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Faculté de biologie
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Ecole de biologie

IMPROVING THE PREDICTION OF PLANT COMMUNITY FUNCTIONAL TRAITS AND SPECIES RICHNESS IN MOUNTAIN GRASSLANDS.

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

par

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January, 2015

Abstract

Aim: To assess the potential of new predictors (land use, light availability, edaphic factors and high resolution topoclimatic predictors) in improving the prediction of plant community functional traits (specific leaf area, vegetative height and seed mass) and species richness in mountainous grasslands.

Location: The western Swiss Alps

Methods: Using 912 vegetation plots previously sampled, we built predictive models for the studied traits using only the coarse resolution topoclimatic predictors that are normally used in modelling studies. Four new sets of 10 plots were then sampled in homogeneous conditions according to these topoclimatic predictors (corresponding to mountain grasslands), and the values of the new predictors gathered. We projected the topoclimatic models on the new plots, and assessed the capacity of the new predictors to explain the residual variance through multi model inference.

Results: We showed that the proposed predictors could help explaining 15.9% (vegetative height) to 36.6% (specific leaf area) of the residual variance in classical topoclimatic models. No group of predictors notably increased the quality of all models. Land use related data were highlighted as the most important factors for both species richness and vegetative height, light availability for seed mass and edaphic factors for specific leaf area. High resolution topographic predictors seemed to be complementary to land use data to improve model quality.

Main conclusions: We showed that prediction of plant community functional traits and species richness could be improved by new predictors as compared to classical topoclimatic models. As some of them can be implemented in models (high resolution topoclimatic predictors, some of the edaphic factors), we suggest that they might be used in future models.

Keywords : community ecology ◆ functional traits ◆ high resolution ◆ land use ◆ modelling ◆ mountain grasslands ◆ seed mass ◆ species richness ◆ specific leaf area ◆ vegetative height

Résumé

Objectif : Etudier le potentiel d'un set de nouveaux prédicteurs (gestion agricole, disponibilité en lumière, facteurs édaphiques et prédicteurs topoclimatiques à haute résolution) pour améliorer la prédiction de traits fonctionnels de communautés de plantes (surface foliaire spécifique, hauteur maximale des feuilles et poids des graines) et de la richesse spécifique dans des prairies de moyenne montagne.

Lieu : Les Préalpes vaudoises

Méthodes : En utilisant 912 relevés floristiques déjà existants, nous avons construits des modèles prédictifs pour chacun de ces traits en n'utilisant que les prédicteurs topoclimatiques à basse résolution généralement utilisés dans les travaux de modélisation. Quatre sets de 10 relevés ont ensuite été échantillonnés dans des conditions homogènes, correspondant à des praires de moyenne montagne, où les valeurs des nouveaux prédicteurs ont également été relevées. En utilisant les projections des modèles topoclimatiques sur ces nouveaux sites, nous avons ensuite étudié la capacité de ces nouveaux prédicteurs à expliquer la variance résiduelle par des techniques d'inférence multi-modèle

Résultats : Nous avons montré que les prédicteurs proposés peuvent expliquer entre 15.9% (hauteur maximale des feuilles) et 36.6% (surface foliaire spécifique) de la variance résiduelle des modèles topoclimatiques classiques. Aucun groupe de prédicteur n'augmentait la précision de chacun des modèles. La gestion agricole était le facteur le plus important pour la richesse spécifique et la hauteur maximale des feuilles, la disponibilité en lumière pour le poids des graines et les facteurs édaphiques pour la surface foliaire spécifique. Les prédicteurs topographiques à haute résolution semblaient être complémentaires à la gestion agricole pour améliorer les modèles.

Conclusions : Nous avons montré que la prédiction des traits fonctionnels de communauté de plantes peut être améliorée par de nouveaux prédicteurs comparativement aux modèles topoclimatiques classiques. Comme certains prédicteurs peuvent être implémentés (prédicteurs topoclimatiques à haute résolution, certains facteurs édaphiques), nous encourageons leur usage dans de futurs travaux.

Introduction

Community ecology is the study of the ensemble of species co-occurring at the same place and time (McGill et al., 2006), and how biotic and abiotic factors will tend to affect its structure, and changes in its structure over sites and time (Pyron, 2010). Especially, it seeks to find some general rules or patterns to explain community composition (MacArthur, 1984). In this attempt, it has long been argued that trying to describe communities on the basis of species not only by their Latin name, but rather through their biological characteristics (also called "traits") could provide better and more generalizable results (Keddy, 1992; McGill et al., 2006). Keddy (1992) cites the example of van der Valk (1981), who created a model for succession in freshwater wetlands, based on life history traits. The generality of the chosen traits enables application of the models in various types of places and flora, whereas a model specifically based on species identity could not have reached such generalization.

Amongst those traits, *functional traits* have specific importance. Functional traits are defined as those traits that have an effect on individual's fitness, via their effects on growth, reproduction or survival (Violle et al., 2007). As they are strongly linked to physiological requirements of species and individuals, they are expected to give more robust conclusions when seeking for general rules shaping communities (McGill et al., 2006). Furthermore, they might give precious insights to ecosystem functioning (Lavorel & Garnier, 2002).

One way to study these functional traits is to compute traits values of an entire community, and to study differences or patterns in these "whole-community" values (Dubuis et al., 2013). This aggregation allows to study general patterns of dependence or causality between trait values and environmental factors, which is of high importance when seeking for general rules shaping communities (Southwood, 1988; Lavorel & Garnier, 2002).

Another important component when trying to characterize communities is species richness. Species richness is defined as the number of species occurring in a given area or system (Díaz & Cabido, 2001). Its importance for ecosystem functioning (Grime, 1998) and proprieties such as resilience (Perterson, Garry et al., 1998) and stability (Tilman et al., 2014) has been widely assessed amongst ecologists.

In the seek for general rules explaining community composition and functioning, a very interesting tool is their modelling as a function of environmental or biotic factors (Keddy, 1992; Küster et al., 2011). This approach gives powerful insights on what could drive the distribution of functional traits, as has been exemplified by Küster et al. (2011). They assessed, by use of this technique, the potential impact of climate and land use changes on distribution of leaf anatomy. Although this method is increasingly used (Pellissier et al., 2010; Sonnier et al., 2010; Dubuis et al., 2011, 2013; Küster et al., 2011), these works are generally based on the habitual topoclimatic predictors, with a traditional 25 x 25 m to 100 x 100 m resolution, and only few works have been dedicated so far to strictly assess in what extent new predictors could improve predictions of trait composition in communities (Garnier et al., 2004; Dubuis et al., 2013).

A notable exception is the study by Dubuis et al. (2013), who tested the influence of edaphic factors on quality of trait models. They showed that inclusion of soil chemical (pH, nitrogen content, phosphorus content) and, to a lesser extent, physical proprieties (soil texture) could significantly improve quality of predictions. Nonetheless, this study focused only on edaphic factors, and other improvements could be attempted

For instance, Dubuis et al. (2013) themselves regretted the absence of land use data in their study. Indeed, land use has been shown to improve prediction of plant abundance (Randin et al., 2009) and to affect grassland floristic composition (Peter et al., 2008) and richness (Zechmeister et al., 2003) in mountainous landscape. It could therefore be expected that land use intensity might have an effect on community trait.

Furthermore, increasing the resolution of the maps of environmental factors has to our knowledge never been attempted in the case of community trait modelling, whereas it has been shown to improve distribution models for some species (Pradervand et al., 2013). On the other hand, maps of environmental factors are always interpolations from point measurement over a study area (see for example Zimmermann & Kienast, 1999). This implies a certain amount of imprecision during their calculation (Guisan & Zimmermann, 2000). Therefore, when trying to increase quality of prediction, another interesting, although time consuming, approach is to resort to point measurements of environmental factors directly on the field, so as to complement or correct environmental maps.

Another point is that Dubuis et al. (2013) were working on an entire elevation gradient, as advised by (McGill et al., 2006) to reach more systematic rules about how community patterns vary over ecological ranges. Nevertheless, there are evidences indicating that the importance of species distribution drivers is not constant over space and time or along productivity gradient (Michalet et al., 2006). Therefore, when working on large environmental gradients, various phenomenons could happen. First, one could loose the effect of some factors, hidden by another that varies more in the study area, as elevation in the case of Dubuis et al. (2013). If a variable varies less than elevation over the study area, it will explain less variance in the data, although it might actually be a main ecological driver. Furthermore, some factors could affect communities in a different way in distinct conditions, as has been shown for land use between high and low elevations (Randin et al., 2009).

In this study, we focused on one very narrow ecological range to assess the potential of a set of new potential predictors in improving the quality of models for three community functional traits and species richness. The selected ecological range corresponded to a lowland mountainous landscape, where grazing is very common. Selected traits were specific leaf area (often designed as SLA), vegetative height and seed mass, which represent the three axes of the leaf-height-seed plant strategy introduced by Westoby (1998). New predictors included land-use data, high-resolution maps of environmental factors, and some *in situ* measurements of light availability and soil proprieties. We then discuss the potential of these predictors as new predictors for further modelling works. We were expecting land-use data to be of high importance, especially on species richness models, because of the high impact of anthropic disturbance on the study area. Point measurements of light availability were expected to be of little impact on model quality, due to high quality of ecological maps over the study area. Soil chemical proprieties were expected to be of high importance, especially for seed mass, following the conclusions of Dubuis et al. (2013).

Methods

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, Fig. 1). It covers 700 km^2, and its elevation

ranges from 375 to 3210 m. Outside of forests, agriculture influences most of the area, with pastures from lowlands to lower alpine zones and meadows mainly at lower elevations (Randin et al., 2009).

