



Context-dependent effects of abandonment vs. grazing on functional composition and diversity of sub-Mediterranean grasslands

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Abstract: Though the interplay of grazing intensity and the availability of resources is a key driver in grassland composition, very few studies focused on trait changes after abandonment along productivity gradients. Through a comparative approach, we aimed to assess the context-dependent effects of long-term grazing cessation on functional composition and diversity in sub-Mediterranean grasslands. We hypothesized that variability of topography, soil and vegetation structure on a fine scale drives the trait-based dynamics after long-term abandonment, also influencing the patterns of functional diversity. On a calcareous mountain ridge of central Italy, we collected data on species cover and traits, site characteristics, soil depth and vegetation structure in 0.5 m × 0.5 m plots located in extensively grazed pastures and in grasslands abandoned since the early 1970s. We analysed patterns of species and traits in relation to environmental variables and management type, and trends in functional diversity (*FD*, Rao's quadratic entropy) along a productivity gradient. We found that grazing cessation reduced the overall *FD* and that the direction of species and trait response after long-term grazing cessation were affected, on a fine scale, by the soil depth / productivity gradient. In dryer conditions, species and functional responses were less affected by abandonment, and were devoted to resistance to both stress and disturbance. In abandoned pastures we detected a significant decrease in *FD* with increasing productivity, leading to a shift from functional strategies devoted to grazing avoidance and tolerance to those devoted to competition for light and resource acquisition. This trend was related to the filtering effect of coarse tall grasses, which spread in highly productive conditions. In grazed grasslands, we detected an overall increasing trend of *FD* with increasing productivity, confirming the key role of extensive grazing in maintaining high levels of *FD*.

Abbreviations: CAME – Herbarium of the University of Camerino, CSR – Competitor, Stress tolerator, Ruderal, CVRE – Cross Validation Relative Error, *FD* – Functional Diversity, ISA – Indicator Species Analysis, IV – Indicator Values, LU – Livestock Unit, MRT – Multivariate Regression Tree, PCA – Principal Components Analysis, RDA – Redundancy Analysis, SE – Standard Error.

Nomenclature for plants: Conti et al. (2005) and Greuter and von Raab-Straube (2008).

Introduction

Research conducted to understand processes underlying species assemblage in abandoned grassland has revealed a few general functional patterns (Díaz et al. 2007). In Temperate and Mediterranean climate, cessation of grazing is accompanied by the disappearance of short-statured and annual plants, early flowering species, and of species with prostrate or rosette morphology. Instead, species characterized by graminoid growth form, presence of storage organs, clonal ability, tall stature, late flowering, large seeds are generally fostered by grazing cessation (Pakeman and Marriot 2010, Peco et al. 2012, Catorci et al. 2013). Moreover, abandonment leads to a transition from functional strategies devoted to grazing avoidance and tolerance to those devoted to competition for light (Louault et al. 2005).

Very few studies focused on trait changes after abandonment along stress gradients, though a key driver in grassland composition is the interplay of grazing intensity and the availability of resources (Grime 2006). Essentially, highly productive habitats have exhibited a stronger correlation between grazing intensity and functional composition than the harsh ones, where a convergence of functional responses to grazing and resource limitation was detected (Rusch et al. 2009). Moreover, high habitat productivity enhances the spread of competitive tall grasses after abandonment (Grime 2001), thus influencing community assembly processes, since tall grasses decrease the amount of light other species can receive and change water regimes and available nutrients of soil (Catorci et al. 2011, Canals et al. 2014).

Since the range of functions provided by a community largely depends on the diversity of functional traits, a useful

approach for investigating ecosystem processes is the analysis of functional diversity (hereafter *FD*), which proved to be widely applicable to grazing systems (Diaz et al. 2007). Recent work has used *FD* to reveal changes in assembly processes along spatial gradients of resource availability and disturbance (e.g., Cornwell and Ackerly 2009, Mason et al. 2011). For instance, local increases in productivity produce a shift in the limiting factors for plant growth, from soil resources to light, thus increasing the intensity of aboveground competition (Tilman 1988). Competition, in turn, can increase similarity among co-existing species by excluding species bearing traits associated with low competitive ability (Mayfield and Levine 2010). Conversely, increased productivity, and hence increased competition for light, should enhance the abundance of fast-growing species, and lead to higher *FD* for vegetative traits (Mason et al. 2011, Spasojevic and Suding 2012, Gross et al. 2013), although the latter may not be true when competition for light is very intense (e.g., Bernard-Verdier et al. 2012). In fact, along a water availability gradient, de Bello et al. (2005) found that *FD* decreased both in more humid and arid conditions, whilst it peaked in intermediate ones, but they considered a relatively small trait set.

Disturbance type and intensity also play an important role as a determinant of the functional structure and *FD* of plant communities (e.g., Carmona et al. 2012, Catorci et al. 2014b). Generally, grazing or mowing cessation leads to a reduction of the overall *FD* (Peco et al. 2012). In fact, disturbance plays a key role in limiting the competitive exclusion of subordinate species by dominant ones (Grime 2001) and in achieving high *FD* values, because non-dominant species differ in many functional features from the dominant species (Thompson et al. 2005).

We focused our study on a traditional sub-Mediterranean pastoral landscape, where a centuries-old history of extensive grazing by domestic herbivores shaped the trait-related species assemblage at the plant community level. As we aimed to understand how environmental heterogeneity on a fine scale conditions *FD*, we set the existence of fine-scale heterogeneity as a basic assumption of our research. Indeed, plant-herbivore interactions are near a steady state, in which small perturbations or changes in disturbance intensity activate feedback loops that push the system back toward equilibrium (Bakker et al. 1983). Moreover, it was stated that plant-herbivores interactions mainly operate through filtering strategies devoted to herbivory tolerance or avoidance (Briske et al., 1996), whose effectiveness is determined by the system productivity level (at both wide and fine scale). This potentially leads to a patchy structure of the vegetation (Augustine and McNaughton 1998, Lessard et al. 2012), enhanced also by different levels of soil erosion (due to the herbivores treading and trampling) mainly correlated to the slope aspect and angle (Evans 1997). Obviously, micro-scale patterns of vegetation composition lead, in turn, to heterogeneous removal of plant material due to selectivity of domestic herbivores (Bakker et al. 1983). This results in a reciprocal fine-scale ecological interaction between herbivore and pastoral system

and reflects the effects of long-term grazing regimes on the plant assemblage at the community level.

