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# WHICH ENVIRONMENTAL FACTORS CAN IMPROVE MODELS OF PLANT SPECIES DISTRIBUTION AT THE SUBALPINE LEVEL?

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# Which environmental factors can improve models of plant species distribution at the subalpine level?

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# Abstract

**Questions** Improving predictions of plant species distribution has been widely studied in alpine regions. However, it is difficult to draw clear conclusions because of the confounding of several factors, as a too wide altitudinal range. In this study, we quantified the importance of variables in a restricted altitudinal range, here at the subalpine level. We tested the importance of three high-resolution variables, namely (1) mean solar radiation at 5 m, (2) curvature at 5 m and (3) slope at 5 m; and six environmental variables, namely (1) slope, (2) exposure, (3) soil pH, (4) mean soil depth, (5) mean organo-mineral horizon depth and (6) carbon-to-nitrogen ratio.

**Location** Subalpine level in the Western Swiss Alps, Switzerland

**Methods** 38 vegetation inventories in four strata of samples with similar topographic and climatic conditions have been done at the subalpine level. Predictions of distribution of 208 plant species have been modelled with four different techniques. Multi-modelling inference analysis with generalized linear mixed models on the residuals of the species distribution models has been implemented, producing importance values for each variable.

**Results** The predictions of the species distribution models are similar between the strata, on the contrary of the observations in the field. The multi-modelling inference on residuals highlighted four variables that seem to be important to improve the predictions of species distribution models: mean solar radiation at 5 m, soil pH, carbon-to-nitrogen ratio and curvature at 5 m.

**Conclusions** Mean solar radiation, soil pH, carbon-to-nitrogen ratio and curvature are important predictor variable for explaining distribution of subalpine plants considered in our study. It would be needed to have more inventories to build models containing many of these variables together, to check if these variables would still be kept in the models when other variables, such as the ones that are typically used.

## Keywords

Species distribution models (SDMs); mountain flora; models on residuals; multi-modelling inference analysis (MMI); subalpine level; high-resolution variables; edaphic variables; Western Swiss Alps

## Abbreviations

AIC = Akaike information criterion; AUC = area under the curve; C:N ratio = carbon-to-nitrogen ratio; DEM = digital elevation model; GIS = geographic information system; GLMM = generalized linear mixed model; MMI = multi-modelling inference analysis; PCA = principle component analysis; SDM = species distribution model; TSS = true skill statistics

# Résumé

**Questions** La prédiction de distribution d'espèces de plantes a été largement étudiée dans les régions alpines, afin de l'améliorer. Cependant il est difficile de tirer des conclusions claires en raison des nombreux facteurs confondants, comme le gradient altitudinal. Dans cette étude, nous avons quantifié l'importance de variables au niveau subalpin. Nous avons testé l'importance de trois variables à haute-résolution, (1) les radiations solaires à 5 m, (2) la courbure à 5 m et (3) la pente à 5 m. Nous avons également testé l'importance de six variables environnementales : (1) la pente, (2) l'exposition, (3) le pH du sol, (4) la profondeur moyenne du sol, (5) la profondeur moyenne de l'horizon organo-minéral et (6) le ratio carbone sur azote.

**Localisation** Etage subalpin dans les Préalpes vaudoises, Suisse.

**Méthodes** Au niveau subalpin, 38 relevés de végétations dans quatre strates d'échantillons ayant des conditions topo-climatiques similaires ont été faits. Les prédictions de distribution de 208 espèces de plantes ont été modélisées avec quatre techniques différentes. Une analyse d'inférence de modèles multiples sur des GLMMs a été implémentée sur les résidus des modèles de distribution, produisant une importance pour chacune des variables.

**Résultats** Les prédictions des modèles sont similaires entre les strates, contrairement aux observations faites sur le terrain. Les modèles sur les résidus ont mis en avant quatre variables qui semblent être importantes pour l'amélioration de la prédiction de distribution d'espèces : les radiations solaires à 5 m, le pH du sol, le ratio carbone sur azote et la courbure à 5 m.

**Conclusions** Les radiations solaires, le pH du sol, le ratio carbone sur azote et la courbure sont d'importantes variables prédictives permettant d'expliquer la distribution des espèces en milieu subalpin. Il nécessiterait d'avoir plus de relevés pour construire des modèles contenant plusieurs de ces variables, ce qui permettrait de contrôler si ces variables seront maintenues dans les modèles comme celles qui sont habituellement utilisées.

# Introduction

Plants interact with each other but also with their environment forming a dynamic system. Plant growth is dependent from its environment and influenced by climatic, topographic or edaphic factors. All these factors form a N-dimensional hyper-volume within which a positive growth rate is maintained. This hyper-volume represents the environmental niche, which contains all the suitable habitats for the species. In reality, species only occur in a part of this niche, which is called the realised niche (Hutchinson, 1957). The realised niche is therefore smaller than the environmental niche due to different biotic factors, such as competition, which can be expressed from environmental surrogates, like climate or soil.

Usually climatic factors such as temperatures or precipitations are used to define the realised plant distribution (Box et al., 1993; Shao & Halpin, 1995; Heegaard, 2002). But edaphic factors, such as soil depth or soil pH, can also be used (Dubuis et al., 2013). Those climatic variables can be obtained by interpolation of measures taken by meteorological stations using Geographic Information System (GIS) (Ninyerola et al., 2000). These variables allow building Species Distribution Models (SDMs) (Thuiller et al., 2005; Hijmans & Graham, 2006).

Nowadays it is known that uncertainties presents in the SDMs can be due to imprecisions in the variables or lack of important variables (Austin & Van Niel, 2011). Part of this problem can result from the interpolation of these variables. These uncertainties contained in the prediction of individual species models can accumulate into larger errors when predicting species assemblage. This situation highlights the importance of using more precise and more accurate environmental predictors to approximate the environmental requirements of species as closely as possible, and to have a more accurate estimation of species distribution. To improve predictive ability of the models, it has been shown that adding new geomorphic (Randin et al., 2009b), edaphic (Dubuis et al., 2013) or topo-climatic

variables at a higher resolution (Lassueur et al., 2006; Pradervand et al., 2013) can improve model predictions.

A few studies have tested different resolutions of variables to see whether high resolution can yield better predictions (Pradervand et al., 2013; Lassueur et al., 2006). No clear improvement was shown, which may be caused by the confounding of several factors along the elevation gradient. Therefore it is important to decrease these factors to calculate an importance of variables. In the lowland, there is a larger effect of the agriculture and other human influence on the landscape, causing stronger effects on plant distributions of the moisture, nutrient and competition than the topography or climatic conditions. This may result because soils, that are already deeper and well differentiated, are also highly fertilized (Dirnböck & Grabherr, 2000; Delarze et al., 1998). As an attempt to decrease the effects of human influence, the study area can be restricted to higher altitudes. In this study, we focused on the subalpine belt, where the effect of agriculture is weaker (Bridge & Johnson, 2000). Moreover at higher altitudes, the influence of climatic and topographic variables is expected to be more pronounced (Ozenda, 2002) and consequently plant life is expected to become also more dependent on topographic and climatic conditions (Pottier et al., 2013).

Indeed a too large altitudinal range and/or human influence could accentuate the uncertainties in models and would have an impact on the predictions of species distribution, particularly when realistic scenarios of the impact of climate change want to be yielded (Randin et al., 2009a; Scherrer et al., 2011; Vicente et al., 2011). These uncertainties also decrease the accuracy of species assemblage predictions (Guisan & Rahbek, 2011; Dubuis et al., 2011; Pottier et al., 2013). Therefore their improvement is needed to have more reliable predictions of plant species distribution.

Here we compare the differences between what have been found in the field and the predictions of species distribution to estimate the uncertainties in species distribution models

based on standard predictors by conducting a stratified sampling in series of sites with similar topographic and climatic conditions. Then we test whether adding new environmental predictors at high resolution and/or edaphic factors could decrease these uncertainties.

# Materials & Methods

In this study, we did a directed sampling, in order to have samples with very similar topo-climatic conditions. This sampling method allows seeing only the error rate at a fine scale (sample scale). After the sampling and the species distribution models (SDMs) of plant distribution, we did a multi-modelling inference analysis on the residuals of the SDMs to see which variables could explain these residuals. In these models, we added different edaphic variables, as soil pH, carbon-to-nitrogen (C:N) ratio, mean soil depth, mean organo-mineral horizon depth, slope and exposure, and fine scale variables as mean solar radiation, curvature and slope. With these models we could identify the most important variables that could improve the predictions of species in the subalpine belt. A summary of the following analysis can be found in the flowchart presented in Fig. 1.

## *Study area*

The study area is located in the Western Swiss Alps (Canton de Vaud, Switzerland, 46°10' to 46°30'N; 6°50' to 7°10'E) and covers ca. 700 $km^2$ (Fig. 2). The elevation gradient ranges from 375 m to 3210 m asl on the top of the Diableret summit. The climate is temperate with annual temperatures ranging from 8°C at low elevation to -5°C at high elevation. The annual precipitations vary from 1200 mm at low elevation to 2600 mm at high elevation (Bouët, 1972). The vegetation belts' succession along the altitudinal gradient is typical from the calcareous Alps, with a colline belt of broadleaf deciduous forests, a montane belt with mixed forests, a subalpine belt with coniferous forests, an alpine belt with meadows and

grasslands vegetation, and finally a nival belt with sparse vegetation of high-elevation species (Randin et al., 2006; Aeschimann & Burdet, 2008).

### *Environmental predictors*

We used four topo-climatic predictors that were previously shown to be important for explaining plant distributions in the study area (Engler et al., 2009; Randin et al., 2009a; Pellisier et al., 2010).

We used one climatic predictor (temperature) and three topographic predictors (solar radiation, slope and topographic position). The climate predictor was computed from the monthly means of the average temperature (°C) and sum of precipitation (mm) data recorded for the period 1961-1990 by the Swiss network of meteorological stations (MeteoSuisse). These data were interpolated across Switzerland based on a 25-m resolution digital elevation model (DEM) (from the Swiss Federal Office of Topography (Swisstopo)) with local thin-plate spline-functions for temperature and a regionalized linear regression model for precipitation (Zimmerman & Kienast, 1999).

The amount of solar radiations received in each month of the year in each pixel was calculated. Solar radiations reflect the quantity of energy that reaches the ground, meaning that they are an estimation of the potential input of energy. Based on the digital elevation model (DEM), the direct, diffuse and reflected solar radiations were computed with the entire area as input and taking into account the local exposure and shading topography using the spatial analyst tool in ArcGIS 10.2.

The slope in degrees was derived from the DEM with the spatial analyst tool in ArcGIS 10.2 using a 3 x 3 pixel moving window.

The topographic position is an integration of topographic positions discriminating convex situations (ridges, bumps) from regular slopes (mountain sides, flat areas) and from

concave situations (valley bottoms, depressions). It was computed by using an ArcInfo Macro Language custom code in ArcGIS 10.2 for the DEM at a 25-m resolution using a 3 x 3 pixel moving window (for more details, see Randin et al., 2009a, 2009c)

### *Sampling strategy*

The sampling was stratified by these four environmental predictor variables, in order to visit samples with similar topographic and climatic conditions from the perspective of models fitted with these variables. Sampling in this way should allow a better quantification of the variability in the observed presence/absence of species, and to attempt explaining it with local predictors not included in the models used for the stratification. The sampling was directed on mean temperature corresponding to altitudes between 1900 and 1950 m, and between 2100 and 2150 m, in order to remain in one type of environmental conditions, here in the subalpine belt. The values for the predictors (mean temperature, global solar radiation, slope and topographic position) were chosen as a function of 912 plots that had been already sampled in this area between 2002 and 2009 (Dubuis et al., 2011) (Fig. 2). For each variable, histogram of the distribution of the values, restricted to elevations between 1900 and 1950 m, and between 2100 and 2150 m, were done. Then, an interval containing the maximum of the values was selected for the sampling.

Firstly, we selected two elevation strata, low and high, based on mean temperature of the growing season, defined between June and August. The temperature intervals were chosen as a function of the altitudes. We selected an interval containing the maximum of temperature values shown on histogram of the distribution of temperatures between 1900 and 1950 m, and an interval containing the maximum of temperature values between 2100 and 2150 m. For that, we used a DEM at a resolution of 25 m. We looked at the mean temperature for two intervals of altitudes: 1900-1950 m (low strata) and 2100-2150 m (high strata). For the low

strata, we used an interval of temperatures between 9.5°C and 9.7°C and for the high strata, we used an interval between 8.7°C and 8.9°C. Each of these intervals corresponded to a sampled range of 1% of the distribution of the temperature restricted to the two strata of elevations (1900 to 1950 m, and 2100 to 2150 m).

Secondly, two other strata - exposure to North or South - were selected based on global solar radiation. “North” was defined between 340° and 20°, corresponding to solar radiations between 115,000 and 145,000 KJ/day, corresponding to a sampled range of 9.09% from the distribution restricted to the two strata of elevations. “South” was defined between 170° and 190°, corresponding to solar radiations between 300,000 and 310,000 KJ/day, corresponding to a sampled range of 3.03% from the distribution restricted to the two strata of elevations (1900 to 1950 m, and 2100 to 2150 m). The interval of values for the “North” strata was larger than the “South” ones, in order to have enough sampled sites exposed in “North”.

Finally, every sampled stratum (low-North, high-North, low-South and high-South) had similar topographic conditions for slope and topographic position. The slope was selected within an interval between 30° and 35°, corresponding to a sampled range of 5.56% from the distribution restricted to the two strata of elevations. Topographic position was selected within a window radius with increments ranging from 100 m to 200 m radius, corresponding to a sampled range of 1.67% from the distribution restricted to the two strata of elevations.

We then selected pixels within these ecological conditions. The sampling was limited to open, non-woody and non-rocked areas. We selected a total of 38 samples: ten samples for the “South” strata (low and high) and nine samples for the “North” strata (low and high) (summary in Table 1 and Fig. 2).

209 ***Data collection***

210 In the field, we recorded the position of each plot using a Trimble GEO Explorer GPS
211 allowing submeter accuracy. We did exhaustive vegetation inventories within 4 $m^2$ and 64 $m^2$
212 for each of the 38 sampled sites. The 4-$m^2$ and the 64-$m^2$ plots had the same lower-left corner.
213 Within the 4-$m^2$ plot, we reported different environmental values, such as field measures of
214 slope and exposure.