Sampling strategy

Plots were sampled over the study area, following a random stratified sampling strategy. In order to get a dataset with groups of plots sharing very homogeneous conditions, four strata of narrow topoclimatic proprieties were created (Table 1). Four topoclimatic predictors were considered as of main importance for functional trait modelling and for physical partitioning of the strata: slope, topographic position, global solar radiation over the growing season (June-August) and mean temperature over the growing season (Dubuis et al., 2011, 2013). Temperature, precipitation and solar radiation data were measured by the Swiss network of meteorological stations (www.meteoswiss.ch) and all predictors were generated at a 25 m resolution from a digital elevation model (Zimmermann & Kienast, 1999). Slope was derived from the elevation model using ArcGIS 10.2 spatial analyst tool (ESRI). Topographic position was computed through moving windows that integrate topographic features at various scales. Positive values indicate ridges and tops, whereas negative values correspond to valleys and sinks. Global solar radiation is the sum of the daily average of potential radiation per month over the whole year. It is calculated on the basis of direct, diffuse and reflected solar radiation reaching the area, and takes into account the exposure of the plot and shading surrounding topography (Zimmermann & Kienast, 1999).

In each of the four strata, the four predictors were kept within very restricted ranges so as to minimize the variance due to topoclimatic factors (Table 1). The four strata were defined as follows; pixels corresponding to mean growing season temperature from 12.2°C to 12.4°C and from 13.2°C to 13.4°C were selected. In each of theses intervals, we then selected pixels with a global solar radiation ranging from either 1600 to 1800 $kJ \cdot day^{-1} \cdot pixel^{-1}$, corresponding to a full North exposure, or from 2800 to 3000 $kJ \cdot day^{-1} \cdot pixel^{-1}$, corresponding to a full South exposure. Global solar radiation for the South-exposed, low mean temperature values stratum (stratum c, Table 1) were actually kept between 2800 and 2900 $kJ \cdot day^{-1} \cdot pixel^{-1}$, as it was possible to gather enough pixels while reducing the range to that extent. We then only kept pixels with a slope between 20 and 25° and a topographic position index between -100 and 0, corresponding to

regular slopes. These restricted ranges represented between 1.3 and 7.2% of the total ranges of the predictors over the whole study area (Table 2, Fig. S1). Ten points were then randomly selected in the open lands of each of these four strata, with some replacement plots in each stratum in case a plot would show impossible to reach or sample during field season.

Vegetation data

42 plots were finally sampled during the field season 2014 (Fig. 1), with at least ten in each stratum. An exhaustive inventory of the vascular plants was performed in a 4 m^2 square. We also estimated visually the cover of each species through an adapted Braun-Blanquet abundance-dominance coefficient (Braun-Blanquet, 1964), where r = 1 to 3 individuals, + = <1%, 1=1 to 5%, 2a=6-15%, 2b=16-25%, 3= 26-50%, 4=51-75%, 5=76-100%. The mid-range value of these classes was used for further analysis.

In addition to these 42 plots, we also disposed of 912 plant inventories sampled between 2002 and 2009 in the same study area. Field methods and size of the plots were the same, but the sampling strategy differed. These inventories were selected with a random-stratified sampling strategy which covered the whole area**,** based on the same ecological predictors but without focus on one particular type of conditions as is the case in our study (Fig. 1; see Dubuis et al. (2013) for more details).

Functional traits

Three functional traits, corresponding to three different characteristics of plant life according to the leaf-height-seed plant strategy presented by Westoby (1998), were retained for analyses. Specific leaf area is the area of one side of a fresh leaf over its dry mass (in $mm^2 \cdot mg^{-1}$; Cornelissen et al., 2003). It is linked to photosynthetic rates and carbon fixation (Lavorel & Garnier, 2002). Vegetative height is the distance between the top photosynthetic tissue and the ground (in m; Dubuis et al., 2013) and is linked to disturbance, stress avoidance and competitivity (Lavorel & Garnier, 2002; Cornelissen et al., 2003). Seed mass is the average dry mass (in mg) of the seeds (Cornelissen et al., 2003). It represents strategies of plant investment in reproduction; smaller seeds can be produced in higher number, but contain limited amount of resources and are expected to yield lower reproductive success (Cornelissen et al., 2003).

For specific leaf area and vegetative height we used data that had previously been collected by Dubuis et al. (2013) for the 240 most abundant species in the same study area. These authors sampled between four and 20 individuals per species in the study area, in contrasting environmental conditions, and calculated an average trait value by species. Only values for *Dactylis glomerata* had to be added from the LEDA trait database (Kleyer et al., 2008). Seed mass information was mainly collected from the LEDA trait database (Kleyer et al., 2008). Missing values were complemented from the Kew seed base (Royal Botanic Gardens Kew, 2014) and literature research (Muller-Schneider, 1986; Pluess et al., 2005; Vittoz et al., 2009).

For each trait, we calculated a weighted mean average for the whole community with cover as weight. Covers were previously rescaled so that the total vegetation cover of a plot would be equal to 100, ignoring the stones, trees and bare soil covers, as well as species for which trait value was missing. Plots for which trait information was available for less than 55% of vegetation cover were discarded. No higher threshold could be applied because of limiting trait data availability. Nonetheless, as we expect missing species to be regularly distributed in the spectrum of trait values, the community means should not be biased. Amongst these 912 plots, 816 had trait data information available for more than 55% of vegetation cover, and 568 in the case of seed mass. Only these plots were retained in further analyses. All trait data were log transformed before performing the analysis, because of non normality of the data. Species richness (SR) was calculated as the total number of species present per plot. No plot was discarded in this case.

New predictors collection

Land-use data

Land-use data was collected by interviews of the farmers managing the grasslands where the plots were localized. Each of them was joined by phone. Questions were asked about the intensity and type of grazing, fertilization and frequency of mowing when applicable. A land-use intensity index (LUI) was then computed as suggested in Blüthgen et al. (2012):

$$LUI = \frac{F_i}{F_R} + \frac{M_i}{M_R} + \frac{G_i}{G_R} \qquad \textbf{(1)}$$

where F_i is the fertilization level for the plot i (m^3 manure · $year^{-1}$ · ha^{-1}), M_i the frequency of mowing per year and G_i the grazing intensity (UGB · days · ha^{-1} · $year^{-1}$), F_R, M_R and G_R their respective means over the data set. An UGB is a Swiss standardized unit for cattle foraging needs (Le Conseil fédéral suisse, 2014)

Light availability

For each plot, we measured a shadow index, as an indication of the shadow due to close objects (mainly trees). It is a complement to the global solar radiation information, which represents the amount of light potentially received by each plot, but considering only the topographic relief for shadows. To do so we measured the angle formed by the horizon and any object projecting a shadow on the plot in the South, South-East and South-West directions. The shadow index was calculated as :

$$SI = 2S_S + S_{SE} + S_{SW} \quad \textbf{(2)}$$

where S_s, S_{SE}, S_{SW} are the horizon-object angle values in the South, South-East and South-West directions respectively.

We also measured the actual exposure of the plot with a compass. Again, this was a complement to global solar radiation, as the latest is calculated on the basis of a digital elevation model (DEM) with a 25 m resolution. Therefore, the measured exposure of the 4 m^2 plot was often quite different to the calculated exposure, for instance because it was located on the side of a bump, changing its actual exposition to sun.

Soil measurements

Soil depth was measured one to three times at each site with an auger. Whenever a depth deeper than 50 cm was reached, digging was stopped and the soil considered as deep. In other cases, we dug until rock was reached, and the mean of the three holes was calculated. Moreover, the depth of the organo-mineral horizon was measured (A horizon, Baize & Jabiol 1995), as an approximation of the amount of organic matter available in the soil. For each plot, a soil sample of the A horizon was collected on the field and dried for laboratory analyses. We measured the pH of the A horizon with a pH meter after diluting soil in water in a 1:2.5 w/v ratio. Organic C and N contents were determined using a Carlo Erba CNS2500 CHN Elemental Analyzer coupled with a Fisons

198 Optima mass spectrometer (Tamburini et al., 2003). A C/N ratio was then computed, as a biologically meaningful summary of nutrient availability (Batjes, 1996).

High resolution environmental predictors

We disposed of high resolution rasters of environmental predictors for the study area, developed by (Pradervand et al., 2013). They developed various predictors at six different scales for the same study area. For the present study, we retained growing degree-days, topographic position and slope as most meaningful predictors at a 5 m resolution, as it yielded the best results in their study. Growing degree-days correspond to the sum of the daily temperatures during the growing season (June, July and August) when temperature above 0°C, and are inferred from the temperature data. Slope and topographic position are similar to that used for stratification of the sampling, but here with a 5 m resolution. For more details about these rasters, see (Pradervand et al., 2013).

Modelling

The models were performed for all the three functional traits and for the species richness following a similar canvas (Fig. 2). All analyses were performed on R 3.1.2 (R Core Team, 2014)

Topoclimatic models

In a first step, we followed the method of Dubuis et al. (2013) so as to assess how much of variance of community trait values could be explained by classical models (i.e., with topoclimatic predictors only, at a 25 m resolution). We first fitted a best GLM model on the 912 plots for which vegetation data was previously available, with only topoclimatic predictors. Selected predictors to fit the models where the same as in Dubuis et al., (2013) (i.e. moisture index, growing degree days, global solar radiation, slope and topographic position, all at 25 m resolution), which had been shown to perform best on trait prediction. Global solar radiation, slope and topographic position have already been explained in the sampling strategy section. Moisture index represents the amount of water potentially available in soil. It is calculated as the mean difference between precipitation and potential evapotranspiration over the growing season. Growing degree days is still the sum of days of the growing season multiplied by the temperature above 0°C, this time at a 25 m scale. The models were created through stepwise

selection. Assumed distribution was Gaussian for the traits, and Poisson for species richness. These models accounted for what was already possible to predict.

We then projected these models on the pixels where the 42 newly sampled plots are situated. On the basis of these projections, we calculated the ordinary residuals of these topoclimatic models for the 42 plots, by computing the difference between the observed and the predicted values for each plot (Zuur et al., 2013). One plot was behaving as an outlier in all models. As it was the only one which had been abandoned for >15 years and that successional process towards forest was already well on its way, we discarded it for the analyses. Trait data was available for over 55% of the plant cover of all the 41 remaining plots. We compared the residuals of the four strata through pairwise Wilcoxon tests with Bonferonni correction for multiple comparisons, so as to address the potential effect of stratification in the design.

