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PREDICTING CHANGES IN SPECIES DISTRIBUTION AFTER 20 YEARS OF CLIMATE CHANGE IN SUBALPINE-ALPINE OPEN LANDS IN THE WESTERN SWISS ALPS

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Abstract

Species distribution models (SDMs) are often used to predict the response of species to climate change. However, predictions are rarely evaluated with independent datasets as inventories realized at different periods are quite sparse. Here, we investigated the impact of climate change on 46 plant species in the Swiss Alps by using SDMs and two independent datasets composed of 69 vegetation plots inventoried in 2002-2003 and 2021-2022. Models were calibrated on plant records collected between 1990-2003, predicted in the past (1991-2000) and present (2011-2020), and evaluated with the independent datasets. We tested if the observed changes in species distribution and abundances can be predicted by SDMs and if changes in model performances (TSS, sensitivity and specificity) can be explained by species ecological preferences. Despite SDMs showing good performances (TSS>0.4), predictions poorly detected the observed changes in presences and abundances over 20 years of climate change. However, changes in TSS and sensitivity were significantly negatively correlated with temperature ecological indicator value, indicating that species growing at higher elevation were better predicted under present climate.
Our study provides a first assessment of the impact of climate change on 46 species in the Alps and highlights the need to consider other environmental parameters in SDMs.

Résumé

Les modèles de distribution d'espèces (SDMs) sont souvent utilisés pour prédire la réponse des espèces face au changement climatique. Cependant, les prédictions sont rarement évaluées avec des jeux de données indépendants car des inventaires réalisés à différentes périodes sont relativement rares. Ici, nous avons étudié l'impact du changement climatique sur 46 espèces de plantes dans les Alpes suisses en utilisant des SDMs et deux jeux de données indépendants composés de 69 placettes inventoriées en 2002-2003 et 2021-2022. Les modèles ont été calibrés avec des registres de plantes collectées entre 1990-2003, prédits dans le passé (1991-2000), dans le présent (2011-2020), et évalués avec les jeux de données indépendants. Nous avons testé si les changements de distribution et d'abondance observés des espèces pouvaient être prédits par les SDMs et si les changements de performances des modèles (TSS, sensibilité et spécificité) pouvaient être expliqués par les préférences écologiques des espèces. Malgré le fait que les SDMs ont de bonnes performances (TSS>0.4), les prédictions détectent mal les changements d'abondance et de présence observés sur 20 ans de changement climatique. Cependant, les changements de TSS et de sensibilité étaient significativement et négativement corrélés avec la température, ce qui indique que les espèces qui poussent plus haut en altitude étaient mieux prédites sous le climat actuel.
Notre étude fournit une première estimation de l'impact du changement climatique sur 46 espèces des Alpes et souligne la nécessité de considérer d'autres paramètres environnementaux lors de l'utilisation de SDMs.

Keywords: Species distribution models (SDMs) – Climate change – Alpine plants – Independent data – Subalpine and alpine belts – Switzerland

Introduction

Climate change is known to affect species distribution and survival (Root et al., 2003). Temperatures in the European Alps increased twice as much compared to the north hemisphere average, with an observed increase of 2°C between the end of the 19th century and the end of the 20th century (Gobiet et al., 2014). Global warming is generally predicted to be greater in higher elevations in the future too (Gobiet et al., 2014). Consequently, mountain's ecosystems are particularly threatened by climate change with multiple potential consequences, such as habitat change, community reshuffling or biodiversity loss (Rogora et al., 2018; Engler et al., 2011). An overall migration of plant species towards summits has already been observed in response to global warming (Pauli & Halloy, 2019), which is reshaping species distribution (Rumpf et al., 2019). As mountain areas possess a high diversity of plants and many endemic species, climate change could lead to a major loss of biodiversity in those ecosystems (Rogora et al., 2018). If conservation measures or political decisions aim at protecting alpine plant species in mountain areas, predictions of future species distribution are needed to better apprehend how species distributions and assemblages might be reshaped under climate change (Guisan et al., 2013).

Species distribution models (SDMs) might provide useful insights to apprehend how climate change will impact species distribution (Guisan & Thuiller, 2005). SDMs allow to statistically define the ecological niche of a species and to spatially predict it in geographic space by linking environmental predictors to records of species presences and absences (Guisan & Zimmermann, 2000) or pseudo-absences (Barbet-Massin et al., 2012; Descombes et al., 2022, Preprint). The predictions can be used to support conservation decisions by indicating species probability of presence in a whole area, under different climatic conditions or different period of time (Guisan et al., 2013). Consequently, SDMs are often used to predict potential species distribution under climate change. Shifts in the distribution of species under climate change can help identify species at risk of future extinction due to the decreased environmental suitability of the sites where the species currently occurs (Guisan & Thuiller, 2005). Predictions can also help finding areas with undiscovered species occurrences (Guisan et al., 2006), as it is essential to have a good knowledge of the population state to plan effective conservation measures (Guisan et al., 2013; McCune et al., 2020). Those information can then be used to define new natural reserves and protect plant population or habitats under threat of climate change (Guisan et al., 2013). However, SDMs need to be reliable to provide sound predictions to support conservation measures or provide guidelines to stakeholders and decision makers.

Different parameters can impact the reliability of SDMs, like the variables used to define the environment or the quality of plant species information for presences and absences, as models are directly based on those data (Guisan et al., 2017). But reliability of models can also vary according to ecological species traits (McCune et al., 2020). Alpine species living in high elevations are adapted to low-temperature conditions, yet communities there tend to shift their composition toward species of warmer and dryer conditions in response to global warming

(Lamprecht et al., 2018), threatening these cold-adapted species. Several studies showed that plants present in wet snowbeds in the Alps are likely to be among the most threated communities due to the snow cover reduction caused by climate change (Liberati et al., 2019; Matteodo et al., 2016). Consequently, using ecological preferences of species might be useful to interpret model results and the reliability of model predictions under climate change, at least for specialist species living in specific ecological conditions.

Predicting species distribution under different future climate change scenarios has become a common approach to assess the potential impact of global warming on species (Descombes et al., 2016; He et al., 2019). But studies rarely rely on independent validation datasets to test the reliability of species distribution predictions. This is mainly because independent datasets collected at different temporal scales (e.g. re-inventoried plots after 20-50 years) with a stratified sampling design are uncommon. For instance, models calibrated on past vegetation inventories can be predicted on present time and predictions compared to recent re-inventoried plots. Few studies used this approach to evaluate models predictions on short-time scale and often with only one or few species (Crepaz et al., 2021; Lou et al., 2019). Lou et al. looked at marsh vegetation change over 40 years by predicting presence and abundance and their results tended to prove that SDMs can be reliably used to predict species distribution under climate change. Knowing species abundance is a key information to understand population state but obtaining abundance data is often difficult and costly. As high abundance could be linked to high environmental suitability (Weber et al., 2017), testing if change of abundance can be predicted by the probabilities of presence obtained from SDMs could be of great use if it proves possible. Furthermore, a recent study assessed shifts in mountain forest communities across 25 years of climate change and found that macroecological properties (richness or average ecological conditions) were successfully predicted by S-SDMs, however the change of composition was not accurately predicted (Scherrer et al., 2017). As forest species have a higher lifespan than grassland species, impacts of climate change could thus be more perceptible for the latter (Scherrer et al., 2017). Overall, investigating the performance of SDMs to predict changes in plant species distribution in response to climate change by using independent validation datasets and for a large set of species as only received limited interest so far.

Here, we resampled after 20 years 71 vegetation inventories realised during summers 2002-2003 in subalpine and alpine open and non-woody lands in the western Swiss Alps. The complete list of species present was recorded on a 4 m^2 surface and their abundance (cover) was estimated. By using opportunistic occurrences from a plant database and randomly selected pseudo-absences, we built SDMs to predict the past (years 1991-2000) and recent (years 2011-2020) distribution of 46 plant species and evaluated their performances under climate change by confronting them to observed past and recent inventories. We asked the three following questions: (1) Can we detect at the species level the observed changes in species abundances of inventoried plots after 20 years of climate change by using predicted probabilities of presence obtained with our SDMs? (2) Can we predict at the species level the changes in plant

distribution after 20 years of climate change? (3) If any, are those changes linked to species ecological preferences?

Methods

Study area

The study area is located in the Western Swiss Alps (Canton de Vaud, Switzerland, 46°10' - 46°30' N; 6°60' - 7°10' E) and is covering an area of ca. 700 km^2 (**Fig. 1**). The elevation ranges from 375 m to 3210 m. The climate is temperate with annual temperatures and precipitations comprised between 8 °C and 1200 mm at 600 m and -5 °C and 2600 mm at 3000 m (Bouët, 1985). The soil is mainly calcareous (Swiss geological maps, www.swisstopo.admin.ch). Humans pressure on vegetation is mainly due to frequent pastures in the area (Randin et al., 2006).

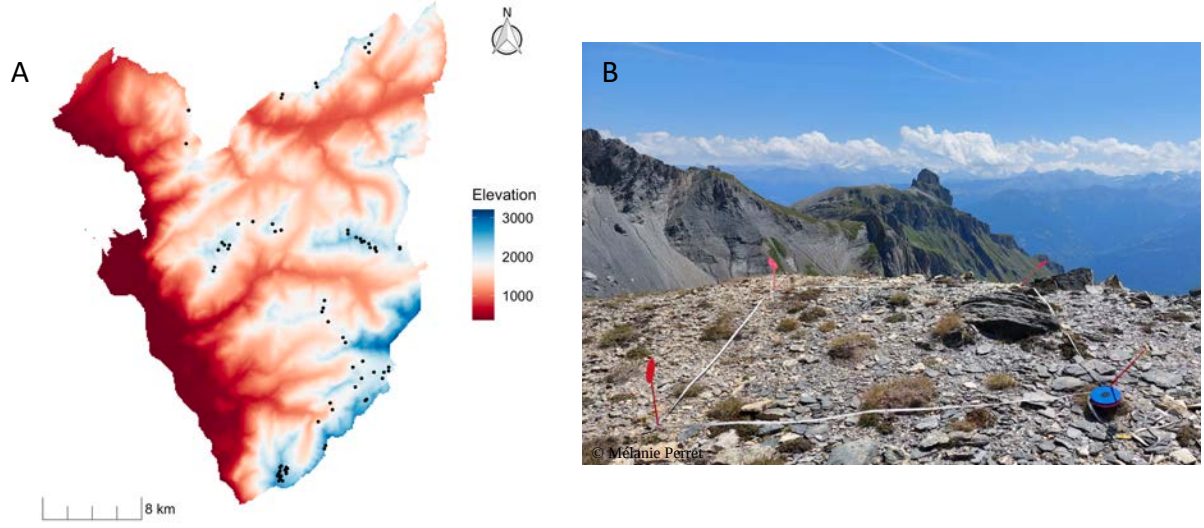

Figure 1. **Panel A**: Map of the study area representing elevation (red-blue gradient) and the independent evaluation plots inventoried in 2002-2003 and 2021-2022 (black dots). **Panel B**: Picture taken during summer 2022 (Frête de Sailles) where we can see the delimitation of the 2 m x 2 m plot.

Species data

Plant inventories

Vegetation inventories were performed during the summers 2002-2003 by recording all vascular plants on 402 plots of 64 m^2 sampled with a random stratified strategy in open and non-woody vegetation (grassland, rock and scree vegetation) in the study area. On each location, plant inventories were made for surfaces of 64 m^2, 16 m^2, 4 m^2 and 1 m^2 nested within each other. The cover of each species occurring in the plot was visually estimated by following

the Braun-Blanquet cover ranges (r = 1-2 individuals, + = < 1%, 1 = 1-5%, 2a = 6-15%, 2b = 16-25%, 3 = 26-50%, 4 = 51-75% and 5 = 76-100%; Randin et al., 2006; Dubuis et al., 2013). We sampled a subset of 71 plots from the pool of plots inventoried in 2002-2003. The 71 selected plots were above 1500 m, presented different exposures, and were well distributed in the study area and along the elevation gradient (**Fig. 1**). They were also chosen manually to optimize the time necessary to reach them by foot (sometimes several hours of walk from the closest road). Our study focuses on subalpine and alpine vegetation because plots at lower elevation should have been already inventoried in spring, which was not possible in the frame of this project. Therefore, plots below 1500 m were not considered. The plots were re-localised thanks to ancient coordinates with the help of a GNSS receiver Trimble R2, schematics, historical species composition of the plots and with pictures if available. Only the 4 m^2 plots were re-inventoried and the cover of each species was estimated by using the Braun-Blanquet cover ranges. The plots were marked with aluminium plates in two opposites corners so that re-localisation will be easier for future inventories. Finally, we retained 69 plots for the analyses because one plot had no species observed and another one had no abundance estimation.

Vegetation data obtained from past (2002-2003) and recent (2021-2022) inventories in the study area were used to evaluate the performances of SDMs as they can be used as two temporal and independent datasets. To ensure sound evaluations of the models, we only selected species with at least 10 occurrences in 2002-2003 inventories (46 species) (**Table S1**). For the analyses, the relative abundance of species estimated with Braun-Blanquet method were transformed into an ordinal scale, where 0 = absent, 1 = one or two individuals, 2 = < 1%, 3 = 1-5%, 4 = 6-15%, 5 = 16-25%, 6 = 26-50%, 7 = 51-75% and 8 = 76-100%, which allows to give more weight to low cover ranges (van der Maarel, 1979).

Plant distribution data

Plant records from the National Data and Information Center of the Swiss Flora (Info Flora: www.infoflora.ch, data extracted in September 2022) were used for the calibration of the SDMs. For the 46 selected species, we retained accurate and valid occurrences (< 100 m) recorded from 1990 to 2003 in Swiss French cantons (Geneva, Vaud, Valais, Neuchatel, Fribourg, and Bern) to have more occurrence records in order to better capture species ecological niche. Data were thinned to have only one observation per raster cell (grid resolution = 100 m) to reduce sampling bias and over-representation of certain environmental conditions in the calibration data (Descombes et al., 2022, Preprint). Finally, occurrences located in a radius of 300 m around the 69 re-inventoried plots were removed to have fully independent datasets for models' evaluation. The 300 m threshold was selected because it has been previously shown to be the best to reduce spatial autocorrelation in model residuals when modelling Swiss plant species at 100 m spatial resolution (Descombes et al., 2022, Preprint). To ensure robust building of the models, we made sure that a minimum of 60 occurrences were present for each species in the calibration data. The number of occurrences for models

calibration vary from 62 to 4361 occurrences (Number of occurrences per species in **Table S1**).

