

## Grazing effects on plant functional group diversity in Mediterranean shrublands

Alexandra D. Papanikolaou · Nikolaos M. Fyllas · Antonios D. Mazaris · Panayiotis G. Dimitrakopoulos · Athanasios S. Kallimanis · John D. Pantis

Received: 6 December 2010 / Accepted: 7 July 2011  
© Springer Science+Business Media B.V. 2011

**Abstract** Grazing is one of the prevalent human activities that even today are taking place inside protected areas with direct or indirect effects on ecosystems. In this study we analyzed the effects of grazing on plant species diversity, plant functional group (PFG) diversity and community composition of shrublands. We analyzed plant diversity data from 582 sampling plots located in 66 protected areas of the Greek Natura 2000 network, containing in total 1102 plant species and subspecies. We also classified a priori all plant species in seven PFGs: annual forbs, annual grasses/sedges, legumes, perennial forbs, perennial grasses/sedges, small shrubs and tall shrubs. For each site, grazing intensity was estimated in four classes (no grazing, low, medium and high grazing intensity). We found that, at the spatial and temporal scale of this study, as grazing intensity increased, so did total species richness. However, each PFG displayed a different response to grazing. Short-lived species (annual grasses or forbs and legumes) benefited from grazing and their species richness and proportion in the community increased with grazing. Perennial grasses and forbs species richness increased with grazing intensity, but their dominance decreased, since their proportion in the community declined. Short shrub species richness remained unaffected by grazing, while tall shrub diversity decreased. Finally, in sites without grazing the spatial pattern of species richness of the different PFGs was not congruent with each other, while in grazed sites they were significantly positively correlated (with the exception of tall shrubs). This finding may imply that grazing is a selective

---

A. D. Papanikolaou · A. D. Mazaris (✉) · J. D. Pantis  
Department of Ecology, School of Biology, U.P. Box 119, 54124 Thessaloniki, Greece  
e-mail: amazaris@bio.auth.gr

N. M. Fyllas  
Ecology and Global Change, School of Geography, University of Leeds, Leeds LS2 9JT, UK

P. G. Dimitrakopoulos  
Biodiversity Conservation Laboratory, Department of Environment, University of the Aegean,  
81100 Mytilene, Greece

A. S. Kallimanis  
Department of Environmental and Natural Resources Management, University of Ioannina, G. Seferi 2,  
30100 Agrinio, Greece

pressure organizing the community structure, and imposing a certain contribution of each PFG. So, in Mediterranean shrublands in protected areas with a long historical record of grazing, it seems that grazing promotes species diversity and its continuation on a portion of the landscape may be a necessary part of an effective management plan.

**Keywords** Mediterranean ecosystems · Grazing · Plant functional groups · Species richness · Community composition

## Introduction

Grazing is considered as one of the most important types of disturbances altering natural processes, affecting species persistence and influencing the structure and composition of plant communities (Olf and Ritchie 1998). However, diversity changes and species responses to potential pressures might not be of the same magnitude across different regions subjected to different pressures, and having discrete evolutionary history and ecological attributes.

The Mediterranean Biome in the ‘old world’ has a high degree of species richness and endemism but is also one of the most imperiled systems of the planet. The current state of vegetation within the Mediterranean biomes has been shaped by natural selection under the pressure of a distinct climate and the contribution of intensive human activities (Naveh 1990; Bergmeier and Dimopoulos 2004; Agra and Ne’eman 2009). This region has been grazed for 9000 years, with many species developing mechanisms to tolerate this disturbance or even take advantage of it (Noy-Meir 1995). Given the long history of human presence in the basin, it has been argued that its high plant diversity is the result of co-evolution of plants and humans (Di Castri 1981). Therefore, although the deteriorative effects of grazing have been acknowledged (Bakker 1989, 1998), contrary results have also highlighted the positive impacts of grazing in natural communities further suggesting that traditional grazing practices should not be considered as disturbances in ecosystems with such a long history of human presence (Montalvo et al. 1993; Verdu et al. 2007). Furthermore, a positive response of species richness to grazing intensity has also been documented, mostly in productive environments (Proulx and Mazumder 1998).

Grazing has been considered a complex disturbance which affects plant communities directly and indirectly (Hay and Kicklighter 2001), as it alters establishment, growth and survivorship rates of different species and at the same time it has an impact on the abiotic component of the ecosystem (Facelli and Springbett 2009). Consequently, significant changes in plant species richness and composition are induced by grazing (Landsberg et al. 1999; Bergmeier and Dimopoulos 2003). Many studies have attempted to define the consequences of grazing on plant communities and have highlighted different responses of species with different functional traits (Noy-Meir et al. 1989; McIntyre et al. 1999; Landsberg et al. 1999; Sternberg et al. 2000; Diaz et al. 2001, 2007). However, these results are often inconsistent and more research is necessary in order to understand how plant species and communities are affected by grazing and the potential variations of its intensity.

