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Environmental factors and management intensity affect in different ways plant diversity and pastoral value of Alpine pastures

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Abstract

Based on a wide dataset of vegetation surveys carried out across the pastures of Western Italian Alps, the objective of the research was to determine the relative importance of management intensity and environmental factors (i.e. topography, climate, bedrock type) on 1) plant diversity and 2) forage quality and productivity (Pastoral Value - PV) of alpine summer pastures. Plant diversity (i.e. Shannon diversity index and species richness) and PV were affected in different ways by both factors, but they showed a hump-shaped relationship with pastoral management intensity. Plant diversity was mainly affected by environmental factors (elevation and total annual precipitation) rather than management intensity. Shannon index and species richness were lower at higher elevations and in locations with higher precipitation, and they were higher on steep sites and calcareous bedrock. However, management intensity had a noteworthy influence on plant diversity. PV was strongly affected by management intensity, whereas environmental factors had limited importance. Differently from plant diversity, PV was not elevation dependent as several vegetation communities with either a low and a high PV occurred within a large range of altitude. PV was higher on flattest sites, in sites with a low level of precipitation, and on calcareous bedrock. Our results highlighted that environmental factors are the main drivers of plant diversity in alpine pastures. Pastures are typically located at higher elevation, are less accessible, and lay in less homogeneous areas where the environmental constraints have a predominant effect on plant community development with respect to management intensity. Contrariwise, the influence of management intensity on PV suggests that an appropriate grazing management can enhance forage productivity and quality for livestock even in harsh environments.

Keywords: Species richness, Shannon diversity index, Alps, Landolt indicator values, grazing livestock, Generalized Linear Mixed Models, Generalized Additive Mixed Models

Highlights

- 3839 vegetation surveys were carried out across pastures of Western Italian Alps
- Plant diversity (PD) and forage Pastoral Value (PV) were computed
- The effects of management intensity and environment on PD and PV were assessed
- PD was mostly affected by environmental factors rather than management intensity
- Management intensity had a larger effect on PV if compared to environmental factors

1. Introduction

Semi-natural grasslands of European Alps are the result of millennial interactions between environmental factors, such as topography and climate, and human management (Bätzing, 2005). Alpine semi-natural grasslands can be grouped into two main categories on the basis of the management type: hay meadows and pastures. Alpine hay meadows are mainly managed by mowing and, most of the times they are also fertilized, while irrigation is an infrequent practice. Meadows are typically located in the valley floors, in the most accessible areas, on fertile soils, and over gentle slopes. They ensure good quality forage suitable for domestic herbivores during the period of vegetative rest, in the form of hay or silage. In some cases, alpine hay meadows are grazed once at the end of the summer (Marini et al., 2007). Alpine pastures, being located at higher altitudes, in the less accessible areas, on less fertile soils and rough terrains (Marini et al., 2011) are generally not suitable for hay-making and, consequently, they are exclusively managed by livestock grazing during summer. As a consequence of the interaction amongst human activities and mountain environment, hay meadows and pastures are an important natural heritage of European Alpine identity with a productive function and a high naturalistic value. Indeed, the higher plant-diversity habitats in European mountains areas are ascribable to meadows and pastures (Väre et al., 2003). Moreover they provide important ecosystem services, such as regulation and maintenance services (e.g. water purification, soil retention, etc.), provisioning services (e.g. food), and cultural services (e.g. nature-based recreation, eco-tourism, local identity, etc.) (Haines-Young and Potschin, 2018). However, socio-economic changes occurring since the middle of 20th century led to a progressive abandonment of agro-pastoral activities in mountain areas, with negative effects on such semi-natural grasslands. Either the reduction or the absence of management practices in semi-natural ecosystems resulted in a dramatic decline of plant diversity (Maurer et al., 2006), in an increase of oligotrophic species, and in an encroachment of dwarf shrubs and trees (Tasser and Tappeiner, 2002). Shrub and tree encroachment is a phenomenon largely occurring at the higher elevation (Tasser and Tappeiner, 2002), where alpine pastures are the main land use. This process reduced the herbage mass and nutritive values of semi-natural grasslands (Kestig et al., 2009; Marriott et al., 2004), with negative effects on the vegetation carrying capacity (i.e., the maximum stocking rate that will achieve a target level of animal performance, in a specified grazing system that can be applied over a defined time without deterioration of the grazing land - Allen et al., 2011). Therefore, to protect these threatened habitats, European policy makers included some hay-meadow and pasture habitats in the European Habitat Directive (92/43/CEE).

Understanding how abiotic environmental factors and human management result in vegetation composition of the semi-natural grasslands is fundamental to adopt appropriate strategies for the maintenance of a high level of both plant diversity and forage productivity and quality. Several studies assessed the relative importance of management and environmental factors on plant diversity, forage yield and quality, and plant species composition of hay meadows in the European Alps (Gusmeroli et al., 2013; Kampmann et al., 2008; Marini et al., 2008, 2007; Pierik et al., 2017) and in central European grasslands (Klimek et al., 2007).

Kampmann et al. (2008) carried out a research in the central Alps on permanent pastures located between 500 and 1300 m a.s.l. However, to date any research has been yet carried out on medium-high altitude pastures, even though they are the majority of alpine grasslands (Ellenberg, 1996). This lack of knowledge is mainly the result of difficulties to quantify the pastoral management intensity directly and effectively as compared to hay meadows. Cutting frequency and the amount of fertilizers applied are good descriptors of hay-meadow management intensity, and both the data are easily retrievable with direct interviews to farmers (Gusmeroli et al., 2013; Marini et al., 2007; Pierik et al., 2017). In general, the cutting frequency ranges between one and three cuts per year (rarely four), depending on altitude and intensity of fertilization. Fertilization occurs once or twice per year with farmyard manure or liquid manure and, occasionally once, with mineral fertilizers (Marini et al., 2007). Since mowing and fertilization are mechanically operated, the management intensity can be considered uniform across the meadow surface, as well as the effects on vegetation communities. With regards to pastures, livestock stocking rate, i.e. number of animals exploiting a given area over a specified period of time (Allen et al., 2011), can be used for the quantification of pastoral management intensity. It expresses an average value of the management intensity all over the pasture and its quantification is retrievable both from direct interview to farmers and from official veterinary service files. However, alpine pastures are generally rough and heterogeneous environments and livestock tend to prefer areas on gentler slopes, closer to water sources, and with a good forage quality and productivity, avoiding the less accessible, less comfortable, and low-quality forage areas (Homburger et al., 2015). This behavior results in an uneven spatial distribution of the stocking rate, i.e. of management intensity, especially when the livestock is free to roam. Sometimes, rotational grazing is used to enhance pasture exploitation by reducing livestock spatial selection. However, even under rotational grazing an uneven spatial distribution of the stocking rate can occur when large paddocks are used (Probo et al., 2014). Therefore, the average stocking rate cannot be a reliable descriptor of the management intensity at the scale at which vegetation composition changes (parcel or paddock scale). In these conditions, the use of proxies can be a valuable and reliable solution for its assessment (Pittarello et al. 2018).

