Learning from model errors: Can land use, edaphic and very high-resolution topo-climatic factors improve macroecological models of mountain grasslands?

Running title: Improvement of macroecological models of mountain grasslands

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Abstract

Aim: Assess the potential of new predictors (land use, edaphic factors and high-resolution topographic and climatic variables, i.e., topo-climatic) to improve the prediction of plant community functional traits (specific leaf area, vegetative height and seed mass) and species richness in models of mountain grasslands.

Location: The western Swiss Alps

Methods: Using 912 grassland plots, we constructed predictive models for community-weighted means of plant traits and species richness using high resolution (25 m) topo-climatic predictors traditionally used in previous modelling studies in this area. In addition, 78 new plots were sampled for evaluation and error assessment in four narrower sets of homogenous conditions based on predictions by the topo-climatic models within two elevation belts (montane and alpine). New, finer-scale predictors were generated from direct field measurements or very high-resolution (5 m) numerical data. We then used multimodel inference to test the capacity of these finer predictors to explain part of the residual variance in the initial topo-climatic models.

Results: We showed that the finer-scale predictors explained up to 44% of the residual variance in the classical topo-climatic models. The very high-resolution topographic position, soil C/N ratio and pH performed notably well in our analysis. Land use (farming intensity) was highlighted as potentially important in montane grasslands, but improvements were only significant for species richness predictions.

Main conclusions: Compared with previously-used topo-climatic models, the new, finer-scale predictors significantly improved the prediction of all traits and species richness in alpine plant communities and that of specific leaf area and richness in montane grasslands. The differences in the importance of the predictors, dependent on both trait and position along the elevation gradient, highlight the different factors that shape the distribution of species and communities along elevation gradients.

Keywords: Alps; Community ecology; Functional traits; Seed mass; Species richness; Specific leaf area; Switzerland; Vegetative height

Introduction

It has long been argued that the description of communities by their biological characteristics (also called "traits") provides better and more generalizable results than descriptions based only on species identities (Keddy, 1992; McGill et al., 2006). Amongst species traits, *functional traits* are related to the fitness of individuals (growth, reproduction or survival; Violle et al., 2007). To understand the distribution of communities and their responses to particular conditions, functional trait values can be calculated at the community level (Dubuis et al., 2013), allowing for the identification of general patterns that cannot be observed when working at the species level. Species richness, usually defined as the number of species in a specified area or system (Díaz & Cabido, 2001), is also widely assessed by ecologists because of its importance in regulating ecosystem properties and functions (Grime, 1998), such as resilience (Perterson, Garry et al., 1998) and stability (Tilman et al., 2014).

In this context, macroecological models (MEM) that relate community properties, such as richness, composition, structure, or function, with environmental or biotic factors are promising tools (Keddy, 1992; Küster et al., 2011; Dubuis et al., 2013). This approach provides powerful insights into the factors that determine the distribution of community properties. For example, Küster et al. (2011) predicted the distribution of functional traits to assess the potential effects of climate and land use changes on the distribution of leaf anatomy. Although MEMs have gained popularity (Pellissier et al., 2010; Sonnier et al., 2010; Dubuis et al., 2011, 2013; Küster et al., 2011; Mod et al., 2015), many studies have been based on similar sets of topographic and climatic (hereafter "topo-climatic") predictors extracted from GIS-derived data. To date, only a few studies have assessed the extent to which other predictors improve the predictions of community trait composition (Garnier et al., 2004; Dubuis et al., 2013). Dubuis et al. (2013) tested the influence of edaphic factors on the quality of trait models and concluded that the inclusion of soil chemical (pH, nitrogen and phosphorus contents) and physical (soil texture) properties significantly improved the quality of the predictions. These authors focused only on edaphic factors but recognized that other predictors, such as land use, could also be included (Dubuis et al., 2013). For example, it is well known that farming intensity affects the floristic composition (Peter et al., 2008) and richness (Zechmeister et al., 2003) of grasslands, and the inclusion of farming management (intensity of grazing or mowing, fertilization) in models improved the prediction of plant abundance (Randin et al., 2009). Therefore, farming intensity could be expected to influence community traits. Furthermore, to our knowledge, very high-resolution environmental maps (< 10 m) have not been incorporated into community trait modelling, although their use has improved the distribution models of some species (Lassueur et al., 2006; Pradervand et al., 2014). By contrast, most climatic data are obtained from interpolations of a limited number of point measurements over a broad study area (e.g., Zimmermann & Kienast, 1999), which results in calculations that are sometimes based on rough approximations, particularly in mountainous regions (Guisan & Zimmermann, 2000). Therefore, a possible approach to increase the quality of predictions is to conduct larger sampling efforts of point measurements of environmental factors in the field, at the locations of species observations, to improve the quality of the predictions.

The evidence suggests that the relative importance of the drivers of species distributions changes over space and time or along productivity gradients (Michalet et al., 2006). In the Alps, the elevation gradient can extend from approximately 400 m to above 4000 m. As advised by the current literature (McGill et al., 2006), Dubuis et al. (2013) studied an entire elevation gradient, seeking a complete understanding of the community variation over a wide ecological range; however, such a large gradient can also buffer the importance of local factors. For example, farming intensity affects communities differently at high and low elevations (Randin et al., 2009), and Pottier et al. (2013) showed that the accuracy of community composition models was dependent on elevation. Thus, there is a clear indication that additional factors may improve community models and that improvement may depend on elevation, but a systematic study has yet to address these questions.

This study aims to assess the potential of a set of new predictor variables (i.e., farming intensity and edaphic and very high-resolution (VHR; 5 m) versus high-resolution (HR; 25 m) topo-climatic factors), measured locally or computed at a fine scale to improve the performance of four community-level macroecological models, namely, species richness (SR) and three functional traits: specific leaf area (SLA), vegetative height (VH) and seed mass (SM). We assessed the potential of the new predictors to explain the error in the previously-used topo-climatic models (hereafter referred to as « classical models »). To identify condition-specific effects of the predictors, we focused on two specific sets of environmental conditions in two disjointed elevation belts (montane and alpine) within the same study area. The potential of the new predictors was assessed for each of the elevational belts separately, and the importance of the different predictors between these two belts was then compared. We expected that the increase in the resolution of the predictors would bring potential to improve the quality of the models, particularly at high elevations where environmental filtering is expected to be stronger (Pottier et al., 2013) and that the farming intensity predictors would be of more primary importance in the lowland.

Materials and Methods

Study design

To assess the predictive power of the new local predictors, we first built generalized linear models (GLM) of community-weighted means of plant traits and species richness based on topo-climatic predictors (see Figure S1 in Supporting Information), as done in previous studies (Zimmermann & Kienast, 1999; Dubuis et al., 2011, 2013). New, finer-scale environmental descriptors (farming intensity and edaphic and VHR topo-climatic factors) were generated from direct field measurements or VHR (5 m) numerical data for a set of newly sampled plots. Small, bivariate linear models (LM) made up of combinations of the new predictors were run on the residuals of the classical models for these new plots. A multimodel inference (MMI) was used to address the capacity of the finer predictors to explain the residual (i.e., unexplained) variance (i.e., deviance in the case of GLMs) in the initial topo-climatic models. Using only the two best predictors highlighted by the MMI, we created a single bivariate (GLM) model per trait, assessed the magnitude of the yielded improvement on the residuals and tested for their significance.

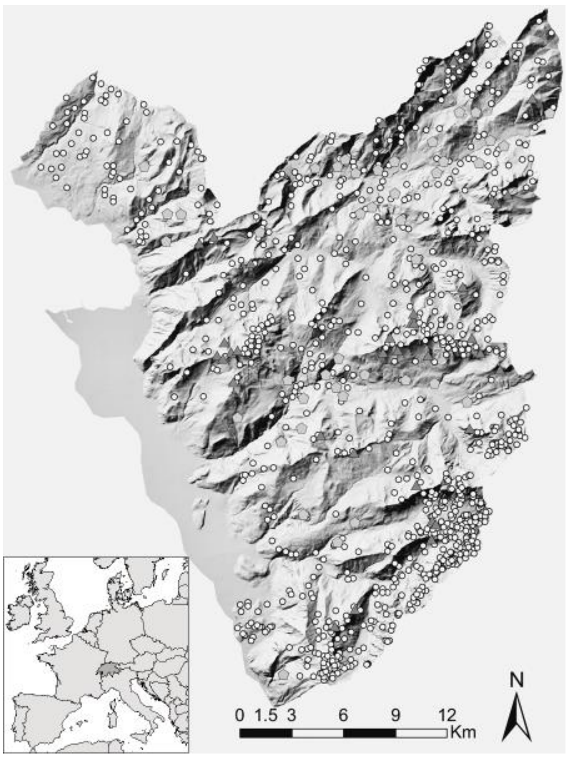

Figure 1. Map of the study area with sample sites (The Alps in Canton de Vaud, Switzerland, 46°10 - 46°30′ N, 6°50 - 7°10′ E). White dots = 912 vegetation plots previously sampled. Triangles = 37 alpine and pentagons= 41 montane vegetation plots sampled for this study.

Vegetation data and predictors

Study area and initial vegetation data

The study area covers 700 km^2 in the western Swiss Alps (Fig. 1), with an elevation ranging from 375 to 3210 m. The vegetation reflects the typical elevation gradient of Central Europe, with broadleaf deciduous forests at the lowest elevations (colline belt), coniferous forests (subalpine) and then alpine grasslands above the treeline (see Dubuis et al. (2013) for more information). Outside of the forests, most of the area is used for agriculture, with pastures in the lowlands to the lower alpine zones and meadows primarily in the colline and montane belts (Randin et al., 2009).

We used 912 plant inventories in 4 m^2 plots sampled between 2002 and 2009 in grasslands and open areas to fit the initial topo-climatic models. These inventories were conducted based on a random-stratified sampling strategy using elevation, slope and aspect as the stratifying factors (Fig. 1; see Dubuis et al. (2013) for more details).

Table 1. Ecological ranges of the two selected elevation strata for the four considered predictors and corresponding proportions of the total available pixels in the study area.

