Soil–plant interactions in a pasture of the Italian Alps

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ABSTRACT

A detailed assessment of a pasture's functioning based on soil properties characterization, floristic composition, and "functional summary" by evaluating competitor–stress tolerator–ruderal (CSR) strategies is provided for a doline in Central Italian Alps.

A floristic survey was carried out at 35 sampling points, representative of the main topographic features, soil and vegetation types; the functional profile at the community level was evaluated by assessing for each species its Grime's CSR strategy; each point was characterized through soil profiles and topsoil (0-10 cm) sampling; pH, soil organic carbon and total nitrogen, available P, soil humus fraction, root density, bulk density, water content, and available water capacity were determined.

Our study showed i) a strong relationship between vegetation, soil properties, topography, and grazing; ii) a prevalence of stress-tolerant strategies; iii) the ability of plant strategy variation to reflect the ecological parameters; and iv) the vegetation potentiality to be an indicator of environmental spatial variability.

Keywords: alpine pasture; spatial variability; soil diversity; plant community; CSR strategy.

INTRODUCTION

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Natural alpine environments are often characterized by great spatial variability in their geomorphological, geological, pedological, and vegetation properties. This variability sometimes occurs at short spatial scales (Aalto et al. 2013) and is strongly conditioned by highly dynamic geomorphic processes.

In alpine ecosystems, soil–plant relationships involve a wide range of essential environmental issues by affecting ecosystem biodiversity, soil potentiality as a carbon sink, and biogeochemical processes, while also representing a valid indicator of the global warming response (Qin et al. 2007; Grand et al. 2016).

The relationships between soil and vegetation in alpine environments have long been studied (Isard 1986; Rose et al. 1988; Gensac 1990; Darmody et al. 2004; Lane et al. 2016). Some studies showed the importance of edaphic factors by investigating physical parameters (texture, soil thickness, surface characteristics; Rubio & Escudero 2000), chemical parameters (pH, but also soil fertility, in particular N and P; Anic et al. 2010, Ahmad et al. 2016), or water availability (Kammer et al. 2013). Other factors, such as climate (Zelnik & Čarni 2013), bedrock (Toure et al. 2015), and topographic aspects (absolute and relative altitude, slope, etc.; Zhang & HuGang 2013), have been investigated to explain vegetation variability and characteristics. Plant cover variability is also affected by management (chemical or organic fertilization, livestock use and grazing intensity (Marini et al. 2008; Teuber et al. 2013). In some cases it has been shown that the soil–vegetation relationship may be expressed in a synthetic way simply using the pedological taxonomy (Gensac 1990; Caria et al. 2013; Grand et al. 2016).

Ecosystem properties are reflected by variation in the adaptive traits of plant species, which may reflect the main ecological gradients shaping plant phenotypes (Di-az et al. 2016). For this reason, plant communities may be effectively described through their functional profile, allowing the comparison of ecosystems within a coherent framework. A successful scheme for the assessment of the functional strategies of plant species is Grime's Competitor–Stress tolerator–Ruderal (CSR) scheme (Grime 1977, reviewed by Grime & Pierce (2012).). CSR theory predicts that the strategies

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of plant species are an adaptive response to a three-way trade-off in the investment of resources between the ability to compete with neighbours (competitive strategy, C), tolerate stress (stress-tolerant strategy, S), or survive disturbance (ruderal strategy, R). The morpho-functional traits of each species can be used to assess its life strategy in the form of coordinates on the C, S, and R axes (Pierce et al. 2017). This theory provides a functional interpretation of plant communities in different ecological conditions and has been successfully used in alpine grasslands and pastures (Caccianiga et al. 2006; Pierce et al. 2007; Li & Shipley 2017). The use of community-weighted mean (CWM) trait values (i.e., values weighted by species abundance at the plot level) allows the application of such an approach at the community level (Garnier et al. 2004; Dubuis et al. 2013) following the mass ratio hypothesis (Grime 1998), which suggests that the traits of the most abundant species have a proportionally higher role in ecosystem functioning. However, except for Moog et al. (2005) on semi-natural grasslands in Germany or Bahr et al. (2012) and Ejrnaes & Bruun (2000) on dry prairies in Denmark, the CSR approach has usually been used without considering soil characteristics; in general, studies have rarely considered the interactions of all the mentioned factors and their relative importance in shaping vegetation patterns.

The objective of this study was to provide a detailed assessment of ecosystem functioning based on quantitative and analytical measurements of soil chemical and physical parameters, biomass and productive measurements, floristic composition, and a "functional summary" (Pierce et al. 2017) provided by an assessment of the CSR strategies; such an assessment was performed for an alpine pasture characterized by high soil and vegetation variability at a detailed scale to provide further insights into the capability of plant strategy variation to reflect the underlying ecological parameters and into the role of biodiversity in perspective of environmental changes

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MATERIALS AND METHODS

Study site

The study site (Figure 1) is a 1.5 ha doline in Valchiavenna (Central Italian Alps, Lombardy; 46° 27' 22" N, 9° 21' 05" E), between 1920 and 1950 m in altitude, used as a cattle pasture under-loaded and grazed mainly by dairy cows, heifers, and calves.

