



Do climate, resource availability, and grazing pressure filter floristic composition and functioning in Alpine pastures?

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Abstract: We studied the floristic composition in the pastures of the Southern Alps (Trento Province, Italy). One hundred and five plots in seven different pasture plant communities were sampled: (1) nitrophilous, (2) montane mesic, (3) subalpine mesic, (4) calcareous montane, (5) calcareous subalpine, (6) acid montane, and (7) acid subalpine pastures. Forward selection and variation partitioning were applied to identify the most important factors controlling the species composition and plant traits in the pastures. Aggregated weighted averages were calculated for each plot using the published values of average height, specific leaf area, and seed mass for each species. Explanatory variables were recorded for each site to reflect climate, soil properties, and grazing pressure. We hypothesised that species composition and functional variation in pastures of the Southern Alps are controlled by three main environmental filters: climate, resource availability, and grazing pressure. We found that variables of climate and soil properties had a major role in explaining the species composition and variations in plant traits, while grazing pressure showed a lower independent effect. Species composition and plant traits depended mainly on temperature, soil fertility, and variables of bedrock type - soil pH. Our results confirm the importance of taking the effects of climate and resource availability into account when describing plant and community functions of grasslands.

Abbreviations: ACID—volcanic and metamorphic acid bedrock; CAL—sedimentary calcareous bedrock; CH—canopy height; DIST—distance to the farm centre; D_SOIL—soil depth; GRAZ—grazing intensity; LHS—leaf-height-seed; MIX—mixed debris; pH—soil pH; PREC—total summer precipitation; P_SOIL—Olsen P in soil; RDA—canonical redundancy analysis; SLA—specific leaf area; SLOPE—slope angle; SM—seed mass; TEM—mean summer temperature; VBAS—volcanic basic bedrock.

Introduction

Since the second half of the 20th century, changes in land use associated with the intensification of agriculture have been the major cause of losses in the biodiversity of farmland at local, regional, and global scales (Norris 2008). Over the last few decades in many European countries, flat and more accessible areas have been managed more intensively, whereas hilly and mountainous areas have been abandoned (MacDonald et al. 2000, Tasser and Tappeiner 2002, Mottet et al. 2006).

In the Italian Alps, summer pastures are still managed in traditional ways, which maintain important grassland habitats of many species, although the number of pastures has declined drastically over the past few decades (Laiolo et al. 2004, Giupponi et al. 2006, Tasser et al. 2007). These summer farms consist mainly of grazed grasslands located

around the centre of the farm (typically a stall). Summer farming creates a landscape with large variation and strong gradients in the effects of grazing animals, which results in very distinct vegetation patterns (Vandvik and Birks 2002a,b). Nitrophilous communities and productive manured grassland dominate the area immediately surrounding the stall. Away from farms, this heavily disturbed and manured vegetation gives way to extensive low-productive perennial grasslands (Vandvik and Birks 2004). A recent census of dairy farming in the Trento province revealed that only 300 of the 700 summer farms listed were actually managed (Provincia Autonoma di Trento, Dipartimento Agricoltura, “unpubl.”). As a result, the species composition of pastures below the tree line has been changing in favour of forest species, with a consequent reduction in biodiversity (Fischer and Wipf 2002). This kind of seminatural grassland needs to be maintained through periodic interventions in manage-

ment, such as mowing and grazing, in order to withhold the encroachment of trees and shrubs (Rook et al. 2004).

Changes in land use constitute a threat to the persistence of these grassland ecosystems (Dullinger et al. 2003, Spiegelberger et al. 2006). Therefore, it is very important to understand the mechanisms leading to the organisation and distribution of these communities to preserve plant diversity and to develop effective agri-environmental schemes, which can maintain and enhance biodiversity.

Environmental conditions and vegetation composition in the European Alps vary due to broad-scale factors such as altitude, precipitation, or geographic location, reflecting different climatic conditions, and fine-scale site factors, like variation in slopes, aspects, and soils (Ellenberg 1996, Wohlgemuth 1998, Moser et al. 2005, Marini et al. 2008). Local grasslands factors have been demonstrated to be important drivers of plant diversity due to different management (Klimek et al. 2007, Raatikainen et al. 2007, Rudmann-Maurer et al. 2008), topography (Sebastià 2004, Bennie et al. 2006), and soil properties (Critchley et al. 2002, Marini et al. 2007).

The characterisation of organisms on the basis of multiple biological attributes, such as physiological, morphological, or life-history traits, has recently emerged as a promising way to study the processes responsible for variation in species composition and ecosystem functioning (e.g., de Bello et al. 2005, Garnier et al. 2007, Pakeman et al. 2009). Westoby (1998) proposed the leaf-height-seed (LHS) ecological strategy as an alternative explanation for plant responses to environmental variation. The LHS scheme differs from other classifications in that it is based on three easily measured “soft” traits (sensu Díaz et al. 2004): 1) specific leaf area (SLA), 2) plant canopy height at maturity, and 3) seed mass. SLA, for instance, contributes to the potential of a plant to respond to a change in exposure to stress, whereas seed mass and plant height influence the ability of a plant to adjust to the effects of disturbance and other environmental changes (Poorter et al. 1990, Westoby 1998).

The European Alps provide interesting study areas to explore the relationships between environmental variables, species composition, and the distribution of plant traits along vertical gradients (elevation). However, these factors and their relative importance for pasture are insufficiently known in the Alps, because only relatively few studies, mostly in the Northern Alps (Muller et al. 2003, Kleijn and Müller-Schärer 2006), have examined species and functional composition of this vegetation community. Since some pasture communities analysed in this study could be considered as habitats of European interest (e.g., alpine and subalpine calcareous grasslands or semi-natural dry grasslands on calcareous substrates), our research also highlights the utility of understanding the factors influencing composition and functioning of plant species. The aim of the present study was to quantify the relative roles of different types of environmental variables in determining the variations of species composition and plant traits in pastures of the Southern Alps. As sug-

gested by Garnier et al. (2007), we hypothesised that species composition and functional variation in pastures of the Southern Alps are controlled by three main environmental filters: i) climate, ii) resource availability, and iii) grazing pressure. Specifically, the following questions were addressed: (1) How do species composition and plant traits change in relation to environmental filters? (2) What are the relative contributions of climate, soil properties, and grazing pressure in controlling plant and community functions?