Environmental predictors

Environmental predictors are used for modelling the distribution of species in SDMs. The predictors were selected based on the results of a study determining the importance of a large set of variables for different plant ecological groups when modelling the distribution of species in Switzerland (Descombes et al., 2020). Overall, we retained eight predictors representing meso-climate, topography and geology that were not correlated between each other (Pearson correlations: $|r| < 0.7$; see Dormann et al., 2013).

Annual sum of precipitation (Prec) and annual temperature average (Tave), used as climatic maps, were created with data from Swiss meteorological stations for two time periods: 1991-2000 for past climate and 2011-2020 for present climate. Those layers were retrieved at 100 m resolution from an ongoing project (unpublished data). Mean normalized difference vegetation index (NDVI) were obtained from Landsat data (espa.cr.usgs.gov) taken from 1st July to 15th September at 30 m resolution and aggregated to 100 m using the bilinear interpolation and for two time periods: 1984-1992 for past climate and 2007-2015 for present climate. Those layers were retrieved from a previous study (Descombes et al., 2020). While the two time periods of the NDVI layers do not perfectly match with the target periods of our project, we do not expect much bias resulting from this. Tave, Prec and NDVI were retrieved for two time periods because they can vary under climate change. In our study area and over a period of 20 years, the range of change in the predictor values is comprised between + 0.4 °C and + 1 °C for the annual temperature average, - 387 mm and + 60 mm for the annual sum of precipitation and -7712 and + 6445 for mean NDVI (**Figure S1**).

Topographic position index (TPI) and topographic roughness index (TRI) were calculated using the "terrain" function from the raster package (Hijmans et al., 2019) in R 4.2.0 (R Core Team, 2018) by using a 100 m resolution digital elevation model (DEM) from Swisstopo (www.swisstopo.admin.ch). Yearly sum of solar radiation (sradyy ; direct and diffuse potential solar radiation) and topographic wetness index (TWI) layers were retrieved from Zimmermann & Kienast (1999) at 25 m spatial resolution and aggregated to 100 m using the bilinear interpolation. A proxy of soil pH (Geology) was derived from the Swiss Geological Survey's geology maps 1:500000 (www.swisstopo.admin.ch) at 100 m resolution. We reclassified lithologies into a gradient of increasing CaCO3 content into six classes (Lehmann et al., 2010) where a value of one indicates acidic bedrocks and a value of six alkaline bedrocks. Soil pH is an important parameter as it can influence nutrient availability to plants and therefore affect plant distributions. Those five geological and topographical predictors were calculated only once because we consider that they are stable within the time frame of our study (20 years).

Species Distribution Models (SDMs)

We modelled the distribution of 46 plant species by relating occurrences data to the eight selected environmental variables. To account for variability among different statistical techniques (Thuiller et al., 2004), species were modelled with an ensemble approach (Araújo & New, 2007) by averaging the results from three statistical algorithms: generalized linear models (GLM; Guisan et al., 2002; McCullagh, 1984), generalized additive models (GAM; Guisan et al., 2002; Hastie & Tibshirani, 1987) and random forest (RF; Breiman, 2001; Prasad et al., 2006). GLMs were performed with stats package version 4.1.2 (R Core Team, 2021b), GAMs with mgcv package version 1.8-38 (Wood, 2021) and RF with randomForest package version 4.7-1 (Cutler & Wiener, 2022) in R 4.1.2 (R Core Team, 2021a). GLMs were calibrated with first and second order polynomial terms and binomial family, GAMs with smooth terms with a maximum degree of freedom of four and binomial family and RF were trained with 5000 trees. As no absences were available for calibration data obtained from Infoflora database, five sets of 5000 pseudo-absences were generated randomly with a minimum distance of 100 m between them (Descombes et al., 2022, Preprint). We ran five iterations of the models with the different sets of pseudo-absences, and presences and pseudo-absences were equally weighted in the calibration of the model.

The contribution (in %) of each predictor in the modelling was assessed by reshuffling randomly each predictor individually (keeping all other predictors unchanged) as it is performed in the biomod2 package (Thuiller et al., 2014). We measured the decrease in prediction accuracy on the reshuffled data with a Pearson correlation (Strobl et al., 2007). The average accuracy loss was transformed to % contribution and this value is reported as a measure of variable importance. We averaged the variable importance by species across all algorithms and replicates.

Single-models were evaluated by repeated split-sampling of the data (training set = 70%, evaluation set = 30%), by five-fold spatial block cross-validation (Roberts et al., 2017) using five strata assigned across 25 regional clusters in the study area, and by the 2002/2003 and 2021/2022 independent datasets. As ensemble approaches show in general better performances than averaged single models (Araújo & New, 2007; Descombes et al., 2022, Preprint), we also evaluated ensemble predictions (average of all single model predictions) against both 2002/2003 and 2021/2022 independent datasets. Wilcoxon tests were done between single models evaluated with independent datasets and ensemble models evaluated with independent datasets for past and present time. The model's accuracies were assessed with the maximization of the True Skill Statistic (TSS; Allouche et al., 2006) and a thresholding technique that maximise the sum of sensitivity (rate of true positive) and specificity (rate of true negative) using functions implemented in the PresenceAbsence package version 1.1.10 (E. Freeman, 2022; E. A. Freeman & Moisen, 2008). We averaged TSS evaluations by species across all algorithms and replicates. We retained all species as they all showed good evaluations (TSS >

0.4; Landis & Koch, 1977) for at least one of the split-sampling and five-fold spatial block cross-validation evaluations.

Finally, predictions of species distribution were made in the study area by averaging predictions of all single-models and replicates in the two time periods: 1991-2000 for past climate and 2011-2020 for present climate.

Analyses of model predictions

We investigated if changes in abundance of species observed on sites after 20 years of climate change can be predicted by our ensemble models. To do so, Kendall rank correlations tests were made for each species between the difference of cover estimated on the field (reclassified between 0 and 8) and the difference of predicted presence probabilities between past and present climate. Only plots with at least one occurrence in the past or in the present were considered as abundance change of species absent in both periods are not relevant. A positive and significant relationship would indicate that changes in abundance observed on the field can be predicted by our models.

We further investigated if our ensemble models calibrated on opportunistic occurrences and randomly selected pseudo-absences are able to predict the observed changes in species presences and absences in the field. For this, we determined the number of plots that are stable (0 => 0 or 1 => 1) and unstable (0 => 1 or 1 => 0) between past and present for observations made on the field and for predictions obtained with the ensemble models. For the latter, we binarized the ensemble predictions by using the threshold obtained by maximising the sum of sensitivity and specificity in ensemble model evaluations. Predictions higher than the threshold were considered as presence while predictions lower than the threshold were considered as absence. We summarized for each 46 species the number of plots that are stable and unstable between past and present in a 4 x 4 contingency table made between observations and ensemble model predictions (16 combinations from the four possible trajectories: 0 => 0, 1 => 1, 1 => 0, 0 => 1, columns: the four trajectories obtained from observations, rows: the four trajectories obtained from predictions). From this contingency table, we then calculated the percentage and number of plots correctly predicted by the models for stable plots and unstable plots and used this evaluation as a measure of the model capacity to predict the observed changes. A high percentage for stable and unstable plot would indicate that ensemble models are able to correctly predict the observed stability or changes in the field, respectively.

We also investigated if ensemble models calibrated on historical occurrence data can predict changes in plant distribution after 20 years of climate change by considering or not predictors varying under climate change in the model predictions (i.e. Tave, Prec and NDVI). For this, we evaluated past and present ensemble predictions with the present independent dataset only by calculating the TSS, sensitivity and specificity. We therefore compare two scenarios: (i) one

where climate change has no influence and predictors are not changing over the last 20 years, and (ii) one where climate change has an influence and predictors (i.e. Tave, Prec and NDVI) are changing over the last 20 years. As the distribution of data was normal, we used paired t-test to assess if there is a significant difference between the model performances of both scenarios. An increase in model performances between both scenarios would indicate that predictions of SDMs including variables varying under climate change enable to better differentiate presences from absences in the independent dataset, and potentially suggest a response of the species to the ongoing climate change. We also calculated the percentage of unstable plots (0 => 1 or 1 => 0) observed for species with model performance increase (TSS increase) and with model performance decrease (TSS decrease). A Wilcoxon test was then done to detect if species with TSS increase have more unstable plots than species with TSS decrease. The same analysis was done with percentage of unstable plots predicted by models.

Finally, to test if the increase or decrease in model performances is linked with species ecological preferences, we used ecological indicators values (EIVs; Landolt et al., 2010). EIVs are subjective ordinal categories ranging generally from one to five that defines a gradient of environmental conditions, and each species possess its own values for each ecological indicator (Descombes et al., 2020; Scherrer & Guisan, 2019). Here, four ecological indicators values were used: temperature (1: alpine/nival stage – 5: collinean stage), soil humidity (1: dry soils – 5: submerged soils), soil reaction (pH) (1: acidic soils – 5: alkaline soils) and soil nutrients (1: nutrient-poor soils – 5: nutrient-rich soils). A Kendall rank correlation was performed between each EIVs and the TSS difference of all species. To detect if sensitivity and specificity follow the same pattern than TSS, we also did Kendall rank correlation between each EIVs and sensitivity difference as well as with specificity difference.

Results

Models evaluation

Single models averaged across algorithms and replicates showed variable performances across the 46 selected species (blue boxplots in **Fig. 2**). Overall, models showed fair to excellent evaluations, with TSS ranging between 0.335 and 0.793 when evaluated with five-fold spatial block cross-validation (mean ± sd = 0.574 ± 0.121) and between 0.433 and 0.829 with split-sampling of the data (mean ± sd = 0.625 ± 0.107; blue boxplots in **Fig. 2**). Single models evaluated on the past and present independent datasets showed lower performances, with TSS ranging between 0.168 and 0.695 when evaluated with the past independent dataset and past climate (mean ± sd = 0.418 ± 0.137) and between 0.168 and 0.678 with the present independent dataset and present climate (mean ± sd = 0.434 ± 0.131; blue boxplots in **Fig. 2**).

Ensemble models showed an overall better performance than single models evaluated on the past independent dataset (paired Wilcoxon test: *p-value* = 0.030) and present independent dataset (paired Wilcoxon test: *p-value* = 1e-05). Therefore, all subsequent analyses and interpretations were performed on the ensemble models predictions. Ensemble models showed TSS ranging between 0.182 and 0.711 when evaluated with the past independent dataset and past climate (mean ± sd = 0.429 ± 0.143) and between 0.200 and 0.732 with the present independent dataset and present climate (mean ± sd = 0.460 ± 0.134; purple boxplots in **Fig. 2**). The evaluation of the ensemble models on the present independent dataset and past climate, simulating a scenario where there is no climate change over the last 20 years, showed TSS ranging between 0.205 and 0.730 (mean ± sd = 0.445 ± 0.141; red boxplot in **Fig. 2**).

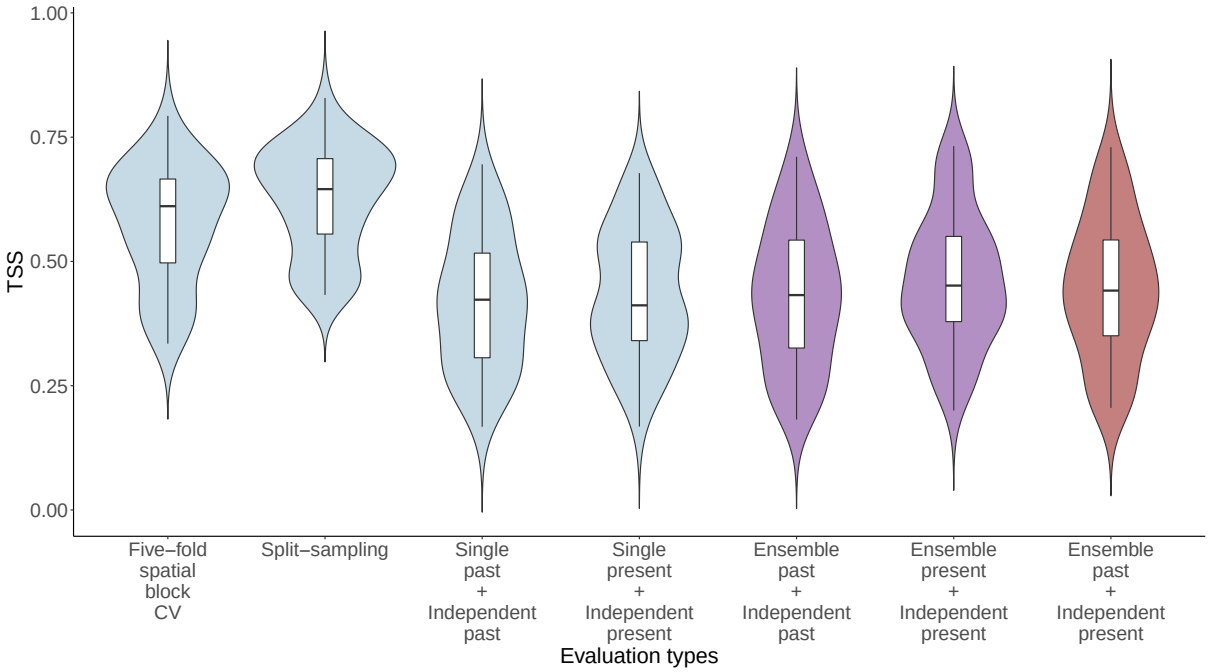

Figure 2. Evaluation of single and ensemble models. The single (blue boxplots) and ensemble models (purple and red boxplots) for the 46 selected plant species were evaluated with TSS and averaged across algorithms (GLM, GAM and RF) and replicates. Models were calibrated on past data, predicted for past and present period and evaluated with past or present datasets (either with calibration or independent datasets). Blue boxplots – five-fold spatial block cross-validation, split-sampling as well as evaluations of past and present predictions evaluated with past and present independent dataset respectively. Purple boxplots – evaluation of past ensemble predictions with the past independent dataset and evaluation of the present ensemble predictions with the present independent dataset. Red boxplot – evaluation of past ensemble predictions with the present independent dataset.

A summary of the number of good and bad models as well as the mean TSS of each evaluation types are presented in **Table 1**. Detailed results for all species and evaluation types are presented in supplementary material (**Table S2**).

Table 1. Number of bad and good models & mean TSS for each evaluation type.