Relative Importance of the new predictors

We then performed a second modelling step, by fitting new GLM models on these residuals, this time including only the new predictors. We assessed the importance of each new predictor in explaining the variance of the residuals using an adapted version of the Multimodel Inference technique presented by Burnham, Anderson, & Huyvaert (2010). We created models with all possible combinations of either four of our predictors, or four of the quadratic plus linear terms of our predictors. Assumed distribution for the residuals of the first models was always Gaussian. The number of predictors was limited to four because of the limited number of observations, according to the rule-of-thumb of 1 predictor for 10 observations of Harrell (2001). Models were then ranked by AICc score as is advised for small sample sizes (Shono, 2000), and an Akaike weight w_i was computed for each model. It is a way to calculate the support obtained by each model, given the set of data and models, based on difference in AICc scores (Burnham & Anderson, 2002):

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(\frac{1}{2}\Delta_r)} \qquad \textbf{(3)}$$

where i is the considered model, R the considered set of models, and Δ_i the difference in AICc scores between model i and the best model in the set (i.e. the one with lowest AIC);

$$\Delta_i = AIC_i - AIC_{\min} \quad \textbf{(4)}$$

Based on these Akaike weights, we estimated the Relative Importance (RI) of each predictor. This RI corresponds to the sum of the Akaike weights for each model where the predictor is present (Burnham & Anderson, 2002). This step permitted us to assess how useful each of the new predictors was, relatively to the others, to help explaining the variance that could not be explained by the classical topoclimatic models (first models).

Percentage of variance explained by the new predictors

So as to quantify the absolute impact of the new predictors, we created a GLM model for each trait and for species richness including the four best predictors according to relative importance. We limited the number of predictors again to four due to the limited number of observations. These models were again run on the residuals of the topoclimatic models, as new predictors are only available for the new plots. We then estimated the improvements due to the four predictors through calculating the percentage of explained variance for each model.

Results

Fieldwork

Elevations of the 42 plots ranged from 1015 to 1324 m. Strata “a” (low elevation, South exposure) and “b” (low elevation, Northern exposure) ranged from 1015 to 1119 m, and strata “c” and “d” (high elevation, South and North exposure respectively) from 1181 to 1324 m.

Relationship between each trait and its most important new predictor are illustrated in Fig. 3. For complete information about all predictors and traits see appendix S2.

Topoclimatic models

The best topoclimatic models and their performances are presented in Table 3**.** They could explain 11.6% (seed mass), 38.4% (species richness) 44.2% (specific leaf area) and 63.8% (vegetative height) of the global variance. The residuals inferred for the 42 new sites from these models are illustrated in appendix S3. Wilcoxon tests for differences between strata were non significant.

364 **Relative importance of the new predictors**

365 The relative importances (RI) of the most important predictors for each trait and for
366 species richness are shown in Fig 4. Weights for some of the related models are shown
367 in appendix S4.

368 *Specific leaf area*

369 Two predictors performed notably better than the others, C/N ratio (RI= 0.79) and A
370 horizon depth (RI = 0.75), followed by slope at 5 m resolution (RI= 0.45) and growing
371 degree days at 5 m resolution (RI = 0.27). The soil pH and shadow index were close to
372 these values (RI= 0.21 and 0.2 respectively). All other linear term predictors had a RI <
373 0.17 and there was a strong break between the relative importance of linear and
374 quadratic terms, the latter being nearly negligible (RI<0.02, Fig. 4A).

375 *Vegetative height*

376 Two predictors performed slightly better than the others, grazing pressure (RI = 0.4)
377 and topographic position at 5 m resolution (RI = 0.36; Fig. 4B), then followed by slope at
378 5 m resolution (RI = 0.25), actual exposure of the plot (RI = 0.23) and C/N ratio (RI =
379 0.22). All other predictors had a RI < 0.2. Quadratic terms had lower values than linear
380 terms.

381 *Seed mass*

382 Quadratic terms of shadow index (RI = 0.57) and soil depth (0.45) performed notably
383 better than other predictors (Fig. 4C). Relative importance of other predictors was then
384 ranging between 0.24 (quadratic term of LUI index) and 0.02 (quadratic term of actual
385 exposure of the plot). Soil physical proprieties were well represented amongst the most
386 important predictors (second, fourth and fifth places for soil depth, quadratic, and then
387 linear terms, and A horizon depth), as well as land use intensity predictors (LUI, third
388 place, grazing pressure, sixth place).

389 *Species richness*

390 Land use intensity index (LUI) and topographic position at 5 m resolution had notably
391 high importance (RI = 0.6 and 0.44 respectively, Fig. 4D), then followed by slope at 5 m
392 resolution (RI= 0.31), C/N ratio (RI = 0.28), pH (RI = 0.23) and growing degree days at

5m resolution (RI = 0.23). All other predictors were under RI = 0.2. Quadratic terms had lower relative importance than linear terms (RI < 0.06).

Percentage of variance explained by the new predictors

The results of the models built with the four best predictors for each trait and for species richness are summarized in Table 4. They respectively explain 36.6% (specific leaf area), 15.9% (vegetative height), 27.2% (seed mass) and 23.4% (species richness) of the residual variance from the first models. Together with the variance already explained by the topoclimatic models (see Table 3), this leads to a total explained variance of 64.6% (specific leaf area), 69.6% (vegetative height), 35.6% (seed mass) and 52.8% (species richness; Fig. 5).

Discussion

We demonstrated that in our conditions, the inclusion of four new predictors could explain 15.9 to 36.6% of the residual variance of habitual topoclimatic models, leading to an increase of the total explained variance from 5.7 to 24.1%. Highlighted predictors were different between traits; there was no new predictor that could be systematically used to improve models.

Biological relationship between traits and highlighted predictors

SLA was strongly influenced by two soil factors: C/N ratio and A horizon depth. These two predictors were expected to represent nutrient availability, A horizon depth showing the amount of organic matter available in the soil and C/N ratio its quality for biological organisms, especially plant growth (Batjes, 1996; Girard et al., 2011). A relationship between SLA and nutrient availability is widely assessed in literature (Meziane & Shipley, 1999; Cornelissen et al., 2003), and the inclusion of edaphic factors had already been shown to improve quality of SLA predictions by Dubuis et al. (2013). It is therefore not surprising to find them as key predictors to improve SLA models. Nevertheless, it is interesting to note that we were expecting a deep A horizon to be synonym of high nutrient availability for the plant, which causes higher SLA values (Cornelissen et al., 2003). The tendency showed to be inverted in our result, with low SLA values related to deep A horizons. This might be because in mature soils, organic matter might indeed accumulate in the topsoil, but in the form of concentrated degradation-resistant materials, therefore not available for the plant (Troeh &

Thompson, 1993). A deeper A horizon would then be synonym of less favourable organic matter degradation conditions, and low nitrogen availability.

Because of the high importance of human activities in the study area, and because of the results of Randin et al. (2009), we were expecting land use to be of high importance when trying to improve community trait predictions in the mountain grasslands. Indeed, vegetative height and species richness both reacted best to land use intensity indicators, with higher species richness in low intensive exploitations and taller species in low grazed exploitations. Interestingly, vegetative height was more related to grazing pasture than to the complete LUI index. This is coherent with ecological theory saying that grazing should favour short against tall plants (Dìaz et al., 2007). Our study also supports the previous studies showing a relation between increasing land use intensity and decreasing species richness (Fischer, 1994; Zechmeister et al., 2003; Niedrist et al., 2008). Nevertheless, it is important to note a possible confounding factor: the two plots with highest LUI index values had been recently mown when inventoried making species hard to distinguish. Nevertheless, other parcels with lower LUI values had also been recently grazed or mown before sampling, and these plots did not behave as outliers.

In both cases of species richness and vegetative height, the land use indicator was directly followed by 5 m resolution slope and topographic position. These high resolution predictors are probably complementary to the land-use information, which is sampled at the scale of the entire parcel (1 to 25 ha in the present study). Indeed, variations in the real land-use intensity might occur within the parcel, as a consequence of variations in the fine scale topography of the site : more flat areas will tend to be more intensively pastured by cattle and easier to reach by the farmer when fertilizing his parcel (personal communications). In this context, 5 m resolution topographic factors might be indicators of fine scale variations in land-use intensity.

Contrarily to our expectations, both vegetative height and seed mass showed an importance of actual light quantity received on the plot, with shadow index being the most important predictor for seed mass, and actual exposure of the plot and shadow index being well ranked amongst vegetative height results. As plant height is a key trait in the competition for light (Falster & Westoby, 2003), which is a vital resource for plants (Raven et al., 2000; Westoby et al., 2002), it makes biologically sense that

increasing the accuracy of the predictors linked to light availability would increase quality of the prediction of vegetative height. Similarly, a relationship between seed mass and shade is already well established in literature (Salisbury, 1942; Leishman et al., 2000; Pakeman et al., 2008), which has even been presented as the main driver in seed size variation (Westoby et al., 1992). Nevertheless, shade is usually measured as the shade at the soil level – taking into account the light obstruction caused by the vegetation itself - rather than on the amount of light actually reaching the vegetation canopy.

Seed mass was also the trait responding the least to topoclimatic models (11.6% of explained variance). The variables retained in these models (slope and both quadratic and linear terms of the moisture index at 25m) would highlight an importance of humidity in controlling seed mass. Similarly, the new predictors used to explain the residuals with multi modelling inference could be related to humidity, with a good representation of soil physical proprieties (soil and A horizon depths). In the silt-rich, loess derived soils of the region, a higher soil depth is linked to a higher water retention potential (Gobat et al., 2010). Increasing the amount of organic matter also affects the water retention potential of the soil (Gobat et al., 2010). This relationship with humidity finds some support in literature (Baker, 1972). Nevertheless, it has been heavily discussed (Westoby et al., 1992; Pakeman et al., 2008), as most of the hypothesized drivers for variation in seed mass (Leishman et al., 2000; Pakeman et al., 2008). Furthermore, instead of an increasing seed mass with shade or dryness of the environment, as Baker (1972) or Salisbury (1942), we found quadratic responses with minimal seed mass at intermediate shade and soil depth, and highest seed mass at intermediate A horizon depth. This difference between studies is difficult to explain, and would need supplementary data to be confirmed. Previous studies have already confirmed that the interpretation of mains drivers of variation in seed mass is equivocal (Salisbury, 1942; Baker, 1972; Westoby et al., 1992; Leishman et al., 2000; Pakeman et al., 2008).