Material and methods

Study area and sampling

The study sites, in total 105 pasture plots (5 m × 5 m), were located in northeast Italy in the Province of Trento (Fig. 1). The geology was heterogeneous with calcareous, siliceous bedrock and mixed sediments. The annual mean temperature was *c.* 8°C at the minimum altitude (1040 m a.s.l.) and *c.* 1°C at the maximum altitude (2382 m a.s.l.). The annual mean rainfall varied between 800–1300 mm year⁻¹. All the selected pastures were located in the highlands, in a landscape characterised by coniferous forests or subalpine scrublands interspersed with grazed grassland, montane hay meadows, and natural alpine and subalpine grasslands. Traditional summer pastures are grazed for two or three months during summer, mainly by cows and sheep, which are then moved back to the bottom of the valley for the rest of the year. The pastures are manured mostly in the form of animal urine and dung, and the area around the stall and other more accessible areas are supplied with farmyard manure.

Floristic data were extracted from an existing dataset containing 323 vegetation plots recorded on the studied grazing areas and belonging to the following seven pasture plant communities (Dainese 2010): (1) nitrophilous pastures (*Rumicetum alpini*), (2) montane mesic pastures (*Festuco commutatae-Cynosuretum*), (3) subalpine mesic pastures (*Poa alpinae*), (4) calcareous montane pastures (*Bromion erecti*), (5) calcareous subalpine pastures (*Seslerio-Caricetum sempervirentis*), (6) acid montane pastures (*Homogyno alpinae-Nardetum*), and (7) acid subalpine pastures (*Sieversio-Nardetum strictae*) (Dainese 2010). In this study, a total of 105 pasture plots (15 for each pasture community) were randomly selected from the dataset (Appendix 1). The phytosociological nomenclature follows Mucina et al. (1993), while the nomenclature of the vascular plants is according to the Flora of the Alps (Äeschmann et al. 2004).

Plant traits

Three functional traits were selected, following the LHS scheme developed by Westoby (1998): specific leaf area (SLA), canopy height (CH), and seed mass (SM). Values for CH were compiled from existing local floras (Äeschmann et al. 2004), and those for SLA and SM from other published sources (Kleyer et al. 2008, Klotz et al. 2002, Liu et al. 2008). The values for SLA, CH, and SM could be ascertained for 70%, 100%, and 80% of the species, respectively. The site-

Table 1. Descriptive statistics of the quantitative explanatory variables used in the analysis of 105 pastures of the Southern Alps.

Variable name and explanation		Unit	Mean	Min	Max
Climate					
TEM	Mean summer temperature	°C	10.88	7.17	14.82
PREC	Total summer precipitation	mm	433	314	526
Soil					
pH	Soil pH		5.07	3.65	7.46
P_SOIL	Available P in soil	mg kg ⁻¹	53.56	9	247
D_SOIL	Soil depth	cm	14.80	2	50
Grazing pressure					
SLOPE	Slope angle	Degree (°)	14.94	1.07	32.12
DIST	Distance to the farm centre	m	299.70	11.48	1225.88
GRAZ	Grazing intensity	LU ha ⁻¹	0.71	0.46	1.41

by-species matrix was combined with the species-by-trait matrix, resulting in a matrix that contains the information of average trait-weighted values per site (the ‘community aggregated traits’, as defined by Garnier et al. 2004). For the more common and abundant species, the values of the three traits were nearly always available, which enabled us to fulfill the rule of thumb recommended by Pakeman and Queded (2007), namely that the sum of weights of the species with missing values should be smaller than 20% in each plot.

Explanatory variables

For each pasture plot, 9 explanatory variables were recorded belonging to three different groups: climate, soil properties, and grazing pressure (Table 1). Since elevation was strongly correlated with temperature ($r = -0.98$, $p < 0.01$, Pearson correlation; Appendix 2), the former variable was not used in subsequent analyses. When considering elevational gradients, it is useful to remember that, elevation cannot be considered as a factor directly controlling the distribution of plant species (Kerr 2001). Elevation is a proxy term for numerous variables that change with elevation. Some

variables, like temperature, are controlled by atmospheric density and have a first order, clinal relationship to elevation as expressed by the adiabatic lapse rate (Carpenter 2005).

The climatic variables were retrieved from existing continuous raster maps with a resolution of 100 m × 100 m derived by spatialising the data of 64 climatic stations located throughout the province (Sboarina and Cescatti 2004). We selected the following climatic variables: (1) mean summer (May–August) temperature (TEM), and (2) total summer (May–August) precipitation (PREC). Temperature was selected as a measure of available energy during the growing season, and precipitation as an indicator of water availability. In the case that pasture plots were located closer than 100 m, the same extrapolated value of TEM and PREC was used.

In each pasture plot, four soil samples were taken at a depth of 0–20 cm, after removing the litter layer, and were bulked prior to analyses. Soil pH (measured in water) and available phosphorus (P_SOIL; mg P kg⁻¹ extracted using Olsen’s reagent) were measured. P_SOIL was selected as a surrogate measure for soil fertility, following studies in which phosphorus has been shown to be the most important soil variable for determining plant and community functions (Marini et al. 2007, Ordoñez et al. 2009). Soil nitrogen (N) was not considered in the analysis, because it gives an indication of the size of the soil N pool but not how much of this pool is actually available for plant uptake (Vitousek and Howarth 1991). Furthermore, soil depth (D_SOIL) was determined for each pasture, as the mean of three measurements. The bedrock variables were obtained from a geological map of the province (Bosellini et al. 1999). The bedrock types were grouped into four qualitative classes: sedimentary calcareous bedrock (CAL), volcanic and metamorphic acid bedrock (ACID), volcanic basic bedrock (VBAS), and mixed debris (MIX).