As far as we know, there is little information on the effect of the fine-scale patchy structure of the soil features (soil depth as a proxy for water regimes and productivity in the study case) on the dynamic processes, after long-term grazing cessation. For this reason, through a comparative approach, we aimed to assess the context-dependent effects of long-term grazing cessation on functional composition and diversity in a traditional extensively grazed pastoral system. Our general hypothesis was that, after grazing cessation, variability of topography, soil and vegetation structure on a fine-scale drives the trait-based dynamic processes, also influencing the patterns of functional diversity.

Since harsh environmental conditions filter species having both drought resistance and avoidance ability, we expected that species composition is less affected by management type (extensive grazing vs. abandonment) in drier than in more productive conditions. Moreover, we expected that in productive conditions, grazing cessation reduces *FD* because promotes the spread of competitive tall grasses, while grazing promotes higher *FD* values, because fosters a greater diversity in strategies of resource acquisition, retention, and reproduction (Grime 2001).

To address these issues, we set the following questions: i) what is the role of soil, topographic and vegetation structure variables on a fine spatial scale as well as of management conditions (extensive grazing or abandonment) in species composition and the trait-related pattern of species assemblage, and ii) what are their effects on functional diversity? iii) how fine-scale gradients affect trends of functional diversity in grazed and abandoned conditions?

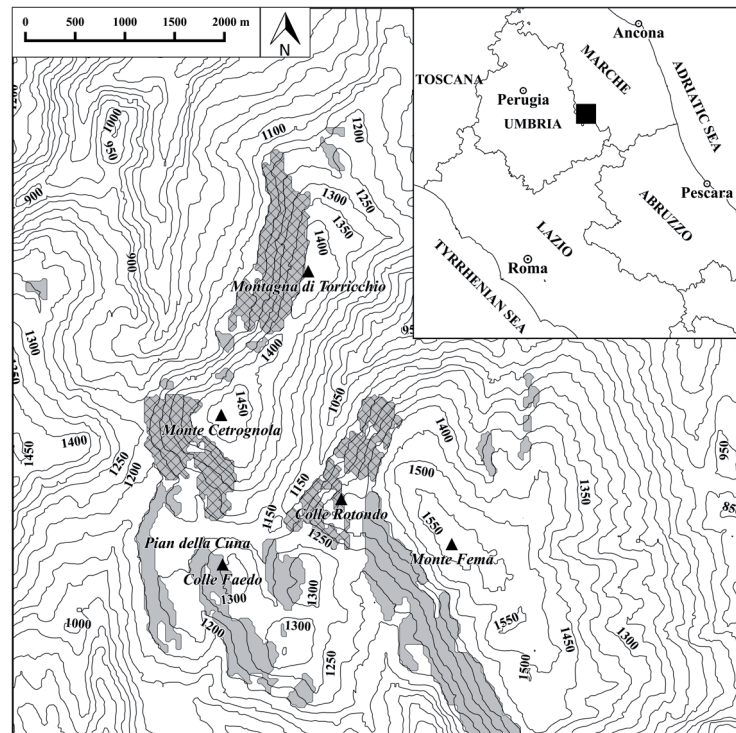
Materials and methods

Study area

The study area is located along the calcareous mountain ridge of central Italy (42°57'20"N; 13°01'00"E), between 1,100 and 1,400 m a.s.l., extended about 3,800 hectares (Figure 1). It lies within the Temperate region, near the border of the Mediterranean one and is characterized by alternation of winter cold stress and summer drought stress. The mean annual rainfall is about 1,200 mm, and the average annual temperature is 9–10°C. Soil depth ranges from about 4–5 to 50–60 cm, mainly depending on slope aspect and angle, which influenced the ratio of soil erosion (see Renard et al. 1991, Cerdà et al. 1995), mainly due to the past activity of domestic herds (Evans 1997).

The studied grassland vegetation (Cesaretti et al. 2009) belongs to the *Potentillo cinerariae-Brometum erecti* Biondi, Pinzi & Gubellini 2004 association (*Phleo ambigu-Bromion erecti* Biondi & Blasi ex Biondi, Ballelli, Allegranza & Zuccarello ex Biondi & Galdenzi 2012 alliance, *Scorzonero villosae-Chrysopogonetalia grylli* Horvatić & Horvat in Horvatić 1963 order, *Festuco-Brometea* Br.-Bl. & Tx. ex Br.-Bl. 1949 class). Beech woods of the *Fagetalia sylvaticae*

Figure 1. Location of the study area (indicated with a small square in the map in the upper right corner) and rationale of sampling design. Grey areas were extracted based on sample stratification criteria. The overlaid grid identifies the areas, each of which included grazed and abandoned grasslands, where $0.5\text{ m} \times 0.5\text{ m}$ plots were randomly chosen.



order compose the actual potential vegetation, thus the considered pastures are all secondary grasslands.

Homogeneous centuries-old history of extensive grazing by sheep and cows characterize the study site, but since the early 1970s grazing activities partially ceased because forbidden (inside the “Montagna di Torricchio” Natural Reserve) or because of farms abandonment. At present, the study area encompasses abandoned areas (since 40 years) and areas grazed by sheep and cows, with a quite homogeneous real livestock pressure of 1.0–1.2 livestock units per hectare (LU/hectare). In the grazed area, traditionally cattle are free to graze, while shepherds herd sheep. Pastoral activities start in June and last until the end of October (Cesaretti et al. 2009). Comparing the real livestock pressure (1.0–1.2 LU/ha) with the theoretical carrying capacity, it can be assumed that the pastoral system undergoes an optimal grazing pressure (Catorci et al. 2012b). Consequently, the seasonal above-ground phytomass is totally removed, hence there is no litter accumulation, and the expansion of dominant species is contained (Grime 2001). Instead, abandoned grasslands are undergoing dynamic processes and are in a transitional state. In the study area there are not large wild herbivores, except for a small number of roe deer, which cannot significantly contribute to the disturbance regime of pastures.

Data collection

To reduce the macro-environmental variability among the observational units (plots) we adopted the following stratifying criteria: geological bedrock (limestone); west-facing slopes (ranging from south-west to north-west); altitude ranging from 1,150 to 1,400 m a.s.l., and slope angles ranging from 10° to 35° . Moreover, we avoided both the upper and

the lower sectors of slopes. Inside the study area, an overall surface of 330 hectares satisfied such criteria; 185 of them were considered for the plots selection, because including both grazed and abandoned grasslands (see Figure 1). The abandoned areas are fenced and thus excluded from grazing by domestic herbivores.

Taking into account the findings of previous studies on the community assembly (e.g., Bartha et al. 2004, Wellstein et al. 2014), we assumed that fine-scale spatial resolution ($0.5\text{ m} \times 0.5\text{ m}$) offers the most appropriate scale of study to detect the fine-scale trait-based assembly rules.