Evaluation Types	Bad Models (TSS < 0.4)	Good Models (TSS > 0.4)	Mean TSS ± SD
K-fold CV	5 (10.87%)	41 (89.13%)	0.57 ± 0.12
Repeated split-sample CV	0 (0%)	46 (100%)	0.63 ± 0.11
Single past + Independent past	21 (45.65%)	25 (54.35%)	0.42 ± 0.14
Single present + Independent present	21 (45.65%)	25 (54.35%)	0.43 ± 0.13
Ensemble past + Independent past	19 (41.30%)	27 (58.70%)	0.43 ± 0.14
Ensemble present + Independent present	16 (34.78%)	30 (65.22%)	0.46 ± 0.13
Ensemble past + Independent present	18 (39.13%)	28 (60.87%)	0.45 ± 0.14

The importance of variable is presented in **Fig. 3**. The four most important predictors to characterize the ecological niche of the 46 selected plant species were the annual temperature average (mean ± sd: 0.611 ± 0.164), topographic roughness index (0.121 ± 0.076), the annual precipitation sum (0.087 ± 0.057), and mean NDVI (0.055 ± 0.031). The predictors had then relatively lower importance, with annual solar radiation sum (0.054 ± 0.062), soil type (0.039 ± 0.044), topographic wetness index (0.021 ± 0.017) and topographic position index (0.012 ± 0.009). Among the four best predictors, three of them vary under climate change in our study (Tave, Prec and NDVI). Variable importance for each species is presented in supplementary material (**Table S3)**.

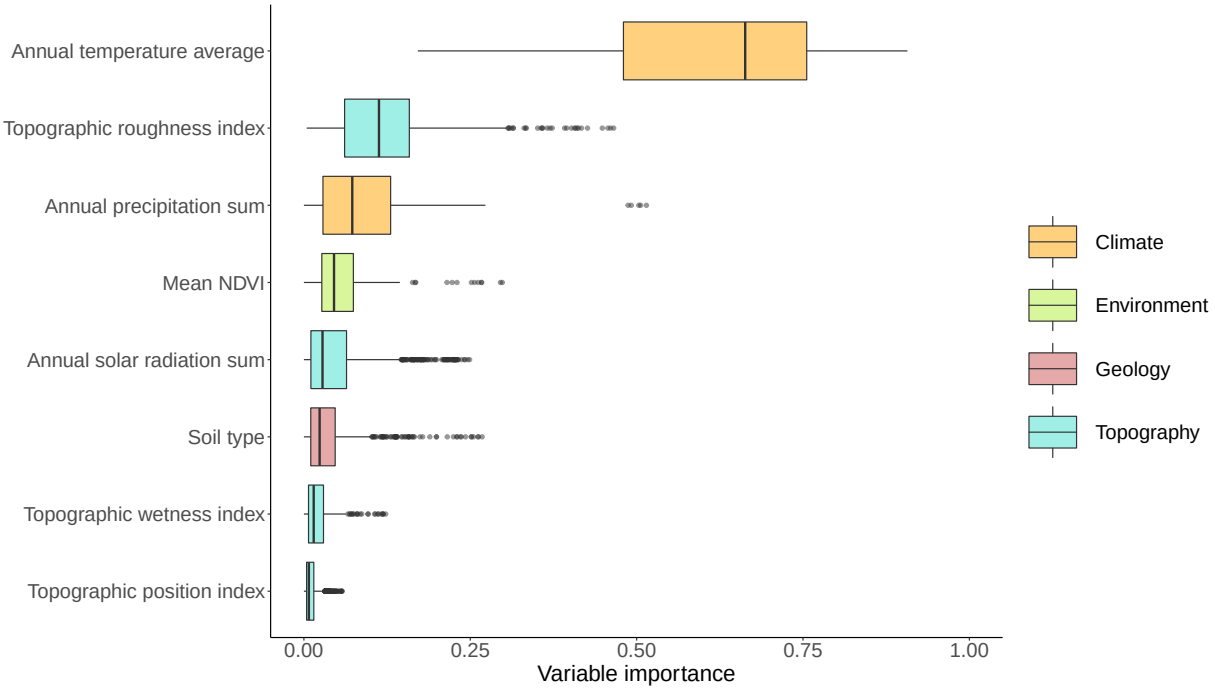

Figure 3. Boxplots showing the importance of variables used to fit SDMs. Contribution of predictors assessed by permutation importance and by meaning results obtained with three algorithms (GLM, GAM and RF), five replicates and then across all species. Variables are classified according to their importance and coloured according to their type. The boxes represent the interquartile range (from 25th to 75th percentile) and the median. The whiskers represent 1.5 times the inter-quartile range. Points are possible outliers.

Predicting changes in plant abundance

Changes observed in the abundances (calculated with median cover) of the 46 selected plant species between past and present plant inventories were in general minor (mean ± sd: 0.367 ± 1.773) and showed important variability with values ranging between - 63 and + 38 (**Table S4**). We found non-significant correlations between the observed change of abundance and the predicted change of presence probability of ensemble models for the 46 selected species (all Kendall's correlation tests: *p-value* > 0.05; see **Table S5**).

Predicting changes in plant distribution

Only minor changes were observed in the presences and absences of the 46 selected plant species between past and present plant inventories, suggesting that they are relatively stable since the last 20 years. On average, 5.955 ± 3.308 % (mean ± sd) of the plots showed a new occurrence (0 => 1), 4.82 ± 3.146 % showed an extinction (1 => 0) and 89.225 ± 4.569 % were stable (either 1 => 1 or 0 => 0; **Table S1**). The changes predicted by the models were a bit higher for unstable plots with on average, 9.767 ± 9.056 % of the plots predicted to have a new occurrence, 9.924 ± 9.834 % to have an extinction and 80.309 ± 6.815 % to be stable (**Table S6**). When both predicted and observed transitions were compared (contingency tables), models generally better predicted plots that remained stable over time than plots with an extinction or a new occurrence. On average, 60.5 ± 11.271 % of plots remaining stable were correctly predicted by the models, while only 18.451 ± 18.376 % of plots presenting an extinction or a new occurrence were correctly predicted by the models (**Table S7)**.

Including or not variables varying under climate change (i.e. Tave, Prec and NDVI) in the model predictions of ensemble models calibrated on historical occurrence data did not improve the model performances. The difference of TSS between past predictions (past climate) evaluated with present dataset and present predictions (present climate) evaluated with present dataset was not significant (paired t-test: *p-value* = 0.383, N = 46). Despite this, TSS values increased for 26 species while it decreased for 20 species. The change of TSS was on average increasing by 0.015 ± 0.116 (mean ± sd) with values ranging from – 0.230 to + 0.270 (**Table S2)**. Sensitivity and specificity increased for 17 and 23 species while they decreased for 19 and 20 species, respectively. The change of sensitivity was on average increasing by 0.007 ± 0.167 with values ranging from - 0.385 to + 0.333, while change of specificity was on average increasing by 0.0083 ± 0.1518 with values ranging from - 0.317 to + 0.321. The TSS increase observed for 26 species is mainly due to an increase of sensitivity (mean ± sd: 0.086 ± 0.157) and less related to changes in specificity (mean ± sd: 0.006 ± 0.160). Detailed results for all species can be found in **Table S8**. Percentage of observed unstable plots vary from 0 % to 13.043 % (mean ± sd: 5.713 ± 3.327 %) for species with TSS increase and from 0 % to 15.942 % (mean ± sd: 4.964 ± 3.163 %) for species with TSS decrease but no significant difference was observed (Wilcoxon test: *p-value* = 0.259). Percentage of predicted unstable plots vary

from 0 % to 34.783 % (mean ± sd: 10.396 ± 9.952 %) for species with TSS increase and from 0 % to 31.884 % (mean ± sd: 9.130 ± 8.703 %) for species with TSS decrease but no significant difference was observed (Wilcoxon test: *p-value* = 0.593).

Changes in TSS were driven by the ecological preferences of the species. We found a significant negative correlation between TSS differences and temperature (Kendall's correlation test: *tau* = -0.448, *z* = -3.854, *p-value* = 0.0001; **Fig. 4A**), but no significant correlations with humidity (Kendall's correlation test: *tau* = 0.200, *z* = 1.783, *p-value* > 0.05; **Fig. 4B**), reaction (Kendall's correlation test: *tau* = -0.113, *z* = -0.953, *p-value* > 0.05; **Fig. 4C**) and nutrients (Kendall's correlation test: *tau* = 0.113, *z* = 0.953, *p-value* > 0.05; **Fig. 4D**). A significant negative correlation between sensitivity differences and temperature were also found (Kendall's correlation test: *tau* = -0.277, *z* = -2.374, *p-value* = 0.018; **Fig. S2A**), but no significant correlations were found for humidity (Kendall's correlation test: *tau* = 0.128, *z* = 1.139, *p-value* > 0.05; **Fig. S2B**), reaction (Kendall's correlation test: *tau* = -0.178, *z* = -1.495, *p-value* > 0.05; **Fig. S2C**) and nutrients (Kendall's correlation test: *tau* = -0.162, *z* = -1.365, *p-value* > 0.05; **Fig. S2D**). Finally, no significant correlations were found between specificity differences and temperature (Kendall's correlation test: *tau* = 0.018, *z* = 0.152, *p-value* > 0.05; **Fig. S3A**), humidity (Kendall's correlation test: *tau* = -0.069, *z* = -0.615, *p-value* > 0.05; **Fig. S3B**), reaction (Kendall's correlation test: *tau* = 0.031, *z* = 0.260, *p-value* > 0.05; **Fig. S3B**) and nutrients (Kendall's correlation test: *tau* = 0.170, *z* = 1.430, *p-value* > 0.05; **Fig. S3D**).

Examples of species predictions and presences/absences observed in past and present are presented for species with the highest TSS increase *(Euphrasia minima*, **Fig. 5A**) and the highest TSS decrease (*Ranunculus tuberosus*, **Fig. 5B**).

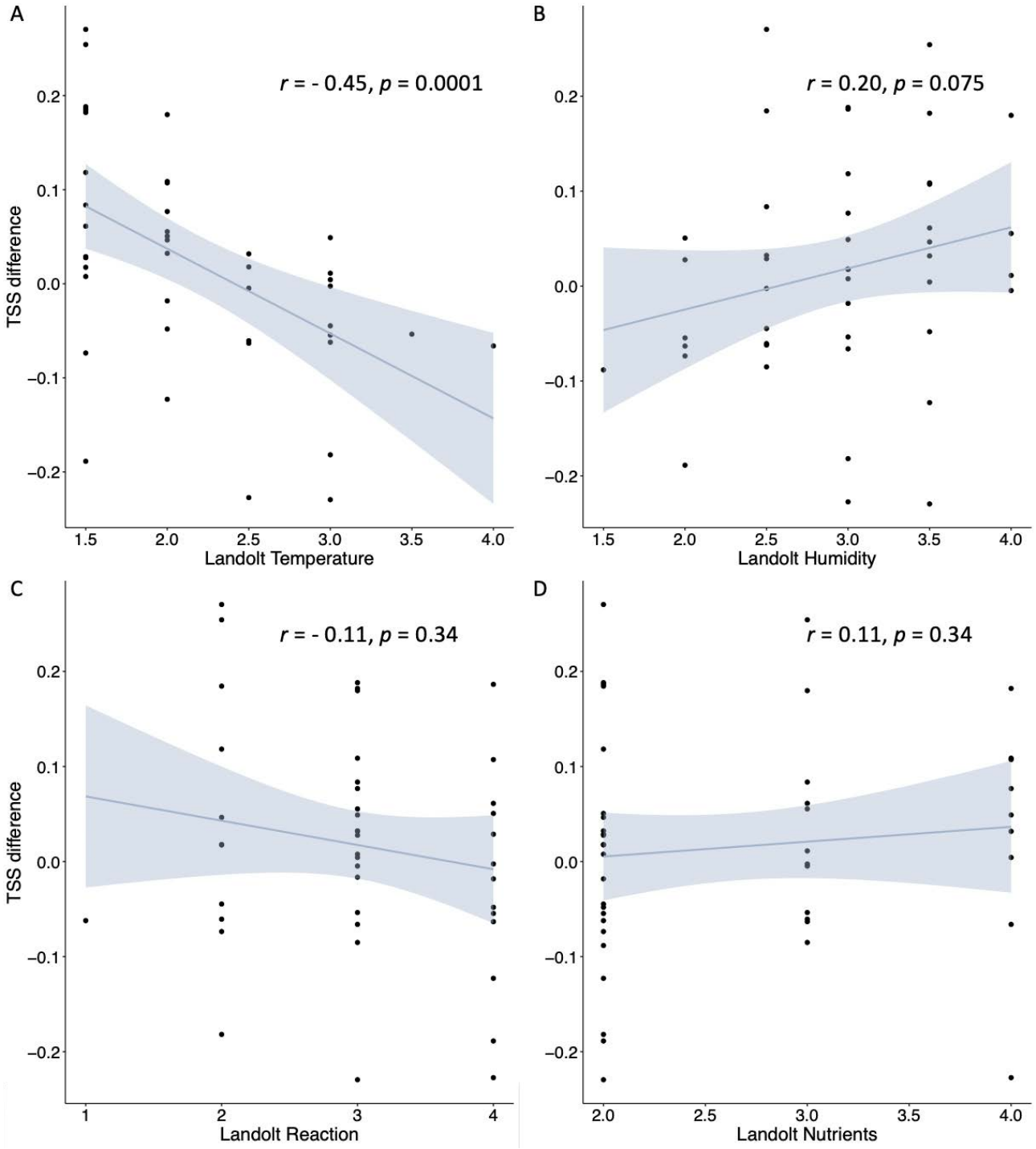

Figure 4. Kendall's correlation for TSS difference between present ensemble predictions evaluated with present independent dataset and past ensemble predictions evaluated with present independent dataset and a selection of ecological indicator values (EIVs) for each species. All EIVs range from 1 to 5 with gradient (A) from alpine/nival stage to collinean stage for Temperature (B) from dry soils to submerged soil for Humidity (C) from acidic soils to alkaline soils for Reaction and (D) from nutrient-poor soils to nutrient-rich soils for Nutrients. The line represents the regression line and the grey area represents the confidence interval. The correlation *tau* and *p-value* are indicated on each panel.

