Capítulo 6

El pastoreo de herbívoros de diferente tamaño no afecta a la diversidad de plantas anuales en pastizales mediterráneos semiáridos

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Rueda, M. & Rebollo, S. *In preparation*. Grazing by different-sized herbivores does not affect annual plant diversity in semi-arid Mediterranean pastures.

Resumen

Diferentes autores han señalado que los gradientes de precipitación y fertilidad del suelo determinan la abundancia de herbívoros de diferente tamaño y sus efectos sobre la vegetación. Ambientes secos e infértiles estarán dominados por una escasa comunidad de pequeños herbívoros, teniendo el pastoreo por múltiples herbívoros efectos negativos sobre la diversidad de plantas. Al contrario, ambientes húmedos y fértiles estarán dominados por una abundante y diversa comunidad de herbívoros que aumentarán la diversidad. Pocos experimentos han testado la aplicabilidad de estas predicciones en comunidades de plantas anuales. En este trabajo estudiamos el efecto de herbívoros grandes *versus* pequeños sobre la diversidad de plantas y los cambios en la abundancia de grupos funcionales en un pastizal mediterráneo semiárido del centro de España durante tres años. Las preferencias de ovejas y conejos silvestres por los diferentes ambientes fueron estimadas mediante conteos de heces. La respuesta de la comunidad de plantas al pastoreo de ovejas y conejos se analizó usando parcelas de exclusión situadas en dos posiciones topográficas: zonas altas y zonas bajas, las cuales variaron en humedad y fertilidad del suelo. En disconformidad con las predicciones, los conejos y las ovejas no mostraron una clara preferencia por lugares con diferente productividad. Una percepción desigual del riesgo de depredación por parte de ambos herbívoros pudo influir en las preferencias de éstos por cada tipo de ambiente. El pastoreo de ovejas y conejos no afectó a la diversidad de plantas tanto en áreas con alta como con baja productividad. Las leguminosas fueron el único grupo fuertemente influido por el pastoreo. La larga historia de pastoreo de los pastizales mediterráneos y la influencia de factores abióticos tales como la variabilidad de las precipitaciónes pueden haber enmascarado los efectos del pastoreo a corto plazo. Son necesarios experimentos a largo plazo para seguir explorando los efectos de la herbivoría sobre la diversidad de plantas anuales. La historia evolutiva de pastoreo por grandes y pequeños herbívoros debería ser tenida en cuenta en aquellos estudios que valoren la respuesta de las plantas a la herbivoría.

Grazing by different-sized herbivores does not affect annual plant diversity in semi-arid Mediterranean pastures

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Abstract

Several authors have pointed out that precipitation and soil fertility gradients determine the abundance of different sized herbivores and their grazing effects. A sparse community of small herbivores will dominate dry and infertile environments, and multiple herbivory will have marked negative effects on plant diversity in these environments. In contrast, an abundant and diverse herbivore community will increase plant diversity in wet and fertile environments. Few experiments have tested the applicability of these predictions in annual plant communities. We explored the effects of large vs. small herbivores on plant diversity and functional groups in a semi-arid Mediterranean pasture in Central Spain over three years. We assessed the preferences of sheep and rabbits for different environments by means of faecal counts. We analysed the response of the plant community to sheep and wild rabbit grazing using replicated fence exclosures in two topographic positions: uplands and lowlands, which differed in soil moisture and fertility. In contrast with predictions, rabbits and sheep did not show a clear preference for different productivity sites. Unequal predation risk perception by small vs. large herbivores may have influenced the preference of different-sized grazers for specific environments. Grazing by sheep and rabbits did not affect plant diversity in either low or high productivity areas. Legumes were the only group strongly influenced by grazing. The long grazing history of Mediterranean pastures and the influence of abiotic factors such as the precipitation availability seemed to override grazing effects in the short-term. Long-term experiments are needed to further explore the effects of herbivory on annual plant diversity. The evolutionary history of grazing by large and small herbivores should be taken into account in those studies assessing plant responses to herbivory.

Keywords: Annual plant community, `dehesa´ ecosystem, different-sized herbivores, herbivore-plant interaction, *Oryctolagus cuniculus*, plant species richness.

1. Introduction

Grassland ecosystems are usually grazed by herbivore assemblages, but the role played by different types of herbivores in maintaining plant species diversity is still not well understood. Recent works have suggested that the impact of herbivory could be explained through differences in herbivore size and habitat productivity (Milchunas and Lauenroth 1993, Proulx and Mazumder 1998, Ritchie and Olff 1999). Several authors have studied the effects of grazing by different sized herbivores (Ritchie *et al.* 1998, Bakker 2003). These studies have mainly taken place on perennial grasslands, but plant responses to grazing may differ between peren-

nial and annual grasslands, as annual species lack temporal continuity in competitive interactions.

Herbivore size largely determines grazer foraging selectivity and food quality requirements (Demment and Van Soest 1985). Food selectivity is limited by the width of the upper mandibular arc (Gordon *et al*. 1996). Large herbivores preferentially graze on multiple plants, as they are less selective, whereas small herbivores can feed on individual plants or even select plant parts. Evidence suggests that large herbivores can survive by foraging on low quality but abundant plants, while smaller herbivores with higher metabolic rates can survive foraging on rare but less abundant, higher-quality plants (Laca and Demment 1996). Therefore, larger grazers foraging on abundant plants would have potentially different effects on plant species diversity than smaller grazers which selectively feed on high quality plants.