Using a GIS generator of random points, we randomly selected the coordinates of the lower left-hand corners of $0.5\text{ m} \times 0.5\text{ m}$ plots inside the two management conditions. Plots falling on rocky outcrops, pathways, areas with dung, mole-hills, and clusters of shrubs and beech trees were not considered.

In all we surveyed 162 plots (80 in grazed and 82 in abandoned grasslands). The field surveys were carried out in June 2011. More specifically, we collected data in both grazed and abandoned plots before June, 20th, the effective beginning date of grazing in the site, which had been agreed with the farmers.

In each plot we recorded: plant species cover value (percent values, visually estimated), slope angle (vertical degree), soil depth (cm, five measurements per plot) litter cover value (percent values, visually estimated), bare soil cover value (percent value of soil covered by rocky debris and small stones, visually estimated), canopy height (cm, measured in ten locations randomly chosen in each plot), and above-ground phytomass ($\text{g}\cdot\text{m}^{-2}$ of dry matter), clipped at 0.5–1.0 cm from ground level and then oven-dried and weighed.

Following the indications of Díaz et al. (2004), de Bello et al. (2005), and Lavorel et al. (2007), we selected a set of traits to encompass the main plant functions related to competitive ability and resource acquisition (life span, horizontal and vertical space occupation, vegetative propagation type, plant height, leaf persistence), resource retention and stress tolerance ability (storage organs, leaf anatomy and persistence, seed weight), reproductive strategies (flowering period, pollination type, seed weight, and type of vegetative propagation), and response to disturbance (life form, type of space occupation and vegetative propagation, plant height, seed weight, and plant palatability). All traits were treated as categorical variables. Appendix 1 shows the list of traits and trait states considered and their respective data sources.

In addition, we collected information on life forms and CSR strategies.

Data analysis

Preliminary data processing. Data on soil depth and herb canopy height were averaged for each plot. The basic descriptive statistics of the environmental variables (slope angle, soil depth, bare soil cover, litter cover, canopy height, and above-ground phytomass) were performed.

To highlight the main environmental gradients acting in the study area and the correlation among the explanatory variables we ran a Principal Components Analysis (PCA), applied to the overall data set and to the two sub-sets composed of plots laid in grazed and in ungrazed grasslands.

To transform binary trait data (presence/absence) into quantitative data (i.e., aggregated cover values of each trait state), we multiplied the “relevés × species cover %” matrix by the “species × trait states” matrix to provide a “relevés × trait state cover %” matrix, which formed the basis for the following analyses. We performed the main descriptive statistics on the aggregated cover values of each trait state in grazed and abandoned plots.

We calculated the aggregated cover of tall grasses (tall graminoids, including tall sedges such as *Carex macrolepis*) in each plot.

To perform PCAs we used the R software (version 2.15.2, R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>) and the *vegan* R-package, version 2.0-10 (*rda* function).

Effect of fine-scale variables and management type on species assemblage and trait composition. To assess the influence of the explanatory variables (canopy height, litter cover, dry matter content, slope angle, bare soil cover, soil depth, and management type) on the species assemblage and identify homogeneous groups of relevés, a constrained clustering using Multivariate regression tree (MRT) analysis (De'ath 2002) with 100 iterations was executed on two matrices, namely “relevés × species (cover %)” and “relevés × explanatory variables”. To choose the optimal size of the tree, an overall error statistic (cross-validation relative error, CVRE) was computed for each test group and partition size (number of groups). For each partition size, the mean and standard er-

ror of all CVRE estimates were computed. We selected the smallest tree (i.e., a tree with fewer splits) within one standard error of the smallest CVRE value (Breiman et al. 1984).

To detect the indicator species set of each group, we performed the Indicator Species Analysis (ISA) on the matrix “relevés × species (cover %)”, using membership in MRT groups as grouping variable. An indicator value is calculated by multiplying the relative abundance of each item in a particular group and the relative frequency of the item occurrence in the sample of that group (Dufrière and Legendre 1997). The number of randomized indicator values higher than the observed ones are used to calculate the probability value (McCune and Grace 2002). We tested the statistical significance ($P < 0.05$) of the observed maximum Indicator Values (IV) using permutation tests with 999 iterations.

To characterize the species sets highlighted by ISA in relation to their life strategies we calculated the frequency distribution of life forms and CSR strategies for each group.

To identify the indicator trait states of each relevé group, we performed ISA on the matrix “relevés × trait state cover %”, using membership in MRT groups as grouping variable.

Basic descriptive statistics of the explanatory variables (mean ± standard deviation, median, 1st and 3rd quartiles) were calculated for each group highlighted by MRT analysis.

To perform MRT and ISA we used R software and the R-packages *mvpart* version 1.6-1 (*mvpart* function) and *labdsv* version 1.6-1 (*indval* function).

Effects of fine-scale variables and management type on functional diversity. We calculated the functional diversity of the two management types using an index based on the quadratic entropy of Rao (1982) that incorporates both the relative abundances of species and a measure of the pairwise functional differences between species. Rao defined quadratic entropy as

$$FD = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j$$

where FD is the sum of the dissimilarity in trait space among all possible pairs of species weighted by the product of the species' relative abundances, S is the number of species, d_{ij} is the distance or dissimilarity between the i -th and j -th species ($d_{ij} = d_{ji}$ and $d_{ii} = 0$), p_i and p_j are the proportions of i -th or j -th species in the sampling unit, so that $p_i p_j$ is the product of the species' relative abundances (Botta-Dukat 2005). In this study we assumed d_{ij} as the dissimilarity between two species, calculated with the formula $\sum_k (x_{i,k} - x_{j,k})^2 / 2$, where i and j are the i -th and j -th species, and k is the category index for each trait (Lepš et al. 2006). We computed FD for each trait by processing the matrices “species × trait states (presence/absence)” and “relevés × species (cover %)”. We also calculated a compound FD index in terms of multiple traits, doing a simple average of the FD values calculated from the single traits in each plot (Botta-Dukat 2005). The FD index was computed using a dedicated Microsoft Excel Macro (Lepš et al. 2006).

Being FD a generalized form of the Gini-Simpson diversity index (Lepš et al. 2006), it is characterized by strong

nonlinearity with respect to species addition, even when all species are equally common (Jost et al. 2010). To avoid possible misinterpretations of the results of statistical elaborations which assume linearity of data distribution (i.e., RDA and linear regression), we transformed Rao's quadratic diversity in effective number of elements, namely the number of elements in an equivalent community composed of equally common elements (trait states in this case). We made this transformation using the algorithm provided by Ricotta and Szeidl (2009) (i.e., $adj-FD=1/(1-FD)$), based on the idea that all equivalent species need to be equally abundant and maximally distinct (all pairwise species dissimilarities $d_{ij} = 1$ for all $i \neq j$, see Ricotta and Szeidl, 2009).

