

# Abandonment in grazing systems: Consequences for vegetation and soil

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Received 11 March 2005; received in revised form 19 September 2005; accepted 23 September 2005

Available online 4 January 2006

## Abstract

Many dehesa zones in marginal areas are suffering from the abandonment of traditional farming practices. Herbivore grazing affects grassland dynamics, changing the species colonisation and extinction relationships via consumption, mechanical disturbance, seed dispersal and altered soil fertility due to dung-borne nutrient input. This paper analyses changes to floristic composition, species richness and heterogeneity as well as soil and light resources in relation to grazing abandonment in two characteristic topography-related types of dehesa habitat (upper slope and lower slope grasslands). Vegetation surveys were undertaken using five replicates in each habitat type in grazed and abandoned grasslands in the Guadarrama range in Central Spain with distric cambisol soils. Additional measurements of light and soil parameters were also undertaken. The results show an effect of grazing on resource availability. In general there was a smaller proportion of fine matter (clay), organic matter, total nitrogen, assimilable potassium and readily available water in abandoned as opposed to grazed zones. We did not find any effect of grazing on phosphorous availability. Abandonment reduces light availability at ground level in lower slope grasslands (wet meadows) but does not produce a significant reduction in upper slope (driest) grasslands, although there is an increased spatial heterogeneity in the availability of light associated with the presence of scattered shrubs. While the total number of species in abandoned zones did not significantly differ from grazed zones, floristic composition changed dramatically with abandonment in both habitat types, with less than 50% of common species. Also, floristic heterogeneity at the small scale increased with abandonment. Designers of agri-environmental policies applied to Mediterranean grasslands should be aware of the risk of widespread grazing abandonment and promote the diversification of grazing regimes across the landscape to maximize species diversity and take advantage of the benefits of low-density grazing in other functions of the ecosystem such as their productivity and stability.

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**Keywords:** Dehesa; Grazing abandonment; Heterogeneity; PAR extinction rate; Species richness; Soil physical and chemical properties

## 1. Introduction

Acceptance of the importance of low intensity farming systems for the conservation of biodiversity in Europe has grown recently (Baldock et al., 1994; Signal et al., 1994). One example of these agrosystems is the *dehesa* or *montado*, whose importance in the European context has been widely acknowledged (Díaz et al., 1997; Peco et al., 2001; Peco, 2002). This agrosystem is an open woodland of *Quercus ilex*

or *Quercus suber* with an understorey of grassland, cereal crops or Mediterranean scrub located on poor sandy acidic soils in the west of the Iberian Peninsula. Traditional extensive management with periodical ploughing, no input of mineral fertilizers, optimum stocking rates (0.2–0.5 LU/Ha) with rough grazing by domestic livestock (mainly cattle and sheep) often including seasonal movements of animals to adjust to productivity limitations, has influenced these systems for centuries (Le-Houérou, 1981). Recent changes in the farming industry are pushing these types of agricultural systems towards intensification in the more productive and populated areas and abandonment in

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marginal zones (Díaz et al., 1997). This dual process of intensification and abandonment, which can coexist even at the local scale, is producing fragmentation of the species-rich semi-natural grasslands which, along with habitat deterioration, are the main factors causing loss of plant populations and species (Harrison and Bruna, 1999; Erikson and Ehrlén, 2001).

One of the natural values of the *dehesa* is its extremely high plant species richness (more than 180 species per 1000 m<sup>2</sup>, approximately 30 species in 20 cm × 20 cm quadrat) (Díaz Pineda et al., 1981; Marañón, 1986). This richness is probably the result of the wide spatial and temporal heterogeneity in the soil and climate conditions, grazing by domestic and wild animals and other low-impact human-induced grassland management practices.

Herbivores can control grassland diversity through mechanisms that affect the colonization-extinction dynamics of the species (Olf and Ritchie, 1998). They are generally regarded as disturbance generators because they consume leaves, fruits and roots and involve mechanical action such as trampling (Crawley, 1997). They also play an important role as dispersers of viable seeds (Malo and Suarez, 1995; Fischer et al., 1996). Herbivores produce changes in the physical and chemical soil properties. Their influence on the spatial distribution of fertility and nutrient cycling due to dung and urine inputs was recognized long ago (Haynes and Williams, 1993; Steinauer and Collins, 1995). Herbivores also produce soil disturbance by pressure or trampling (Shankar and Singh, 1996), which can increase site regeneration and soil heterogeneity and thus create more opportunities for coexistence (Grubb, 1977) but can also create widespread erosion processes that reduce plant diversity (Milchunas et al., 1988).