215 The species list found in the 4-$m^2$ sampled sites was then reduced in order to contain
216 only species in common with the ones found in the 912 vegetation samples and with a
217 minimum of 30 occurrences in the 912 samples (119 species). This list was the species that
218 could be modelled. This list of 119 species was then reduced to 75 to contain species with a
219 minimum of 5 occurrences in our 4-$m^2$ plots and a minimum of 30 occurrences in the 912
220 plots.

221

222 ***Soil measures & soil analyses***

223 In the field, we also took different soil measures, such as soil depth with an auger and
224 the organic horizon depth corresponding to the organo-mineral horizon (horizon-A). We also
225 took soil samples in the organo-mineral horizon, at two corners of the 4-$m^2$ plot for lab
226 analyses. For the analyses, the mean soil depth per sample and mean horizon-A depth per
227 sample were used.

228 Soil samples were analyzed in the lab in order to measure the soil pH and the amount
229 of carbon (C), hydrogen (H) and nitrogen (N). The samples were first air-dried, then sieved at
230 2 mm. Soil pH was measured with a pH meter after diluting soil in water in a 1:2.5 soil/water
231 proportion (Page, 1982). Carbon, hydrogen and nitrogen contents analysis were performed
232 using a Carlo Erba CNS2500 CHN Elemental Analyzer coupled with a Fisons Optima mass

233 spectrometer (Tamburini et al., 2003). For the analyses, the amount of C, H, N was
234 transformed into a C:N ratio per sample.
235

236 ***Species distribution models***

237 We used the 'biomod2' library (Thuiller et al., 2013) in the R software (3.03, R
238 Foundation for Statistical Computing, Vienna, Austria) to model the distribution of 208 plant
239 species and using the four topo-climatic variables at a resolution of 25 m: mean temperature
240 during the growing season, global solar radiation, slope and topographic position (SDMs on
241 208 species) (Guisan & Zimmermann, 2000). The 208 species were extracted from the 912
242 vegetation plots sampled between 2002 and 2009, with a minimum of 30 occurrences. We
243 used four different modelling techniques (two regression methods and two classification
244 methods): generalized additive models (GAM), generalized boosted models (GBM),
245 generalized linear models (GLM), and random forests (RF) (Elith et al., 2006). We used a
246 repeated (15 times) split-sample cross-validation approach for evaluating the models. Each
247 model was fitted using 80% of the plots and evaluated using the area under the curve of a
248 receiver-operating characteristic plot (AUC; Hanley & Mcneil, 1982) and the true skill
249 statistics (TSS; Allouche et al., 2006) calculated on the excluded 20% partition. The projected
250 distributions for all individual species were then stacked to obtain a probability of presence
251 per species and per plot. For each model, the predicted probabilities were transformed into
252 binary presence/absence data and then the associated binary predictions were stacked for each
253 species.

254 To verify the capacity of the models to predict the distribution of the species present in
255 our samples, an external validation was done. For that we projected 75 species having a
256 minimum of 5 occurrences in our 4-$m^2$ samples and a minimum of 30 occurrences in the 912

vegetation samples, and we recalculated the AUC values according to this independent dataset (SDMs on 75 species).

### *Comparison between the observations and the predictions*

In order to compare the observations and the predictions, we calculated the species richness in the observations in the 4-$m^2$ plots, in the 64-$m^2$ plots, the observations reduced to 75 species, the predictions and the predictions reduced to 75 species. The species richness for the predictions was calculated by summing the binary presence/absence for each sample. The similarity between the observed samples for all the species in the 4-$m^2$ plots and for the observations reduced to the species used for the models (119 species) has been tested by hierarchical clustering using the 'vegan' library. The similarity between the predicted samples has been tested too.

### *Models on residuals*

Thanks to Principle Component Analyses (PCAs), we selected nine variables with pairwise correlations < 0.7 to limit the risk of multi-colinearity, including variables directly recorded in the field and GIS variables at high resolution. From the field variables, we kept slope, exposure, soil pH, mean soil depth, mean horizon-A depth and C:N ratio. We also selected three high-resolution variables at 5 m: curvature, slope and mean solar radiation (mean of 15$^{th}$ June, 15$^{th}$ July and 15$^{th}$ August). These variables were calculated with the same GIS approach used for the sampling variables, but from a DEM at 1 m.

Generalized linear mixed models (GLMMs) were implemented with the residuals of the models (SDMs on 208 species), ranging from $-1$ to $+1$, as the response variables and the nine environmental variables as predictors. The residuals have been calculated as $1 -$ the probability of presence of each species in each sample if the species was present in the

observations (reduced to 75 species), or as 0 – the probability of presence if the species was not present in the observations (reduced to 75 species). The stratum was added as random factor. GLMMs were fitted with the 'lme4' library in R, with a Gaussian distribution for the residuals. We fitted GLMMs with all possible combinations of the predictors, allowing a maximum of four variables per model (Grueber et al., 2011). We fitted models with linear and/or quadratic terms for all variables and with only the null model (only the random factor). Then for each of the 75 species, we performed a multi-modelling inference analysis (MMI) using the 'MuMIn' library to obtain the importance of variables (Grueber et al., 2011; Symonds & Moussalli, 2010). MMI avoids the problem of selecting a 'best' model out of several competing and sometimes nearly equivalent models. Instead, MMI calculates relative AIC weights for all models. These AIC weights, which sum to one across all the models, can be used to calculate the importance of variables, as the sum of the AIC weights across all models that contained the variable. Indeed this importance can be estimated as a percentage.

To visualize the results, a co-inertia analysis was performed with the 'ade4' library on the 75 species. A co-inertia analysis jointly fit two principal component analyses, in a way that each is reciprocally constrained by the other. It thus applies to two different data matrices. The first PCA was performed on the residuals of each species in each sample. The second PCA was performed on the values of the four most important variables for each site: mean solar radiation at 5 m, soil pH, C:N ratio and curvature at 5 m. In the ordination graphs, we highlighted the plant species as a function of their AUC values from the external validation (SDMs with 75 species) or in function of their ecological indicator values, to better understand the ecological meaning of our most important variables (Landolt et al., 2010). We used the light indicator value to assess the meaning of mean solar radiation, the acidity indicator value for soil pH, the nitrogen indicator value for C:N ratio and the humidity indicator value for curvature.

# Results

## *Data collection*

Across our 38 samples, we recorded a total of 245 different plant species in the 4-$m^2$ plots and 304 different plant species in the 64-$m^2$ plots. For the following analysis we focused on the 4-$m^2$ plots to have the same resolution as the predictions. There were 119 species in common between the 4-m2 plots and the 30 occurrences dataset of the 912 plots. A total of 75 species showed a minimum of 5 occurrences in our 4-$m^2$ plots and 30 occurrences in the 912 plots for external validation of the models.

## *Comparison between the observations and the predictions*

### *Species richness*

The mean species richness observed in the field was 35.97 species per sample for the 4-$m^2$ plots and 57.16 species per sample for the 64-$m^2$ plots. The species richness values were significantly different between the observations in the 4-$m^2$ and in the 64-$m^2$ plots (Wilcoxon signed rank test, *P*-value <0.001) (Fig. 3). The species richness for the reduced species list (i.e. 75 species that have a minimum of 5 occurrences in our inventories and a minimum of 30 occurrences in the 912 inventories) had a mean of 22.53 species per sample for the observations and 10.32 species per sample for the predictions (Fig. 3).

With the binary projections, the models (SDMs with 208 species) predicted a mean of 46.71 species per sample. The species richness values between the predictions and the observations (in the 4-$m^2$ and in the 64-$m^2$ plots) were significantly different (Wilcoxon signed rank test, *P*-value <0.001). The number of species predicted in the samples was in-between the richness observed in the 4-$m^2$ and the 64-$m^2$ plots.

### *Similarity in plant composition*

The uncertainties associated to the predictions could be visualized through the hierarchical clustering. In the field, the hierarchical clustering revealed that the strata are not grouped together and they have an average similarity of plant composition of only 28.61%, ranging from 25.22% to 34.71% (Fig. 4A). With the observations reduced to the species that can be modelled (119 species), the hierarchical clustering revealed also that the strata are not grouped together and that they have a similarity of plant composition of only 31.49%, ranging from 28.53% to 42.69% (Fig. 4B). As expected, the hierarchical clustering showed that the predicted samples (SDMs on 208 species) are grouped by stratum. They have a similarity of plant composition ranging from 64.22% to 72.98%, and with a mean similarity of 69.34% (Fig. 4C).

## ***Species distribution models***

The evaluation metrics (AUC) values, of the cross-validation models (SDMs on 208 species), ranged from 0.66 (poor) to 0.96 (excellent). The vast majority (98.5%) were over 0.7 (useful models according to Swets (1988)) (Fig. 5). The mean AUC value was 0.82 (Fig. 5). The lowest AUC values were for *Alchemilla coriacea aggr*. (0.68), *Hieracium bifidum aggr*. (0.66) and *Silene vulgaris s.l.* (0.66). The highest AUC values were for *Holcus lanatus* (0.96), *Lolium perenne* (0.95) and *Ranunculus bulbosus* (0.94). The evaluation metrics (TSS) values, of the SDMs on 208 species, ranged from 0.35 (poor) to 0.85 (excellent), with less than the half of the species (41.5%) over 0.6 (useful models according to Swets (1988)) (Fig. 5). The mean TSS value was 0.58 (Fig. 5). The lowest TSS values were for *Hieracium bifidum aggr.* (0.35), *Silene vulgaris s.l.* (0.36) and *Alchemilla coriacea aggr.* (0.37). The highest TSS values were for *Glechoma hederacea sstr.* (0.85), *Holcus lanatus* (0.84) and *Lolium perenne* (0.82).

356 For the external validation to verify the predictive capacity of the models (SDMs on
357 75 species), the AUC values ranged from 0.63 to 0.95 and a mean AUC value of 0.82 (Fig. 5,
358 Appendix S1). Furthermore the vast majority (96%) were over 0.7. The lowest AUC values
359 were for *Parnassia palustris* (0.63), *Alchemilla conjuncta aggr*. (0.69) and *Pedicularis foliosa*
360 (0.70). The highest AUC values were for *Alchemilla vulgaris aggr*. (0.95), *Trifolium medium*
361 (0.93) and *Astrantia major* (0.92). The TSS values ranged from 0.30 to 0.85 and a mean TSS
362 value of 0.57 (Fig. 5). Less than the half of the species (43.2%) were over 0.6. The lowest
363 AUC values were for *Parnassia palustris* (0.30), *Alchemilla conjuncta aggr*. (0.36) and
364 *Leontodon helveticus* (0.38). The highest TSS values were for *Astrantia major* (0.75),
365 *Trifolium medium* (0.77) and *Alchemilla vulgaris aggr.* (0.85). For the following sections, we
366 will focus on the AUC values.
367 The probabilities of presence for the 208 species ranged between 0.04 and 0.93; see
368 Appendix S1 in supplementary material for the probabilities of presence for the 75 species.
369

370 ***Models on residuals***

371 The models fitted to the residuals of the first model (SDMs on 208 species) produced a
372 total of 38,325 GLMMs, with 255 models per species with linear terms only, 255 models per
373 species with linear and quadratic terms, and 75 null models.
374 The multi-modelling inference analysis gave median importance values ranging from
375 <0.001% to 15.6%. The most important variables were mean solar radiation at 5 m with a
376 median importance of 15.6%, soil pH with a median importance of 8.7%, C:N ratio with a
377 median importance of 7.3% and curvature at 5 m with a median importance of 2.0% (Table 2
378 and Fig. 6).
379 Mean solar radiation was very important (over 70%) for three species: *Phleum*
380 *hirsutum* (86%), *Scabiosa lucida* (84%) and *Pimpinella major* (82%). Curvature seemed to be

important (over 60%) for *Ranunculus montanus aggr.* (65.7%). Soil pH seemed to be very important (over 70%) for *Carex sempervirens* (79%). The C:N ratio was very important (over 70%) for *Sesleria caerulea* (97%), *Alchemilla vulgaris aggr.* (93%), *Hypericum maculatum aggr.* (84%), *Aposeris foetida* (78%) and *Gentiana verna* (74%).

The co-inertia analysis did not allow separating the plant species in groups related to their reaction to light, humidity, acidity or nitrogen, see Appendix S2 in supplementary material (Fig. S2.1-2.5). It supposed that these variables would not especially affect plants with particular ecological conditions.

# Discussion

In this study, we investigated which environmental variables usually missing in traditional species distribution models could optimize their predictive ability in a mountain landscape. The directed sampling, with four strata identified sites with similar topographic and climatic conditions, sampling a range between 1% and 9% of the totality of the local range of the variables restricted to the two strata of elevations (1900 to 1950 m, and 2100 to 2150 m). The species distribution models (SDMs on 208 species) predicted similar plant communities between the strata, with a similarity of plant composition of 69.34%. On the contrary, in the field, the samples from the same strata had a similarity of plants composition of only 33.19%. The most important variables identified by the MMI approach (GLMMs) on the residuals of the first models (SDMs on 208 species), were mean solar radiation at 5 m, soil pH, C:N ratio and curvature at 5 m with importance of 15.6%, 8.7%, 7.3%, 2.0% respectively.

## *High-resolution variables*

The most important variable missing in previous models was mean solar radiation at a fine scale (5 m) with a median importance of 15.6%. Solar radiations reflect the quantity of

energy that reaches the ground. This variable should thus be very important for light-sensitive plants. It did prove very important for three plant species in particular: - *Phleum hirsutum*, *Scabiosa lucida* and *Pimpinella major* - with an importance over 80%. According to its light indicator value (Landolt index), *Phleum hirsutum* is a species that grows only in sunny habitats, but also occurring in partial shade (light value 4). However, *Scabiosa lucida* and *Pimpinella major* are semi-shade plants, rarely in full light, but generally with more than 10% relative illumination (light value 3). So light does not seem to be a limiting factor for these species, although solar radiations seem to be important for them.