We performed the main descriptive statistics on *FD* values of traits in grazed and abandoned plots. We compared *FD* values of the two types of management using Wilcoxon Mann-Whitney tests. Results of tests were corrected for multiple comparisons using the Holm correction.

To model the responses of functional diversity driven by environmental and vegetation features at a fine spatial scale in the two management types, we performed a canonical redundancy analysis (RDA) of the "relevés \times trait transformed *FD* value" matrix, constrained by canopy height, dry matter and litter cover (productivity-related variables), slope, bare soil cover, and soil depth in the soil (topographic and soil features) and management type (grazing/abandonment). RDA axes were tested using permutation tests (999 iterations).

To run Wilcoxon Mann-Whitney tests and RDA we used the R-packages *stats* version 3.0-2 (*wilcox.test* function) and *vegan* version 2.0-10 (*rda* function), respectively.

Comparison of *FD* trends in grazed and abandoned conditions. As PCA depicted a main gradient linked to soil depth and phytomass production, we used PCA axis 1 object scores as a single composite variable. We examined in each management condition the relationships between this composite variable and transformed *FD* values of the overall trait set and of traits singly considered, and the abundance of competitive tall grasses, using nonparametric linear regression analyses when data did not meet the assumptions for simple linear regression. Significance of regressions was assessed using the F-test and the Theil-Sen test for simple linear regression and nonparametric linear regression, respectively. Results of tests were corrected for multiple comparisons using the Holm correction.

To perform linear regressions we used the R-packages *stats* version 3.0-2 (*lm* function) and the *mblm* version 0.12 (*mblm* function). To validate linear models assumptions we used the *gvlma*, version 1.0.0.2 R-package (*gvlma* function).

Results

Preliminary data processing

PCA axis 1, explaining 53.17% of the total variance, was mainly related to canopy height, dry matter content, soil depth, and bare soil cover (Figure 2a). PCA axis 2, explaining 16.35% of the total variance, depicted a secondary gradient

linked to slope angle. Canopy height, dry matter content, litter cover, and soil depth, were positively correlated to each other, while were negatively correlated to bare soil cover. Positive correlations between soil depth, and the productivity-related variables (canopy height, dry matter content, and litter cover) were found both in grazed and in ungrazed grasslands (Figure 2b,c), indicating the existence across the study area of a gra-

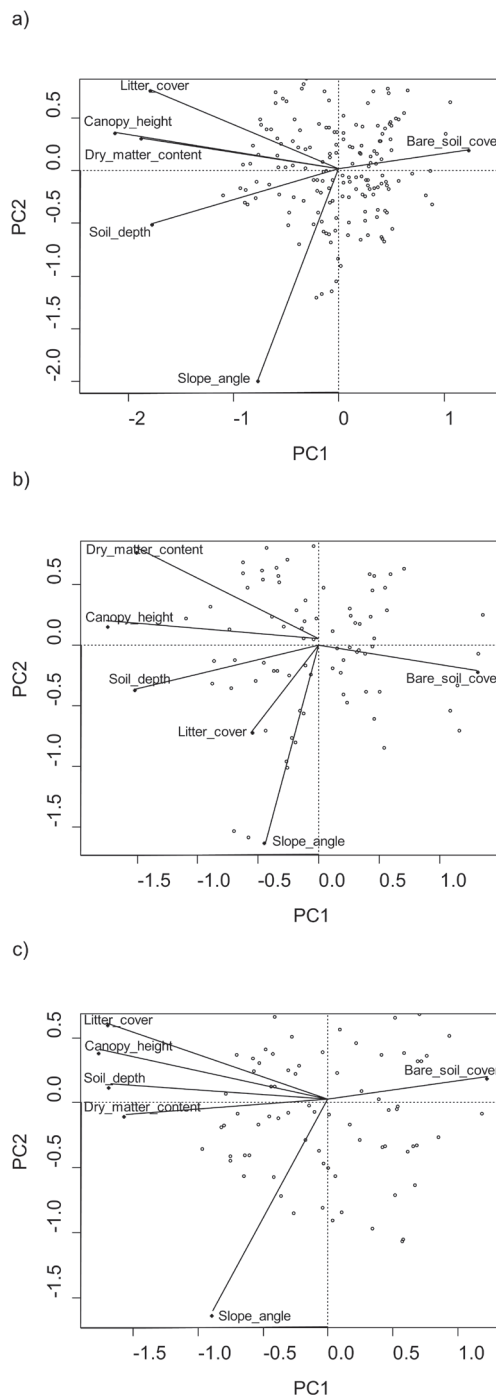


Figure 2. Principal Components Analysis biplot (scaling 2) for the environmental variables data set (soil depth, bare soil cover, litter cover, canopy height, dry matter content, slope angle), performed using all the plots (a), and two sub-sets composed of plots laid in grazed pastures (b) and in abandoned ones (c).

Table 1. Values of functional diversity index (quadratic entropy of Rao) in the two differently managed grasslands, computed for each trait and for multiple traits and significance values of differences between the two management conditions obtained using Wilcoxon Mann-Whitney test. Significant values after Holm correction are indicated in italics. SD: standard deviation.

Trait	Management type										<i>P</i> (1-tailed)
	Grazed					Abandoned					
	Mean	SD	Median	1st quartile	3rd quartile	Mean	SD	Median	1st quartile	3rd quartile	
Life span	0.0657	0.0594	0.0425	0.0171	0.0905	0.0127	0.0290	0.0000	0.0000	0.0058	<0.001
Vegetative propagation type	0.5961	0.0441	0.5905	0.5673	0.6249	0.5503	0.0947	0.5615	0.4899	0.5997	<0.001
Storage organs type	0.5358	0.0643	0.5156	0.4898	0.5679	0.5092	0.1203	0.5127	0.4290	0.5525	0.030
Leaf persistence	0.3948	0.0970	0.4023	0.3102	0.4601	0.3825	0.1272	0.3849	0.2704	0.4729	0.276
Leaf anatomy	0.5899	0.0884	0.6039	0.5355	0.6309	0.5632	0.1288	0.5670	0.4864	0.6254	0.020
Pollination	0.5144	0.0609	0.5204	0.4894	0.5478	0.4947	0.0789	0.5044	0.4779	0.5282	0.016
Seed weight	0.6353	0.0535	0.6403	0.5847	0.6654	0.5947	0.0918	0.6081	0.5371	0.6450	<0.001
Horizontal space occupation	0.6773	0.0534	0.6745	0.6391	0.7055	0.6274	0.0979	0.6251	0.5707	0.6741	<0.001
Vertical space occupation	0.7219	0.0519	0.7247	0.6846	0.7470	0.6726	0.1025	0.6726	0.6038	0.7208	<0.001
Palatability	0.4647	0.0569	0.4831	0.4444	0.4982	0.4295	0.1027	0.4562	0.3880	0.4908	0.001
Plant height	0.6069	0.0656	0.6179	0.5758	0.6445	0.5747	0.1042	0.5805	0.5109	0.6424	0.004
Flowering period	0.5763	0.0829	0.5763	0.5138	0.6246	0.5967	0.0933	0.6057	0.5414	0.6437	0.033
Overall trait set	0.5251	0.0337	0.5302	0.5120	0.5435	0.4882	0.0539	0.4968	0.4667	0.5192	<0.001