Pastoral management is one of the most important drivers of the amount of nutrients in the soil of alpine pastures as their removal and accumulation strictly depend on livestock grazing and deposition of dung and urine, respectively (Jewell et al., 2007; Koch et al., 2018). Hence, nutrient balance in the soil is co-determined by nutrient outputs (forage intake) and inputs (livestock urine and fecal depositions). Even though, in alpine environments, the grazing livestock can remove nutrients from a large portion of the pasture and return them to few small patches (i.e. overgrazed areas characterized by a nitrophilous vegetation), an intensive pastoral management generally results in a high addition of nutrients. Vice-versa, a low management pressure results in a low addition of nutrients in the soil. This assumption is supported by Koch et al. (2018), who found a strong relation between the total number of GPS positions and the number of dung pats counted in surveyed plots, and by White et al. (2001), who found that the number of excretions was highly correlated

to the time spent by cattle in the same area. Based on this concept, the nutrient indicator value proposed by Landolt et al. (2010) (hereafter 'N Landolt') can be used as a proxy of pastoral management intensity. A value ranging from 1 to 5 is attributed to each plant species of a given vegetation community, and the mean value for that community can be computed either by weighting (Pittarello et al., 2016) or not weighting (Güsewell et al., 2012; Strebel and Bühler, 2015) single species values with their corresponding abundance. High average N Landolt values are related to vegetation communities occurring in nutrient-rich conditions, whereas low average N Landolt values are related to those occurring in nutrient-poor conditions. Indeed, Pittarello et al. (2016) found that vegetation communities receiving a low organic fertilization by grazing livestock had lower N Landolt values compared to those receiving a higher organic fertilization. N Landolt can be considered as a reliable and cost-effective proxy of fertilization rate and, therefore, of pastoral management intensity (Güsewell et al., 2012).

The forage productivity and quality can be expressed through the Pastoral Value (PV), which is a unique and synthetic index derived from sward botanical composition summarizing forage yield, quality, and palatability for livestock (Daget and Poissonet, 1969). Being an index taking the botanical composition into account, PV is more constant and less influenced by temporal fluctuations than other parameters of forage quality and quantity, such as the aboveground biomass (Daget and Poissonet, 1969). Because of its reliability, PV has been widely adopted in different environments such as Mediterranean forest lands (Bianchetto et al., 2015), Mediterranean oak wood pastures (Franca et al., 2018), Patagonian Steppe (Golluscio et al., 2015), Pampa of Argentina (Vecchio et al., 2019), and semi-natural temperate European grasslands (Fanlo et al., 2015; Gillet et al., 2016; Probo et al., 2016).

Based on a wide dataset of vegetation surveys carried out across the pastures of Western Italian Alps, the aim of the present research was to fill the gap of knowledge in the evaluation of the relative importance of management intensity and environmental factors (i.e. topography, climate, bedrock type) on 1) plant diversity and 2) PV of alpine summer pastures.

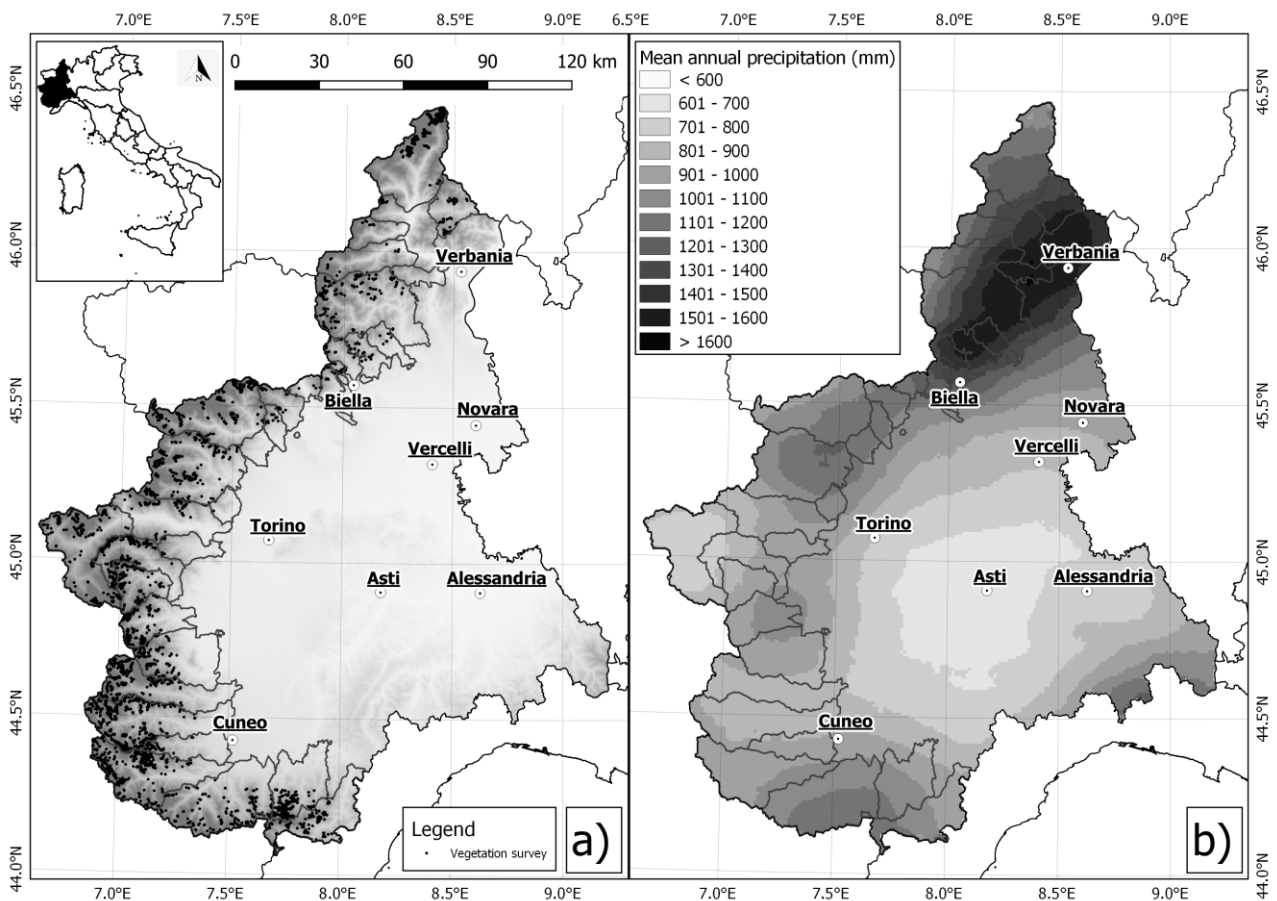
2. Material and Methods

2.1. Study area

The research was carried out across summer pastures of 32 alpine valleys of Western Italian Alps, Piedmont Region (Figure 1a). Pastures, mainly grazed by domestic livestock (i.e. cattle, sheep and goats), covered an area of more than 187.000 ha. The elevation ranged from 494 to 2912 m a.s.l., while mean total annual precipitation measured in the period 1977 – 2007 ranged from 640 mm to 1600 mm of western sectors and northern part, respectively (ARPA Piemonte, 2010) (Figure 1b). About 70% of study area extended on siliceous bedrock (mainly gneiss and granite), whereas the remaining 30% occurred on calcareous bedrock (mainly calc-schists, dolomite, and limestones) (Regione Piemonte 2006). Vegetation consisted of semi-natural pastures developed over a wide spectrum of soil nutrient conditions (e.g. from nutrient poor *Nardus*

stricta to nitrophilous *Rumex alpinus* vegetation communities), elevation (e.g. from low-land *Lolium perenne* to alpine *Carex curvula* and *Salix herbacea* vegetation communities), and water soil availability (e.g. from xero-thermic *Bromus erectus* to humid *Deschampsia caespitosa* vegetation communities) (Cavallero et al. 2007).

