



UNIL | Université de Lausanne

Faculté de biologie
et de médecine

Ecole de Biologie

Predicting spatial patterns of functional traits

**Travail de Maîtrise universitaire ès Sciences en comportement,
évolution et conservation**
Master Thesis of Science in Behavior, Evolution and Conservation

par

Leila Rossier

Directeur : Professeur, Antoine Guisan
Superviseur (s) : Anne Dubuis, Docteur, Julien Pottier
Expert (s) : Docteur, Cécile Albert
DEE

(14 janvier, 2011)

Predicting spatial patterns of functional traits

Rossier Leila¹, Dubuis Anne¹, Pottier Julien ¹, Pellissier Loïc ¹, and Guisan Antoine^{1,2}

¹ Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland.

² Faculty of Geography and Paleontology, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland.

*Corresponding author: Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, CH-1015

Lausanne, Switzerland; Fax +41 21 692 42 65; E-mail: leila.rossier@unil.ch

Abstract

Functional traits are measurable plant features used by ecologists to understand and describe relationships between plants and their environment. As a result, a series of functional traits measured on a species can theoretically give indications on its ecology, life strategy and capability to cope with a particular environment. By extension traits can be aggregated at the community level to give insight on the ecosystem processes, services and resilience. This kind of information is particularly useful when studying plant communities in a global change context.

This study aims at testing the possible use of habitat suitability models to predict patterns of functional traits within communities in space, and explore which environmental predictors are best appropriate for this purpose.

The study took place in the western Swiss Alps, in Canton de Vaud. We measured three functional traits (specific leaf area, leaf dry matter content and height) for the 240 most common angiosperm species. With these traits, a set of functional indices (community weighted mean, Rao's index, functional richness, functional dispersion, functional divergence and functional evenness) was calculated for 202 vegetation plots. We used generalised additive models to relate indices for each plot to environmental predictors. Three different groups of environmental predictors were used to build the models: topoclimatic predictors, chemical edaphic and physical edaphic predictors. A variation partitioning analysis was performed to assess the respective contribution of the three different groups of predictors.

Our results show that it is possible to obtain good models for some functional patterns (community weighted mean of the trait, functional richness, Rao's index), while weak

predictive power is constantly obtained for functional evenness. As topo-climatic environmental variables proved the most important predictors; it was possible to project the model across the entire study area.

Our study showed that models for functional traits provide a powerful tool to assess ecological patterns in the landscape, with a more mechanistic orientation than simple species distribution models. This kind of models should prove useful for the prediction of plant communities.

Keywords: plant functional traits, habitat suitability modeling, SLA, LDMC, height, functional diversity, functional indices.

Introduction

An ecological community is not simply made of co-occurring species, but is a dynamic interactive system of interdependent populations. The study of ecological community highlights the interactions between species both in space and time, considering their abundances, distributions, structures and relationships (Putman 1996).

Functional properties of a community are widely used in ecology to quantify ecosystem properties or services (Küster *et al.* 2010). Functional traits are at the basis of that scientific approach. They can be defined as any morphological, physiological or phenological feature measurable at an individual level affecting its fitness and that can be seen as a surrogate of a function (Violle *et al.* 2007). Moreover plant communities are related to their environment: a variation exists in their functional traits dependent to the environmental conditions (Küster *et al.* 2010) and ecologists use this characteristic to give insight in a species strategy or fitness. Functional traits are considered adaptive if the phenotype occurring in a particular environment enhances the individual performance in that environment (e.g., improved resource acquisition, growth, survival and/or reproduction) relative to alternative phenotypic states (Ackerly 2003).

For this study, we selected three important functional traits, according to the literature (Albert *et al.* 2010, Lavergne *et al.* 2004, Roche *et al.* 2004, Reich *et al.* 1999, Wilson *et al.* 1999). The vegetative height, is associated with the competitive vigour of a plant, the specific leaf area (SLA), provides a measure of the allocation of biomass to light harvesting (Ackerly and Cornwell 2007) and finally the leaf dry matter content (LDMC) gives an indication of the leaf water content corresponding to the leaf content in mesophyll, the photosynthetic tissue (Grime *et al.* 1997). These traits are used as

surrogate of more complex functions as they are easy to measure in the field. The resulting data are quantitative and they allow a good understanding of the abilities of each species to catch the resources.

LDMC and SLA are negatively correlated (Cortez *et al.* 2007, Roche *et al.* 2004) and the trade-off between them characterizes two different strategies: a species with a high SLA (respectively a low LDMC) get light efficiently and is able to produce new leaves along the growing season (Albert *et al.* 2010, Cornelissen 2003, Reich *et al.* 1999). A species with low SLA (respectively high LDMC) grows more slowly, but is better able to keep nutrients and allocates resources to defensive chemicals (Coley 1988), it is also more resistant to physical hazards, for example against herbivory, wind or hail (Leishman *et al.* 2007).

If several traits are considered together, each species can be placed at a particular position in a functional niche space. Rosenfeld (2002) defined the functional niche as “analogous to the Hutchinsonian niche, except that the axes represent functional attributes or process rates, in place of environmental variables”. It is the functional space where the species are distributed (Figure 1).

A community formed by a group of species can be described from a functional point of view with indices characterizing the respective positions of the species in the functional space and this has the potential to reveal the processes that structure that community (Mouchet *et al.* 2010). Then it is useful to describe the functional diversity that is characterizing the distribution of functional units in the trait space. Indices characterizing functional diversity can be calculated for one or a set of trait (i.e. in a one- or multi-dimensional trait space).

The first and most simple index to describe a trait in a community is the community weighted mean for that particular trait. It corresponds to the mean of the trait value for

each species in the community weighted by its abundance. The formula is the following and the meanings of letters stand in table 1:

$$CWM = \sum_{i=1}^n \frac{A_s}{A} \times T_s$$

Villeger, Mason and Moullot (2008) proposed a framework splitting that diversity in three different aspects: evenness, divergence and richness. First functional evenness (Feve) quantifies the regularity with which the functional space is filled by species, weighted by their abundance (Mouchet *et al.* 2010). (Figure 2)

Then, functional divergence (FDiv) describes the distribution of abundance within the volume of functional trait occupied by species (Villeger, Mason and Moullot 2008), Figure 3. It is computed as the ratio of the sum of the distance between species to the centroid, weighted by the relative abundance of each species; this centroid is the centre of the convex hull surrounding the functional space.

The last index is the functional richness (Fric) (Cornwell *et al.* 2006, Villeger, Mason and Moullot 2008), which represents the number of different trait values in the functional space. (Figure 4) It is calculated as the area of convex hull between all species in the functional space. This index is not influenced by the respective abundances of the species.

Finally more complex indices exist that encompass several aspects of functional diversity. Botta-Dukat (2005) proposed an index of functional diversity based on Rao's quadratic entropy (Q) (Rao 1982) that incorporates both the relative abundances of species and a measure of the pairwise functional differences between species. The Rao's index is the mean functional dissimilarity between two randomly selected individuals, weighted by the product of species proportions (which can be based on any measure of species abundance, e.g. biomass, cover) (de Bello *et al.* 2010).

111 The Rao's index equals the Simpson's diversity index (Botta-Dukat 2005); the Simpson's
112 index represents the potential maximum value that the Rao's index can reach if species
113 are completely different (de Bello *et al.* 2007). (Figure 5)

114 The last type of index used in this study is the dispersion. It is the average distance to the
115 centroid (i.e. multivariate dispersion), when all species have equal abundances (i.e.
116 presence-absence data), as originally described by Anderson (2006). Laliberte and
117 Legendre (2010) improved this index accounting for species abundances. The centroid
118 is shifted towards the most abundant species, and then a weighted average distance to
119 this new centroid is computed using again the relative abundances as weights. This
120 index is correlated with Rao (Laliberte and Legendre 2010). (Figure 6)

121 All the above-mentioned indices can be computed only for places where the plant
122 community is known and where a vegetation inventory has been previously achieved.

123 Species diversity influences the resilience and resistance of ecosystems to
124 environmental change (Chapin *et al.* 2000). Moreover empirical and theoretical support
125 is accumulating for the idea that functional diversity might affect short-term ecosystem
126 resource dynamics and long-term ecosystem stability (Diaz and Cabido 2001). Beyond a
127 specific functional composition enables community to be more resistant against
128 invasion (Prieur-Richard and Lavorel 2000). For instance, leaf structure has been shown
129 to be related to leaf palatability and digestibility for herbivores (Hanley *et al.* 2007) and
130 consequently to litter quality and nutrient cycling (Cortez *et al.* 2007). A better
131 knowledge of the functional attributes of plant communities helps us to understand how
132 communities are organized and which types of interactions exist between the plant
133 species forming a particular community. This knowledge helps us to adapt our policy
134 and management to have the best yield and preserve the landscape.

But as they are good indicators of ecosystem functions, it could be useful to generalize this information, for example for management purposes.

In this study we propose to use statistical modeling to predict spatial patterns of functional traits. Statistical predictive models relate presences and absences of species (Guisan and Zimmermann 2000, Franklin 1998) or communities (Fischer 1990) to environmental factors to predict their distribution. These models have become an increasingly important tool to address various issues in ecology, biogeography, evolution, and more recently, in conservation biology and climate change research (Guisan and Thuiller 2005). Several relationships have been demonstrated between climatic factors and aspects of plants and afterwards between climatic factors and functional traits. For example Mooney and Dunn (1970) showed the convergent evolution of Mediterranean-climate and evergreen sclerophyll shrubs. More recently, Diaz, Cabido and Casanoves (1998) detected, on a quantitative, statistically conservative basis, consistent linkages between climatic factors and numerous plant traits, over a broad spectrum of environmental conditions and plant growth forms. Barboni *et al.* (2004) showed that most plant traits show different trends in the gradient of abundance with respect to climate, depending on life form, leaf type and leaf phenology in a Mediterranean-climate.

Consequently, we expect that the functional attributes of a community respond to the same environmental factors than single species (Zimmermann and Kienast 1999) and accordingly to be predictable with the same techniques.

Previous studies have predicted relative proportion of leaves (Küster *et al.* 2010) or flower morphology (Pellissier *et al.* 2010), but to our knowledge, continuous traits values, and more interestingly patterns of functional diversity have never been predicted in this way. We used a set of topo-climatic and edaphic factors to predict

160 patterns of functional traits and functional diversity described with the indices detailed
161 above.