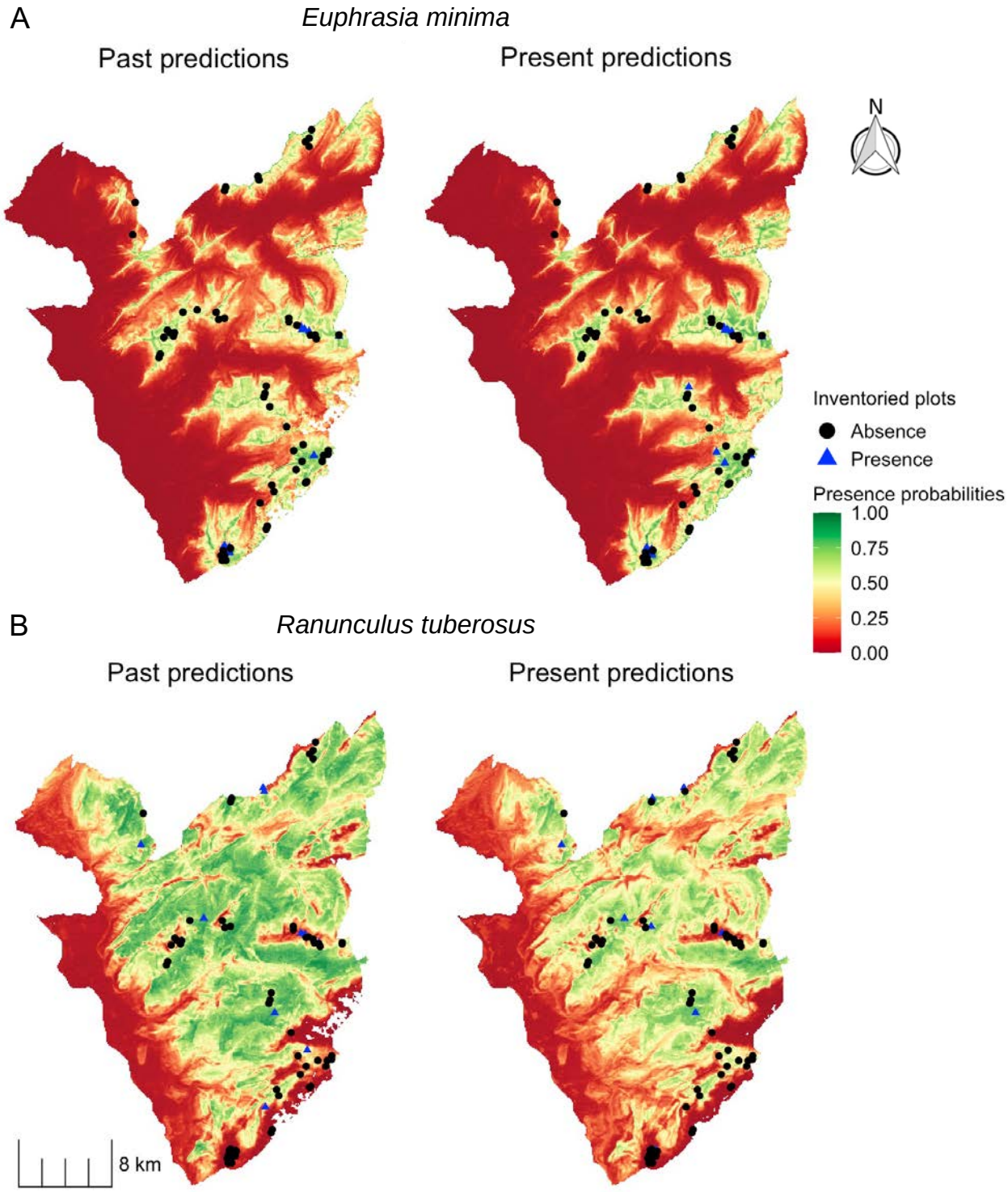

Figure 5. Maps with ensemble models predictions for past and present. Red-green gradient represents the presence probabilities (red: low presence probabilities, green: high presence probabilities), black dots the absence and blue triangles the presence of the species for past (2002-2003) and present (2021-2022) inventoried plots.

Discussion

Our study investigated the impact of climate change on the distribution and abundance of 46 plant species in the Swiss Alps by using SDMs and two independent evaluation datasets composed of 69 vegetation plots inventoried in 2002-2003 and revisited in 2021-2022. Overall, we found that, in the frame of our study design and datasets, our SDMs calibrated on opportunistic occurrences and randomly selected pseudo-absences are not able to predict the observed changes in species abundance. Similarly, and despite SDMs showing in general good performances (TSS > 0.4), ensemble models showed poor capacities to predict the observed changes in species presences in the inventoried plots (only 18.45 ± 18.38 % of the changes correctly predicted). Furthermore, including or not variables varying under climate change (i.e. Tave, Prec and NDVI) in the predictions of ensemble models calibrated on historical occurrence data did not improve significantly the model performances. While the number of species showing an increase or decrease in model performance (TSS) was quite similar, an increase of performance was mainly driven by a higher rate of true positive (sensitivity). Finally, we found that changes in TSS and sensitivity were significantly negatively correlated with the temperature EIV. Together, our results suggest that the SDMs used in our study are not able to capture adequately the changes observed during the last 20 years of climate change on the 69 inventoried plots. Despite this, our study provides a first assessment of the impact of climate change on 46 species in the Swiss Alps and provides guidelines for future studies.

Models' evaluation

All averaged single-models evaluations with repeated split-sampling and five-fold spatial block cross-validation provided good results, except models for five species (i.e. *Anthoxanthum odoratum* aggr., *Leontodon hispidus subsp. hispidus*, *Lotus corniculatus* aggr., *Trifolium pratense*, *Trifolium repens subsp. repens*) having a TSS < 0.4 with the five-fold cross-validation. The latter is not surprising as those five species have a large ecological amplitude, which might be an explanation why SDMs have some difficulties to predict them. Finally, ensemble models showed an overall better performance than single models, as it has been observed in previous studies (Araújo & New, 2007; Descombes et al., 2022, Preprint).

The four most important variables for modelling the 46 selected plant species in our study area were annual temperature average (Tave), topographic roughness index (TRI), annual precipitation sum (Prec) and mean normalized difference vegetation index (NDVI). This is in accordance with other studies showing that those predictors were the best among a large set of variables (Descombes et al., 2020). It is interesting to note that three of them (Tave, Prec and NDVI) are also the ones changing between past and present climate. Consequently, predictions of SDMs are susceptible to change between past and present climate. The principal driver of those changes should be the temperature as it is the most important variable, resulting in an overall migration of the ecological niche of species to higher elevations (see Fig. 5).

Evaluations performed for averaged single-models and ensemble models made with both independent evaluation datasets gave sometimes weaker TSS performances compared to repeated split-sampling and five-fold spatial block cross-validation performed on the calibration data. In particular, evaluations made with independent datasets have nevertheless an important variability between species which could be explained by different limitations which are listed at the end of the discussion section.

Predicting change in plant abundance

The species-level relationships between change of abundance observed on the field and probabilities of presence obtained with SDMs calibrated on opportunistic occurrences and randomly selected pseudo-absences were not significant. Predicting abundance with presence probabilities has been shown to be a difficult task because there might be no direct link between the two or because the models are not enough complex to capture all the information needed to find this link (Dallas & Hastings, 2018). A study found no correlation between probability of occurrences and observed abundance for a bracken fern (*Pteridium aquilinum*) and suggested that abundance and distribution are maybe influenced by different environmental factors, which could explain why it is sometimes impossible to link those two parameters (Nielsen et al., 2005). Weber et al. (2017) performed a meta-analysis to test if there is a positive correlation between species abundance and environmental suitability obtained with SDMs. The lowest correlation was found for plants, which could indicate that environmental suitability is not the only important parameters influencing plants abundance (Weber et al., 2017). Indeed, demographic processes are modifying species range and consequently abundance. A study suggested that demographic strategies can change according to the environmental conditions faced by different populations or species, which impact their local persistence or extinction (Csergő et al., 2017). Competition could also impact plants abundance by causing plants to move to less favourable habitats, which can results with some species having their highest abundance under suboptimal conditions (Cabral & Kreft, 2012; McGill, 2012). However, a study looking at the butterfly *Parnassius apollo* (Gutiérrez et al., 2013) and another one studying small reptiles, arboreal marsupial, diurnal birds and vascular plants (Pearce & Ferrier, 2001) found a link between abundance and habitat suitability for some species. Finally, in our study, we transformed the visually estimated Braun-Blanquet abundance-dominance scale into ordinal classes with unequal range of cover (as in SDMs by Guisan et al., 1998). This was maybe a limitation to this specific analysis as this method allows to record only large change of cover (Vittoz & Guisan, 2007). Therefore, using more precise cover estimation could improve the relationship and be considered for future inventories.

Predicting change in plant distribution

Changes observed in the presences and absences of the 46 selected plant species between past and present plant inventories generally showed that stable plots (species still present or absent: 89.23 % on average) are more frequent than unstable plots (species appearance: 5.96 %; or extinction: 4.82 %) (Table S1). This suggests that the distribution of those species was relatively stable during the last 20 years in our study area. A study looking at range dynamic of mountain plants found species-specific variations, with some species having an expansion and other a contraction of their range size (Rumpf et al., 2018), indicating that species responses to climate change are also species-specific. This could explain why we did not observe a general trend for species distribution change in our study. As we had to select species with enough observations to evaluate our SDMs, the selected species tend to be frequent, and sometimes dominant, in our study area, which implies that they have maybe a more stable population dynamic or present a larger ecological amplitude than rarer and often specialized species that are also more susceptible to respond to ongoing climate change (Vincent et al., 2020). Consequently, the selected species may not be a representative set of subalpine and alpine plant species, but rather a representative set of the most frequent ones in the study area.

SDMs predicted on average more stable (species still present or absent: 80.31 %) than unstable plots (species appearance: 9.77 %; or extinction: 9.92 %), but models tended to predict much more unstable plots than observed in the field. This simple comparison suggests that, in the field, species distributions are much more stable than expected under climate change during the last 20 years and that there might be a lag in the response of plants to the actual climate change (Alexander et al., 2018; Dullinger et al., 2012; Rumpf et al., 2019). Species range shift under climate change can be delayed by lag in colonization of new suitable sites (colonization credit) or in population extinction at unsuitable sites (extinction debt), and Rumpf et al. (2019) found that species adapted to cold conditions are more subject to extinction debts while colonization credit is more common for warmth-adapted species. This lag in species response can result in a mismatch between sites considered as climatically suitable and sites occupied by species, as found by a previous study (Dullinger et al., 2012). However, one should also consider the fact that the models could also overpredict the number of appearance or extinction if the calibration datasets were not representative of the species ecological niche, which can result in biased predictions due to niche truncation (Chevalier et al., 2022). Finally, our SDMs were not able to adequately predict the observed changes in presences and absences in plant inventories, because only 18.45 % of the plots presenting an extinction or a new occurrence were correctly predicted by the models. The low performance of our models to predict those changes might result from the fact that we did not consider some important ecological parameters in our models, which can strongly influence the dynamic of species in the field, such as stochastic events and ecological drift (Hubbell, 2001), biological interactions (plant-animal or plant-plant competition; HilleRisLambers et al., 2013), inter-annual climate or population fluctuations (Csergő et al., 2017; Gardner et al., 2021), or some ecological parameters such as soil pH, soil moisture or microclimatic conditions (Descombes et al., 2020; Lembrechts et al., 2019; Randin et al., 2009). Nevertheless, further studies are necessary to understand how plants will respond to climate change and how those changes could be predicted by modelling approaches.

Ensemble models calibrated on historical occurrence data and predicted in the present (2011-2020 period) with a set of predictors changing under climate change did not show significant improvements in model performances compared to a scenario where predictors do not change compared to the calibration period (1991-2000). This suggests that most of the 46 selected plant species did not respond to the current climate change, as we would have otherwise observed a general increase in model performance. This result is in line with our previous observation that presences and absences of the 46 selected plant species between past and present plant inventories are in general stable and that only few changes are occurring. While the number of species showing an increase or decrease in model performance is quite similar, an increase of performance for 26 species is reported and mainly driven by a higher rate of true positive (sensitivity).

Changes in model performances (TSS and sensitivity) were significantly negatively correlated with the temperature ecological indicator value (EIV; Landolt et al., 2010). This implies that species growing in higher elevations (e.g. *Ligusticum mutellina*, *Polygonum viviparum*, *Potentilla aurea*) are better predicted in our models when considering variable varying under climate change, while the ones growing in lower elevations (e.g. *Aster bellidiastrum, Potentilla erecta, Ranunculus tuberosus*) are better predicted when we consider a scenario where predictors do not change compared to the calibration period (1991-2000). A study looking at plant assemblage predictions in the same study area found that accuracy of stacked-species distribution models (S-SDMs) varies along environmental gradients, but obtained the opposite trend with sensitivity decreasing and specificity increasing along elevation (Pottier et al., 2013).

Those results showing variation in model accuracy along elevation indicate that it is necessary to control the quality of evaluations over space to fully understand quality of predictions (Hanspach et al., 2011). Because species living in higher elevations are adapted to cold conditions and are particularly vulnerable to global warming (Pauli & Halloy, 2019), the latter might explain why we observe an increase in model performances for high elevation species. Hence, high elevation species might already have responded to climate change and are therefore better predicted by our models when considering variables varying under climate change. In contrast, lower elevation species were less impacted until now and might not yet have responded to climate change. This implies that species distributions should have changed more for species better predicted (increase of TSS) than for species less well predicted (decrease of TSS) if species with TSS increase have already responded to climate change. Consequently, species better predicted (TSS increase) should have more changes (appearances or extinctions) in inventoried plots than species less well predicted (TSS decrease). And models should also predict more unstable plots for those species. But for observations and predictions, we found no significant differences between unstable and stable plots for species with increase or decrease of TSS. These results could be explained by the fact that species have maybe not responded to climate change as we expected or that some parameters were missing in our models. Cotto et al. (2017) developed eco-evolutionary model (combining niche modelling with demographic and genetic simulations) to predict the response of alpine plants to climate change. They found a delay in range losses for perennial species as they stay in unsuitable habitats for more time than what was predicted by the niche modelling, and especially for species that are the most abundant. It can be explained by the fact that long lifespan of adults prevents rapid evolution as population turnover is limited, but it favours persistence of population. It thus results in an increase of maladapted individuals which cause a decrease in population size that occurs faster than species range reduction. This implies that evolutionary and demographic processes at local scale happen faster than species range change, therefore, state of local populations is maybe only weakly related to species range change (Csergő et al., 2017). Consequently, monitoring local population size could be more useful than presence-absence surveys to understand species range evolution and response to climate change (Cotto et al., 2017). The results of this previous study show that SDMs that include only environmental information are maybe not always adapted to fully understand species distribution under future climate, which could explain why we were not able to find conclusive results, especially over such a small period (20 years).