Predictor	Total range over the study area	Stratum	Montane		Alpine	
			Sampling range	Proportion [%]	Sampling range	Proportion [%]
Mean temperature June-August [°C]	2.8 – 18.3		12.2 – 13.4	7.75	8.9 – 9.7	6.44
Global solar radiation [$kJ \bullet day^{-1} \bullet pixel^{-1}$]	313.3 – 3106.8	South	2800 – 3000	7.20	3000 – 3100	3.03
		North	1600 – 1800	7.20	1150 – 1450	9.09
Slope [°]	0 – 80		20 – 25	6.25	30 – 35	5.56
Topographic position index	-699 – 1054		-100 – 0	5.70	100 – 200	1.67

Sampling strategy and new plots

A random-stratified design based on mean temperature, global solar radiation and topographic position was then used to sample the new plots in the grassland areas (see Appendix 1, Table S1 for a presentation of the 25 m resolution predictors used in this study). To obtain data from groups of plots sharing very similar macro-environmental conditions, we selected plots in both montane and alpine grasslands in two sets of very precise ecological conditions corresponding mainly to southern and northern exposure (Table 1; see supplement to methods in Appendix 1). In each combination of ecological conditions we would expect nearly identical plant communities based on the topo-climatic models.

A total of 41 montane and 37 alpine grassland plots were sampled (Fig. 1) during the summer of 2014 (June-August). Inventories of all vascular plants were made in 4 m^2 plots following the same methods and plot size used in the previous inventories. We estimated the cover of each species using the same adapted Braun-Blanquet (1964) abundance-dominance scale (r, 1-3 individuals; +, < 1%; 1, 1-5%; 2a, 6-15%; 2b. 16-25%; 3, 26-50%; 4, 51-75%; 5, 76-100%). The mid-range values of these classes were used for further analyses.

Functional traits

Three functional traits were considered, corresponding to three different characteristics of plant life (Westoby, 1998). Specific leaf area (SLA) is the area of one side of a fresh leaf per dry mass of the leaf (Cornelissen et al., 2003) and is linked to photosynthetic and carbon fixation rates (Lavorel & Garnier, 2002). Vegetative height (VH) is calculated as the distance between the top photosynthetic tissue and the ground and is linked to disturbance, stress avoidance and competition (Lavorel & Garnier, 2002). Seed mass (SM) is the average dry mass of the seeds and represents the strategy of plant investment in reproduction (Cornelissen et al., 2003). For SLA and VH, data previously collected for the same study area were used (Dubuis et al., 2013). SM data were gathered from databases or literature (Kleyer et al., 2008; Royal Botanic Gardens Kew, 2014; Müller-Schneider, 1986; Römermann et al., 2005; Pluess et al., 2005; Vittoz et al., 2009; Klotz et al., 2002). We calculated cover-weighted means for the entire plant community (i.e., weighted mean). Plots were discarded whenever trait information was available for less than 60% of the vegetation cover. No new plots had to be discarded. More information about trait value computation can be found in Supporting Information (Appendix S1). Species richness was calculated for all plots as the total number of species per plot.

New predictors

An overview of the new predictors is available in Supporting Information, Appendix 1 (Table S2). Farming intensity data were collected for the 41 montane grasslands from interviews with farmers. A land use intensity index (LUI) was then computed, as suggested in Blüthgen et al. (2012):

$$LUI = \frac{F_i}{F_R} + \frac{M_i}{M_R} + \frac{G_i}{G_R}$$

where F_i is the fertilization level for the plot *i* (m^3 of manure·$year^{-1}$·ha^{-1}), M_i is the frequency of mowing per year, G_i is the grazing intensity (UGB·days·ha^{-1}·$year^{-1}$) and F_R, M_R and G_R are their respective means for the data set. A UGB is a standardized unit for cattle foraging requirements (1 UGB = one cow). For the 37 alpine plots no interviews were conducted. In the alpine plots, grazing pressure is always diluted across vast areas with high topographic and grazing heterogeneity. Details would therefore be of little value.

For all plots, we measured the true aspect with a compass. The total depth of the soil was measured with an auger. A soil sample of the organo-mineral horizon (Baize & Jabiol, 1995) was collected and air-dried. The pH of the sample was measured with a pH meter after dilution in water in a 1:2.5 w/v ratio. We measured the organic C and N contents with a Carlo Erba CNS2500 CHN Elemental Analyser coupled with a Fisons 198 Optima mass spectrometer (Tamburini et al., 2003). The C/N ratio was used as a biologically relevant summary of nutrient availability (Batjes, 1996).

Pradervand et al. (2014) developed different very high resolution (VHR) predictors for the same study area using modelling processes instead of interpolation. We retained growing degree-days, topographic position and slope at a 5 m resolution because these predictors yielded the best results in the previously published species distribution models (Pradervand et al., 2014). Growing degree-days corresponded to the sum of the daily temperatures during the growing season (June, July and August) when temperatures were above 3°C. For more details on these raster maps, see Pradervand (2015), Descombes et al. (2015) and Appendix 1.

Modelling

The models were run for the three functional traits – SLA, VH and SM - and for species richness (SR) following a similar canvas (Fig. S1 in Appendix S1). All analyses were performed using R statistical software (version 3.3.2; R Core Team, 2016).

Topo-climatic models

Classical topo-climatic models (GLM) were built following the method of Zimmermann & Kienast (1999) using the same high-resolution (HR) topo-climatic predictors, i.e., moisture index, growing degree-days, global solar radiation, slope and topographic position (25 m resolution). The moisture index is the mean difference between precipitation and potential evapotranspiration over the growing season. The moisture index represents the amount of water potentially available in the soil (see Appendix 1 for more details about the HR predictors). Using these predictors, a GLM was fitted with the 912 available vegetation plots for each of the three traits and for SR. All trait values were log transformed before analyses to meet the normality assumption of the data. Models were selected through a backwards stepwise selection based on AIC. The family and link functions were set to Gaussian and identity for the three traits and Poisson and logarithm for SR.

We used the 912 vegetation plots previously available to fit our classical 25 m topo-climatic models. These plot data had been collected following a random stratified sampling strategy over the main environmental gradients. This approach allows the most accurate distribution models to be built for species (Hirzel & Guisan, 2002) and for functional traits (McGill et al., 2006; Dubuis et al., 2011, 2013; Küster et al., 2011). To further assess the predictive power of the finer local predictors, we projected the topo-climatic models on the 78 new plots and calculated the ordinary residuals at these sites. We did so by comparing the predictions to the actual observations (Zuur et al., 2013), which means focusing on the “error” of the model within these plots, an appropriate approach towards model improvement (Jenkins et al., 2003). To address the potential effect of stratification in the design, we compared the residuals of the different strata within each elevation belt using a Kruskal-Wallis test. One new plot in the alpine belt behaved as an outlier. As the outlier occurred on an extremely steep slope and the vegetation was heathland instead of grassland for all other plots, it was discarded in the following analyses.

Relative importance of the new predictors

To calculate the relative performance of the new predictors, we performed a second modelling step by fitting new models to these residuals, this time using simple linear models (LM) and including the new, local variables as predictors. Adapting the approach recently developed by Breiner et al. (2015), we constructed ensembles of small models using all possible combinations of two predictors at a time (i.e., in each small model) or a combination of the linear and quadratic terms of these predictors. The number of predictors in each small model was limited to four (when both quadratic and linear terms were included) in the final models according to Harrell’s rule-of-thumb of 10 observations per parameter estimate (Harrell, 2001). The quadratic terms were always considered together with their respective linear terms to allow the capture of a proper quadratic curve response by the model. Potential overfitting issues were addressed through an RMSE analysis (see Appendix 1). The importance of each new predictor in explaining the variance in the residuals was assessed across the ensemble of models using multimodel Inference (MMI; Burnham et al., 2011). We used the ‘MuMIn’ R package (Barton, 2014) to rank the models by AICc score, and an Akaike weight was computed for each model (Burnham & Anderson, 2002). These Akaike weights were used to estimate the relative importance (RI) of each predictor (for more details see Appendix 1). This permitted the assessment of the usefulness of each of the new predictors relative to the others in explaining the error of the classical topo-climatic models.

Because farming intensity was only available for the lower plots, the two elevation belts were analysed separately. The montane plots were analysed twice: once with farming intensity to evaluate the importance of this category of predictor, and once without farming intensity for direct comparison with the alpine plots.

Percentage of deviance explained by the new predictors

To quantify the effects of the new predictors, we fitted a final model (GLM) for each of the three traits and for SR, including the two best predictors (with quadratic terms when applicable) according to the relative importance values previously calculated by MMI. These models were run on the residuals of the topo-climatic models to evaluate the proportion of the residual variance that could be explained by the new predictors. The family was set to Gaussian for the residuals of all traits and species richness. We estimated the potential for model improvement with the new predictors by calculating the percentage of residual deviance that could be explained by this new modelling step. We tested whether this increase in explained variance was significant by creating models with random new variables based on a normal distribution in the same way that our best models were created. This step was repeated 10,000 times. We then tested whether the amount of explained variance was significantly above the 95% quantile of the distribution of random values.

Results

The HR topo-climatic models explained 44.3% of the total deviance for SLA, 63.9% for VH, 8.3% for SM and 38.4% for SR for the 912 vegetation plots that covered the entire study area. The details are presented in the supplementary material (Table S3 in Appendix S2). The results of the Kruskal-Wallis tests among the elevation belts were non-significant, indicating no stratification in the residuals.

No predictor was identified as most important in the models fitted on the residuals (Fig. 2). The overfitting analysis indicated that none of these models were significantly overfitted. When farming intensity was not considered (Fig. 2, middle panel), the edaphic factors performed well in the montane grasslands. The C/N ratio was the most important predictor for SLA and VH in the montane belt, while soil depth and pH were the most important predictors for SM and SR, respectively (Fig. 2, upper and middle panels).

In contrast, the VHR (5 m) topo-climatic predictors were more important in the alpine grasslands. Notably, the topographic position was identified as the most important local predictor to model SLA and SR and the second most important predictor for VH (Fig. 2, lower panel). The VHR growing degree-days was important to model VH and SR.