Considering that animals graze freely during the day and are gathered at night in the farm centre (barn, milking shed,

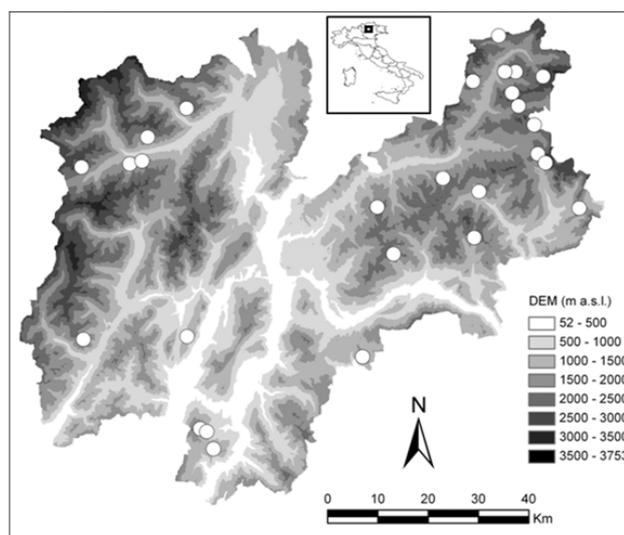


Figure 1. Location of the study area in the Italian Alps and distribution of grazing areas studied.

or other assembly point for the animals), the spatial gradient extending from farm centre to surrounding vegetation was assumed – *a priori* – to parallel a gradient of decreasing animal influence on vegetation, as demonstrated by Vandvik and Birks (2002a,b). Furthermore, topography (slope) was assumed to be a further key factor driving grazing pressure in the pastures, e.g., sloping pastures are grazed less intensively than flat pastures. Based on these considerations, two proxy indicators of grazing pressure were quantified: slope (SLOPE) and distance to the farm centre (DIST). Slope was calculated on the basis of a digital model of elevation with a cell size of 10 m × 10 m. Finally, a grazing intensity index (GRAZ) for each pasture plot was estimated considering the average stock density for each type of pasture community, expressed in livestock units (LU) divided by pasture community size, in order to standardise this index between the communities.

A central and recurrent problem in building models of species distribution is identifying the appropriate scale for modelling (Wiens 2002). A first possible mismatch can occur between the ‘resolution’ at which species data were sampled and the one at which environmental predictors are available (Guisan and Thuiller 2005). Although climatic variables were measured using coarse-scale maps, this resolution should be able to distinguish species and community replacement along a climatic gradient, e.g., montane pastures compared to subalpine pastures, given that these variables are operating at a broad scale.

Data analysis

Prior to analysis, the data on species composition were Hellinger-transformed to express species abundance as a square-root-transformed proportionate abundance in each sampling. Legendre and Gallagher (2001) have shown that this transformation makes data on species presence-absence or abundance amenable to linear ordination methods such as principal component analysis (PCA) or canonical redundancy analysis (RDA). The plant functional traits were log₁₀-transformed (Westoby 1998) and standardised to mean zero and unit standard deviation (Pakeman et al. 2009).

Given that multicollinearity among explanatory variables can hamper the identification of the most causal variables (MacNally 2000), the Pearson correlation matrix was calculated. In the case of highly correlated variables ($r > 0.60$), only one of them was used to avoid multicollinearity; elevation was excluded from the analyses (Appendix 2). Forward selection on each set of explanatory variables (climate, soil, and grazing pressure) was run separately to select those variables that contributed significantly ($P \leq 0.05$ after 999 random permutations) to explaining the variation in species composition and plant traits. To minimise the problems of the classical forward selection, the double-step procedure proposed by Blanchet et al. (2008) was applied. This procedure corrects for the overestimation of the proportion of explained variance by using two stopping criteria: 1) 0.05 significance level, and 2) adjusted- R^2 ($Adj-R^2$) of the global model. Thus,

one runs a multiple regression with all explanatory variables included and uses the $Adj-R^2$ of this model as another stopping criterion. Only these selected variables were used in subsequent analyses. The analysis was performed using the function ‘forward.sel’ in the ‘Packfor’ package in R (available at https://r-forge.r-project.org/R/?group_id=195).

Variation partitioning (Borcard et al. 1992), using the estimation procedure proposed by Peres-Neto et al. (2006), was employed for quantifying the proportion of variation in species composition and functional traits explained by the variation in each of the three combinations of explanatory variables. All the partial regression analyses were tested for significance with the Monte Carlo permutation test ($n = 999$). The total variation was decomposed into seven components: the pure effect of climate (C), soil (S), and grazing pressure (G) factors; three first-order joint components ($C \cap S$, $C \cap G$, and $S \cap G$); and the joint component among the three groups ($C \cap S \cap G$). The variation explained was reported in each model as the adjusted R^2 (R^2_{adj}), which takes the number of predictor variables and sample size into account to prevent the inflation of R^2 values (Peres-Neto et al. 2006). When a negative R^2_{adj} was obtained, we interpreted it as a zero value (Peres-Neto et al. 2006), meaning that not all fractions of one variation partitioning always add up to a perfect 100%. In interpreting variation partitioning, one must consider that the amount of explained variability included also reflects the reduction of dimensionality (so that we can expect higher values for single response variables than those for total species composition) and is also dependent on the number of explanatory variables in the model. The R-language functions ‘varpart’, ‘rda’, and ‘anova.cca’ in the ‘vegan’ library were used (Oksanen et al. 2008).

After that, redundancy analysis (RDA) diagrams were used to describe and visualise the relations between explanatory variables, species composition, and plant traits across pasture communities. RDA was carried out using CANOCO for Windows ver. 4.5 (ter Braak and Šmilauer 2002). All the explanatory variables recorded were included in the RDA diagrams to get an overview of the relations. For data on community composition, it often does not make sense to display the scores of all species, given that some species are rare, and no relevant information can be provided about their ecological preferences, while other species might not be characterised well by the explanatory variables used in the analysis (Lepš and Šmilauer 2003). For clarity, ordination plots are limited to those plant species with a fit range $>10\%$. The fit range provides a measure for the variance explained by an individual species (Lepš and Šmilauer 2003).

Results

Species composition

In the regression model of species composition, both the considered climatic variables (TEM and PREC) were significant (Table 2). Almost all the soil variables (pH, P_SOIL, CAL, ACID, VBAS, and D_SOIL) were significant. The

Table 2. Summary of the significant explanatory variables (climate, soil and grazing pressure) obtained by forward selection procedure in the multiple regression models of plant species composition and functional traits. *F*= the *F* statistic; *P*=the *P*-value statistic; *R*²=coefficient of determination of the variable selected; Adj-*R*²=the cumulative adjusted coefficient of determination of the variable selected; *df*=degrees of freedom. Variable abbreviations: TEM, mean summer temperature; PREC, total summer precipitation; pH, soil pH; P_SOIL, Available P in soil; CAL, calcareous bedrock; ACID, volcanic and metamorphic acid bedrock; VBAS, volcanic basic bedrock; MIX, mixed debris; D_SOIL, soil depth; SLOPE, slope angle; DIST, distance to the farm centre; GRAZ, grazing intensity.