Following the variety of findings regarding disturbance regimes a series of hypotheses have been put forward to describe the observed patterns. Among them dominant is the ‘intermediate disturbance hypothesis’ (IDH) that infers highest species richness at sites that experience an indeterminate level of disturbance (Connell 1978; Huston 1979). According to IDH, at high intensity of disturbance few species are able to persist and the overall

diversity is low. On the other hand, without disturbance the community structure will be driven by interspecific competition, where few competitively superior species will exclude the majority of the species, leading to a species poor community. At moderate levels, disturbance allows moderation of competitive interactions without pushing species outside their physiological tolerance and thus helps maximize diversity (Connell 1978; Sousa 1984; Petraitis et al. 1989; Shea et al. 2004). The ‘*disturbance reversal hypothesis*’ infers to a negative association of a pressure with species diversity in low productivity ecosystems (see Proulx and Mazumder 1998). For example, Osem et al. (2007) found that species richness was positively affected by grazing in the most productive Mediterranean semiarid rangeland sites in Israel, but it was unaffected or decreased with grazing in the less productive locations. However previous studies that provided support to either of these hypotheses tend to be biased towards specific species or sites, with analyses of plants response to disturbance regimes, such as grazing, along a coarse regional level remaining scarce.

Towards the protection of biological diversity, the international community has established networks of protected areas. In the European Union such a network, named Natura 2000 (EU 2007) has been developed aiming to protect species or habitats of conservation interest. Some of the sites included in this network have previously being protected under different statuses (e.g. National Parks) controlling or forbidding human-related activities. On the other hand, many sites that are listed within national networks do still support some kind of human-related activities. To what extent disturbances such as grazing affect species diversity and community composition at protected sites has received limited attention, while the existence of potential patterns of species responses to grazing at broader scales remains unspecified.

In this study we investigated the response of natural ecosystems in Natura 2000 protected sites, by examining how species richness, plant functional groups (PFGs) richness and community composition vary along grazing gradients in the Mediterranean. We further examined the degree of congruence of species richness among the different PFGs and the potential differences in functional composition under levels of grazing intensity aiming to understand whether grazing could act as a selective pressure organizing natural communities.

## Methods

### Data summary

In this study, we used a dataset containing 1102 plant species and subspecies that were recorded within the Greek Natura 2000 network of protected areas which comprises sites regarded as important for the maintenance of biodiversity (Dimitrakopoulos et al. 2004; Kallimanis et al. 2008). The sampling plots were located in the habitat types: (a) low formations of *Euphorbia* close to cliffs, (b) thermo-Mediterranean and pre-desert scrub, (c) *Sarcopoterium spinosum* phryganas and (d) Endemic phryganas of the *Euphorbio-Verbascion*, which correspond to scrub and/or herbaceous vegetation association as described by CORINE land use types (for a detailed description of the selected habitat types please check: EUR27-Interpretation Manual of European Union Habitats).

In order to standardize for the differences in sampling effort we maintained in our analysis only sampling plots of a fixed size, i.e. 100 m<sup>2</sup>. The final dataset included 19203 occurrence records sampled across 582 sampling plots located in 66 sites across Greece

(on average 8.81 plots per site). Species recorded in these plots were a priori classified into seven PFGs according to Flora Europaea. The selected PFGs were based on the existing literature on plant functional traits in Mediterranean and other types of ecosystems (Lavorel et al. 1997; Hooper and Vitousek 1997; Sternberg et al. 2000; Troumbis et al. 2000; Joshi et al. 2001; Dimitrakopoulos et al. 2005; Spehn et al. 2005; Petchey and Gaston 2006). PFGs defined were: (a) annual forbs ( $n = 300$  species), (b) annual grasses/sedges ( $n = 67$  species), (c) legumes ( $n = 129$  species), (d) perennial forbs ( $n = 404$  species), (e) perennial grasses/sedges ( $n = 69$  species), (f) small shrubs (<150 cm) ( $n = 94$  species) and (g) tall shrubs (>150 cm) ( $n = 39$  species).

Within the Natura 2000 database, grazing intensity is recorded into three levels, ranging from a value of 0 for undisturbed sites to a value of 3 for highly grazed ones. This semi-quantitative scheme for assessing intensity of human impacts, including grazing, has been applied for all European protected sites included in the Natura 2000 network. This estimation is guided by a common directive throughout EU and serves as a tool for assessing potential threats within the Natura 2000 sites. This grazing intensity scale is based on experts' opinion while no additional information on the species or population of grazing animals was available. In the present study, grazing intensity aggregates to a single measure different components that could describe such an event like frequency, extent, intensity per se and duration of the phenomenon (Shea et al. 2004).

#### Data analysis

For each of the 582 studied plots, total and within functional group species richness was calculated as the number of different species encountered. To explore for potential differences in species richness and PFG responses to grazing we performed our analysis into two subsets of the PFGs classified dataset, consisting of grazed ( $n = 499$ ) and undisturbed plots ( $n = 83$ ). In both cases species richness did not followed a normal distribution (Shapiro-Wilks Normality Test) and thus a set of non parametric tests were applied. Potential differences in species richness for undisturbed and disturbed plots were examined using Wilcoxon test. For multiple comparisons along the grazing intensity gradient a Kruskal–Wallis test was performed, followed by a post-hoc Kruskal–Wallis procedure using the *pgirmess* R package based on the algorithm described in Siegel and Castellan (1988).