Material and Methods

Study area

The study area is located in the western Swiss Alps (Vaud, Switzerland, 46°10' to 46°30'N; 6°60' to 7°10'E). It covers 700km² with elevation ranging from 375 meters to 3210 meters (Figure 7). The climate of this region is temperate. The annual mean temperatures and total precipitations vary, respectively, from 8 °C and 1200mm at 600m elevation to -5°C and 2600mm at 3000m elevation (Bouët 1985). Human impact is important in this region; agriculture is quite intensive up to subalpine areas (addition of fertilizer, frequent mowing and intense grazing in places). Moreover tourism is developed in some part of the area, with ski resorts and hiking treks.

Sampled species

The most common angiosperm species (240 in total, see complete list in table 3 in the Appendix) of the study area were sampled.

The collect took place between 7 and 12 am during the summer 2010. The sampling was realized as much as possible in contrasted exposures, slopes and elevation to cover as much as possible of the total distribution range of each species and get a picture of the intra-specific trait variation. Between 4 and 20 individuals per species were sampled.

One well-developed entire leaf was collected per individual. The leaves were put into a plastic bag with water and kept at cool temperature in an icebox to be sure they stay saturated in water until measurement in the lab. In the field, the height of the highest leaf of the plant was also measured. In the lab, the leaves were weighted to obtain the fresh mass, scanned and analyzed with the software "Medición de Objetos" (V.4.2 ©

1999-2000) to calculate their surface, finally they were dried in an air oven at 60°celsius during 3 days and weighted again to measure their dry mass (Cornelissen *et al.* 2003).

Traits measured

The vegetative height was measured in the field as the distance between the top of the photosynthetic tissue and the ground in mm. Specific leaf area (SLA) was calculated as the ratio of leaf surface to its dry mass, expressed in mm² mg⁻¹. Leaf dry matter content (LDMC) is the ratio of leaf dry mass to its saturated fresh mass (in mg g⁻¹), these two traits were measured according to the protocol proposed by Cornelissen *et al.* (2003) and Garnier *et al.* (2001).

Topo-climatic and soil predictors

Five topo-climatic predictors were extracted from GIS maps obtained from a DEM and meteorological stations data (see for calculations, Randin *et al.* 2009a): 1) degree day in [day * deg] (fddeg0), which is calculated with this formula:

$$Ddeg = \sum_{j=1}^n \max[0, (T_j - T_0)]$$

(Tuhkanen 1980)

where T₀ is the minimum temperature which allows plant growth and T_j is the daily mean temperature; 2) the moisture index, which is the difference between the average daily precipitation and the average daily potential evapotranspiration in [0.1mm/month] (fmmind68); 3) slope in [deg] (fslope); 4) solar radiation in [Kj/day] (fsumradyy) and; 5) topographic position (ftopos). Two groups of edaphic predictors were also considered; chemical variables (the pH, the content in nitrogen and phosphorus) and physical variables (the texture, i.e. the respective percentage of clay, silt and sand).

210

211 ***Vegetation data***

212 The vegetation data (species occurrences) used in our analysis derive from fieldwork
213 conducted between 2002 and 2009 in the study area (Randin *et al.*, 2009a, b, Dubuis *et*
214 *al.* in review). In total, 912 4m² vegetation plots were inventoried according to a
215 random-stratified sampling design (Hirzel and Guisan 2002) based on elevation, slope
216 and aspect. All plant species were inventoried and, in 252 plots, pH, nitrogen content
217 and texture of the soil were also measured. The sampling was limited to open non-
218 woody vegetation. For further analyses, we kept only those plots for which we had trait
219 data for more than 80% of the relative vegetation cover. This corresponded to 195 plots
220 for which we had all edaphic and topo-climatic data, 202 plots with topo-climatic data
221 and chemical edaphic data and 605 plots with climatic predictors only.

222

223 ***Indices***

224 With the three traits (height, SLA and LDMC), several functional diversity indices were
225 calculated.

226 The first one, the community weighted mean (CWM) was calculated as the mean of each
227 trait for each species of the community weighted by the abundances of the species
228 (Lavorel *et al.* 2008).

229 We used the function dbFD from the “FD” R package (Laliberte and Legendre 2010) to
230 compute the three following indices described by Villeger, Mason and Mouillot (2008).

231 Functional evenness (Feve) is calculated with the minimum spanning tree linking all
232 species of the community in the functional space. Functional divergence (Fdiv), for
233 several traits functional divergence relates to how abundance is distributed within the
234 volume of functional trait space occupied by species (Laliberte and Legendre 2010). The

function dbFD cannot calculate Fdiv for one trait; it works only for traits together. Functional richness (Fric) is measured as the convex hull volume for all traits together, and as a range when only one trait is considered, it does not take into account the abundance of species. Rao's index was computed with the method from de Bello *et al.* (2009). And finally, an index measured dispersion: the Functional dispersion (FDis) (Laliberte and Legendre 2010).

In this study, the functional diversity was described in total by 20 indices; each index was calculated for each trait separately (one-dimensional trait space) and all traits together (tri-dimensional trait space) except for Fdiv, which cannot be calculated for each trait separately, and CWM, which cannot be calculated for all traits together.

Statistical analyses and modelling

The spatial distribution of each index was modeled with generalized linear model (GLM) (Nelder *et al.* 1972) and with generalized additive models (GAM) (Guisan, Edwards and Hastie 2002) assuming a Gaussian distribution implemented in R 2.11.1.

GLMs were tested with a polynomial of degree 2 and the GAMs were run with 4 degrees of freedom. Following an exploratory approach, we ran three types of models for each index; models with topo-climatic predictors (202 plots), models with topo-climatic and chemical soil predictors (202 plots) and models with topo-climatic, chemical and physical soil predictors (195 plots).

The fit of the model was estimated by calculating the adjusted geometric mean square improvement R² (Nagelkerke 1991), rescaled to a maximum of 1 and adjusted for the number of observations and predictors in the model.

The evaluation of predictive power of the models was done with a repeated (100times) split-sample procedure. An evaluation dataset was obtained by randomly splitting the

original dataset into two 70%-30% partitions, using the 70% partition for fitting the models and the 30% left out partition for independently evaluating them. For each split-sample repetition and for each model, a Spearman's rank correlation between observed and predicted index value was calculated on the evaluation data set. The final evaluation value is the mean of the 100 correlations.

To understand the respective importance of the three classes of predictors (topo-climatic, chemical and physical attributes of the soil) in the models, a variation partitioning based on partial correlation analyses (Figure 8) was realized on GAM models with 4 degrees of freedom. This approach allows in our case partitioning of variation into height identifiable fractions of deviance (1) pure topo-climatic (CL), (2) pure chemical attributes of the soil (CH), (3) pure physical attributes of the soil (PH), (4) shared chemical and physical properties of the soil (CH-PH), (5) shared topo-climatic and chemical properties of the soil (CL-CH), (6) shared topo-climatic and physical properties of the soil (CL-PH), (7) shared the three classes (CL-CH-PH), (8) unexplained variation (see Borcard *et al.* (1992) and Randin *et al.* (2009) for implementation).

As continuous soil maps do not exist for our study area, projections were calculated for the GAM models with 4 degrees of freedom containing only topo-climatic predictors. 605 plots were used to calibrate the models.

Projections were realized for the following models: the community weighted mean, the functional richness index and the Rao's index for all traits separately.

Results

Traits measurement

A total of 1714 leaves were collected during the summer 2010. The average of each species was realized for each trait. Together with data from a previous field campaign we obtained the three traits for 240 species. The list of the plant species is displayed in table 3 in the Appendix.

Models

Here we present only GAMs results, as GLMs yielded globally similar results, they are presented in table 4 of the Appendix. Table 2 shows the evaluation of predictive power (Rho) and fit (d2adj) for all models with the three different groups of predictors.

For one-dimensional indices, the evaluation values were in most cases better than those of tri-dimensional indices. For one-dimensional indices, CWM and Fric gave the best results. For tri-dimensional indices, Fric had the best model.

The height was the trait, giving the better models, followed by LDMC, SLA, and all traits together. For one-dimensional indices, the evaluation values were in most cases better than those of tri-dimensional indices. For one-dimensional indices, CWM and Fric gave the best results. For tri-dimensional indices, Fric had the best model. Fdis gave good evaluation values for height, but very bad evaluation values for SLA and all traits together. Feve gave bad evaluation values for all models.

For one-dimensional indices, the predictive power and the fit increased with adjunction of soil chemical attributes for CWM and Fric indices. Adjunction of the physical attributes of soil increased the predictive power and the fit of all indices of LDMC and Fric of height. For SLA, the predictive power increased but the fit decreased when chemical and physical attributes of the soil were added.

305

306 ***Variation partitioning***

307 The respective importance of the three different groups of environmental variables
308 (topo-climatic, physical and chemical) in the models was determined with a variation
309 partitioning analysis (Figure 9, table 5 in Appendix). The total variance explained in the
310 models was between 25% and 70%.

311 Climatic predictors explained the greatest proportion of variance in our models
312 (between 10 and 35%). Soil chemical properties explained only a little part of the
313 variance (less than 15%), except for the LDMC indices, for which they proved more
314 important (about 20%). Soil physical composition played a minor role in explaining the
315 variance (less than 10%). The variances of functional evenness indices were largely
316 unexplained (around 70%), as were the functional diversity indices for SLA.

317 As regards to the interactions, those between soil predictors (chemical and physical)
318 explained less than those containing climatic predictors.

319

320 ***Projection maps***

321 All projections displayed in this section result from models with topo-climatic predictors
322 only. We choose to show maps for CWM, Fric and Rao as their models gave overall good
323 evaluation results.

324 Figure 10 represents projections of CWM model for each trait. The first map (Figure
325 10a) gives information about the height of the vegetation. Plant species showed high
326 growth in the plains, and then their size decreases with increasing altitude. Plants
327 growing on northern slope are smaller than those on southern slopes. The second map
328 (Figure 10b) represents CWM for SLA. In the plain, between 400 and 800 meters the leaf
329 area is big, in mid-altitude it is intermediate, and becomes very small at the top. This

index follows the same pattern as the previous map, with greater variation in space. The third map (Figure 10c) represents leaf dry mass content. High values were most of the time found on the peaks and low values were in the plain and on valleys. The three previous projections (Figure 10) predicted high plants with high SLA and low LDMC, in low altitude and short plants with low SLA and high LDMC on the peaks.