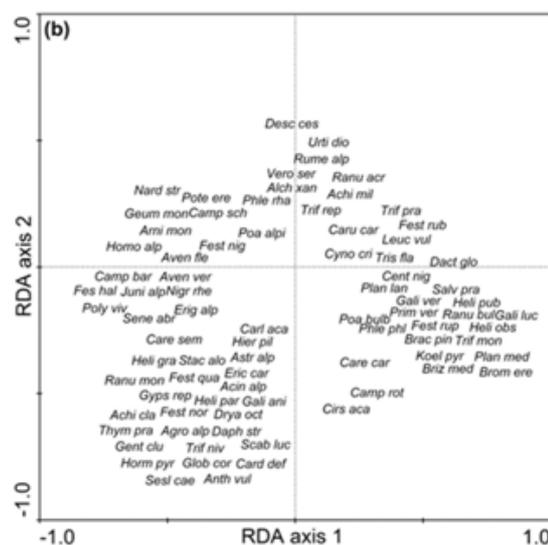
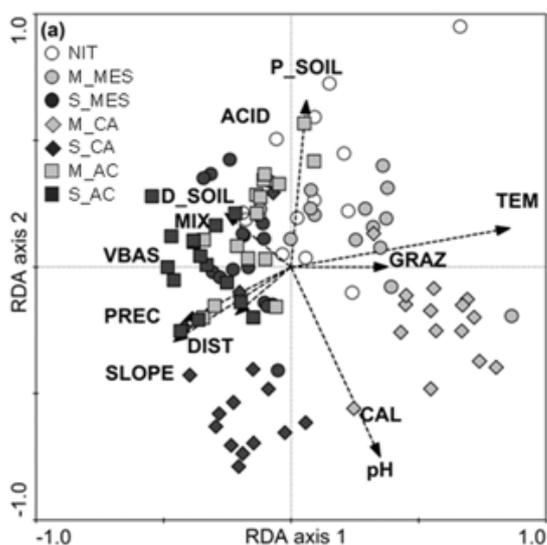
	<i>F</i>	<i>P</i>	<i>R</i> ²	Model			
				Adj <i>R</i> ²	<i>d.f.</i>	<i>F</i>	<i>P</i>
Species composition							
Climate				10.4	2,102	6.13	0.001
TEM	10.13	0.001	9.0				
PREC	2.75	0.001	2.4				
Soil				17.2	6,98	4.16	0.001
pH	9.23	0.001	8.2				
P_SOIL	7.17	0.001	6.0				
VBAS	2.65	0.002	2.2				
CAL	2.11	0.004	1.7				
ACID	1.85	0.014	1.5				
D_SOIL	1.91	0.015	1.5				
Grazing pressure				6.8	3,101	3.08	0.001
SLOPE	4.03	0.001	3.8				
DIST	3.26	0.001	3.0				
GRAZ	2.23	0.007	2.0				
Functional traits							
Climate				15.6	1,103	19.77	0.001
TEM	19.77	0.001	16.1				
Soil				19.7	3,101	9.34	0.001
P_SOIL	14.75	0.001	12.5				
pH	6.66	0.002	5.4				
MIX	4.95	0.004	3.8				
Grazing pressure				6.1	2,102	4.43	0.001
SLOPE	5.73	0.002	5.3				
GRAZ	3.01	0.030	2.7				

analysis selected all the variables of grazing pressure: SLOPE, DIST, and GRAZ. Soil variables together explained the greatest amount (over 17%) of the variation of species composition. Climatic variables accounted for 10.4% of the species compositional variation, while grazing pressure accounted for 6.8%.

In the ordination diagram, the first axis accounted for 10.1% of the total variation and separated pasture communities mainly by temperature and to a lesser extent by grazing pressure (Fig. 2). Montane pastures located in warmer sites showed higher grazing pressure than subalpine pastures located instead in colder sites. The second axis accounted for 9.4% of the total variation and divided the pasture communities according to soil fertility (nitrophilous and mesic pastures) and bedrock type – soil pH (calcareous vs. acid pastures).

In the variation partitioning of species composition, the total variance explained was 29.4% (Fig. 4a). Soil (14.2%) showed the most important pure effect, followed by climate (7.2%), while grazing pressure explained only a small (3.0%)

Figure 2. Redundancy analysis (RDA) diagrams of species composition occurring in the 105 pasture plots: (a) explanatory variables and pastures communities, (b) species (only plant species with a fit-range above 10% are shown, n=81). Axes 1 and 2 explain 10.1% and 9.4% of the floristic variance, respectively. Numeric explanatory variables are represented by dotted-line arrows and nominal explanatory variables by triangles. Abbreviations for communities: NIT, nitrophilous pastures; M_MES, mountain mesic pastures; S_MES, subalpine mesic pastures; M_CA, calcareous mountain pastures; S_CA, calcareous subalpine pastures; M_AC, acid mountain pastures; S_AC, acid subalpine pastures. Explanatory variable abbreviations: ACID, volcanic and metamorphic acid bedrock; CAL, calcareous bedrock; D_SOIL, soil depth; DIST, distance to the farm centre; GRAZ, grazing intensity; MIX, mixed debris; P_SOIL, Available P in soil; pH, soil pH; PREC, total summer precipitation; SLOPE, slope angle; TEM, mean summer temperature; VBAS, volcanic basic bedrock. For abbreviations for species names, see Appendix 1.