We still lack a general model to predict the vegetation response to grazing pressure in terms of species diversity. Herbivores are generally thought to increase species diversity, but some studies suggest weak or even negative effects (see review in Olf and Ritchie, 1998). The intermediate disturbance theory (Grime, 1973), which predicts maximum diversity at intermediate disturbance levels, has been used by some authors to explain single-mode relationships (Naveh and Whittaker, 1979). Thus, zones with low grazing intensity have less species as a result of competitive exclusion, but when grazing pressure is excessive, diversity falls because of mortality in species, which are less resistant to this type of disturbance. This model was complicated by the inclusion of evolutionary grazing history and habitat type, mainly defined by climate and productivity (Milchunas et al., 1988). The model predicts that semiarid-grasslands with a long history of grazing only respond with a moderate decrease in diversity under increasing grazing intensity, while under more humid conditions, the effect of grazing should be more intense. The reason for this differing response is that in subhumid environments, the major limiting factor for plants is light while in semiarid environments it is water. Adaptations that

enhance survival in semiarid environments may promote grazing tolerance or avoidance because water stress and grazing stress are similar in the sense that both result in a loss of plant organs. In subhumid environments, divergent selection pressure (competition for light and grazing tolerance) maintains species pools that permit switches in plant species and competition modes that depend on grazing intensity.

The conceptual model proposed by Milchunas et al. (1988) has generally been supported by meta-analysis over a global range of environments (Milchunas and Lauenroth, 1993). In the Mediterranean Basin there have been numerous short-term exclosure experiments to analyse the effect of grazing on grassland communities, especially in central Spain (Montalvo et al., 1993; Ortega et al., 1996; Peco et al., 1998), and Israel (Noy-Meir et al., 1989; Noy-Meir, 1995; Noy-Meir, 1998). In most cases, the observed effects are consistent with the predictions of Milchunas et al. model (1988) for sub-humid grasslands with a long evolutionary history of grazing, with more species richness in the grazed areas. Exceptions to this pattern have also been found on very poor soils with a non-significant reduction of species richness after grazing exclusion (Hadar, 1996).

The importance of long-term series (more than 20 years) for analysing the effects of climate and land use change is widely recognized (Bakker et al., 1996). Unfortunately, very few long-term experimental series are available for the analysis of the effect of grazing, primarily due to the difficulty of maintaining such experiments due to the lack of human and material resources for long-term projects. One alternative is to analyse spatial series (chronosequences) corresponding to different levels of grazing that have been in action for a long period. In the present study, we used land-use history to differentiate grazed and abandoned situations. This natural experiment (*sensu* Diamond, 1986) has the advantage of permitting the observation of differences in grazing patterns that have been at work in the landscape for decades and can include replications that are harder to achieve in grazing trials, while at the same time avoiding the undesirable effects caused by exclosures.

In this paper, we analyse the effect of long-term grazing abandonment on floristic composition and vegetation richness in *dehesa* grasslands of central Spain. Because, we can expect the effect to depend on the productivity of the microhabitat, we propose a small-scale approach that is similar to Ossen et al. (2004), comparing neighbouring topographic microenvironments (south- and north-facing slopes, hilltop and wadi shoulders). Our hypothesis is that grazing abandonment produces smaller changes in floristic composition and vegetation richness in upper slope dry/unproductive habitats than in lower slope wet/more productive habitats. At the species level, we analyse individual species responses to grazing and the consistency of these responses in relation to habitat type.

Finally, we analyse the spatial variability of light, water availability and soil resources and the effect of grazing

abandonment on this patterns to try to propose the mechanisms underlying the species responses.

## 2. Materials and methods

### 2.1. Study area

The study area was 35 km north of Madrid at an altitude of 900 m in the Sierra de Guadarrama (UTM 30 T VL 446 mE 4508 mN). The climate is continental Mediterranean with an average of 550 mm annual rainfall and heavy interannual fluctuations (standard deviation: 83.01).

The area is mainly covered by *dehesas* (open savannah-like woodlands) of *Quercus ilex* subsp. *ballota* and an open grassland understorey with a high percentage (>90%) of annual species. These grasslands have been grazed traditionally by sheep and cattle since the Middle Ages. In the 15th century, the property was split between two municipalities. Part of the *dehesa* is still used communally for cattle grazing all year round, at low stocking densities (less than 0.5 livestock units/ha), while the other part passed into private hands and was ploughed occasionally and grazed until it was abandoned at least 30 years ago. The abandoned area has been invaded by woody species in the upper slope habitats, mainly *Lavandula stoechas* subsp. *pedunculata*, *Cytisus scoparius* and *Juniperus oxycedrus* (Traba, 2000) but still has a high cover (70–90%) of herbaceous species, mainly annuals. In the more humid habitats, which appear on the wadi shoulders, the woody species disappear and perennial tussock-grasses dominate. Grazed and abandoned areas have the same physical features: gentle slopes (<5%) on shallow acidic soils (distric cambisol) and a gneiss substratum.

### 2.2. Vegetation sampling

In grazed and abandoned zones, we differentiated two topography-related habitat types: dry grasslands on the upper part of the slopes and wet meadows on the lower part of the slopes (wadi).

In spring 2000, we chose five 10 m × 10 m plots in each habitat type in both grazed and abandoned areas. We recorded the presence of all species in 10 quadrats (20 cm × 20 cm) set at random in each plot.