Figure 1 - (a) Distribution of 3839 vegetation surveys in the Western Italian Alps (represented on Digital Terrain Model). (b) Mean total annual precipitation map of Piedmont region. Grey lines represent the borders of the 33 Alpine valleys.



2.2. Vegetation surveys

Vascular plant species composition was analyzed in 3839 vegetation surveys performed between 2001 and 2007. Vegetation surveys were carried out in the 32 valleys of the Alpine area, each corresponding roughly to a catchment basin. The surveys occurred over a wide range of ecological conditions (i.e. thermic, intermediate, snow-bed, and shrub-encroached vegetation communities) and soil nutrient content (i.e. from oligotrophic to nitrophilous vegetation communities). Each of them consisted in a 25-m linear transect along which all plant species touching a steel needle at every 50 cm-interval were identified and recorded (Daget and Poissonet, 1971). Through this method occasional plant species were often missed and, therefore, a

complete list of all other plant species found within a 1-m buffer area around the transect line (vegetation plot) was also recorded (Probo et al., 2016). Floristic nomenclature followed Pignatti (1982).

The frequency of occurrence (f_i) for each plant species recorded in the linear transects was calculated by dividing the number of occurrences by 50, which was the total measurements per vegetation transect. Then, the f_i was used to compute the Species Relative Abundance (SRA_i) at each vegetation survey according to the following formula:

$$SRA_i = \frac{f_i}{\sum_{i=1}^n f_i} \cdot 100(\%)$$

By converting f_i to percentage, the proportion of different species was assessed (Daget and Poissonet, 1971). We attributed a SRA value of 0.3% (Tasser and Tappeiner, 2005) to all the occasional plant species not found along the linear transect but within vegetation plots.

2.3. Computation of response variables

Plant diversity. Species richness and Shannon diversity index were used to express plant diversity. Species richness was the number of plant species in each vegetation plot while Shannon diversity index (hereafter “H’”) was calculated for each vegetation survey according the following formula (Magurran, 1988):

$$H' = - \sum_{i=1}^{i=n} \left\{ \frac{SRA_i}{100} \cdot \log_2 \left(\frac{SRA_i}{100} \right) \right\}$$

where SRA_i is the SRA for the species i .

Pastoral Value (PV). An Index of Specific Quality (ISQ) was attributed to each plant species according to its productivity, morphology, structure, palatability and preference by livestock (Cavallero et al., 2007). The ISQ ranged from 0 (low-quality species) to 5 (high-quality species) (Daget and Poissonet, 1971). PV, which ranges from 0 (low) to 100 (high), was computed to quantify forage productivity and quality according to the formula of Daget and Poissonet (1969):

$$PV = \sum_{i=1}^n (SRA_i \cdot ISQ_i) \cdot 0.2$$

where ISQ_i is the ISQ value for the species i .

Descriptive statistics of response variables are shown in Table 1.

Table 1 - Mean, standard deviation of mean (SD), coefficient of variation (CV%), minimum, and maximum values of forage productivity and quality, plant diversity indexes, management intensity, and environmental variables of surveyed summer pastures of Western Italian Alps.

	Variable	Unit	Mean	SD	CV%	min	max
Response variables	Forage productivity and quality						
	Pastoral Value (PV)	-	20.7	9.48	45.82	0.0	63.5
	Plant diversity indexes						
	Species richness	-	34	12.5	36.76	5	88
	Shannon diversity Index (H')	-	3.7	0.66	17.84	0.9	5.5
Explanatory variables	Management intensity						
	N Landolt	-	2.5	0.34	13.49	1.7	4.2
	Climate						
	Total annual precipitation	mm	1013.70	166.37	16.41	725	1580
	Topography						
	Elevation	m	2033.9	373.83	18.38	494	2912
	Slope	°	20.7	9.78	47.20	0.3	56.2
	Southness	°	112.9	47.88	42.43	0.0	180.0

2.4. Computation of explanatory variables

Management intensity. N Landolt value (Landolt et al., 2010) was attributed to each plant species and the mean N Landolt was calculated for each vegetation transect using presence/absence data. N Landolt was considered as a proxy of pastoral management intensity according to Güsewell et al. (2012) and Pittarello et al. (2018).

Environmental factors. Topographic variables, namely elevation, slope, and aspect, were determined for each vegetation survey from a 10-m resolution digital elevation model (Regione Piemonte, 2008). Aspect was transformed into southness ($\text{southness} = 180 - |\text{aspect} - 180|$) to avoid circular variable issues (Chang et al., 2004). As climate proxy we used total mean annual precipitation of the period 1977 – 2007 determined for each vegetation survey on a 1-km resolution raster grid derived from long-term datasets of 386 weather stations spread over the region (ARPA Piemonte, 2010). Additionally, each vegetation survey was attributed to siliceous or calcareous bedrock based on Piedmont geological map (Regione Piemonte, 2006). Spatial analyses were carried out with QGIS 2.18.18 software (QGIS Development team, 2018) and SAGA (Conrad et al., 2015). Descriptive statistics for explanatory variables are reported in Table 1.

2.5. Data analysis

To carry out a preliminary exploration of the relations between vegetation composition and environmental factors, a multivariate constrained ordination approach was adopted. Three matrices were used: 1) a botanical matrix, containing the SRA of the most frequent species, i.e. species occurring in at least 1 % of the

vegetation surveys, 2) an explanatory variable matrix, including N Landolt, elevation, slope, southness, bedrock type, and total mean annual precipitation, and 3) a supplementary matrix, including species richness, H' , and PV. A preliminary Detrended Correspondence Analysis (Hill and Gauch, 1980) on the botanical matrix showed an axis length greater than four and a Canonical Correspondence Analysis (CCA) was therefore used (Ter Braak and Smilauer, 2002). A Mantel test (999 permutations) was performed prior to CCA to detect the multivariate correlation between the botanical and explanatory variable matrices. The CCA was carried out by using the botanical composition as first matrix and the management and environmental factors as secondary matrix. The third matrix was used to assess the relations of plant diversity and PV with vegetation composition and the explanatory variables. Pearson's correlation was computed amongst explanatory and supplementary variables, with the first axes of CCA explaining more than 80% of total variance.

Generalized Additive Mixed Models (GAMMs) and Generalized Linear Mixed Models (GLMMs) were used in sequence to assess the relative importance of management and environmental factors (i.e. explanatory variables) on species richness, H' and PV (i.e. response variables). The 'Alpine valley' in which vegetation surveys occurred was considered as random factor to account for spatial auto-correlation. A correlation analysis was performed on explanatory variables to exclude highly collinear variables ($r > |0.70|$) from subsequent analyses. For H' and PV, being continuous data variables, a normal distribution was specified when model residuals were normally distributed, otherwise a gamma distribution was used. Species richness, being a count data variable, was modeled with both Poisson and negative binomial distributions and best models were selected according to the lower Akaike Information Criterion (AIC).

GAMMs were performed to assess if the relations between response and continuous explanatory variables were described by either linear (i.e. negative or positive) or more complex (e.g. unimodal) relationships. Since Generalized Additive Models use non-parametric smoothers for fitting a curve through a scatterplot of two variables (Crawley, 2007), explanatory variables were modeled by setting the default non-parametric smoothed function [i.e. $s(x)$, where x is a specific explanatory variable]. To analyze the influence of Alpine valleys as random factor, it was treated as a smooth term, i.e. we set $bs = "re"$ (Wood, 2008). The shape of the relationships was evaluated through visual interpretation of GAMM output plots.