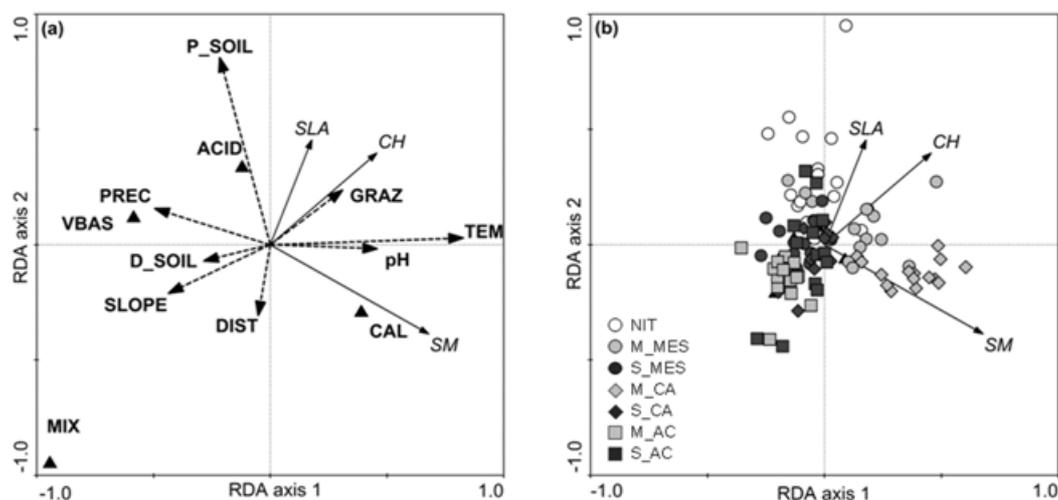


Figure 3. Redundancy analysis (RDA) diagrams of plant traits occurring in the 105 pastures: (a) explanatory variable and plant traits, (b) pasture communities and plant traits. Axes 1 and 2 explain 23.3% and 17.1% of the plant traits variance, respectively. Numeric explanatory variables are represented by dotted-line arrows, nominal explanatory variables by triangles and plant traits by solid-line arrows. Abbreviations for communities: NIT, nitrophilous pastures; M_MES, mountain mesic pastures; S_MES, subalpine mesic pastures; M_CA, calcareous mountain pastures; S_CA, calcareous subalpine pastures; M_AC, acid mountain pastures; S_AC, acid subalpine pastures. Explanatory variable abbreviations: ACID, volcanic and metamorphic acid bedrock; CAL, calcareous bedrock; D_SOIL, soil depth; DIST, distance to the farm centre; GRAZ, grazing intensity; MIX, mixed debris; P_SOIL, Available P in soil; pH, soil pH; PREC, total summer precipitation; SLOPE, slope angle; TEM, mean summer temperature; VBAS, volcanic basic bedrock. Plant traits abbreviations: CH, canopy height; SLA, specific leaf area; SM, seed mass.

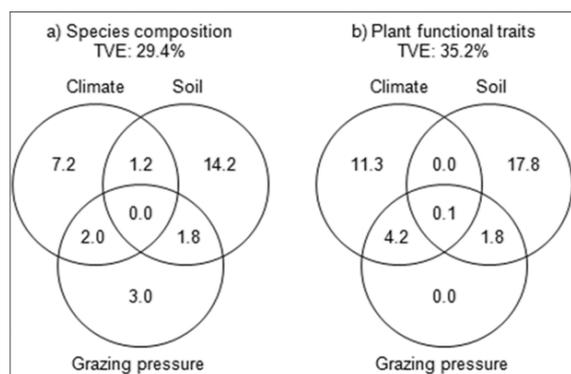


Figure 4. Results of partitioning variance (adjusted R^2 in %) from climate, soil and grazing pressure sources for (a) species composition and (b) plant functional traits. Adjusted fractions of total variation explained (TVE) were estimated following the procedure of Peres-Neto et al. (2006).

proportion of it. The share effect of each pair of explanatory variables was weak (*c.* 1-2%).

Plant traits

In the model of plant traits, TEM was the only significant climatic variable (Table 2). Significant soil variables were P_SOIL, pH, and MIX. Among the grazing pressures were selected SLOPE and GRAZ. Soil variables together explained the greatest amount of the variation (19.7%), as found in species composition. Climatic variables accounted

for 15.6% of the functional variation, while grazing pressure accounted for 6.1%.

In the ordination diagram, the first axis accounted for 23.3% of the total variation and was determined mainly by temperature, grazing pressure, and bedrock type (Fig. 3). Plant height and seed mass were positively correlated with temperature; in addition, seed mass was positively correlated with calcareous bedrock. Moreover, a reduction of grazing pressure, due to both environmental constraints (slope) and lower grazing intensity, tends to favour species with lower specific leaf area and stature. The second axis captured 17.1% of the total variation and was mainly determined by soil fertility. Specific leaf area was positively correlated with soil fertility.

The amount of variation captured by the three groups was 35.2% (Fig. 4b). Soil (17.8%) and climate (11.3%) alone explained the largest proportions of the variation. Variation in grazing pressure was shared with climate (4.2%) and soil (1.8%).

Discussion

Species-environment relationships

The results show a significant species-climatic gradient. Along the elevational gradient, temperature plays an important role in forming specific communities, separating montane pastures (*Festuco commutatae-Cynosuretum* and *Bromion erecti*) from subalpine pastures (*Poion alpinae*, *Seslerio-Caricetum sempervirentis*, and *Sieversio-Nardetum strictae*). The ordination of species composition shows not

only replacement of montane by subalpine species with decreasing temperature, but also highlights a gradient of grazing pressure. There is evidence that grazing pressure, due to both environmental constraints (slope) and lower grazing intensity, tends to decline in subalpine pastures. The results probably reflect that topographic and soil-related site characteristics determine the spatial distribution of the land use within the study region, as reported by several studies (White et al. 2004, Klimek et al. 2007, Tasser et al. 2007, Rudmann-Maure et al. 2008). Pastures located in colder sites have a lower economic yield potential, due to a shorter growing season and more difficulties in management, which can lead to a lower management pressure. Mottet et al. (2006) in the Pyrenees and Kampmann et al. (2008) in the Swiss Alps have shown that slope and elevation can be driving forces in decision making for type of management.

Models of species composition also show a significant role of soil fertility. As demonstrated by several authors (e.g., Critchley et al. 2002, Marini et al. 2007), phosphorus is a key soil factor explaining the variation of species composition. The ordination analysis shows a decreasing trend of soil fertility from nitrophilous pastures > mesic pastures > calcareous and acid pastures. Moreover, variables of bedrock type – soil pH distinguish communities that occur on acid bedrock (*Homogyno alpinae-Nardetum* and *Sieversio-Nardetum strictae*) from those on calcareous bedrock (*Bromion erecti* and *Seslerio-Caricetum sempervirentis*).

