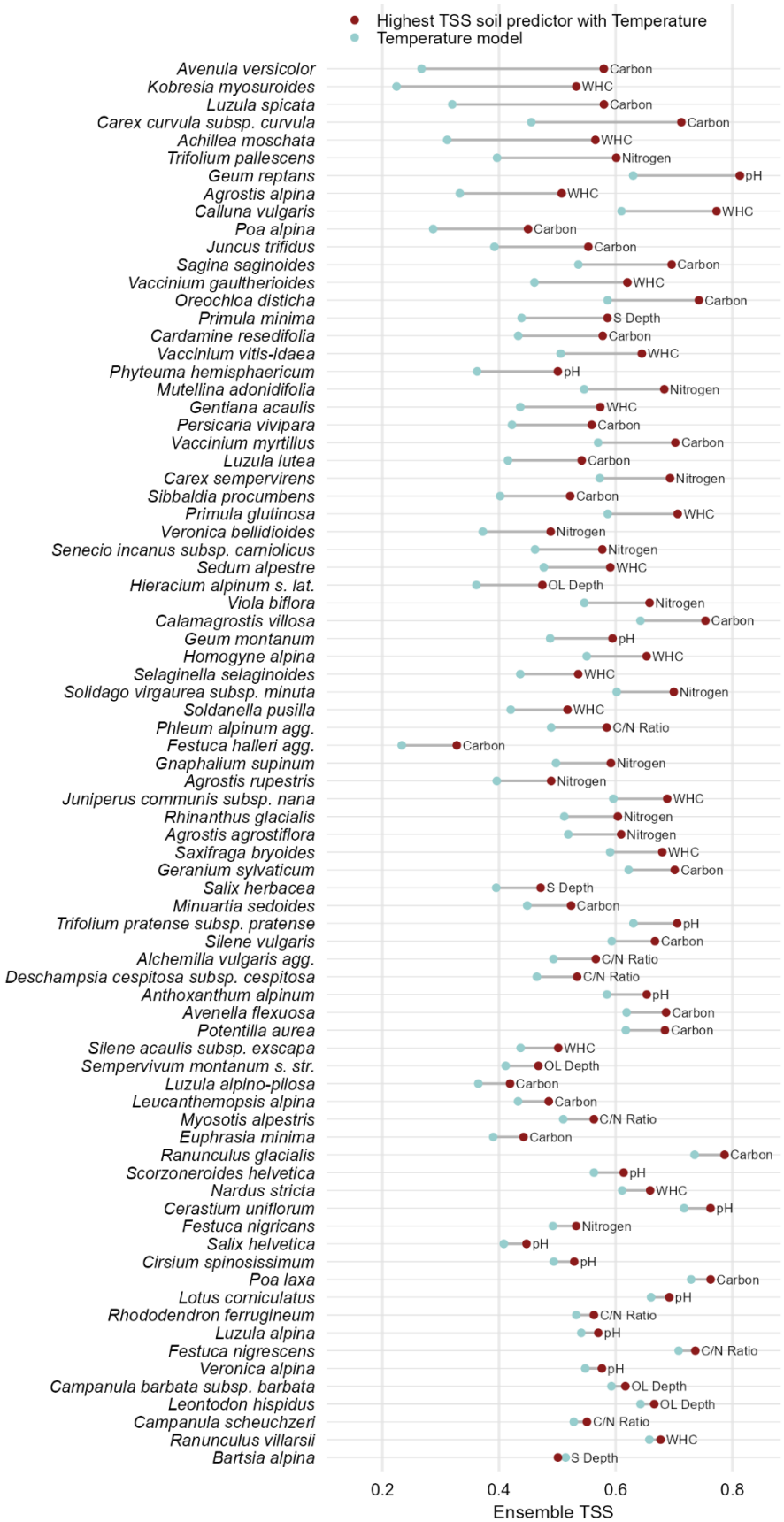

Figure 4. Soil predictors with the highest TSS per species for all models with Temperature, compared with single-predictor Temperature models. Species are sorted from the largest to smallest TSS increase. Organic Layer Depth = OL Depth, Soil Depth = S Depth.

Question 2: Patterns in predictive performance according to species ecological properties

Functional traits

In linear regression analysis of functional traits against ΔTSSsoil of the four soil predictors with the highest ΔTSSsoil results (Carbon, Nitrogen, WHC, pH), statistically significant or marginally significant relationships were revealed with: leaf_nitrogen, LT_50, and osmot_potential (Fig. 5). No significant relationships were revealed with vegetative height, LDMC, SLA, leaf_carbon, or succulence. ΔTSSsoil of the four soil predictors had significant negative relationships with LT_50 and leaf_nitrogen (P-values < 0.033, R^2 values > 0.090), i.e. species adapted to colder temperatures and low leaf nitrogen content (=lower LT_50/leaf_nitrogen) had a higher TSS improvement following the addition of the soil predictors (=higher ΔTSSsoil). ΔTSSsoil of pH had a positive relationship with osmot_potential, i.e. species with higher osmot_potential generally saw a higher TSS improvement following the addition of pH, although this was on the threshold for statistical significance (P-value = 0.050, R^2 = 0.076). Overall, LT_50 explained 30.6% of the variance of ΔTSSsoil when including pH in the models, 28.6% in the case of Carbon, 26.9% for WHC, and 21.4% for Nitrogen.