Before modelling data with GLMMs, continuous explanatory variables were standardized (Z-scores) to allow the assessment of their size effect by scrutinizing model parameters (β coefficients). A GLMM analysis was carried out for each response variable by including the linear terms of all explanatory variables. Moreover, when the shape of the relationship between response and explanatory variables resulting from GAMMs showed a curvature, a higher power (e.g. quadratic, cubic, etc. depending on the shape) of response variables was also included in the model. According to the GAMM output plots, the GLMM of species richness, H' , and PV included the quadratic term of N Landolt, whereas for all others explanatory variables a linear term was specified. To assess the pure importance of each single explanatory variable, the interactions amongst variables were not specified in the GLMMs. To estimate the variance explained by the models, marginal and

conditional R_{GLMM}^2 were computed. Marginal R_{GLMM}^2 measures the proportion of variance explained by fixed factors, whereas conditional R_{GLMM}^2 measures the proportion of variance explained by both fixed and random factors, i.e. by the whole model (Nakagawa and Schielzeth, 2013). GAMM and GLMM assumptions (i.e., homogeneity, normality, independence) were graphically checked using Pearson residuals (Zuur et al., 2009). All statistical analyses were performed using R software, version 3.5.2. (R Core Team, 2018). GAMMs were carried out with the 'gam' function of the 'mgcv' package (Wood, 2011). GLMMs were performed with the 'glmmTMB' function of 'glmmTMB' package (Benthem et al., 2017). Marginal and conditional R_{GLMM}^2 coefficients were computed using the function 'r.squaredGLMM', package 'MuMIn' v.1.43.6 (Barton, 2019). The Mantel test, DCA and CCA were run with the 'mantel', 'decorana' and 'cca' functions, respectively, of 'vegan' package (Oksanen et al., 2019).

3. Results

During the vegetation surveys, a total of 1013 plant species was recorded. The botanical and the explanatory variable matrices were significantly correlated at Mantel test ($r = 0.33$, $P < 0.001$), i.e. the grasslands with similar botanical composition were associated to similar management and environmental characteristics. Significant correlations among plant species and the explanatory variables were observed, with 87% of the variance explained by the first three axes of CCA (Figure 2a-b). The correlation matrix for explanatory and supplementary variables, and with the first three axes of CCA is reported in Table 2. Along axis 1, plant composition was mainly affected by the contrasting effect of management intensity (N Landolt) and elevation. Pastures more intensively managed were associated to higher PV ($r = 0.65$, $P < 0.001$), and they were generally located at lower elevation. Plant species associated to a high N Landolt and PV were those typical of meso-eutrophic vegetation communities, i.e. dominated by *Festuca pratensis* Hudson, *Phleum pratense* L., *Poa pratensis* L., *Taraxacum officinale* s.l., *Trifolium repens* L., and *Trisetum flavescens* (L.) Beauv. High-elevation pastures were dominated by snow-bed species (e.g. *Alchemilla pentaphyllea* L., *Salix herbacea* L., and *Salix retusa* L.) and by wind-exposed and cryophile swards on edges (e.g. dominated by *Carex curvula* All. and *Elyna myosuroides* Vill. Fritsch). The axis 2 separated plant species mainly along a slope gradient (Figure 2a). Species richness and H' had the highest level of correlation with axis 2 ($r = -0.47$; $P < 0.001$ and $r = -0.31$; $P < 0.001$, respectively). Plant species associated to steep slopes were those typical of thermic slopes (e.g. *Festuca scabriculumis* (Hackel) Richter, *Helictotrichon parlatorei* (Woods) Pilger, and *Sesleria varia* (Jacq.) Wettst.), shrub-encroached vegetation communities (e.g. dominated by *Juniperus nana* Willd and *Vaccinium myrtillus* L.), and species-rich vegetation communities (e.g. dominated by *Bromus erectus* Hudson and *Brachypodium rupestre* (Host) R. et S.). Axis 3 of CCA (Figure 2b), explaining the 15% of total variance, separated plant species occurring on siliceous bedrock and with a high level of precipitation (e.g. *Potentilla erecta* (L.) Rauschel, *Calluna vulgaris* (L.) Hull, and *Festuca tenuifolia* Sibth.) from those related to calcareous

bedrock and dry environments (e.g. *Astragalus danicus* Retz., *Helictotrichon arlatorei*, *Helictotrichon sedenense* (Clarion) Holub), and *Onobrychis montana* DC.).

Table 2 – Correlation matrix with Pearson’s coefficients amongst the first three CCA axes, explanatory, and supplementary variables. Only significant correlations (P<0.05) are shown.

		axis 1	axis 2	axis 3	N_Landolt	Precipitation	Slope	Southness	Elevation	Calcareous bedrock	Siliceous bedrock	Species richness	H'	PV
CCA axes	axis 1				0.87	0.24	-0.12	0.07	-0.69	0.16	-0.16	0.17	0.15	0.60
	axis 2			0.08	0.28	0.05	-0.40	-0.27	0.42	0.09	-0.09	-0.47	-0.31	0.24
	axis 3		0.08		-0.05	0.59	-0.08		-0.24	0.46	-0.46	-0.29	-0.30	-0.13
Explanatory variables	N_Landolt	0.87	0.28	-0.05		0.21	-0.24		-0.50	0.14	-0.14		0.06	0.65
	Precipitation	0.24	0.05	0.59	0.21			0.03	-0.45	0.39	-0.39	-0.20	-0.19	0.04
	Slope	-0.12	-0.40	-0.08	-0.24			0.24				0.18	0.16	-0.29
	Southness	0.07	-0.27			0.03	0.24		-0.03	0.09	-0.09			-0.05
	Elevation	-0.69	0.42	-0.24	-0.50	-0.45		-0.03		-0.25	0.25	-0.29	-0.17	-0.29
	Calcareous bedrock	0.16	0.09	0.46	0.14	0.39		0.09	-0.25		-1.00	-0.19	-0.17	0.04
	Siliceous bedrock	-0.16	-0.09	-0.46	-0.14	-0.39		-0.09	0.25	-1.00		0.19	0.17	-0.04
Supplementary variables	Species richness	0.17	-0.47	-0.29		-0.20	0.18		-0.29	-0.19	0.19		0.75	
	H'	0.15	-0.31	-0.30	0.06	-0.19	0.16		-0.17	-0.17	0.17	0.75		0.08
	PV	0.60	0.24	-0.13	0.65	0.04	-0.29	-0.05	-0.29	0.04	-0.04		0.08	