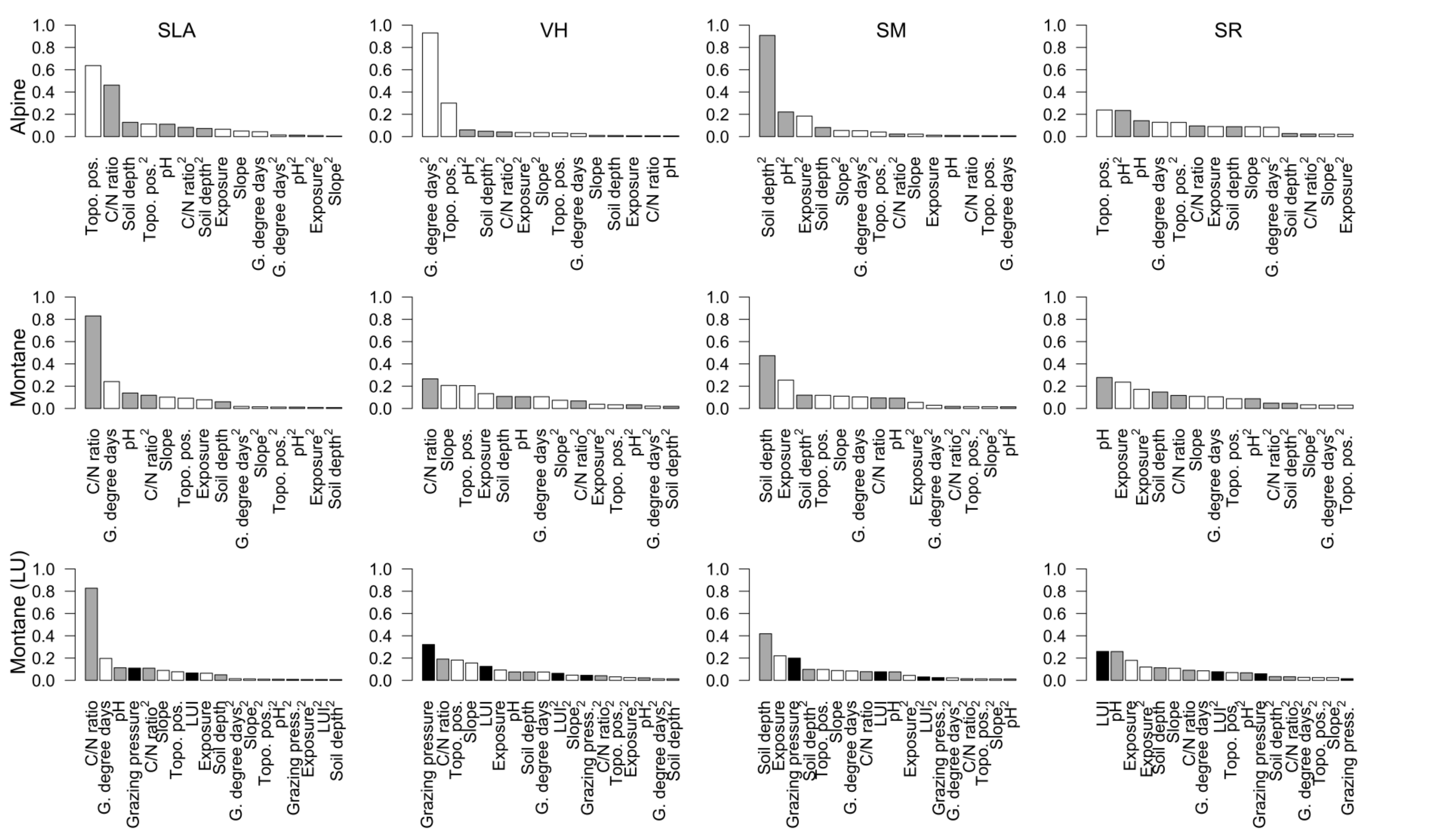

Figure 2**. The relative importance (RI) of the new predictors in the GLMs fitted to the residuals of the topo-climatic models for the alpine (upper panel) and montane grasslands when land use is (lower panel) or is not (middle panel) included. Community traits are specific leaf area (SLA), vegetation height (VH), seed mass (SM) and species richness (SR). White = very high-resolution topo-** climatic predictors; grey = edaphic factors; black = land use data; C/N ratio = C/N ratio of soil organic material; pH = pH of the organo-mineral horizon; Soil depth = depth of the soil down to bedrock; G. degree-days = sum of degree-days in the growing season; Topo. pos = topographic position (convex or concave) calculated at a 5 m resolution; Slope = slope measured in the field; Exposure = exposure of the plot measured in the field; Grazing pres. = grazing pressure; LUI = farming (land use) intensity (a combination of fertilization, mowing frequency and grazing pressure).

When comparing the models with and without farming intensity, grazing pressure was the most important variable to predict VH, and the LUI index was highlighted as the most important for SR. The relative ranking of the predictors was only slightly affected by the inclusion of farming intensity in all models (Fig. 2, lower panel).

Table 2. Most important new predictors for each community trait and for species richness in the best models based on very-high resolution topoclimatic predictors (5 m), farming intensity and values measured in the field. The D^2 values are calculated on the residual deviance of the topoclimatic models (25 m resolution). Individual D2 values for each variable are presented in Appendix S2, Table S4. Predictors are listed in order of importance.

	Montane grasslands – with farming intensity			**Montane grasslands – without farming intensity**			**Alpine grasslands – farming intensity not available**		
	Retained predictors	**AIC**	**D^2**	**Retained predictors**	**AIC**	**D^2**	**Retained predictors**	**AIC**	**D^2**
SLA	C/N ratio Deg. days	-148.4	0.27	C/N ratio pH	-148.44	0.26	C/N ratio Topo. pos.	-87.7	0.34
VH	Graz. pres. C/N ratio	-41.7	0.12	C/N ratio Slope	-43.8	0.07	Topo. pos. Topo. pos.^{2} Deg. days Deg. days^2	-27.4	0.27
SM	Soil depth Exposure	1.7	0.14	Soil depth Exposure	1.7	0.14	Soil depth Soil depth^2 pH pH^2	-24.1	0.44
SR	LUI pH	311.3	0.16	Expo Expo^2 pH	310.43	0.14	Topo. pos. pH pH^2	279	0.27

SLA = specific leaf area; VH = vegetative height; SM = seed mass; SR = species richness; C/N ratio = soil organic carbon to nitrogen ratio; pH = soil pH of the organo-mineral horizon; Soil depth = depth of the soil down to bedrock; Slope = slope of the plot measured in the field; Exposure = exposure measured in the field; Deg. days = growing degree-days; Topo. pos. = topographic position (convex or concave) calculated at a 5 m resolution; Graz. pres. = grazing pressure; LUI index = farming (land use) intensity.

The models constructed with the two best predictors for each trait and SR are summarized in Table 2. In the montane grasslands, the new predictors explained an additional 14.8% of the total deviance for SLA, 4.4% for VH, 13.1% for SM and 9.9% for SR (Fig. S2). When farming intensity was not included, these percentages decreased to 2.7% for VH and 8.8% for SR. In the alpine grasslands, the new predictors (particularly the VHR topographic position) explained an additional 18.9% of the total deviance for SLA, 9.8% for VH, 40% for SM and 16.6% for SR. This increase in explained deviance was significantly different from what could be achieved with random variables for all traits and SR in the alpine grasslands (p-values between 0.001 and 0.036, Fig. S2). In the montane grasslands, the amount of explained deviance was significantly higher than random simulations for SLA with and without farming intensity information and for SR when farming intensity was included (Fig. S2).

Discussion

The addition of locally measured or very high resolution (VHR; 5 m) predictors derived from GIS data, soil characteristics and VHR topography, to model community properties such as traits and species richness explained additional variance compared to models used in previous studies using traditional predictors. Indeed, these new local variables explained up to 44% of the residual variance in the traditional topo-climatic (25 m) models. The most important variables were different between the grassland types, with a slight shift from edaphic variables at low elevations to VHR topographic variables at high elevations. Adding the local variables could improve the quality of the models for specific leaf area (SLA) and species richness (SR) at mid elevations (montane belt) and for all traits except for seed mass (SM) at higher elevations (alpine belt).

Farming intensity

In this study, farming intensity ranked high as a potential predictor for VH and SR, but surprisingly, it only produced significant improvement in the case of SR. However, based on the significant human activity in the study area, we expected the farming intensity to be more important when modelling the community traits in the montane grasslands. Therefore, it seems that the impact of farming was not fully captured by our estimation of the grazing pressure and by the LUI index proposed by Blüthgen et al. (2012). Particularly, our analyses did not account for possible interactions with other factors, such as correlations between land use and topography, which might affect the consequences of farming intensity. Indeed, cows are not expected to graze homogeneously on a bumpy field, nor could a farmer mow a flat patch similar to a slope. Yet, as Randin et al. (2009) found that categories of land use (mowing versus grazing, fertilization levels) improved the models of species abundance, there seems to be a real potential for adding farming intensity into the models. Accurate spatial information on these processes remains difficult to obtain, and better ways to compute this information will need to be identified in future studies.

Edaphic factors

Soil properties, especially the C/N ratio and soil pH, were important predictors, showing up most often within the two best new variables (Figure 2; Table 2). These two predictors represent the availability of nutrients and toxic elements, respectively (Dubuis et al., 2011). These are particularly important indicators of plant growth (Batjes, 1996; Girard et al., 2011). Therefore, it is not surprising that the C/N ratio was consistently within the two best predictors for SLA in both elevation belts. The relationship between SLA and nutrient availability has been widely assessed in the literature (e.g., Cornelissen et al., 2003), and the inclusion of edaphic factors has been demonstrated to improve the quality of predictions of SLA (Dubuis et al., 2013). In a previous study, two soil chemical properties, pH and carbon isotopic ratios, were predicted across the geographic area (Buri, 2014), and additional maps are currently being developed for other soil properties (Buri et al. In press). If the C/N ratio could be similarly mapped, C/N ratio and pH would provide high potential for model improvement, especially for SLA.

Very high resolution (VHR) predictors

Although the improvements brought by the use of VHR data may seem obvious (5 m resolution being closer to the 2 x 2 m plots size), a previous study revealed that using 5 m or 25 m topo-climatic predictors resulted in species distribution models of similar performance (Pradervand et al., 2014). In our study, VHR topo-climatic predictors, especially topographic position and growing degree-days, contributed significantly to the improvement of the SLA, VH and SR models within the alpine belt. Topographic position is closely linked to microclimatic and edaphic conditions because it represents potential shelters against the wind and places with an accumulation of snow or cold air and is related to soil distribution. Similarly, growing degree-days are expected to be very sensitive to microtopography in the alpine environment (Köner, 2003). This result highlights the importance of micro-topographic information in the alpine areas, where the communities are primarily regulated by climatic, microclimatic and partly related soil conditions. Because topographic position is relatively easy to infer and implement in models (Pradervand et al., 2014), it is a promising candidate for further improvement of community trait models.