The mean annual air temperature, measured by three meteorological stations located inside or very near the study area and characterized by different exposure types (north, plain, and south), is 3.1 °C; the mean annual precipitation is about 1300 mm (45%–50% as snow). During the vegetative period (June–September), the mean air temperature is 10.3 °C, the mean precipitation is about 600 mm, and the mean solar radiation is 19.3 MJ m^{-2} d^{-1}.

The doline shows strong topographic variability (maximum height difference of 30 m): in the northern part there is a rounded summit, the south-facing steep slope is subjected to water and wind erosion, while the flat bottom is sometimes subjected to water stagnation. Close to the doline at the west and east, respectively, there are a rolling plain surface covered by earth hummocks and a low-marked impluvium zone.

The study site has a carbonate (marble, crystalline limestone) substrate and a discontinuous felsic (mainly schist) glacial cover. Due to the different thicknesses of glacial deposits and because of slightly developed periglacial phenomena (earth hummocks, nivation, gelifluction, ploughing blocks) in the absence of permafrost, the soil characteristics are very variable and the pattern of vegetation is intricate.

The main soil types (IUSS Working Group WRB, 2015) are Leptosols and Cambisols, to a smaller extent Umbrisols, and more rarely Podzols (Comolli et al. 2011).

The study area was characterized from the pedological, vegetation, and topographic points of view. Thirty-five sampling points were selected as representative of the main soil and vegetation types and of the main topographic features (Figure 1).

Vegetation sampling

A floristic survey was carried out at each sampling point to detect the occurrence and abundance of plant species and to outline the main plant communities. Vegetation sampling was performed during the growing season (20th July) through point-quadrat analysis. Thirty-five plots, each consisting of a 0.5 × 0.5 m quadrat with a 10 cm grid, were considered. At each node of the grid, the plant species touching the grid and the vertical line passing through the node were identified, and the number of contacts, which is a good indicator of relative abundance, was recorded. The overall number of contacts can also be considered a proxy for the biomass of the whole community (Redjadj et al. 2012). After the floristic survey, at each sampling point, a soil core sample was taken down to 10 cm (core diameter 10 cm; sampled volume 785 cm^3) for determination of the root biomass. Extraction of roots from the cores was carried out by presoaking the sampled soil overnight in a solution of EDTA (40 g L^{-1}) to facilitate washing. After that, roots were washed, picked out, separated into three diameter classes (<2 mm; 2–5 mm; >5 mm), and oven dried at 80 °C for 24 h to determine the following dry masses of the root biomass, expressed as g dm^{-3}: total (totRoots), <2 mm diameter (very fine, vfRoots), 2–5 mm diameter (fine, fRoots). There were no roots with diameter >5 mm. At 15 sampling point, roots were also sampled in the deeper layers (10–20 cm and 20–30 cm layers).

Twelve-year aboveground biomass data of the main types of the doline's vegetation are available; they were collected by mowing the grass at about 3 cm height within exclusion cages of 2 × 1 m. The mowing was performed at maximum vegetative development (between 15th and 30th July) and was repeated on the regrowth at the end of the season (September).

The functional profile of each vegetation type was evaluated by assessing for each species its Grime's CSR strategy through the approach proposed by Pierce et al. (2017). Such an approach allows the assessment of the competitive, stress-tolerant, and ruderal components of a species' strategy, expressed as a percentage, using a few leaf traits: the leaf area (LA), leaf dry matter content (LDMC), and specific leaf area (SLA). These parameters were calculated from the values of leaf fresh weight, leaf dry weight, and leaf area data obtained by previous studies (Caccianiga et al.

2006; Pierce et al. 2007; Pierce et al. 2017), an available comprehensive dataset (Cerabolini et al. 2010), and other data (Caccianiga and Cerabolini, unpublished).

For each sampling point, the CWM of the CSR average scores was calculated by weighting by the overall frequency of the observed species.

Soil sampling and laboratory analyses

Immediately after the vegetation sampling, besides the soil core sample for the determination of root biomass, another sample was collected down to 10 cm (core diameter 10 cm; sampled volume 785 cm^3) for soil organic carbon (SOC) content and bulk density (BD) determination, and other soil analyses. Sometimes (11 cases for roots and 3 cases for SOC) the sample depth was shallower than 10 cm due to the presence of the fractured rock substrate near the soil surface.

On the collected soil samples, the following parameters were determined: pH in water (pHw; soil-to-solution ratio 1:2.5); SOC and total nitrogen (totN) by dry combustion with a Flash EA 1112 NC-Soil elemental analyzer (Thermo Fisher Scientific CN, Pittsburgh, USA) after removal of carbonates, if present, by hot HCl treatment); soil texture (four fractions) by sieving and sedimentation after dispersion with sodium hexametaphosphate; and available P (avP) according to Bray & Kurtz (1945).