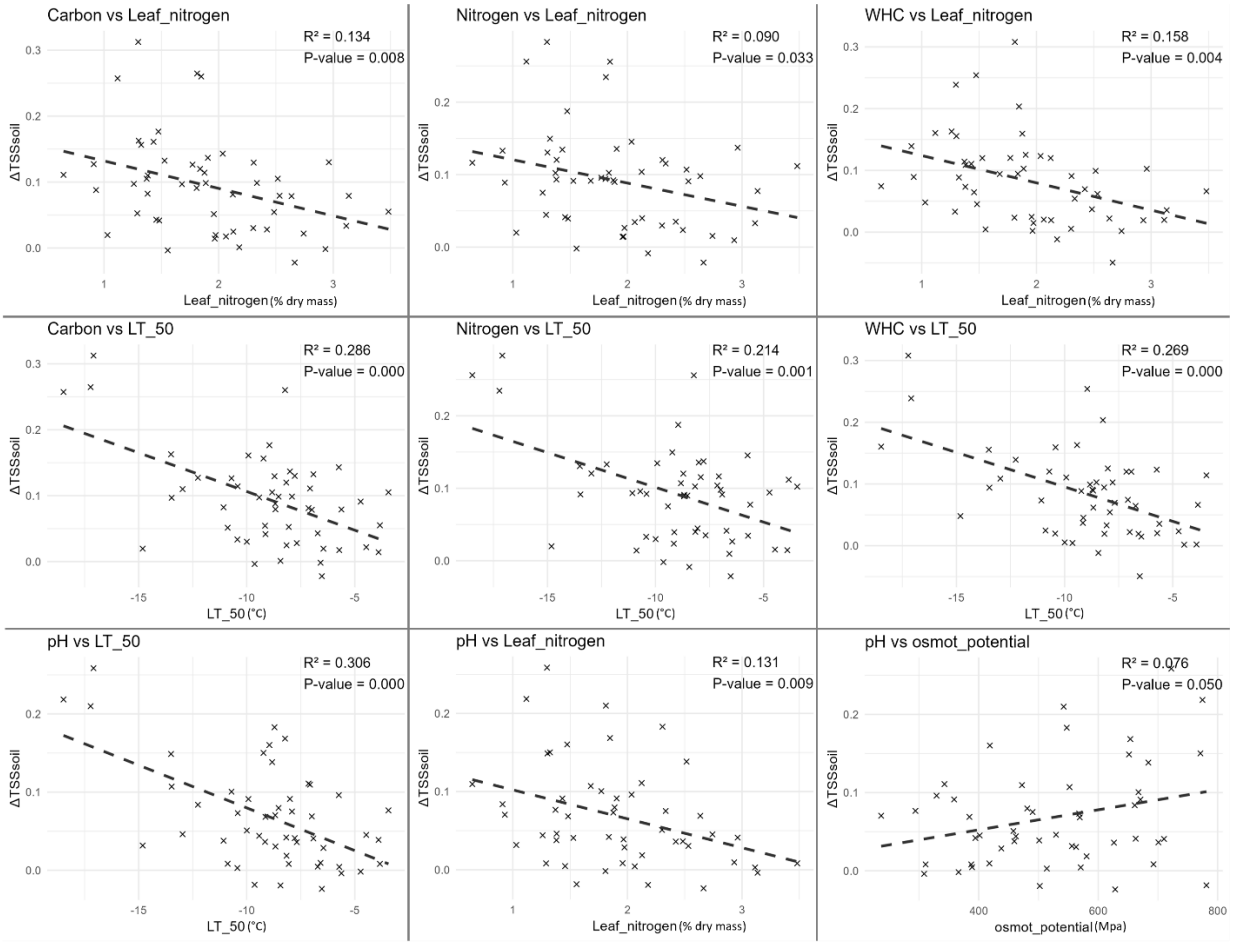

Figure 5. Statistically significant linear regressions of species functional traits against ΔTSSsoil of soil predictors: Carbon, Nitrogen, WHC, and pH. Each cross represents a species.

Strong correlations occurred between the ΔTSSsoil values of soil predictors (Table 2A). The ΔTSSsoil values of Carbon and Nitrogen were extremely strongly correlated, and both of these were also strongly correlated with the ΔTSSsoil of WHC and pH. The ΔTSSsoil of WHC and pH were slightly less strongly correlated. Table 2A also shows a higher strength of correlation of ΔTSSsoil compared with the raw data of the variables themselves. By contrast, correlations between the functional traits themselves were moderate between LT_50 and osmot_potential and LT_50 and leaf_nitrogen, and weak between leaf_nitrogen and osmot_potential (Table 2B).

Table 2. Pearson's correlation coefficients (r) between: (A) ΔTSSsoil and raw data of the four soil predictors selected for regression analysis, (B) the three functional traits which showed significant regressions with ΔTSSsoil of the four soil predictors.

(A)	*Predictors*	*ΔTSSsoil (r)*	*Raw data (r)*
	Carbon - Nitrogen	0.970	0.945
	Carbon - WHC	0.883	0.825
	Carbon - pH	0.869	-0.543
	Nitrogen - WHC	0.857	0.754
	Nitrogen - pH	0.852	-0.510
	WHC - pH	0.793	-0.540

(B)	*Functional traits*	*r*
	LT_50 - osmot_potential	-0.547
	LT_50 - leaf_nitrogen	0.505
	leaf_nitrogen - osmot_potential	-0.320

EIVs

The ΔTSSsoil of Carbon, Nitrogen, WHC and pH, all had significant negative relationships with EIV Nutrients and EIV Moisture (P-values < 0.033, R^2 values > 0.060). For EIV of Nutrients, relationships were closest with the ΔTSSsoil of WHC (P-value = 0.002, R^2 = 0.125), and the ΔTSSsoil of Carbon (P-value = 0.005, R^2 = 0.102). For EIV of Moisture, relationships were closest with the ΔTSSsoil of Carbon (P-value = 0.012, R^2 = 0.082), and the ΔTSSsoil of pH (P-value = 0.016, R^2 = 0.076). EIV of Temperature had significant negative relationships with the ΔTSSsoil of both pH and Carbon (P-values = 0.046, R^2 values = 0.053). However, due to imbalances in the numbers of species represented in different EIV Landolt categories - for example, a disproportionate number of species represented with an EIV Nutrients value of 2 - these linear regression results should be interpreted with caution (Fig. 6). All EIVs were correlated weakly (maximum Pearson's correlation coefficient, r = 0.44).