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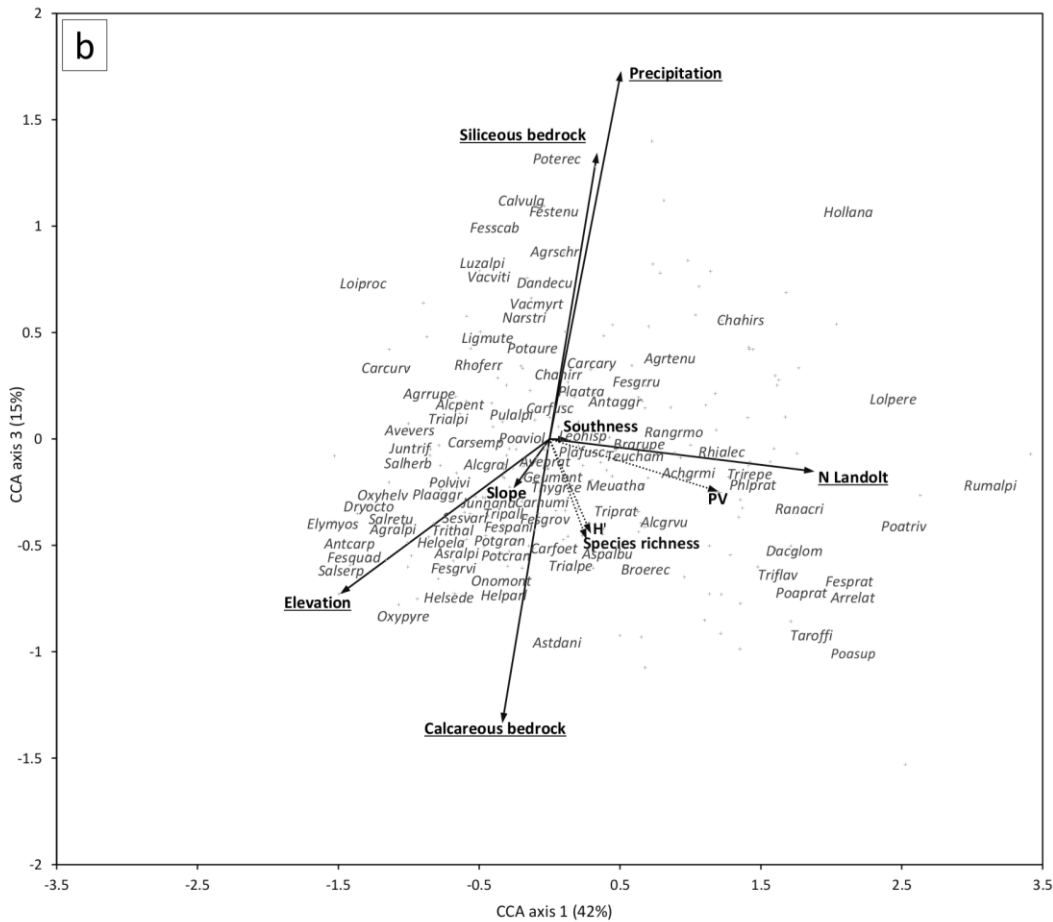
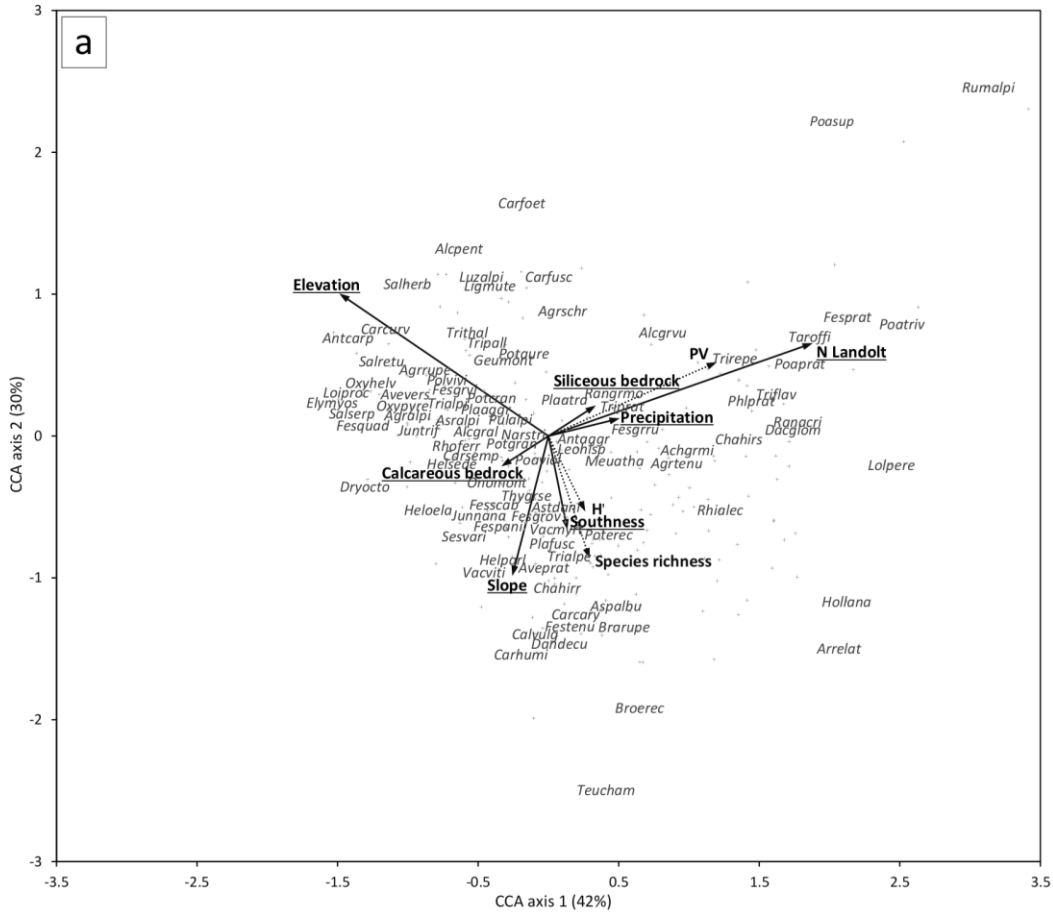