### 2.3. Soil sampling and analysis

Ten randomly selected soil samples were taken in September 1999 in each zone and habitat type. Core samplers measuring 5 cm diameter and 10 cm deep were used to extract the soil samples, which were then air dried and sieved with 2 mm mesh. The analysed parameters were: organic matter (Walkley and Black, 1934), total nitrogen (Kjeldahl), exchangeable phosphorous and potassium (extraction by acetate-EDTA: Läkanen and Enviö, 1971;

Cottenie et al., 1975; measure with spectrophotometer except for phosphorus (colorimeter)), sand and clay (Day, 1965) and readily available water (the amount of water between “field capacity” and the “wilting point”). Water content in soil was analysed by gravimetric techniques (Richards, 1954). The units used to present the soil data are g/kg dry soil except for phosphorous and potassium: mg/100 g dry soil.

### 2.4. Measurements of light extinction rate

Photosynthetic active radiation (PAR) was measured using a radiometer (Delta OHM HD 9021) on a sunny autumn day between 12:00 and 14:00 in order to characterize the light environment at the time of germination in each zone and habitat type. Autumn was selected because most of the germination is concentrated in this period in the area (Ortega et al., 1996). Ten measurements were taken at ground level at 10 randomly selected sampling points in each zone and habitat type. Ten measurements were also taken above the plant canopy. The PAR extinction rate through vegetation was calculated as  $E = ((P - F) / P) \times 100$ , where  $P$  is the mean incidence of PAR above the plant canopy and  $F$  is the mean incidence of PAR at ground level.

### 2.5. Data analysis

To analyse changes in floristic composition, Canonical correspondence analysis (CCA) ordination was performed on species frequency data using CANOCO 4.5 (ter Braak and Smilauer, 2002). Conditional effects show the amount of additional variation contributed by each variable when added to the model (ter Braak and Smilauer, 2002). A forward selection process was used to rank the variables in order of their importance in determining the species data. The significance of the variable at the time it was included in the model was tested using a Monte Carlo permutation test using 499 permutations. The inertia from the conditional effects was used to derive the multivariate correlation ratio (MCR), which represents the proportion of variation explained by the individual factors.

Individual species abundance trends in relation to the grazing regime were identified using frequency data at the plot scale. In each habitat type, species were classified in relation to grazing as increasers, decreasers or indifferent species using *t*-test. Grazing increasers were species significantly more frequent in grazed than abandoned sites. Grazing decreasers were species significantly more frequent in abandoned sites. Indifferent species were species that did not show significant differences in frequency between grazed and abandoned sites. Only species present in more than 10% of the samples were used for this species response groups analysis. Finally, the Jaccard index was used to calculate the similarity in species composition between the quadrats of each plot and, the mean value of dissimilarity (1, Jaccard index) was used as an indicator of floristic

heterogeneity at the quadrat scale. To test differences in relation to grazing and habitat type in species richness and floristic heterogeneity at the quadrat scale, soil parameters and light extinction rate, we used a two-way ANOVA. Appropriate transformations were applied if necessary to adjust to the models requirements. The SPSS 11.5 package (1989–2003) was used in all statistical analyses.

### 3. Results

#### 3.1. Floristic composition

The total number of species found was 187, with 114 in the grazed zone and 157 in the abandoned zone. The percentage of floristic similarity between these two zones measured by the Jaccard index with presence/absence data was only 43%, with 32 exclusive species in the grazed zones, 75 exclusive to the abandoned zones and 80 common species. In the upper slope habitats, the percentage of floristic similarity between grazed and abandoned zones was 40% while in the lower slope habitat it was 36%.

In the CCA, the major split on the first axis was between habitat types while the second axis separated grazed from abandoned plots (Fig. 1). Overall, these variables account for 25.70% of the variance in the data (Table 1). The sum of all unconstrained eigenvalues was 3.67. Both factors and the interaction term were significant under the Monte Carlo permutation test ( $P < 0.01$ ).

#### 3.2. Response groups

A total of 62 species were classified in relation to grazing in upper and lower slope habitats (Table 2). Only four species appeared simultaneously in the response groups in upper slope and lower slope habitats: *Spergularia purpurea*,

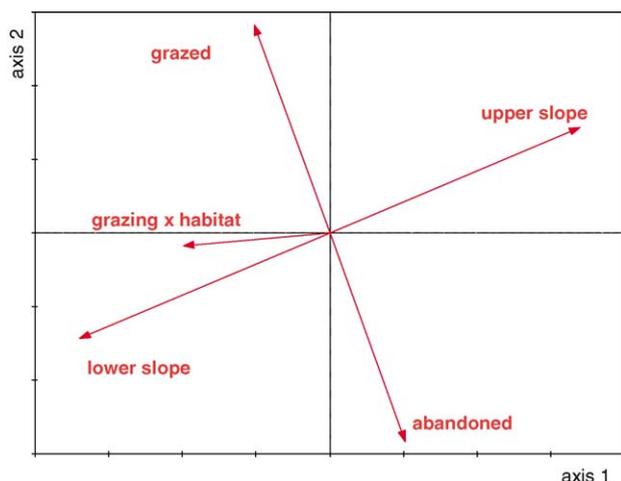


Fig. 1. Ordination showing the first two axes of the CCA. Factors are grazing (grazed, abandoned) and habitat type (upper slope, lower slope). Length of the vectors indicates the strength of the correlations between categories of factors and the CCA axes. Details of these variables in Table 1.