To explore the potential impact of grazing on community composition we estimated the relative contribution of each PFG, as the ratio of species belonging to this PFG to the total number of species in the plot, and repeated the analyses described above. For each plot we additionally estimated the Simpson index of functional diversity, grouping “as a species” taxa categorized in the same PFG. The Simpson index ( $D$ ) was estimated using the formula:

$$D = \frac{1}{\sum_{i=1}^n p_i^2}$$

where  $p_i$  the proportion of PFG<sub>*i*</sub> (sum of species belonging to this PFG to the total number of species in the plot), with  $i$  ranging from 1 to 7 (seven a priori defined PFGs). In all cases this metric followed a normal distribution and variances were equal between the different levels of grazing intensity, and thus Analysis of Variance along with the Tukey post-hoc test were used to explore for differences in functional composition as a response to grazing.

We finally used the Spearman correlation test to examine the degree of congruence of species richness among the different PFGs under levels of grazing intensity.

Spatial autocorrelation is known to influence biological data, further leading to biased results and misleading conclusions. In our study the spatial distribution of the sampling plots at the grazed and ungrazed sites could have an influence in the analysis. However, in our case, this seems unlikely since our sample 100 m<sup>2</sup> plots were dispersed throughout Greece, with average distance separating them 51.160 km. We additionally tested for a potential effect of distance on species richness by simple Mantel tests between similarity matrices produced by the species richness data (using Euclidian distances) and by geographical distances between sampling plots. The analysis revealed no significant correlations ( $P > 0.05$ ) indicative of a no significant effect of spatial autocorrelation.

In addition, inference could be affected if grazed and ungrazed sites are different in terms of basic biophysical attributes, e.g. if groups of sites (i.e. grazed or ungrazed) could have a lower than average diversity due to their environmental conditions. To avoid such complications we selected to analyze data from specific habitat types so as to standardize for environmental conditions. We also tested for this potential source of bias by performing independent samples *t*-test and Mann–Whitney tests to investigate for significant differences in mean altitude, mean and maximum annual temperature between grazed and ungrazed sites and sampling plots. Data on mean annual temperature were obtained from WorldClim climate grids (version 1.4, <http://www.worldclim.org/>, for more details see Hijmans et al. 2005). All tests demonstrated no significant difference (in all cases  $P > 0.05$ ) in the studied attributes between grazed and ungrazed plots at a site or sampling plot level.

## Results

### Species richness and functional diversity under disturbance regimes

Mean plot level species richness and functional group richness for grazed and undisturbed plots are summarized in Table 1. Total species richness was higher in grazed than in undisturbed plots ( $W = 13147$ ,  $P < 0.01$ ), while along the grazing intensity gradient a gradual increase in species richness was found. The difference in functional diversity, as measured by Simpson's index, was not significant in grazed relative to undisturbed plots ( $W = 18075.5$ ,  $P = 0.063$ ), or along the grazing gradient ( $F = 0.973$ ,  $P = 0.324$ ).

Species richness of annual forbs, annual grasses, legumes, perennial forbs and perennial grasses was significantly higher at sampling plots that were subjected to grazing (in all cases  $P < 0.05$ ; Table 1). Short and tall shrubs presented a neutral response to grazing, with species richness not significantly changing between grazed and undisturbed sites (Table 1).

Within PFGs species richness responded in an individualistic way to gradients of grazing intensity (Table 1; Fig. 1). Based on the Kruskal–Wallis multiple comparison tests, species richness of annual forbs, annual grasses, legumes and perennial forbs followed a similar pattern, exhibiting the highest richness under a higher grazing intensity (in all cases  $P < 0.001$ ; Table 1). Species richness of perennial grasses showed a gradual increase with grazing intensity although this relationship was marginally non-significant ( $P = 0.055$ ) (Fig. 1). Species richness of tall shrubs was significantly different along the grazing regime with higher values obtained at relatively low disturbance intensities

**Table 1** Differences in species richness, PFGs species richness and Simpson metric of functional diversity between grazed and undisturbed plots, and along the grazing gradient