For all functional traits, the use of weighted average species values instead of direct field measurements could have biased the results. Nevertheless, this is a common approach in the literature (see for example Cornwell & Ackerly, 2009; Dubuis et al., 2013) and is often necessary due to the time or resource limitations of measuring traits for all species in all plots (990 in this study). Furthermore, the results of Cornwell & Ackerly (2009) suggest that the contribution of intraspecific variability would be very low compared to those of other ecological processes when studying shifts in trait values amongst ecological gradients.

Conclusions

We demonstrated that in the montane and alpine grasslands of the western Swiss Alps, part of the remaining variance in the standard topo-climatic models (25 m resolution) of plant community functional traits can be explained by new, complementary local predictors, i.e., edaphic and very high-resolution (5 m) topo-climatic predictors.

Because different responses were observed along the elevation gradient, the selection of environmental variables used to fit models ought to be considered more cautiously in relation to elevation. Studies that combine modelling with field verification are promising, and future studies could replicate this type of analysis and assess the other parts of the elevation range that were not investigated in this study.

Finally, two of these predictors, the 5 m resolution topographic position and the soil C/N ratio, yielded particularly good results. The very high-resolution topographic position is relatively easy to implement in models, and the ability to obtain predicted maps of soil chemical composition is rapidly progressing. Therefore, these variables are good candidates to improve macroecological models.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix 1. Complements to Materials and methods

Appendix 2. Complements to Results

Appendix 3. Correlations between predictors and community weighted means of the traits.

Data accessibility

Floristic data are available at the National Data and Information Center on the Swiss Flora (www.infoflora.ch).

Biosketch

The spatial ecology group at the University of Lausanne (www.unil.ch/ecospat) specializes in predictive habitat distribution modelling at the species, community and habitat types levels.

Author contributions: J-N.P., A.G. and P.V. conceived the initial idea and designed the study and statistical analyses; M.E.A.B and M.B. collected the data with the help of the acknowledged persons; A.B. supervised the soil measurements; M.E.A.B analysed the data; M.B. assisted in the analyses; M.E.A.B, J-N.P., A.G. and P.V. wrote the manuscript in collaboration with A.B and M.B.

Appendix S1. Supplement to Materials and Methods

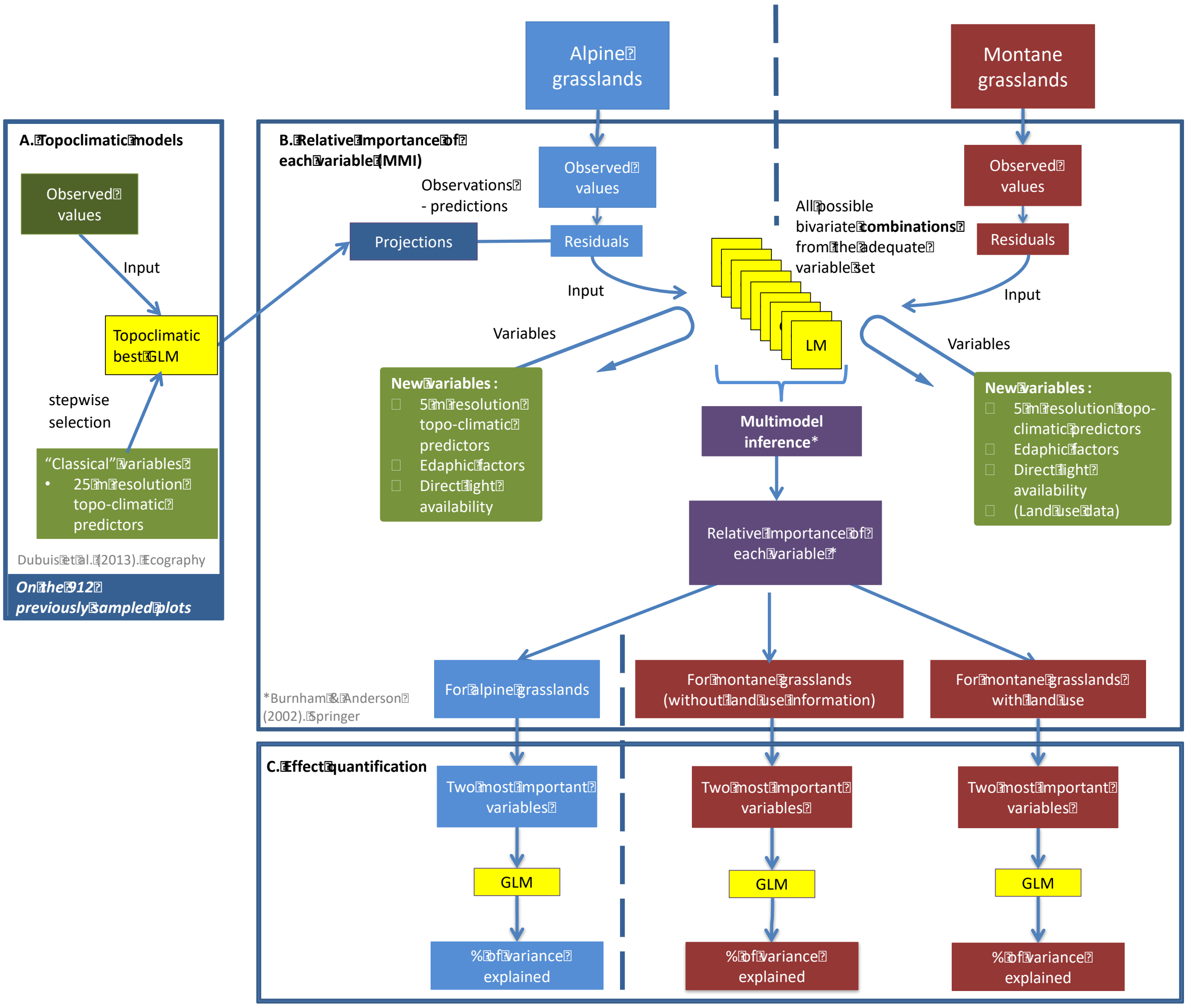

Figure S1. General workflow of the study. We first created a set of models using the classical 25 m predictors, calibrated on 912 pre-existing vegetation plots (Panel A.). This accounted for the best state of knowledge in community modeling (Dubuis et al. 2013). We then focused on the residuals of these models as to see how much of the remaining variance could possibly be improved by a set of more local variables (Table S2). For this, we projected the classical models on a set of newly sampled plots, for which we had additional information, and calculated the residuals for these new plots. For each elevation belt, we created a set of new models through bivariate combinations of our new, local predictors and classified these in their potential to explain the remaining variance through multimodel inference (Panel B.). We used this classification to select the two variables with highest potential. We tested the significance of the improvements obtained by these two variables through randomization tests (Panel C).

Category	Variable	Definition
Coarse resolution predictors [25 m resolution]	Moisture index	Mean difference between precipitation and potential evapotranspiration over the growing season (water potentially available in soil)
	Growing degree-days	Sum of the daily temperatures during the growing season (June, July and August - when temperatures > 3°C
	Global solar radiation	Sum of the daily average of potential radiation per month over the year
	Slope	Slope of the grasslands
	Topographic position	Index where positive values = ridges and tops, negative values = valleys and sinks
	Mean temperature	Mean temperature over the growing season

Table S1. Presentation of the “classical” 25 m variables used in this study.

Calculation of the 25 m resolution topo-climatic predictors

The temperature, growing degree days and solar radiation were measured by the Swiss network of meteorological stations (www.meteoswiss.ch), and the predictors were all generated at a 25 m resolution following Zimmermann and Kienast (1999). The slope was derived from the elevation model using the ArcGIS 10.2 spatial analyst tool (ESRI). The topographic position was computed through moving windows that integrated topographic features at various scales, with positive values indicating ridges and tops and negative values corresponding to valleys and sinks. The global solar radiation is the sum of the daily average of potential radiation per month over the entire year (Müller, 1984) and was calculated based on the direct, diffuse and reflected solar radiation that reached the area, accounting for the slope, aspect and shading of the surrounding topography (Kumar et al., 1997). The moisture index is the mean difference between precipitation and potential evapotranspiration over the growing season. It represents the amount of water potentially available in soil.

Details of the sampling strategy for the new plots

Our goal was to obtain groups of plots sharing very similar macro-environmental topo-climatic conditions, so as to allow identifying which local variables may further explain part of the residual variation (i.e. not explained by the topo-climatic HR variables). We first stratified the sampling within two elevation belts (montane and alpine) based on four HR topo-climatic predictors of primary ecological importance: slope, topographic position (indicating ridges or sinks), global solar radiation over the growing season (June-August) and mean temperature over the growing season (Dubuis et al., 2011, 2013). Within each of these two elevation belts, two strata were further created by combining situations of temperature, exposure (North and South) and slope. The strata were defined as illustrated in Table 1 and Table S1: pixels with a mean growing season temperature from 12.2°C to 13.4°C, a global solar radiation from 1600 to 1800 kJ $\cdot$ day^{-1} $\cdot$ pixel^{-1} (North) or from 2800 to 3000 kJ $\cdot$ day^{-1} $\cdot$ pixel^{-1} (South), with a slope between 20° and 25° and a topographic position index between -1 and 0, for the montane grasslands; pixels with a mean growing season temperature from 8.7°C to 9.7°C, global solar radiation from 1150 to 1450 kJ ›day^{-1} ›pixel^{-1} (North) or from 3000 to 3100 kJ ›day^{-1} ›pixel^{-1} (South), slopes from 30° to 35° and topographic position indices between 1 and 2 for the alpine grasslands. These restricted ranges represented between 1.7% and 9.1% of the total ranges of the predictors over the entire study area (Table 1).