Table 1  
Canonical correspondence analysis

Factors	Inertia conditional effects	$P$	MCR (%) per factor
Habitat	0.54	0.002	14.71
Grazing	0.44	0.002	11.99
Habitat $\times$ grazing	0.37	0.002	10.10

MCR: multivariate correlation ratio.

which always appeared in the group of grazing increasers but with a higher significance level in the case of upper slope habitats, and *Spergula arvensis*, *Vulpia ciliata* and *Vulpia muralis*, which change group when the habitat changes. *Vulpia ciliata* is thus a grazing decreaser in upper slope habitats but indifferent in lower slope habitats, *Vulpia muralis* is indifferent in upper slope habitats but a grazing increaser in lower slope habitats, and *Spergula arvensis* is a grazing increaser in upper slope habitats and indifferent in lower slope habitats.

#### 3.3. Species richness and heterogeneity

At the quadrat scale, we found significant differences in richness between habitats (Table 3) with greater richness in the upper slope habitat (Fig. 2a). The effect of grazing on species richness was not significant but the interaction between factors was marginally significant ( $p < 0.1$ ), indicating possible differences between habitats in this effect. Species heterogeneity (1, Jaccard index) was only marginally different between habitats (Table 3), but highly significant between grazed and abandoned plots, with more heterogeneity in abandoned plots in all habitat types (Fig. 2b).

#### 3.4. Light, water availability and soil resources

We found significant differences in PAR extinction rate in the autumn between grazed and abandoned zones (Table 4), with a higher extinction rate in the abandoned zones (Fig. 3a). Surprisingly, no differences were found between habitats.

We also found significant differences in soil parameters for grazing and habitat type (Table 4). Grazing produces a reduction in the percentage of sand and an increase in the percentage of clay in all habitats (Fig. 3b and c). There was also a general increase in total nitrogen, organic matter and available water (Fig. 3d–f) in the grazed in comparison with the abandoned zones. Finally, grazing had no significant effect on phosphorus levels (Fig. 3g) while in the case of potassium (Fig. 3h), the two analysed factors showed a strong interaction (Table 4), with more potassium in the grazed than in the abandoned zones in the upper slope habitat, while the opposite was the case in the lower slope habitat. Both habitats also differed overall in the rest of the soil parameters (Fig. 3). Hence, the upper slope habitat was richer in sand and phosphorus than the lower slope habitat. The latter, however,

Table 2  
Plant species for which a grazing response was identified in each habitat type

Grazing increasers	P	Indifferent	Grazing decreaseers	P
<b>Upper slope</b>				
<i>Anthemis arvensis</i> <sup>a</sup>	***	<i>Aira caryophyllea</i>	<i>Agrostis castellana</i> <sup>a</sup>	***
<i>Aphanes microcarpa</i> <sup>a</sup>	**	<i>Andryala integrifolia</i>	<i>Asterolinon linum-stellatum</i>	*
<i>Astragalus pelecinus</i>	*	<i>Brassica barrelieri</i>	<i>Avena barbata</i>	*
<i>Crassula tillaea</i>	*	<i>Galium parisiense</i>	<i>Campanula lusitanica</i>	*
<i>Erodium cicutarium</i> <sup>a</sup>	**	<i>Ornithopus compressus</i> <sup>a</sup>	<i>Coronilla repanda</i> <sup>a</sup>	***
<i>Filago lutescens</i> <sup>a</sup>	*	<i>Trifolium campestre</i>	<i>Holcus setiglumis</i>	*
<i>Herniaria hirsuta</i> <sup>a</sup>	**	<i>Xolantha guttata</i> <sup>a</sup>	<i>Jasione montana</i> <sup>a</sup>	**
<i>Hypochoeris glabra</i> <sup>a</sup>	**	<i>Vulpia muralis</i> <sup>a</sup>	<i>Lathyrus angulatus</i>	*
<i>Moenchia erecta</i>	*		<i>Lavandula stoechas</i> <sup>a</sup>	***
<i>Plantago coronopus</i> <sup>a</sup>	*		<i>Linaria spartea</i>	*
<i>Poa bulbosa</i> <sup>a</sup>	***		<i>Mibora minima</i> <sup>a</sup>	***
<i>Rumex acetosella</i>	*		<i>Sanguisorba minor</i>	*
<i>Spergula arvensis</i> <sup>a</sup>	**		<i>Silene scabriflora</i> <sup>a</sup>	***
<i>Spergularia purpurea</i> <sup>a</sup>	***		<i>Teesdalia coronopifolia</i>	***
<i>Trifolium glomeratum</i> <sup>a</sup>	**		<i>Vulpia ciliata</i>	*
<i>Trifolium subterraneum</i>	*			
<i>Trifolium suffocatum</i> <sup>a</sup>	*			
<b>Lower slope</b>				
<i>Juncus bufonius</i> <sup>a</sup>	*	<i>Bromus hordaceus</i>	<i>Anthoxanthum aristatum</i> <sup>a</sup>	*
<i>Merendera pyrenaica</i>	**	<i>Crepis capillaris</i>	<i>Briza minor</i>	*
<i>Poa annua</i>	**	<i>Festuca rothmaleri</i>	<i>Festuca ampla</i>	*
<i>Spergularia purpurea</i>	*	<i>Juncus acutiflorus</i>	<i>Trifolium strictum</i>	*
<i>Trifolium cernuum</i> <sup>a</sup>	***	<i>Lotus angustissimus</i>		
<i>Trifolium micranthum</i>	***	<i>Montia minor</i>		
<i>Trifolium ornithopodioides</i>	*	<i>Ranunculus bulbosus</i>		
<i>Vulpia muralis</i> <sup>a</sup>	**	<i>Scirpus setaceus</i> <sup>a</sup>		
		<i>Spergula arvensis</i>		
		<i>Vulpia ciliata</i>		