dent of productivity unrelatedly to management conditions. The basic descriptive statistics of the measured variables are shown in Appendix 2, showing, in particular, very low mean values of litter cover (\pm SD) in grazed plots ($1.3\% \pm 0.7\%$), confirming the existence in the past years of a quite homogeneous and total forage consumption by herbivores. Instead, the mean litter cover value (\pm SD) of abandoned plots was largely higher ($41.9\% \pm 33.5\%$).

The main descriptive statistics of trait states abundance in grazed and in abandoned plots are reported in Appendix 3.

Effect of fine-scale variables and management type on species assemblage and trait composition

MRT analysis generated a tree composed of three leaves (CVRE = 0.951, SE = 0.022) (Figure 3). The variable discriminating between the two branches in the first node was bare soil cover, while type of management marked the second partition. The first group (presence of bare soil) was composed of both grazed and abandoned plots; the two subgroups (absence of bare soil), were composed of grazed or abandoned plots respectively.

For each group, Appendix 4 shows the descriptive statistics of environmental and vegetation features, the indicator species and the indicator traits, as well as the characteristics of the indicator species with regard to life forms and CSR strategies. Plots with bare soil showed lower soil depth, dry matter content, and canopy height values than the other groups. Chamaephytes (suffruticose and reptant) were highly represented. In plots without bare soil, grazed conditions were characterized by scapose therophytes and scapose or rosulate hemicryptophytes; abandoned conditions by caespitose hemicryptophytes, suffruticose and succulent chamaephytes.

The presence of bare soil, linked to lower soil depth values, favoured stress tolerant and ruderal species; in plots without bare soil, thus with higher soil depth values, grazing fostered the CSR-strategists, while abandonment promoted competitive and competitive-stress tolerant species.

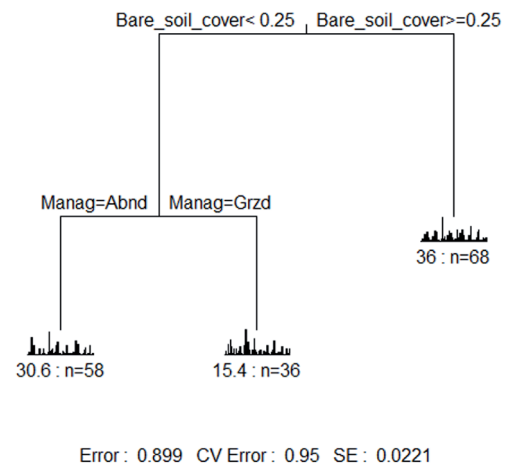
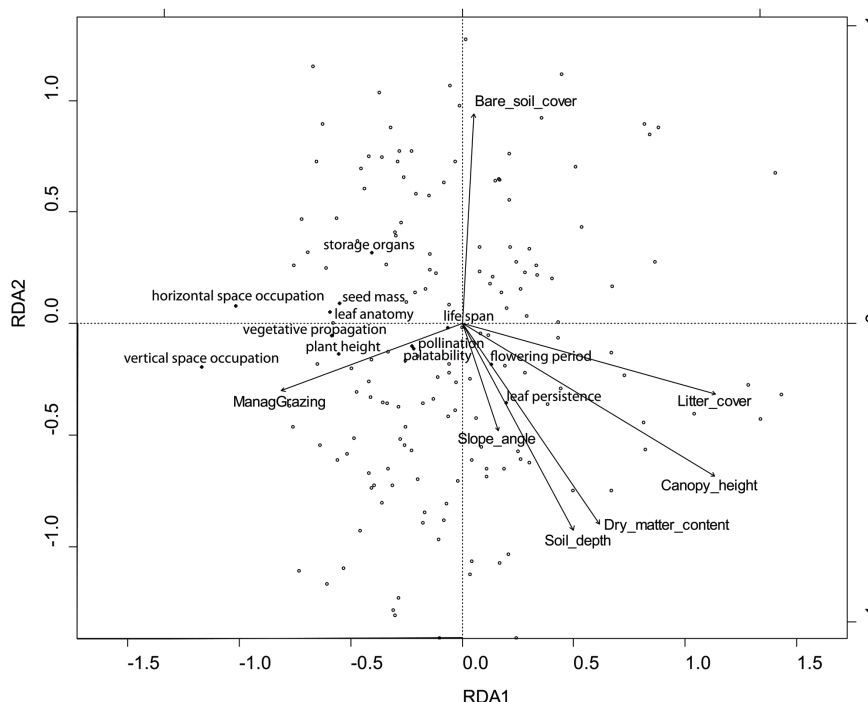


Figure 3. The Multivariate regression tree for the species data set, constrained by their explanatory variables. The threshold values shown for each partition of the tree correspond to the mean of the two limit values of the considered variables at the break between the branches. The relative abundances of the species are shown in histograms at the tips of the branches, with the species in the same order as in the input file. Under each histogram, the sum of squared errors for the group and the number of relevés in the leaf (n) are indicated. Below each tree the residual error (Error), the cross-validation error (CV Error) and standard error (SE) are indicated. Manag: management type; Abnd: abandoned; Grzd: grazed.