Contrarily to our expectations, our results partially contradict those of Dubuis et al. (2013), who found that soil chemical proprieties explain a significant part of the variance in seed mass in the same study area. Furthermore, we did not find any correlation between seed mass and temperature, which has been highlighted in various

works (Pakeman et al., 2008; Dainese & Sitzia, 2013). Nevertheless, these authors worked on a much broader elevation or geographical range, whereas we focussed on short gradients. Therefore, we see a plausible explanation for both these last apparent contradiction: soil proprieties and temperature might be important to distinguish seed mass variations *amongst* a wide gradient of different ecological conditions, and not *within* the restricted range of ecological conditions and vegetation types studied here.

Potential for prediction

Soil proprieties showed to be important predictors, appearing in three of the four final models. Soil chemical proprieties were already shown as possible to be modelled across a geographic area (Burri, in prep), and such maps are currently being developed for the study area (Burri, unpublished work). These could be valuable information to implement in future models. Nevertheless, currently, physical soil information, such as soil or A horizon depths, cannot be inferred from remote sources and therefore still have to be measured in the field for each plot. As they do not exist as maps, they cannot be used as predictors for model projections.

The same applies to our fine scale measurements of light availability; as such, they do not exist as maps for the study area, and are difficult to sample. Nevertheless, the results of our study showed that the light availability related predictors normally used in topoclimatic models were not as complete as expected, especially for seed mass. Remote sensing approaches nowadays permit to detect changes in the earth surface up to the single tree level, and such approaches are already being applied in forestry (Morsdorf et al., 2004). Moreover, Pradervand et al. (2013) already developed maps of solar radiation at a 1 m resolution, although not accounting for tree cover. Taken together, these elements could be useful hints to improve models quality, especially for seed mass, as direct light availability measurements showed to be much more important in our study than was primarily expected.

High resolution topoclimatic predictors were highlighted in three of the four final models. As these predictors are nowadays relatively easy to infer and implement in models (Pradervand et al., 2013), it is an interesting hint for further improvement of the models. Nevertheless, for vegetative height and species richness, they accompany land-use information, probably refining it. Our study does not show whether they would be able to perform so well without land-use information.

In the context of this study, land use was highlighted as a major new predictor for both vegetative height and species richness, and was also quite important to explain seed mass. Nevertheless, it is important to remember that land use is often a very difficult piece of information to obtain. It rarely exists as maps and was a very time consuming step in our study, as only available with precision after discussing with the farmer. Furthermore, Randin et al. (2009) showed that this factor could improve species abundance models over the entire elevation range zone in the same study area but improvement was specifically for species occurring in lower areas, where anthropic disturbance occur. Therefore, it would be important to verify if land use is still as important when extending modelling efforts to a broader ecological range.

Limitations

Because of trait data availability, we had to put the threshold for minimum cover proportion with trait data information at 55%, although literature advices a value of 80% (Pakeman & Quested, 2007). A higher threshold would have discarded some of the 42 plots used in the second modelling step, what would have reduced the statistical power of our analyses. However, as we expect missing species to be regularly distributed in the spectrum of trait values, the community means ought not to be biased in one or the other direction. Caution should nevertheless be taken in future works to sample more trait data for the study area, and whenever possible, high trait-data availability thresholds should also be applied.

Another limitation in this work is the fact that we used a restricted environmental gradient. The strength of this approach is to allow detection of small variations that would normally be lost in the background of a larger gradient, or that could operate differently amongst different ecological conditions. But on the other hand, it is therefore difficult to extrapolate the validity of these results to other ecological conditions. One important step before implementing the suggested predictors in models should be to test them in other ecological conditions. It would also be interesting to test the importance of land-use data outside the range of highly managed mountain grasslands, and the efficiency of high-resolution topoclimatic predictors when uncoupled from land use data.

Conclusions

We showed that, in grasslands of the Western Swiss Alps, some part of the remaining variance in classical topoclimatic models (25 m resolution) could be explained by new complementary predictors: land use, edaphic and high resolution topoclimatic predictors (5 m). Some of them (land use, soil physical proprieties) are complicated to obtain and do not exist as maps for projections. Still, they may yield important improvement in model quality and should therefore not be omitted in future work, at least when projection is not needed. On the other hand, predictors such as high resolution environmental predictors or chemical soil composition, could be implemented in future modelling works, and therefore offer promising clues for community trait and species richness models improvement.

Acknowledgements

Many thanks to Christian Purro, Loïc Liberati, Olivia Chavaillaz and Samuel Jordan for their help during the field work, to the Service Cantonal d'Agriculture for their help in the search of the parcels' farmers, and to the farmers and owners themselves for allowing me to perform analyses on their lands and answering my questions. Many thanks also to all my fellow master students and to the ecospat group members for their help and support during this project. Especially huge thanks to Mélanie Beauverd for her help and the so many exchanges all along this project.

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Tables:

Table 1 : Ranges of topoclimatic predictors used in the stratification of the sampling strategy.

Stratum	Mean temperature (°C)	Slope (°)	Topographic position (unit-less)	Global solar radiations ($kJ \cdot day^{-1} \cdot pixel^{-1}$)
a "Low elevation, South exposure"	13.2-13.4	20-25	-100-0	2800-3000
b "Low elevation, North exposure"	13.2-13.4	20-25	-100-0	1600-1800
c "High elevation, South exposure"	12.2-12.4	20-25	-100-0	2800-2900
d "High elevation, North exposure"	12.2-12.4	20-25	-100-0	1600-1800

Table 2 : Fractions of the total available ecological range represented by the studied strata (mountain grasslands)

Predictor	**Total range over the study area**	**Restricted ranges retained in sampling**	**Percentage**
Mean temperature June-August (°C)	2.8- 18.3	13.2-13.4 12.2-12.4	1.3%
Slope (°)	0 – 80	20-25	6.25%
Topographic position (unit-less)	-699 – 1054	-100-0	5.7%
Global solar radiation ($kJ \cdot day^{-1} \cdot pixel^{-1}$)	313.3 – 3106.8	2800-3000 1600-1800	7.2%

745
746 **Table 3 Summary of topoclimatic models for the four traits and species richness.** Retained
747 predictors = predictors retained by the stepwise selection process. These models were
748 calibrated on plots previously sampled by Dubuis et al.(2013), using only 25 x 25 m topoclimatic
749 predictors.

Trait	**Retained predictors**	**AIC**	**% explained variance**
Specific leaf area	• Growing degree days • Global solar radiation • Slope • Topographic position • Moisture index • Global solar radiation^2 • Slope^2 • Moisture index^2	-1788.5	44.20%
Vegetative height	• Growing degree days • Slope • Moisture index • Growing degree days^2 • Topographic position^2 • Moisture index^2	-397.1	63.80%
Seed mass	• Slope • Moisture index • Moisture index^2	-113.5	11.60%
Species richness	• Growing degree days • Slope • Topographic position • Growing degree days^2 • Global solar radiation^2 • Slope^2 • Topographic position^2 • Moisture index^2	10356.9	38.40%

750

751

752
753 **Table 4 : AIC and percentage of explained residual variances** for the four models built with
754 the four most important predictors for each trait and for species richness. Percentages are
755 expressed in percentage of the residual variance from the first modeling step.

Trait	**Retained best predictors**	**AIC**	**% of explained variance**
Specific leaf area	• C/N ratio • A horizon depth • Slope (5 m resolution) • Growing degree days (5 m resolution)	-154.75	36.6 %
Vegetative height	• Grazing pressure • Topographic position (5 m resolution) • Slope (5 m resolution) • Exposition	-39.75	15.9 %
Seed mass	• Shadow index (linear and quadratic terms) • Soil depth (linear and quadratic terms)	-9.6894	27.2 %
Species richness	• LUI index • Topographic position (5 m resolution) • Slope (5 m resolution) • C/N ratio	297.35	23.4%

756

Figures:

Fig. 1 : Map of the study area, with vegetation plots newly inventoried in 2014 (orange triangles) and previously inventoried (2002-2009, white dots; Dubuis et al., 2013)