For Fric for height (Figure 11a), no high values were predicted. In the plain up to mid-elevation the richness was medium, and very low on the peaks. The values were highest in the south-exposed slopes. For Fric for SLA (Figure 11b), the highest richness was predicted at low altitude. For Fric for LDMC (Figure 11c), high values were predicted on the peaks, and low values in the plain or at very high altitude (around 3000 meters) (right bottom of the map).

The maps for Rao's indices showed more variation in space than the previous maps. Values of Rao's index for height (Figure 12a) were higher in the plain and on the south-exposed slopes, and smaller on the mountain tops and in the north-exposed slopes. Figure 12b presented Rao's index for SLA. Low values were found on the peaks (bottom of the map) and high values are spread across the other peaks. Mid-values were obtained in the plain. Rao's index values for LDMC (Figure 12c) gave high values on the peaks and low values in the valley.

Discussion

Our explorative approach allowed us to analyse our extensive data set, to underline which indices were easy to model, and which of them could be successfully projected in

our study area. Additionally, different patterns of plant communities could be represented and we found what predictors were important in this regard.

Functional traits models

Our results underline the power of the models for height, because this trait depends especially on climatic variables and has been shown to be strongly correlated with temperature (Barboni *et al.* 2004) and consequently strongly correlated with an altitudinal gradient. The models for SLA gave not so good values for predictive power and fit, except for CWM and because of this the projections maps for Fric and Rao gave unclear patterns, with high values spread across the other peaks. The better model for LDMC was Fric and the other gave us bad values for predictive power and fit for the models with only topo-climatic predictors, because as showed before, LDMC needs soil predictors to give better predicted maps. An explanation for those results can be found in the measurement of these traits; for height we measured only one time each sample, whereas for LDMC and SLA two measurement steps were done, and maybe for SLA the surface measurements are biased.

Concerning one-dimensional indices, CWM and Fric were the ones giving the highest fit and predictive power values. From an ecological point of view they represent more simple measures, unlike the other diversity indices; CWM represents the average trait weighted by the abundance of each species, Fric is the number of different traits in the functional space and it is not weighted by the relative abundances of species. On the contrary, Feve shows constantly weaker predictive power and weaker fit values, because this index is ecologically more complex. As a result, it is difficult to predict how the traits are distributed in functional space, because the available predictors did not play an important role in the models for Feve. This index is more influenced by other

factors such as the competition between plant species or land-use. Rao's index gave good results for height, in the average for LDMC and really weak predictions for SLA. These results in part from same explanations described before, namely the measurement of the traits was different.

Our results show that it is not possible to obtain fair prediction for multi-dimensional indices. This is probably due to the fact that some traits (SLA and LDMC in our case) are negatively correlated (Roche *et al.* 2004) and therefore could cancel each other, producing confuse patterns.

Globally, the more predictors are used, the greater the fit, but the lower the predictive power. In our case, models were really improved when chemical predictors were added, but when physical predictors were added to the former, the too great number of predictors made it impossible to improve both the predictive power and the fit. These results are over fitted and cannot give correct predictions on independent data. It would be necessary to test if models with only physical predictors added to topo-climatic would give better results than the other models.

Variation partitioning

The climatic predictors explain the greatest part of the variation in our models. This can be explained by the topography of our study area, which encompasses a large altitudinal gradient, causing climatic conditions to be highly dissimilar between the plain and the peaks and offering very diverse environment for the species to grow in. Several studies have shown that plants and therefore ecosystem processes are related to climatic conditions Thuiller *et al.* (2004), Chapin *et al.* (2000). More recently, Pellissier *et al.* (2010) showed the impact of the climate on the growth of the plants and on the functional traits, namely they showed a decreasing trend of plant size with increasing

altitude in grasslands, an increasing proportion of plants with mainly vegetative reproduction and of species pollinated by insects with possible selfing toward higher altitudes.

Height and SLA were more explained by climatic predictors than LDMC, which needs edaphic predictors to obtain good predictive power and fit values. LDMC is more influenced by soil factors than the other traits, because it is related to the storage of plant resources, which is itself linked to the quantity of nutrients present in the soil and indirectly linked with the pH that influence nutrient availability.

Spatial predictions

Because continuous soil maps do not exist for our entire study area, it is currently impossible to project the models with chemical and physical soil predictors.

Among traits, height was the easiest to project and shows clear patterns with high plants in the plain and smaller plants toward higher altitude, because this trait depends especially on climatic variables (Wilson *et al.* 1999). Well known strategies are represented in the CWM maps; on the one hand at low elevations high plants with high SLA and low LDMC are found, because there the plants are not limited by light, availability of water and nutrients, and the growing season is long enough to allow them to complete their life cycle. On the other hand at high altitudes, plants have limited time to grow and complete their life cycle, because of snow persisting during a long period, shortening their growing season. Moreover, plants receive less solar radiations and temperatures fluctuate much between day and night. Furthermore the impact of the exposure is visible in the CWM maps; this predictor is linked with the quantity of solar radiation during the day with plants exposed to south obtaining more light than plants growing in northern slopes, which have an influence on the traits and distinctly on

height. These harsh conditions at high elevations constrain plants growth, resulting in their short stature, with high LDMC and low SLA.

These predicted patterns follow an altitudinal gradient and confirm the study of Pellissier *et al.* (2010), which showed a decreasing trend of plant size with increasing altitude in grasslands. Moreover our projections are consistent with the expectation that LDMC is negatively correlated with SLA (Cortez *et al.* 2007) and SLA is negatively correlated with the altitudinal gradient (Roche *et al.* 2004, Pierce *et al.* 1994).

The functional diversity (Fric and Rao) maps picture quite similar patterns, namely richness in traits. But both show different characteristic; while Fric counts the richness in traits, Rao quantifies trait differences and count them.

For Fric measured on height, we never obtained the maximum possible values, likely because of the intense intra-specific competition, one never finds at the same place small, medium and high plants. The Fric SLA map shows higher values at low altitude (many different leaf types) and then decrease until the highest altitude; because the inter-specific competition is too hard to permit the growth of high-stature and small-stature plants in the same place.

The patterns showed in the map for Fric LDMC is the opposite, the richness in trait is high also at high altitude. This is explained by the presence of two different leaf shapes; on rocks, some species have succulent leaves as *Saxifraga* genus, *Thlaspi rotundifolium* or *Primula Auricula* while on shallow soils species have rather dry leaves as *Agrostis* genus, *Carex* genus or *Poa Minor* to survive to harsh conditions. The two strategies enable plants in two opposite ways to avoid the dryness, to resist to the frost and to be more resistant to variation in temperature (Korner 2003).

Rao's map for height shows clear patterns compared with the other; in the plain we obtain the higher values of Rao, which means that the distances between traits are

larger and represent a more diversified type of traits than on the peaks. Rao's map for SLA reveals patterns that are more difficult to interpret and the values for predictive power and fit are the worst of our maps projections. Rao's map for LDMC gives us clear patterns: the plants are similar on the traits level in plain, because they are not limited by water availability or at least less than at high altitude and this explain why the values of Rao are close to zero there.

Future prospects

As our study confirmed that it is possible to model functional trait patterns along environmental gradients, we could use this approach to estimate the changes in trait distribution under future environmental scenarios, as done in Küster *et al.* (2010), but using quantitative traits and at a much finer scale. Having knowledge about the future distribution of vegetation type could prove particularly interesting in our study area. For example, it would allow predicting, through LDMC or SLA, the forage quality and profitability. Cornellissen *et al.* (1999) showed that high SLA and consequently low LDMC leaves plants species reduced the litter quality, moreover Duru *et al.* (2008) showed, that plants with lower LDMC had higher plant component digestibility, but lower leaf proportion. An increase in temperature could represent a problem, as it has been demonstrated that temperature influences LDMC (Buxton 1996) and that high temperatures increase plant development rate, reducing leaf / stem ratio and digestibility coefficients (Andueza *et al.* 2010). This could impact livestock farming, a quite important economic activity for the area.

It is one example of issue that encourages us having a better knowledge about functional aspect of ecosystems.

478 With this study, we confirmed the usefulness of trait-centred models. This approach can
479 provide a modelling tool with a more mechanistic orientation, an important quality that
480 is likely to provide us with more robust projections (Küster *et al.* 2010).

481 Acknowledgements

482

483 I acknowledge especially Anne Dubuis, for her help all along my project. Thanks to Julien
484 Pottier for constructive discussions, explanations and advices and Loïc Pellissier for his
485 statistics codes. Thanks to Antoine Guisan and all the “Bioassemble” team. Many thanks
486 to all people, who helped me during the field campaign; especially Pascal Vittoz for
487 plants determination and Phillipe Châtelain for lab work and the collect. Finally, I would
488 like to thank François Bonnet and his family for their hearty welcome in Pont-de-Nant.

References

- Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* **164**:S165-S184.
- Ackerly, D. D., and W. K. Cornwell. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* **10**:135-145.
- Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology* **24**:1192-1201.
- Anderson, M. J., K. E. Ellingsen, and B. H. McCord. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* **9**:683-693.
- Andueza, D., P. Cruz, A. Farruggia, R. Baumont, F. Picard, and B. Michalet-Doreau. 2010. Nutritive value of two meadows and relationships with some vegetation traits. *Grass and Forage Science* **65**:325-334.
- Barboni, D., S. P. Harrison, P. J. Bartlein, G. Jalut, M. New, I. C. Prentice, M. F. Sanchez-Goni, A. Spessa, B. Davis, and A. C. Stevenson. 2004. Relationships between plant traits and climate in the Mediterranean region: A pollen data analysis. *Journal of Vegetation Science* **15**:635-646.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. PARTIALLYING OUT THE SPATIAL COMPONENT OF ECOLOGICAL VARIATION. *Ecology* **73**:1045-1055.
- Botta-Dukat, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* **16**:533-540.
- Bouët, M. 1985. Climat et météorologie de la Suisse romande. Payot Lausanne.
- Buxton, D. R. 1996. Quality-related characteristics of forages as influenced by plant environment and agronomic factors. *Animal Feed Science and Technology* **59**:37-49.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. *Nature* **405**:234-242.
- Coley, P. D. 1988. Effects of plant-growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**:531-536.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**:335-380.
- Cornelissen, J. H. C., N. Perez-Harguindeguy, S. Diaz, J. P. Grime, B. Marzano, M. Cabido, F. Vendramini, and B. Cerabolini. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* **143**:191-200.
- Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering: Convex hull volume. *Ecology* **87**:1465-1471.
- Cortez, J., E. Garnier, N. Perez-Harguindeguy, M. Debussche, and D. Gillon. 2007. Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant and Soil* **296**:19-34.
- de Bello, F., S. Lavergne, C. N. Meynard, J. Leps, and W. Thuiller. 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science* **21**:992-1000.