Curvature is also important, with a median importance of 2.0%. This variable has a similar overall meaning as topographic position, because it represents areas that are convex, concave or flat. But curvature identifies these topographic situations within a narrow neighbourhood and thus reflects finer scale process of drainage. Curvature can also impact plants, because it indirectly translates variations in humidity, and likely also in soil depth and soil pH (Randin et al., 2009a). Curvature appears to be important for *Ranunculus montanus aggr.* with an importance of 65.7%. According to its humidity indicator value (Landolt index), *Ranunculus montanus aggr.* is a species that grows on moderately dry to moderately damp soils, with a wide ecological range (humidity value of 3). At the first sight, the humidity does not seem to be a limiting factor for this species, although curvature seems to be important for it.

A sampling restricted to a small part of environmental gradients across the study area is expected to better reveal the predictive potential of variables at high resolution. In previous studies, divergent results have been found, but these studies were performed over larger extent and along larger altitudinal ranges. Lassueur et al. (2006) found no significant explanation for curvature, which could be explained by a too wide altitudinal range considered. However, they found that northness (NS), which is related to solar radiations, was

431 the most significant explanatory variables at such fine scale showing similar results as we
432 found. Pradervand et al. (2013) found that the best model performance were obtained for
433 models with a resolution of 5 m, but the differences compared with other resolutions
434 (resolutions of 2 m, 10 m, 25 m, 50 m and 100 m) were too small or not significant to derive
435 any meaningful conclusion. Guisan et al. (2007b) found no differences in predictive power
436 between models built for trees with predictors at 100 m and 1 km. Guisan et al. (2007a) found
437 for most of the bird and plant data sets considered that lowering the predictor resolution ten
438 times cause only a slight decrease of the model's predictive power. These results show that
439 topographic variables can have different importance when a too wide altitudinal range is
440 taken into account, but their resolutions can affect the uncertainties of models. Therefore the
441 importance of variables could be better estimated when a local range, restricted to a small
442 altitudinal range, is selected. Indeed a local range allows decreasing the confounding of
443 several factors along the elevation gradient.
444

445 ***Edaphic variables***

446 As also expected, our results show that edaphic factors can also improve the predictive
447 ability of SDMs, with soil pH showing a median importance of 8.7%. Soil pH is important,
448 because some plants can only grow on acidic or basic soils (Aerts & Chapin, 2000). High soil
449 pH can prevent the release of important ions (such as nitrogen), causing nutrient deficiency
450 (Gobat et al, 2004). Low soil pH can also cause nutrient deficiencies because ions such as
451 nitrogen can form chemical complexes with other ions and become unavailable for plants
452 (Gobat et al, 2004). Soil pH appears particularly important for *Carex sempervirens*, with an
453 importance of 79.0%, although this species is considered as in different to pH with a Landolt
454 value of 3 (lightly acid to neutral soils).

455 C:N ratio also shows some importance for improving SDMs, with a median
456 importance of 7.3%. C:N ratio expresses the amount of N used as nutrients by plants (Dubuis
457 et al., 2013). Therefore, its amount has a direct impact on plant growth and, consequently, on
458 the formation of plant communities. This variable is influenced by soil pH because its
459 availability depends on the acidity of soil. C:N ratio proved particularly important *for Sesleria*
460 *caerulea*, *Alchemilla vulgaris aggr.*, *Hypericum maculatum aggr.*, *Aposeris foetida* and
461 *Gentiana verna* (97.0%, 93.0%, 84.0%, 78.0%, 74.0% respectively). *Sesleria caerulea* and
462 *Gentiana verna* are present in sites that are more or less infertile (nitrogen value of 2), and
463 *Hypericum maculatum aggr*. and *Aposeris foetida* are in sites of intermediate fertility
464 (nitrogen value of 3). *Alchemilla vulgaris aggr.* has no specific nitrogen value, because it can
465 live everywhere. Globally, these species do not seem to depend on the nitrogen richness in the
466 soil.

467 As these soil variables are very important for plant distribution, it would be important
468 to have mapped representation of these variables. Mapped representation of soil proprieties is
469 needed for the entire region in order to put them in the SDMs, because they have been
470 collected in the field and only for the sampled sites that have been visited. These maps allow
471 seeing the effect of these variables along the global altitudinal gradient. Unfortunately
472 predictor maps of soil proprieties, such as soil pH or ions concentration, are difficult to obtain,
473 so these maps are still rarely available. Moreover this kind of maps is not available for our
474 study area. Producing such data will likely prove important for making progress in future
475 studies.

476

477 ***Future perspectives***

478 A limitation restricted to our dataset is the number of species that can be modelled. As
479 this number is limited, only 119 species out of a total of 245 species observed in the field,

could be modelled. Moreover one cannot add too many variables in the models in order to keep enough power, because it has been shown that a model is likely to be reliable only when the number of predictors is less than 10% of the sample size (Harrell, 2001).

For future studies, it would be interesting to be able to build models containing many of these important variables together. For that, more inventories along the altitudinal gradient would be needed. This would allow checking if these variables would still be kept in the models when other variables, such as the ones that are typically used (e.g. topo-climatic). In order to check if soil variables would really improve SDMs, more inventories would be needed to estimate the soil variables impact on the accuracy of the predictions. Improving the prediction of species distribution at a fine scale in particularly complex landscapes may allow yielding more realistic scenarios of the impact of climate change on plant distribution (Randin et al., 2009a; Scherrer et al., 2011; Vicente et al., 2011). And it could improve the accuracy of species assemblage predictions at high elevations (Guisan & Rahbek, 2011; Dubuis et al., 2011; Pottier et al., 2013).

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# Figures

**Figure 1** Flowchart of the analyses done in this study. 1) Sampling strategy done with distribution of topo-climatic variables from 912 samples already done in the study area: mean temperature during the growing season, global solar radiation, slope and topographic position. 2) Data collection with a total of 245 species observed in 38 samples (in the 4-$m^2$ plots). 3) Species selection to have only the species in common in the two databases (119 species). This list has been restricted to have only species with a minimum of 5 occurrences in our plots and a minimum of 30 occurrences in the 912 plots (75 species). 4) Species distribution models to project the species in the 38 plots (SDMs on 208 species). 5) External validation to verify the capacity of the dataset using 75 species (SDMs on 75 species). 6) Comparison of the observations and the predictions by comparing the species richness and by hierarchical clustering. 7) Models on the residuals with a multi-modelling inference analysis (GLMMs on the residuals of the SDMs on 208 species), to obtain an importance of variables. Then co-inertia analyses have been done to visualize the results and to see if there is pattern between the AUC values, Landolt indices of light, acidity, nitrogen and humidity.

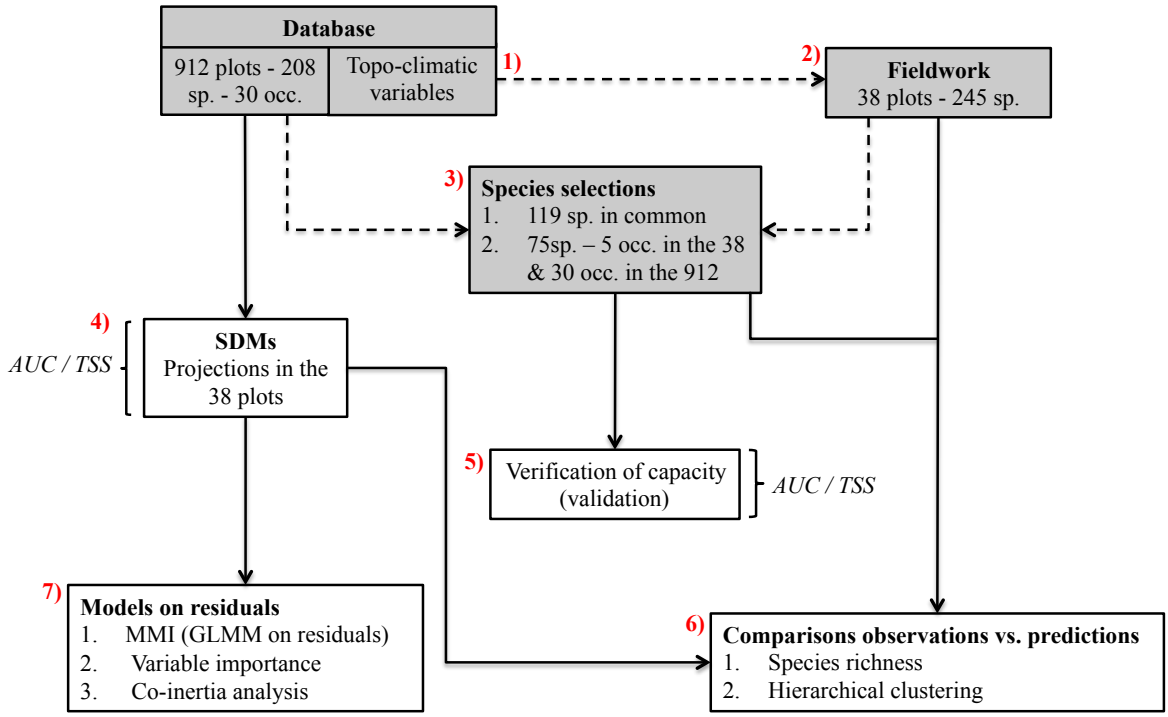
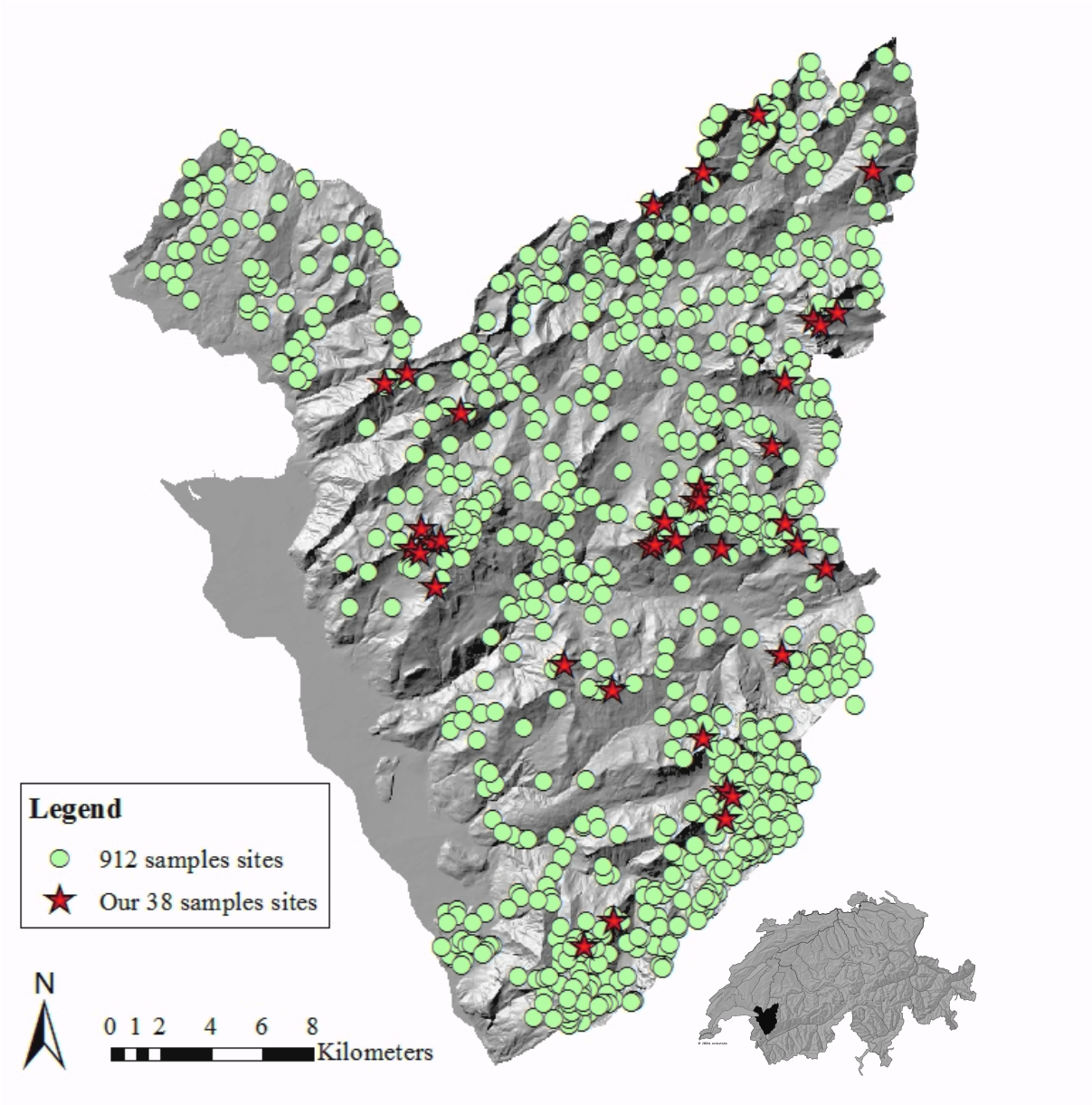
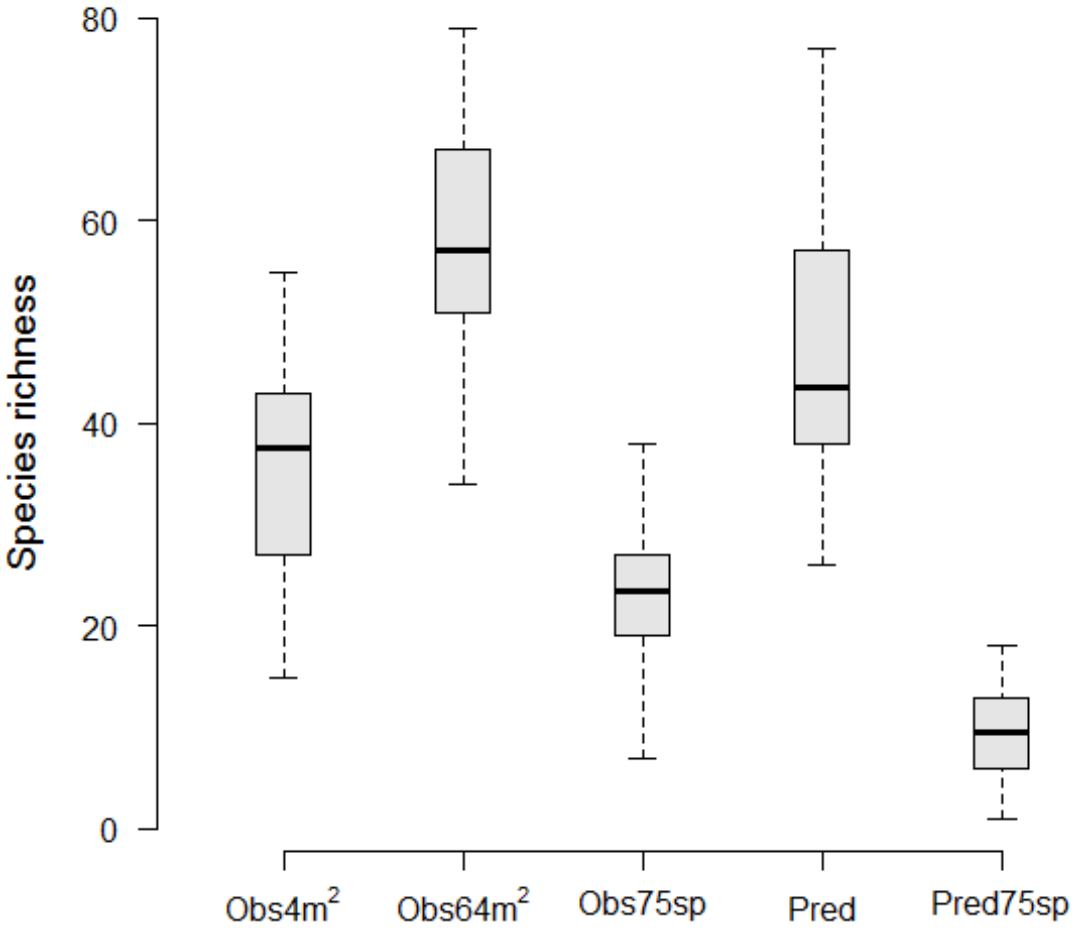