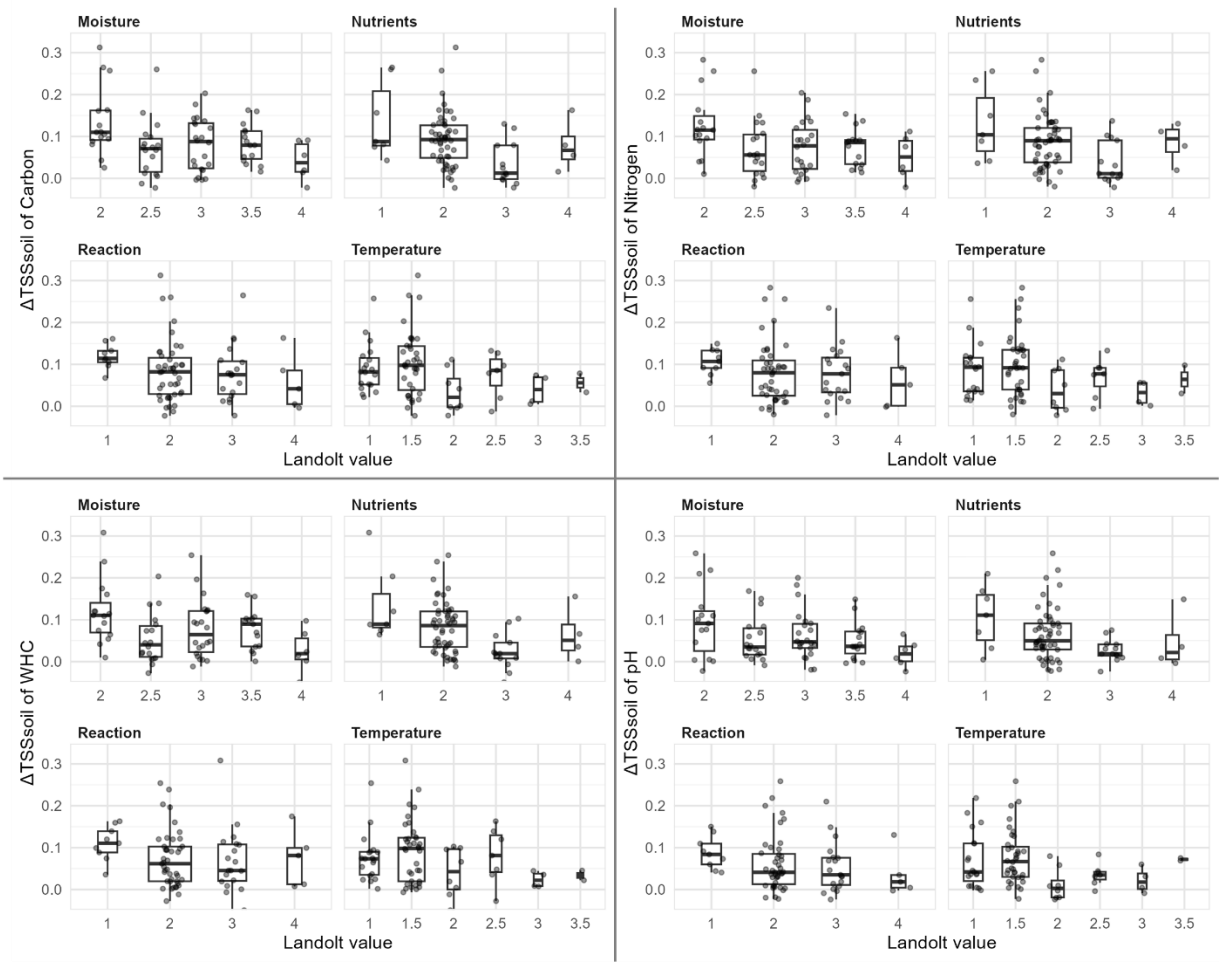

Figure 6. Distribution of ΔTSSsoil values for the soil predictors: Carbon, Nitrogen, WHC, and pH, within categories of the EIVs of: Moisture, Nutrients, Reaction and Temperature. Each dot represents a species, with boxplot width dependent on the number of species within each Landolt value category.

Discussion

What is the relative importance of various soil properties in explaining the above-treeline distribution of alpine plant species, in relation to a climate predictor?

Among the seven soil variables studied in this thesis, as single predictors, Carbon, Nitrogen and WHC were the most important for the overall distribution of plant species on Mt Schrankogel, when considering their predictive power averaged across all plant species. When included with a climate predictor, Carbon, Nitrogen and WHC were still the most predictive, but pH also joined this group due to the significantly higher improvement in predictive power when Temperature was included in pH models compared with Carbon, Nitrogen and WHC. However, when considering the descriptive metric of the percentage of species for which soil variable was the most predictive when included in the

climate model, Carbon was the most predictive soil variable for the highest percentage of species. Within this metric, Nitrogen was in a second group along with WHC and pH, as being the second "best" predictors.