- de Bello, F., J. Leps, S. Lavorel, and M. Moretti. 2007. Importance of species abundance for assessment of trait composition: an example based on pollinator communities. *Community Ecology* **8**:163-170.
- de Bello, F., W. Thuiller, J. Leps, P. Choler, J. C. Clement, P. Macek, M. T. Sebastia, and S. Lavorel. 2009. Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science* **20**:475-486.
- Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* **16**:646-655.
- Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* **9**:113-122.
- Duru, M., P. Cruz, A. H. K. Raouda, C. Ducourtieux, and J. P. Theau. 2008. Relevance of Plant Functional Types based on Leaf Dry Matter Content for Assessing Digestibility of Native Grass Species and Species-Rich Grassland Communities in Spring. *Agronomy Journal* **100**:1622-1630.
- Fischer, H. S. 1990. Simulating the distribution of plant communities in an alpine landscape.
- Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science* **9**:733-748.
- Garnier, E., B. Shipley, C. Roumet, and G. Laurent. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* **15**:688-695.
- Grime, J. P., K. Thompson, R. Hunt, J. G. Hodgson, J. H. C. Cornelissen, I. H. Rorison, G. A. F. Hendry, T. W. Ashenden, A. P. Askew, S. R. Band, R. E. Booth, C. C. Bossard, B. D. Campbell, J. E. L. Cooper, A. W. Davison, P. L. Gupta, W. Hall, D. W. Hand, M. A. Hannah, S. H. Hillier, D. J. Hodkinson, A. Jalili, Z. Liu, J. M. L. Mackey, N. Matthews, M. A. Mowforth, A. M. Neal, R. J. Reader, K. Reiling, W. RossFraser, R. E. Spencer, F. Sutton, D. E. Tasker, P. C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**:259-281.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**:993-1009.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147-186.
- Hanley, M. E., B. B. Lamont, M. M. Fairbanks, and C. M. Rafferty. 2007. Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology Evolution and Systematics* **8**:157-178.
- Hirzel, A., and A. Guisan. 2002. Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling* **157**:331-341.
- Korner, C. 2003. Limitation and stress - always or never ? *Journal of Vegetation Science* **14**:141-143.
- Küster, E. C., S. M. Bierman, S. Klotz, and I. and Kühn. 2010. Modelling the impact of climate and land use change on the geographical distribution of leaf anatomy in a temperate flora. *Ecography*.
- Laliberte, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**:299-305.
- Lavergne, S., J. D. Thompson, E. Garnier, and M. Debussche. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* **107**:505-518.

- Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quetier, A. Thebault, and A. Bonis. 2008. Assessing functional diversity in the field - methodology matters! *Functional Ecology* **22**:134-147.
- Leishman, M. R., T. Haslehurst, A. Ares, and Z. Baruch. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist* **176**:635-643.
- Mooney, H. A., and E. L. Dunn. 1970. Convergent Evolution of Mediterranean-Climate Evergreen Sclerophyll Shrubs. *Evolution* **24**:292-&.
- Mouchet, M. A., S. Villegger, N. W. H. Mason, and D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* **24**:867-876.
- Mouillot, D., N. W. H. Mason, and J. B. Wilson. 2007. Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia* **152**:729-737.
- Nagelkerke, N. J. D. 1991. A NOTE ON A GENERAL DEFINITION OF THE COEFFICIENT OF DETERMINATION. *Biometrika* **78**:691-692.
- Nelder, J. A., and Wedderburn, R. W. 1972. GENERALIZED LINEAR MODELS. *Journal of the Royal Statistical Society Series A-General* **135**:370-&.
- Pellissier, L., B. Fournier, A. Guisan, and P. Vittoz. 2010. Plant traits co-vary with altitude in grasslands and forests in the European Alps. *Plant Ecology* **211**:351-365.
- Pierce, L. L., S. W. Running, and J. Walker. 1994. Regional-Scale Relationships of Leaf-Area Index to Specific Leaf-Area and Leaf Nitrogen-Content. *Ecological Applications* **4**:313-321.
- Prieur-Richard, A. H., and S. Lavorel. 2000. Do more diverse plant communities greater resistance to invasions? *Revue D Ecologie-La Terre Et La Vie*:37-51.
- Putman, R. J. 1996. *Community ecology*. Chapman & Hall, London [u.a.].
- Randin, C. F., H. Jaccard, P. Vittoz, N. G. Yoccoz, and A. Guisan. 2009. Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science* **20**:996-1008.
- Rao, C. R. 1982. DIVERSITY AND DISSIMILARITY COEFFICIENTS - A UNIFIED APPROACH. *Theoretical Population Biology* **21**:24-43.
- Reich, P. B., D. S. Ellsworth, M. B. Walters, J. M. Vose, C. Gresham, J. C. Volin, and W. D. Bowman. 1999. Generality of leaf trait relationships: A test across six biomes. *Ecology* **80**:1955-1969.
- Roche, P., N. Diaz-Burlinson, and S. Gachet. 2004. Congruency analysis of species ranking based on leaf traits: which traits are the more reliable? *Plant Ecology* **174**:37-48.
- Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. *Oikos* **98**:156-162.
- Thuiller, W., S. Lavorel, G. Midgley, S. Lavergne, and T. Rebelo. 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology* **85**:1688-1699.
- Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. *Acta phytogeog. Suecia*:1-105.
- Villegger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**:2290-2301.
- Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* **116**:882-892.

632 Wilson, P. J., K. Thompson, and J. G. Hodgson. 1999. Specific leaf area and leaf dry matter
633 content as alternative predictors of plant strategies. *New Phytologist* **143**:155-
634 162.

635 Zimmermann, N. E., and F. Kienast. 1999. Predictive mapping of alpine grasslands in
636 Switzerland: Species versus community approach. *Journal of Vegetation Science*
637 **10**:469-482.

Table 3: List of the 240 species for which trait data are available

<i>Achillea atrata</i>	<i>Carex flacca</i>	<i>Galium anisophyllum</i>
<i>Achillea millefolium</i>	<i>Carex leporina</i>	<i>Galium megalospermum</i>
<i>Acinos alpinus</i>	<i>Carex nigra</i>	<i>Galium pumilum</i>
<i>Adenostyles alliariae</i>	<i>Carex pallescens</i>	<i>Gentiana acaulis</i>
<i>Adenostyles glabra</i>	<i>Carex panicea</i>	<i>Gentiana bavarica</i>
<i>Agrostis alpina</i>	<i>Carex sempervirens</i>	<i>Gentiana campestris sstr</i>
<i>Agrostis capillaris</i>	<i>Carex sylvatica</i>	<i>Gentiana lutea</i>
<i>Agrostis rupestris</i>	<i>Carlina acaulis subsp caulescens</i>	<i>Gentiana purpurea</i>
<i>Agrostis schraderiana</i>	<i>Carum carvi</i>	<i>Gentiana verna</i>
<i>Agrostis stolonifera</i>	<i>Centaurea jacea sstr</i>	<i>Geranium sylvaticum</i>
<i>Ajuga reptans</i>	<i>Centaurea montana</i>	<i>Geum montanum</i>
<i>Alchemilla conjuncta aggr</i>	<i>Centaurea scabiosa sl</i>	<i>Geum rivale</i>
<i>Alchemilla glabra aggr</i>	<i>Cerastium arvense sl</i>	<i>Glechoma hederacea sstr</i>
<i>Alchemilla vulgaris aggr</i>	<i>Cerastium fontanum sl</i>	<i>Globularia cordifolia</i>
<i>Alchemilla xanthochlora aggr</i>	<i>Cerastium latifolium</i>	<i>Gnaphalium supinum</i>
<i>Allium schoenoprasum</i>	<i>Chaerophyllum aureum</i>	<i>Gypsophila repens</i>
<i>Androsace chamaejasme</i>	<i>Chaerophyllum hirsutum aggr</i>	<i>Hedysarum hedysaroides</i>
<i>Anemone narcissiflora</i>	<i>Cirsium acaule</i>	<i>Helianthemum nummularium sl</i>
<i>Anthoxanthum odoratum aggr</i>	<i>Cirsium oleraceum</i>	<i>Helictotrichon pubescens</i>
<i>Anthriscus sylvestris</i>	<i>Cirsium spinosissimum</i>	<i>Helictotrichon versicolor</i>
<i>Anthyllis vulneraria sl</i>	<i>Clinopodium vulgare</i>	<i>Heracleum sphondylium sl</i>
<i>Aposeris foetida</i>	<i>Crepis aurea</i>	<i>Hieracium bifidum aggr</i>
<i>Arabis alpina sl</i>	<i>Crepis pyrenaica</i>	<i>Hieracium lactucella</i>
<i>Arnica montana</i>	<i>Cruciata laevipes</i>	<i>Hieracium pilosella</i>
<i>Arrhenatherum elatius</i>	<i>Cynosurus cristatus</i>	<i>Hieracium villosum aggr</i>
<i>Aster bellidiastrum</i>	<i>Daucus carota</i>	<i>Hippocrepis comosa</i>
<i>Astrantia major</i>	<i>Deschampsia cespitosa</i>	<i>Holcus lanatus</i>
<i>Athamanta cretensis</i>	<i>Doronicum grandiflorum</i>	<i>Homogyne alpina</i>
<i>Bartsia alpina</i>	<i>Dryas octopetala</i>	<i>Hypericum maculatum sl</i>
<i>Bellis perennis</i>	<i>Epilobium anagallidifolium</i>	<i>Hypochaeris radicata</i>
<i>Brachypodium pinnatum</i>	<i>Erigeron uniflorus</i>	<i>Knautia arvensis</i>
<i>Briza media</i>	<i>Euphorbia cyparissias</i>	<i>Knautia dipsacifolia sstr</i>
<i>Bromus erectus sstr</i>	<i>Euphrasia minima</i>	<i>Laserpitium latifolium</i>
<i>Bromus hordeaceus</i>	<i>Euphrasia salisburgensis</i>	<i>Lathyrus pratensis</i>
<i>Calamagrostis varia</i>	<i>Festuca ovina aggr</i>	<i>Leontodon autumnalis</i>
<i>Caltha palustris</i>	<i>Festuca pratensis sl</i>	<i>Leontodon helveticus</i>
<i>Campanula barbata</i>	<i>Festuca quadriflora</i>	<i>Leontodon hispidus sl</i>
<i>Campanula cochleariifolia</i>	<i>Festuca rubra aggr</i>	<i>Leontodon montanus</i>
<i>Campanula glomerata sl</i>	<i>Festuca violacea aggr</i>	<i>Leucanthemum vulgare aggr</i>
<i>Campanula scheuchzeri</i>	<i>Filipendula ulmaria</i>	<i>Ligusticum mutellina</i>
<i>Carduus defloratus sl</i>	<i>Fragaria vesca</i>	<i>Linaria alpina sstr</i>
<i>Carex atrata aggr</i>	<i>Galeopsis tetrahit</i>	<i>Linum catharticum</i>
<i>Carex ferruginea</i>	<i>Galium album</i>	<i>Lolium multiflorum</i>