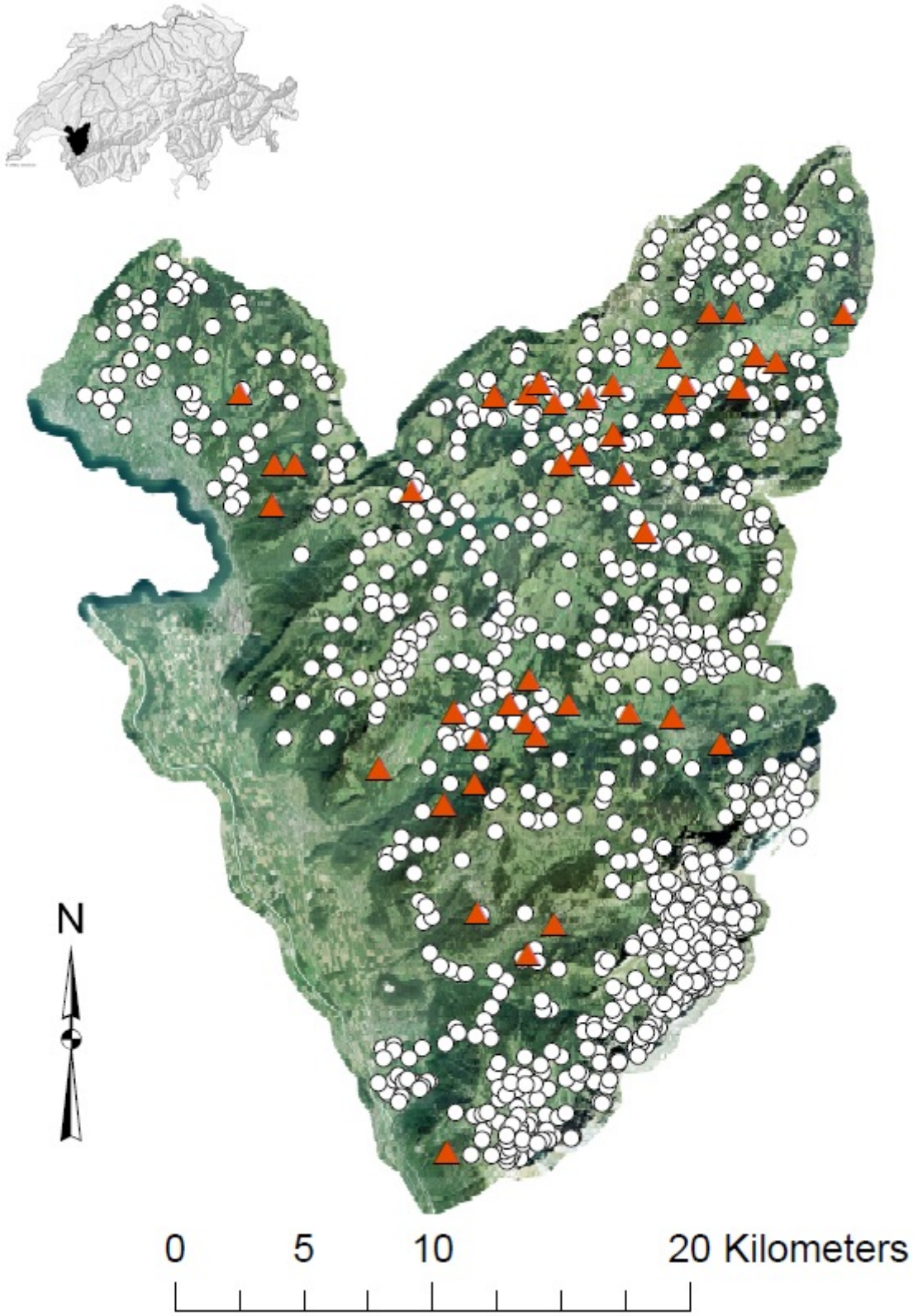


Fig. 2 Scheme of the statistical analyses canvas.

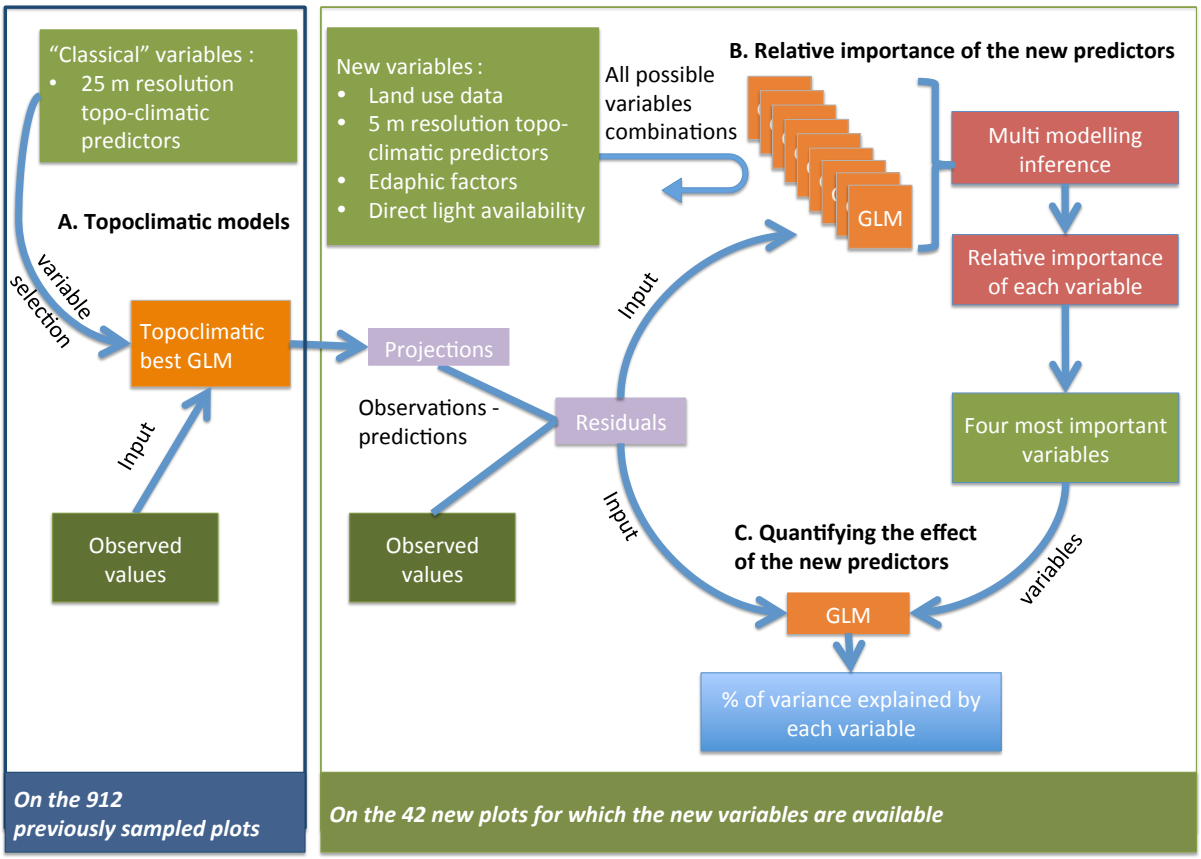


Fig. 3 : Relationship between each trait and its most important new predictor. SLA = specific leaf area, VH = vegetative height, SM = seed mass, SR = species richness. Complete information is available in S2.

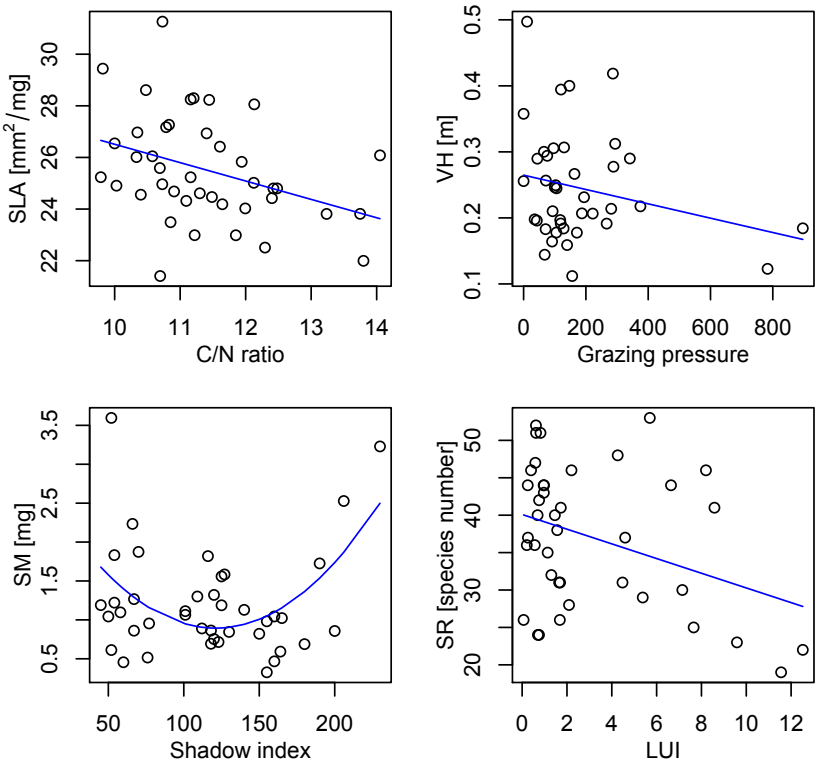


Fig. 4 : Relative Importance for the ten best predictors in explaining residuals of the first models. A = specific leaf area, B = vegetative height, C = seed mass, D = species richness. Topographic pos. = topographic position, LUI = Land Use Intensity index, G. degree days = growing degree days.