It is unsurprising that across all species, Temperature was a significantly better predictor than most soil variables. This corroborates with many findings of thermal conditions playing the major role in predicting plant distributions, with climate variables regularly reported as the most important overall predictors (Buri et al., 2020; Ni and Vellend, 2024). However, substantial interspecies variability in the performance of a climate predictor compared to soil predictors is also not unexpected (Löffler and Pape, 2020). In my thesis, Temperature was only a marginally better predictor than Carbon, for which it had, on average, a TSS value 0.05 higher than Carbon. Buri et al. (2020) included the stable isotope carbon-13 as a predictor, finding this to be the most important predictor in soil-only SDMs. Measurements of carbon content in soil may perform well because they do not only describe soil properties but, simultaneously, act as a proxy for topographical attributes important for plant distribution in an alpine landscape, e.g. snow melt-out dates (Buri et al., 2020).

Furthermore, the fact that Carbon, Nitrogen, WHC and pH included in the Temperature models, all yielded a significantly higher predictive power compared to Temperature as a single predictor, shows a major contribution of soil properties in plant SDMs. The presence of WHC in the group that significantly improved the climate models, corroborates the finding of Cianfrani et al. (2019), which also showed the significant improvement of plant SDMs by the addition of a metric of soil water availability. In terms of the predictive performance of pH, it had a similar importance compared to Nitrogen when included in the climate model, but was not very effective on its own. This result clearly depends on the bedrock heterogeneity of the study area which was low in my thesis. By contrast, the study area of Dubuis et al. (2013) included both calcareous and siliceous substrates and consequently found that pH was a more important predictor than total nitrogen content.

In terms of the improvement in predictive power per species, from the "best" Temperature + soil model compared to the Temperature model, the contribution of soil variables – mostly Carbon, Nitrogen, WHC and pH – was considerable for a large fraction of species. And, overall, for 42% of species, a soil variable used as a single predictor had a higher predictive power than Temperature as a single predictor. The most impactful soil variables; Carbon, Nitrogen, WHC and pH, all yielded similar improvements in the predictive power of the climate models. In addition, there was a strong correlation in the improvement in predictive power between all four of these variables, and in

particular between model improvement by Carbon and Nitrogen. The strong correlation of their ΔTSSsoil values suggest that model improvement by all four variables eventually emerge from the effect of one overarching soil-gradient, probably the one between humus-rich, well-developed soils and less-developed, raw soils (Hagedorn et al., 2019) which occur in intricate mosaics in an alpine landscape.

Are there patterns in the relative sensitivity of SDMs to soil variables?

The improvement in the predictive power of the Temperature models following the addition of the soil variables, Carbon, Nitrogen, WHC, and pH, were most strongly correlated with the functional traits: leaf nitrogen and LT_{50}. These are traits indicative of stress tolerance and linked to competitiveness, in terms of the ability of plants to maintain photosynthetic rates in harsh conditions such as short growing seasons and below-freezing summer temperatures (Körner, 2003). Since all the correlations were negative, the higher the contribution of soil variables for model performance, the lower the percentage of leaf nitrogen and the lower the temperature which the species could tolerate. Put simply, a higher impact of soil on the SDMs was correlated with a greater tolerance to stress.

In the case of the correlations of the importance of soil variables with leaf nitrogen content, the negative relationships imply plant species with a low leaf nitrogen content can be modelled more precisely with the inclusion of soil variables. These relationships are related to stress tolerance due to leaf nitrogen's role in photosynthetic activity, since the involved enzymes, such as Rubisco, are rich in nitrogen (Field, 1986). A high leaf nitrogen content means high photosynthetic activity and therefore high growth rates. This is indicative of highly competitive plant species which may have more strategies for nitrogen acquisition and favour well-developed, humus-rich soils i.e. a non-stressful environment (Lambers et al., 2008). In contrast, species with low leaf nitrogen content confer higher tolerance to photosynthetic stress and thus the ability to grow on raw soils with a lower available pool of nitrogen, and accordingly, low carbon content and low WHC (Schroeder et al., 2023).

Concurrently, if stress-tolerant species have low growth rates and are poor competitors, they would rarely grow at sites with well-developed soils where they are competitively replaced. Alpine species generally have higher leaf nitrogen contents compared with species at lower elevations (Leuschner and Ellenberg, 2017). This might suggest that alpine species with low leaf nitrogen content would occur in the most poorly developed soils which are vulnerable to drought and low nutrient extremes, and where productivity is limited by these extreme conditions (Zhao et al., 2022). Furthermore, the

significant relationship between leaf nitrogen and model improvement following the addition of pH, likely results from low-competitive species occurring on slowly developing, raw soils which tend to have higher pH (Körner, 2003; Zhao et al., 2022). In contrast, it has been shown that plants that occur in well-developed, humus-rich soils have relatively high nitrogen contents (Körner, 2003), and in alpine climates these soils tend to have lower pH via acidification from slow re-mineralisation of carbon-rich plant material (Tian et al., 2017). Therefore, these relationships may be reflective of both a nutrient and pH-gradient in species distributions (Li et al., 2022), where soil variables are more predictive of species occurring in less-developed soils.