For BD determination, soil cores were oven dried at 105 °C for 24 h and weighed; in the case of soils containing rock fragments (>2 mm diameter), the soil volume and mass were proportionally reduced to obtain the fine earth BD. The SOC content was also calculated on an area basis (C_{stock}, kg m^{-2}, 0–10 cm depth) considering the soil BD and rock fragment volume.

The soil particle density (PD) was estimated according to PD (g cm^{-3}) = 2.65 − 0.02SOM (%), where SOM (soil organic matter) was calculated as SOC (%) × 1.724. The total soil porosity (totPor) was calculated from PD and BD.

Soil humus fractions were determined according to Anderson & Schoenau (2008) to obtain the carbon and nitrogen contents of fulvic acids (C_{FA}, N_{FA}), humic acids (C_{HA}, N_{HA}), and humin (C_{HUM}, N_{HUM}).

Throughout the vegetative season, the soil temperature at 5 cm depth and soil water content at 0–8 cm depth were measured every two weeks at each sampling plot, and the measurements were then averaged. The soil water content was measured using a portable TDR system (IMKO Micromodultechnik, GmbH, Ettlingen, Germany) and then converted (using the measured BD) to the water-filled pore space (WFPS).

The morphologic and topographic features of the doline were obtained from a digital terrain map (DTM) with a 2 m resolution.

The mean solar radiation for the vegetation period (June–September) was calculated for each sampling point in ArcGIS Desktop (ESRI 2011, Release 10) using the DTM.

After the topsoil sampling, a soil profile was opened at each of the 35 sampling points until a depth of about 100 cm or until the rock substrate. The soil was described and sampled by horizons (FAO 2006). Laboratory analyses were carried out on all the collected samples using the methods indicated above and, for Fe and Al fractionation only, using the official Italian methods (MiPAF 2000); soils were then classified using the WRB taxonomic system (IUSS Working Group WRB 2015). Based on the characteristics of the soil, taking into account the horizons A and B (thus excluding C and R), the available water content (AWC) was calculated for each sampled point; the empirical equations of Ghanbarian-Alavijeh & Millàn (2010) were used, considering the measured BD for the 0–10 cm layer and an estimated BD value for the underlying layer (Hallet et al. 1998).

The intensity of water erosion was qualitatively evaluated on the basis of the bare soil percentage by direct observation and using remote sensing images.

The list of all investigated parameters and their abbreviations are shown in Table 1.

Statistical analyses

A clustering procedure was used to identify the main vegetation types using the Chord distance and Unweighted Pair-Group Method using arithmetic Averages (UPGMA) as a clustering method. In order to test the relationships between soil properties and vegetation types, the linear mixed model

(LMM) procedure was performed (Bolker et al. 2009) to test for autocorrelation among the model residuals (Searle et al., 2009). If linear model assumptions on the residuals distribution were not satisfied, a Gaussian anamorphosis transformation (using ISATIS release 13.01 of software package Geovariances 2013) of the response variable was performed. To compare the –2 log likelihood fitting criteria of different models (spatial, nonspatial), a likelihood ratio test was performed.

Statistical analyses were performed using PROC MIXED (Littel et al., 2006) of SAS (release 9.4, SAS Institute). The spatial covariance function of residuals was iteratively determined using the statement REPEATED by estimating the partial sill, range, and nugget effect parameters (Littell et al. 2006). The statistical difference between means was assessed through contrast analysis using the instruction LSMEANS.

The relationships between soil properties, environmental variables, and plant species were investigated using canonical correlation analyses (CCA; CANOCO version 4.5). Only the most abundant plant species (i.e., those with the highest number of recorded contacts) were included in the CCA. We selected the five most abundant species for each of the five vegetation types; as some species dominated in more than one vegetation type, a total of 14 species was included in the analysis. The Monte Carlo permutation test was performed in order to assess both the significance of the environmental variables and the ordination axes. To reduce the data set complexity and noise in the variance components, one from each pair of highly correlated variables was removed from the analysis (Perez-Riverol et al. 2017).

The CSR life strategy was also interpreted by principal component analysis (PCA; CANOCO version 4.5) mapping C, S, and R coordinates, soil and environmental variables, and vegetation types into the same space to investigate their correlations.

RESULTS

Vegetation

The main vegetation types identified by cluster analysis were 1. communities dominated by bentgrass (*Agrostis schraderiana*) (B); 2. *Nardus stricta* pastures (N); 3. rich pasture dominated by tall grasses and forbs (*Phleum pratense, Poa alpina, Alchemilla vulgaris, Deschampsia caespitosa*) (RP); 4. *Sesleria varia* grasslands (SV); and 5. earth hummocks (EH) (Table S1).

The number of contacts was the highest for RP, followed by EH, B, N and SV; the average number of species was higher for SV and N than for the other vegetation types (Figure 2a,b).

The annual aboveground biomass production measured for the main vegetation types showed great differences (Figure 2c): RP vegetation produced more than the others; N pasture and earth hummocks gave intermediate biomass; while B and SV (considered together) were characterized by lower production. The average water content of the biomass was instead similar between the vegetation types (64%–68%; data not shown). The totRoots biomass (about 80% represented by vfRoots) averaged to 4.9 g dm^{-3}, with a minimum of 1.8 and a maximum of 13.2 g dm^{-3}. Most of the roots, except for those from earth hummocks, which have a more homogeneous distribution with depth, were amassed in the first 10 cm (Table 2), with no statistical differences among vegetation types.