Limitations

Several limitations linked to the sampling design might have impacted the results presented in this study. First, our independent datasets are relatively small as they are composed of 69 plots with species presences and absences which might not be representative enough of the species distribution and ecology in the study area. Second, the re-localisation of the plots in the field was sometimes very difficult and some plots might have been shifted by a few meters. Consequently, some species could have been missed or included because the plot could not be relocated precisely (Kapfer et al., 2017). However, the re-inventoried plots were the ones for which enough information was available to obtain a satisfactory relocation. Third, the identity of the observer could also be a possible bias in our independent datasets as the botanists that made the inventories were not the same in 2002-2003 and 2021-2022 (Vittoz & Guisan, 2007). Fourth, the climate inter-annual variability could have impacted species detections in some cases as summer 2022 was particularly dry (Kapfer et al., 2017). A potential example of this problem in our study could be *Crocus albiflorus*, for which we observed an important decrease

of presences from 12 to 3 occurrences between past and present inventories. This species is a geophyte that blooms between March and June, dries out during summer and is difficult to detect if a drought event previously occurred. Fifth, calibration data could also be spatially biased if sampling effort for some species were concentrated in specific area during the 1990-2003 period, which could have led to missing information concerning the species niche (and thus model fitting). However, we do not expect that calibration data have a major impact on our results because we took care to have large calibration datasets filtered by spatial thinning. Finally, some important predictors were not included in our models or not properly mapped (Mod et al., 2016; Scherrer & Guisan, 2019). For instance, EIVs for soil pH and humus have been shown to be good predictors for mountain plants in previous studies (Buri et al., 2020; Descombes et al., 2020; Scherrer & Guisan, 2019). Other parameters such as snow cover, that is impacting physiology of plants (overwinter survival, productivity, reproductive success) and nutrients availability, that is a stress factor, have been shown to improve predictive performance for plants (Niittynen & Luoto, 2018). But those different data were unfortunately unavailable for the past and present periods investigated in our study.

Conclusion

Our study provides a first assessment of the impact of climate change on a large set of 46 species in the Alps and provides valuable guidelines for future studies. Despite good model performances, our SDMs were not able to capture adequately the changes observed during the last 20 years of climate change on the 69 inventoried plots. The 46 species selected showed few changes in their observed distribution during the last 20 years, implying that those species did not respond yet to climate change or that those changes are not visible within our dataset as it is relatively small. Consequently, even if our models predicted changes (mainly due to temperature change recorded in this region over the past 20 years) in the distribution of species, we were not able to corroborate those predictions with 20 years of field observations. Unknown parameters could have also prevented us from proper interpretation of our results, as species distributions can be impacted by many factors, such as stochastic events, geomorphic disturbances, or micro-topographic habitats, that are quite frequent in alpine landscapes (Carlson et al., 2013; Giaccone et al., 2019). Nevertheless, further studies comparing predictions to independent temporal datasets are necessary, as SDMs need to be reliable to provide sound predictions to base conservation measures on them.

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Supplementary Material

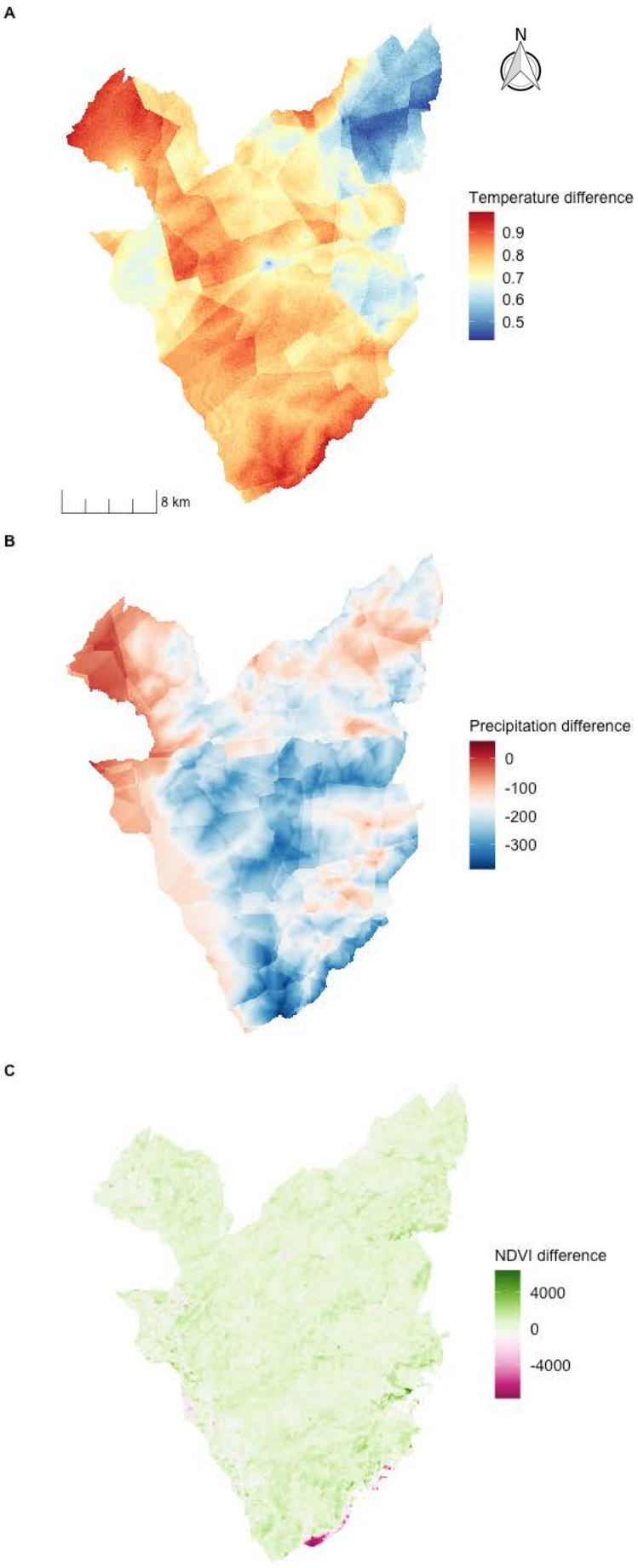

Figure S1. Predictors change in our study area over 20 years. Panel A: Change of annual temperature average ranges between + 0.4 and + 1°C. Panel B: Change of annual sum of precipitation ranges between - 387 mm and + 60 mm. Panel C: Change of NDVI mean ranges between - 7712 and + 6445.

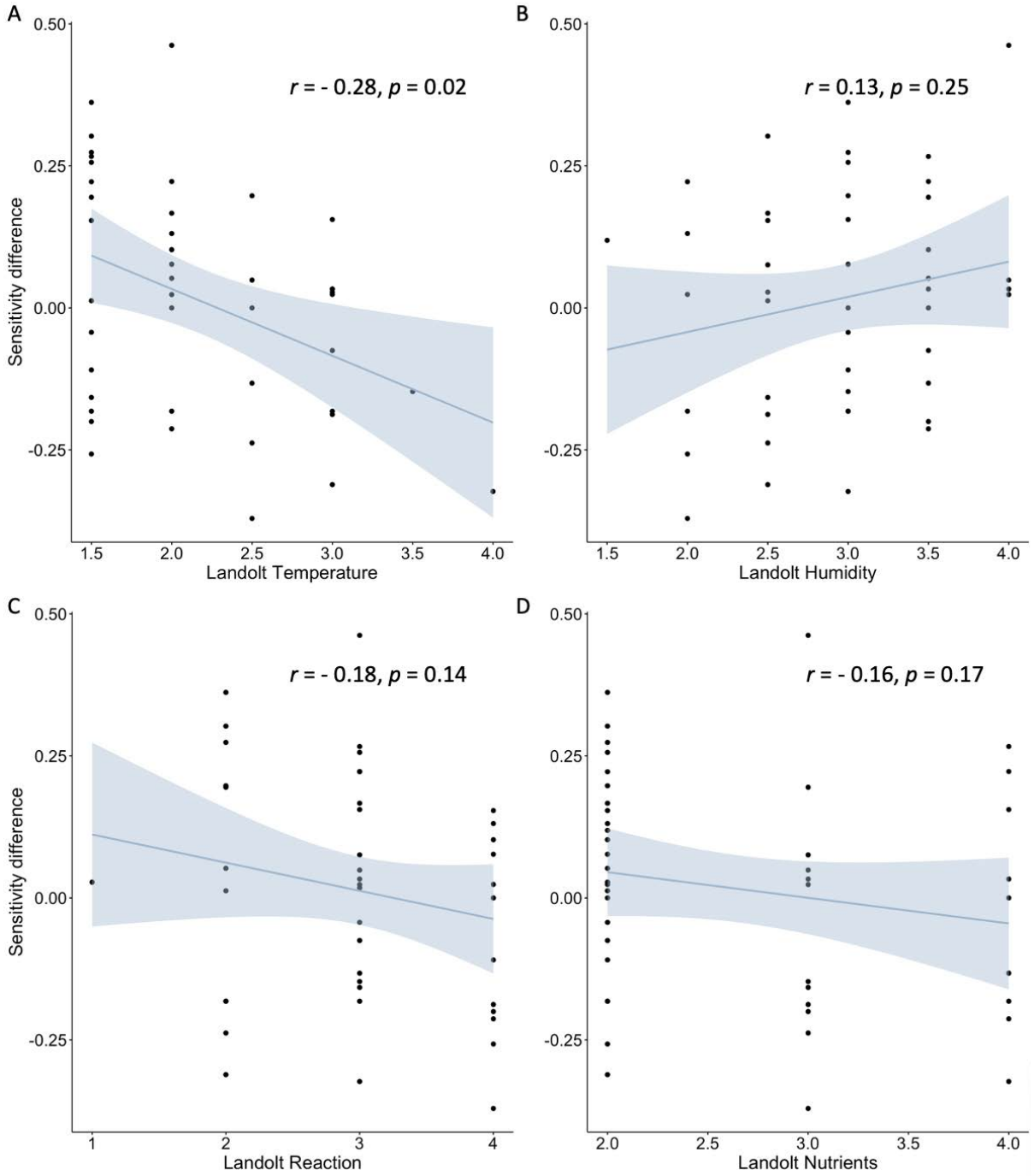

Figure S2. Kendall's correlation for sensitivity difference between present ensemble predictions evaluated with present independent dataset and past ensemble predictions evaluated with present independent dataset and a selection of ecological indicator values (EIVs) for each species. All EIVs range from 1 to 5 with gradient (A) from alpine/nival stage to collinean stage for Temperature (B) from dry soils to submerged soil for Humidity (C) from acidic soils to alkaline soils for Reaction and (D) from nutrient-poor soils to nutrient-rich soils for Nutrients. The line represents the regression line and the grey area represent the confidence interval. The correlation *tau* and *p-value* are indicated on each panel.

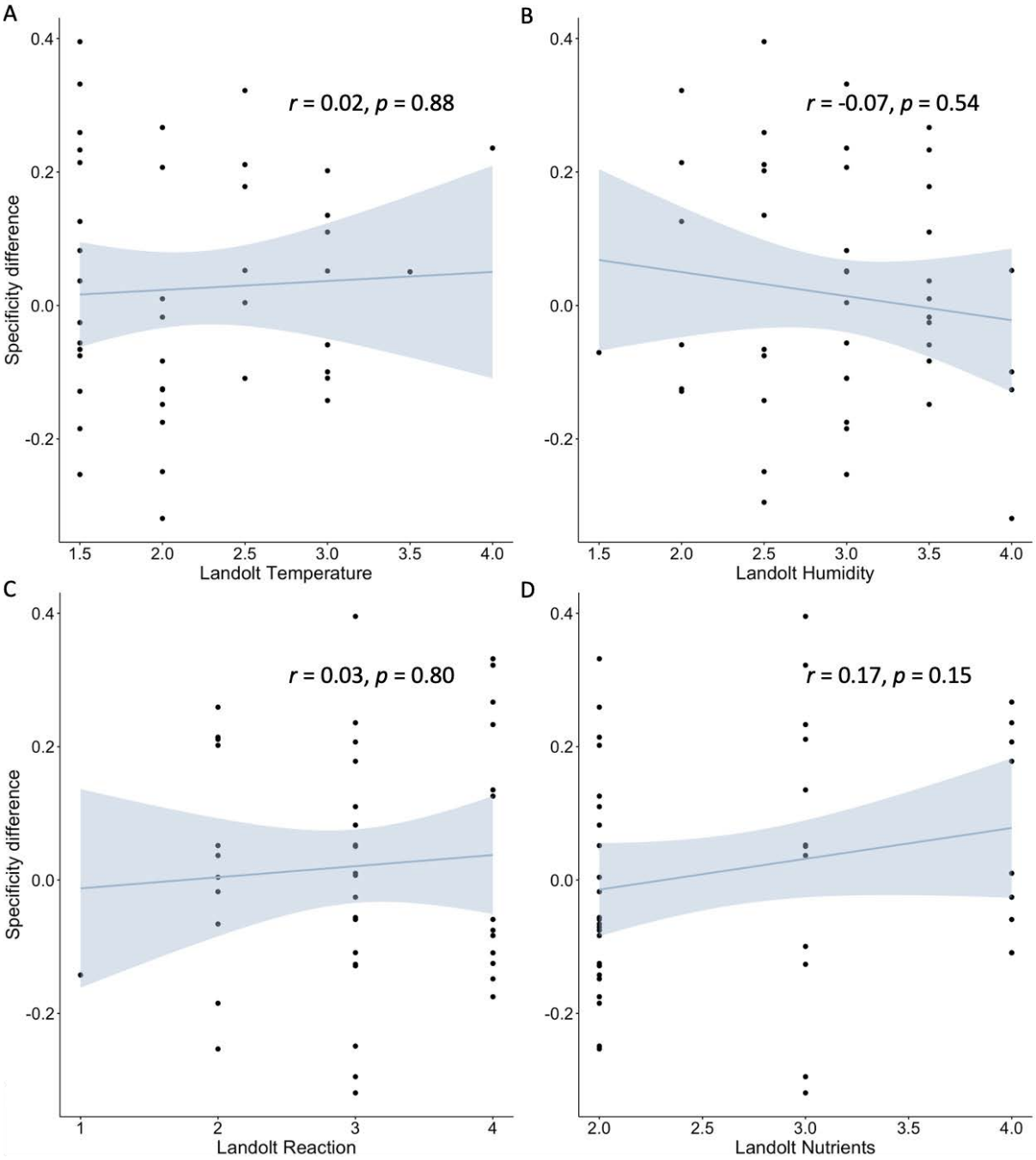

Figure S3. Kendall's correlation for specificity difference between present ensemble predictions evaluated with present independent dataset and past ensemble predictions evaluated with present independent dataset and a selection of ecological indicator values (EIVs) for each species. All EIVs range from 1 to 5 with gradient (A) from alpine/nival stage to collinean stage for Temperature (B) from dry soils to submerged soil for Humidity (C) from acidic soils to alkaline soils for Reaction and (D) from nutrient-poor soils to nutrient-rich soils for Nutrients. The line represents the regression line and the grey area represent the confidence interval. The correlation *tau* and *p-value* are indicated on each panel.