However, there is another relationship we can see based on the types of species for which soil variables were important predictors; many were dominant graminoids of grasslands, especially of higher elevations like *Carex curvula* and *Kobresia myosuroides*. Here, the significant effect of soil variables in their models suggests an importance of soil conditions for their distribution at the alpine-subnival ecotone, where these species require a level of development and stabilisation of soils which is only realised in patches in high alpine environments (Bürli et al., 2021). For example, soil conditions, topography and disturbances are perhaps more important factors than thermal factors for a grass like *Oreochloa disticha* which tolerates climatic conditions at the alpine-subnival ecotone, but rarely occurs on scree and associated raw substrates, and which moreover is competitively inferior to a dominant high-elevation graminoid like *Carex curvula* (Doležal and Šrůtek, 2002). Alpine graminoid species also have strong stress-tolerator traits such as very low LT_{50} values and growth forms for morphological avoidance of low temperature extremes, for the ability to occur in colder and less competitive environments (Körner, 2003), which may also contribute to the significant relationships found between leaf nitrogen and LT_{50} and the model improvements via soil variables.

The significant relationships with LT_{50} may have similar reasons to those with leaf nitrogen content. Plants at higher elevations are exposed to more frequent and more extreme frosts in summer (Körner, 2003). At the same time, soils are poorly developed at these elevations. Therefore, species with a low LT_{50} threshold i.e. high freezing tolerance, tend to occur in the least developed soils with low Carbon and Nitrogen content, low WHC, and above-average pH. These relationships suggest soil variables may be more important for predicting the distribution of those species which pass the crucial abiotic filter of the ability to tolerate extreme summer frosts (Pescador et al., 2016). Generally, species in more facilitative - as opposed to competitive - environments also have higher tolerance to environmental stresses and fewer traits conferring competitiveness, which also suggests that species with higher freezing tolerance should be concentrated in the less-developed soils where competition is less of a

limiting factor for plants to grow (Pellissier et al., 2018; Choler et al., 2001). In the case of the high-elevation graminoids discussed in the previous paragraph, the correlation of the importance of soil variables to high freezing tolerance may similarly be related to their distribution in more-developed soil remnants at the subnival ecotone. The higher susceptibility to drought that plants occurring on less-developed soils would endure (Zhao et al., 2022), may be another reason for the relationship with LT_{50}. Since adaptations for freezing tolerance, like high concentrations of osmotically active compounds, are also conducive of drought tolerance (Sierra-Almeida et al., 2016; Pescador et al., 2016), it is likely plants with low LT_{50} values would occur in raw soils that are physiologically the driest (i.e. low WHC). This may also contribute to the relationship with the importance of soil variables, perhaps, especially the importance of WHC as a predictor increasing for plants with high freezing tolerance.

This relates to the positive relationship we found between soil pH and a trait of drought tolerance; osmotic potential. A greater importance of pH had a relationship – on the threshold of statistical significance – with higher osmotic potential of species. Since above-average pH is indicative of less-developed soils that are more susceptible to drought (Zhao et al., 2022), species with higher osmotic potential are more capable of growing at these sites, meaning pH may be a good predictor of species with high drought tolerance. Although we might also expect the predictive power of WHC – effectively a measurement of the drought tolerance of soil (Cianfrani et al., 2019) – to correlate with osmotic potential, these results suggest above-average pH, rather than low WHC, is more indicative of less-developed soils and therefore the occurrence of drought tolerant species.

In summary, a greater importance of soil variables is understood in models for species with traits that confer tolerance to stress, such as summer frost, low nutrient availability, and low water availability. This is consistent with the EIV analysis, where the importance of Carbon, Nitrogen, WHC, and pH as predictors was associated with species with lower Landolt values for EIV Moisture and EIV Nutrients. Lower values for EIV Moisture indicate species which occur in drier soils and therefore have a higher tolerance to drought, and lower values for EIV Nutrients indicate species which occur in nutrient-poor soils and have higher nutrient stress-tolerance i.e. capability to grow in low nutrient environments (Leuschner and Ellenberg, 2017). Therefore, a similar trend is suggested here compared with the relationships with the functional traits. There are exceptions in these results if species are assessed individually in Figure 4, and as seen by the wide variation in the predictive capability of the soil variables in different EIV Landolt categories in Figure 6. However, there is a trend that points to a

gradient of soil conditions being most important for species occurring in less-developed, raw soils to less important for species occurring in well-developed, humus-rich soils.

Conclusions

The results of this thesis concur with the view that the distribution of many alpine plant species strongly depends on particular soil conditions. It importantly suggests that less-developed, raw soils are important for species with specific characteristics in terms of stress-tolerance. For plant species which occur in higher stress environments – indicated by more extreme functional traits – the effect of temperature on their distributions likely has less importance compared with environmental predictors which can better confer this stress (Steinbauer et al., 2022). The role of facilitation in less-developed soils where stress is greater, should also be noted as perhaps making soil conditions good predictors of plant species in communities driven more by facilitation than competition (Blonder et al., 2018). Range shifts of plants in response to climate change, especially upward movement, may therefore be constrained, with raw soils at the highest elevations not being appropriate for species migrating from below (Hagedorn et al., 2019). This relates to the significant contribution of soil conditions in plant SDMs that was found on a latitudinal gradient and in climate change projections caused a restriction in the ability for species to migrate polewards (Ni and Vellend, 2024). It is likely that the development of soil - being extremely slow even in lower-alpine environments (Leuschner and Ellenberg, 2017) - would not be fast enough to provide the more developed soils that plants from lower elevations may need to be able to survive at higher elevations. On the other hand, in high alpine to subnival remnants of more developed soil, such as where the soil-dependent graminoids may be more dominant, these may be colonised by especially mobile, competitive plants which, under warming, may not require such freezing tolerance (Rumpf et al., 2018).