<sup>a</sup> Species present in more than 40% of the samples.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

had more clay, organic matter, nitrogen total and water retention capacity than the upper slope habitat.

## 4. Discussion

### 4.1. Floristic composition and species responses

Although the main factor explaining changes in the floristic composition of the studied communities was the topography-related productivity gradient, often an important factor in Mediterranean environments (González-Bernáldez and Díaz-Pineda, 1980; Casado et al., 1985), the abandon-

ment of long-term grazing is also associated with profound changes in floristic composition. The grazed and abandoned zones only share approximately 40% of the species, while the other 60% are exclusive to grazed or abandoned zones. This result coincides with findings by other authors who recognize that livestock grazing has a considerable effect on community structure and floristic composition (Milchunas and Lauenroth, 1993; Bullock et al., 1995). However, the

Table 3  
Two way-ANOVAs for species richness and heterogeneity

Parameters	Habitat		Grazing		Habitat × grazing	
	F	P	F	P	F	P
Species richness	5.33	*	0.25	n.s.	3.09	n.s.
Species heterogeneity	3.7	n.s.	17.35	***		n.s.

n.s.: non significant ( $n = 5$ ).

\*  $P < 0.05$ .

\*\*\*  $P < 0.001$ .

Table 4  
Two way-ANOVAs for soil parameters

Parameters	Habitat		Grazing		Habitat × grazing	
	F	P	F	P	F	P
PAR	0.83	n.s.	18.95	***	0.40	n.s.
Clay	83.64	***	9.98	**	1.42	n.s.
Sand	94.71	***	10.28	**	0.01	n.s.
Total nitrogen	89.76	***	29.22	***	2.21	n.s.
Organic matter	65.62	***	18.29	***	2.76	n.s.
Available water	78.28	***	6.77	**	0.23	n.s.
Phosphorous	39.52	***	1.32	n.s.	2.11	n.s.
Potassium	2.47	n.s.	2.41	n.s.	9.96	n.s.

n.s.: non significant ( $n = 5$ ).

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

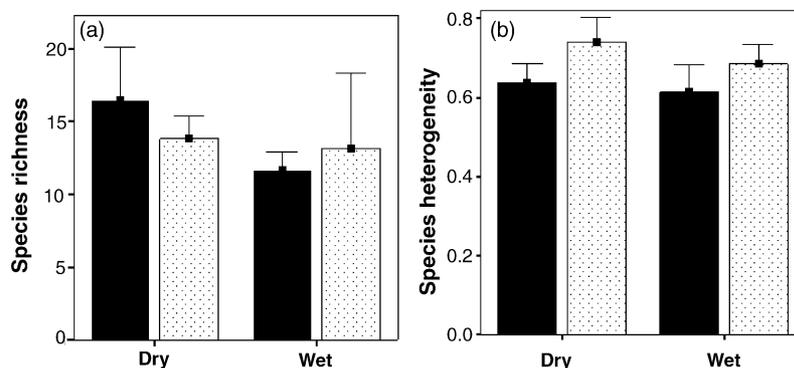


Fig. 2. Species richness (number of species) and heterogeneity (1 – Jaccard index) observed in 20 cm × 20 cm quadrats in relation to habitat type (upper slope, lower slope) and grazing (grazed: dark bars; abandoned: light bar). Error bars show 95.0% CI of mean.

mean dissimilitude between grazed and abandoned zones in our study (Fig. 2) had an equivalent magnitude in upper and lower slope pastures, which does not corroborate the hypothesis of Milchunas et al. (1988) that the changes in floristic composition with abandonment will be greater in moister zones.