<i>Lolium perenne</i>	<i>Polygonum viviparum</i>	<i>Soldanella alpina</i>
<i>Lotus corniculatus aggr</i>	<i>Potentilla aurea</i>	<i>Solidago virgaurea sl</i>
<i>Luzula alpinopilosa</i>	<i>Potentilla crantzii</i>	<i>Stachys officinalis sl</i>
<i>Luzula multiflora</i>	<i>Potentilla erecta</i>	<i>Taraxacum alpinum aggr</i>
<i>Luzula sieberi</i>	<i>Primula auricula</i>	<i>Taraxacum officinale aggr</i>
<i>Lysimachia nummularia</i>	<i>Primula elatior sstr</i>	<i>Thesium alpinum</i>
<i>Medicago lupulina</i>	<i>Primula farinosa</i>	<i>Thlaspi rotundifolium aggr</i>
<i>Minuartia verna</i>	<i>Pritzelago alpina sstr</i>	<i>Thymus praecox subsp polytrichus</i>
<i>Molinia caerulea</i>	<i>Prunella grandiflora</i>	<i>Thymus pulegioides sstr</i>
<i>Myosotis alpestris</i>	<i>Prunella vulgaris</i>	<i>Tofieldia calyculata</i>
<i>Nardus stricta</i>	<i>Pulsatilla alpina sl</i>	<i>Tragopogon pratensis sl</i>
<i>Onobrychis montana</i>	<i>Ranunculus aconitifolius</i>	<i>Trifolium badium</i>
<i>Onobrychis viciifolia</i>	<i>Ranunculus acris sl</i>	<i>Trifolium medium</i>
<i>Ononis repens</i>	<i>Ranunculus alpestris</i>	<i>Trifolium pratense sl</i>
<i>Origanum vulgare</i>	<i>Ranunculus bulbosus</i>	<i>Trifolium repens sstr</i>
<i>Oxytropis jacquinii</i>	<i>Ranunculus montanus aggr</i>	<i>Trifolium thalii</i>
<i>Parnassia palustris</i>	<i>Ranunculus repens</i>	<i>Trisetum distichophyllum</i>
<i>Pedicularis foliosa</i>	<i>Rhinanthus alectorolophus</i>	<i>Trisetum flavescens</i>
<i>Petasites paradoxus</i>	<i>Rhododendron ferrugineum</i>	<i>Trollius europaeus</i>
<i>Phleum hirsutum</i>	<i>Rumex acetosa</i>	<i>Tussilago farfara</i>
<i>Phleum pratense</i>	<i>Rumex alpestris</i>	<i>Vaccinium gaultherioides</i>
<i>Phleum rhaeticum</i>	<i>Rumex alpinus</i>	<i>Vaccinium myrtillus</i>
<i>Phyteuma orbiculare</i>	<i>Rumex obtusifolius</i>	<i>Vaccinium vitis.idaea</i>
<i>Phyteuma spicatum</i>	<i>Salix herbacea</i>	<i>Valeriana dioica</i>
<i>Pimpinella major</i>	<i>Salix reticulata</i>	<i>Valeriana montana</i>
<i>Pimpinella saxifraga aggr</i>	<i>Salix retusa</i>	<i>Valeriana tripteris</i>
<i>Plantago alpina</i>	<i>Salvia pratensis</i>	<i>Veratrum album subsp lobelianum</i>
<i>Plantago atrata sstr</i>	<i>Sanguisorba minor sl</i>	<i>Veronica alpina</i>
<i>Plantago lanceolata</i>	<i>Saxifraga aizoides</i>	<i>Veronica aphylla</i>
<i>Plantago major sl</i>	<i>Saxifraga biflora sl</i>	<i>Veronica chamaedrys</i>
<i>Plantago media</i>	<i>Saxifraga moschata sl</i>	<i>Veronica officinalis</i>
<i>Poa alpina</i>	<i>Saxifraga oppositifolia</i>	<i>Vicia cracca sstr</i>
<i>Poa cenisia</i>	<i>Saxifraga paniculata</i>	<i>Vicia sativa sl</i>
<i>Poa minor</i>	<i>Scabiosa lucida</i>	<i>Vicia sepium</i>
<i>Poa pratensis</i>	<i>Senecio doronicum</i>	<i>Viola biflora</i>
<i>Poa supina</i>	<i>Sesleria caerulea</i>	
<i>Poa trivialis sl</i>	<i>Silene acaulis</i>	
<i>Polygonum bistorta</i>	<i>Silene vulgaris sl</i>	

Table 4: GLMs results with topo-climatic and chemical soil predictors.

	GLMs with topo-climatic and chemical soil predictors (202 plots)	
	Rho Cross-validation	Adj ²
Height		
CMW(H)	0.670258	0.490726
Fric	0.691352	0.521706
Rao	0.592594	0.386752
Feve	0.117261	0.043801
Fdis	0.540646	0.340144
LDMC		
CWM(LDMC)	0.347867	0.203916
Fric	0.525773	0.336978
Rao	0.4143	0.253831
Feve	0.132681	0.055751
Fdis	0.414621	0.242409
SLA		
CMW(SLA)	0.670926	0.499633
Fric	0.244617	0.083192
Rao	0.134028	0.047193
Feve	0.225942	0.090682
Fdis	0.086725	0.023006
All traits together		
Fdiv	0.131466	0.055124
Fric	0.366958	0.163281
rao	0.214065	0.09699
Feve	0.193491	0.071692
Fdis	0.155096	0.08008

Table 5: Values of the variation partitioning

Indices	Climatic	Physical	Chemical	CH+PH	CL+CH	CL+PH	CL+CH+PH	Unexplained
Vegh	0.2968	0.05431	0.06264	-0.003	0.0722	0.0731	0.066699	0.37749
FricH	0.3479	0.05662	0.031	0.0163	0.1019	0.0858	0.045403	0.31504158
RaoH	0.2457	0.06343	0.0584	0.0008	0.0892	0.046	0.037782	0.45874426
FdisH	0.1694	-0.0815	0.07971	-0.028	-0.029	0.0996	0.14956	0.64035908
FeveH	0.1344	0.05547	0.03614	0.0073	0.0384	0.0043	-0.000428	0.72451986
LDMC	0.1284	0.06771	0.176	0.0279	0.097	0.0152	-0.002076	0.48990747
FricLDMC	0.2438	0.04597	0.07672	0.0291	0.0624	0.0706	-0.012582	0.48409849
RaoLDMC	0.1392	0.03617	0.18236	0.0411	0.1083	0.025	-0.008208	0.47609004
FdisLDMC	0.1396	0.03765	0.20798	0.0278	0.1156	0.0183	-0.00999	0.46313248
FeveLDMC	0.1208	0.06726	0.09936	-0.008	0.0434	0.0176	-0.009974	0.66943058
SLA	0.3288	0.02009	0.11239	0.0357	0.1496	0.0464	-0.004191	0.31115669
FricSLA	0.127	0.02205	0.09619	0.0024	0.0245	0.012	0.020413	0.69556906
RaoSLA	0.1435	0.02452	0.05582	0.038	0.0147	0.0054	0.006496	0.71159449
FdisSLA	0.1636	0.02876	0.04958	0.0215	0.0115	0.0044	0.00629	0.71433747
FeveSLA	0.116	0.0538	0.05166	0.0051	0.0298	0.0447	0.019548	0.67934177
Fdiv	0.1694	0.08599	0.07971	-0.003	0.0371	0.0086	-0.018605	0.64035908
Fric	0.1571	0.02108	0.07198	0.0029	0.036	0.0268	0.023797	0.66026522
Rao	0.0911	0.0899	0.12824	0.0537	0.0368	0.0063	0.059776	0.53419117
Feve	0.0989	0.09229	0.08216	-0.018	0.0327	0.0412	0.001638	0.66945132
Fdis	0.0935	0.09912	0.15781	0.0415	0.0299	-0.004	0.047523	0.53431159

Table 1: Abbreviations of the formula

Abbreviations	meaning
A	total abundance
As	abundance of species S
c	community
d	derivative
dist	distance
e	subscript of an edge
G	centroïd
s	species
Sc	set of species present in community c
t	trait
V	convex hull
Xts	mean value of trait t in species s
Z	sample vector of all traits, used for the purpose of computing integrals over trait space

Table 2: a) Evaluation of GAM Models with topo-climatic predictors b) Evaluation of GAM Models with topo-climatic and chemical soil predictors c) Evaluation of GAM Models with topo-climatic, chemical and physical soil predictors. The cross-validation is a rho coefficient of correlation between predicted and observed values. In the second column is the variance explained by each model, i.e. the adjusted d2.