Table 2. Results of regression analyses showing the relation between adjusted functional diversity values ($adj.-FD=1/(1-FD)$, where FD is the quadratic entropy of Rao) for traits singly considered and the overall trait set and PCA axis 1 object scores, in grazed and abandoned plots. Regressions were performed using simple regression analysis, when assumptions for linear regression were satisfied, and nonparametric regression analysis when one or more assumptions were violated. F -test and Theil-Sen test were run to obtain significance values of slopes (P) in simple regression and nonparametric regression analyses. Significant values for single traits after Holm correction are indicated in italics. (*) Regression performed using nonparametric regression analysis

Trait	Management type					
	Grazed			Abandoned		
	Slope estimate	Intercept estimate	P	Slope estimate	Intercept estimate	P
Life span	0.0000	1.0489	0.859*	0.0000	1.0000	0.066*
Vegetative propagation type	-0.1895	2.5088	0.052	0.3424	2.2824	<0.001
Storage organs type	0.2814	2.1047	0.015	0.4327	2.1112	<0.001
Leaf persistence	-0.4000	1.7221	<0.001	-0.3219	1.5646	<0.001
Leaf anatomy	0.3173	2.9135	<0.001*	0.3872	2.4368	<0.001*
Pollination	-0.0299	2.1136	0.141*	0.0684	2.0334	0.001*
Seed weight	-0.1479	2.7686	0.307	0.4468	2.5438	<0.001
Horizontal space occupation	0.5059	3.0971	<0.001*	0.7763	2.8417	<0.001*
Vertical space occupation	0.0068	3.5938	0.976	0.4430	3.1295	0.009
Palatability	-0.1726	1.8979	0.004	0.0706	1.7651	0.231
Plant height	0.1858	2.6269	0.039*	0.3330	2.5037	<0.001*
Flowering period	-0.3152	2.4157	0.041	-0.1051	2.4619	0.327
Overall trait set	-0.0301	2.1415	0.033*	0.1469	2.0269	<0.001*

Figure 4. Redundancy analysis ordination graph (scaling 2) for adjusted functional diversity values ($adj.-FD=1/(1-FD)$, where FD is the quadratic entropy of Rao) of plant traits, using soil depth, bare soil cover, litter cover, canopy height, dry matter content, slope angle, and management type as constraining variables.



The detailed results of ISA for species and trait states are shown in Appendix 5.

Effects of fine-scale variables and management type on functional diversity

The main descriptive statistics of FD values for each trait and the overall trait set in grazed and abandoned plots, and

the significance values of comparisons between the two management conditions are provided in Table 1. FD values were significantly greater in grazed than in abandoned plots for the overall trait set, as well as for life span, vegetative propagation type, seed weight, horizontal and vertical space occupation, and palatability.

The total explained variance for FD , constrained by the considered explanatory variables, was 22.2% ($adj.-R^2$). The

first axis of RDA ($P = 0.001$) explained 83.9% of the constrained variance and was linked to canopy height and litter cover, and secondly to type of management; the second axis ($P = 0.001$) was related to bare soil cover, soil depth, and dry matter, and explained 7.4% of the constrained variance (Figure 4). All the FD values were negatively correlated to canopy height, litter cover, dry matter, and abandoned condition, except for flowering period and leaf persistence (positively linked to soil depth, and dry matter), and storage organs (positively related to bare soil cover) (Figure 4).

Comparison of FD trends in grazed and abandoned conditions

Regression analyses showed a significant trend of the overall FD in grazed grasslands along the environmental gradient depicted by PCA axis 1 scores, namely increasing values with increasing soil depth/phytomass production. A significant trend was detected in ungrazed grasslands as well, but in the opposite direction (Table 2, Figure 5).

FD of life span and flowering period had not significant relation with the gradient neither in grazed nor in ungrazed condition (Table 2). Some traits showed the same FD trends in both management types, namely decrease in leaf anatomy

and horizontal space occupation and increase in leaf persistence FD values with increasing productivity (Table 2).

FD of vegetative propagation, storage organs, pollination, seed weight, plant height, and vertical space occupation showed significant decreasing trends with increasing productivity in abandoned grasslands but not in the grazed ones (Table 2). On the contrary, FD of plant palatability showed significant increasing trends with increasing productivity in grazed grasslands but not in the abandoned ones (Table 2).

Abundance of competitive tall grasses showed a significant increasing trend in both management types ($P < 0.001$) with the increase in soil depth / phytomass production. The slope of the regression line was higher in abandoned than in grazed plots (Figure 6).

Discussion

Effect of fine-scale variables and management type on species assemblage and trait composition

MRT analysis grouped grazed and ungrazed plots, when characterized by shallow soil (Figure 3, Appendix 4), highlighting little floristic differences between the two management conditions. Likewise, several authors (e.g., Vitasović Kosić et al. 2011, Klimeš et al. 2013) found that the species

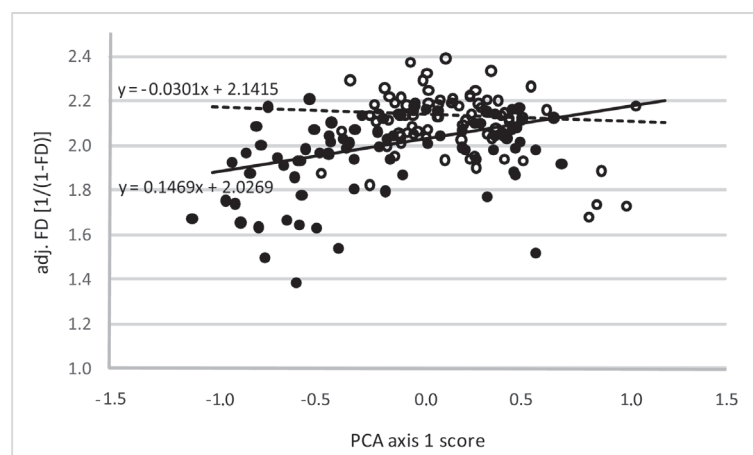


Figure 5. Scatterplot diagram and regression lines ($P < 0.001$) obtained from the nonparametric linear regression analyses between adjusted functional diversity values ($adj.-FD=1/(1-FD)$, where FD is the quadratic entropy of Rao) for the overall trait set and PCA axis 1 object scores in grazed and abandoned plots (white dots - grazed plots; black dashed line - regression line of grazed plots; black dots - abandoned plots; black solid line - regression line of abandoned plots).

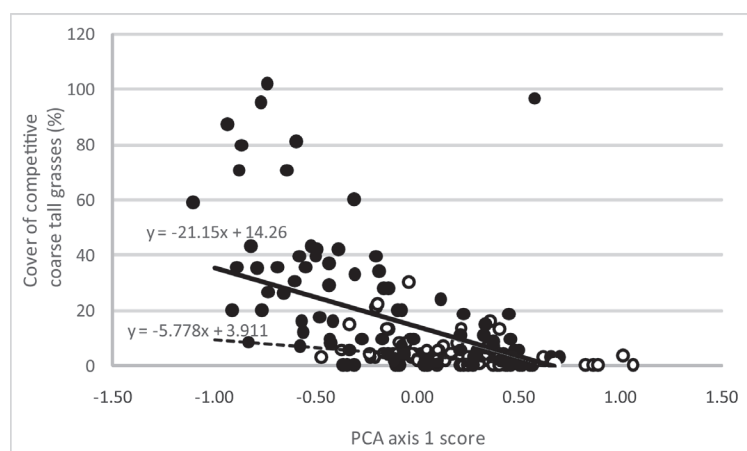


Figure 6. Scatterplot diagram and regression lines ($P < 0.001$) obtained from non-parametric regression analyses between the abundance of competitive tall grasses (*Brachypodium rupestre*, *Sesleria nitida*, and *Carex macrolepis*) and the PCA axis 1 object scores in grazed and abandoned plots (white dots - grazed plots; black dashed line - regression line of grazed plots; black dots - abandoned plots; black solid line - regression line of abandoned plots).

composition of dry habitat is little affected by grazing cessation, since harsh conditions strongly filter species having both drought resistance and avoidance ability (Coughenour 1985, Chapin et al. 1990, Peltzer and Wilson 2001).