We should therefore more routinely include soil parameters in SDMs, especially for climate change predictions. Carbon content – the best soil predictor for the largest number of species and, across all species, a predictor not significantly worse than the climate predictor used in this thesis – is quite simple to measure, and would improve distribution models for many species. Nitrogen content and pH are also simple to measure and would assist models, although Nitrogen and Carbon were highly correlated variables. Determining the WHC requires further sampling effort of the soil depth and organic layer depth but is also an important predictor for some species. Interpolation of soil variables across an entire study area remains a challenge especially in topo-climatically diverse landscapes where sampling can be extremely costly (Lannuzel et al., 2021). To build SDMs with the most eco-

physiologically meaningful predictors would require increased field sampling (Löffler and Pape, 2020) and should therefore further motivate the search for proxies or indicators, such as via remote sensing.

References

Allouche, O., Tsoar, A. and Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology*, *43*(6), pp.1223-1232.

Alvarez, N., Thiel-Egenter, C., Tribsch, A., Holderegger, R., Manel, S., Schönswetter, P., Taberlet, P., Brodbeck, S., Gaudeul, M., Gielly, L. and Küpfer, P., 2009. History or ecology? Substrate type as a major driver of spatial genetic structure in Alpine plants. *Ecology Letters*, *12*(7), pp.632-640.

Austin, M.P. and Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. *Journal of biogeography, 38*(1), pp.1-8.

Austin, M.P., 1980. Searching for a model for use in vegetation analysis. *Vegetatio*, *42*, pp.11-21.

Blonder, B., Kapas, R.E., Dalton, R.M., Graae, B.J., Heiling, J.M. and Opedal, Ø.H., 2018. Microenvironment and functional-trait context dependence predict alpine plant community dynamics. *Journal of Ecology*, *106*(4), pp.1323-1337.

Buri, A., Grand, S., Yashiro, E., Adatte, T., Spangenberg, J.E., Pinto-Figueroa, E., Verrecchia, E. and Guisan, A., 2020. 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.

Bürli, S., Theurillat, J.P., Winkler, M., Lamprecht, A., Pauli, H., Rixen, C., Steinbauer, K., Wipf, S., Abdaladze, O., Andrews, C. and Barančok, P., 2021. A common soil temperature threshold for the upper limit of alpine grasslands in European mountains. *Alpine Botany*, *131*(1), pp.41-52.

Chauvier, Y., Descombes, P., Guéguen, M., Boulangeat, L., Thuiller, W. and Zimmermann, N.E., 2022. Resolution in species distribution models shapes spatial patterns of plant multifaceted diversity. *Ecography, 2022*(10), p.e05973.

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), p.e01433.

Choler, P., Michalet, R. and Callaway, R.M., 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology*, *82*(12), pp.3295-3308.

Chytrý, K., Helm, N., Hülber, K., Moser, D., Wessely, J., Hausharter, J., Kollert, A., Mayr, A., Rutzinger, M., Winkler, M. and Pauli, H., 2023. Limited impact of microtopography on alpine plant distribution. *Ecography*, p.e06744.

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*, pp.57-70.

Coudun, C., Gégout, J.C., Piedallu, C. and Rameau, J.C., 2006. Soil nutritional factors improve models of plant species distribution: an illustration with Acer campestre (L.) in France. Journal of *Biogeography, 33*(10), pp.1750-1763.

Descombes, P., Walthert, L., Baltensweiler, A., Meuli, R.G., Karger, D.N., Ginzler, C., Zurell, D. and Zimmermann, N.E., 2020. Spatial modelling of ecological indicator values improves predictions of plant distributions in complex landscapes. *Ecography, 43*(10), pp.1448-1463.

Doležal, J. and Šrůtek, M., 2002. Altitudinal changes in composition and structure of mountain-temperate vegetation: a case study from the Western Carpathians. *Plant Ecology*, *158*, pp.201-221.

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P. and Guisan, A., 2013. 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.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araujo, M.B., Pearman, P.B., Le Lay, G., Piedallu, C., Albert, C.H. and Choler, P., 2011. 21st century climate change threatens mountain flora unequally across Europe. *Global change biology, 17*(7), pp.2330-2341.

Field, C.H., 1986. The photosynthesis-nitrogen relationship in wild plants. *On the economy of plant form and function*, pp.25-55. *Cambridge University Press: New York*.

Gégout, J.C., Hervé, J.C., Houllier, F. and Pierrat, J.C., 2003. Prediction of forest soil nutrient status using vegetation. *Journal of Vegetation Science*, *14*(1), pp.55-62.

Hagedorn, F., Gavazov, K. and Alexander, J.M., 2019. Above-and belowground linkages shape responses of mountain vegetation to climate change. *Science*, *365*(6458), pp.1119-1123.

Havström, M., Callaghan, T.V. and Jonasson, S., 1993. Differential growth responses of Cassiope tetragona, an arctic dwarf-shrub, to environmental perturbations among three contrasting high-and subarctic sites. *Oikos*, pp.389-402.

IUSS Working Group WRB, 2022. World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps. 4th edition. *International Union of Soil Sciences (IUSS)*. Vienna, Austria.

Jasper, K., Calanca, P. and Fuhrer, J., 2006. Changes in summertime soil water patterns in complex terrain due to climatic change. *Journal of Hydrology*, *327*(3-4), pp.550-563.

Körner, C. and Hiltbrunner, E., 2021. Why is the alpine flora comparatively robust against climatic warming? *Diversity, 13*(8), p.383.