Trait-environment relationships

Concerning plant traits, a change in plant size and seed mass was observed along the temperature gradient. Short size and prostrate stature are certainly the most prominent characteristics of alpine plants (Körner 1989, Pellissier et al. 2010), and our analysis shows a decreasing trend of plant size with decreasing temperature. The decrease in plant stature with altitude represents an adaptation of plants to cold climates, because by reducing stature and spread, plants can increase the temperature of leaves and soil (Friend and Woodward 1990, Körner 2003). Moreover, the aerial parts of low-growing plants tend to be insulated from desiccation by snow cover when the ground is frozen and no water is available to the roots (Grime 2002). The decline in seed mass with reduction of temperature may be due to environmentally induced plastic responses to a decline in resource availability (e.g., lower temperatures at higher elevations may reduce photosynthetic rates), while the short growing seasons may reduce the time for seed development and seed provisioning, thereby reducing mature-seed mass, as reported by several authors (Baker 1972, Totland and Birks 1996). In addition, calcareous montane pastures are positively correlated with seed mass. The positive association between seed mass and pH was also found by Tautenhahn et al. (2008), who explained this relation as an adaptive stress response due to higher competition on alkaline soils. Furthermore, larger seed mass may act as a buffer against poor environmental conditions, e.g., lower availability of water (summer precipi-

tation) and nutrients as found in calcareous montane pastures; in addition, the seedlings produced are more capable of resisting environmental hazards, and reserves are needed for environmental-resistance mechanisms (Leishman and Westoby 1994).

Plants with leaf traits that allow a fast use of nutrients and growth but for shorter times, like high SLA, were found in fertile pastures managed more intensively, while the reverse occurred in pastures with lower fertility and grazing pressure where conservation of nutrients is arguably more important. Our results support previous studies (Kahmen and Poschlod 2004, Garnier et al. 2007, Pakeman et al. 2009, Seifan et al. 2010) and confirm the presence of a functional trade-off between rapid acquisition of resources and conservation of resources in responses to changes in soil fertility and grazing pressure.

Our study has indicated that the LHS ecological strategy could yield relevant information on key aspects of pasture functioning. The traits selected here, canopy height, specific leaf area, and seed mass, could be used to capture the functioning of plant species and communities. Our results reveal that replacement of species along gradients of temperature, fertility, and grazing pressure occurs concomitantly with changes in resource use, plant size, and seed mass. The availability of energy, water, and resources are important components in the response of plants to pasture functioning.

Partitioned species-environment and trait-environment relationships

The variation partitioning approach has allowed a quantification of the relative roles of climatic, soil, and grazing pressure factors in determining the composition and functional structure of pastures in the Southern Alps. The availability of environmental energy (temperature), soil fertility (Olsen P in soil), and bedrock type – soil pH (calcareous vs. acid bedrock) are the most important factors, among those tested, that control species and functional composition in pastures of the Southern Alps. The variation partitioning shows a low degree of overlap between components of climate, soil, and grazing pressure, indicating independent environmental filters that control species distribution and plant traits. Almost all of the variation is related to the unique effect of variables of soil (c. 14-18%) and climate (c. 7-11%) in models of both the species composition and plant traits, respectively. Our observations are consistent with previous studies (e.g., Díaz et al. 1998, Vandvik and Birks 2002a,b, de Bello et al. 2005, Marini et al. 2007, Raatikainen et al. 2007, Pakeman et al. 2009, Lüth et al. 2010) that have shown a remarkable filtering effect of soil properties and climate on species and functional composition of grasslands. However, the models highlight a weak effect of grazing pressure (3-0%), mainly related to the shared components with climate and/or soil (c. 4-6%). The lower independent effect of grazing pressure could be due to two possibilities: (i) the scale at which grazing pressure was measured is not sensitive enough for highlighting the relation with floristic composition and

plant traits, or (ii) grazing is not a variable but a constant in this system (i.e., to highlight these differences the sampling should be evaluated between grazed pastures and abandoned ones). In addition, when habitat filtering becomes the main limiting factor (i.e., when temperature or soil fertility is low), grazing pressure is expected to have less of an effect on functional diversity (Díaz et al. 1999). It also has to be kept in mind that the measured variables of soil chemistry are linked not only to the natural fertility of the site, but also to inputs of long-term management (Marini et al. 2007).

Conclusion

By combining ordination analysis and variation partitioning, the present study shows some relationships between species composition, plant traits, and environmental variables in pastures of the Italian Alps. The observed patterns of species and functional composition cannot be attributed to a single explanation, but rather to a combination of natural and biotic factors. The analyses highlight the presence of three main environmental filters that determine the variations of species composition and plant traits in pastures of the Southern Alps: i) temperature, ii) soil fertility, and iii) bedrock type – soil pH (acid vs. calcareous substrate). These findings confirm the importance of taking the effects of climate and resource availability into account when describing plant and community functions of grasslands (Marini et al. 2007, Pake-man et al. 2009). Further studies considering additional (e.g., farm extension, type of grazers) or better predictors, as for variables of grazing pressure, may therefore be necessary to improve the models of species composition and plant traits.