These plots, characterized by low values of dry matter, litter cover, and canopy height, showed a prevalence of suffruticose and reptant chamaephytes among the indicator species (Appendix 4) besides of tubers and prostrate habit as indicator traits (Appendix 5). As stated by Catorci et al. (2013), in Mediterranean dry pastures the presence of tubers is typical of species with fast growing and early flowering strategy, compelled by the summer drought stress and allowed by the mobilisation of reserves stored during the previous growing season (Bolmgren and Cowan 2008). Moreover, this finding is consistent with Cornwell and Ackerly (2009) who indicated that low productivity selects for species with resource-retaining strategies. Prostrate habit (as that of dwarf shrubs like suffruticose and reptant chamaephytes) is the typical growth form of plants growing in habitats with water shortage, since they minimize the loss of nutrients rather than maximizing their uptake (Skarpe 2001).

With regard to plots without bare soil (therefore with deeper soil and higher productivity), MRT separated grazed and ungrazed conditions from a floristic point of view. They also differ in litter cover, canopy height and dry matter, which were greater in abandoned plots (Appendix 4). The abandoned condition fostered caespitose species like grasses (leafy stem with narrow leaves) (Appendix 5), an observation consistent with previous findings (Peco et al. 2012, Catorci et al. 2013), and substantially related to the high cover value of the competitive coarse tall grasses *Brachypodium rupestre*, *Carex macrolepis*, and *Sesleria nitida* (Figure 6). Rhizomes, mid-late spring flowering, scleromorphic/mesomorphic leaves, plant height 41-60 cm, heavy seeds and unpalatability, which are indicator trait states of abandoned condition, characterize them. Actually, these functional features are typical of dominant, invasive tall grasses (Grime 2001). On the other hand, the need of subordinate plants to face competition with tall grasses is expressed by a specific group of indicator trait states. Firstly, sedge space occupation type increases the probability of locating nutrient-rich pockets and of escaping competition with highly competitive species for nutrients and water (Muthukumar et al. 2004). Succulent leaves allow plants to store water resources and tolerate their depletion by dominant tall grasses (Catorci et al. 2011). Bulbs and light seeds (0.51-2.00 mg) reflect the short time available to complete the reproductive cycle (Moles and Westoby 2006) before the start of the growth period of dominant grasses (Catorci et al. 2012a). Finally, the absence of herbivory during summer may explain the abundance of mid to late summer flowering strategy and summer green leaves, which are indicator trait states of ungrazed plots.

The indicator species set of productive (without bare soil) grazed plots was characterized by hemicryptophytes and therophytes. The former are mostly CSR strategists (Appendix 4), typical of habitats in which the level of competition is restricted by moderate intensities of stress or disturbance (Grime 2001). Therophytes, with only sexual re-

production (indicator trait state), are ruderal species and are related to treading and trampling by large herbivores (Kohler et al. 2006). Likewise, annual life span, self-pollination, short stature (height less than 20 cm) and rosette leaf arrangement (indicator trait states of productive grazed plots) are related to soil disturbance (treading and trampling) and are escape strategies (Noy-Meir et al. 1989, Lavorel et al. 2007, Kahmen and Poschlod 2008). The indication by ISA of species with heavy seeds (10.1-50.0 mg) is consistent with Wu et al. (2009), who associated larger seed mass to moderate grazing intensity. In addition, tap roots (indicator trait state) highlight a strategy by which plants can face the herbivory during the drought period by storing resources and deepening their root to reach the wettest soil layer, thus allowing for leaf re-growth (Catorci et al. 2012a). Early spring flowering (indicator trait state) may be viewed as a strategy allowing plants to predate the period of grazing, which traditionally starts on June 1st, and drought stress (Briske 1996) and is usually fostered by moderate grazing (Grime 2001). Finally, it was postulated that grazing of domestic herbivores is effective in controlling the spread of unpalatable tall grasses and increase the forage quality (Milchunas et al. 1995, Catorci et al. 2014a). In fact, palatability emerged as indicator of grazed plots.

Effects of fine-scale variables and management type on functional diversity

Our results indicated that in the sub-Mediterranean climate, abandonment leads to a reduction of the overall *FD* (Table 1, Figure 4), since *FD* of most of the traits was negatively correlated to canopy height, litter cover, dry matter, besides abandoned condition (Figure 4). Our findings follow Grime's prediction (2006) that disturbance should promote trait differentiation by suppressing competitive dominance and allowing the coexistence of functionally dissimilar species. Moreover, grazing increase heterogeneity in spatial (de Bello et al. 2006) and temporal (Catorci et al. 2014c) resource distribution and promote the coexistence of species with dissimilar resource acquisition strategies on a fine spatial scale (Pugnaire et al. 2004). In fact, we found that in the grazed condition, *FD* was particularly higher for traits related to space occupation, plant height, and type of vegetative propagation (Figure 4). This may be due to the optimal grazing pressure in relation to the productivity of the system (Catorci et al. 2012b), and may also reflect the coexistence of different avoidance and tolerance strategies (Briske 1996), whose spread depends on the interplay of primary production and disturbance intensity (Bullock 1996). In addition, trampling might be beneficial for *FD*, because sward gaps are colonized by species with efficient space occupation strategies like clonal ability (de Kron et al. 2005) or annual life history (Grime 2001). The higher *FD* of seed weight under grazing is in accordance with the prediction of Laliberté et al. (2013) that disturbance should promote differentiation of traits related to dispersal, because it increases the likelihood that species with different regeneration niches could co-occur (Grubb 1977).

Only leaf persistence and flowering period *FDs* showed a weak positive association with dry matter (Figure 4) that

is with the increase of productivity. Catorci et al. (2012a), argued that where tall canopies and thick herb layer are likely to limit reproductive and vegetative performances, the subordinate species adopt functional strategies to differentiate their flowering period by predated or delaying the reproductive period compared to that of dominant species, which exploits the period with the most favourable climatic conditions (Ansquer et al. 2009). This implies a more numerous set of strategies, and thus a higher *FD*. Similarly, to avoid competition, non-competitive species need to optimize their photosynthetic returns, differentiating the time period in which leaves can photosynthesize, as well as the length of the period of photosynthesis. Obviously, the higher *FD* of flowering time and leaf persistence in productive conditions is also allowed by the lower summer drought stress (thus by the longer growing period) experienced by plants growing on deeper soils.