Körner, C., 2003. Alpine plant life: functional plant ecology of high mountain ecosystems (2. ed.). *Berlin: Springer*.

Lambers, H., Raven, J.A., Shaver, G.R. and Smith, S.E., 2008. Plant nutrient-acquisition strategies change with soil age. *Trends in ecology and evolution*, *23*(2), pp.95-103.

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F., Theurillat, J.P. and Urmi, E., 2010. *Flora indicative: Ecological inicator values and biological attributes of the flora of Switzerland and the Alps: ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Haupt Verlag.

Lannuzel, G., Balmot, J., Dubos, N., Thibault, M. and Fogliani, B., 2021. High-resolution topographic variables accurately predict the distribution of rare plant species for conservation area selection in a narrow-endemism hotspot in New Caledonia. *Biodiversity and Conservation*, *30*(4), pp.963-990.

Leuschner, C. and Ellenberg, H., 2017. *Ecology of Central European non-forest vegetation: coastal to alpine, natural to man-made habitats: vegetation ecology of Central Europe, Volume II* (Vol. 2). Springer.

Li, Y., Xu, H., Chen, J., Xiao, Y., Ni, Y., Zhang, R., Ye, W. and Lian, J., 2022. Effects of soil resource availability on patterns of plant functional traits across spatial scales. *Ecology and Evolution*, *12*(2), p.e8587.

Little, C.J., Wheeler, J.A., Sedlacek, J., Cortés, A.J. and Rixen, C., 2016. Small-scale drivers: the importance of nutrient availability and snowmelt timing on performance of the alpine shrub Salix herbacea. *Oecologia*, *180*, pp.1015-1024.

Liu, C., White, M. and Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of biogeography*, *40*(4), pp.778-789.

Löffler, J. and Pape, R., 2020. Thermal niche predictors of alpine plant species. *Ecology*, *101*(1), p.e02891.

Matias, L., Castro, J. and Zamora, R., 2011. Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. *Global Change Biology*, *17*(4), pp.1646-1657.

Matijević, V., 2024. Interaction, distribution, and modelling of mountain plant vegetation as a response to soil properties in the study area of Schrankogel Mountain, Austria. *University of Vienna*.

Michalet, R., Gandoy, C., Joud, D., Pagès, J.P. and Choler, P., 2002. Plant community composition and biomass on calcareous and siliceous substrates in the northern French Alps: comparative effects of soil chemistry and water status. *Arctic, Antarctic, and Alpine Research*, *34*(1), pp.102-113.

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.

Ni, M. and Vellend, M., 2024. Soil properties constrain predicted poleward migration of plants under climate change. *New Phytologist*, *241*(1), pp.131-141.

Pellissier, L., Descombes, P., Hagen, O., Chalmandrier, L., Glauser, G., Kergunteuil, A., Defossez, E. and Rasmann, S., 2018. Growth-competition-herbivore resistance trade-offs and the responses of alpine plant communities to climate change. *Functional Ecology*, *32*(7), pp.1693-1703.

Pescador, D.S., Sierra-Almeida, Á., Torres, P.J. and Escudero, A., 2016. Summer freezing resistance: a critical filter for plant community assemblies in Mediterranean high mountains. *Frontiers in Plant Science*, *7*, p.194.

R Core Team. 2024. R: A Language and Environment for Statistical Computing. Vienna, Austria.

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.

Rumpf, S.B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N.E. and Dullinger, S., 2018. Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences*, *115*(8), pp.1848-1853.

Sardans, J. and Peñuelas, J., 2012. The role of plants in the effects of global change on nutrient availability and stoichiometry in the plant-soil system. *Plant physiology*, *160*(4), pp.1741-1761.

Scherrer, D. and Guisan, A., 2019. Ecological indicator values reveal missing predictors of species distributions. *Scientific Reports, 9*(1), p.3061.

Scherrer, D. and Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of biogeography*, *38*(2), pp.406-416.

Schroeder, L., Robles, V., Jara-Arancio, P., Lapadat, C., Hobbie, S.E., Arroyo, M.T. and Cavender-Bares, J., 2024. Drivers of plant diversity, community composition, functional traits, and soil processes along an alpine gradient in the central Chilean Andes. *Ecology and Evolution*, *14*(2), p.e10888.

Sierra-Almeida, A., Reyes-Bahamonde, C. and Cavieres, L.A., 2016. Drought increases the freezing resistance of high-elevation plants of the Central Chilean Andes. *Oecologia*, *181*, pp.1011-1023.

Soudzilovskaia, N.A., Elumeeva, T.G., Onipchenko, V.G., Shidakov, I.I., Salpagarova, F.S., Khubiev, A.B., Tekeev, D.K. and Cornelissen, J.H., 2013. Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences*, *110*(45), pp.18180-18184.

Steinbauer, K., Lamprecht, A., Winkler, M., Di Cecco, V., Fasching, V., Ghosn, D., Maringer, A., Remoundou, I., Suen, M., Stanisci, A. and Venn, S., 2022. Recent changes in high-mountain plant community functional composition in contrasting climate regimes. *Science of the Total Environment*, *829*, p.154541.

Syphard, A.D. and Franklin, J., 2009. Differences in spatial predictions among species distribution modeling methods vary with species traits and environmental predictors. *Ecography, 32*(6), pp.907-918.

Tian, L., Zhao, L., Wu, X., Fang, H., Zhao, Y., Yue, G., Liu, G. and Chen, H., 2017. Vertical patterns and controls of soil nutrients in alpine grassland: Implications for nutrient uptake. *Science of the Total Environment*, *607*, pp.855-864.