The distribution of Grime's life strategies showed small variations among the investigated communities (Figure 3), within which the species mainly exhibited a stress-tolerant attitude (Table S1): the bentgrass community was mainly composed of different stress tolerators, with *Agrostis schraderiana* dominant*;* in *Sesleria varia* grasslands, species mainly showed stress-tolerant (S) (*Sesleria varia, Carex caryophyllea, Poa alpina, Helianthemum oelandicum*) and stress-tolerant–ruderal (SR) (*Hippocrepis comosa*) strategies; earth hummocks were characterized by few species, mainly stress tolerators (*Nardus stricta, Agrostis schraderiana, Vaccinium uliginosum*) and SR (*Trifolium alpinum, Avenella flexuosa*); *Nardus stricta* pastures included species showing an S strategy, with *Nardus stricta* dominant and *Festuca nigrescens* and *Agrostis schraderiana* much less frequent. Rich pastures were marked by a wider range of strategies, with dominance of the S species (*Agrostis schraderiana, Poa alpina, Festuca nigrescens, Deschampsia caespitosa*) and the presence

of other species which mainly exhibited relatively generalist strategies, such as *Alchemilla vulgaris* and *Trifolium pratense*, with stress-tolerant–competitive (SC) and R attitudes, respectively.

Soil

The representative soil types which characterized the investigated doline are shown in Table 3. They were mainly Leptosols and Cambisols, all rich in SOC content in the topsoil. Leptosols, shallow and lowly developed soils, were mainly located along steeper slopes with southern exposure and limited by carbonate bedrock, which influenced their base saturation and reaction (Rendzic Leptosols; 10–15 cm thick; base saturation (BS) > 50%; pH > 6.0). Where slopes were still steep but marbles were slightly deeper, we found a few thin soils with thick (25–35 cm) surface horizon, low BS, and high SOC (Leptic Umbrisols).

The most widespread soil type at the study site was Cambisol, slight to moderately developed soil, which mainly differed in thickness and saturation status. In flat and moist areas of the lower part of the doline, these soils were thick (until 100 cm deep) and with high base saturation (Eutric Cambisols), while along the slight slopes and in the high plain part, not as wet as the bottom of the sinkhole, we mainly found thinner soils, desaturated in bases (Dystric Cambisols) and rich in rock fragments. In areas with thick glacial cover rich in highly weathered schist, Cambisols passed gradually towards Podzols, with evidence of cryoturbation caused in the past by frost action; these soils, classified as Dystric Cambisols (Protospodic) – Entic Podzols, were deep, very acid, with strong silt content and few rock fragments, more compacted, and with less organic matter than the other soils.

When considering only the first layer (0–10 cm depth, but slightly less for three points), the SOC and Ntot contents were high and very variable, ranging between 2.2% and 13.6% and 0.2% and 1.2%, respectively (Table 4); the average C/N ratio (±SE) was 10.9 ± 0.2. The average avP content was 23.6 ± 2.9 mg kg^{-1}; the surface soil texture was mainly sandy loam; and the pHw varied over a wide range, from very acid (4.3) to neutral (7.1) values.

The average soil temperature (at 5 cm depth) during the grazing season was 16.1 °C, ranging between 12.7 and 19.3 °C; the WFPS (mean ± SE) was 42.6% ± 1.58%, varying between 24.3% and 59.9%.

Soil–plant interactions

At the top of the slope, where soil was poorly developed, thin, and limited by highly fractured bedrock, the typical vegetation was *Sesleria varia* grassland (Figure 4). The south-facing slope was moderate to high in terms of gradient (25%–51%) and soil erosion was often strong (activated by cattle grazing, but mainly due to runoff and snow and wind erosion); here, the distribution pattern of *Sesleria varia* and *Agrostis schraderiana* communities was very intricate, with patches often less than 1-meter-wide, making their separation difficult. However, soils under *Sesleria varia* grassland (Rendzic Leptosols) usually differed from those under bentgrass (Leptic Umbrisols) showing a neutral instead of acidic reaction and higher total porosity due to their low bulk density. In flat or gently sloped areas, particularly at the concave bottom of the doline, the prevailing vegetation was rich pasture, and soils were mainly deep Eutric Cambisols with intense biological activity by earthworms in the topsoil. Along water flow zones and near flat areas, *Nardus stricta* pastures spread over moderately deep and sometimes thin Dystric Cambisols, with low pH and common rock fragment content. In areas with weathered shale substrate, where soils were very acidic and deep, there was a significant presence of earth hummocks, with a pattern of small reliefs and depressions (about 40 cm difference between the top and bottom of the hummocks); the depressed areas are strongly compacted by cattle transit, resulting in water stagnation following prolonged rainy events.