Figure 2 - Biplot ordination diagram of the canonical correspondence analysis (CCA) among species (codes and crosses), environmental (solid arrows) and supplementary (dashed arrows) variables, a) axes 1 and 2, b) axes 1 and 3. Only species with a species relative abundance (SRA) greater than 3% were indicated by codes while others were represented by crosses. Species codes (centered on scores): Achgrmi - *Achillea gr. millefolium*; Agralpi - *Agrostis alpina*; Agrrupe - *Agrostis rupestris*; Agrschr - *Agrostis schraderana*; Agrtenu - *Agrostis tenuis*; Alcgral - *Alchemilla gr. alpina*; Alcgrvu - *Alchemilla gr. vulgaris*; Alcprnt - *Alchemilla pentaphyllea*; Alogera - *Alopecurus gerardi*; Antcarp - *Antennaria carpathica*; Antaggr - *Anthoxanthum odoratum*; Arcuvau - *Arctostaphylos uva-ursi*; Arrelat - *Arrhenatherum elatius*; Aspalbu - *Asphodelus albus*; Asralpi - *Astragalus alpinus*; Astdani - *Astragalus danicus*; Aveflex - *Avenella flexuosa*; Aveprat - *Avenula pratensis*; Avevers - *Avenula versicolor*; Brarupe - *Brachypodium rupestre*; Broerac - *Bromus erectus*; Calvulg - *Calluna vulgaris*; Carcary - *Carex caryophyllea*; Carcurv - *Carex curvula*; Carfoet - *Carex foetida*; Carfusc - *Carex fusca*; Carhumi - *Carex humilis*; Carpilu - *Carex pilulifera*; Carrosa - *Carex rosae*; Carsemp - *Carex sempervirens*; Cartend - *Carex tendae*; Chahirs - *Chaerophyllum hirsutum*; Chahirr - *Chamaecytisus hirsutus*; Chebonu - *Chenopodium bonus-henricus*; Dacglom - *Dactylis glomerata*; Dandecu - *Danthonia decumbens*; Descaes - *Deschampsia caespitosa*; Dryocto - *Dryas octopetala*; Elymyos - *Elyna myosuroides*; Fesgrha - *Festuca gr. halleri*; Fesgrov - *Festuca gr. ovina*; Fesgrru - *Festuca gr. rubra*; Fesgrvi - *Festuca gr. violacea*; Fespani - *Festuca paniculata*; Fesprat - *Festuca pratensis*; Fesquad - *Festuca quadriflora*; Fesscab - *Festuca scabriculmis*; Festenu - *Festuca tenuifolia*; Geumont - *Geum montanum*; Helnumm - *Helianthemum nummularium*; Heloela - *Helianthemum oelandicum*; Helparl - *Helictotrichon parlatorei*; Helsede - *Helictotrichon sedenense*; Hollana - *Holcus lanatus*; Juntrif - *Juncus trifidus*; Junnana - *Juniperus nana*; Leohelv - *Leontodon helveticus*; Leohisp - *Leontodon hispidus*; Ligmute - *Ligusticum mutellina*; Loiproc - *Loiseleuria procumbens*; Lolpere - *Lolium perenne*; Luzalpi - *Luzula alpino-pilosa*; Meuatha - *Meum athamanticum*; Narstri - *Nardus stricta*; Onomont - *Onobrychis montana*; Oxyhelv - *Oxytropis helvetica*; Oxypyre - *Oxytropis pyrenaica*; Phlalpi - *Phleum alpinum*; Phlprat - *Phleum pratense*; Plaatra - *Plantago atrata*; Plafusc - *Plantago fuscescens*; Plaaggr - *Plantago gr. alpina/serpentina*; Poaalpi - *Poa alpina*; Poachai - *Poa chaixii*; Poaprat - *Poa pratensis*; Poasup - *Poa supina*; Poatriv - *Poa trivialis*; Poaviol - *Poa violacea*; Polbist - *Polygonum bistorta*; Polvivi - *Polygonum viviparum*; Potaure - *Potentilla aurea*; Potcran - *Potentilla crantzii*; Poterac - *Potentilla erecta*; Potgran - *Potentilla grandiflora*; Pulalpi - *Pulsatilla alpina*; Ranacri - *Ranunculus acris*; Rangrmo - *Ranunculus gr. montanus*; Rhialec - *Rhinanthus alectorolophus*; Rhofer - *Rhododendron ferrugineum*; Rumalpi - *Rumex alpinus*; Salherb - *Salix herbacea*; Salreti - *Salix reticulata*; Salretu - *Salix retusa*; Salserp - *Salix serpyllifolia*; Sesvari - *Sesleria varia*; Taroffi - *Taraxacum officinale*; Teucham - *Teucrium chamaedrys*; Thygrse - *Thymus gr. serpyllum*; Trialpe - *Trifolium alpestre*; Trialpi - *Trifolium alpinum*; Tripall - *Trifolium palleescens*; Triprat - *Trifolium pratense*; Trirepe - *Trifolium repens*; Trithal - *Trifolium thalii*; Triflav - *Trisetum flavescens*; Urtodio - *Urtica dioica*; Vacgaul - *Vaccinium gaultherioides*; Vacmyrt - *Vaccinium myrtillus*; Vacviti - *Vaccinium vitis-idaea*.

Since correlation coefficients higher than $|0.70|$ were not detected, all the explanatory variables were included in GAMMs and GLMMs. GAMMs of species richness and H' showed that all explanatory variables were significant, whereas for PV the only not significant variable was southness (Table 3). The visual interpretation of the shape of GAMM output plots pointed out clear unimodal relations between N Landolt and species richness, H' , and PV, whereas for all the other explanatory variables the relationships were linear (Figure 3). Plant diversity indexes showed a flat peak, i.e. a plateau in which highest species richness and H' values were reached within a wide range of N Landolt values (approximately from 2.3 to 3.3). Instead, PV peaked around a N Landolt value of 3.4.

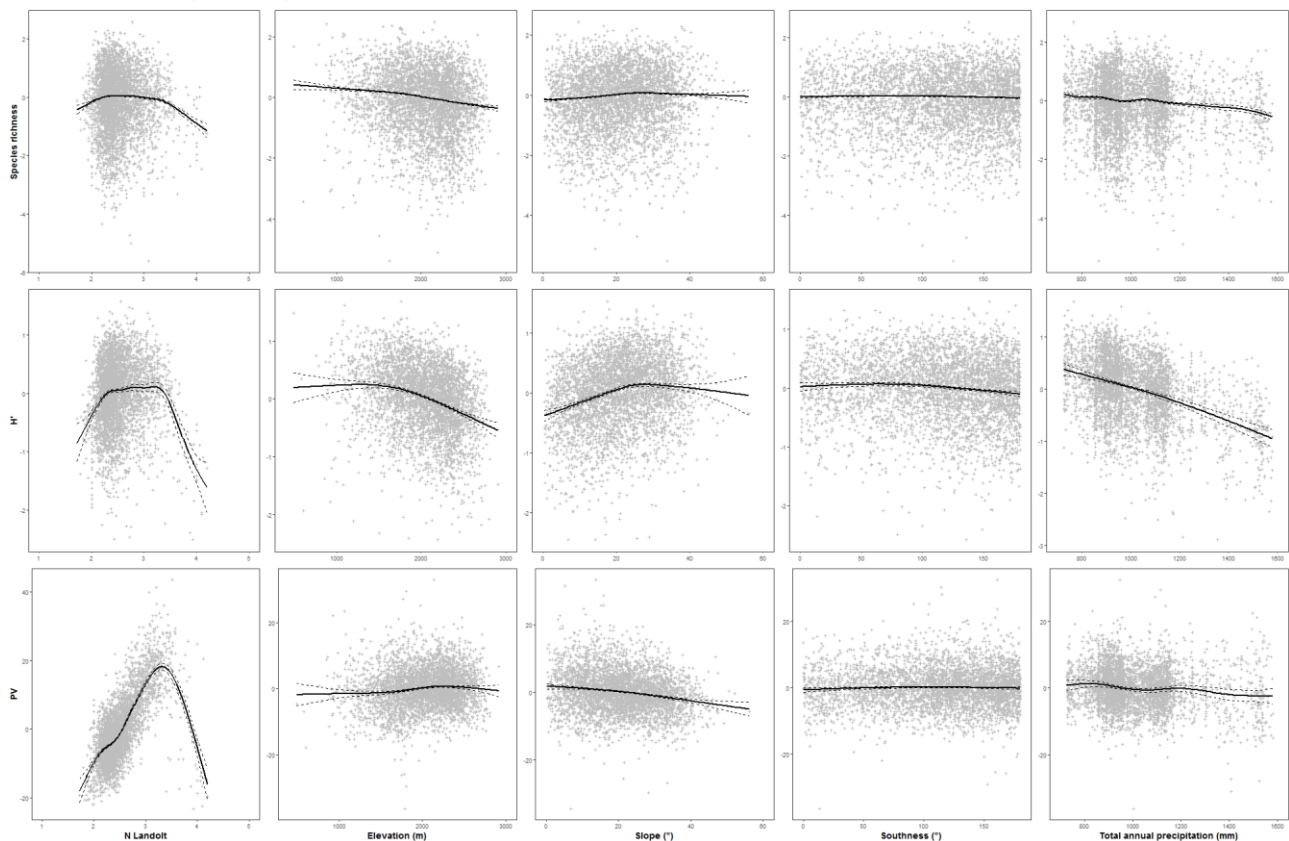
Table 3 - Results of Generalized Additive Mixed Models (GAMMs) showing the effects of management intensity (N Landolt), and environmental variables on species richness, Shannon diversity index (H'), and Pastoral Value (PV). Asterisks represent statistical significance: *, P < 0.001; **, P < 0.01; *, P < 0.05; n.s., not significant (P ≥ 0.05). edf: effective degree of freedom. Ref.df: reference degrees of freedom**