We also detected a series of local species indicators of the grazing level. We found groups of grazing increasers and decreasers in both habitats, as well as species that were indifferent to grazing. These group responses can be very useful for the identification of functional responses types (Noy-Meir et al., 1989; Díaz et al., 2001; Bullock et al., 2001). In a previous study in the upper slope dry grasslands of the same study area, Peco et al. (2005) found that amongst the grazing increasers, the predominant species were cryptophytes, prostrate species, species with medium specific leaf area, early flowering, unassisted seeds and clonal reproduction, while the predominant grazing decreasers were chamaephytes, taller plants, species with heavy leaf dry weight, late flowering species, species with heavy seeds and fruits with adhesive structures. The grazing indicator value of these species should, however, be approached with caution as at the regional level, they can return inconsistent responses (Stohlgren et al., 1999; Vesik and Westoby, 2001). Although there is a higher degree of consistency at the local level (McIntyre et al., 2003), in our case, of the 18 common species with the work by Peco et al. (2005) in dry habitats, all showed consistent behaviour. Nevertheless, three of the four species that were common to the two habitat types in this study lost their indicator status with the change of habitat. These discrepancies, while moderate at the local level, might indicate that not only the functional traits of the species give them adaptive advantages with respect to grazing: in many cases, the individual response of the species depends on the traits of the rest of the species in the community and their relative abundance.

#### 4.2. Species richness and heterogeneity

Contrary to our expectations, we did not find any significant differences in species richness in relation to

abandonment in either upper slope or lower slope habitats. In the experimental design, we assumed that the differences in productivity linked to topography and greater water and nutrient availability in the lower slope zones in contrast to the upper slope zones would be large enough to detect different productivity-related trends in the response of richness to grazing (Milchunas et al., 1988), also found in Mediterranean environments along local topography-related productivity gradients (Ossen et al., 2002). Although the rainfall conditions in our study area were similar to the latter study area, our extremely poor soils prevented the differences in productivity between the high and low slope zones (150 and 250 g/m<sup>2</sup>, respectively, according to Montalvo (1992)) from being as notable as those reported by the former authors (<200 g/m<sup>2</sup> on hilltop and up to 700 g/m<sup>2</sup> on the wadi shoulders). The productivity ranges in our sampling plots yielded results that concur with the proposal by Milchunas et al. (1988) for semiarid environments in which plant growth and diversity is primarily limited by soil resources (mainly water and minerals) and not by light, as in the more productive habitats. A 5-year enclosure experiment by Montalvo et al. (1993) on an altitudinal gradient that included our study area found that enclosure tended to reduce the number of species. Nevertheless, these effects were very small (2–3 species) and not consistent between years or topographic positions, suggesting that the effect of the weather conditions on species richness in one particular year can interfere with the effect of the enclosure, especially in grasslands dominated by annual species (Peco et al., 1998). Noy-Meir (1998) also points out that there is little evidence of response by richness to grazing in oligotrophic grasslands, which are invadable by small shrubs, mentioning a paper by Hadar (1996) in which grazing exclusion also lacked a significant effect on richness. While all papers discussed in this section evaluate the effects of grazing in short-term enclosure experiments, in our case the focus is on long-term abandonment (more than 30 years). This difference might also explain the discrepancies, because while it might be true that grassland enclosure causes a decline, albeit only slight, in the number of species, the colonization processes in abandoned pasture by forest species confined