Functional traits

SLA is the area of one side of a fresh leaf per the dry mass of the leaf (Cornelissen et al., 2003) and is linked to photosynthetic rates and carbon fixation (Lavorel & Garnier, 2002). VH is the distance between the top photosynthetic tissue and the ground and is linked to disturbance, stress avoidance and competition (Lavorel & Garnier, 2002; Cornelissen et al., 2003). SM is the average dry mass of the seeds (Cornelissen et al., 2003) and represents the strategy of plant investment in reproduction, i.e., smaller seeds are produced in higher numbers but are expected to have lower reproductive success because of the limited amount of resources (Cornelissen et al., 2003). For SLA and VH, we used data previously collected by Dubuis et al. (2013) for the 240 most abundant species in this study area. These authors sampled generally ten (4-20) individuals per species in contrasted environmental conditions and calculated an average trait value for each species. Values for two species were obtained from the literature (Aeschimann et al., 2004; Kleyer et al., 2008). The information on SM was collected from the LEDA trait database (Kleyer et al., 2008) and missing values were complemented from the Kew seed base (Royal Botanic Gardens Kew, 2014) or with a literature (Muller-Schneider, 1986; Klotz et al., 2002; Pluess et al., 2005; Römermann et al., 2005; Vittoz et al., 2009).. For each trait, we calculated an average, cover-weighted value for the entire plant community (i.e. weighted mean). Whenever trait information was available for less than 60% of the vegetation cover, the plot was discarded. 807 of the ancient plots were kept for SLA and VH analyses and 552 for SM. None of the new plots had to be discarded. Species richness was calculated for all plots as the total number of species per plot.

Category	Variable	Definition
Very-high Resolution [5 m resolution]	Growing degree-days (G. degree days)	Sum of the daily temperatures during the growing season (June, July and August) when temperatures is > 3°C
	Topographic position (Topo. pos.)	Positive values = ridges and tops, negative values = valleys and sinks
	Slope	Slope of the grassland
Edaphic factors	pH	pH of the soil organo-mineral horizon
	C/N ratio	C/N ratio of the soil organo-mineral horizon
	Soil depth	Soil depth
Farming intensity*	Grazing pressure	Farming intensity measure where only grazing is taken into account
	Land Use Intensity index (LUI)	Farming intensity metric where grazing, fertilization and mowing are taken into account. See main text for details about computation

Table S2. Presentation of the new variables tested in this study. *The farming intensity information is only available for montane grasslands.

Presentation of the new predictors

Farming intensity data was collected for the 41 montane grasslands from interviews with the farmers. A land use intensity index (LUI) was then computed as suggested in Blüthgen et al. (2012):

$$LUI = \frac{F_i}{F_R} + \frac{M_i}{M_R} + \frac{G_i}{G_R}$$

where F_i is the fertilization level for the plot i (m^3 of manure·year^{-1}·ha^{-1}),M_i is the frequency of mowing per year, G_i is the grazing intensity (UGB·days·ha^{-1}·year^{-1}) and F_R, M_R and G_R their respective means for the data set. A UGB is a standardized unit for cattle foraging requirements (1 UGB = one cow).

For the 37 alpine plots, no interviews were conducted. These plots are rarely or very sparsely fertilized, but some are grazed by cows or sheep in summer. However, grazing pressure is always diluted across large areas with high topographic and grazing heterogeneity. Details would therefore be of little value. The other new predictors were all measured in the 78 plots.

For each plot, we measured the true aspect with a compass to complement the global solar radiation data calculated on an elevation model with a resolution of 25 m.

The total depth of soil was measured with an auger (mean of 2-4 measurements per plots). When depth exceeded 50 cm, the soil was classified as deep. For each plot, a soil sample of the organo-mineral horizon (Baize & Jabiol, 1995) was collected, air-dried and sieved at 2 mm for laboratory analyses. Its pH was measured with a pH meter, after dilution in water in a 1:2.5 w/v ratio. We measured the organic C and N contents with a Carlo Erba CNS2500 CHN Elemental Analyser, coupled with a Fisons 198 Optima mass spectrometer (Tamburini et al., 2003). The C/N ratio was used as a biologically relevant summary of nutrient availability (Batjes, 1996).

Pradervand et al. (2014) developed different VHR predictors for the same study area issued from modelling processes instead of interpolating. We retained growing degree-days, topographic position and slope at a 5 m resolution because these predictors yielded the best results in previously published species distribution models (Pradervand et al, 2014). Growing degree-days corresponded to the sum of the daily temperatures during the growing season (June, July and August) when temperatures were above 3°C and were inferred from temperature data loggers established in the study area in 2012. Topographic position and slope were calculated from a digitalized elevation model with a resolution of 2 m acquired by LIDAR. For more details on these raster maps, see Pradervand (2015) and Descombes et al. (2015).

Overfitting issues

In our multimodel inference approach, we built models formed of all bivariate combinations of our new variables (Fig. S1, panel B). We addressed potential overfitting issues through Root Mean Square Error (RMSE; Caruana & Niculescu-Mizil, 2004; Liu et al., 2011) analysis. For all the models, we split the data in a training and testing sets of 70% and 30% of the data, respectively. We then assessed whether the models were overfitted through a RMSE: if the model is overfitted, the error is going to be higher on the testing than on the training test, and the subtraction of both terms will be higher than 0. We performed 30 steps of data splitting, and inferred a distribution of the subtraction term. We tested whether 0 was outside the 95% quantile of the distribution. None of the resulting p-values were significant, indicating no overfitting.

Calculation of the Akaike weight and the relative importance of the new predictors

To compare the support obtained by each model based on the combination of the four new predictors and their quadratic terms, we calculated an Akaike weight (w_i) based on the differences in AICc scores (Burnham & Anderson, 2002):

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

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

$$\Delta_i = AIC_i - AIC_{\min}$$

The relative importance (RI) of a predictor corresponds to the sum of the Akaike weights for each model in which the predictor is included (Burnham & Anderson, 2002).

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Appendix S2. Complements to Results

Table S3. Predictors retained in the topoclimatic models (25 m resolution) and evaluation of these models for the three community traits and for species richness. These models were established on the 912 plots that were distributed within the entire study area.

Trait	Predictor	Unit	Coefficients	p-values	AIC	D^2
Specific leaf area	Growing deg. Days	°C	$7.46 \bullet 10^{-05}$	< 0.001		
(log transformed)	Glob. Rad.	kJ/ (day · pixel)	$8.89 \bullet 10^{-07}$	0.082		
	Slope	°	0.0011	0.150		
	Topo. pos.	unit-less	$-5.73 \bullet 10^{-05}$	0.010	-1781.8	0.44
	Moisture Index	1/10 mm	$-8.52 \bullet 10^{-05}$	0.003		
	Glob. Rad.^{2}	kJ/ (day · pixel)	$-2.12 \bullet 10^{-12}$	0.060		
	Slope^2	°	$-4.04 \bullet 10^{-05}$	0.008		
	Moisture Index^2	1/10 mm	$4.72 \bullet 10^{-08}$	0.023		
	Intercept		1.15	< 0.001		
Vegetative height	Growing deg. days	°C	0.001	< 0.001		
(log transformed)	Slope	°	0.003	< 0.001		
	Topo. pos.	unit-less	$9.64 \bullet 10^{-05}$	0.110		
	Moisture Index	1/10 mm	-0.0002	0.003	-394.7	0.64
	d ^{2}	°C	$-1.21 \bullet 10^{-07}$	< 0.001		
	Topo. pos.^{2}	unit-less	$4.2 \bullet 10^{-07}$	0.049		
	Moisture Index^2	1/10 mm	$-2.42 \bullet 10^{-07}$	< 0.001		
	Intercept		-1.45	< 0.001		
Seed mass	Glob. Rad.	kJ/ (day · pixel)	$3.84 \bullet 10^{-06}$	0.100		
(log transformed)	Slope	°	0.004	< 0.001		
	Moisture Index	1/10 mm	-0.00031	< 0.001	-20.9	0.08
	Glob. Rad.^{2}	kJ/ (day · pixel)	$-8.05 \bullet 10^{-12}$	0.120		
	Moisture Index^2	1/10 mm	$3.42 \bullet 10^{-07}$	< 0.001		
	Intercept		-0.57	0.037		

Table S3. Continues

Species richness	Growing deg. days	°C	0.00062	< 0.001	10356.9	0.38
	Slope	°	0.02	< 0.001		
	Topo. pos.	unit-less	0.0011	< 0.001		
	Growing deg. days ^{2}	°C	$- 1.72 \bullet 10^{-07}$	< 0.001		
	Glob. Rad.^{2}	kJ/ (day · pixel)	$-3.21 \bullet 10^{-12}$	< 0.001		
	Slope^2	°	-0.0002	< 0.001		
	Topo. pos. ^{2}	unit-less	$4.53 \bullet 10^{-07}$	0.085		
	Moisture Index^2	1/10 mm	$-1.51 \bullet 10^{-06}$	< 0.001		
	Intercept		3.07	< 0.001		

AIC is the value of Aikake Information Criterion, and D^2 is the proportion of the total deviance explained by the model. Growing deg. days = growing degree-days; Glob rad = global solar radiation; Topo. pos. = topographic position.

The result of the Kruskal-Wallis tests performed on their residuals for the newly sampled plots were non-significant, indicating no stratification in the residuals.

Table S4. Overview of the separate D^2 values of the retained predictors when put into separate univariate models. D^2 values are calculated on the residual deviance of the topoclimatic models (25 m resolution).

	Montane grasslands – with farming intensity		**Montane grasslands – without farming intensity**		**Alpine grasslands – farming intensity not available**	
	Retained predictors	**Separate D^2**	**Retained predictors**	**Separate D^2**	**Retained predictors**	**Separate D^2**
SLA	C/N ratio	0.21	C/N ratio	0.21	C/N ratio	0.24
	Deg. days	0.03	pH	0.0004	Topo. pos.	0.25
VH	Graz. pres.	0.08	C/N ratio	0.06	Topo. pos. (linear + quadratic)	0.12
	C/N ratio	0.06	Slope	0.04	Deg. days (linear + quadratic)	0.33
SM	Soil depth	0.10	Soil depth	0.10	Soil depth (linear + quadratic)	0.37
	Exposure	0.06	Exposure	0.06	pH (linear + quadratic)	0.17
SR	LUI	0.07	Expo (linear + quadratic)	0.14	Topo. pos.	0.06
	pH	0.08	pH	0.08	pH (linear + quadratic)	0.13

SLA = specific leaf area; VH = vegetative height; SM = seed mass; SR = species richness; C/N ratio = soil organic carbon to nitrogen ratio; pH = soil pH of the organo-mineral horizon; Soil depth = depth of the soil down to bedrock; Slope = slope of the plot measured in the field; Exposure = exposure measured in the field; Deg. days = growing degree-days; Topo. pos. = topographic position (convex or concave) calculated at a 5 m resolution; Graz. pres. = grazing pressure; LUI index = farming (land use) intensity.