	a) GAMs models with topo-climatic predictors (202 plots)		b) GAMs models with topo-climatic and chemical soil predictors (202 plots)		c) GAMs models with topo- climatic and chemical and physical soil predictors (195 plots)	
	Rho Cross- validation	Adj2	Rho Cross- validation	Adj2	Rho Cross- validation	Adj2
Height						
CWM (H)	0.647556	0.511065	0.6546565	0.555819	0.63168	0.598826
Fric	0.676343	0.558357	0.6872746	0.587989	0.69004	0.662241
Rao	0.560432	0.409577	0.5552645	0.453396	0.54596	0.513224
Feve	0.161703	0.163803	0.1141	0.180962	0.04451	0.230596
Fdis	0.516365	0.371628	0.515464	0.409026	0.4906	0.469328
LDMC						
CWM (LDMC)	0.279483	0.223995	0.3734309	0.330814	0.41335	0.480491
Fric	0.453693	0.318357	0.5263343	0.424262	0.51372	0.484686
Rao	0.294336	0.2293	0.453883	0.391148	0.45626	0.49468
Feve	0.077349	0.120889	0.0686331	0.164644	0.16694	0.288786
Fdis	0.273614	0.221057	0.4121068	0.383461	0.45828	0.499065
SLA						
CWM (SLA)	0.632562	0.509251	0.6616606	0.597016	0.66202	0.66992
Fric	0.209098	0.149787	0.2214369	0.18312	0.21402	0.246563
Rao	0.031741	0.131507	0.1696111	0.208129	0.1221	0.245629
Feve	0.202492	0.174948	0.1542226	0.200662	0.09768	0.242251
Fdis	0.056992	0.149188	0.2049796	0.209944	0.18156	0.27716
Traits together						
Fdiv	0.178117	0.168517	0.1763961	0.213246	0.18219	0.319998
Fric	0.334094	0.224482	0.335776	0.25478	0.30554	0.295824
Rao	0.122815	0.135481	0.26081	0.263953	0.37371	0.433613
Feve	0.177929	0.154102	0.127312	0.193369	0.20027	0.287991
Fdis	0.033634	0.101554	0.2146746	0.240246	0.3588	0.425322

Figures

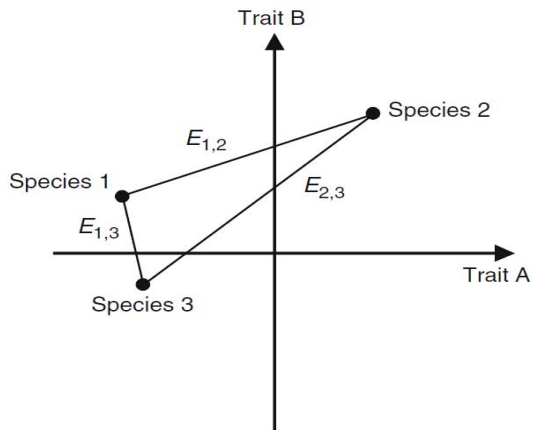


Figure 1

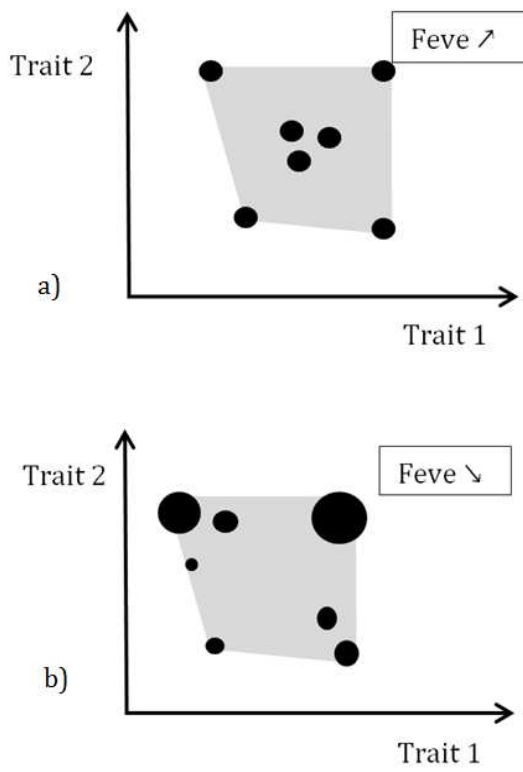
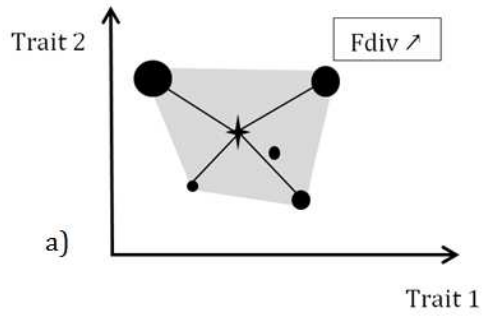


Figure 2

$$Feve = \frac{\sum_{e \in E} \min \left[\frac{\text{dist}(e) / (\frac{A_e}{A})}{\sum_{e' \in E} \text{dist}(e') / (\frac{A_{e'}}{A})}, \frac{1}{|S_c| - 1} \right] - \frac{1}{|S_c| - 1}}{1 - \frac{1}{|S_c| - 1}}$$



$$Fdiv = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}$$

$$\Delta d = \sum_{s \in S_c} \frac{A_s}{A} (dG_s - \overline{dG})$$

$$\Delta|d| = \sum_{s \in S_c} \frac{A_s}{A} |dG_s - \overline{dG}|$$

$$G_t = \left(\frac{1}{|V|}\right) \sum_{s \in V} X_{ts}$$

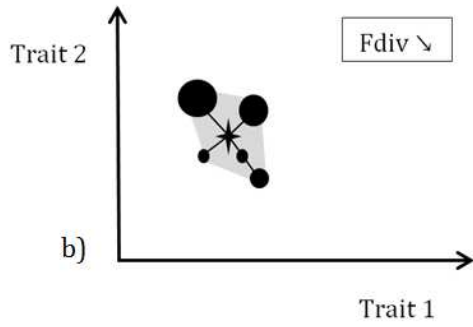
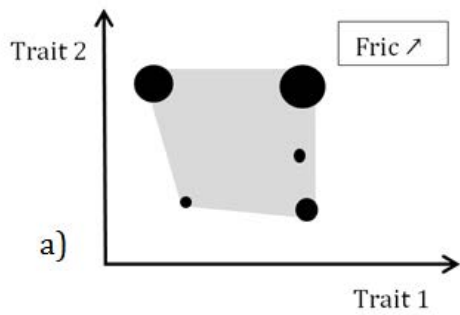


Figure 3



$$Fric = \int \max(f_{s \in S_c}(Z)) dZ$$

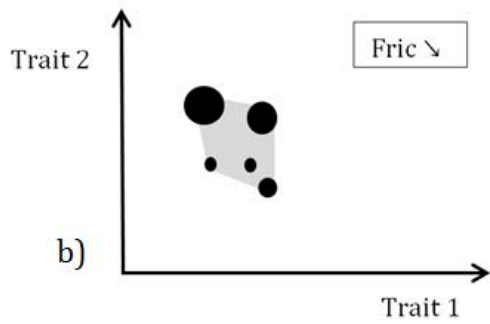
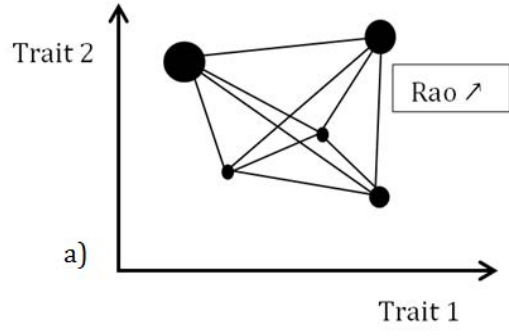


Figure 4



$$Rao = \sum_{s \in S_c} \sum_{s' \in S_c} \frac{A_s A_{s'}}{A^2} dist(s, s')$$

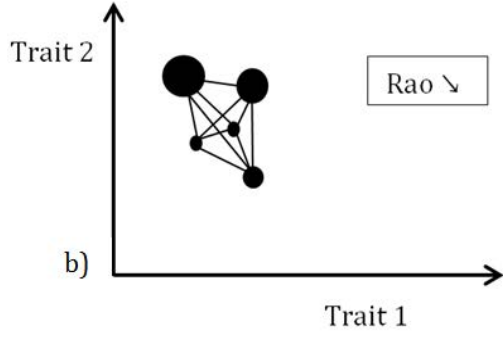
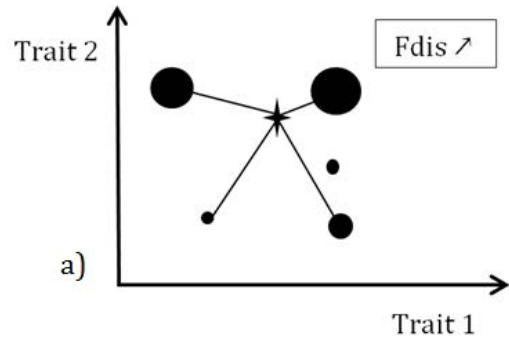
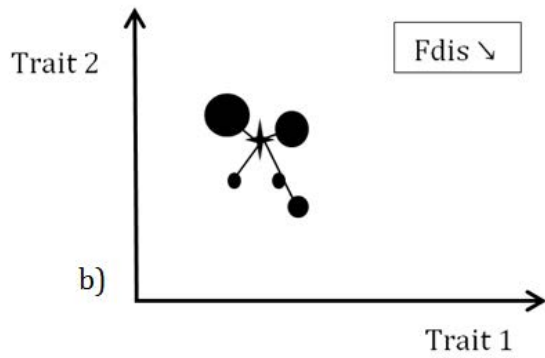