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References

- Äschimann, D., K. Lauber, D.M. Moser and J.P. Theurillat. 2004. *Flora Alpina*. Zanichelli, Bologna.
- Baker, H.G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997-1010.
- Bennie, J., M.O. Hill, R. Baxter and B. Huntley. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *J. Ecol.* 94: 355-368.
- Blanchet, F.G., P. Legendre and D. Borcard. 2008. Forward selection of explanatory variables. *Ecology* 89: 2623-2632.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.
- Bosellini, A., A. Castellarin, G.V. Dal Piaz and M. Nardin. 1999. *Carta litologica e dei lineamenti strutturali del Trentino (1:200 000)*. Servizio Geologico della Provincia Autonoma di Trento, Trento.
- Carpenter, C. 2005. The environmental control of plant species density on a Himalayan elevation gradient. *J. Biogeogr.* 32: 999-1018.
- Critchley, C.N.R., B.J. Chambers, J.A. Fowbert, R.A. Sanderson, A. Bhogal and S.C. Rose. 2002. Association between lowland grassland plant communities and soil properties. *Biol. Conserv.* 105: 199-215.
- Dainese, M. 2010. *Classification and biodiversity patterns in pastures of province of Trento*. PhD dissertation, Department of Environmental Agronomy and Crop Production, University of Padova, Padova, Italy.
- de Bello, F., J. Lepš and M.T. Sebastià. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *J. Appl. Ecol.* 42: 824-833.
- Díaz, S., M. Cabido and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9: 113-122.
- Díaz, S., M. Cabido, M. Zak, E.M. Carretero and J. Aranibar. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in centralwestern Argentina. *J. Veg. Sci.* 10: 651-660.
- Díaz, S., J.G. Hodgson, K. Thompson, M. Cabido, J.H.C. Cornelissen, A. Jalili, G. Montserrat-Martí, J.P. Grime, F. Zarrinkamar, Y. Asri, S.R. Band, S. Basconcelo, P. Castro-Díez, G. Funes, B. Hamzehee, M. Khosnevi, N. Pérez-Harguindeguy, M.C. Pérez-Rontomé, F.A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Deghan, L. De Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador and M.R. Zak. 2004. The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* 15: 295-304.
- Dullinger, S., T. Dirnböck, J. Greimler and G. Grabherr. 2003. A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. *J. Veg. Sci.* 14: 243-252.
- Ellenberg, H. 1996. *Vegetation Mitteleuropas mit den Alpen*. 5th edn. Verlag Eugen Ulmer, Stuttgart
- Fischer, M. and S. Wipf. 2002. Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadow. *Biol. Conserv.* 104: 1-11.
- Friend, A.D. and F.I. Woodward. 1990. Evolutionary and ecophysiological responses of mountain plants to the growing season environment. *Adv. Ecol. Res.* 20: 59-124.
- Garnier, E., J. Cortez, G. Billès, M.L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill and J.P. Toussaint. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630-2637.
- Garnier, E., S. Lavorel, P. Ansquer, H. Castro, P. Cruz, J. Dolezal, O. Eriksson, C. Fortunel, H. Freitas, C. Golodets, K. Grigulis, C. Jouany, E. Kazakou, J. Kigel, M. Kleyer, V. Lehsten, J. Lepš, T. Meier, R. Pake-man, M. Papadimitriou, V.P. Papanastasis, H. Quested, F. Quétier, M. Robson, C. Roumet, G. Rusch, C. Skarpe, M. Sternberg, J.P. Theau, Á. Thébault, D. Vile and M.P. Zarovali. 2007. A standardized methodology to assess the effects of land use change on plant traits, communities and ecosystem functioning in grasslands. *Ann. Bot.* 99: 967-985.
- Giupponi, C., M. Ramanzin, E. Sturaro and S. Fuser. 2006. Land use change, biodiversity and agricultural policy in the Belluno province, Italy. *Environ. Sci. Policy* 9: 163-173.

- Grime, J.P. 2002. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. 2nd edn. John Wiley & Sons Ltd.
- Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8: 993-1009.
- Kahmen, S. and P. Poschold. 2004. Plant functional trait responses to grassland succession over 25 years. *J. Veg. Sci.* 15: 21-32.
- Kampmann, D., F. Herzog, P. Jeanneret, W. Konold, M. Peter, T. Walter, O. Wildi and A. Lüscher. 2008. Mountain grassland biodiversity: impact of site conditions versus management type. *J. Nat. Conserv.* 16: 12-25.
- Kerr, J. 2001. Global biodiversity patterns: from description to understanding. *Trends Ecol. Evol.* 16: 424-425.
- Kleyer, M., R.M. Bekker, I.C. Knevel, J.P. Bakker, K. Thompson, M. Sonnenschein, P. Poschold, J.M. van Groenendael, L. Klimeš, J. Klimešová, S. Klotz, G.M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J.G. Hodgson, A.K. Jacke, I. Kühn, D. Kunzmann, W.A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H.J. Steendam, O. Tackenberg, B. Wilmann, J.H.C. Cornelissen, O. Eriksson, E. Garnier and B. Peco. 2008. The LEDA traitbase: a database of life-history traits of North-west European flora. *J. Ecol.* 96: 1266-1274.
- Kleijn, D. and H. Müller-Schärer. 2006. The relation between unpalatable species, nutrients and plant species richness in Swiss montane pastures. *Biodivers. Conserv.* 15: 3971-3982.
- Klimek, S., A.R.G. Kemmermann, M. Hofmann and J. Isselstein. 2007. Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors. *Biol. Conserv.* 134: 559-570.
- Klotz, S., I. Kühn and W. Durka. 2002. *BIOFLOR—Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland*. Schriftenreihe für Vegetationskunde 38, Bonn.
- Körner, C., 1989. The nutritional status of plants from high altitudes: a worldwide comparison. *Oecologia* 81: 379-391.
- Körner, C., 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. 2nd edn. Springer-Verlag, Berlin.
- Laiolo, P., F. Dondero, E. Ciliento and A. Rolando. 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* 41: 294-304.
- Legendre, P. and E.D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.
- Leishman, M.R. and M. Westoby. 1994. The role of seed size in seedling establishments in dry soil conditions: experimental evidence from semi-arid species. *J. Ecol.* 82: 249-258.
- Lepš, J. and P. Šmilauer. 2003. *Multivariate Analysis of Ecological Data Using Canoco*. Cambridge University Press, Cambridge.
- Liu, K., R.J. Eastwood, S. Flynn, R.M. Turner and W.H. Stuppy. 2008. *Seed information database* (release 7.1, May 2008) <www.kew.org/data/sid>
- Lüth, C., E. Tasser, G. Niedrist, J. Dalla Via and U. Tapeiner. 2010. Plant communities of mountain grasslands in a broad cross-section of the Eastern Alps. *Flora* 206: 433-443.
- MacDonald, D., J.R. Crabtree, T.D. Wiesinger, N. Stamou, P. Fleury, J. Gutierrez Lazpita and A. Gibon. 2000. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *J. Environ. Manag.* 59: 47-69.
- MacNally, R. 2000. Regression and model-building in conservation biology, biogeography, and ecology: the distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. *Biodivers. Conserv.* 9: 655-671.
- Marini, L., M. Scotton, S. Klimek, J. Isselstein and A. Pecile. 2007. Effects of local factors on plant species richness and composition of Alpine meadows. *Agric. Ecosyst. Environ.* 119: 281-288.
- Marini, L., F. Prosser, S. Klimek and R.H. Marrs. 2008. Water-energy, land-cover and heterogeneity drivers of the distribution of plant species richness in a mountain region of the European Alps. *J. Biogeogr.* 35: 1826-1839.
- Moser, D., S. Dullinger, T. Englisch, H. Niklfeld, C. Plutzer, N. Sauberer, H.G. Zechmeister and G. Grabherr. 2005. Environmental determinants of vascular plant species richness in the Austrian Alps. *J. Biogeogr.* 32: 1117-1127.
- Mottet, M., S. Ladet, N. Coqué and A. Gibon. 2006. Agricultural land-use change and its drivers in mountain landscapes: A case study in the Pyrenees. *Agric. Ecosyst. Environ.* 114: 269-310.
- Mucina, L., G. Grabherr, T. Ellmauer and S. Wallnöfer. 1993. *Die Pflanzengesellschaften Österreichs*. Gustav Fischer, Jena.
- Muller, P., S. Gusewell and P.J. Edwards. 2003. Impacts of soil conditions and agricultural land use on plant species richness of Alpine pastures in the south of Glarus. *Bot. Helv.* 113: 15-36.
- Norris, K. 2008. Agriculture and biodiversity conservation: opportunity knocks. *Conserv. Lett.* 1: 2-11.
- Oksanen, J., R. Kindt, P. Legendre, R.B. O’Hara and M.H.H. Stevens. 2008. *Vegan: community ecology package*. R package version 1.15-1. <<http://r-forge.r-project.org/projects/vegan/>>
- Ordoñez, J.C., P.M. van Bodegom, J.P.M. Witte, I.J. Wright, P.B. Reich and R. Aerts. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecol. Biogeogr.* 18: 137-149.
- Pakeman, R.J. and H.M. Quested. 2007. Sampling plant functional traits: What proportion of the species need to be measured? *Appl. Veg. Sci.* 10: 91-96.
- Pakeman, R.J., J. Lepš, M. Kleyer, S. Lavorel, E. Garnier and the VISTA consortium. 2009. Relative climatic, edaphic and management controls of plant functional trait signatures. *J. Veg. Sci.* 20: 148-159.
- Pellissier, L., B. Fournier, A. Guisan and P. Vittoz. 2010. Plant traits co-vary with altitude in grasslands and forests in the European Alps. *Plant Ecol.* 211: 351-365.
- Peres-Neto, P.R., P. Legendre, S. Dray and D. Borcard. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614-2625.
- Poorter, H. and C. Remkes. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83: 553-559.
- Raatikainen, K.M., R.K. Heikkinen and J. Pykälä. 2007. Impacts of local and regional factors on vegetation of boreal semi-natural grasslands. *Plant Ecol.* 189: 155-173.
- Rook, A.J., B. Dumont, J. Isselstein, K. Osoro, M.F. WallisDeVries, G. Parente and J. Mills. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biol. Conserv.* 119: 137-150.
- Rudmann-Maurer, K., A. Weyand, M. Fischer and J. Stöcklin. 2008. The role of landuse and natural determinants for grassland vegetation composition in the Swiss Alps. *Basic Appl. Ecol.* 9: 494-503.
- Sboarina, C. and A. Cescatti. 2004. *Il clima del Trentino. Distribuzione spaziale delle principali variabili climatiche*. Report 33. Centro di Ecologia Alpina, Trento.