	Undisturbed	Grazed	W	P	Grazing Intensity				P
					Absent	Low	Medium	High	
Number of plots	83	499			83	124	129	246	
Total species richness	22.18	34.79	13147	<0.01	22.18 <sup>a</sup>	31.9 <sup>b</sup>	31.90 <sup>b</sup>	37.76 <sup>c</sup>	<0.01
Annual forbs	4.07	10.28	12161	<0.01	4.07 <sup>a</sup>	8.65 <sup>b</sup>	7.91 <sup>b</sup>	12.34 <sup>c</sup>	<0.01
Annual grasses	0.60	3.61	6726	<0.01	0.60 <sup>a</sup>	3.62 <sup>b</sup>	3.02 <sup>c</sup>	3.91 <sup>b</sup>	<0.01
Legumes	2.71	4.53	15631	<0.01	2.71 <sup>a</sup>	4.11 <sup>a</sup>	4.09 <sup>a</sup>	4.97 <sup>b</sup>	<0.01
Perennial forbs	5.65	6.95	16436	<0.01	5.65 <sup>a</sup>	5.80 <sup>a</sup>	7.74 <sup>b</sup>	7.12 <sup>b</sup>	<0.01
Perennial grasses	1.78	2.31	17841	<0.05	1.78	2.16	2.36	2.36	0.055
Small shrubs	5.57	5.61	21231	0.712	5.57	5.77	5.23	5.74	0.494
Tall shrubs	1.80	1.50	22944	0.105	1.80 <sup>a</sup>	1.79 <sup>ab</sup>	1.54 <sup>ab</sup>	1.34 <sup>b</sup>	0.030
Simpson's D	4.18	4.40	18076	0.063	4.18 <sup>a</sup>	4.65 <sup>b</sup>	4.35 <sup>a</sup>	4.29 <sup>a</sup>	<0.01

Significant difference obtained by the post hoc test between pairs of grazing intensity are depicted using the superscripts a, b and c, where the same letter indicates no significant difference

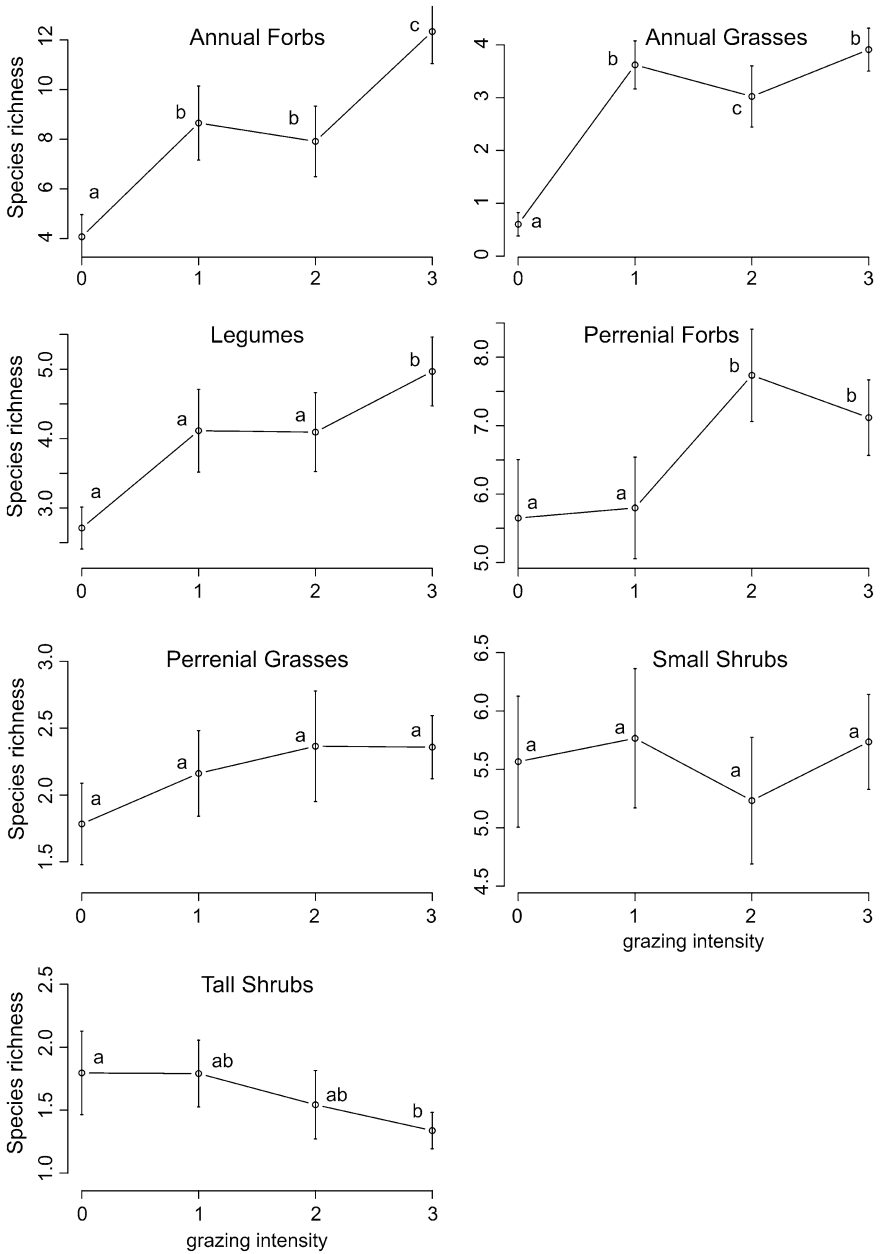
( $P < 0.001$ ) (Fig. 1). No significant differences were obtained for species richness of short shrubs.