Concerning surface soil characteristics, SV and EH greatly differed from the other vegetation types (Figure 5, Table S2). The *Sesleria varia* community significantly ($p < 0.05$) differed in terms of pH (the highest values), BD, and clay content (the lowest values) from the other vegetation groups; it exhibited, in common with EH, lower avP than the other vegetation types. EH was instead characterized by significantly ($p < 0.05$) higher BD, CN, and silt and lower SOC_{stock}, C_{HA}, and C_{FA} than the other communities. The vegetation types N, RP, and B mainly had similar values for most

of the investigated parameters, with intermediate values for CN, BD, pH, and textural fractions and highers value of SOC_{stock}, C_{HA}, and C_{FA} than EH and SV. Concerning the soil water content, the SV and B vegetation types were significantly drier than N and RP, while EH showed intermediate WFPS values.

The parameter with the highest discriminating power was SOC_{stock}. B, RP, and EH significantly differed from each other, with the highest values for B and the lowest values for EH; RP showed intermediate values, similar to SV and N.

The CCA resulted in high eigenvalues and cumulative percentage variances of the species–environment data, which were indicative of distinctive species assemblages across the different vegetation types (Table 5, Figure 6); the cumulative constrained variability explained by the first two axes was 60.7%. The species–environmental parameter correlations were 0.965 for axis 1 and 0.880 for axis 2. The main identified ecological gradient was that of soil pH, temperature, and erosion risk, marked by base-requiring species such as *Sesleria varia*, *Helianthemum oleandicum*, *Hippocrepis comosa*, and *Carex caryophyllea*. Axis 2 identified a second gradient coinciding with higher C/N ratio, BD, and silt content and lower C_{stock} with dominant *Vaccinium myrtillus* and *Avenella flexuosa*; to a lesser extent, *Trifolium alpinum*; *Phleum alpinum*, and *P. pratense* seem to be linked to soils characterized by higher water content and avP.

We conducted PCA to compare the CSR strategies with respect to soil and environmental properties. The first two factors explained 61% of the total variance: Factor 1 accounted for 41% and Factor 2 for 20%.

Despite the mean life strategy in the study site being stress tolerant, there was a clear distinction between conditions favoring ruderal, competitive, and stress-tolerant components (Figure 7). The stress-tolerant component was weakly correlated with WFPS and avP characterizing the resting areas; the ruderal component was associated to conditions favoring slow organic matter mineralization (high C/N) such as those in the earth hummock areas, while competitiveness was positively correlated with pHw.

DISCUSSION

We selected an alpine pasture that exhibited a wide range of plant communities and soil conditions. This study showed evidence of strong relationships between vegetation (floristic composition, vegetation types, and life strategies) and soil chemical (pHw, avP, SOC, CN) and physical (BD, AWC, texture) properties, climatic and pedoclimatic parameters (T, WFPS, Rad, AWC), topography (slope, erosion), and livestock grazing.

It has long since been demonstrated that mutual soil–plant relationships produce spatial patterning in soil properties and that individual plant performance and plant communities may respond to soil variability (Rubio & Escudero 2000; Casa & Castrignanò 2008; Ferré et al. 2014). In mountain areas, such variability is exacerbated by heterogeneity in the geomorphology and lithology of the soil parent material. In accordance with this, changes along the topographic gradient from dry calcareous to damp acidic soils, reflecting variations in soil fertility and conditions of stress and disturbance, were observed.

The investigated doline mainly exhibited stress-tolerant strategies, although the kinds of stress were different. In the upper part of the south-facing slope, on shallow soils, stress related to sub-alkaline reactions and dry conditions favored the presence of *Sesleria varia*, *Carex caryophyllea, Poa alpina,* and *Helianthemum oleandicum*. Biomass production was restricted, but biodiversity was high, in accordance with the "unimodal diversity–productivity relationship" or "humped-back model" which implies that the highest levels of biodiversity occur at intermediate levels of productivity rather than at the highest ones (Grime 2006; Adler et al. 2011). Where disturbances caused by erosion and cattle transit were higher, species with the stress-tolerant–ruderal (SR) strategy appeared. Grazing is known to have the potential to modify ecosystems and change their structure and function (Hobbs et al. 1996)—in this case, by promoting erosion through mechanical disturbance of the soil surface (Pietola et al. 2005).

With decreasing slope, in particular along the water flow areas, another stress-tolerant species, *Nardus stricta*, prevailed; this species is often dominant under acidic and nutrient-poor conditions (Landolt et al. 2010) and, thus, in communities characterized by low productivity, forage quality, and palatability. Bentgrass communities occurred nearby on convex slopes and, thus, under intermediate topographic conditions between *Nardus stricta* communities and those linked to steeper slopes. These communities share the overall ecological profile of *Nardus*-dominated pastures, with a slight displacement towards the C and R corners of the CSR triangle. For both communities, the dominant S strategy is an expected consequence of low productivity, the main driver of stress tolerance syndrome (Grime 2006).