**Figure 2** Map of the study area. The 912 green circles represent the vegetation inventories done between 2002 and 2006; the red stars represent our 38 plots separated in four strata with similar topographic and climatic conditions.



656 **Figure 3** Species richness for the observations and the predictions datasets. The species
657 richness values are significantly different between the observations in the 4-$m^2$ plots, in the
658 64-$m^2$ plots, the observations reduced to 75 species, the predictions and the predictions
659 reduced to 75 species (Wilcoxon signed rank test, *P*-value <0.001). The predictions have
660 species richness in between the species richness values observed in the 4-$m^2$ and in the 64-$m^2$
661 plots.




662

**Figure 4** Similarity of plant composition. (A) Hierarchical clustering of all the plant observations in the field. These are not clearly grouped by strata, as shown by the similarity of only 28.61%. (B) Hierarchical clustering of the plant observations restricted to the species that can be modelled (119 species). The plots are not clearly grouped by strata, as shown by the similarity of only 33.19%. (C) Hierarchical clustering of the predictions of the species (SDMs on 208 species). There are grouped by strata, with a similarity of 69.34%.

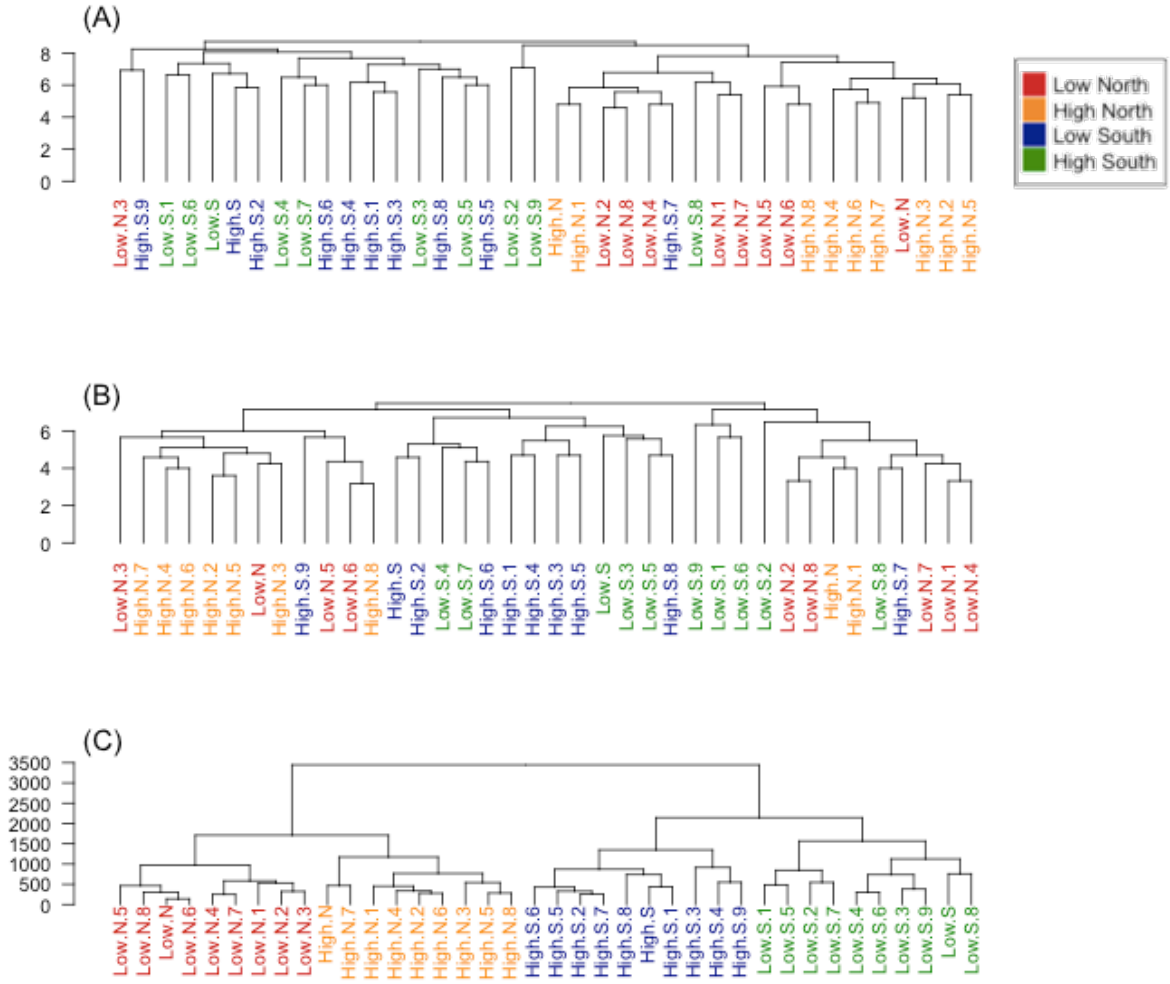


**Figure 5** Evaluation metrics for the SDMs (cross-validation and external validation). The AUC for the cross-validation (SDMs on 208 species) had a mean value of 0.82 and the TSS had a mean value of 0.58 (in red). The mean AUC for the external validation (SDMs on 75 species) was 0.82 too and the mean TSS was 0.57 (in blue).

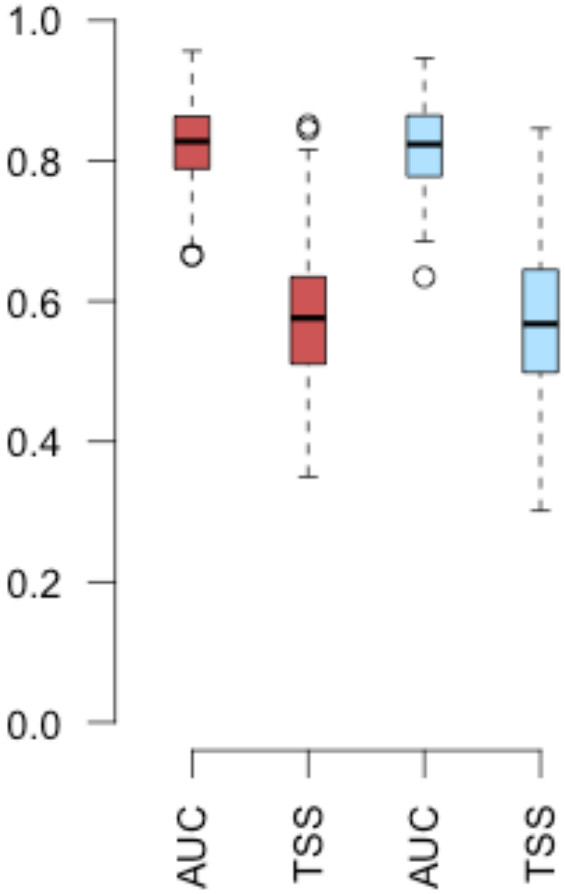
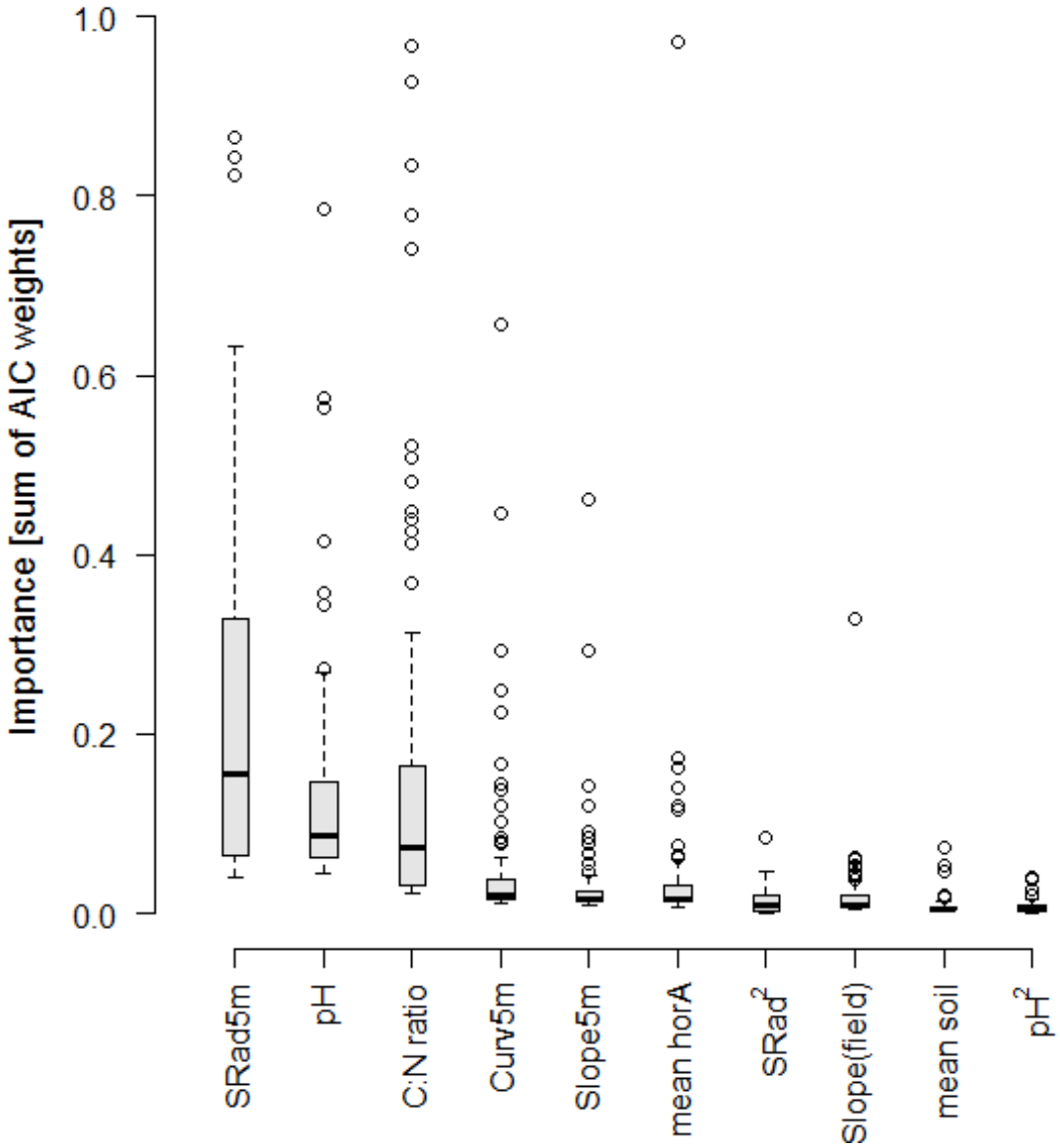


**Figure 6** Importance of variables. The ninth most important variables in the models fitted to the residuals of the SDMs on 208 species are represented. The most important variables are mean solar radiation at 5 m, soil pH, C:N ratio and curvature at 5 m with a median importance of 15.6%, 8.7%, 7.3% and 2.0% respectively. “SRad5m” represents mean solar radiation at 5 m, “Curv5m” represents curvature at 5 m and “meanhorA” represents mean horizon-A depth.