The enhanced *FD* of below-ground storage in the driest conditions (Figure 4) may indicate that in these settings niche partitioning is of increased importance, because it allows for exploitation of soil resources (Spasojevic and Suding 2012); it probably results in a highly complex pattern of strategies devoted to their acquisition and storage.

Comparison of FD trends in grazed and abandoned conditions

Our findings indicate that different management conditions affected the trends of the overall *FD* along the fine-scale gradient depicted by PCA axis 1. Indeed, the overall *FD* increased under grazing disturbance and decreased in ungrazed conditions with increasing productivity (Figure 5). These outcomes are likely related to the already quoted control of the spread of dominant tall grasses (see Figure 6) and to the total depletion of forage production operated by herbivores, thus avoiding litter accumulation (see Appendix 2). In fact, litter can reduce seed germination, establishment of individuals (Eriksson 1995), and growth of established plants (Facelli and Pickett 1991), thus likely contributing to decrease of the overall number of functional strategies characterizing the system (Catorci et al. 2011). Likewise, the spread of competitive species, leads to the competitive exclusion of functionally dissimilar species and to the increase trait similarity between coexisting competitive species, due to the increased competition for light and soil resources (Grime 2006, Bernard-Verdier et al. 2012). Our results are consistent with Janecěk et al. (2013) who asserted that the responses to abandonment often depend on productivity, but are in contrast with de Bello et al. (2006), who found a negative effect of grazing on functional diversity in the moistest locations.

We found that *FD* response of different traits to management followed a quite complex and not constant pattern with respect to the considered soil depth / productivity gradient.

Firstly, *FD* of some traits (life span and flowering period) did not show any significant trend. Actually, they might be considered as strategy linked to the macro-climatic conditions rather than to fine-scale environmental features, since

flowering period, largely compelled by both winter cold stress and summer drought stress, is basically related to air temperature, humidity, and photoperiod (e.g., White 1995, Fitter et al. 1995, Diekmann 1996). Although annual life span emerged as indicator of the MRT group including grazed plots of more productive conditions (Appendix 4, Appendix 5), probably differences in *FD* of life span did not emerge since the mean cover value of annual and biennial plants remained very low in any condition and showed little variation (Appendix 3) and, as stated by de Bello et al. (2005), *FD* is little or not affected when variations involve species with low abundance and frequency.

Otherwise, *FD* of some traits, mostly linked to resources acquisition and water loss prevention (leaf anatomy, horizontal space occupation, and leaf persistence) showed the same trend along the gradient in grazed and abandoned plots (Table 2). This suggests the existence of a similar variation pattern in the two management systems related to the set of strategies aimed to tolerate drought stress, consisting in a wider range of leaf anatomies, and space occupation types (Grime 1977), at the more xeric extreme of the gradient, and to avoid competition with the dominant species with a more numerous set of leaf persistence types at the more productive end of the gradient.

Another group of traits, mostly related to plant foraging and dispersal strategies, resources storage and competition for light (vegetative propagation, storage organs, plant height, pollination, seed weight, and vertical space occupation) did not show significant trends of *FD* in grazed grasslands along the considered gradient. Instead, they showed a decreasing trend with increasing productivity in abandoned grasslands, thus with the enhancement of competitive dominant species, which negatively filter the trait pool of the subordinate ones. This confirms the statements of several authors on the positive effect of disturbance (see Díaz et al. 2007), in that it avoided the loss of part of the local trait pool, especially in the most productive conditions.

With regard to palatability, the *FD* trend was significantly affected by grazing. In dry conditions, the lower *FD* values suggest a prevalence of species with avoidance strategies because, as argued by Díaz et al. (2001), livestock acts removing species that lack adaptations to avoid defoliation. The increasing *FD* values in more productive conditions indicate that the optimal grazing pressure characterizing the study area allowed the coexistence of palatable species with those having avoidance strategies. Instead, *FD* of palatability did not show any trend in ungrazed plots, because of the prevalence of unpalatable species over palatable ones along the whole gradient, namely species with tough leaves, woody and/or spiny stems or branches in the least productive plots and dominant coarse tall grasses in the most productive conditions.

Conclusions

Our findings demonstrated that fine-scale variability of productivity and related variables (soil depth, bare soil cover,

etc.) plays a key role on the dynamic processes after long-term grazing cessation, involving species, traits and *FD*. Firstly, we confirmed the hypothesis that a convergence of species composition and functional responses to grazing and resource limitation characterized habitats with low productivity. Instead, in productive conditions grazing cessation led to changes in both species and functional composition. Particularly, competitive coarse tall grasses were fostered by abandonment chiefly leading to a shift from functional strategies devoted to grazing avoidance and tolerance to those devoted to competition for light and slow resources acquisition. These changes caused a reduction of the overall *FD* in abandoned condition, likely because of the reduction of available spatial and temporal niches. Our results indicate that the overall *FD* increased under grazing disturbance and decreased in ungrazed conditions with increasing productivity and that, after grazing cessation, the trends of *FD* of the different traits are conditioned by the soil depth / productivity gradient.

The *FD* of traits mostly related to macroclimatic features did not show any trend in grazed and abandoned conditions along the considered gradient. Instead, *FD* of traits, mostly linked to the resources acquisition and water loss prevention (leaf anatomy, horizontal space occupation, and leaf persistence) showed the same trend along the gradient in grazed and abandoned plots. Another group of traits mostly related to plant foraging and dispersal strategies, resources storage and competition for light did not show significant trends of *FD* in grazed grasslands along the considered gradient, but showed a decreasing trend with increasing productivity in abandoned grasslands. This result confirms the key role of extensive grazing in maintaining high levels of functional diversity, also in sub-Mediterranean climate.

It was demonstrated that productive grasslands are less resistant to change in species composition after management cessation than the dry ones (Hirst et al. 2005, Bennie et al. 2006). Our findings allow us to argue that this statement is true also at a finer spatial scale, with regard not only to species composition, but also to functional diversity.

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Electronic Appendices

Appendix 1. Traits and corresponding trait states analysed in the present study.

Appendix 2. Descriptive statistics for environmental variables.

Appendix 3. Descriptive statistics for traits.

Appendix 4. Descriptive statistics of environmental and vegetation structure features, indicator trait states and indicator species.

Appendix 5. Indicator species and trait states.

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