In the flat zones at the bottom of the doline, where soils were deep, rich in nutrients, and damp, species with stress-tolerant (S), stress-tolerant–competitive (SC), and stress-tolerant–ruderal (SR) attitudes grew. Rich pastures were characterized by high biomass and a low number of species with high nutrient acquisition, high photosynthetic efficiency, and fast growth (Grime 2001); such species usually form tall and uniform stands with plastic biomass allocation to leaves and roots to maximize nutrient acquisition. Here, livestock rest, which increases the nutrient turnover rates and selective grazing, trampling, and soil compaction (Manier & Hobbs 2007; Jones et al. 2010). Patchy concentrations of nutrients, together with local stress factors such as temporary water stagnation, provide contrasting microsites for a range of life strategies; thus, dominant species include both S strategists, such as *Festuca nigrescens*, and species with a relatively high C component, like *Phleum pratense*. However, it should be considered that in spite of being the most productive and exhibiting the highest C component, these communities share the overall S strategy of the whole ensemble of investigated plant communities.

Despite the high aboveground productivity, the root biomass in the investigated surface layers of the rich pastures was not different from that of the other vegetation types. Cambisols of the stable areas were deep, but most of the roots were in the surface layer, and only a small part was deeper (10–30 cm); this is in accordance with what was found for tundra (an environment comparable with ours),

which was characterized by 80%–90% of the root mass occurring in the upper 0.3 m of the profile (Jackson et al. 1996). The lower root/shoot ratio in this community is probably linked to its higher nutrient status with respect to the other investigated communities, as this ratio is expected to increase under low nutrient availability because of greater allocation of nutrients to root growth and increased root longevity (Chapin III 1980).

The earth hummocks represented a separate case; this vegetation type developed above acidic soils in the level or near-level areas with low drainage and characterized by an alternation of raised and depressed areas due both to periglacial phenomena and livestock trampling, to which corresponded an alternation of stress-tolerant–ruderal and stress-tolerant strategies. The raised areas were characterized by shrub species of the subalpine heathlands (*Vaccinium uliginosum*), *Trifolium alpinum*, and high cover of *Avenella flexuosa*, to which the ruderal component is mainly due. The depressed areas, more compacted due to livestock transit and, thus, often damp after rainy events, showed flora which was instead comparable to that of a typical *Nardus stricta* grassland, with species tolerant to trampling and to high water availability, such as *Agrostis schraderiana*.

CONCLUSIONS

~~Our study provided a detailed description of i) soil types and characteristics, ii) vegetation types, iii) floristic composition, and iv) plant life strategies, assessing their relationships at a large spatial scale in an alpine pasture.~~ Overall, this study demonstrated the high spatial heterogeneity of soil properties and vegetation related to high variability in the topography, soil parent material, and pedoclimate. Moreover, vegetation pattern proved to be a valid indicator of environmental spatial variability resulting from all the factors working together; considering its spatial heterogeneity, and making use of its explanatory power for soil and morphology changes, it could be used to evaluate most of the biogeochemical processes related to the soil–vegetation complex. The use of CWM values effectively summarizes the overall ecosystem properties, even if they do not necessarily reflect the unique possible optimal strategies of the respective communities (Muscarella & Uriarte

2016), and a wide spectrum of strategies may occur in each plot, enhanced by the high small-scale variability of environmental parameters.

Our results highlight the importance of the use of complementary approaches to vegetation study, from quantitative data of the above- and belowground biomass to qualitative information provided by detailed floristic survey and functional approaches that may help to shed light on the processes underpinning community arrangement and functioning.

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Table 1. Investigated soil properties, environmental variables, vegetation, and their abbreviations.

Soil properties, environmental variables and	Unit	Abbreviation
Soil organic carbon content of the 0-10 cm mineral soil layer	%	SOC
Soil organic carbon stock of the 0-10 cm	kg m^{-2}	SOC_{stock}
C:N ratio of the 0-10 cm mineral layer		CN
pH in water of the 0-10 cm mineral layer		pH_w
Available phosphorus content of the 0-10 cm mineral layer	mg kg^{-1}	avP
Bulk density of the 0-10 cm mineral layer	g cm^{-3}	BD
Coarse sand content of the 0-10 cm minerale layer	g kg^{-1}	cSand
Soil porosity	%	totPor
Silt content of the 0-10 cm minerale layer	g kg^{-1}	
Clay content of the 0-10 cm minerale layer	g kg^{-1}	
Water filled pore space at 0-8 cm depth	%	WFPS
Total, very fine and fine total root biomass	g dm^{-3}	totRoots, vfRoots, fRoots
carbon and nitrogen content of fulvic acids	g kg^{-1}	C_{FA}, N_{FA}
carbon and nitrogen content of humic acids	g kg^{-1}	C_{HA}, N_{HA}
carbon and nitrogen content of humin	g kg^{-1}	C_{HUM}, N_{HUM}
slope	%	
Solar radiation	MJ m^{-2} d^{-1}	Rad
Soil temperature at 5 cm depth	°C	T
Available water content	mm	AWC
Intensity of erosion		Eros
Rich pasture		RP
Earth hummocks		EH
Sesleria varia grassland		SV
Bentgrass		B
Nardus stricta pasture		N

Table 2. Total root density (g dm^{-3}) for each vegetation type in the three investigated layers.