- Sebastiá, M.T. 2004. Role of topography and soils in grassland structuring at the landscape and community scales. *Basic Appl. Ecol.* 5: 331-346.
- Seifan, M., K. Tielborger, D. Schloz-Murer and T. Seifan. 2010. Contribution of molehill disturbances to grassland community composition along a productivity gradient. *Acta Oecol.* 36: 569-577.
- Spiegelberger, T., D. Matthies, H. Müller-Schärer and U. Schaffner. 2006. Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps. *Ecography* 29: 541-548.
- Tasser, E. and U. Tappeiner. 2002. Impact of land use changes on mountain vegetation. *Appl. Veg. Sci.* 5: 173-184.
- Tasser, E., J. Walde, U. Tappeiner, A. Teutsch and W. Noggler. 2007. Land-use changes and natural reforestation in the Eastern Central Alps. *Agric. Ecosyst. Environ.* 118: 115-129.
- Tautenhahn, S., H. Heilmeyer, L. Götzenberger, S. Klotz, C. Wirth and I. Kühn. 2008. On the biogeography of seed mass in Germany – distribution patterns and environmental correlates. *Ecography* 31: 457-468.
- ter Braak, C.J.F. and P. Šmilauer. 2002. *CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca.
- Totland, O. and H.J.B. Birks. 1996. Factors influencing inter-population variation in *Ranunculus acris* seed production in an alpine area of southwestern Norway. *Ecography* 19: 269-278.
- Vandvik, V. and H.J.B. Birks. 2002a. Partitioning floristic variance in Norwegian upland grasslands into within-site and between-site components: are the patterns determined by environment or by land-use? *Plant Ecol.* 162: 233-245.
- Vandvik, V. and H.J.B. Birks. 2002b. Pattern and process in Norwegian upland grasslands: a functional analysis. *J. Veg. Sci.* 13: 123-134.
- Vandvik, V. and H.J.B. Birks. 2004. Mountain summer farms in Røldal, western Norway – vegetation classification and patterns in species turnover and richness. *Plant Ecol.* 170: 203-222.
- Vitousek, P.M., and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry* 13: 87-115.
- Westoby, M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant Soil* 199: 213-227.
- White, T.A., D.J. Barker and J.M. Kenneth. 2004. Vegetation diversity, growth, quality and decomposition in managed grasslands. *Agric. Ecosyst. Environ.* 101: 73-84.
- Wiens, J.A. 2002. Predicting species occurrences: progress, problems, and prospects. In: J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall and F.B. Samson (eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Covelo, CA, pp. 739-749.
- Wohlgemuth, T. 1998. Modelling floristic species richness on a regional scale: a case study in Switzerland. *Biodivers. Conserv.* 7:159-177.

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Appendices

Appendix 1. Species composition of the seven main pasture communities, given as mean of percentage cover for the most important species.

Appendix 2. Pearson correlations between explanatory variables.

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