Table S1. Overview of the species datasets. Table summarizing for each species the number of occurrences used to calibrate the SDMs, the number of occurrences observed during past (2002-2003) and present (2021-2022) inventories, and the percentage and number of plots observed that were stable (0 → 0 and 1 → 1) or unstable (0 → 1 and 1 → 0) between past and present predictions (1: presence and 0: absence).

Species	Occurrences number model calibration	Occurrences number past observations	Occurrences number present observations	Plots percentage 0 → 0 (Number of plots)	Plots percentage 1 → 1 (Number of plots)	Plots percentage 0 → 1 (Number of plots)	Plots percentage 1 → 0 (Number of plots)
Agrostis capillaris	2269	17	21	68.12 (47)	23.19 (16)	7.25 (5)	1.45 (1)
Alchemilla conjuncta aggr.	308	13	14	75.36 (52)	14.49 (10)	5.8 (4)	4.35 (3)
Alchemilla vulgaris aggr.	1592	29	28	53.62 (7)	36.23 (25)	4.35 (3)	5.8 (4)
Anthoxanthum odoratum aggr.	3594	31	30	50.72 (35)	39.13 (27)	4.35 (3)	5.8 (4)
Anthyllis vulneraria	2275	12	14	76.81 (53)	14.49 (10)	5.8 (4)	2.9 (2)
Aster bellidiastrum	929	11	12	81.16 (56)	14.49 (10)	2.9 (2)	1.45 (1)
Bartsia alpina	615	11	12	78.26 (54)	11.59 (8)	5.8 (4)	4.35 (3)
Briza media	2968	12	14	78.26 (54)	15.94 (11)	4.35 (3)	1.45 (1)
Campanula scheuchzeri	975	35	37	36.23 (25)	40.58 (28)	13.04 (9)	10.14 (7)
Carduus defloratus subsp. defloratus	332	11	13	76.81 (53)	11.59 (8)	7.25 (5)	4.35 (3)
Carex sempervirens	1038	29	34	47.83 (33)	39.13 (27)	10.14 (7)	2.9 (2)
Crepis aurea	517	11	11	79.71 (55)	11.59 (8)	4.35 (3)	4.35 (3)
Crocus albiflorus	591	12	3	79.71 (55)	1.45 (1)	2.9 (2)	15.94 (11)
Dactylis glomerata	3864	13	10	78.26 (54)	11.59 (8)	2.9 (2)	7.25 (5)
Deschampsia cespitosa	1661	10	15	73.91 (51)	10.14 (7)	11.59 (8)	4.35 (3)
Euphrasia minima	517	14	17	73.91 (51)	18.84 (13)	5.8 (4)	1.45 (1)
Festuca rubra aggr.	3577	32	33	46.38 (32)	40.58 (28)	7.25 (5)	5.8 (4)
Galium anisophyllon	568	30	31	47.83 (33)	36.23 (25)	8.7 (6)	7.25 (5)
Geranium sylvaticum	1681	17	16	72.46 (50)	20.29 (14)	2.9 (2)	4.35 (3)
Geum montanum	407	14	12	76.81 (53)	14.49 (10)	2.9 (2)	5.8 (4)
Helictotrichon versicolor	309	14	11	79.71 (55)	15.94 (11)	0 (0)	4.35 (3)
Homogyne alpina	1101	28	26	55.07 (38)	33.33 (23)	4.35 (3)	7.25 (5)
Leontodon hispidus subsp. hispidus	634	32	32	44.93 (31)	37.68 (26)	8.7 (6)	8.7 (6)
Leucanthemum vulgare aggr.	3477	18	22	68.12 (47)	26.09 (18)	5.8 (4)	0 (0)
Ligusticum mutellina	185	21	22	66.67 (46)	28.99 (20)	2.9 (2)	1.45 (1)
Lotus corniculatus aggr.	4361	27	29	53.62 (37)	34.78 (24)	7.25 (5)	4.35 (3)
Luzula multiflora aggr.	1145	16	18	71.01 (49)	20.29 (14)	5.8 (4)	2.9 (2)
Nardus stricta	1304	16	19	72.46 (50)	23.19 (16)	4.35 (3)	0 (0)
Phleum alpinum aggr.	522	17	23	62.32 (43)	20.29 (14)	13.04 (9)	4.35 (3)
Plantago alpina	591	17	20	69.57 (48)	23.19 (16)	5.8 (4)	1.45 (1)

Plantago atrata subsp. atrata	393	14	20	68.12 (47)	17.39 (12)	11.59 (8)	2.9 (2)
Poa alpina	1172	30	30	49.28 (34)	36.23 (25)	7.25 (5)	7.25 (5)
Polygonum viviparum	951	23	28	59.42 (41)	33.33 (23)	7.25 (5)	0 (0)
Potentilla aurea	638	20	21	65.22 (45)	24.64 (17)	5.8 (4)	4.35 (3)
Potentilla crantzii	485	13	10	78.26 (54)	11.59 (8)	2.9 (2)	7.25 (5)
Potentilla erecta	2310	11	11	81.16 (56)	13.04 (9)	2.9 (2)	2.9 (2)
Ranunculus montanus	62	24	19	63.77 (44)	26.09 (18)	1.45 (1)	8.7 (6)
Ranunculus tuberosus	930	10	8	81.16 (56)	7.25 (5)	4.35 (3)	7.25 (5)
Salix retusa	266	11	10	79.71 (55)	10.14 (7)	4.35 (3)	5.8 (4)
Scabiosa lucida	785	14	20	66.67 (46)	15.94 (11)	13.04 (9)	4.35 (3)
Selaginella selaginoides	755	15	13	73.91 (51)	14.49 (10)	4.35 (3)	7.25 (5)
Sesleria caerulea	1048	16	21	63.77 (44)	17.39 (12)	13.04 (9)	5.8 (4)
Soldanella alpina	520	20	17	63.77 (44)	17.39 (12)	7.25 (5)	11.59 (8)
Trifolium pratense	4062	22	21	65.22 (45)	27.54 (19)	2.9 (2)	4.35 (3)
Trifolium repens subsp. repens	1400	15	18	72.46 (50)	20.29 (14)	5.8 (4)	1.45 (1)
Trollius europaeus	1441	13	11	79.71 (55)	14.49 (10)	1.45 (1)	4.35 (3)

Table S2. Evaluation of models and ensemble models. Single models (GLM, GAM and RF) were evaluated separately with five-fold spatial block cross-validation, repeated split-sampling as well as with past and present independent datasets. Ensemble models (average of all single model predictions) for past and present periods were evaluated with past and present independent datasets respectively. Ensemble model for past period was also evaluated with present independent dataset. The number of species' occurrences in plots inventoried in 2002-2003 (past) and in 2021-2022 (present) are also indicated.

	Single models (average)				Ensemble models			Nb occurrences	
Species	**Five-fold spatial block CV**	**Repeated split-sampling**	**Single past + Independent past**	**Single present + Independent present**	**Ensemble past + Independent past**	**Ensemble present + Independent present**	**Ensemble past + Independent present**	**Independent past**	**Independent present**
Agrostis capillaris	0.4890	0.5550	0.5544	0.4067	0.5554	0.4464	0.4911	17	21
Alchemilla conjuncta aggr.	0.6446	0.6883	0.2905	0.1678	0.2981	0.2000	0.2182	13	14
Alchemilla vulgaris aggr.	0.5273	0.5796	0.3803	0.3081	0.3560	0.3301	0.3258	29	28
Anthoxanthum odoratum aggr.	0.3821	0.4483	0.5151	0.5397	0.4992	0.5385	0.5308	31	30
Anthyllis vulneraria	0.4191	0.4961	0.2702	0.2691	0.2281	0.2766	0.3649	12	14
Aster bellidiastrum	0.5743	0.6335	0.4855	0.3722	0.5517	0.4035	0.5263	11	12
Bartsia alpina	0.7206	0.7045	0.2422	0.3743	0.2649	0.4079	0.2281	11	12
Briza media	0.4927	0.5426	0.6953	0.6024	0.7105	0.6753	0.7299	12	14
Campanula scheuchzeri	0.5335	0.6829	0.2322	0.3995	0.2378	0.4755	0.3919	35	37
Carduus defloratus subsp. defloratus	0.5447	0.6039	0.4204	0.3605	0.4263	0.3777	0.4409	11	13
Carex sempervirens	0.6305	0.6452	0.2383	0.2838	0.1897	0.2832	0.2555	29	34
Crepis aurea	0.7019	0.7351	0.6641	0.6777	0.7069	0.7320	0.6552	11	11
Crocus albiflorus	0.6157	0.6457	0.5734	0.5808	0.5789	0.4697	0.6970	12	3
Dactylis glomerata	0.4311	0.4516	0.6171	0.5371	0.6195	0.5322	0.5983	13	10
Deschampsia cespitosa	0.4102	0.4953	0.3680	0.2886	0.4254	0.3593	0.3481	10	15
Euphrasia minima	0.6170	0.7252	0.3939	0.6400	0.4195	0.6912	0.4208	14	17
Festuca rubra aggr.	0.4069	0.4635	0.4560	0.4103	0.4383	0.4116	0.4722	32	33
Galium anisophyllon	0.5261	0.5903	0.3072	0.2622	0.3718	0.2895	0.2572	30	31
Geranium sylvaticum	0.5603	0.5720	0.4421	0.4436	0.4400	0.4858	0.4540	17	16
Geum montanum	0.7049	0.7631	0.4349	0.5263	0.4065	0.4956	0.4781	14	12
Helictotrichon versicolor	0.7928	0.8288	0.5110	0.5168	0.5273	0.5596	0.6332	14	11
Homogyne alpina	0.6469	0.6758	0.5328	0.5512	0.5566	0.5912	0.5447	28	26
Leontodon hispidus subsp. hispidus	0.3347	0.4564	0.4008	0.3606	0.4426	0.3902	0.3927	32	32
Leucanthemum vulgare aggr.	0.4202	0.4577	0.6028	0.4131	0.6176	0.3985	0.4836	18	22
Ligusticum mutellina	0.6820	0.7331	0.4387	0.6291	0.4435	0.6750	0.4207	21	22

Lotus corniculatus aggr.	0.3369	0.4326	0.3924	0.3887	0.3836	0.4086	0.4250	27	29
Luzula multiflora aggr.	0.5660	0.6311	0.6068	0.5129	0.6179	0.5033	0.5654	16	18
Nardus stricta	0.6679	0.7230	0.5172	0.6601	0.4858	0.6874	0.6695	16	19
Phleum alpinum aggr.	0.6605	0.6976	0.2875	0.4188	0.2240	0.4565	0.3478	17	23
Plantago alpina	0.7534	0.7698	0.4296	0.5459	0.4536	0.5622	0.4439	17	20
Plantago atrata subsp. atrata	0.7055	0.7412	0.1929	0.2452	0.2364	0.2694	0.2082	14	20
Poa alpina	0.5595	0.6616	0.1675	0.3221	0.1821	0.4231	0.2410	30	30
Polygonum viviparum	0.6135	0.6496	0.2377	0.4443	0.3043	0.5044	0.3162	23	28
Potentilla aurea	0.6802	0.7117	0.4257	0.6478	0.4867	0.7232	0.5387	20	21
Potentilla crantzii	0.6751	0.7076	0.3060	0.3399	0.3283	0.4068	0.3780	13	10
Potentilla erecta	0.5309	0.5561	0.6310	0.5486	0.6207	0.4906	0.6724	11	11
Ranunculus montanus	0.6615	0.7006	0.3319	0.3431	0.3250	0.3789	0.2716	24	19
Ranunculus tuberosus	0.6335	0.6342	0.3111	0.3828	0.3441	0.3791	0.6086	10	8
Salix retusa	0.6672	0.7183	0.3503	0.5026	0.3401	0.5627	0.3763	11	10
Scabiosa lucida	0.6088	0.6449	0.3487	0.2461	0.3844	0.2531	0.4418	14	20
Selaginella selaginoides	0.7293	0.7537	0.4659	0.5025	0.5000	0.5192	0.5673	15	13
Sesleria caerulea	0.5102	0.5554	0.2738	0.2240	0.2500	0.2560	0.2054	16	21
Soldanella alpina	0.6438	0.6988	0.6076	0.5365	0.6571	0.5543	0.4989	20	17
Trifolium pratense	0.3537	0.4496	0.4523	0.3867	0.4836	0.3869	0.4405	22	21
Trifolium repens subsp. repens	0.3920	0.4612	0.5600	0.5410	0.5481	0.5948	0.5458	15	18
Trollius europaeus	0.6513	0.6860	0.2659	0.3253	0.2514	0.3527	0.3574	13	11

Table S3. Variable importance for each species. Contribution of predictors in the modelling for each species assessed by permutation importance and by meaning results obtained with three algorithms (GLM, GAM and RF) and five replicates. Sraddy: direct and diffuse potential solar radiation, TWI: topographic wetness index, Prec: annual sum of precipitation, Tave: annual temperature average, NDVI: mean normalized difference vegetation index, TPI: topographic position index, TRI: topographic roughness index, Geology: soil pH.