	0-10 cm			10-20 cm			20-30 cm	
Vegetation	N	Mean	Std. Err.	N	Mean	Std. Err.	N	Mean	Std. Err.
B - Bentgrass	9	5.17	0.80	3	1.56	1.26		-	-
RP - Rich pasture	10	5.35	0.70	4	0.99	0.60	4	0.93	0.30
SV - *Sesleria varia* grassland	5	8.16	1.97	3	1.56	1.26		-	-
EH - Earth hummock	4	8.04	2.17	4	3.83	1.42	4	1.46	0.30
N - *Nardus stricta* pasture	7	6.20	0.95	3	0.99	0.28	3	1.39	0.28

Table 3. Main properties of representative soil profiles (taxonomy according to IUSS Working Group WRB, 2015).

Horizon	Depth (cm)	Colour (moist)	Rock fragments	Structure	Roots	pH H_2O	SOC (g kg^{-1})	C:N ratio	Textural class	Notes
Soil profile #1 – Leptic Umbrisol (Siltic) (representative of bentgrass vegetation)										
A1	0-11	10YR 2/1	few, f	granular, f	common, vf-f	4.1	116	10.3	silty loam	
A2	11-27	10YR 3/3	many, m-f	sub. blocky, f-m	very few, vf-f	5.0	54	8.9	silty loam	
R	27+									fractured marble
Soil profile #2 – Dystric Leptic Cambisol (Humic) (representative of *Nardus stricta* pasture)										
A	0-7	10YR 2/1	absent	granular, f	common, vf-f	4.9	126	11.6	loamy sand	
BAw1	7-15	10YR 3/2.5	common, vf-f	sub. blocky, f	few, vf-m	4.7	40	10.4	silty loam	
BAw2	15-42	10YR 3.5/4	common, vf-f	sub. blocky, f	few, f	5.3	27	11.5	sandy loam	
R	42-60		abundant, vf-f	single grain	very few, vf					fractured marble
Soil profile #3 – Eutric Cambisol (Humic, Loamic) (representative of rich pasture vegetation)										
Ah	0-5	10YR 2/1	absent	granular, f	common, vf-f	5.7	82	10.5	loam	earthworms
A	5-15	10YR 3.5/3	few, vf-f	granular, m	very few, mf-f	5.5	31	9.2	loam	
Bw1	15-26	10YR 4/4	few, vf-f	sub. blocky, f-m	very few, vf	5.7	15	10.0	loam	
Bw2	26-34	2.5Y 4.5/4	few, vf-f	sub. blocky, f-m	very few, vf	6.0	14	9.8	loam	
C1	34-55	2.5Y 5/4	common, vf-m	massive	very few, vf	5.9	3		loam	
C2	55-95	2.5Y 5/3	common, vf-m	massive	absent	6.0	2		loam	
Soil profile #4 – Rendzic Leptosol (Humic) (representative of *Sesleria varia* grassland)										

A1	0-3	10YR 2/1	common, vf-f	granular, f	many, vf	6.3	114	9.8	sandy loam	
A2	3-10	10YR 2/1	frequent, vf-m	granular, f	few, vf	6.7	70	9.3	sandy loam	total carbonates: 3 g kg^{-1}
R/A	10-40	10YR 2/3	abundant, f-vc			7.2	62	9.1		fractured marble; total carbonates: 420 g kg^{-1}
Soil profile #5 – Dystric Cambisol (Humic, Siltic, Relictiturbic, Protospodic) (representative of earth hummocks vegetation)										
A	0-5	10YR 3/3	absent	granular, m	common, vf-m	4.5	43	10.2	silty loam	
AB	5-11	10YR 3.5/4	absent	granular, m	few, vf-m	4.3	29	10.2	silty loam	
Bw (Bs)	11-30	10YR 5/5	few, vf	sub. blocky, m	few, vf-m	4.4	11	8.5	silty loam	
CB1	30-55	10YR 5/6	few, vf	platy (lithogenic)	very few, vf-f	4.7	1		silty loam	
CB2	55-80	1Y 5/6	common, vf	platy (lithogenic)	very few, vf	5.9	0		silty loam	
C	80-120	2.5Y 5.5/6	many, vf-m	massive	absent	7.6	0		sandy loam	total carbonates: 351 g kg^{-1}

Legend for rock fragments, structure and roots: vf: very fine; f: fine; m: medium; c: coarse; vc: very coarse. Textural classes according to Soil Survey Division Staff (1993).

Table 4. Main statistics of soil properties in the 0–10 cm layer. For abbreviations of variables, see Table 1.