Interestingly, total species richness was highest at the plots with highest grazing intensity, in contrast with the Simpson's index of functional diversity, which peaked at low grazing intensities (Table 1), indicating that at ungrazed plots there is a more equal representation of the species present, while as grazing intensity increases few species increase their dominance, while many rare ones are also present.

Focusing on the species composition of the different plots, we analyzed the proportion of species that each PFG contributes. A non-parametric pairwise comparison demonstrated that the relative contribution of annual forbs and annual grasses at the local communities significantly increased under grazing ( $P < 0.01$ ) while it did not significantly change for legumes ( $P = 0.644$ ). On the contrary, the contribution of perennial forbs, grasses, short and tall shrubs decreased under grazing pressure ( $P < 0.01$ ).

#### Degree of congruence of species richness among the different PFGs

In undisturbed plots, with few exceptions, no two functional groups appear to be congruent (Table 2). In other words, the spatial pattern of species richness of one PFG was independent of the spatial pattern of species richness of any other PFG. The only exception was a significant negative association between the species richness of annual forbs and that of tall shrubs ( $r_s = -0.37$ ,  $P < 0.05$ ). On the other hand the spatial pattern of species richness of all PFGs (with the exception of tall shrubs) was strongly congruent on grazed sites. This



**Fig. 1** Responses of species richness of the different PFGs to gradients of grazing intensity. Mean values and standard deviation for each group of plots for different PFGs under different grazing intensity are presented. Significant differences obtained by the post hoc test between pairs of grazing intensity are depicted using the superscripts a, b and c, where the same letter indicates no significant difference (for example for annual forbs species richness differed significantly between sites of no grazing and grazing intensity of 1, 2 and 3; between sites of grazing intensity of 1,2 and 3 but no difference were obtained between sites of grazing intensity 1 and 2, for tall shrubs species richness was only different between no grazing and grazing intensity three sites). See Table 1 for non parametric multiple comparisons

**Table 2** Congruence between species richness of PFGs under different grazing regimes as expressed through the Spearman's correlation coefficient

	Medium grazing intensity											
	Annual grasses	Legumes	Perennial forbs	Perennial grasses	Small shrubs	Tall shrubs	Annual grasses	Legumes	Perennial forbs	Perennial grasses	Small shrubs	Tall shrubs
No disturbance												
Annual forbs	NS	0,34**	0,51**	NS	NS	-0,37*	0,53**	0,64**	0,43**	0,43**	NS	NS
Annual grasses		NS	NS	NS	NS	NS	0,59**	0,26**	0,53**	0,35**	NS	NS
Legumes			0,25*	NS	NS	NS		0,33**	0,37**	NS	NS	NS
Perennial forbs				NS	NS	NS			0,33**	NS	NS	-0,22*
Perennial grasses					0,28*	NS				0,25**	NS	NS
Small shrubs						NS					NS	NS
Low grazing intensity												
Annual forbs	0,57**	0,63**	0,55**	0,30**	0,62**	NS	0,70**	0,65**	0,45**	0,16*	0,19**	NS
Annual grasses		0,56**	0,24*	0,28**	0,45**	NS		0,67**	0,48**	0,19**	0,19**	NS
Legumes			0,39**	0,33**	0,52**	NS			0,36**	0,15*	NS	NS
Perennial forbs				0,37**	0,64**	NS				0,26**	0,24**	NS
Perennial grasses					0,52**	0,31**				0,36**	NS	NS
Small shrubs						NS					NS	NS

Significance levels \*  $P < 0.05$ , \*\*  $P < 0.01$ , NS not statistically significant correlation



was observed both overall and in all levels of grazing intensity. All associations were positive and significant, with the only exception of tall shrubs (Table 2).

## Discussion

Mediterranean plants are generally known to be adapted to disturbances and their communities usually present a fast post-disturbance recovery (Lavorel et al. 1999). Our results showed that in Greek Natura 2000 protected areas as grazing pressure intensified plant species richness increased, at least at the spatial and temporal scale of this study. Furthermore, our results suggest that plant functional groups (PFGs) in Mediterranean ecosystems respond in discrete ways to grazing pressure. More specifically, species with short life span increased in both diversity and dominance, while woody species were either unaffected or declined.