	species richness ¹				H' ²				PV ²			
	edf	Ref.df	Chi.sq	P	edf	Ref.df	F	P	edf	Ref.df	F	P
N Landolt	6.77	7.86	326.20	***	7.51	8.43	30.68	***	7.32	8.30	415.20	***
Elevation	4.03	5.04	552.46	***	3.05	3.87	54.04	***	3.89	4.88	6.96	***
Slope	4.91	6.05	220.22	***	3.74	4.70	44.00	***	2.19	2.80	39.10	***
Southness	2.80	3.48	26.13	***	2.58	3.21	10.52	***	1.97	2.46	1.68	n.s.
Total annual precipitation	7.97	8.71	153.78	***	2.01	2.55	51.04	***	5.42	6.59	2.29	*
Alpine valley (random factor)	25.91	31.00	822.94	***	25.06	31.00	7.45	***	25.98	31.00	6.93	***

¹ Family distribution: negative binomial

² Family distribution: Gaussian

Figure 3 - Relationships of management intensity (N Landolt) and environmental factors (elevation, slope, southness, and total annual precipitation) with each response variable: species richness, Shannon diversity index (H'), and Pastoral value (PV). The solid lines represent the predicted values by Generalized Additive Mixed Models (GAMM) whereas the dashed lines are the estimated 95 % confidence intervals.



GLMM results showed that all the explanatory variables significantly described species richness (Table 4). In order of importance the significant factors affecting species richness were elevation, total annual precipitation, bedrock type, slope, quadratic term of N Landolt, linear term of N Landolt, and southness. Species richness showed a negative relationship with elevation, total annual precipitation, and southness, while it was positively affected by slope, linear term of N Landolt, and calcareous bedrock.

GLMM showed that all explanatory variables significantly affected H' (Table 4). Total annual precipitation was the factor with the higher effect size, followed by elevation, bedrock type and the linear term of N Landolt (which had a similar absolute estimate value), slope, the quadratic term of N Landolt, and southness. Results showed that H' was higher on calcareous bedrock with respect to siliceous bedrock. Total annual precipitation, elevation, and southness had a negative linear relation with H' and the linear terms of N Landolt and slope were positively related to H' .

Results of GLMM showed that, in order of importance, the significant factors affecting PV were the linear term of N Landolt, slope, quadratic term of N Landolt, bedrock type, and total annual precipitation (Table 4). Elevation and southness did not show any significant effect. The linear term of N Landolt was positively related to PV while total annual precipitation and slope had a negative effect on it. According to GLMM estimates, PV was higher on calcareous than on siliceous bedrock.

The unimodal relationship showed by GAMMs was confirmed by all GLMMs, where both the linear and quadratic term of N Landolt were significant and had a positive and negative effect, respectively. An opposite sign of the two terms of the curve equation means that the increase of the values of the dependent variable is less than linear because the quadratic term is exerting a downward force on them. Therefore, the trend will reach a maximum level and then head downward.

Model residuals were normally distributed, and they did not show any trend when plotted against both fitted values and each predictor. The inclusion of 'Alpine valley' as random factor increased the explained variance in the GLMM of species richness, H' , and PV. Indeed, in all GLMMs the conditional R^2_{GLMM} (i.e. estimated explained variance by fixed + random factors) was always higher than marginal R^2_{GLMM} (i.e. estimated explained variance by fixed factors) (Table 4).

Table 4 - Results of Generalized Linear Mixed Models (GLMMs) showing the effects of management intensity (N Landolt) and environmental factors on species richness, Shannon diversity index (H'), and Pastoral Value (PV). Asterisks represent statistical significance: *, P < 0.001; **, P < 0.01; *, P < 0.05; n.s., not significant (P ≥ 0.05). Marginal and conditional R^2_{GLMM} measure the proportion of variance explained by fixed effects and the proportion of variance explained by both fixed and random effects, respectively. The column "Rank" indicates the rank of importance of each explanatory variable in the GLMM.**

	species richness ¹				H' ²				PV ²			
	Rank	Stand. β^*	s.e.†	P	Rank	Stand. β	s.e.	P	Rank	Stand. β	s.e.	P
Intercept		3.56	0.029	***		3.83	0.046	***		22.15	0.513	***
N Landolt	6	0.04	0.007	***	4	0.15	0.022	***	1	7.74	0.164	***
N Landolt ²	5	-0.06	0.003	***	6	-0.10	0.006	***	3	-1.15	0.069	***
Elevation	1	-0.14	0.006	***	2	-0.19	0.013	***		0.19	0.146	n.s.
Slope	4	0.06	0.005	***	5	0.12	0.010	***	2	-1.33	0.116	***
Southness	7	-0.01	0.005	**	7	-0.04	0.010	***		-0.03	0.112	n.s.
Total annual precipitation	2	-0.11	0.012	***	1	-0.25	0.022	***	5	-0.71	0.249	**
Bedrock type (Siliceous)	3	-0.08	0.010	***	3	-0.15	0.022	***	4	-0.81	0.254	**
Marginal R^2_{GLMM}		0.57				0.23				0.48		
Conditional R^2_{GLMM}		0.92				0.32				0.54		

¹Family distribution: negative binomial

²Family distribution: Gaussian

*Standardized coefficient of the variables

†Standard errors of standardized coefficients (β).

4. Discussion

The large amount of data gathered across the Northwestern Italian Alps, exploring a wide range of ecological, climatic, topographic, and management conditions, allowed us to assess the relative importance of environmental and management factors in affecting plant diversity (i.e. species richness and H'), forage productivity and quality (i.e. PV), and plant species composition of pastures. Plant diversity and PV were affected in different ways by environmental factors and management intensity, but both of them showed a hump-shaped relationship with the intensity of pastoral management as expressed by N Landolt. The wide range of N Landolt values at which plant diversity indexes peaked started from low values and ended up at medium values, suggesting that with a low to medium management intensity the species richness and H' can be maximized. Instead, PV peaked in correspondence of medium-high management intensity levels. These results confirm the findings of Pittarello et al. (2018) who investigated such relationships for the montane/sub-alpine and alpine pastures, separately.

Plant diversity

In our study, H' and species richness of alpine pastures were mainly affected by environmental factors rather than management intensity. Alpine pastures are located at high elevation, are less accessible, and lay in less homogeneous areas where the environmental constraints (i.e. short vegetative season, low temperatures, shallow soils, etc.) have a predominant effect on plant community development with respect to management intensity. However, management intensity had a remarkable importance in conditioning H' and species

richness, comparable to that of bedrock type and slope and even higher than southness. As found by Nervo et al. (2017), management intensity has a relatively higher importance in determining H' compared to species richness, since the addition of soil nutrient mostly affects the cover of plants belonging to specific ecological groups (e.g. oligotrophic and mesotrophic species) with respect to the number of plant species. Conversely, in hay meadows, Marini et al. (2007) and Marini et al. (2008) reported a stronger influence of management intensity on species richness when compared to environmental variables. As hay meadows typically occur where the environmental constraints have less importance compared to alpine pastures, the management practices and their intensity are the main drivers of plant diversity.