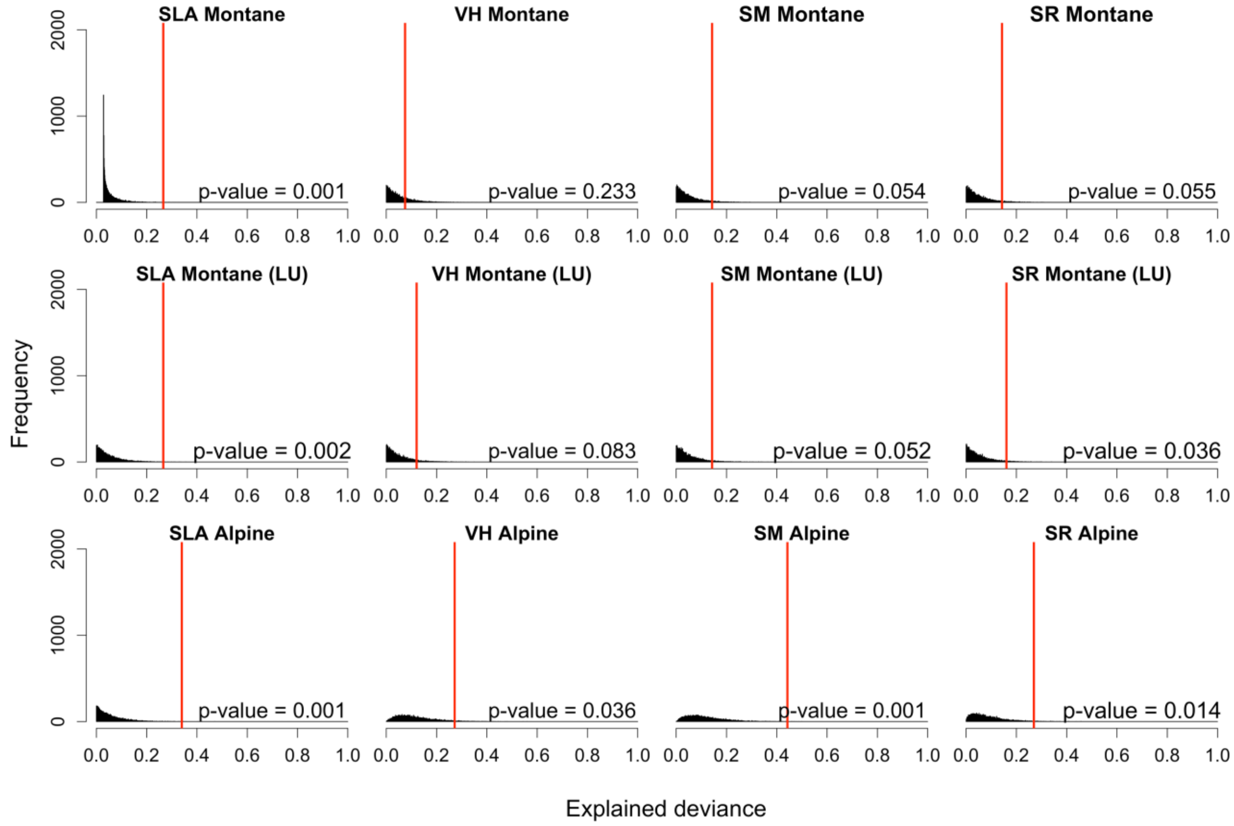

Figure S2. The amount of the remaining deviance (vertical line) that could be explained by the two most important variables for the three community traits and species richness at each elevation strata compared to random variables (black histograms). The p-values indicate whether the values are significantly outside the 95% confidence interval of the distribution. Abbreviations of the community traits are similar to those in Figures 2, 3 and 4.

Appendix S3. Correlations between predictors and community weighted means of the traits.

Figure S3. Correlation between the original data and the new predictors. A = correlation with the linear term (blue line). B = quadratic correlation (red dashed line). CWM = community weighted mean of the considered trait; Topo. pos. = topographic position (5 m); G. degree days = growing degree days; LUI = farming (land use) intensity.