	N	Mean	Median	Minimum	Maximum	Std. Dev.	Std. Error	Coeff. Var.(%)
Slope	35	22.31	25.00	0.00	51.00	18.11	3.06	81
BD	35	0.71	0.70	0.41	1.02	0.14	0.02	20
totPor	35	70.06	70.66	60.29	81.14	5.09	0.86	7
pHw	35	5.1	4.8	4.3	7.1	0.7	0.1	14
SOC	35	8.0	7.8	2.2	13.6	2.7	0.4	34
totN	35	0.8	0.8	0.2	1.2	0.3	0.1	36
CN	35	10.9	10.9	8.7	14.2	1.1	0.2	10
C_{FA}	35	11.56	11.45	4.85	17.51	2.86	0.48	25
C_{HA}	35	20.95	21.18	5.11	32.36	6.91	1.17	33
C_{HUM}	35	41.19	40.34	12.51	80.76	16.06	2.71	39
N_{FA}	35	1.14	1.07	0.48	1.69	0.32	0.05	28
N_{HA}	35	2.00	1.99	0.27	3.25	0.72	0.12	36
N_{HUM}	35	3.35	3.14	0.76	6.77	1.52	0.26	45
avP	35	23.57	20.41	2.86	67.48	17.36	2.93	74
Sand	35	556	582	355	781	89.09	15.06	16
Silt	35	372	363	178	554	81.42	13.76	22
Clay	35	72	72	41	106	15.41	2.61	21
T	35	16.1	15.9	12.7	19.3	1.9	0.32	12
WFPS	34	42.6	42.5	24.3	59.9	9.2	1.58	22

Table 5. Canonical correlation analysis (CCA) for the 14 most abundant plant species in relation to the considered environmental variables (soil properties of the 0-10 cm layer). Marginal (Lambda1) and conditional (LambdaA) effect scores (variance partitioning) are reported. P: ** < 0.01; * P < 0.05; + P < 0.1; ns= not significant. For abbreviations of variables, see table 1.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues:	0.484	0.358	0.193	0.111
Species-environment correlation:	0.965	0.880	0.778	0.808
Cumulative percentage variance of species data and species-environment relation:	34.9	60.7	74.6	82.7
Variable	**Lambda1**	**LambdaA**	**P**	**F**
pH_w	0.42	0.42	**	8.62
CN	0.23	0.24	**	5.74
Eros	0.41	0.14	**	3.79
Silt	0.21	0.11	*	2.95
WFPS	0.12	0.07	+	2.00
Rad	0.11	0.07	*	2.07
T	0.17	0.06	+	1.88
SOC_{stock}	0.18	0.06	ns	1.66
C_{HUM}	0.3	0.04	ns	1.33
avP	0.23	0.04	ns	1.27
Slope	0.19	0.04	ns	1.14
Clay	0.13	0.03	ns	1.13
C_{FA}	0.17	0.03	ns	0.89
AWC	0.12	0.02	ns	0.65
BD	0.2	0.02	ns	0.44

Figure 1. Study area: a) geographic position of the study area; b) the doline; c) the earth hummock vegetation; d) locations of the sampling points.

Figure 2. Vegetation types of the investigated doline: a) number of contacts; b) number of species; and c) aboveground biomass (2006–2018).

SV: *Sesleria varia* grassland; RP: reach pasture; N: *Nardus stricta* pasture; EH: earth hummocks; B: bentgrass.

Figure 3. Functional profiling through Grime's CSR model (R: ruderal strategy; C: competitive strategy; S: stress-tolerant strategy) for each sampling point of the investigated vegetation types (SV: *Sesleria varia* grassland; RP: reach pasture; N: *Nardus stricta* pasture; EH: earth hummocks; B: bentgrass).

Figure 4. Schematic representation of soil–plant relationships along a topographic transect in the investigated doline. The dotted line approximately represents the depth of the substrate.

B: bentgrass; RP: reach pasture; SV: *Sesleria varia* grassland; EH: earth hummocks; N: *Nardus stricta* pasture.

Figure 5. Box plots for the comparison of soil properties among vegetation types (B: bentgrass; RP: reach pasture; SV: *Sesleria varia* grassland; EH: earth hummocks; N: *Nardus stricta* pasture).

Different letters indicate statistically significant differences ($p < 0.05$) in the response variable among vegetation types in the mixed model.

For abbreviations of variables, see Table 1.

Figure 6. CCA analysis of plant species in relation to the considered soil and environmental variables. Significant variables (at $p < 0.05$) are reported within rectangles.

Species abbreviations: *Agrostis schraderiana*: *Agr_schr*; *Alchemilla vulgaris*: *Alch_vul*; *Carex caryophyllaea*: *Car_car*; *Festuca nigrescens*: *Fest_nig*; *Heliantemum oleandicum*: *Hel_olea*; *Hippocrepis comosa*: *Hipp_com*; *Nardus stricta*: *Nard_str*; *Phleum alpinum*: *Phl_alp*; *Phleum pratense*: *Phl_prat*; *Poa alpina*: *Poa_alp*; *Sesleria varia*: *Sesl_var*; *Trifolium alpinum*: *Trif_alp*; *Vaccinum uliginosum*: *Vacc_uli*.

For abbreviations of variables, see Table 1.

Figure 7. PCA analysis. Plot of CSR components, considered soil and environmental variables, and vegetation types. For abbreviations of variables, see Table 1.