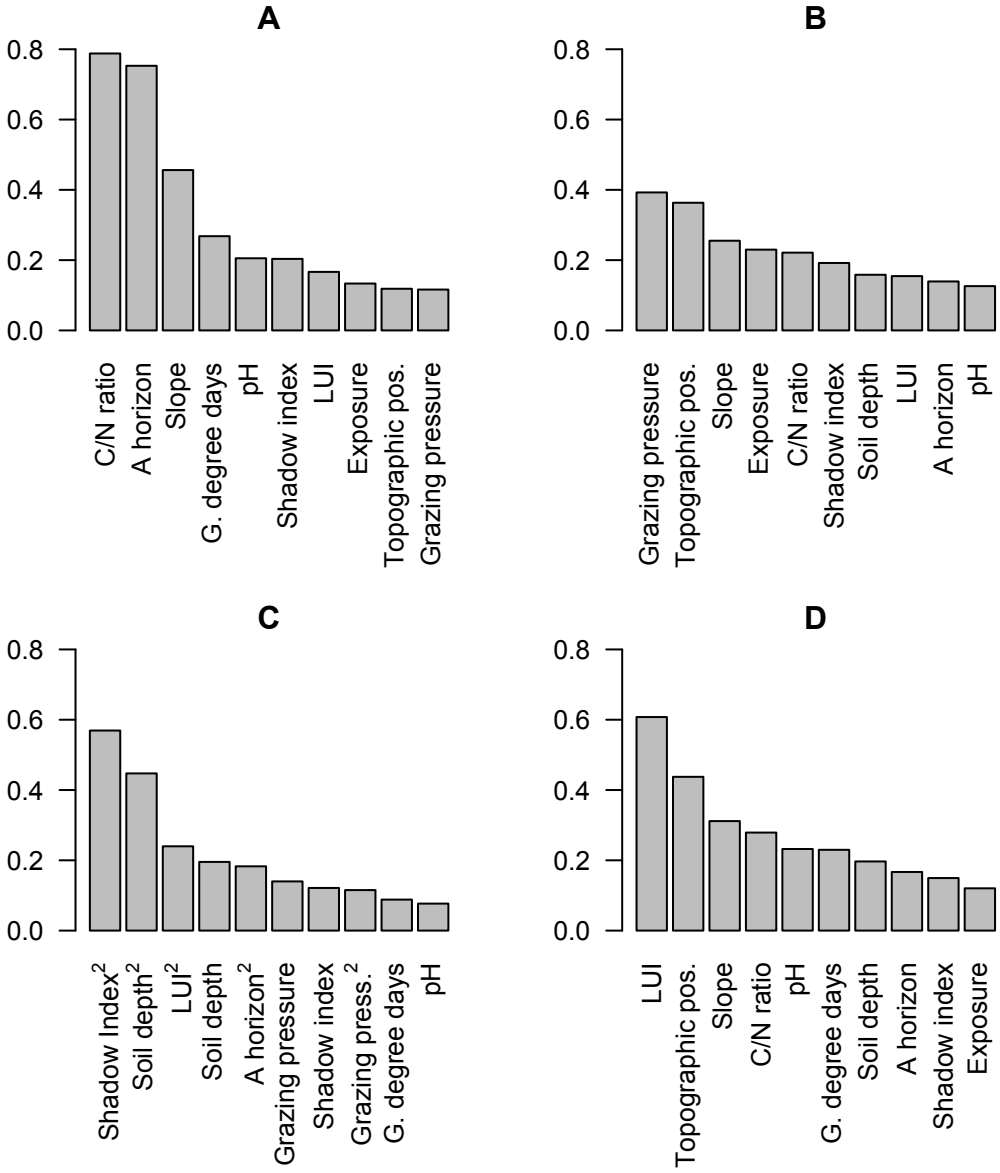
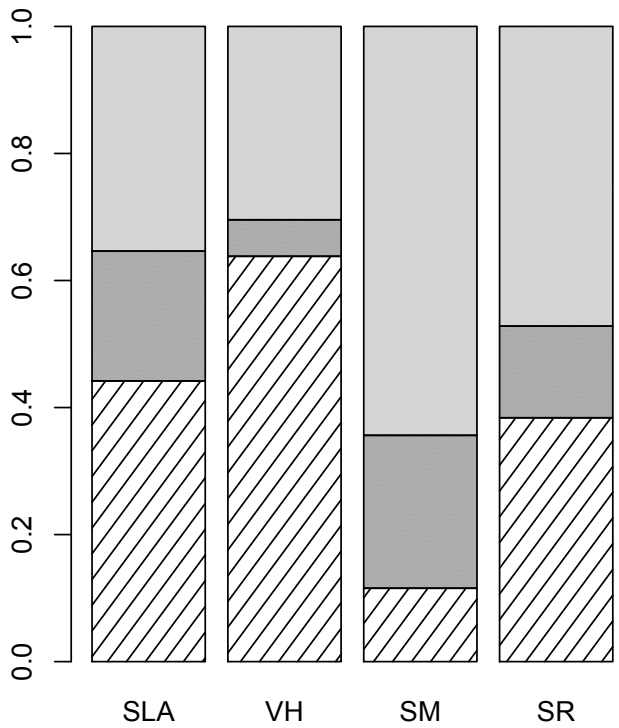


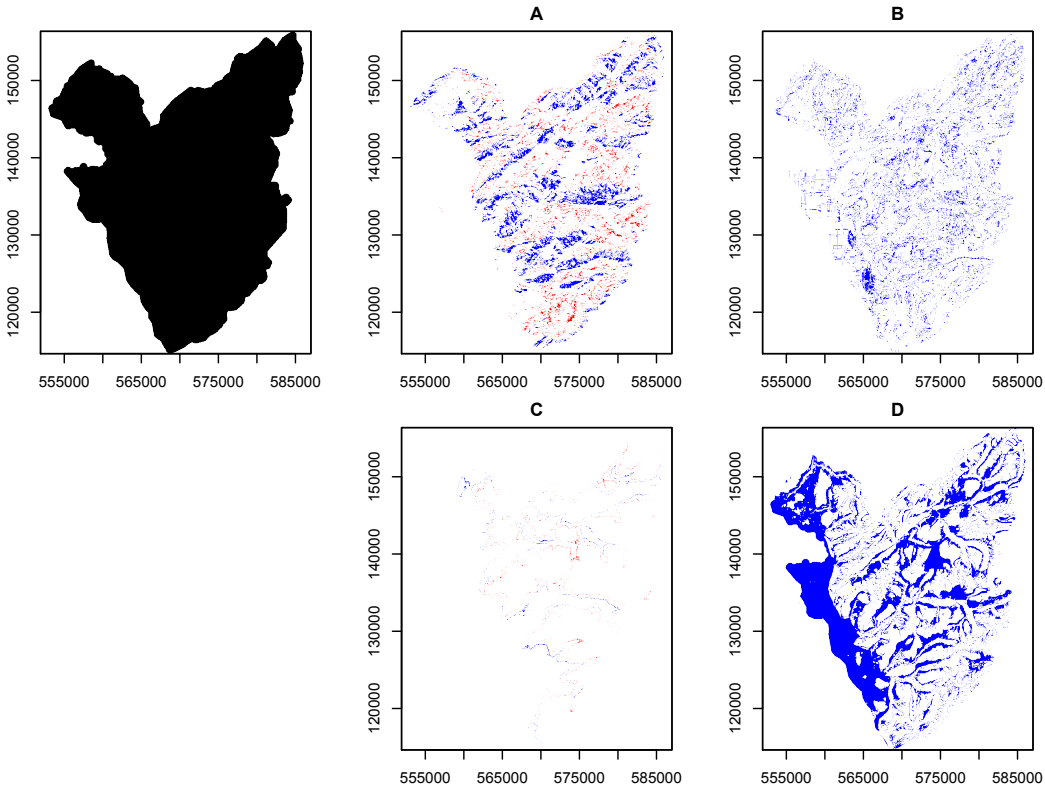
Fig. 5 : percentage of explained variance for the four models. Dashed lines = variance explained by the first models (topoclimatic predictors, calibrated on the plots previously sampled; Dubuis et al., 2013); dark grey = supplementary variance explained by the second models (four most important new predictors, calibrated on the plots sampled in the field season 2014); light grey = unexplained variance.



Supporting information:

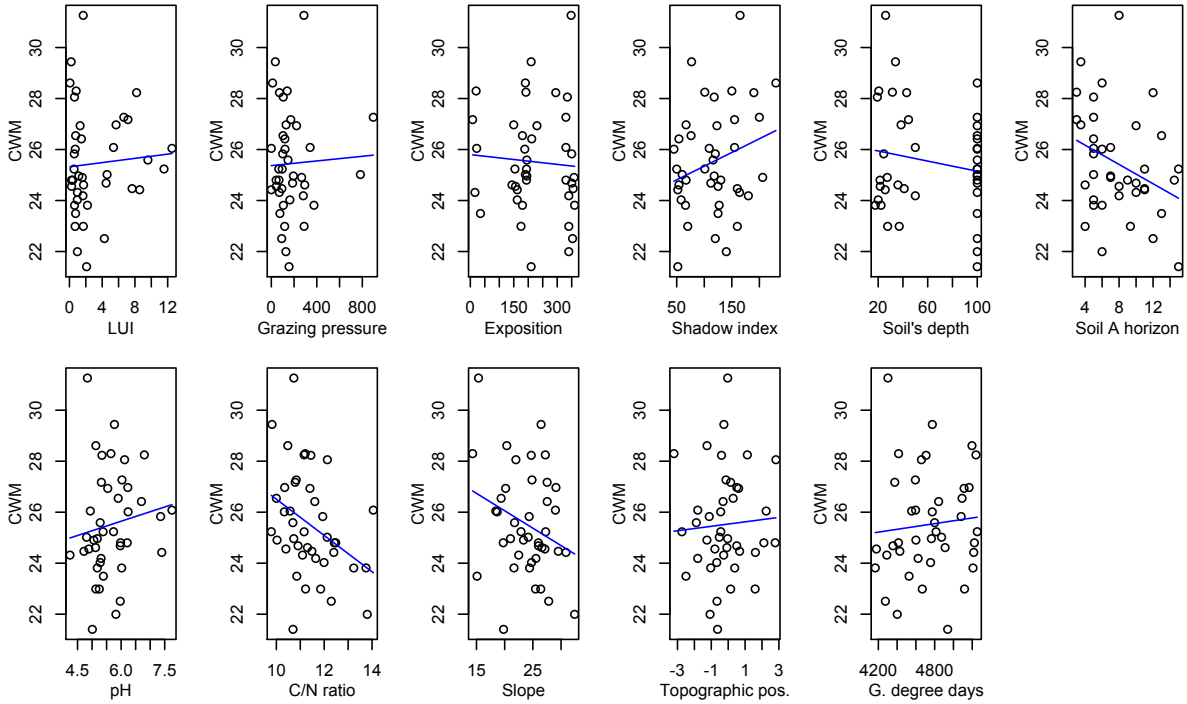
Appendix S1

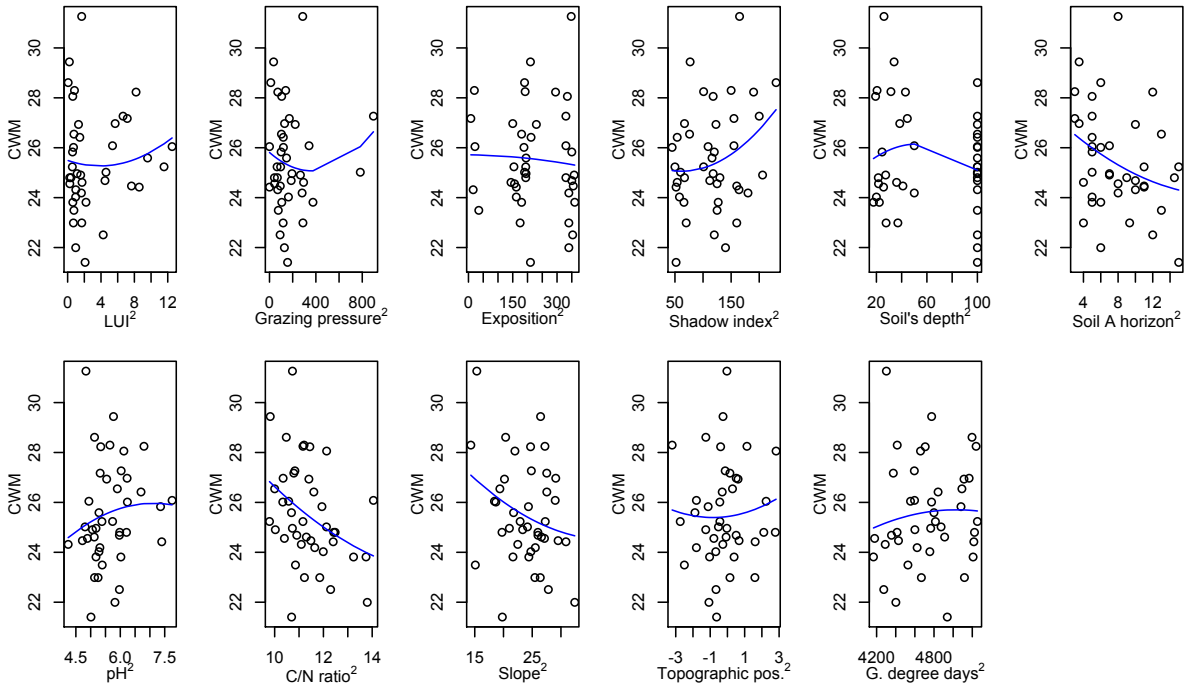
Ranges of predictors used for the sampling strategy and their distribution over the study area**.** A = global solar radiation, B = slope, C = mean temperature, D = Topographic position. Blue and red show the different strata when applicable. In black is the entire study area



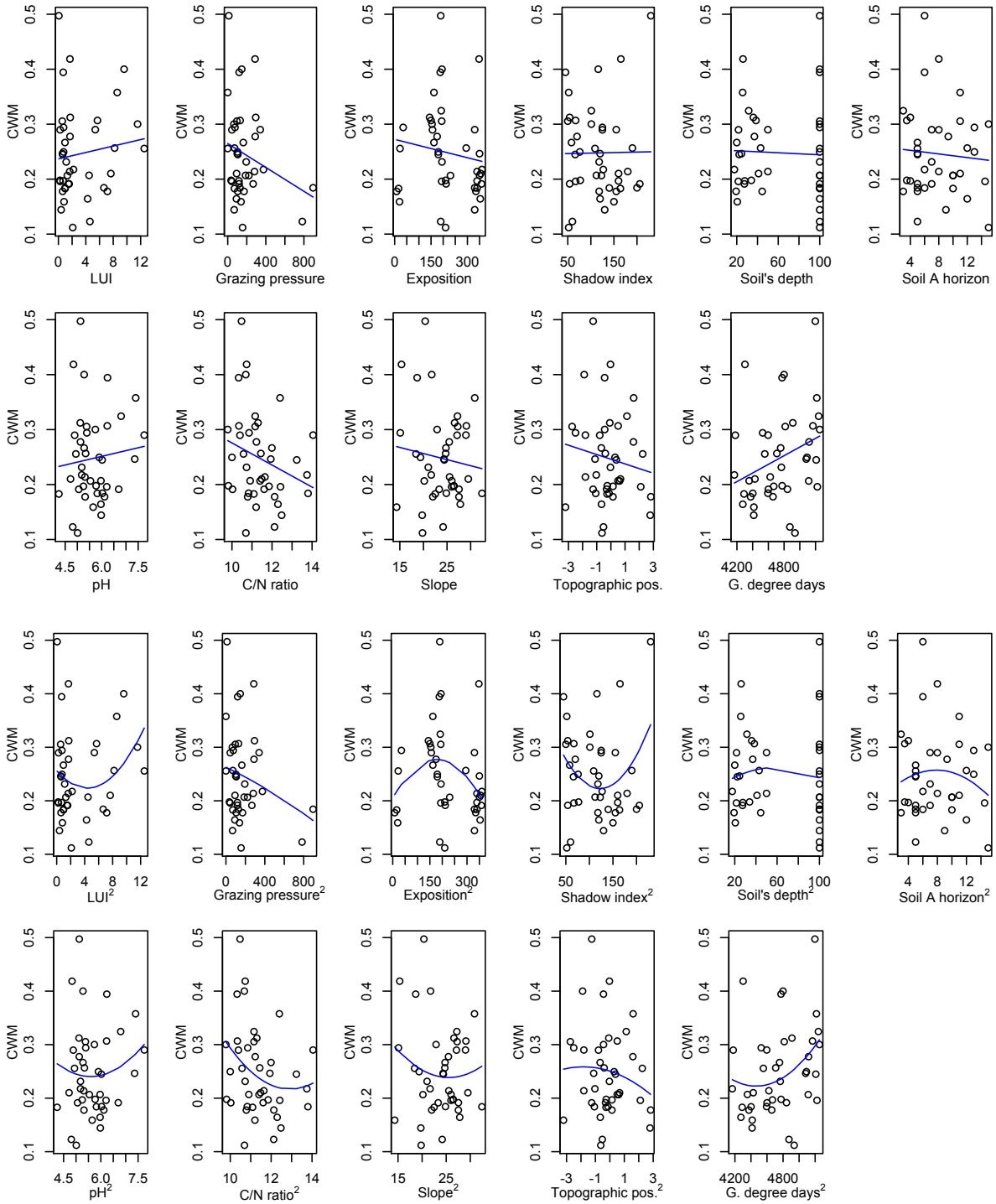
Appendix S2: relationship between traits and predictors

Appendix S2A: **Specific leaf area** as a function of each new potential new predictor. CWM = community weighted mean ($mm^2 \cdot mg^1$), G. degree days = growing degree days, Topographic pos. = topographic position.