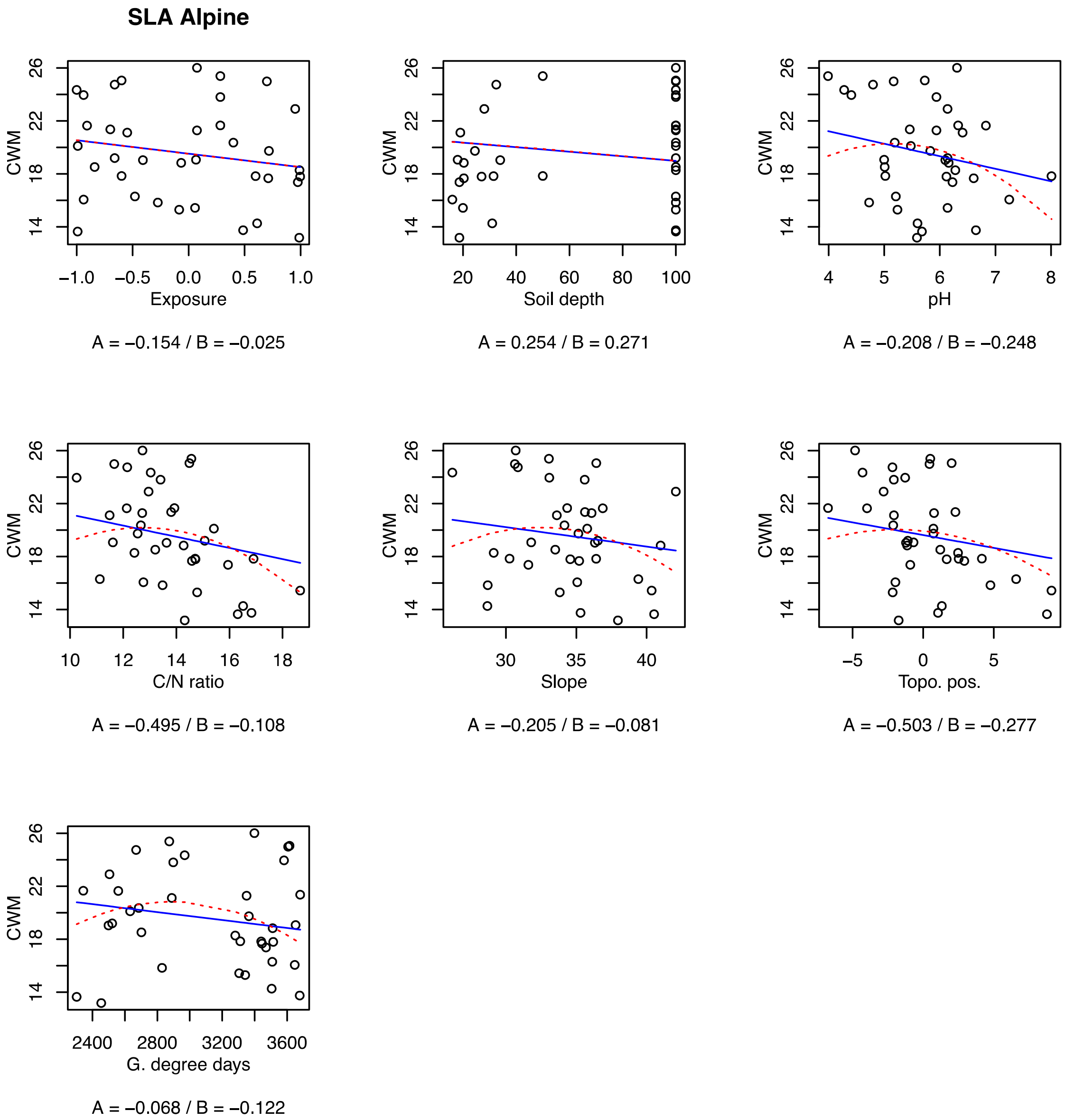

Figure S3. Continued

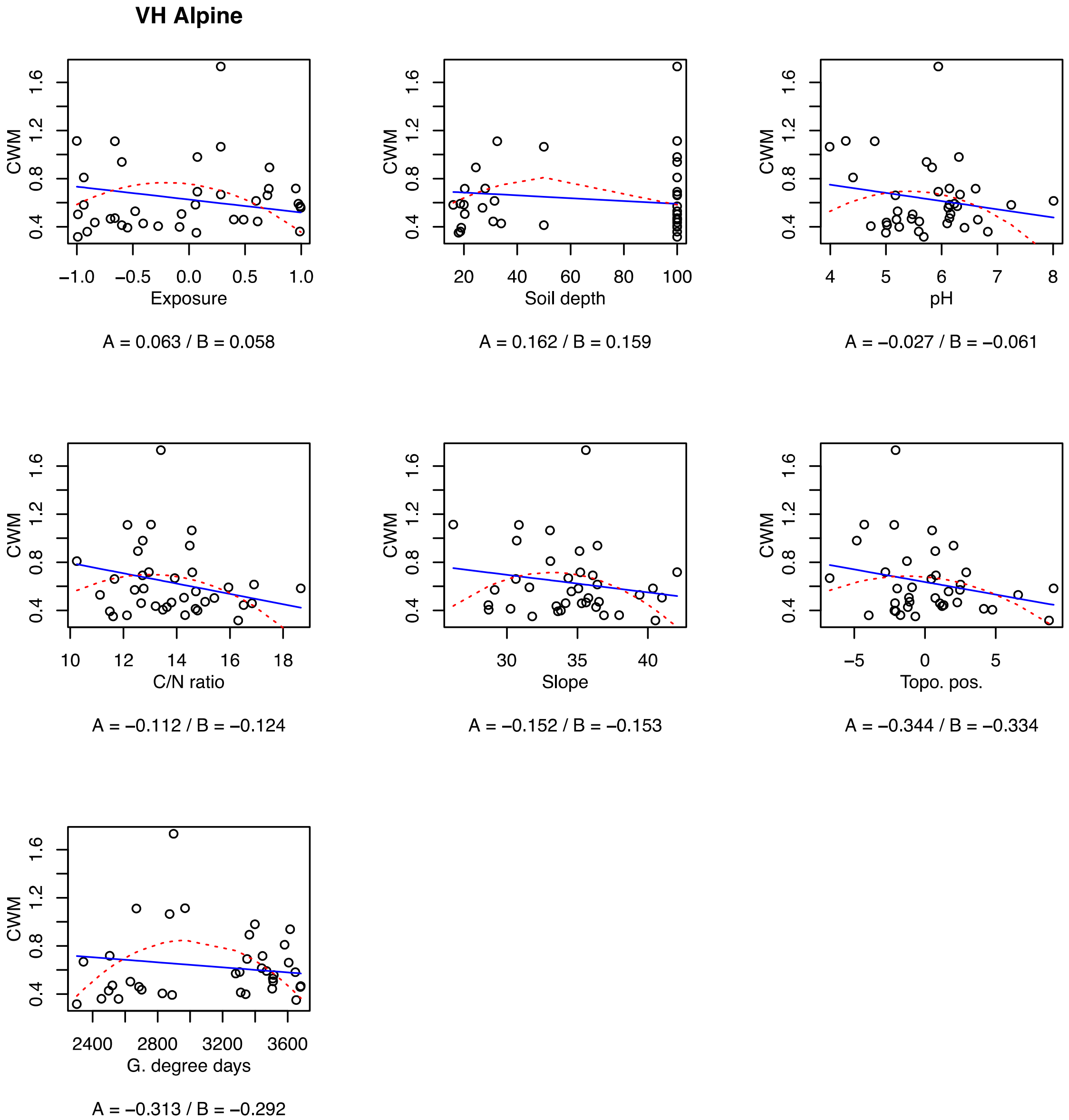

Figure S3. Continued

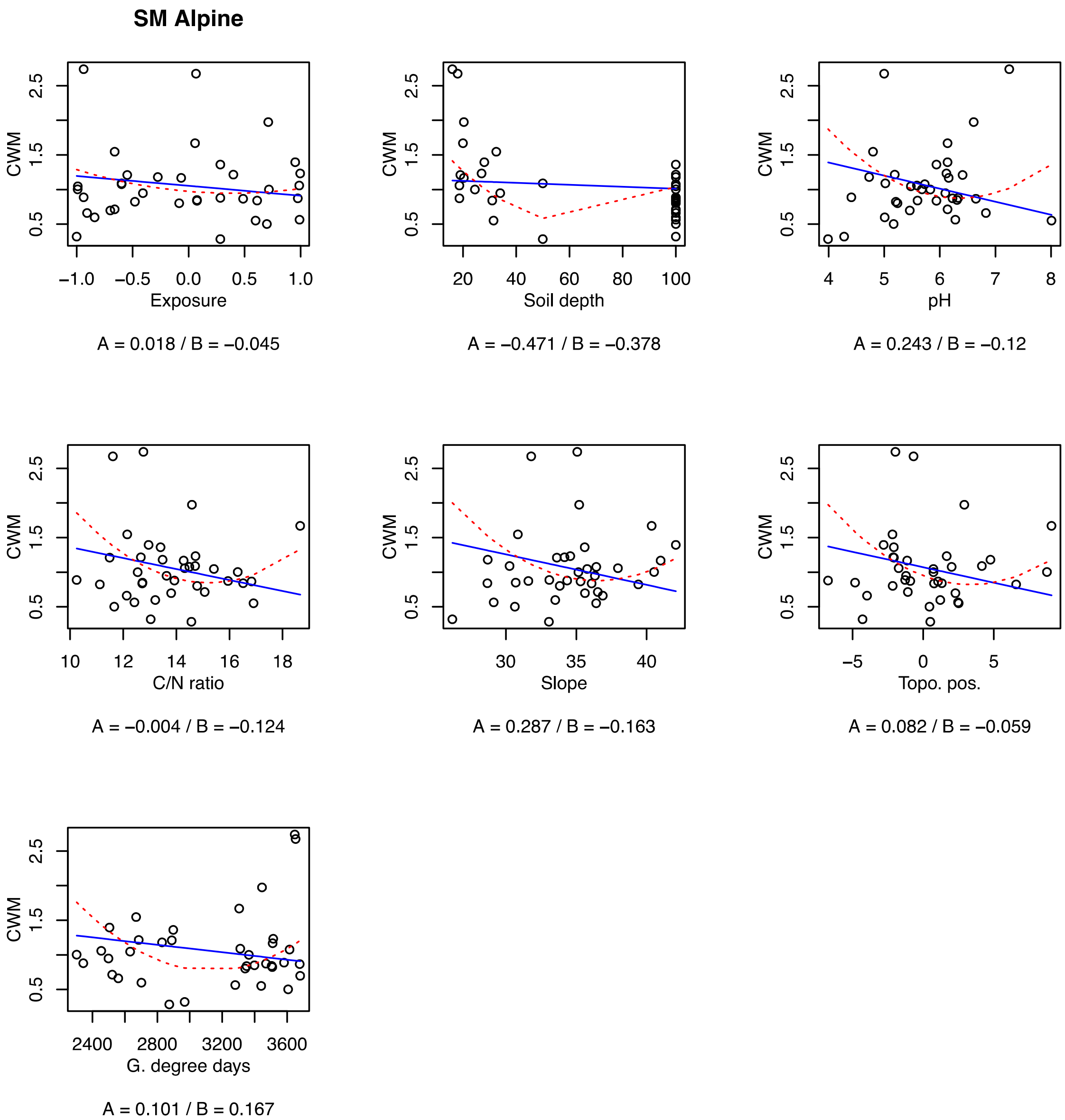

Figure S3. Continued

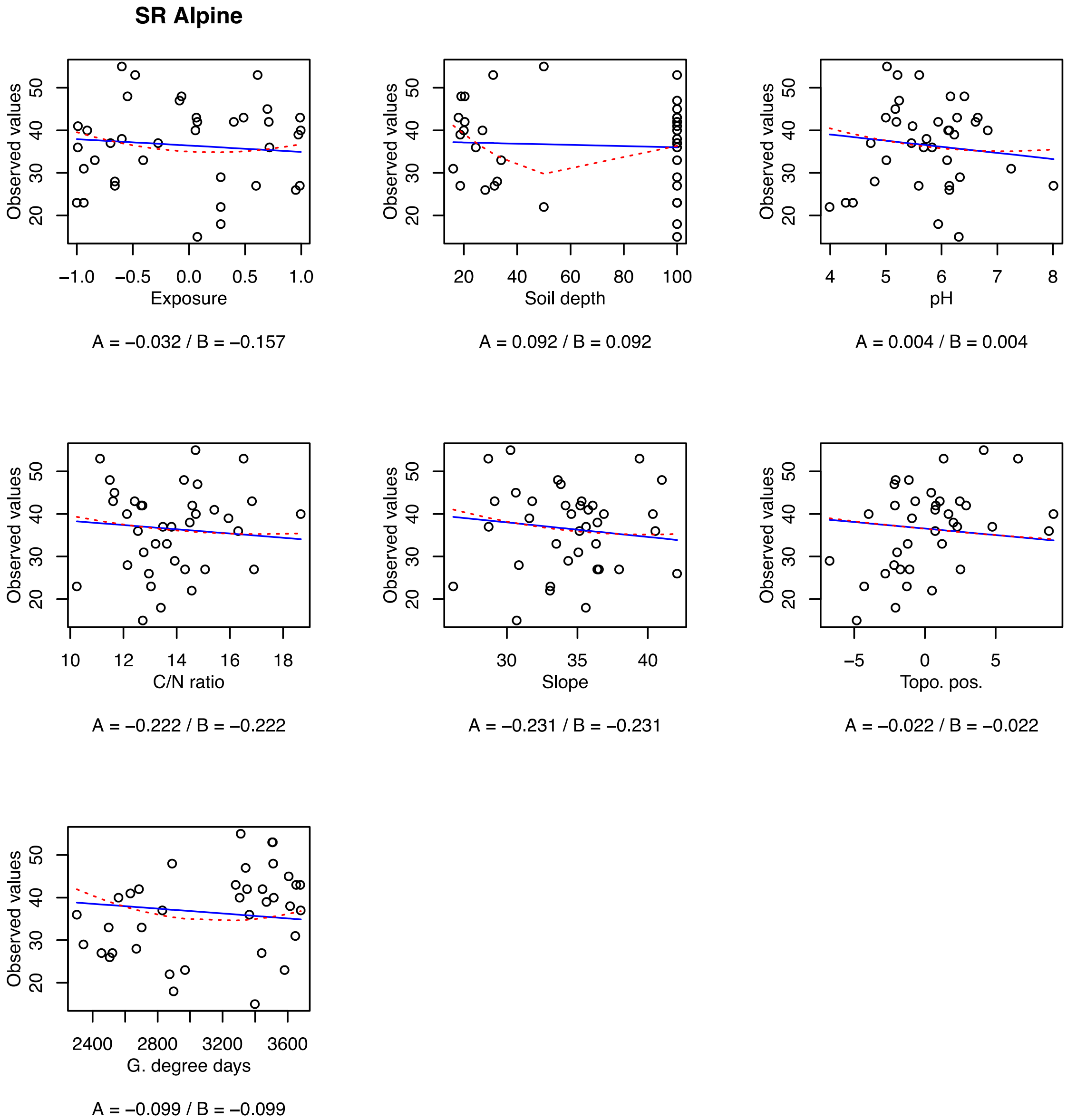