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.

Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan Publisher, New York.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D.A., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J. and Kuhn, M., 2019. Welcome to the Tidyverse. *Journal of open source software*, *4*(43), p.1686.

Wookey, P.A., Robinson, C.H., Parsons, A.N., Welker, J.M., Press, M.C., Callaghan, T.V. and Lee, J.A., 1995. Environmental constraints on the growth, photosynthesis and reproductive development of Dryas octopetala at a high Arctic polar semi-desert, Svalbard. *Oecologia*, *102*, pp.478-489.

Wookey, P.A., Welker, J.M., Parsons, A.N., Press, M.C., Callaghan, T.V. and Lee, J.A., 1994. Differential growth, allocation and photosynthetic responses of Polygonum viviparum to simulated environmental change at a high arctic polar semi-desert. *Oikos*, pp.131-139.

Zhao, Y., Wang, X., Jiang, S., Xiao, J., Li, J., Zhou, X., Liu, H., Hao, Z. and Wang, K., 2022. Soil development mediates precipitation control on plant productivity and diversity in alpine grasslands. *Geoderma*, *412*, p.115721.

Appendix

Appendix 1: For each species, the predictor which resulted in the largest TSS increase after the addition of each soil predictor to the Temperature model (ΔTSSsoil)

Species	*ΔTSSsoil*	*Predictor with highest ΔTSSsoil*
Avenula versicolor	0.3125	Carbon
Kobresia myosuroides	0.3080	WHC
Luzula spicata	0.2602	Carbon
Carex curvula subsp. curvula	0.2573	Carbon
Achillea moschata	0.2540	WHC
Trifolium pallescens	0.2043	Nitrogen
Geum reptans	0.1829	pH
Agrostis alpina	0.1746	WHC
Calluna vulgaris	0.1630	WHC
Poa alpina	0.1628	Carbon
Juncus trifidus	0.1611	Carbon
Sagina saginoides	0.1599	Carbon
Vaccinium gaultherioides	0.1594	WHC
Oreochloa disticha	0.1564	Carbon
Primula minima	0.1473	Soil Depth
Cardamine resedifolia	0.1448	Carbon
Vaccinium vitis-idaea	0.1392	WHC
Phyteuma hemisphaericum	0.1383	pH
Mutellina adonidifolia	0.1372	Nitrogen
Gentiana acaulis	0.1371	WHC
Persicaria vivipara	0.1368	Carbon
Vaccinium myrtillus	0.1325	Carbon
Luzula lutea	0.1264	Carbon
Carex sempervirens	0.1204	Nitrogen
Sibbaldia procumbens	0.1199	Carbon
Primula glutinosa	0.1199	WHC
Veronica bellidioides	0.1164	Nitrogen
Senecio incanus subsp. carniolicus	0.1153	Nitrogen
Sedum alpestre	0.1140	WHC
Hieracium alpinum s. lat.	0.1131	Organic Layer Depth
Viola biflora	0.1118	Nitrogen
Calamagrostis villosa	0.1115	Carbon
Geum montanum	0.1070	pH
Homogyne alpina	0.1027	WHC
Selaginella selaginoides	0.0993	WHC
Solidago virgaurea subsp. minuta	0.0979	Nitrogen
Soldanella pusilla	0.0974	WHC
Phleum alpinum agg.	0.0952	C/N Ratio
Festuca halleri agg.	0.0943	Carbon
Gnaphalium supinum	0.0941	Nitrogen

Agrostis rupestris	0.0933	Nitrogen
Juniperus communis subsp. nana	0.0923	WHC
Rhinanthus glacialis	0.0919	Nitrogen
Agrostis agrostiflora	0.0908	Nitrogen
Saxifraga bryoides	0.0893	WHC
Geranium sylvaticum	0.0791	Carbon
Salix herbacea	0.0762	Soil Depth
Minuartia sedoides	0.0752	Carbon
Trifolium pratense subsp. pratense	0.0752	pH
Silene vulgaris	0.0741	Carbon
Alchemilla vulgaris agg.	0.0724	C/N Ratio
Deschampsia cespitosa subsp. cespitosa	0.0691	C/N Ratio
Anthoxanthum alpinum	0.0683	pH
Avenella flexuosa	0.0675	Carbon
Potentilla aurea	0.0670	Carbon
Silene acaulis subsp. exscapa	0.0645	WHC
Sempervivum montanum s. str.	0.0559	Organic Layer Depth
Luzula alpino-pilosa	0.0544	Carbon
Leucanthemopsis alpina	0.0526	Carbon
Myosotis alpestris	0.0525	C/N Ratio
Euphrasia minima	0.0519	Carbon
Ranunculus glacialis	0.0514	Carbon
Scorzoneroides helvetica	0.0509	pH
Nardus stricta	0.0480	WHC
Cerastium uniflorum	0.0452	pH
Festuca nigricans	0.0399	Nitrogen
Salix helvetica	0.0389	pH
Cirsium spinosissimum	0.0351	pH
Poa laxa	0.0335	Carbon
Lotus corniculatus	0.0311	pH
Rhododendron ferrugineum	0.0303	C/N Ratio
Luzula alpina	0.0292	pH
Festuca nigrescens	0.0286	C/N Ratio
Veronica alpina	0.0286	pH
Campanula barbata subsp. barbata	0.0239	Organic Layer Depth
Leontodon hispidus	0.0237	Organic Layer Depth
Campanula scheuchzeri	0.0226	C/N Ratio
Ranunculus villarsii	0.0192	WHC
Bartsia alpina	-0.0132	Soil Depth