# Tables

**Table 1** Summary of the four sampling strata. The four strata have very similar topographic and climatic conditions selected with four environmental variables: mean temperature, global solar radiation, slope and topographic position. The total number of samples is 38 sites.

| Strata | Mean temperature [°C] | Global solar radiation [KJ/day] | Slope [°] | Topographic position [m radius] | Number of samples |
|---|---|---|---|---|---|
| Low - North | 9.5 – 9.7 | 115,000 – 145,000 | 30 – 35 | 100 – 200 | 9 |
| Low - South | 9.5 – 9.7 | 300,000 – 310,000 | 30 – 35 | 100 – 200 | 10 |
| High - North | 8.7 – 8.9 | 115,000 – 145,000 | 30 – 35 | 100 – 200 | 9 |
| High - South | 8.7 – 8.9 | 300,000 – 310,000 | 30 – 35 | 100 – 200 | 10 |

**Table 2** Importance of variables in the models fitted to residuals of the SDMs on 208 species. Mean solar radiation at 5 m, soil pH, C:N ratio and curvature at 5 m were the most important variables. The importance was calculated as the sum of the AIC weights of each model in which the variable was present, which can be related to a percentage of importance.

| **Variables** | **Importance [%]** |
|---|---|
| Mean solar radiation | 15.6 |
| Soil pH | 8.7 |
| C:N ratio | 7.3 |
| Curvature at 5 m | 2.0 |
| Slope at 5 m | 1.7 |
| Mean horizon-A depth | 1.6 |
| Mean solar radiation$^2$ | 1.0 |
| Slope (field) | 1.0 |
| Mean soil depth | 0.5 |
| Soil pH$^2$ | 0.4 |
| C:N ratio$^2$ | $6.66 \times 10^{-02}$ |
| Exposure | $4.64 \times 10^{-02}$ |
| Curvature at 5 m$^2$ | $5.38 \times 10^{-03}$ |
| Mean horizon-A depth$^2$ | $3.40 \times 10^{-03}$ |
| Slope at 5 m$^2$ | $2.73 \times 10^{-03}$ |
| Slope (field) $^2$ | $3.71 \times 10^{-04}$ |
| Mean soil depth$^2$ | $1.41 \times 10^{-04}$ |
| Exposure$^2$ | $4.81 \times 10^{-07}$ |

# Supplementary material

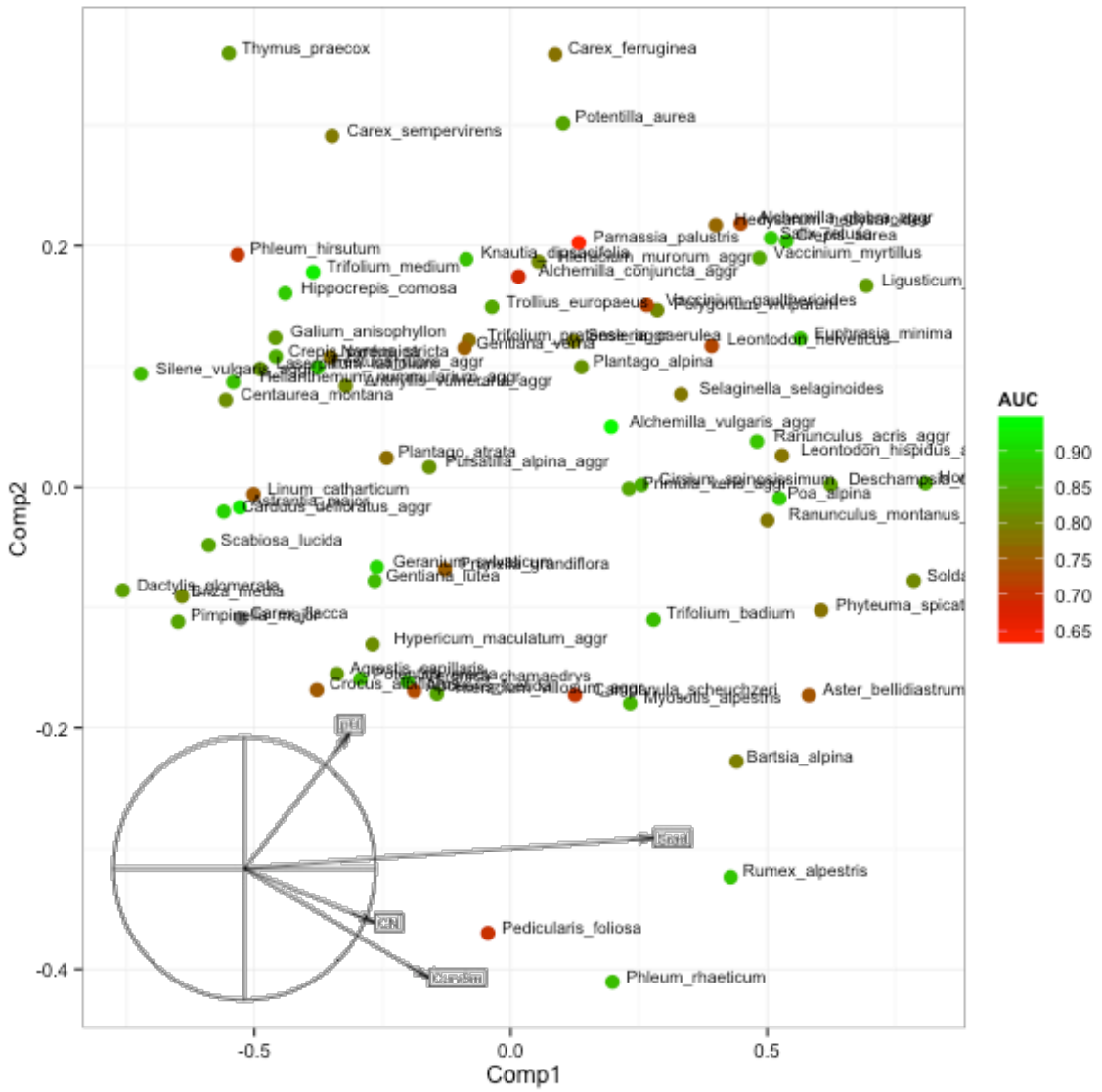
**Appendix S1** The 75 species used for the MMI, sorted by their AUC values (SDMs on 75 species) and their probabilities of presence in each plot. The probabilities range between 0.04 and 0.933. In the first table, there are the probabilities of presence in the plots of the low strata ("North" and "South", and between 1900 and 1950 m). In the second one, the probabilities of presence for the plots in the high strata ("North" and "South", and between 2100 and 2150 m) are shown.