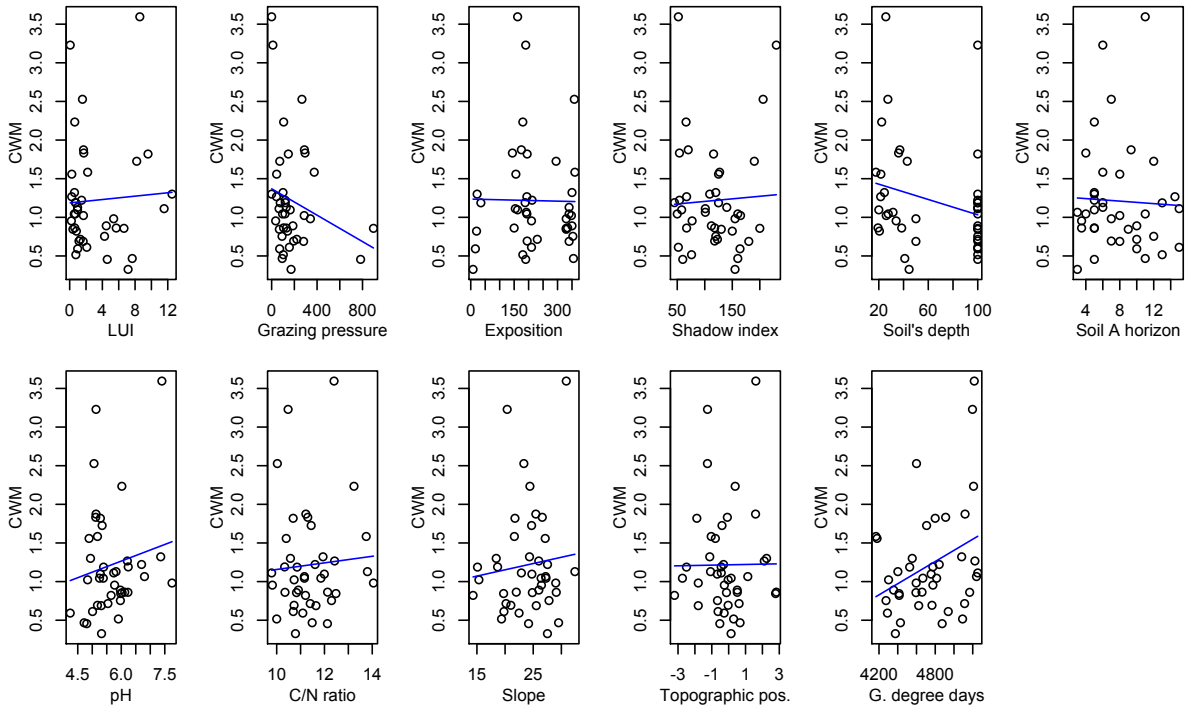


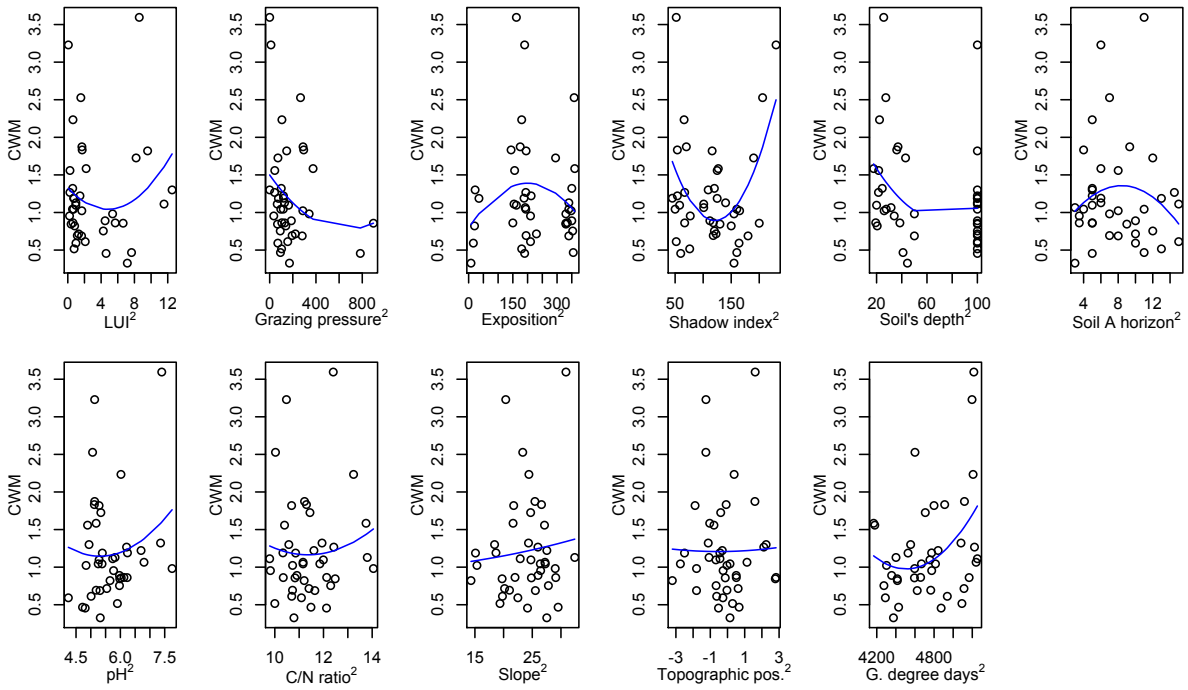


Appendix S2B: Vegetative height. CWM = community weighted mean (m), G. degree days = growing degree days, Topographic pos. = topographic position.

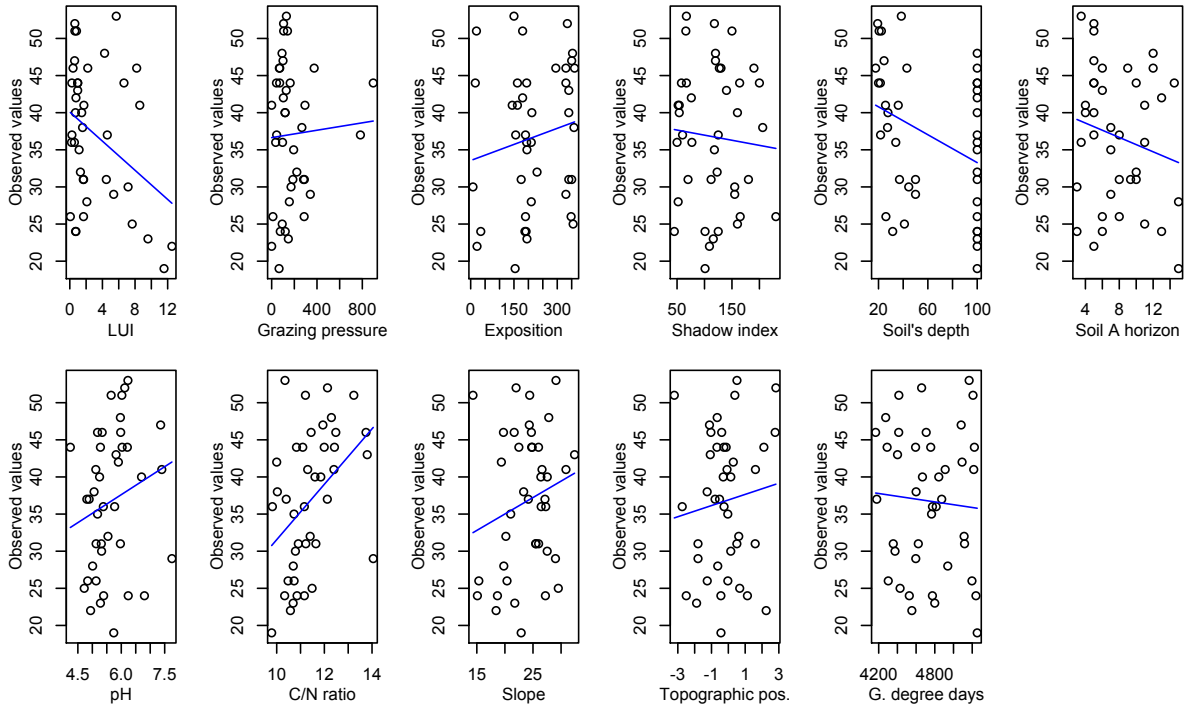


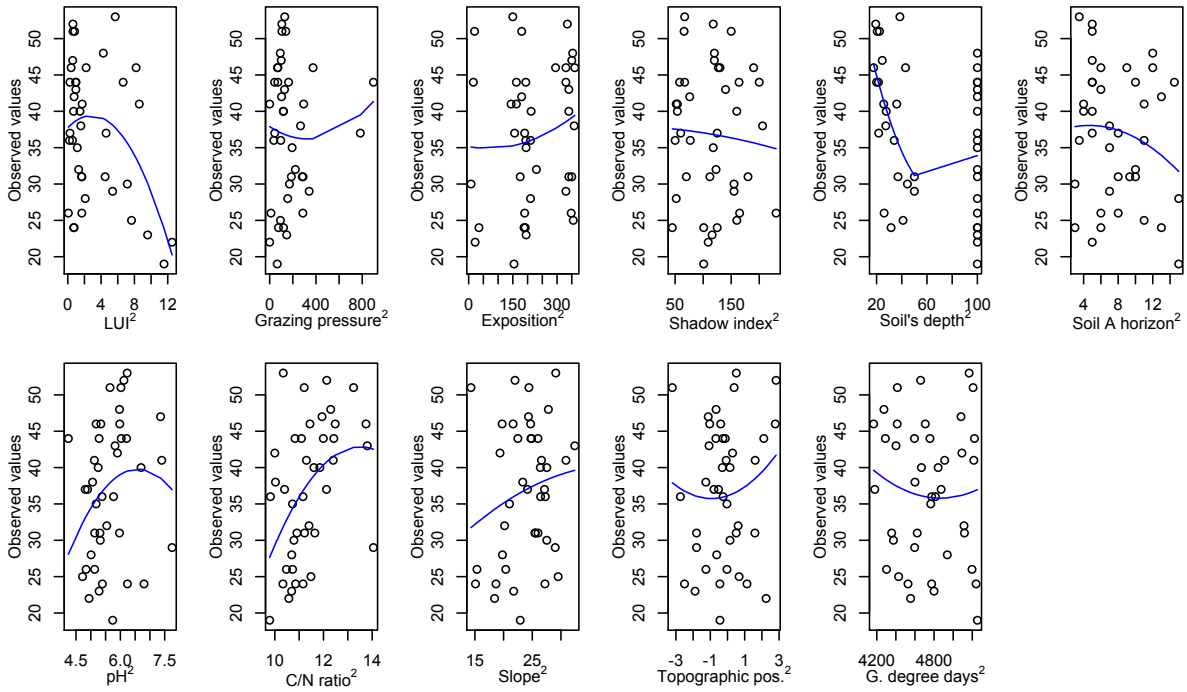
Appendix S2C: Seed mass. CWM = community weighted mean (mg), G. degree days = growing degree days, Topographic pos. = topographic position.





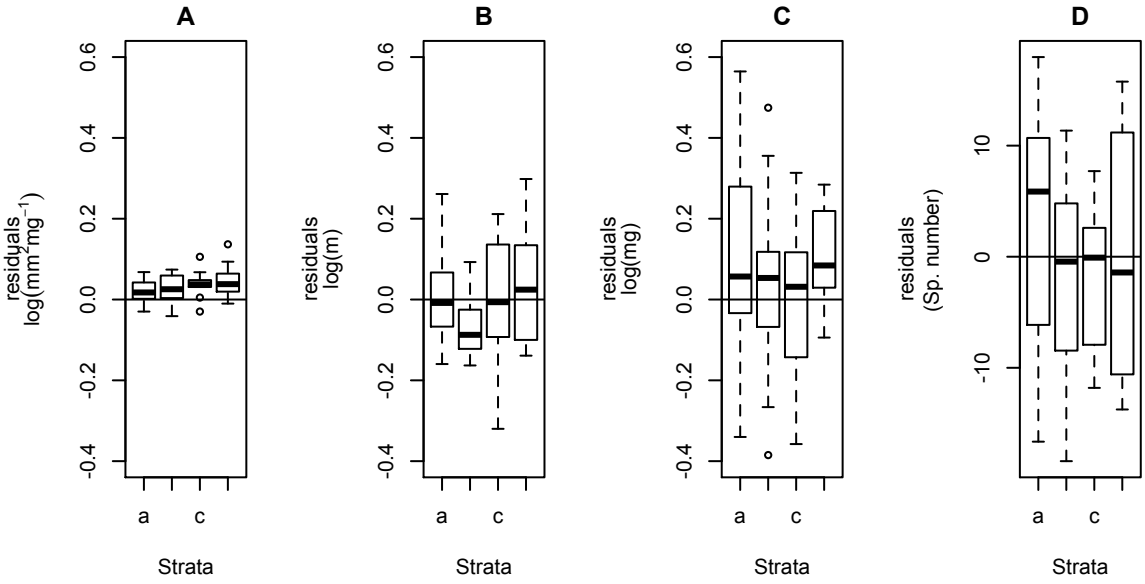
Appendix S2D: Species Richness. Observed values = observed number of species per plot, G. degree days = growing degree days, Topographic pos. = topographic position.





Appendix S3:

Plot of the residuals of the topoclimatic models for the A) specific leaf area B) vegetative height C) seed mass D) species richness obtained for the 42 new plots.



Appendix S4 :

Weights of the 15 best models for A) specific leaf area B) vegetative height C) seed mass D) species richness. Variables included in each models are designed by the following code: 1 = C/N ratio, 2 = topographic position, 3 = growing degree days, 4 = exposition, 5 = shadow index, 6 = LUI index, 7 = pH. 8 = Grazing pressure, 9 = 5 m resolution slope, 10 = A horizon depth, 11 = soil depth. 12-22 = quadratic term of these variables, in the same order. 23 = null model.