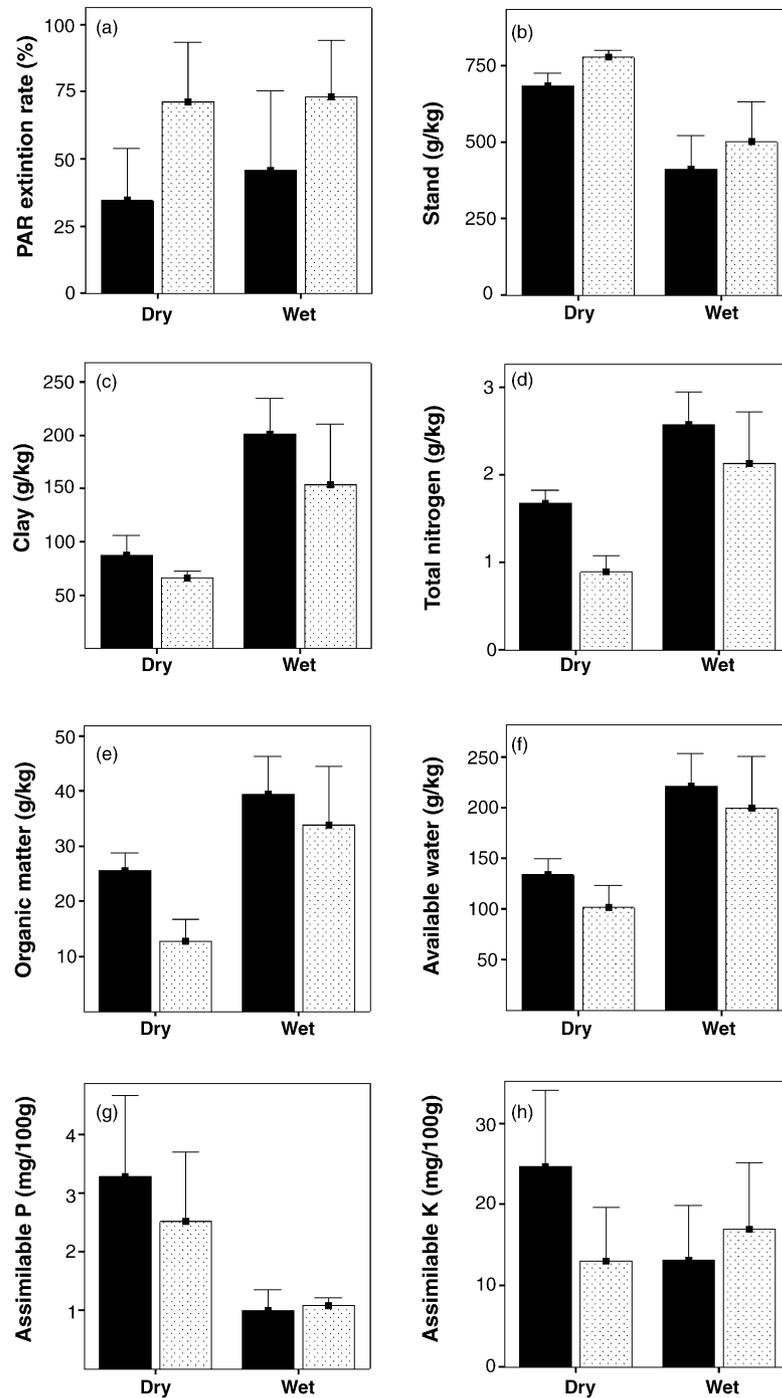


Fig. 3. Soil parameters observed in relation to habitat (upper slope, lower slope grasslands) and grazing (grazed grassland: dark bars; abandoned grassland: light bar). Error bars show 95.0% CI of mean.

to natural grazing refuges (Noy-Meir, 1998) are slower and were thus not recorded in the above-mentioned experiments.

Grazing abandonment does seem to produce an increase in small-scale spatial heterogeneity in both topographic positions. This may be linked to the role of livestock as a seed disperser (Malo and Suarez, 1995; Poschlod et al., 1996) and hence as a homogeniser of floristic composition,

reducing the tendency of the seed banks to be spatially clumped (Pake and Venable, 1996; Bertiller, 1998; Marone et al., 1998). Another possible explanation is that the increased heterogeneity with no grazing could simply be the effect of scrub invasion into a uniform grassy sward. This is not the case of the lower slope zones in which there is no scrub invasion. In the upper slope zones this possible explanation has been discarded reanalysing the values of

intraplots heterogeneity without *Lavandula pedunculata*, the only scrub present in the samples. The average heterogeneity for grazed and ungrazed zones shows very similar values as those in Fig. 2 (0.66 and 0.78 for grazed and abandoned zones, respectively) and also significantly different ( $P < 0.001$ ).

#### 4.3. Grazing and resource availability

The absence of livestock involves changes in the vegetation structure that are obvious to the eye. In upper slope zones there is an invasion by low shrubs with an open structure that coinhabit the zone with pastures still dominated by annual species. Bare soil covers 9%, a similar level to grazed zones, and 20% of the soil is occupied by a lichen crust. In lower slope zones, on the other hand, the pasture becomes denser, reducing the amount of bare soil (around 5%), roughly half of the bare soil area in grazed zones (Sánchez, 2001). These changes in the structure also involve changes in the light-resource environment. While abandonment produces a reduction in the light available at ground level in lower slope pastures, in upper slope pastures it does not lead to a generalized loss of the luminosity level on the ground, although it creates a more diverse lighting environment due to the effect of thickets. Whatever the case, the mean difference in the rate of light extinction between grazed and abandoned zones in both types of habitat is 30%, with a quite high measured level of average open ground PAR ( $934.79 \mu\text{Einstein/s/m}^2$  for an average cloudless September day), characteristic of Mediterranean environments, enabling less emphasis to be placed on light as a structuring factor for these open communities.

The main differences in the soil parameters are linked to a topographic gradient in which the low slope zones have higher proportions of clay, organic matter, total nitrogen and water availability. This result corroborates previous findings in Mediterranean environments (Ruiz et al., 1980). Although they have a smaller effect, grazing by large herbivores seems to also influence the soil characteristics, particularly in the upper slope zones. Extensive grazing thus seems to increase fertility (nitrogen and potassium) and water availability, probably through the input of organic matter in faeces and nutrient redistribution. Nitrogen recycling through dung and urine is often given as an explanation of increased mineralization rates under grazing (Ruess and McNaughton, 1987) since herbivore dung is more easily decomposable than most plant litter due to the favourable C/N ratio of dung (Pastor et al., 1993; Hobbs, 1996; Frank and Groffman, 1998). However, the effects of herbivores on nitrogen cycling depend on the habitat type and herbivore species through differences in the spatial patterns of dung deposition and volume (Bakker et al., 2004). In addition, herbivores can have an indirect effect on nutrient cycling when they influence the vegetation composition, resulting in changed nutrient input through litter (Pastor et al., 1993; Ritchie et al., 1998; Olofsson and Osaken, 2002). The organic matter