| Species | AUC | Low S1 | Low S2 | Low S3 | Low S4 | Low S5 | Low S6 | Low S7 | Low S8 | Low S9 | Low S10 | Low N1 | Low N2 | Low N3 | Low N4 | Low N5 | Low N6 | Low N7 | Low N8 | Low N10 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Alchemilla vulgaris aggr.* | 0.946 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 |
| *Trifolium medium* | 0.927 | 0.008 | 0.007 | 0.007 | 0.007 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Astrantia major* | 0.924 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Geranium sylvaticum* | 0.899 | 0.009 | 0.009 | 0.009 | 0.009 | 0.010 | 0.009 | 0.009 | 0.009 | 0.009 | 0.225 | 0.176 | 0.312 | 0.137 | 0.155 | 0.108 | 0.133 | 0.257 | 0.195 | 0.117 |
| *Carduus defloratus aggr.* | 0.896 | 0.038 | 0.050 | 0.052 | 0.062 | 0.038 | 0.035 | 0.037 | 0.036 | 0.035 | 0.038 | 0.054 | 0.064 | 0.065 | 0.041 | 0.059 | 0.044 | 0.059 | 0.034 | 0.056 |
| *Poa alpina* | 0.889 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Hippocrepis comosa* | 0.885 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.011 | 0.010 | 0.010 | 0.010 | 0.010 | 0.012 | 0.010 | 0.012 | 0.011 | 0.009 |
| *Salix retusa* | 0.883 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.016 | 0.015 | 0.015 | 0.015 | 0.015 | 0.015 | 0.016 | 0.015 | 0.014 | 0.015 |
| *Festuca rubra aggr.* | 0.881 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Crepis aurea* | 0.881 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 |
| *Rumex alpestris* | 0.879 | 0.279 | 0.334 | 0.281 | 0.300 | 0.294 | 0.404 | 0.263 | 0.211 | 0.166 | 0.023 | 0.017 | 0.016 | 0.017 | 0.013 | 0.018 | 0.013 | 0.023 | 0.013 | 0.014 |
| *Ranunculus acris aggr.* | 0.878 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 |
| *Euphrasia minima* | 0.876 | 0.368 | 0.588 | 0.509 | 0.543 | 0.474 | 0.408 | 0.351 | 0.457 | 0.333 | 0.024 | 0.026 | 0.030 | 0.031 | 0.023 | 0.027 | 0.026 | 0.029 | 0.022 | 0.025 |
| *Veronica chamaedrys* | 0.873 | 0.019 | 0.019 | 0.018 | 0.017 | 0.019 | 0.018 | 0.018 | 0.020 | 0.019 | 0.016 | 0.015 | 0.014 | 0.014 | 0.016 | 0.015 | 0.016 | 0.014 | 0.015 | 0.014 |
| *Knautia dipsacifolia* | 0.873 | 0.035 | 0.024 | 0.032 | 0.028 | 0.021 | 0.022 | 0.029 | 0.023 | 0.031 | 0.009 | 0.019 | 0.012 | 0.010 | 0.009 | 0.010 | 0.009 | 0.011 | 0.010 | 0.010 |
| *Helianthemum nummularium aggr.* | 0.871 | 0.014 | 0.011 | 0.014 | 0.015 | 0.011 | 0.011 | 0.013 | 0.010 | 0.012 | 0.032 | 0.044 | 0.046 | 0.056 | 0.038 | 0.045 | 0.034 | 0.041 | 0.037 | 0.047 |
| *Trifolium badium* | 0.871 | 0.042 | 0.026 | 0.033 | 0.032 | 0.024 | 0.033 | 0.046 | 0.026 | 0.034 | 0.416 | 0.414 | 0.575 | 0.249 | 0.124 | 0.426 | 0.144 | 0.571 | 0.270 | 0.238 |
| *Phleum rhaeticum* | 0.870 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Potentilla erecta* | 0.865 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 |
| *Gentiana lutea* | 0.862 | 0.012 | 0.013 | 0.013 | 0.013 | 0.012 | 0.012 | 0.012 | 0.013 | 0.013 | 0.014 | 0.013 | 0.013 | 0.013 | 0.014 | 0.013 | 0.013 | 0.013 | 0.014 | 0.013 |
| *Silene vulgaris aggr.* | 0.861 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.024 | 0.012 | 0.026 | 0.008 | 0.008 | 0.008 | 0.008 | 0.024 | 0.008 | 0.008 |
| *Myosotis alpestris* | 0.858 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.037 | 0.038 | 0.032 | 0.014 | 0.015 | 0.020 | 0.015 | 0.034 | 0.017 | 0.014 |
| *Cirsium spinosissimum* | 0.852 | 0.013 | 0.012 | 0.013 | 0.013 | 0.012 | 0.013 | 0.013 | 0.012 | 0.013 | 0.156 | 0.033 | 0.043 | 0.020 | 0.018 | 0.023 | 0.018 | 0.240 | 0.018 | 0.019 |
| *Crepis pyrenaica* | 0.848 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.006 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Homogyne alpina* | 0.847 | 0.101 | 0.181 | 0.137 | 0.214 | 0.213 | 0.206 | 0.110 | 0.136 | 0.089 | 0.275 | 0.203 | 0.163 | 0.252 | 0.251 | 0.205 | 0.200 | 0.214 | 0.105 | 0.173 |
| *Primula veris aggr.* | 0.842 | 0.019 | 0.014 | 0.020 | 0.019 | 0.012 | 0.018 | 0.018 | 0.013 | 0.019 | 0.008 | 0.009 | 0.009 | 0.008 | 0.008 | 0.009 | 0.008 | 0.009 | 0.008 | 0.009 |
| *Trollius europaeus* | 0.842 | 0.013 | 0.012 | 0.013 | 0.013 | 0.013 | 0.014 | 0.013 | 0.013 | 0.013 | 0.063 | 0.028 | 0.056 | 0.013 | 0.013 | 0.013 | 0.013 | 0.150 | 0.013 | 0.012 |
| *Scabiosa lucida* | 0.841 | 0.028 | 0.024 | 0.023 | 0.020 | 0.035 | 0.030 | 0.026 | 0.037 | 0.030 | 0.350 | 0.212 | 0.283 | 0.138 | 0.274 | 0.230 | 0.241 | 0.271 | 0.367 | 0.204 |
| *Vaccinium myrtillus* | 0.841 | 0.009 | 0.010 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Potentilla aurea* | 0.840 | 0.009 | 0.010 | 0.010 | 0.010 | 0.009 | 0.010 | 0.009 | 0.010 | 0.009 | 0.014 | 0.015 | 0.017 | 0.016 | 0.014 | 0.016 | 0.015 | 0.016 | 0.013 | 0.016 |
| *Hieracium villosum aggr.* | 0.837 | 0.006 | 0.007 | 0.006 | 0.006 | 0.007 | 0.006 | 0.006 | 0.007 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 |
| *Pimpinella major* | 0.836 | 0.011 | 0.010 | 0.010 | 0.010 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.027 | 0.022 | 0.020 | 0.017 | 0.021 | 0.020 | 0.020 | 0.022 | 0.026 | 0.017 |
| *Dactylis glomerata* | 0.832 | 0.020 | 0.026 | 0.024 | 0.024 | 0.018 | 0.018 | 0.020 | 0.019 | 0.019 | 0.008 | 0.008 | 0.009 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Deschampsia cespitosa* | 0.830 | 0.104 | 0.141 | 0.130 | 0.153 | 0.149 | 0.109 | 0.099 | 0.138 | 0.096 | 0.038 | 0.046 | 0.058 | 0.050 | 0.034 | 0.049 | 0.035 | 0.052 | 0.034 | 0.045 |
| *Thymus praecox* | 0.827 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.012 | 0.011 | 0.011 | 0.010 | 0.011 | 0.011 | 0.011 | 0.012 | 0.011 | 0.010 |
| *Ligusticum mutellina* | 0.827 | 0.010 | 0.011 | 0.010 | 0.011 | 0.011 | 0.011 | 0.010 | 0.010 | 0.010 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 |
| *Galium anisophyllon* | 0.824 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.008 | 0.009 | 0.009 | 0.008 | 0.008 | 0.008 | 0.008 | 0.009 | 0.008 | 0.008 |
| *Agrostis capillaris* | 0.823 | 0.050 | 0.046 | 0.050 | 0.049 | 0.037 | 0.038 | 0.044 | 0.040 | 0.047 | 0.039 | 0.062 | 0.058 | 0.044 | 0.047 | 0.040 | 0.039 | 0.042 | 0.072 | 0.051 |
| *Laserpitium latifolium* | 0.820 | 0.025 | 0.016 | 0.019 | 0.017 | 0.020 | 0.022 | 0.023 | 0.021 | 0.025 | 0.169 | 0.154 | 0.160 | 0.040 | 0.140 | 0.112 | 0.138 | 0.187 | 0.176 | 0.042 |
| *Plantago alpina* | 0.818 | 0.145 | 0.084 | 0.128 | 0.112 | 0.104 | 0.121 | 0.144 | 0.104 | 0.126 | 0.021 | 0.022 | 0.024 | 0.022 | 0.020 | 0.023 | 0.019 | 0.023 | 0.030 | 0.021 |
| *Pulsatilla alpina aggr.* | 0.814 | 0.052 | 0.053 | 0.049 | 0.051 | 0.062 | 0.070 | 0.062 | 0.062 | 0.051 | 0.054 | 0.016 | 0.038 | 0.015 | 0.016 | 0.015 | 0.015 | 0.040 | 0.016 | 0.015 |
| *Hypericum maculatum aggr.* | 0.810 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.007 | 0.008 | 0.008 | 0.007 | 0.008 | 0.008 | 0.008 | 0.007 | 0.008 | 0.008 | 0.008 | 0.007 | 0.008 |
| *Centaurea montana* | 0.808 | 0.020 | 0.019 | 0.022 | 0.021 | 0.016 | 0.015 | 0.020 | 0.018 | 0.019 | 0.028 | 0.021 | 0.029 | 0.014 | 0.013 | 0.014 | 0.014 | 0.033 | 0.015 | 0.014 |
| *Soldanella alpina* | 0.806 | 0.014 | 0.012 | 0.015 | 0.013 | 0.012 | 0.012 | 0.013 | 0.012 | 0.013 | 0.011 | 0.012 | 0.015 | 0.011 | 0.011 | 0.012 | 0.011 | 0.021 | 0.012 | 0.013 |
| *Briza media* | 0.805 | 0.010 | 0.011 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.012 | 0.013 |
| *Anthyllis vulneraria aggr.* | 0.804 | 0.105 | 0.072 | 0.117 | 0.099 | 0.086 | 0.057 | 0.090 | 0.107 | 0.121 | 0.041 | 0.036 | 0.030 | 0.029 | 0.036 | 0.030 | 0.032 | 0.029 | 0.037 | 0.030 |
| *Polygonum viviparum* | 0.803 | 0.008 | 0.008 | 0.008 | 0.008 | 0.009 | 0.009 | 0.008 | 0.008 | 0.008 | 0.009 | 0.008 | 0.008 | 0.009 | 0.009 | 0.009 | 0.012 | 0.009 | 0.008 | 0.008 |
| *Hieracium murorum aggr.* | 0.802 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.018 | 0.020 | 0.056 | 0.018 | 0.017 | 0.022 | 0.016 | 0.028 | 0.018 | 0.018 |
| *Sesleria caerulea* | 0.792 | 0.178 | 0.063 | 0.098 | 0.146 | 0.071 | 0.076 | 0.109 | 0.067 | 0.081 | 0.062 | 0.156 | 0.127 | 0.131 | 0.054 | 0.097 | 0.048 | 0.103 | 0.068 | 0.082 |
| *Bartsia alpina* | 0.792 | 0.017 | 0.018 | 0.018 | 0.018 | 0.017 | 0.016 | 0.017 | 0.017 | 0.018 | 0.498 | 0.483 | 0.575 | 0.354 | 0.234 | 0.497 | 0.158 | 0.569 | 0.367 | 0.393 |
| *Carex sempervirens* | 0.787 | 0.064 | 0.079 | 0.082 | 0.081 | 0.078 | 0.066 | 0.067 | 0.086 | 0.067 | 0.288 | 0.324 | 0.570 | 0.233 | 0.182 | 0.387 | 0.112 | 0.368 | 0.378 | 0.288 |
| *Selaginella selaginoides* | 0.782 | 0.102 | 0.112 | 0.103 | 0.111 | 0.109 | 0.110 | 0.104 | 0.101 | 0.100 | 0.011 | 0.011 | 0.012 | 0.012 | 0.012 | 0.011 | 0.012 | 0.012 | 0.011 | 0.012 |
| *Ranunculus montanus aggr.* | 0.782 | 0.271 | 0.204 | 0.244 | 0.306 | 0.239 | 0.290 | 0.300 | 0.218 | 0.254 | 0.017 | 0.017 | 0.017 | 0.019 | 0.016 | 0.017 | 0.016 | 0.017 | 0.017 | 0.020 |
| *Leontodon hispidus aggr.* | 0.779 | 0.008 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Phyteuma spicatum* | 0.778 | 0.026 | 0.047 | 0.033 | 0.037 | 0.033 | 0.030 | 0.027 | 0.032 | 0.027 | 0.009 | 0.010 | 0.010 | 0.010 | 0.010 | 0.009 | 0.010 | 0.010 | 0.009 | 0.010 |
| *Carex ferruginea* | 0.778 | 0.041 | 0.036 | 0.043 | 0.042 | 0.036 | 0.035 | 0.040 | 0.036 | 0.039 | 0.192 | 0.117 | 0.208 | 0.086 | 0.104 | 0.103 | 0.085 | 0.243 | 0.153 | 0.119 |
| *Nardus stricta* | 0.777 | 0.025 | 0.015 | 0.018 | 0.019 | 0.012 | 0.014 | 0.016 | 0.014 | 0.019 | 0.257 | 0.513 | 0.547 | 0.289 | 0.094 | 0.453 | 0.094 | 0.555 | 0.136 | 0.257 |
| *Trifolium pratense aggr.* | 0.774 | 0.055 | 0.071 | 0.070 | 0.087 | 0.059 | 0.051 | 0.055 | 0.061 | 0.053 | 0.097 | 0.101 | 0.061 | 0.088 | 0.092 | 0.078 | 0.082 | 0.072 | 0.067 | 0.076 |
| *Plantago atrata* | 0.772 | 0.158 | 0.113 | 0.125 | 0.133 | 0.147 | 0.128 | 0.132 | 0.171 | 0.159 | 0.412 | 0.309 | 0.286 | 0.166 | 0.293 | 0.245 | 0.270 | 0.373 | 0.342 | 0.155 |
| *Hedysarum hedysaroides* | 0.762 | 0.028 | 0.022 | 0.025 | 0.025 | 0.022 | 0.022 | 0.023 | 0.022 | 0.022 | 0.059 | 0.078 | 0.107 | 0.082 | 0.061 | 0.089 | 0.060 | 0.097 | 0.076 | 0.076 |
| *Gentiana verna* | 0.755 | 0.077 | 0.089 | 0.081 | 0.087 | 0.095 | 0.079 | 0.079 | 0.095 | 0.075 | 0.134 | 0.155 | 0.236 | 0.182 | 0.130 | 0.174 | 0.143 | 0.182 | 0.135 | 0.176 |
| *Prunella grandiflora* | 0.754 | 0.337 | 0.195 | 0.306 | 0.201 | 0.334 | 0.328 | 0.339 | 0.314 | 0.354 | 0.019 | 0.017 | 0.017 | 0.018 | 0.019 | 0.017 | 0.017 | 0.017 | 0.020 | 0.018 |
| *Crocus albiflorus* | 0.749 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.009 | 0.010 |
| *Linum catharticum* | 0.748 | 0.025 | 0.032 | 0.031 | 0.030 | 0.045 | 0.030 | 0.025 | 0.030 | 0.026 | 0.019 | 0.020 | 0.020 | 0.023 | 0.020 | 0.023 | 0.023 | 0.022 | 0.020 | 0.020 |
| *Aster bellidiastrum* | 0.742 | 0.014 | 0.015 | 0.014 | 0.014 | 0.015 | 0.015 | 0.014 | 0.015 | 0.014 | 0.015 | 0.014 | 0.014 | 0.015 | 0.015 | 0.015 | 0.015 | 0.016 | 0.014 | 0.015 |
| *Alchemilla glabra aggr.* | 0.727 | 0.021 | 0.020 | 0.020 | 0.022 | 0.020 | 0.020 | 0.020 | 0.019 | 0.019 | 0.019 | 0.020 | 0.022 | 0.021 | 0.018 | 0.022 | 0.019 | 0.022 | 0.018 | 0.020 |
| *Aposeris foetida* | 0.726 | 0.018 | 0.027 | 0.025 | 0.023 | 0.021 | 0.019 | 0.020 | 0.020 | 0.018 | 0.013 | 0.013 | 0.020 | 0.014 | 0.013 | 0.013 | 0.012 | 0.017 | 0.016 | 0.014 |
| *Leontodon helveticus* | 0.723 | 0.044 | 0.039 | 0.041 | 0.040 | 0.045 | 0.045 | 0.044 | 0.048 | 0.044 | 0.052 | 0.047 | 0.046 | 0.052 | 0.051 | 0.048 | 0.050 | 0.049 | 0.054 | 0.045 |
| *Vaccinium gaultherioides* | 0.721 | 0.023 | 0.027 | 0.030 | 0.034 | 0.025 | 0.023 | 0.023 | 0.024 | 0.023 | 0.307 | 0.282 | 0.374 | 0.131 | 0.118 | 0.206 | 0.143 | 0.423 | 0.102 | 0.100 |
| *Campanula scheuchzeri* | 0.706 | 0.116 | 0.061 | 0.107 | 0.069 | 0.177 | 0.162 | 0.116 | 0.142 | 0.162 | 0.131 | 0.091 | 0.146 | 0.093 | 0.155 | 0.122 | 0.090 | 0.118 | 0.247 | 0.118 |
| *Phleum hirsutum* | 0.703 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.014 | 0.013 | 0.080 | 0.057 | 0.067 | 0.036 | 0.060 | 0.066 | 0.073 | 0.075 | 0.067 | 0.065 |
| *Pedicularis foliosa* | 0.699 | 0.021 | 0.024 | 0.021 | 0.022 | 0.019 | 0.018 | 0.017 | 0.018 | 0.019 | 0.191 | 0.147 | 0.259 | 0.183 | 0.169 | 0.285 | 0.208 | 0.190 | 0.105 | 0.192 |
| *Alchemilla conjuncta aggr.* | 0.685 | 0.026 | 0.019 | 0.021 | 0.024 | 0.020 | 0.021 | 0.022 | 0.021 | 0.023 | 0.183 | 0.093 | 0.160 | 0.053 | 0.126 | 0.063 | 0.082 | 0.166 | 0.095 | 0.085 |
| *Parnassia palustris* | 0.634 | 0.348 | 0.119 | 0.191 | 0.177 | 0.177 | 0.235 | 0.323 | 0.159 | 0.227 | 0.176 | 0.175 | 0.256 | 0.133 | 0.157 | 0.199 | 0.134 | 0.248 | 0.271 | 0.119 |