Grazing is one type of disturbance often associated with the intermediate disturbance hypothesis (IDH), where species richness reaches maximum values at intermediate levels of disturbance (e.g. Mwendera et al. 1997). Our findings oppose in part this hypothesis (see also Grime 1973; McIntyre and Lavorel 1994), with most PFGs demonstrating a monotonic increasing pattern with grazing intensity. Our results indicate that different PFGs respond differently to grazing with some supporting and others rejecting the IDH. A plausible explanation for the lack of support to the IDH may refer to the history of the Mediterranean landscapes. At the Mediterranean region, ecosystems have coevolved with human activities, such as grazing, since antiquity. However, we think this is only part of the explanation, since even in Greek forests there is clear evidence that overgrazing leads to depleted, species poor communities (e.g. Chaideftou et al. 2009). A more pertinent explanation might be that since our data were collected in protected areas, it is likely that the maximum observed grazing intensity is less than the intermediate intensity of grazing observed outside protected areas, and thus we are only looking at part of the picture, i.e. at the first half of the IDH response. A third possibility might refer to the type of habitats (typical Mediterranean shrublands) we analyzed. On the one hand, without grazing it is expected that shrublands would remain at areas, which could not support a forest because of their limited resources or harsh environmental and topographic conditions. But with grazing, areas that could support forests would remain shrublands. In this latter case, disturbances could allow a trade-off in individual species ability and response to immigration, colonization and extinction (Sousa 1984; Petraitis et al. 1989) favoring a wider array of species.

As a final note on IDH we should mention that when applied to whole communities, the differences in life history of species present become important. There is a large disparity in the way in which different species experience the same disturbance regime. For example, an intermediate disturbance frequency for a community of annual plants is not expected to be the same as for a community of long-lived shrubs. Thus, the disturbance frequency that maximizes the richness of one plant functional group is not expected to be the same for another group. And in this context we might argue that different PFGs seem to illustrate different parts of the hump shaped relationship described by IDH.

Short-lived plant species benefited from grazing disproportionately, increasing both their species richness and their proportion in the species composition. This is in accordance with previous studies that have demonstrated an increase in species richness of annual plants under grazing (e.g. Pakeman 2004; Diaz et al. 2007). Lavorel et al. (1999) suggested that “grazing favors small and disfavors tall species”, with tall grasses and tall forbs

presenting higher recruitment in ungrazed sites. The short life span and high seed dispersal allow annual forbs and grasses to establish new individuals at gaps created by grazing. Similarly, legumes' life history traits with the small-sized, short-lived species of a prostrate habit in addition to small seeds and small germination fraction seem to be favored by grazing as they could effectively occupy potential gaps developed (McIntyre et al. 1995; Aboling et al. 2008). In any case, our results provide further support to previous suggestions that in dry ecosystems such as the Mediterranean, grazing could favor relative short-lived species, given the convergence of species adaptations to both grazing and drought pressures (Milchunas et al. 1988; Verdu et al. 2007).

We also found that species richness of perennial forbs and grasses increased in grazed plots compared to undisturbed ones. This was contrary to expectations that the richness of perennial species decreases with grazing intensity (Diaz et al. 2007). Perennial forbs and grasses could be resistant to grazing due to several physiological adaptations. Growth by underground meristems, large seeds leading to high germination rates (Aboling et al. 2008) and biochemical repellents (Noy-Meir et al. 1989) are some of these characteristic adaptations. On the other hand, a plausible explanation for the observed pattern could be that several short-lived species (i.e. life span of 2 or 3 years) were included in this PFG, and thus could drive the overall responses of this group towards a more short-lived strategy.

Recent studies on woody plant response to grazing (Vesk et al. 2004; De Bello et al. 2005) reveal a more complicated pattern compared to earlier conceptual models (Milchunas and Lauenroth 1993). On a global scale, Diaz et al. (2007) identified a neutral response of woody species even in areas expected to be favored by such type of disturbances like dry rangelands. Our results indicate a different response of short compared to tall shrubs. In particular short shrubs species richness had a neutral response to grazing, with a negative response identified for tall shrubs. The long history of grazing in the Mediterranean basin may have led to key adaptations of both small and tall shrubs that could operate in a variety of ecosystems and under different climate and productivity conditions, enabling them to persist under different levels of grazing (Agra and Ne'eman 2009). However grazing usually results in a comparatively higher damage in tall plants whose structural configuration exposes a greater surface to grazers (Hadar et al. 1999; Lavorel et al. 1999). This result is in line with a previous study conducted in a dense matorral system in Greece, where grazing did not significantly affect total species richness, although the importance of tall shrubs was replaced by that of smaller shrubs adapted to more intense disturbance regimes (Alados et al. 2004).

The observed differential increase in species richness of different PFGs is also causing a shift in the community structure. In the grazed plots annual plants dominate, while in the undisturbed plots perennials and shrubs are the dominant functional groups. So even though perennial plant species richness increased, their proportion in the community's species composition decreased. So perhaps it is not perennial species richness per se that is affected by grazing but their contribution to community species composition. Such differences in the functional attributes of different PFGs and the way they interact with disturbances could be an important step forward to better understand the response of ecosystems to different levels of disturbance (McIntyre et al. 1999) and definitely require further attention.