Figure 5



$$Fdis = \frac{\sum_{s \in S_c} A_s dG_s}{A}$$



$$G_t = \frac{\sum_{t=1}^T \sum_{s \in S_c} A_s x_{ts}}{A}$$

Figure 6

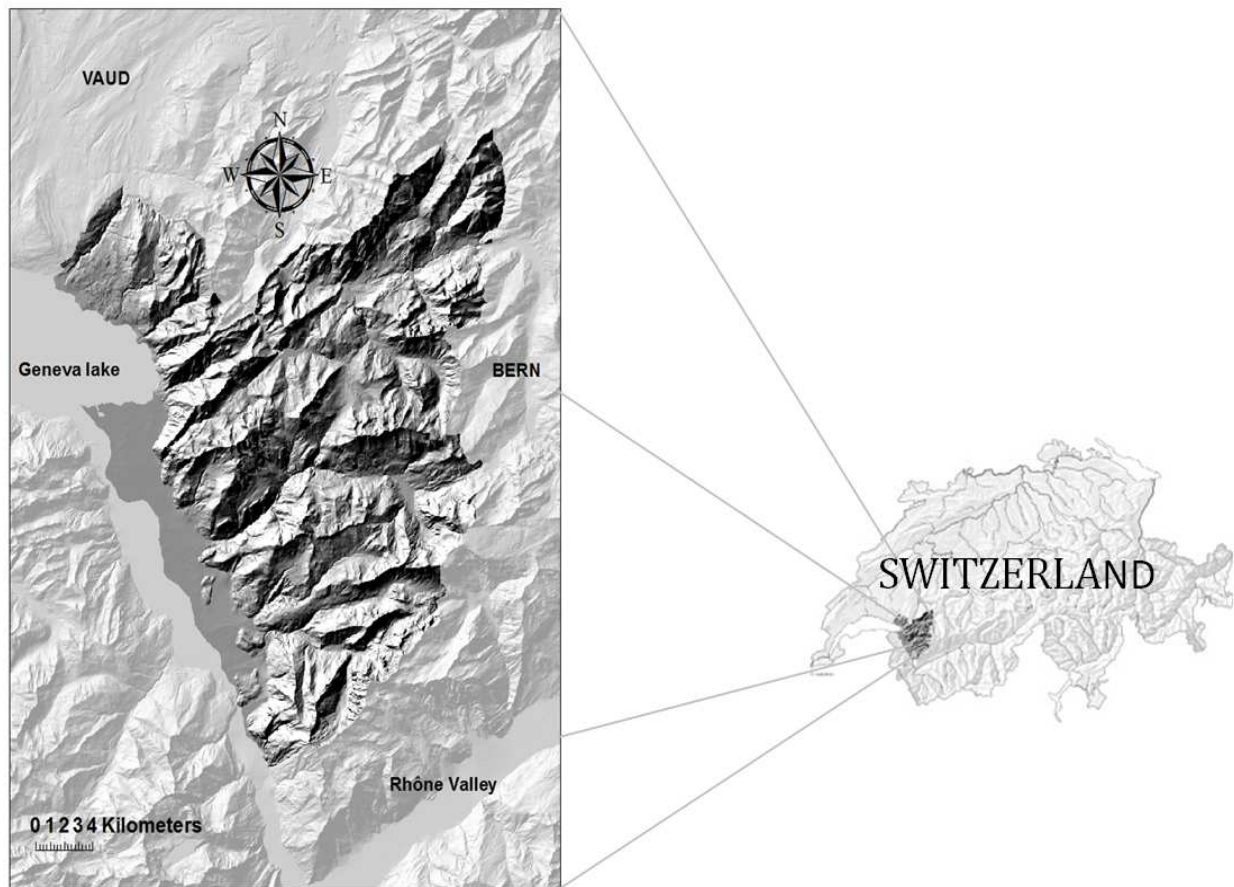


Figure 7

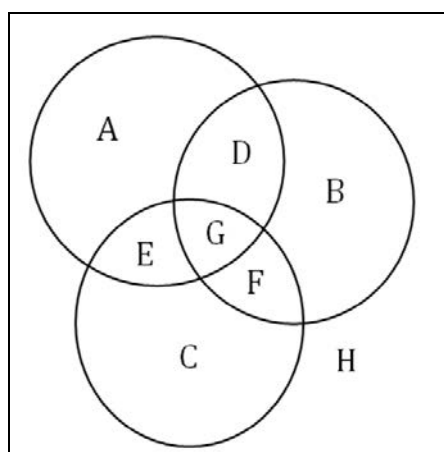


Figure 8

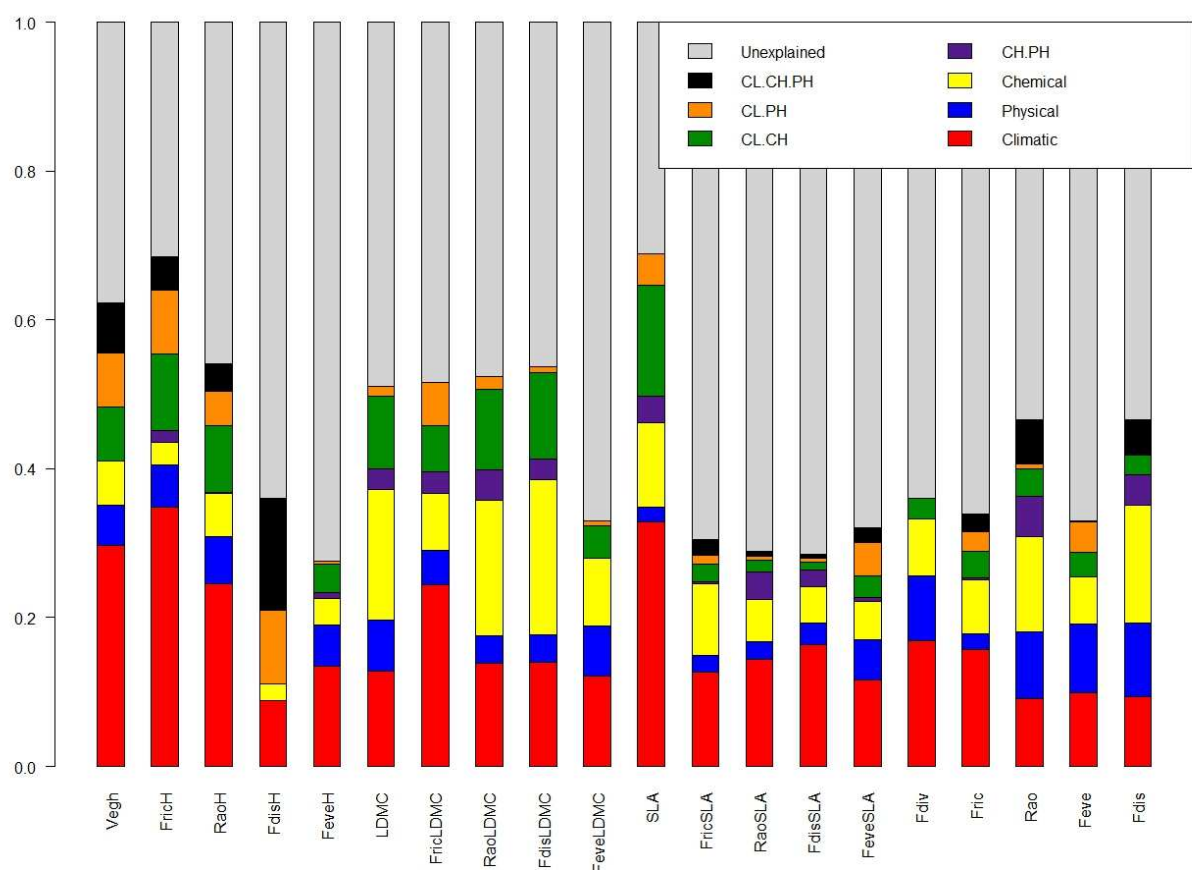


Figure 9

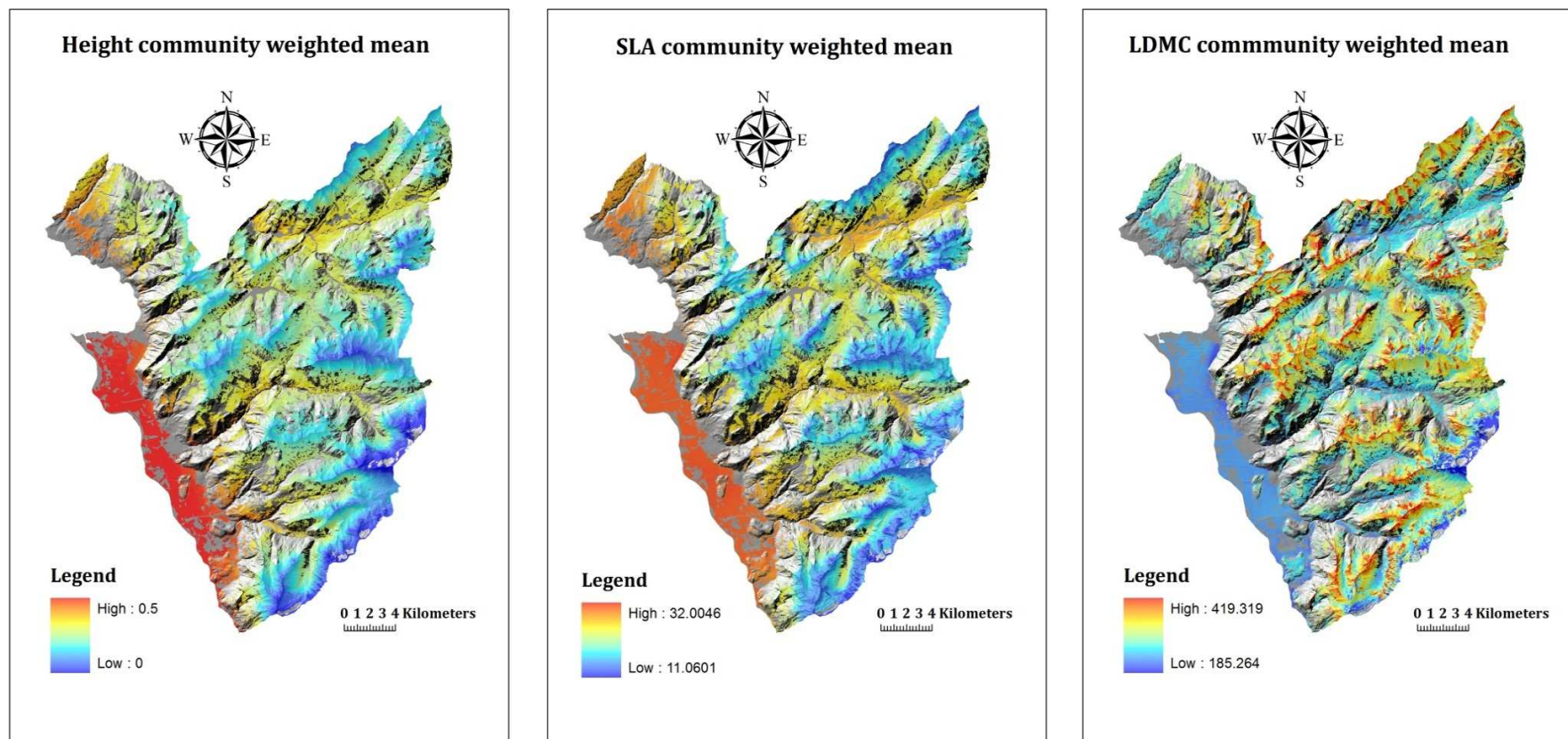


Figure 10

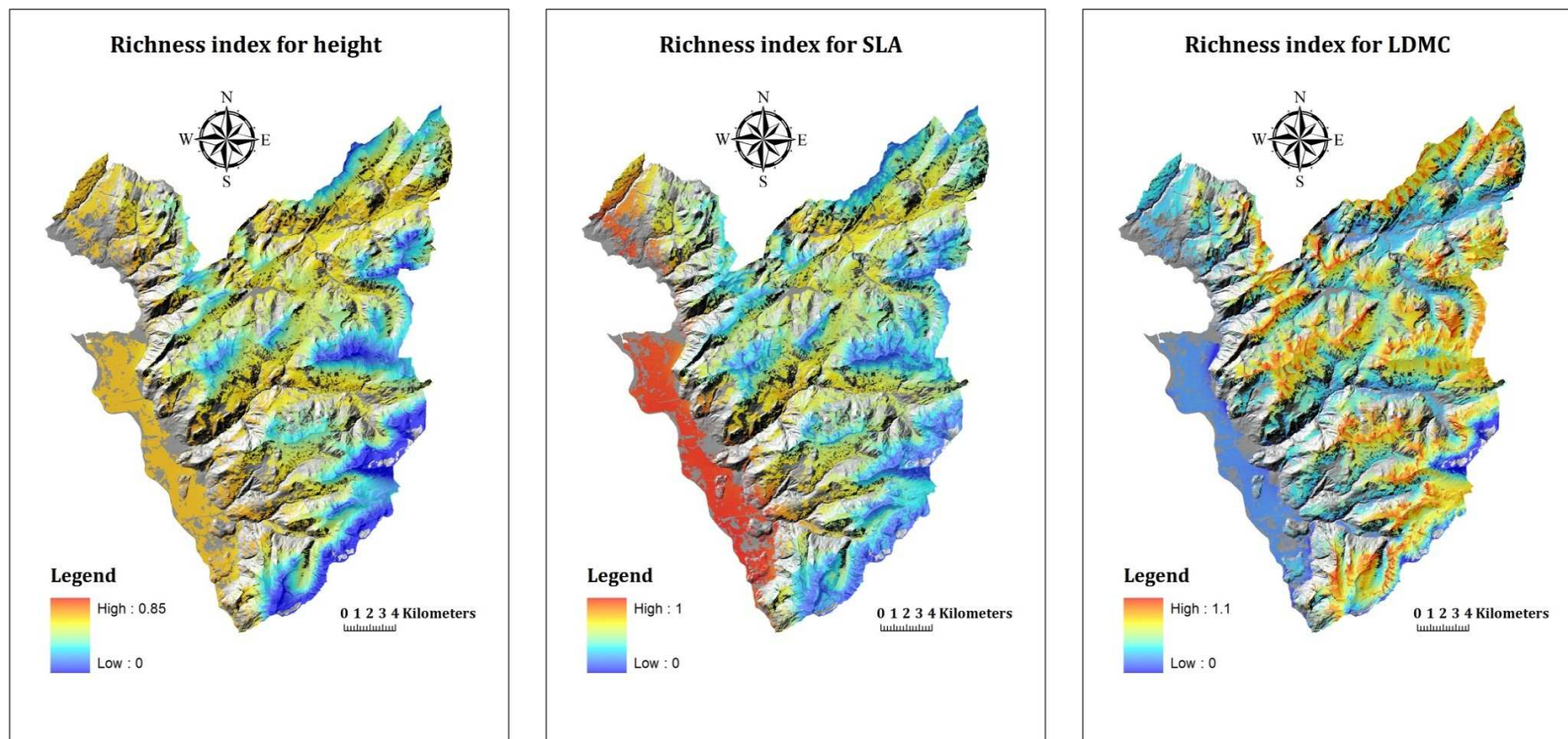


Figure 11

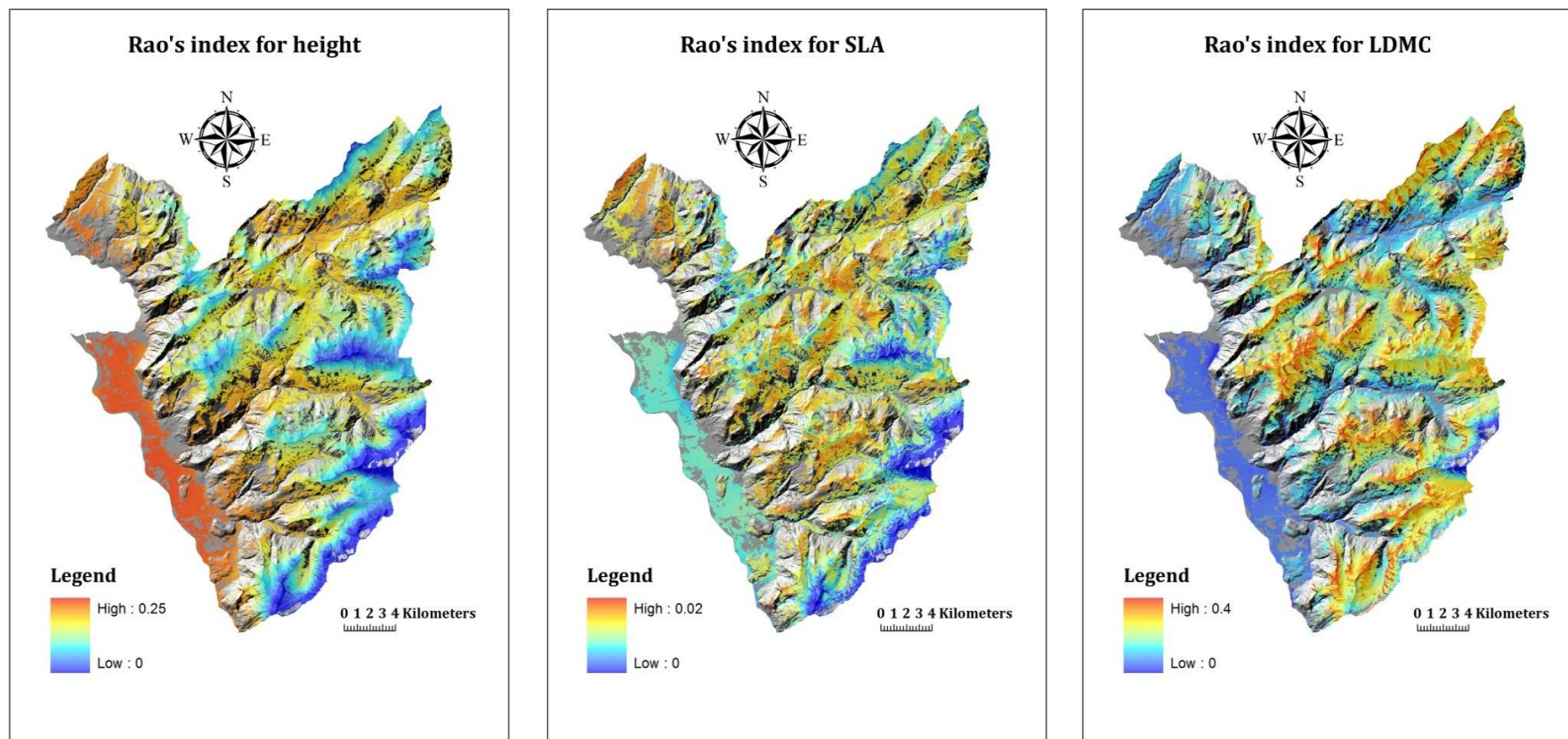


Figure 12

Legends

Figure 1: Concept of distances between species in function-trait Euclidean space, which is assumed to represent the functional niche (Rosenfeld 2002). In the present study the trait space is three-dimensional. This Figure is adapted from Mouillot, Mason and Wilson (2007).

Figure 2: a) high Feve; b) low Feve. The functional space is here composed by two traits; the black circles represent the species, their size being proportional to abundance and the grey surface represents the convex hull.

Figure 3: a) high Fdiv; b) low Fdiv. The functional space is here composed by two traits; the black circles represent the species, their size being proportional to abundance. The black star is the centroid of the convex hull (grey surface).

Figure 4: a) high Fric; b) low Fric. The functional space is here composed by two traits; the black circles represent the species, their size being proportional to abundance and the grey surface represents the convex hull.

Figure 5: a) high Rao; b) low Rao. The functional space is here composed by two traits; the black circles represent the species, their size being proportional to abundance. The black lines represent the distance between each pair.