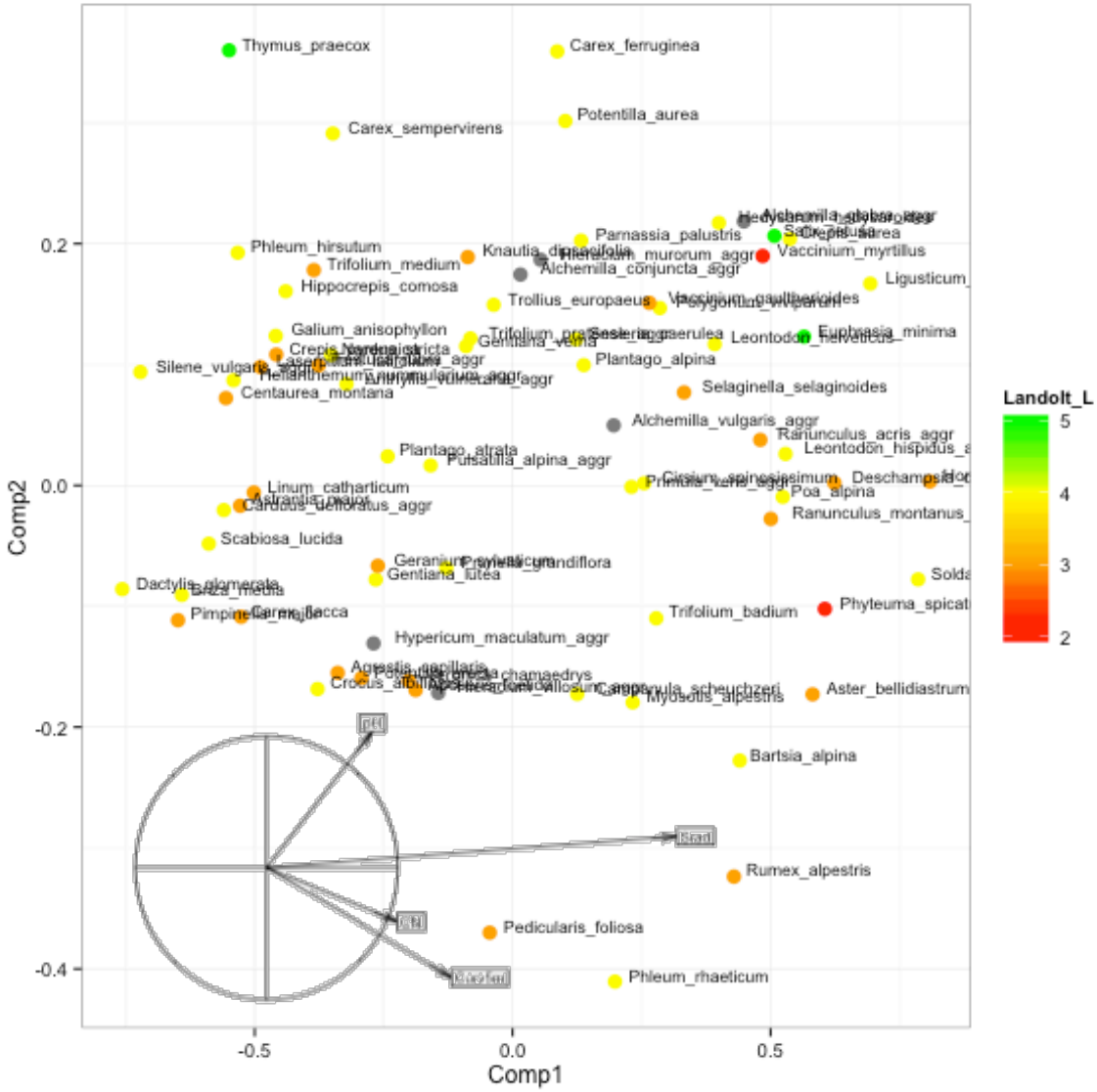
| Species | AUC | High S1 | High S2 | High S3 | High S4 | High S5 | High S6 | High S7 | High S8 | High S9 | High S10 | High N1 | High N2 | High N3 | High N4 | High N5 | High N6 | High N7 | High N8 | High N10 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Alchemilla vulgaris aggr.* | 0.946 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 |
| *Trifolium medium* | 0.927 | 0.008 | 0.008 | 0.008 | 0.008 | 0.007 | 0.007 | 0.008 | 0.008 | 0.008 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Astrantia major* | 0.924 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Geranium sylvaticum* | 0.899 | 0.008 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.539 | 0.448 | 0.426 | 0.526 | 0.435 | 0.379 | 0.468 | 0.480 | 0.483 | 0.342 |
| *Carduus defloratus aggr.* | 0.896 | 0.014 | 0.020 | 0.019 | 0.019 | 0.021 | 0.026 | 0.021 | 0.016 | 0.020 | 0.022 | 0.028 | 0.025 | 0.018 | 0.024 | 0.022 | 0.018 | 0.022 | 0.017 | 0.023 |
| *Poa alpina* | 0.889 | 0.015 | 0.017 | 0.016 | 0.011 | 0.011 | 0.011 | 0.011 | 0.015 | 0.011 | 0.008 | 0.009 | 0.009 | 0.013 | 0.013 | 0.021 | 0.009 | 0.009 | 0.009 | 0.010 |
| *Hippocrepis comosa* | 0.885 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.009 | 0.008 | 0.008 | 0.009 | 0.008 | 0.008 | 0.008 | 0.008 | 0.009 | 0.008 |
| *Salix retusa* | 0.883 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 |
| *Festuca rubra aggr.* | 0.881 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Crepis aurea* | 0.881 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.013 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 |
| *Rumex alpestris* | 0.879 | 0.344 | 0.282 | 0.241 | 0.358 | 0.389 | 0.328 | 0.197 | 0.160 | 0.279 | 0.017 | 0.030 | 0.023 | 0.015 | 0.017 | 0.018 | 0.032 | 0.033 | 0.013 | 0.025 |
| *Ranunculus acris aggr.* | 0.878 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 |
| *Euphrasia minima* | 0.876 | 0.387 | 0.512 | 0.478 | 0.451 | 0.565 | 0.542 | 0.506 | 0.240 | 0.493 | 0.027 | 0.036 | 0.030 | 0.022 | 0.026 | 0.028 | 0.034 | 0.029 | 0.021 | 0.030 |
| *Veronica chamaedrys* | 0.873 | 0.024 | 0.023 | 0.024 | 0.021 | 0.023 | 0.021 | 0.025 | 0.025 | 0.022 | 0.021 | 0.025 | 0.025 | 0.020 | 0.019 | 0.018 | 0.020 | 0.026 | 0.021 | 0.018 |
| *Knautia dipsacifolia* | 0.873 | 0.172 | 0.188 | 0.170 | 0.229 | 0.143 | 0.312 | 0.156 | 0.184 | 0.235 | 0.020 | 0.015 | 0.013 | 0.021 | 0.014 | 0.014 | 0.013 | 0.013 | 0.014 | 0.015 |
| *Helianthemum nummularium aggr.* | 0.871 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.019 | 0.021 | 0.014 | 0.013 | 0.013 | 0.013 | 0.013 | 0.014 | 0.013 | 0.013 |
| *Trifolium badium* | 0.871 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.011 | 0.010 | 0.010 | 0.010 | 0.033 | 0.023 | 0.016 | 0.194 | 0.130 | 0.015 | 0.020 | 0.018 | 0.023 | 0.018 |
| *Phleum rhaeticum* | 0.870 | 0.011 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.011 | 0.010 | 0.009 | 0.009 | 0.009 | 0.010 | 0.010 | 0.010 | 0.010 | 0.009 | 0.010 | 0.010 |
| *Potentilla erecta* | 0.865 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 |
| *Gentiana lutea* | 0.862 | 0.027 | 0.018 | 0.018 | 0.016 | 0.020 | 0.016 | 0.024 | 0.037 | 0.016 | 0.016 | 0.018 | 0.020 | 0.029 | 0.043 | 0.020 | 0.023 | 0.027 | 0.031 | 0.048 |
| *Silene vulgaris aggr.* | 0.861 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.024 | 0.025 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Myosotis alpestris* | 0.858 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.018 | 0.019 | 0.018 | 0.058 | 0.077 | 0.018 | 0.024 | 0.019 | 0.052 | 0.049 |
| *Cirsium spinosissimum* | 0.852 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.017 | 0.016 | 0.015 | 0.218 | 0.030 | 0.015 | 0.015 | 0.015 | 0.017 | 0.017 |
| *Crepis pyrenaica* | 0.848 | 0.014 | 0.013 | 0.012 | 0.010 | 0.012 | 0.009 | 0.011 | 0.014 | 0.010 | 0.008 | 0.008 | 0.009 | 0.020 | 0.024 | 0.009 | 0.009 | 0.009 | 0.015 | 0.011 |
| *Homogyne alpina* | 0.847 | 0.124 | 0.124 | 0.087 | 0.091 | 0.181 | 0.135 | 0.102 | 0.050 | 0.108 | 0.064 | 0.076 | 0.075 | 0.059 | 0.076 | 0.062 | 0.074 | 0.080 | 0.042 | 0.086 |
| *Primula veris aggr.* | 0.842 | 0.059 | 0.076 | 0.088 | 0.047 | 0.044 | 0.077 | 0.038 | 0.052 | 0.059 | 0.014 | 0.011 | 0.011 | 0.014 | 0.015 | 0.046 | 0.021 | 0.011 | 0.019 | 0.015 |
| *Trollius europaeus* | 0.842 | 0.011 | 0.011 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.011 | 0.012 | 0.012 | 0.011 | 0.011 | 0.153 | 0.057 | 0.011 | 0.012 | 0.011 | 0.025 | 0.013 |
| *Scabiosa lucida* | 0.841 | 0.014 | 0.013 | 0.016 | 0.021 | 0.026 | 0.019 | 0.027 | 0.015 | 0.020 | 0.091 | 0.082 | 0.061 | 0.075 | 0.058 | 0.041 | 0.055 | 0.067 | 0.071 | 0.043 |
| *Vaccinium myrtillus* | 0.841 | 0.014 | 0.013 | 0.013 | 0.012 | 0.013 | 0.012 | 0.013 | 0.013 | 0.012 | 0.009 | 0.009 | 0.009 | 0.010 | 0.010 | 0.009 | 0.009 | 0.009 | 0.010 | 0.010 |
| *Potentilla aurea* | 0.840 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.011 | 0.011 | 0.013 | 0.011 | 0.013 | 0.012 | 0.012 | 0.012 | 0.011 | 0.012 |
| *Hieracium villosum aggr.* | 0.837 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 | 0.006 |
| *Pimpinella major* | 0.836 | 0.013 | 0.010 | 0.011 | 0.011 | 0.011 | 0.010 | 0.010 | 0.012 | 0.010 | 0.025 | 0.023 | 0.020 | 0.039 | 0.031 | 0.024 | 0.031 | 0.022 | 0.031 | 0.028 |
| *Dactylis glomerata* | 0.832 | 0.036 | 0.044 | 0.037 | 0.052 | 0.045 | 0.054 | 0.039 | 0.031 | 0.046 | 0.009 | 0.009 | 0.010 | 0.008 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 |
| *Deschampsia cespitosa* | 0.830 | 0.129 | 0.132 | 0.099 | 0.095 | 0.147 | 0.132 | 0.110 | 0.066 | 0.105 | 0.041 | 0.044 | 0.045 | 0.036 | 0.046 | 0.039 | 0.043 | 0.036 | 0.031 | 0.045 |
| *Thymus praecox* | 0.827 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.009 | 0.009 | 0.008 | 0.009 | 0.009 | 0.008 | 0.009 | 0.009 | 0.009 | 0.008 |
| *Ligusticum mutellina* | 0.827 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.010 | 0.011 | 0.011 | 0.011 |
| *Galium anisophyllon* | 0.824 | 0.013 | 0.013 | 0.013 | 0.012 | 0.013 | 0.012 | 0.013 | 0.013 | 0.012 | 0.010 | 0.010 | 0.011 | 0.012 | 0.013 | 0.011 | 0.011 | 0.011 | 0.014 | 0.012 |
| *Agrostis capillaris* | 0.823 | 0.068 | 0.089 | 0.081 | 0.077 | 0.068 | 0.082 | 0.061 | 0.061 | 0.081 | 0.065 | 0.059 | 0.061 | 0.068 | 0.070 | 0.062 | 0.056 | 0.064 | 0.053 | 0.077 |
| *Laserpitium latifolium* | 0.820 | 0.020 | 0.017 | 0.019 | 0.020 | 0.017 | 0.017 | 0.018 | 0.022 | 0.019 | 0.077 | 0.066 | 0.043 | 0.232 | 0.154 | 0.046 | 0.180 | 0.065 | 0.146 | 0.121 |
| *Plantago alpina* | 0.818 | 0.149 | 0.164 | 0.144 | 0.205 | 0.135 | 0.177 | 0.123 | 0.136 | 0.184 | 0.042 | 0.037 | 0.035 | 0.043 | 0.030 | 0.028 | 0.044 | 0.028 | 0.036 | 0.039 |
| *Pulsatilla alpina aggr.* | 0.814 | 0.017 | 0.017 | 0.018 | 0.026 | 0.032 | 0.025 | 0.033 | 0.017 | 0.023 | 0.013 | 0.017 | 0.016 | 0.019 | 0.019 | 0.012 | 0.012 | 0.017 | 0.012 | 0.012 |
| *Hypericum maculatum aggr.* | 0.810 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Centaurea montana* | 0.808 | 0.047 | 0.053 | 0.049 | 0.058 | 0.048 | 0.071 | 0.046 | 0.046 | 0.071 | 0.034 | 0.033 | 0.032 | 0.284 | 0.240 | 0.041 | 0.037 | 0.031 | 0.114 | 0.063 |
| *Soldanella alpina* | 0.806 | 0.020 | 0.022 | 0.021 | 0.023 | 0.019 | 0.077 | 0.018 | 0.020 | 0.025 | 0.025 | 0.018 | 0.019 | 0.041 | 0.020 | 0.021 | 0.017 | 0.017 | 0.018 | 0.021 |
| *Briza media* | 0.805 | 0.011 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.011 | 0.011 | 0.012 | 0.011 | 0.012 | 0.012 | 0.012 | 0.012 | 0.011 | 0.012 |
| *Anthyllis vulneraria aggr.* | 0.804 | 0.128 | 0.135 | 0.142 | 0.109 | 0.148 | 0.181 | 0.139 | 0.124 | 0.185 | 0.083 | 0.064 | 0.108 | 0.077 | 0.048 | 0.053 | 0.138 | 0.081 | 0.065 | 0.072 |
| *Polygonum viviparum* | 0.803 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 |
| *Hieracium murorum aggr.* | 0.802 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.012 | 0.018 | 0.016 | 0.014 | 0.016 | 0.015 | 0.014 | 0.014 | 0.014 | 0.017 | 0.025 |
| *Sesleria caerulea* | 0.792 | 0.067 | 0.070 | 0.062 | 0.103 | 0.062 | 0.096 | 0.054 | 0.053 | 0.087 | 0.103 | 0.089 | 0.056 | 0.102 | 0.071 | 0.057 | 0.091 | 0.051 | 0.075 | 0.083 |
| *Bartsia alpina* | 0.792 | 0.018 | 0.017 | 0.016 | 0.015 | 0.018 | 0.018 | 0.016 | 0.016 | 0.017 | 0.365 | 0.294 | 0.349 | 0.516 | 0.448 | 0.303 | 0.307 | 0.296 | 0.443 | 0.465 |
| *Carex sempervirens* | 0.787 | 0.040 | 0.051 | 0.053 | 0.050 | 0.044 | 0.062 | 0.043 | 0.037 | 0.056 | 0.161 | 0.144 | 0.112 | 0.220 | 0.241 | 0.201 | 0.139 | 0.103 | 0.303 | 0.289 |
| *Selaginella selaginoides* | 0.782 | 0.038 | 0.045 | 0.045 | 0.053 | 0.048 | 0.062 | 0.048 | 0.038 | 0.044 | 0.011 | 0.010 | 0.011 | 0.011 | 0.012 | 0.011 | 0.010 | 0.010 | 0.010 | 0.011 |
| *Ranunculus montanus aggr.* | 0.782 | 0.086 | 0.110 | 0.097 | 0.134 | 0.100 | 0.144 | 0.096 | 0.082 | 0.127 | 0.016 | 0.018 | 0.017 | 0.015 | 0.017 | 0.016 | 0.016 | 0.017 | 0.017 | 0.016 |
| *Leontodon hispidus aggr.* | 0.779 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.008 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 |
| *Phyteuma spicatum* | 0.778 | 0.016 | 0.017 | 0.017 | 0.016 | 0.019 | 0.016 | 0.019 | 0.016 | 0.016 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 |
| *Carex ferruginea* | 0.778 | 0.069 | 0.134 | 0.086 | 0.067 | 0.059 | 0.097 | 0.058 | 0.067 | 0.085 | 0.253 | 0.228 | 0.258 | 0.464 | 0.445 | 0.349 | 0.195 | 0.227 | 0.220 | 0.293 |
| *Nardus stricta* | 0.777 | 0.011 | 0.012 | 0.011 | 0.013 | 0.011 | 0.014 | 0.011 | 0.012 | 0.014 | 0.393 | 0.212 | 0.064 | 0.534 | 0.342 | 0.111 | 0.067 | 0.064 | 0.208 | 0.400 |
| *Trifolium pratense aggr.* | 0.774 | 0.045 | 0.051 | 0.048 | 0.060 | 0.076 | 0.062 | 0.057 | 0.037 | 0.072 | 0.058 | 0.095 | 0.087 | 0.049 | 0.051 | 0.065 | 0.079 | 0.098 | 0.054 | 0.074 |
| *Plantago atrata* | 0.772 | 0.044 | 0.043 | 0.045 | 0.051 | 0.042 | 0.051 | 0.045 | 0.046 | 0.051 | 0.079 | 0.064 | 0.042 | 0.119 | 0.066 | 0.047 | 0.054 | 0.051 | 0.062 | 0.052 |
| *Hedysarum hedysaroides* | 0.762 | 0.021 | 0.031 | 0.024 | 0.024 | 0.023 | 0.027 | 0.023 | 0.021 | 0.026 | 0.091 | 0.076 | 0.064 | 0.078 | 0.069 | 0.068 | 0.058 | 0.059 | 0.062 | 0.075 |
| *Gentiana verna* | 0.755 | 0.039 | 0.046 | 0.054 | 0.057 | 0.049 | 0.058 | 0.042 | 0.035 | 0.053 | 0.145 | 0.123 | 0.186 | 0.104 | 0.142 | 0.154 | 0.109 | 0.106 | 0.108 | 0.134 |
| *Prunella grandiflora* | 0.754 | 0.203 | 0.108 | 0.164 | 0.304 | 0.114 | 0.162 | 0.197 | 0.181 | 0.191 | 0.021 | 0.025 | 0.019 | 0.022 | 0.018 | 0.018 | 0.023 | 0.022 | 0.019 | 0.026 |
| *Crocus albiflorus* | 0.749 | 0.010 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.010 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.010 | 0.009 | 0.009 | 0.009 | 0.009 | 0.010 |
| *Linum catharticum* | 0.748 | 0.052 | 0.056 | 0.052 | 0.038 | 0.051 | 0.048 | 0.049 | 0.045 | 0.047 | 0.028 | 0.030 | 0.032 | 0.031 | 0.039 | 0.033 | 0.032 | 0.032 | 0.030 | 0.036 |
| *Aster bellidiastrum* | 0.742 | 0.013 | 0.013 | 0.013 | 0.012 | 0.013 | 0.012 | 0.013 | 0.012 | 0.012 | 0.012 | 0.012 | 0.013 | 0.012 | 0.013 | 0.013 | 0.013 | 0.013 | 0.012 | 0.013 |
| *Alchemilla glabra aggr.* | 0.727 | 0.015 | 0.016 | 0.016 | 0.017 | 0.016 | 0.017 | 0.016 | 0.015 | 0.017 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.016 | 0.015 | 0.015 | 0.015 | 0.017 |
| *Aposeris foetida* | 0.726 | 0.013 | 0.014 | 0.014 | 0.013 | 0.015 | 0.014 | 0.014 | 0.013 | 0.014 | 0.011 | 0.009 | 0.010 | 0.009 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 | 0.010 |
| *Leontodon helveticus* | 0.723 | 0.029 | 0.027 | 0.030 | 0.037 | 0.038 | 0.034 | 0.041 | 0.030 | 0.033 | 0.056 | 0.060 | 0.066 | 0.043 | 0.038 | 0.042 | 0.057 | 0.076 | 0.064 | 0.039 |
| *Vaccinium gaultherioides* | 0.721 | 0.016 | 0.018 | 0.017 | 0.018 | 0.021 | 0.022 | 0.018 | 0.016 | 0.022 | 0.052 | 0.047 | 0.043 | 0.113 | 0.116 | 0.041 | 0.046 | 0.051 | 0.045 | 0.050 |
| *Campanula scheuchzeri* | 0.706 | 0.044 | 0.036 | 0.055 | 0.046 | 0.033 | 0.037 | 0.040 | 0.038 | 0.045 | 0.066 | 0.081 | 0.034 | 0.064 | 0.044 | 0.042 | 0.091 | 0.058 | 0.075 | 0.050 |
| *Phleum hirsutum* | 0.703 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.013 | 0.050 | 0.048 | 0.110 | 0.100 | 0.091 | 0.095 | 0.096 | 0.074 | 0.116 | 0.086 |
| *Pedicularis foliosa* | 0.699 | 0.012 | 0.013 | 0.013 | 0.019 | 0.013 | 0.014 | 0.013 | 0.012 | 0.015 | 0.034 | 0.027 | 0.030 | 0.027 | 0.030 | 0.026 | 0.030 | 0.030 | 0.030 | 0.030 |
| *Alchemilla conjuncta aggr.* | 0.685 | 0.027 | 0.063 | 0.040 | 0.033 | 0.029 | 0.025 | 0.027 | 0.027 | 0.046 | 0.079 | 0.090 | 0.092 | 0.335 | 0.254 | 0.121 | 0.119 | 0.146 | 0.119 | 0.120 |
| *Parnassia palustris* | 0.634 | 0.070 | 0.079 | 0.085 | 0.194 | 0.075 | 0.126 | 0.076 | 0.074 | 0.128 | 0.219 | 0.126 | 0.063 | 0.250 | 0.071 | 0.065 | 0.108 | 0.068 | 0.143 | 0.121 |