We found that in undisturbed plots, only for a few pairs of PFGs the spatial pattern of species richness were congruent. A plausible explanation for this pattern is that without grazing, the edaphic environment becomes increasingly important. In this sense, the variation apparent in the ungrazed plots might be indicative of the difference in composition related to such edaphic differences between studied sites; but we lack data to verify this

hypothesis. However, in grazed plots, with the exception of tall shrubs, for all other functional groups there was strong and positive correlation in their pattern of species richness. This was observed in all levels of grazing intensity. Given that grazing homogenizes vegetation, these results are likely to suggest that it acts as a selective regime towards organizing plant communities that consist of a certain proportion of species from each functional group. In addition, our results suggest that in disturbed sites where shrub species are effectively controlled, smaller PFGs are gaining the space released and enhance their species diversity (Noy-Meir and Briske 2002). It should be noted that we did not identify any negative association in species richness between the smaller functional groups, which could indicate that all of those groups benefit from the removal or elimination of the highly competitive tall woody plants. In this manner, we suggest that for total species richness to increase all groups (except shrubs) need to increase and one cannot do so at the expense of the others, which could imply that grazing imposes certain assembly rules on the community that undisturbed areas lack.

The establishment of protected areas represents a first step towards mitigating environmental degradation and halting biodiversity loss. Effective management and conservation of these complex traditional landscapes requires strategies that would be based on a better understanding of both ecological and social aspects of change. Especially in the Mediterranean human presence is closely related to the evolution of biological diversity. In such cases, grazing does not seem to affect the potential for an area to be of high biodiversity value. Furthermore, traditional grazing practices seems to promote species coexistence and biodiversity, especially of short-lived species, while at the same time grazing seems to impose a community structure that is much more organized (as far as PFG proportions are concerned) than undisturbed plots. As the results of our study demonstrated grazed plots had greater diversity than ungrazed plots, i.e. grazing increased alpha diversity; this does not imply that for maximizing total plant diversity at the landscape level (gamma diversity) the entire landscape should be grazed. In Mediterranean forests there is low overlap in species composition of the vegetation and seed bank between grazed and ungrazed plots (Chaideftou et al. 2011). A series of studies from different regions including the Mediterranean have shown that even within some growth forms such as annuals and geophytes which normally benefit from grazing there is proportion of species, albeit small, that occur only at lightly grazed and ungrazed sites (Noy-Meir and Oron 2001; Todd and Hoffman 2009; Cingolani et al. 2005). Therefore, it is important to mention that, grazing as a sole management practice is likely to be detrimental to diversity in the long term. Thus total biodiversity is best conserved if both grazed and ungrazed areas exist in the landscape. Therefore we argue that the continuation of grazing in part of the landscape, even in protected areas, is necessary for effective management.

**Acknowledgments** The work of ADM, ASK and JDP was partially supported by the EU FP7 SCALES project ('Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal and Ecological Scales'; project #226852).

## References

- Aboling S, Sternberg M, Perevolotsky A et al (2008) Effects of cattle grazing timing and intensity on soil seed banks and regeneration strategies in a Mediterranean grassland. *Commun Ecol* 9:97–106
- Agra H, Ne'eman G (2009) Woody species as landscape modulators: their effect on the herbaceous plants in a Mediterranean maquis. *Plant Ecol* 205:165–177

- Alados CL, ElAich A, Papanastasis VP et al (2004) Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecol Modell* 180:523–535
- Bakker JP (1989) Nature management by grazing and cutting. Kluwer, Dordrecht
- Bakker JP (1998) The impact of grazing to plant communities. In: Wallis De Vries MF, Bakker JP, Van Wieren SE (eds) *Grazing and conservation management*. Kluwer, Dordrecht, pp 137–184
- Bergmeier E, Dimopoulos P (2003) The vegetation of islets in the Aegean and the relation between the occurrence of islet specialists, island size, and grazing. *Phytocoenologia* 33:447–474
- Bergmeier E, Dimopoulos P (2004) Wood pasture in an ancient submediterranean oak forest. *Ecol Medit* 30:5–14
- Chaideftou E, Thanos CA, Bergmeier E et al (2009) Seed bank composition and above-ground vegetation in response to grazing in sub-Mediterranean oak forests (NW Greece). *Plant Ecol* 201:255–265
- Chaideftou E, Thanos CA, Bergmeier E et al (2011) The herb layer restoration potential of the soil seed bank in an overgrazed oak forest. *J Biol Res* 15:47–57
- Cingolani AM, Posse G, Collantes MB (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *J Appl Ecol* 42:50–59
- Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310
- De Bello F, Leps J, Sebastia MT (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *J Appl Ecol* 42:824–833
- Di Castri F (1981) Mediterranean-type shrublands of the world. In: Di Castri F, Goodall DW, Specht RL (eds) *Mediterranean-type shrublands*. Elsevier, Amsterdam, pp 1–52
- Diaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J Appl Ecol* 38:497–508
- Diaz S, Lavorel S, McIntyre S et al (2007) Plant trait responses to grazing—a global synthesis. *Glob Change Biol* 13:313–341
- Dimitrakopoulos PG, Memtsas D, Troumbis AY (2004) Questioning the effectiveness of the Natura 2000 Special Areas of Conservation strategy: the case of Crete. *Glob Ecol Biogeogr* 13:199–207
- Dimitrakopoulos PG, Galanidis A, Siamantziouras ASD et al (2005) Short-term invasibility patterns in burnt and unburnt experimental Mediterranean grassland communities of varying diversities. *Oecologia* 143:428–437
- EU (2007) *Interpretation Manual of European Union Habitats, EUR27*. European Commission, DG Environment, Brussels, pp 144
- Facelli JM, Springbett H (2009) Why do some species in arid lands increase under grazing? Mechanisms that favour increased abundance of *Maireana pyramidata* in overgrazed chenopod shrublands of South Australia. *Austral Ecol* 34:588–597
- Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347
- Hadar L, Noy-Meir I, Perevolotsky A (1999) The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. *J Veg Sci* 10:673–682
- Hay M, Kicklighter C (2001) *Grazing, effects of encyclopedia of biodiversity*. vol 3. Academic Press, San Diego, pp 265–276
- Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305
- Huston M (1979) General hypothesis of species-diversity. *Am Nat* 113:81–101
- Joshi J, Schmid B, Caldeira MC et al (2001) Local adaptation enhances performance of common plant species. *Ecol Lett* 4:536–544
- Kallimanis AS, Mazaris AD, Tzanopoulos J et al (2008) How does habitat diversity affect the species–area relationship? *Glob Ecol Biogeogr* 17:532–538
- Landsberg J, Lavorel S, Stol J (1999) Grazing response groups among understorey plants in arid rangelands. *J Veg Sci* 10:683–696
- Lavorel S, McIntyre S, Landsberg J et al (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol Evol* 12:474–478
- Lavorel S, Rochette C, Lebreton JD (1999) Functional groups for response to disturbance in Mediterranean old fields. *Oikos* 84:480–498
- McIntyre S, Lavorel S (1994) Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. *Conserv Biol* 8:521–531
- McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes—their relationship to disturbance responses in herbaceous vegetation. *J Ecol* 83:31–44
- McIntyre S, Lavorel S, Landsberg J et al (1999) Disturbance response in vegetation towards a global perspective on functional traits. *J Veg Sci* 10:621–630

- Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol Monogr* 63:327–366
- Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized-model of the effects of grazing by large herbivores on grassland community structure. *Am Nat* 132:87–106
- Montalvo J, Casado MA, Levassor C et al (1993) Species-diversity patterns in mediterranean grasslands. *J Veg Sci* 4:213–222
- Mwendera EJ, Saleem MAM, Woldu Z (1997) Vegetation response to cattle grazing in the Ethiopian Highlands. *Agric Ecosyst Environ* 64:43–51
- Naveh Z (1990) Ancient mans impact on the Mediterranean landscape in Israel—ecological and evolutionary perspectives. In: Bottema S, Entjes-Nieborg G, Van Zeist W (eds) *Man's role in the shaping of the East Mediterranean Landscape*. AA Balkema, Rotterdam, pp 43–50
- Noy-Meir I (1995) Interactive effects of fire and grazing on structure and diversity of mediterranean grasslands. *J Veg Sci* 6:701–710
- Noy-Meir I, Briske DD (2002) Response of wild wheat populations to grazing in Mediterranean grasslands: the relative influence of defoliation, competition, mulch and genotype. *J Appl Ecol* 39:259–278
- Noy-Meir I, Oron T (2001) Effects of grazing on geophytes in Mediterranean vegetation. *J Veg Sci* 12:749–760
- Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of mediterranean grassland plants to grazing and protection. *J Ecol* 77:290–310
- Olf H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. *Trends Ecol Evol* 13:261–265
- Osem Y, Perevolotsky A, Kigel J (2007) Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small scale spatial and temporal variation in primary productivity. *J Ecol* 90:936–946
- Pakeman RJ (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *J Ecol* 92:893–905
- Petchev OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecol Lett* 9:741–758
- Petraitis PS, Latham RE, Niesenbaum RA (1989) The maintenance of species-diversity by disturbance. *Quart Rev Biol* 64:393–418
- Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79:2581–2592
- Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol Lett* 7:491–508
- Siegel S, Castellan JWW (1988) *Nonparametric statistics for the behavioural sciences*. McGraw-Hill Book Company, New York
- Sousa WP (1984) The role of disturbance in natural communities. *Ann Rev Ecol Syst* 15:353–391
- Spehn EM, Hector A, Joshi J et al (2005) Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol Monogr* 75:37–63
- Sternberg M, Gutman M, Perevolotsky A et al (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *J Appl Ecol* 37:224–237
- Todd SW, Hoffman MT (2009) A fence line in time demonstrates grazing-induced vegetation shifts and dynamics in the semiarid Succulent Karoo. *Ecol Appl* 19:1897–1908
- Troumbis AY, Dimitrakopoulos PG, Siamantziouras ASD et al (2000) Hidden diversity and productivity patterns in mixed Mediterranean grasslands. *Oikos* 90:549–559
- Verdu JR, Moreno CE, Sanchez-Rojas G et al (2007) Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosphere Reserve. *Biol Conserv* 140:308–317
- Vesk PA, Leishman MR, Westoby M (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *J Appl Ecol* 41:22–31