Species	sradyy	TWI	Prec	Tave	NDVI	TPI	TRI	Geology
Agrostis capillaris	0.0789	0.0195	0.0775	0.5692	0.0603	0.0129	0.1638	0.0179
Alchemilla conjuncta aggr.	0.0158	0.0076	0.3246	0.5086	0.0144	0.0126	0.0188	0.0975
Alchemilla vulgaris aggr.	0.0687	0.0161	0.0463	0.6294	0.0483	0.0118	0.1568	0.0226
Anthoxanthum odoratum aggr.	0.1381	0.0218	0.0900	0.4374	0.0615	0.0175	0.2101	0.0236
Anthyllis vulneraria	0.2087	0.0671	0.1811	0.2525	0.0561	0.0117	0.0834	0.1395
Aster bellidiastrum	0.0118	0.0293	0.0496	0.6718	0.0485	0.0311	0.1282	0.0298
Bartsia alpina	0.0102	0.0059	0.0359	0.8166	0.0473	0.0054	0.0668	0.0120
Briza media	0.2032	0.0219	0.0852	0.5045	0.0387	0.0116	0.1008	0.0341
Campanula scheuchzeri	0.0147	0.0081	0.0706	0.7959	0.0360	0.0088	0.0542	0.0116
Carduus defloratus subsp. defloratus	0.0479	0.0928	0.1305	0.4772	0.0180	0.0466	0.0225	0.1646
Carex sempervirens	0.0358	0.0195	0.0438	0.7792	0.0318	0.0079	0.0373	0.0447
Crepis aurea	0.0065	0.0054	0.0422	0.7118	0.0788	0.0067	0.1340	0.0146
Crocus albiflorus	0.0201	0.0136	0.0230	0.6525	0.0847	0.0106	0.1799	0.0157
Dactylis glomerata	0.2016	0.0227	0.1046	0.4807	0.0345	0.0149	0.0888	0.0521
Deschampsia cespitosa	0.0139	0.0336	0.1418	0.2743	0.1623	0.0374	0.3153	0.0214
Euphrasia minima	0.0057	0.0065	0.0824	0.7994	0.0277	0.0088	0.0602	0.0094
Festuca rubra aggr.	0.1348	0.0214	0.1048	0.4181	0.0503	0.0144	0.2193	0.0369
Galium anisophyllon	0.0138	0.0126	0.0434	0.7922	0.0289	0.0059	0.0427	0.0605
Geranium sylvaticum	0.0366	0.0119	0.0616	0.6736	0.0953	0.0116	0.0823	0.0272
Geum montanum	0.0179	0.0043	0.0937	0.7740	0.0361	0.0039	0.0646	0.0054
Helictotrichon versicolor	0.0061	0.0049	0.1113	0.7761	0.0423	0.0097	0.0399	0.0097
Homogyne alpina	0.0138	0.0251	0.0477	0.7038	0.0445	0.0049	0.1531	0.0072
Leontodon hispidus subsp. hispidus	0.0573	0.0538	0.0652	0.3135	0.0859	0.0375	0.3565	0.0303
Leucanthemum vulgare aggr.	0.1615	0.0433	0.0888	0.4498	0.0478	0.0160	0.1354	0.0574
Ligusticum mutellina	0.0090	0.0041	0.1433	0.7679	0.0510	0.0028	0.0185	0.0033
Lotus corniculatus aggr.	0.2097	0.0346	0.1979	0.3015	0.0497	0.0139	0.1302	0.0625
Luzula multiflora aggr.	0.0429	0.0216	0.0555	0.4750	0.1082	0.0131	0.2724	0.0113
Nardus stricta	0.0273	0.0085	0.0474	0.6794	0.0515	0.0057	0.1743	0.0058
Phleum alpinum aggr.	0.0076	0.0059	0.0251	0.7731	0.0734	0.0067	0.1063	0.0018
Plantago alpina	0.0060	0.0058	0.0267	0.7467	0.0521	0.0096	0.1422	0.0111
Plantago atrata subsp. atrata	0.0322	0.0062	0.0722	0.6966	0.0469	0.0082	0.0845	0.0531
Poa alpina	0.0095	0.0129	0.0722	0.7068	0.0160	0.0080	0.1399	0.0346
Polygonum viviparum	0.0085	0.0177	0.0614	0.7646	0.0317	0.0053	0.0923	0.0186
Potentilla aurea	0.0057	0.0199	0.0400	0.7127	0.0691	0.0132	0.1350	0.0043
Potentilla crantzii	0.0662	0.0118	0.0851	0.6142	0.0176	0.0087	0.0720	0.1244
Potentilla erecta	0.0667	0.0294	0.0969	0.4433	0.1614	0.0122	0.1715	0.0187
Ranunculus montanus	0.0458	0.0297	0.1765	0.5697	0.0576	0.0157	0.0775	0.0275
Ranunculus tuberosus	0.0361	0.0184	0.1589	0.5622	0.0479	0.0054	0.1030	0.0682
Salix retusa	0.0318	0.0216	0.0413	0.7647	0.0204	0.0058	0.0757	0.0386
Scabiosa lucida	0.0371	0.0084	0.0556	0.7761	0.0373	0.0073	0.0292	0.0492
Selaginella selaginoides	0.0210	0.0097	0.0675	0.7109	0.0387	0.0076	0.1239	0.0208
Sesleria caerulea	0.0526	0.0361	0.1356	0.4173	0.0561	0.0154	0.0709	0.2160
Soldanella alpina	0.0141	0.0100	0.0248	0.8002	0.0540	0.0026	0.0798	0.0146
Trifolium pratense	0.1617	0.0217	0.1097	0.4157	0.0482	0.0158	0.1904	0.0368
Trifolium repens subsp. repens	0.0372	0.0264	0.1235	0.4643	0.0634	0.0144	0.2529	0.0178
Trollius europaeus	0.0163	0.0170	0.0486	0.6935	0.0860	0.0081	0.1228	0.0077

Table S4. Change of observed abundance (converted into Braun-Blanquet range median) between past and present inventories for each species. Only plots with at least one observation in the past or in the present were considered. Mean abundance change ± standard deviation. Minimum and maximum change. Number of plots with an increase, decrease or no change of abundance.

Species	Mean ± sd	Minimum change	Maximum change	Plots number with increase of abundance	Plots number with decrease of abundance	Plots number with no change of abundance
Agrostis capillaris	0.8864 ± 8.7095	-27.5	17.5	9	5	8
Alchemilla conjuncta aggr.	2.3559 ± 8.6588	-7.5	27.5	7	6	4
Alchemilla vulgaris aggr.	2.3141 ± 6.124	-7.5	20	14	8	10
Anthoxanthum odoratum aggr.	0.2191 ± 4.0587	-7.5	10	13	12	9
Anthyllis vulneraria	1.2844 ± 3.187	-3	10	8	2	6
Aster bellidiastrum	0.7385 ± 2.7991	-0.5	10	4	3	6
Bartsia alpina	0.0033 ± 1.3618	-2.5	4	6	6	3
Briza media	-0.1 ± 1.8822	-3	4	5	4	6
Campanula scheuchzeri	-0.1114 ± 0.6236	-2.5	4	10	13	21
Carduus defloratus subsp. defloratus	1.5969 ± 3.6112	-3	10	8	4	4
Carex sempervirens	2.8347 ± 10.3236	-17.5	38	15	8	13
Crepis aurea	0.4714 ± 6.3648	-17.5	10.5	5	4	5
Crocus albiflorus	-0.4357 ± 0.8015	-3	4	2	11	1
Dactylis glomerata	-1.63 ± 7.5375	-27.5	7.5	4	7	4
Deschampsia cespitosa	-1.275 ± 7.1053	-17.5	10.5	9	6	3
Euphrasia minima	0.2222 ± 0.6215	-0.5	4	6	1	11
Festuca rubra aggr.	-4.4459 ± 10.9461	-37.5	20.5	9	20	8
Galium anisophyllon	0.4306 ± 1.2333	-2.5	4	12	6	18
Geranium sylvaticum	1.1579 ± 2.5984	-2.5	7.5	7	4	8
Geum montanum	-0.1625 ± 1.6132	-3	4	3	6	7
Helictotrichon versicolor	0.9643 ± 4.0452	-7.5	10	4	4	6
Homogyne alpina	1.5806 ± 3.9892	-2.5	17.5	13	7	11
Leontodon hispidus subsp. hispidus	3.7079 ± 9.2272	-10	35	21	9	8
Leucanthemum vulgare aggr.	1.2068 ± 3.336	-2.5	10	11	4	7
Ligusticum mutellina	-1.7565 ± 4.1118	-10	4	4	8	11
Lotus corniculatus aggr.	2.3891 ± 5.4612	-2.5	27.5	16	5	11
Luzula multiflora aggr.	0.3 ± 0.7969	-0.5	4	8	3	9
Nardus stricta	-1.4763 ± 20.7656	-52.5	25	12	5	2
Phleum alpinum aggr.	-0.2865 ± 6.5453	-17.5	20	14	8	4
Plantago alpina	0.7429 ± 6.0381	-10	17.5	9	4	8
Plantago atrata subsp. atrata	0.7773 ± 2.0836	-2.5	7.5	13	5	4
Poa alpina	0.8314 ± 2.691	-2.5	10.5	9	9	17
Polygonum viviparum	0.0893 ± 1.0352	-2.5	4	7	3	18
Potentilla aurea	1.0437 ± 2.8038	-3	10	10	5	9
Potentilla crantzii	0.0367 ± 0.7624	-0.5	4	4	6	5
Potentilla erecta	1.3462 ± 3.0096	-2.5	10	7	3	3
Ranunculus montanus	0.8 ± 2.6379	-2.5	10	6	7	12
Ranunculus tuberosus	-0.1808 ± 1.0891	-2.5	4	4	8	1
Salix retusa	-7.1143 ± 18.0014	-63	7.5	5	7	2
Scabiosa lucida	1.85 ± 4.8449	-2.5	20	14	7	2
Selaginella selaginoides	0.0833 ± 0.7685	-0.5	4	3	7	8
Sesleria caerulea	-0.618 ± 5.0917	-17.5	7.5	12	8	5
Soldanella alpina	0.44 ± 1.1486	-0.5	4	9	8	8
Trifolium pratense	1.125 ± 5.8692	-10	17.5	11	8	5
Trifolium repens subsp. repens	2.4237 ± 4.8007	-7.5	10.5	12	5	2
Trollius europaeus	0.2214 ± 2.3234	-3	4	7	7	0

Table S5. Kendall's correlation between observed change of abundance and predicted change of presence probability for each species. *p-value* is the significance level of the test statistic (threshold: *p-value* < 0.05), *z* is the value of the test statistic and *tau* is the correlation coefficient (*tau* ranges from -1 to +1).

Species	*p-value*	*z*	*tau*
Agrostis capillaris	0.5503	-0.5974	-0.1009
Alchemilla conjuncta aggr.	0.8330	0.2108	0.0396
Alchemilla vulgaris aggr.	0.4108	0.8225	0.1117
Anthoxanthum odoratum aggr.	0.5757	-0.5597	-0.0741
Anthyllis vulneraria	0.3261	0.9820	0.2035
Aster bellidiastrum	0.9482	-0.0650	-0.0147
Bartsia alpina	0.0877	-1.7076	-0.3656
Briza media	0.4194	-0.8074	-0.1730
Campanula scheuchzeri	0.3058	-1.0241	-0.1207
Carduus defloratus subsp. defloratus	0.7476	-0.3219	-0.0624
Carex sempervirens	0.6398	-0.4679	-0.0594
Crepis aurea	0.2963	1.0445	0.2421
Crocus albiflorus	0.6788	-0.4142	-0.0896
Dactylis glomerata	0.6076	0.5134	0.1052
Deschampsia cespitosa	0.5047	0.6671	0.1232
Euphrasia minima	0.3368	-0.9605	-0.1854
Festuca rubra aggr.	0.6459	0.4594	0.0569
Galium anisophyllon	0.7693	0.2932	0.0385
Geranium sylvaticum	1.0000	0.0000	0.0000
Geum montanum	0.8117	-0.2383	-0.0473
Helictotrichon versicolor	0.7282	-0.3476	-0.0752
Homogyne alpina	0.1655	1.3868	0.1936
Leontodon hispidus subsp. hispidus	0.3995	-0.8426	-0.1034
Leucanthemum vulgare aggr.	0.1395	1.4777	0.2525
Ligusticum mutellina	0.3763	-0.8848	-0.1495
Lotus corniculatus aggr.	1.0000	0.0000	0.0000
Luzula multiflora aggr.	0.8620	-0.1738	-0.0310
Nardus stricta	0.0670	1.8318	0.3237
Phleum alpinum aggr.	0.6682	-0.4287	-0.0647
Plantago alpina	0.2733	1.0954	0.1935
Plantago atrata subsp. atrata	0.0655	-1.8417	-0.3113
Poa alpina	0.2020	-1.2758	-0.1649
Polygonum viviparum	0.1853	-1.3246	-0.1999
Potentilla aurea	0.4284	-0.7919	-0.1267
Potentilla crantzii	0.8356	-0.2076	-0.0431
Potentilla erecta	0.8500	-0.1891	-0.0421
Ranunculus montanus	0.8801	0.1508	0.0238
Ranunculus tuberosus	0.2803	-1.0797	-0.2536
Salix retusa	0.8229	0.2238	0.0469
Scabiosa lucida	0.3998	-0.8419	-0.1348
Selaginella selaginoides	0.2585	-1.1300	-0.2120
Sesleria caerulea	0.1894	1.3124	0.2020
Soldanella alpina	0.1497	1.4405	0.2273
Trifolium pratense	0.8918	0.1360	0.0218
Trifolium repens subsp. repens	0.1396	1.4772	0.2622
Trollius europaeus	0.3064	1.0229	0.2301

Table S6. Changes in species presences or absences predicted by the SDMs. Percentage and number of plots predicted to be stable (0 → 0 and 1 → 1) or unstable (0 → 1 and 1 → 0) between past and present predictions (1: presence and 0: absence).