Figure S3. Continued

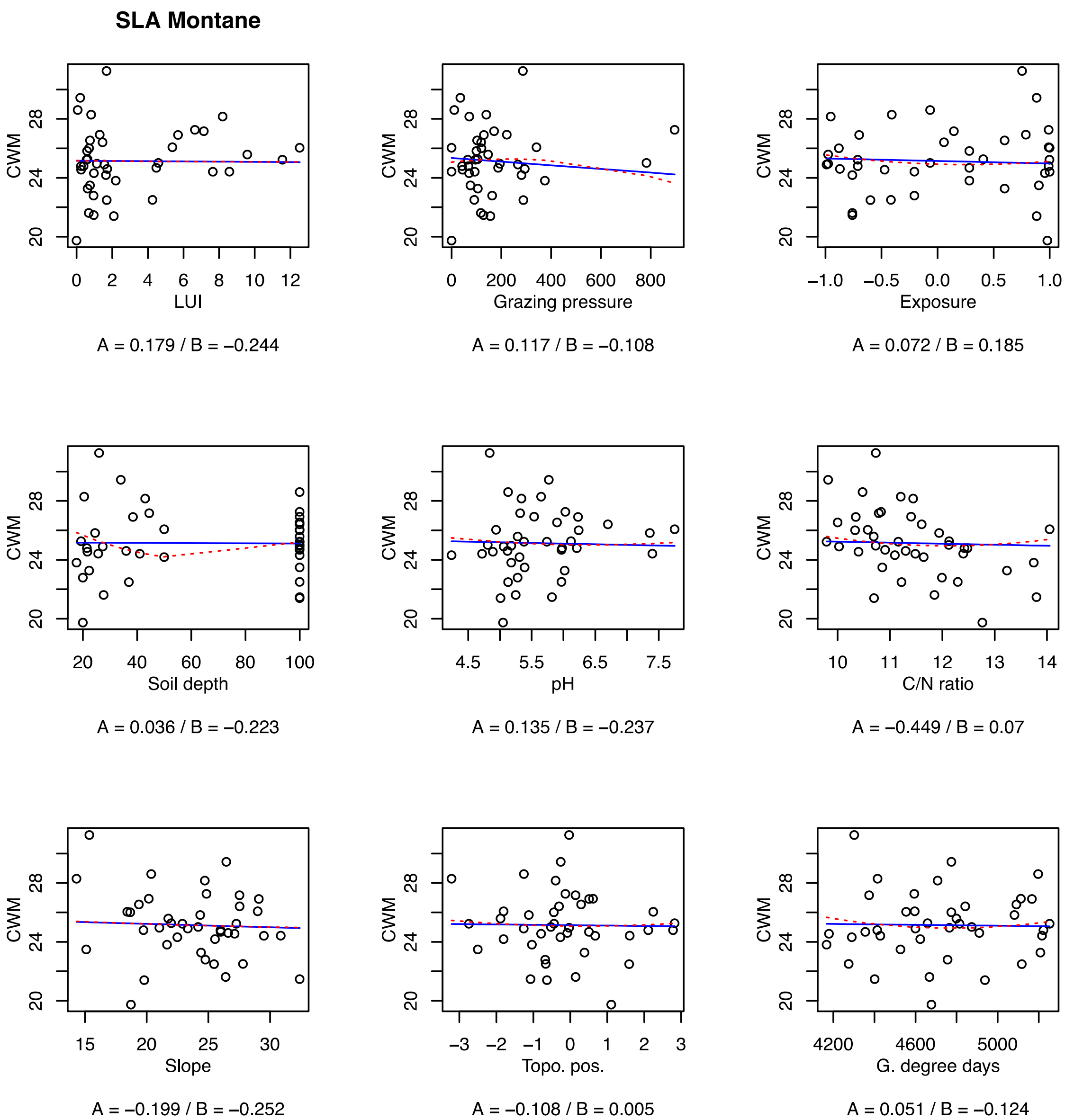

Figure S3. Continued

VH Montane

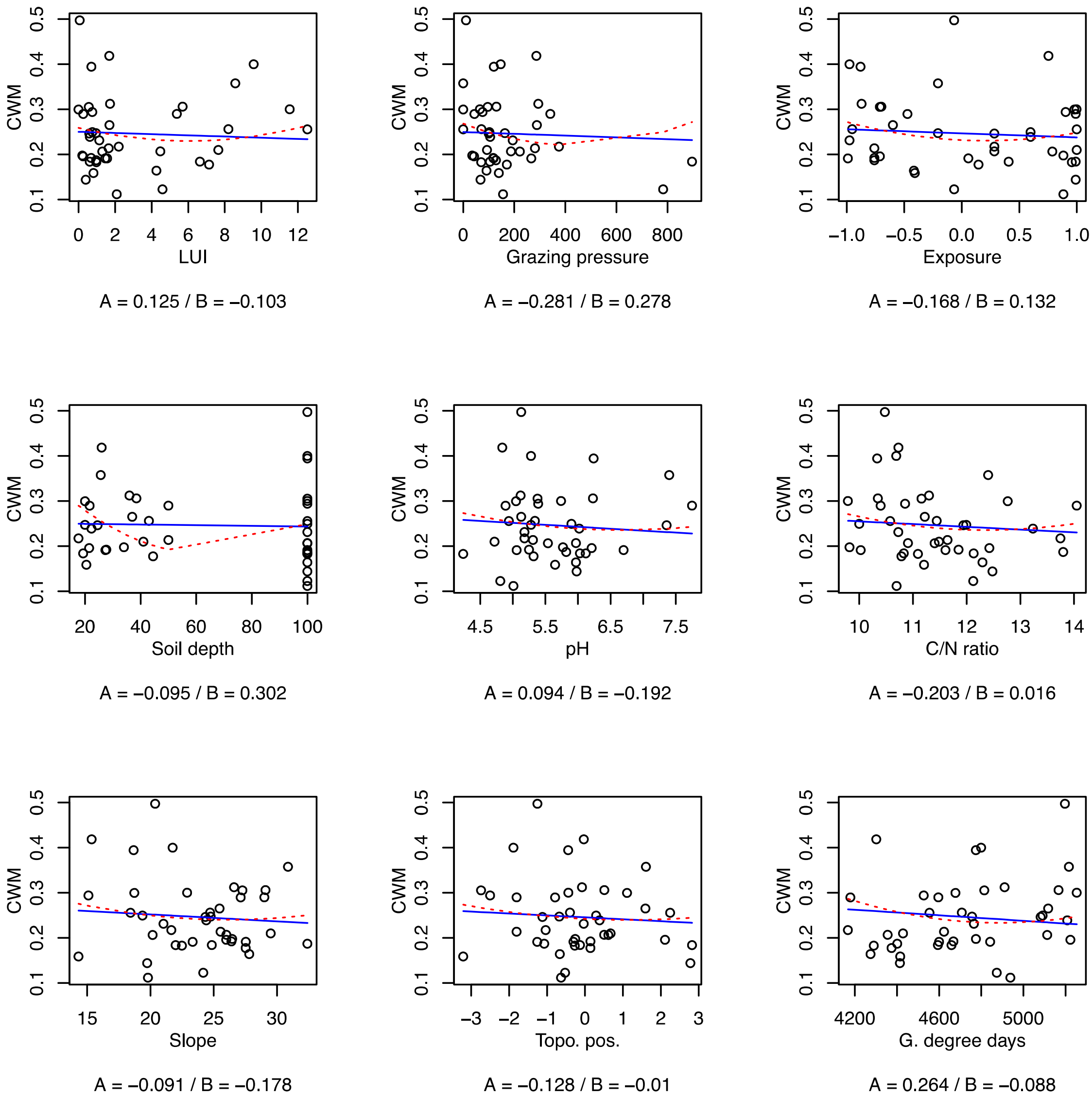

Figure S3. Continued

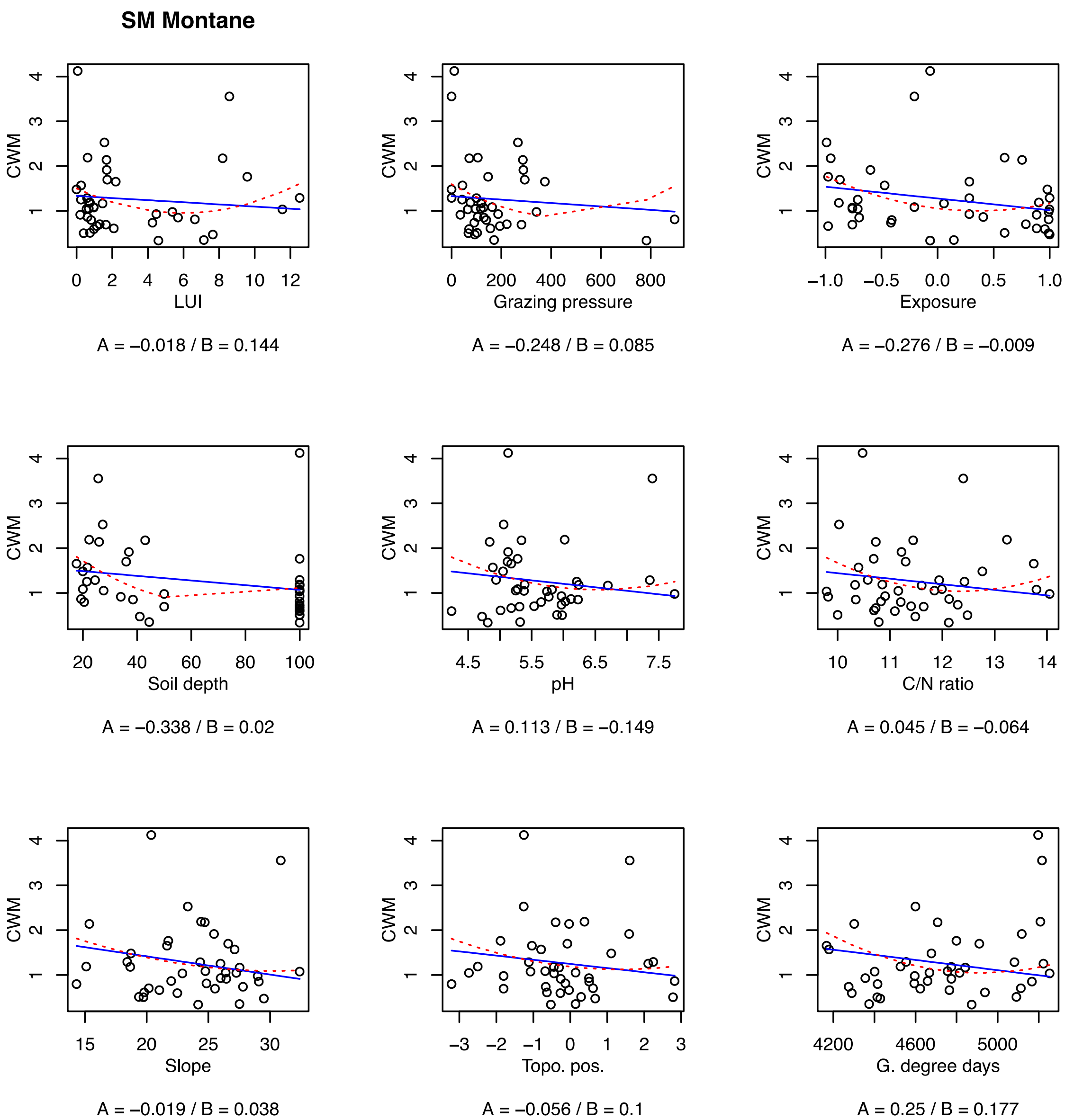

Figure S3. Continued