Figure 6: a) high Fdis; b) low Fdis. The functional space is here composed by two traits; the black circles represent the species, their size being proportional to abundance. The black star is the centroid of species balanced by their abundance. The black lines are the distance between the centroid and species.

Figure 7: The study area

Figure 8: Illustration of our variation partitioning, the letters represent each category of predictors can explain the variance in our models. A: Chemical, B: Physical, C: Topo-climatic, D: Chemical + Physical, E: Topo-climatic + Chemical, F: Physical + Topo-climatic, G: Topo-climatic + Physical + Chemical, H: Unexplained.

Figure 9: Variation partitioning for functional indices model. Each bar represent one model: 1) CWM for height, 2) Fric for height, 3) Rao for height, 4) Fdis for height, 5) Feve for height, 6) CWM for LDMC, 7) Fric for LDMC, 8) Rao for LDMC, 9) Fdis for LDMC, 10) Feve for LDMC, 11) CWM SLA, 12) Fric SLA, 13) Rao SLA, 14) Fdis SLA, 15) Feve SLA, 16) Fdiv for all traits, 17) Fric for all traits, 18) Rao for all traits, 19) Feve for all traits, 20) Fdis for all traits. The variation in the model is explained by topo-climatic predictors is represented in red, physical edaphic predictors in blue, chemical edaphic predictors in yellow, interaction between chemical and physical predictors in purple, interaction between topo-climatic and chemical predictors in green, interaction between topo-climatic and physical predictors in orange, interaction between all predictors in black and unexplained variation in grey.

Figure 10: Projections of the model for community weighted mean for a) height, b) SLA and c) LDMC.

Figure 11: Projections of the model for Fric for a) height, b) SLA and c) LDMC.

Figure 12: Projections of the model for Rao's index for a) height, b) SLA and c) LDMC.