In the present study, elevation and total annual precipitation were the two factors which mostly affected plant diversity. H' and species richness were lower at higher elevation and in locations with higher levels of precipitation. It is known that as the altitude increases, the environmental constraints for plant species increase as well, hence the abundance of plant species functionally adapted to persist in the harsh conditions of alpine environments progressively decreases with the elevation (Körner, 2003). Precipitation in alpine environment can be both in liquid (i.e. rainfall) or solid (i.e. snow) states and it can represent a limiting factor for plant species growth when exceeding specific levels. An excess of precipitation determines an impoverishment of nutrients in the soil due to leaching, so that only the best-adapted plant species monopolize limiting resources and lead other species to a reduction or elimination (Grime, 1979; Huston, 1994). For instance, in alpine valleys associated with frequent and abundant precipitation (i.e. sub-oceanic areas), optimal conditions for the growth of *Nardus stricta* occur, whose presence results in an increase of its dense litter layer and of the competitiveness against other plant species (Chadwick, 1960; Pittarello et al., 2017b). Moreover, a high amount of snow can be a limiting factor for the growth of several plant species as the prolonged snow cover duration reduces the vegetative period (Körner, 2003).

Our results highlighted a higher plant diversity on steeper sites, supporting the findings of other research conducted in mountain areas (Kampmann et al., 2008; Marini et al., 2007; Zhang et al., 2018). Indeed, steep sites are characterized by a high number of microhabitats supporting the co-existence of plant species with different ecological niches. In addition, in these sites the low accumulation of nutrients hampers the dominance of few nutrient-demanding plant species. Plant species associated to steeper sites were those belonging to some habitats of Natura 2000 Network (Habitat Directive 92/43/CEE) characterized by a high plant diversity, such as habitat 6240* (Sub-pannonic steppic grasslands) (e.g. *C. humilis* and *T. chamaedrys*) and 6210* (Semi-natural dry grasslands and scrubland facies on calcareous substrates - Festuco-Brometalia) (e.g. *B. erectus*, *B. rupestris*, and *C. caryophyllea*).

According to GLMM results, plant diversity was lower on south-oriented slopes. This result was in contrast to Wohlgemuth et al. (2008), who found that south-facing slopes were more species-rich than those on northern slopes, based on data gathered across the whole Switzerland. However, in our research, for species richness and H' either, the effect of southness was the lowest amongst all explanatory variables as shown by

GAMM plots, which exhibited a flat relation between it and plant diversity. For these reasons, we would consider the effect of this factor negligible in conditioning plant diversity and PV in Alpine environments. Species richness and H' were higher on calcareous bedrock with respect to siliceous one, confirming the findings of several other studies carried out in mountain environments (Ewald, 2003; Partel, 2002; Wohlgemuth, 2002, 1998; Pittarello et al., 2017b). Calcareous substrates were widely available over large areas and for a long time during the Quaternary period, so that many species adapted to high-pH soils (Partel, 2002). Moreover, due to the larger number of microhabitats (Körner, 2003), grasslands on calcareous bedrock can host a higher number of plant species with different ecological needs if compared to grasslands on siliceous bedrock.

Pastoral Value

The management intensity had a larger effect on PV compared to environmental factors. Indeed, the effect of N Landolt (standardized $\beta = 7.74$) was more than five-fold higher than the one of significant environmental factors (total annual precipitation, slope, and bedrock type). Conversely, in alpine hay meadows the forage quality, of which PV is a proxy, was affected by ecological factors (Gusmeroli et al., 2013; Pierik et al., 2017). More specifically, Gusmeroli et al. (2013) found that management did not affect the forage quality, whereas Pierik et al. (2017) assessed that ecological factors were more important than management. However, in both studies, N Landolt was included amongst ecological factors rather than management ones. Landolt indicator values indicate habitat conditions (Landolt et al., 2010), but in some circumstances such conditions can be affected by an external factor. For instance, hay meadows receive nutrients addition mainly through manure and/or fertilizers, whereas alpine pastures through fecal and urine deposition by livestock. For this reason, in these cases the indicator value for nutrient content in the soil can be considered as proxy for management intensity, both in hay meadows and grazed pastures (Güsewell et al., 2012; Lonati et al., 2018). Indeed, Dietschi et al. (2007) and Peter et al. (2008) found that high levels of manure and/or fertilizer inputs and frequent cuts in mountain meadows were significantly related to high values of indicator for soil nutrients.

While plant diversity decreased with elevation, PV was not elevation dependent. Several vegetation communities with a low PV (i.e. lower than 10, on average) and with a high PV (i.e. higher than 30, on average) occurred from low to high altitudes. For instance, communities with a very low PV, such as *Molinia arundinacea* and *Festuca scabriculumis* dominated ones, occurred from 600 m to 1700 m a.s.l. and from 1500 to 2700 m a.s.l., respectively. Similarly, vegetation communities with a high PV, such as those dominated by *Festuca gr. rubra* and *Agrostis tenuis* and by *Dactylis glomerata* occurred from 500 m to 2600 m a.s.l. and from 800 m to 2300 m a.s.l., respectively.

Contrary to species richness, PV was negatively affected by slope as steeper areas of pastures are generally underexploited by livestock (Pittarello et al., 2017a) and therefore they receive a low nutrient supply through the deposition of urine and feces. Hence, plant species with medium-high ISQ, which typically are nutrient-

demanding (Pittarello et al., 2019), are less abundant in the steepest sites and the PV of vegetation communities is low.

Bedrock type and total annual precipitation were the two less important factors in explaining PV due to their low estimate coefficient values. PV was higher in pastures on calcareous bedrock as they likely host a lower proportion of unpalatable plant species compared to siliceous bedrock. Similarly to species richness, PV assumed high values when the level of precipitation was low. A high level of precipitation determines a nutrient loss due to leaching (Di and Cameron, 2002) and when the nutrient content in the soil is low, nutrient-poor plant species dominate over the nutrient-demanding ones (Chapin et al., 1986). The dominance of nutrient-poor plant species, such as *N. stricta*, which typically have low ISQ (Perotti et al., 2018; Ravetto Enri et al., 2017), could explain the low PV of pastures characterized by high precipitation. Indeed, in our study *N. stricta* vegetation community was amongst the most widespread ones, accounting for almost the 15 % of all vegetation surveys.

5. Conclusions

Our results highlighted that environmental factors, such as elevation and total annual precipitation, are the main drivers of the plant diversity in alpine pastures, even though management intensity had a noteworthy influence. Conversely, the Pastoral Value was strongly influenced by management intensity rather than by environmental factors, suggesting that even in harsh environments such as alpine pastures an appropriate grazing management can enhance forage productivity and quality for livestock. Grazing management is the only governable factor in alpine pastures to preserve plant diversity and to maintain a high level of forage productivity and quality. Consequently, a livestock stocking rate in equilibrium with the vegetation carrying capacity should be adopted to maximize both plant diversity and forage quality and productivity, while reducing the negative effects of over- and under-grazing on vegetation.

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