Species	Plots percentage 0 → 0 (Number of plots)	Plots percentage 1 → 1 (Number of plots)	Plots percentage 0 → 1 (Number of plots)	Plots percentage 1 → 0 (Number of plots)
Agrostis capillaris	53.62 (37)	26.09 (18)	0 (0)	20.29 (14)
Alchemilla conjuncta aggr.	15.94 (11)	68.12 (47)	15.94 (11)	0 (0)
Alchemilla vulgaris aggr.	23.19 (16)	72.46 (50)	4.35 (3)	0 (0)
Anthoxanthum odoratum aggr.	53.62 (37)	33.33 (23)	2.9 (2)	10.14 (7)
Anthyllis vulneraria	39.13 (27)	43.48 (30)	13.04 (9)	4.35 (3)
Aster bellidiastrum	31.88 (22)	52.17 (36)	14.49 (10)	1.45 (1)
Bartsia alpina	42.03 (29)	23.19 (16)	34.78 (24)	0 (0)
Briza media	63.77 (44)	20.29 (14)	11.59 (8)	4.35 (3)
Campanula scheuchzeri	18.84 (13)	52.17 (36)	1.45 (1)	27.54 (19)
Carduus defloratus subsp. defloratus	44.93 (31)	23.19 (16)	0 (0)	31.88 (22)
Carex sempervirens	21.74 (15)	56.52 (39)	20.29 (14)	1.45 (1)
Crepis aurea	59.42 (41)	20.29 (14)	0 (0)	20.29 (14)
Crocus albiflorus	40.58 (28)	47.83 (33)	7.25 (5)	4.35 (3)
Dactylis glomerata	57.97 (40)	14.49 (10)	0 (0)	27.54 (19)
Deschampsia cespitosa	33.33 (23)	52.17 (36)	13.04 (9)	1.45 (1)
Euphrasia minima	39.13 (27)	40.58 (28)	1.45 (1)	18.84 (13)
Festuca rubra aggr.	39.13 (27)	39.13 (27)	0 (0)	21.74 (15)
Galium anisophyllon	15.94 (11)	62.32 (43)	21.74 (15)	0 (0)
Geranium sylvaticum	44.93 (31)	37.68 (26)	0 (0)	17.39 (12)
Geum montanum	43.48 (30)	26.09 (18)	24.64 (17)	5.8 (4)
Helictotrichon versicolor	42.03 (29)	34.78 (24)	0 (0)	23.19 (16)
Homogyne alpina	59.42 (41)	30.43 (21)	5.8 (4)	4.35 (3)
Leontodon hispidus subsp. hispidus	36.23 (25)	47.83 (33)	0 (0)	15.94 (11)
Leucanthemum vulgare aggr.	36.23 (25)	37.68 (26)	26.09 (18)	0 (0)
Ligusticum mutellina	46.38 (32)	31.88 (22)	13.04 (9)	8.7 (6)
Lotus corniculatus aggr.	40.58 (28)	43.48 (30)	8.7 (6)	7.25 (5)
Luzula multiflora aggr.	59.42 (41)	27.54 (19)	13.04 (9)	0 (0)
Nardus stricta	52.17 (36)	34.78 (24)	10.14 (7)	2.9 (2)
Phleum alpinum aggr.	37.68 (26)	42.03 (29)	14.49 (10)	5.8 (4)
Plantago alpina	44.93 (31)	24.64 (17)	30.43 (21)	0 (0)
Plantago atrata subsp. atrata	18.84 (13)	60.87 (42)	0 (0)	20.29 (14)
Poa alpina	34.78 (24)	40.58 (28)	18.84 (13)	5.8 (4)
Polygonum viviparum	44.93 (31)	33.33 (23)	18.84 (13)	2.9 (2)
Potentilla aurea	50.72 (35)	26.09 (18)	18.84 (13)	4.35 (3)
Potentilla crantzii	30.43 (21)	53.62 (37)	11.59 (8)	4.35 (3)
Potentilla erecta	47.83 (33)	36.23 (25)	4.35 (3)	11.59 (8)
Ranunculus montanus	39.13 (27)	27.54 (19)	2.9 (2)	30.43 (21)
Ranunculus tuberosus	59.42 (41)	28.99 (20)	0 (0)	11.59 (8)
Salix retusa	36.23 (25)	30.43 (21)	1.45 (1)	31.88 (22)
Scabiosa lucida	43.48 (30)	40.58 (28)	1.45 (1)	14.49 (10)
Selaginella selaginoides	60.87 (42)	23.19 (16)	11.59 (8)	4.35 (3)
Sesleria caerulea	79.71 (55)	5.8 (4)	14.49 (10)	0 (0)
Soldanella alpina	56.52 (39)	30.43 (21)	10.14 (7)	2.9 (2)
Trifolium pratense	37.68 (26)	44.93 (31)	4.35 (3)	13.04 (9)
Trifolium repens subsp. repens	53.62 (37)	28.99 (20)	15.94 (11)	1.45 (1)
Trollius europaeus	37.68 (26)	46.38 (32)	5.8 (4)	10.14 (7)

Table S7. Changes in species presences or absences observed in plant inventories and confirmed by model predictions. Percentage and number (in brackets) of unstable (0 → 1 and 1 → 0) and stable (0 → 0 and 1 → 1) plots that are correctly predicted by the SDMs.

Species	Percentage and number of unstable plots correctly predicted	Percentage and number of stable plots correctly predicted
Agrostis capillaris	0 (0)	69.84 (44)
Alchemilla conjuncta aggr.	42.86 (3)	32.26 (20)
Alchemilla vulgaris aggr.	14.29 (1)	61.29 (38)
Anthoxanthum odoratum aggr.	0 (0)	77.42 (48)
Anthyllis vulneraria	33.33 (2)	47.62 (30)
Aster bellidiastrum	0 (0)	48.48 (32)
Bartsia alpina	42.86 (3)	50 (31)
Briza media	0 (0)	80 (52)
Campanula scheuchzeri	6.25 (1)	60.38 (32)
Carduus defloratus subsp. defloratus	25 (2)	54.1 (33)
Carex sempervirens	22.22 (2)	50 (30)
Crepis aurea	16.67 (1)	76.19 (48)
Crocus albiflorus	0 (0)	51.79 (29)
Dactylis glomerata	42.86 (3)	69.35 (43)
Deschampsia cespitosa	27.27 (3)	48.28 (28)
Euphrasia minima	20 (1)	60.94 (39)
Festuca rubra aggr.	11.11 (1)	63.33 (38)
Galium anisophyllon	27.27 (3)	53.45 (31)
Geranium sylvaticum	20 (1)	60.94 (39)
Geum montanum	16.67 (1)	55.56 (35)
Helictotrichon versicolor	66.67 (2)	57.58 (38)
Homogyne alpina	12.5 (1)	78.69 (48)
Leontodon hispidus subsp. hispidus	0 (0)	64.91 (37)
Leucanthemum vulgare aggr.	50 (2)	58.46 (38)
Ligusticum mutellina	33.33 (1)	66.67 (44)
Lotus corniculatus aggr.	0 (0)	62.3 (38)
Luzula multiflora aggr.	0 (0)	74.6 (47)
Nardus stricta	0 (0)	71.21 (47)
Phleum alpinum aggr.	16.67 (2)	54.39 (31)
Plantago alpina	80 (4)	60.94 (39)
Plantago atrata subsp. atrata	20 (2)	38.98 (23)
Poa alpina	10 (1)	55.93 (33)
Polygonum viviparum	20 (1)	60.94 (39)
Potentilla aurea	28.57 (2)	70.97 (44)
Potentilla crantzii	0 (0)	43.55 (27)
Potentilla erecta	0 (0)	61.54 (40)
Ranunculus montanus	28.57 (2)	51.61 (32)
Ranunculus tuberosus	25 (2)	65.57 (40)
Salix retusa	14.29 (1)	46.77 (29)
Scabiosa lucida	8.33 (1)	59.65 (34)
Selaginella selaginoides	0 (0)	73.77 (45)
Sesleria caerulea	30.77 (4)	76.79 (43)
Soldanella alpina	15.38 (2)	78.57 (44)
Trifolium pratense	0 (0)	59.38 (38)
Trifolium repens subsp. repens	20 (1)	70.31 (45)
Trollius europaeus	0 (0)	47.69 (31)

Table S8. TSS, sensitivity and specificity change when considering or not climate change. TSS, sensitivity and specificity values for evaluation of the past climate predictions with the present independent dataset (ensemble past + independent present). TSS, sensitivity and specificity values for evaluation of the present climate predictions with the present independent dataset (ensemble present + independent present). Difference of TSS, sensitivity and specificity (Difference). TSS is ordered from maximum increase to maximum decrease.

	TSS			Sensitivity			Specificity		
Species	**Ensemble past + Independent present**	**Ensemble present + Independent present**	**Difference**	**Ensemble past + Independent present**	**Ensemble present + Independent present**	**Difference**	**Ensemble past + Independent present**	**Ensemble present + Independent present**	**Difference**
Euphrasia minima	0.5385	0.6912	**0.2704**	0.5385	0.9412	**0.0588**	0.5385	0.75	**0.2115**
Ligusticum mutellina	0.4207	0.675	**0.2543**	0.5909	0.9091	**0.3182**	0.8298	0.766	**-0.0638**
Polygonum viviparum	0.3162	0.5044	**0.1882**	0.5357	0.8214	**0.2857**	0.7805	0.6829	**-0.0976**
Salix retusa	0.3763	0.5627	**0.1864**	0.8	0.8	**0**	0.5763	0.7627	**0.1864**
Potentilla aurea	0.5387	0.7232	**0.1845**	0.8095	0.9524	**0.1429**	0.7292	0.7708	**0.0416**
Poa alpina	0.241	0.4231	**0.1821**	0.6	0.8333	**0.2333**	0.641	0.5897	**-0.0513**
Bartsia alpina	0.2281	0.4079	**0.1798**	0.6667	0.9167	**0.25**	0.5614	0.4912	**-0.0702**
Plantago alpina	0.4439	0.5622	**0.1183**	0.75	0.95	**0.2**	0.6939	0.6122	**-0.0817**
Phleum alpinum aggr.	0.3478	0.4565	**0.1087**	0.8696	0.8696	**0**	0.4783	0.587	**0.1087**
Ranunculus montanus	0.2716	0.3789	**0.1073**	0.6316	0.5789	**-0.0527**	0.64	0.8	**0.16**
Campanula scheuchzeri	0.3919	0.4755	**0.0836**	0.8919	0.7568	**-0.1351**	0.5	0.7188	**0.2188**
Crepis aurea	0.6552	0.732	**0.0768**	1	0.8182	**-0.1818**	0.6552	0.9138	**0.2586**
Plantago atrata subsp. atrata	0.2082	0.2694	**0.0612**	0.8	0.8	**0**	0.4082	0.4694	**0.0612**
Soldanella alpina	0.4989	0.5543	**0.0554**	0.9412	0.8235	**-0.1177**	0.5577	0.7308	**0.1731**
Sesleria caerulea	0.2054	0.256	**0.0506**	0.4762	0.381	**-0.0952**	0.7292	0.875	**0.1458**
Trifolium repens subsp. repens	0.5458	0.5948	**0.049**	0.7222	0.8889	**0.1667**	0.8235	0.7059	**-0.1176**
Homogyne alpina	0.5447	0.5912	**0.0465**	0.7308	0.7308	**0**	0.814	0.8605	**0.0465**
Galium anisophyllon	0.2572	0.2895	**0.0323**	0.9677	1	**0.0323**	0.2895	0.2895	**0**
Geranium sylvaticum	0.454	0.4858	**0.0318**	0.8125	0.75	**-0.0625**	0.6415	0.7358	**0.0943**
Potentilla crantzii	0.378	0.4068	**0.0288**	0.7	1	**0.3**	0.678	0.4068	**-0.2712**
Carex sempervirens	0.2555	0.2832	**0.0277**	0.9412	0.9118	**-0.0294**	0.3143	0.3714	**0.0571**
Nardus stricta	0.6695	0.6874	**0.0179**	0.7895	0.9474	**0.1579**	0.88	0.74	**-0.14**
Geum montanum	0.4781	0.4956	**0.0175**	0.5833	0.9167	**0.3334**	0.8947	0.5789	**-0.3158**
Deschampsia cespitosa	0.3481	0.3593	**0.0112**	0.8667	0.9333	**0.0666**	0.4815	0.4259	**-0.0556**
Anthoxanthum odoratum aggr.	0.5308	0.5385	**0.0077**	0.6333	0.6667	**0.0334**	0.8974	0.8718	**-0.0256**
Alchemilla vulgaris aggr.	0.3258	0.3301	**0.0043**	0.6429	0.9643	**0.3214**	0.6829	0.3659	**-0.317**
Leontodon hispidus subsp. hispidus	0.3927	0.3902	**-0.0025**	0.9062	0.6875	**-0.2187**	0.4865	0.7027	**0.2162**
Trollius europaeus	0.3574	0.3527	**-0.0047**	0.9091	0.8182	**-0.0909**	0.4483	0.5345	**0.0862**

Lotus corniculatus aggr.	0.425	0.4086	**-0.0164**	1	0.7586	**-0.2414**	0.425	0.65	**0.225**
Alchemilla conjuncta aggr.	0.2182	0.2	**-0.0182**	1	1	**0**	0.2182	0.2	**-0.0182**
Agrostis capillaris	0.4911	0.4464	**-0.0447**	0.7619	0.5714	**-0.1905**	0.7292	0.875	**0.1458**
Selaginella selaginoides	0.5673	0.5192	**-0.0481**	0.6923	0.7692	**0.0769**	0.875	0.75	**-0.125**
Trifolium pratense	0.4405	0.3869	**-0.0536**	0.8571	0.7619	**-0.0952**	0.5833	0.625	**0.0417**
Briza media	0.7299	0.6753	**-0.0546**	0.8571	0.8571	**0**	0.8727	0.8182	**-0.0545**
Festuca rubra aggr.	0.4722	0.4116	**-0.0606**	0.6667	0.6061	**-0.0606**	0.8056	0.8056	**0**
Luzula multiflora aggr.	0.5654	0.5033	**-0.0621**	0.7222	0.7778	**0.0556**	0.8431	0.7255	**-0.1176**
Carduus defloratus subsp. defloratus	0.4409	0.3777	**-0.0632**	0.9231	0.5385	**-0.3846**	0.5179	0.8393	**0.3214**
Dactylis glomerata	0.5983	0.5322	**-0.0661**	0.7	0.6	**-0.1**	0.8983	0.9322	**0.0339**
Helictotrichon versicolor	0.6332	0.5596	**-0.0736**	0.9091	0.8182	**-0.0909**	0.7241	0.7414	**0.0173**
Leucanthemum vulgare aggr.	0.4836	0.3985	**-0.0851**	0.9091	0.9091	**0**	0.5745	0.4894	**-0.0851**
Anthyllis vulneraria	0.3649	0.2766	**-0.0883**	0.9286	0.7857	**-0.1429**	0.4364	0.4909	**0.0545**
Aster bellidiastrum	0.5263	0.4035	**-0.1228**	1	1	**0**	0.5263	0.4035	**-0.1228**
Potentilla erecta	0.6724	0.4906	**-0.1818**	1	0.8182	**-0.1818**	0.6724	0.6724	**0**
Scabiosa lucida	0.4418	0.2531	**-0.1887**	0.85	0.6	**-0.25**	0.5918	0.6531	**0.0613**
Crocus albiflorus	0.697	0.4697	**-0.2273**	1	1	**0**	0.697	0.4697	**-0.2273**
Ranunculus tuberosus	0.6086	0.3791	**-0.2295**	0.625	0.625	**0**	0.9836	0.7541	**-0.2295**