deposited with the faeces also assists soil stability, retaining fine particles through the formation of clay-humic complexes. We have seen that in the absence of livestock, the fine fraction declines, possibly due to increased erosion in the absence of structuring organic matter. The lower concentration of soil organic matter in abandoned areas probably makes soil aggregate less stable and more susceptible to breakdown under the effect of raindrop splashing. Through the same process, livestock seems to have a positive effect on the water retention ability of soil. In the case of phosphorous, no significant differences linked to grazing were found, although the upper slope habitat had more assimilable phosphorous than the lower slope habitat. This result may be due to the *dehesa* structure of the grasslands, with scattered trees in the drier habitats and scrub invasion following the abandonment of grazing. It is generally accepted that both trees and shrubs are able to increase phosphorous availability through the input from their leaf litter and their ability to extract this nutrient from deeper soil layers (González Bernáldez et al., 1969; Moro et al., 1997; Gallardo, 2003). In the case of the lower slope grasslands, the lack of the tree and shrub storey, even in abandoned states, could be related to the lower phosphorous availability in these habitats. A positive relationship between increased soluble phosphorous in the soil and grazing intensity has been detected in heavily grazed woodlands of SW Australia (Yates et al., 2000). In contrast, however, only marginal effects were found in the case of low to moderate grazing in Californian oak woodlands (Dahlgren et al., 1997).

#### 4.4. Richness and resource availability

This work is of limited value for linking richness to resource availability, as both the PAR and the soil samples were taken using the same sampling design but in different years and plots from the richness measurements. However, the comparison of the measurements in the four analysed situations (grazing and habitat type), permit several hypotheses to be advanced on the operation of these pastures. Although there were no significant differences in overall richness in relation to grazing, in the upper slope habitat, there is a slightly significant tendency ( $P < 0.10$ ) for grazed zones to have more richness than the abandoned zones, while in the lower slope zones there are no differences in richness between these two groups of plots. The explanation that we can provide is based on the particular effect of the livestock as a modifying agent of the nutrient cycle and the high availability of gaps that characterize grasslands on such poor soils. Here, grazing abandonment seems to have a different effect, depending on the local topography-related productivity. In the upper slope habitat, abandonment does not cause a problem of competition for canopy resources (light) as the light environment becomes more heterogeneous while there are still gaps with a high light availability, however the soils become impoverished and plant growth and diversity is limited by soil resources

(mainly water and minerals). When livestock provide nutrient input and the water retention ability, the soils produce a slight increase in richness. The probability of colonization via endozoochorous (Malo and Suarez, 1995) and epizoochorous (Fischer et al., 1996) dispersal also increases, a most important factor in a community in which there is a predominance of small-seeded species lacking specialized dispersal structures (Azcárate et al., 2002). In the lower slope habitat, on the other hand, the soil fertility conditions are somewhat better although they are still low and, together with the low rainfall, do not lead to an excessive spread of the canopy after abandonment, which may explain the lack of effects in this habitat. The low richness in the most productive habitats in grazed zones may also be due to excessive pressure by cattle in these microenvironments, a focal point for livestock when the driest zones are exhausted (De Miguel et al., 1989).

## 5. Conclusion

The results presented here show that the impact of low-intensity grazing in dehesa systems not only affects the vegetation structure and composition but also the physical and hydrological properties, light availability at the ground level and soil chemistry. These effects may have important consequences for nature conservation in these valuable agrosystems. Long-term grazing abandonment causes the loss of more than 60% of grassland species in dehesas. Although the zones invaded by scrub are also very species-rich, widespread abandonment can produce a reduction in floristic richness at the landscape scale on account of the different floristic composition in grazed and abandoned zones. Moderate grazing improves fertility in very poor soils and can promote species richness at the local scale and vegetation cover, which enhances protection from soil erosion. It also improves the water retention ability of the soil, which can have important consequences for seed germination and seedling establishment in environments where the main limiting factor for these processes is water (Espigares and Peco, 1993). Finally, although it was not evaluated in this study, there is no doubt that grazing can control the accumulated biomass, reduce the fire hazard and the consequent degrading processes in vegetation and soil. At the landscape scale it is therefore advisable to combine areas with different types of grazing pressure to maximize species diversity at the landscape level and use the benefits of low-density grazing in other functions of the ecosystem such as productivity and stability.

## Acknowledgements

We are grateful to C. Levassor for her help in the field work. The study was supported by the Spanish Ministry of Science and Technology (projects AMB 990382 and REN

2003-01562) and Spanish Ministry of Education and Culture (FPI scholarships to F.M.A. and A.M.S.).

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