**Appendix S2** Co-inertia analysis fitted the PCA of the residuals of the species distribution models (on 208 species) and the PCA of the values of the most important variables for each plot. The co-inertia analysis did not allow separating the plant species in groups related to their reaction to light, humidity, acidity or nitrogen.

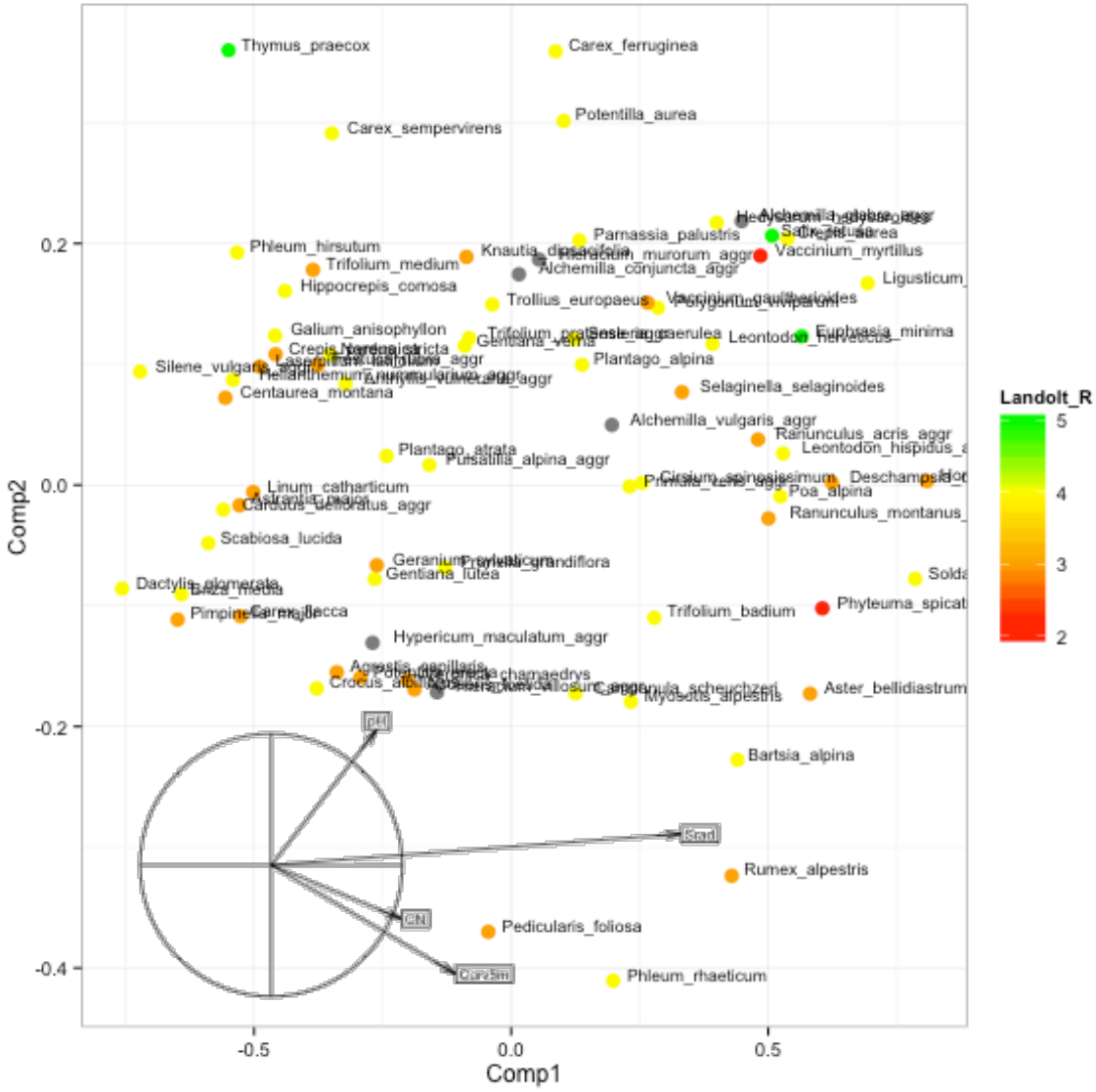
**S2.1** Co-inertia analysis showing the plant species with the most important variables. In colour, the AUC values of the SDMs on 75 species, from the higher values (in green) to the lower ones (in red). "Srad" corresponds to mean solar radiation, "pH" for soil pH, "CN" corresponds to C:N ratio, "Curv5m" corresponds to curvature at 5 m.



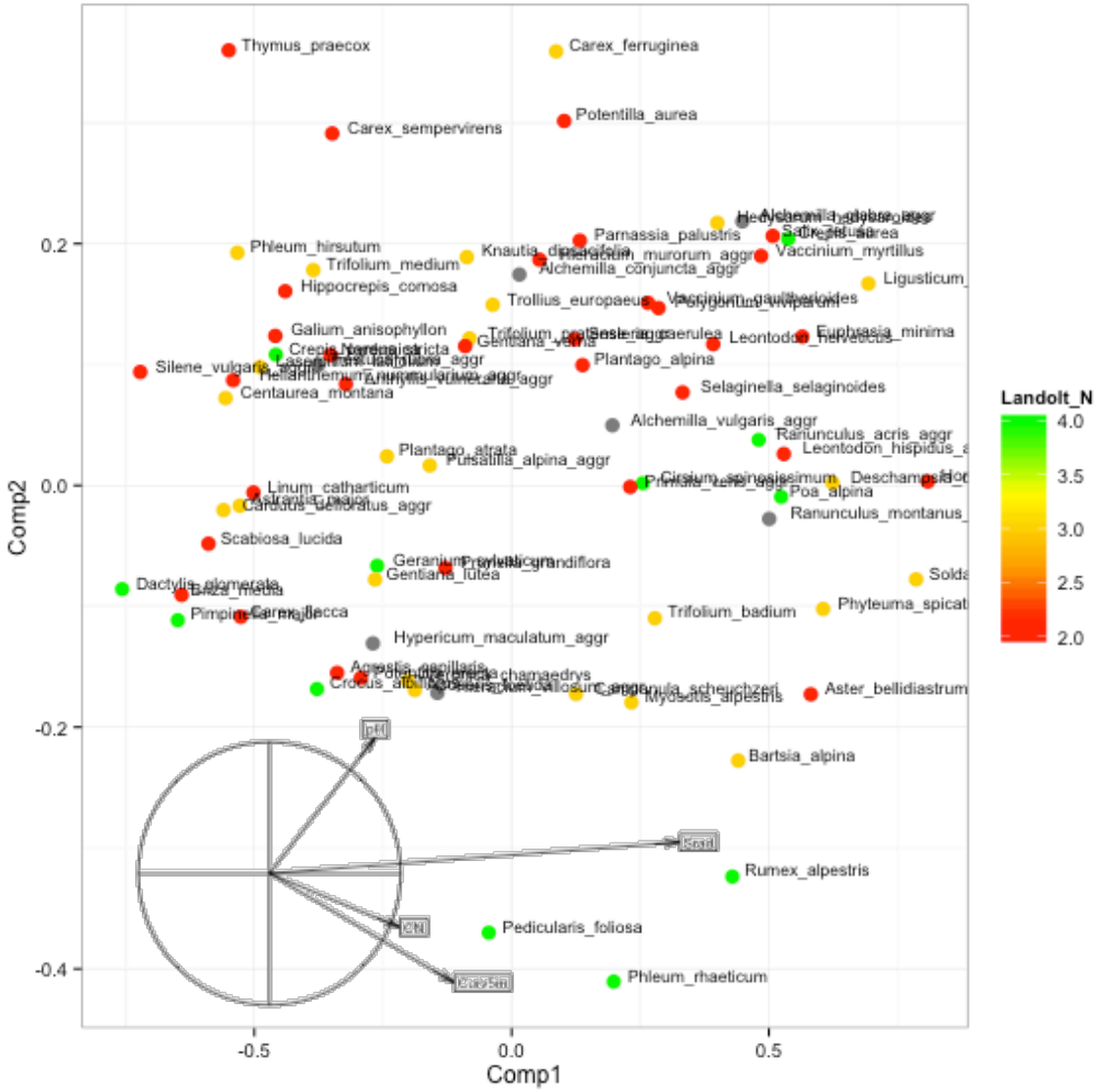
**S2.2** Co-inertia analysis showing the plant species with the most important variables. The colours represent the ecological values of light (L index values) from the higher values (in green) to the lower ones (in red). “Srad” corresponds to mean solar radiation, “pH” for soil pH, “CN” corresponds to C:N ratio, “Curv5m” corresponds to curvature at 5 m.



**S2.3** Co-inertia analysis showing the plant species with the most important variables. The colours represent the ecological values of acidity (R index values) from the higher values (in green) to the lower ones (in red). “Srad” corresponds to mean solar radiation, “pH” for soil pH, “CN” corresponds to C:N ratio, “Curv5m” corresponds to curvature at 5 m.



**S2.4** Co-inertia analysis showing the plant species with the most important variables. The colours represent the ecological values of nitrogen (N index values) from the higher values (in green) to the lower ones (in red). “Srad” corresponds to mean solar radiation, “pH” for soil pH, “CN” corresponds to C:N ratio, “Curv5m” corresponds to curvature at 5 m.



**S2.5** Co-inertia analysis showing the plant species with the most important variables. The colours represent the ecological values of humidity (F index values) from the higher values (in green) to the lower ones (in red). “Srad” corresponds to mean solar radiation, “pH” for soil pH, “CN” corresponds to C:N ratio, “Curv5m” corresponds to curvature at 5 m.