The resources for which plants compete (water, light, nutrients, etc) affect palatability of dominant species (Coley *et al*. 1985). As a consequence, local resources may influence grazing intensity and thus whether herbivores will mediate plant extinction rates by preventing competitive exclusion. Therefore, the effects of different-sized herbivores should vary predictably across environmental gradients such as soil fertility and precipitation that determine primary productivity (van de Koopel *et al*. 1996).

Ritchie and Olff (1999) proposed a conceptual model that identifies limiting resources for plants (water, soil fertility and light) and their influence on the effects of large vs. small herbivores. In this model, the authors suggest that low productivity environments (dry and infertile) favour a plant community that only would support a few small herbivores. These herbivores are likely to select rare, palatable species, increasing, therefore, plant extinction rates. Additionally, herbivore assemblages may have

marked negative effects on plant diversity and species composition, as few plants are grazing tolerant in these environments. An increase in moisture, that results in wet and infertile soils, may lead to higher large herbivore abundance if productivity supports their intake requirements. In this case, multiple herbivores would have weak or negative effects on plant diversity and species composition because large herbivores would be consuming low-quality plants, and small herbivores high-quality plants. In dry and fertile environments, dominant plant species tend to be palatable and support high densities of many herbivore species. These plant species are likely to tolerate herbivory because of good regrowth opportunities, thus foraging by multiple herbivores would have little effect on plant diversity. In highly productive environments (wet and fertile), dominant plants are light competitors in the absence of grazing. Strong light competitor species have low palatability (Fryxell 1991) and likely would be disfavoured to all except large herbivores when mature. Grazing by large herbivores opens the canopy, so that a few grazing-tolerant plant species replace tall species. Thus, the reduction of dominant plants by large herbivores leads to a plant community with more abundant high-quality plants where multiple herbivores enhance plant diversity.

Semi-arid grasslands of the Mediterranean basin are characterised by annual communities and extremely high diversity values (Pineda *et al*. 1981). These ecosystems have a marked seasonality in soil resources, mainly water and nitrogen, which limits primary productivity (Seligman and Van Keulen 1989). An undulating topography and high inter-annual rainfall variability often results in the patchy distribution of these limiting resources (Noy-Meir 1973). This heterogeneity can cause wide spatial and temporal variations in primary productivity within the same local area (Osem *et al*. 2004). These grasslands have a long history of grazing by domestic large herbivores (Noy-Meir 1998). Iberian Mediterranean grasslands have also

been historically grazed by the European wild rabbit (*Oryctolagus cuniculus* (L.)) which can reach high local densities. Wild rabbit is a keystone species in this ecosystem, where at least 39 predator species prey on it (Delibes and Hiraldo 1981). Rabbit effects on vegetation attributes within its native ecosystem have seldom been studied (but see Soriguer 1983, Petterson 2001). This knowledge can complete our understanding about the ecological role of this herbivore in Iberian Mediterranean grasslands.

The aim of the present study was to assess the role of different-sized herbivores in regulating the structure of annual plant communities in Mediterranean semi-arid grasslands. We conducted the experiment in a Mediterranean `dehesa´ of central Spain. Dehesa ecosystems are mosaic landscapes of scrubland and pastures that support the highest densities of wild European rabbits in the Iberian Peninsula (Blanco 1998). In these types of ecosystems, topography determines nutrient distribution and water run-off and meaningful differences in productivity between uplands and lowlands may be found. We studied the effects of large (sheep) and small-sized (rabbits) herbivores in two environments with different productivity by means a replicate size-selective fence experiment which exclude sheep and rabbits-plus-sheep. Our main hypotheses were: a) in the less productive upland environments (dry and infertile), we expected mainly grazing by small herbivores, which would reduce plant species diversity through selective foraging on rare and palatable species; b) in the more productive lowland environments (humid and fertile), we expected higher grazing pressure by both herbivores, which would enhance plant diversity. We studied grazing responses through a community parameters and functional group approach. We considered legumes as high quality plant species; tall and short species in order to assess changes in light competitors, and grasses, legumes and composites as more abundant plant families of our system.

2. Material and methods

Study area

The research was conducted in a 330 ha dehesa located in the south-west of Madrid, Central Spain (40º 23´ N, 4º 12´ W) during 2002, 2003 and 2004. Mean elevation is 690 m. Climate is semi-arid continental Mediterranean with marked seasons. Mean annual temperature and precipitation are 12.6º C and 432.6 mm. Precipitation is characterised by a high year-to-year fluctuation in timing and amount, and by a pronounced summer drought. The amount of annual precipitation during the experiment was 676, 550 and 584 mm, respectively.

The substrate is sandy to sandy-loamed textured, upon a fractured bedrock of granite. There is a gentle undulating topography. Vegetation physiognomy is a typical dehesa system: sparsely punctuated holm oak trees *Quercus ilex* on a pasture matrix. There are also extensive areas of the Mediterranean shrub *Lavandula stoechas* L. Herbaceous vegetation is highly diverse (111 species) and mainly composed of annual species which die at the beginning of the summer drought (June-July) (Fernandez-Alès *et al.* 1993). In slopes and uplands the herbaceous community is mainly composed of short postrate plants. In the lowlands, vegetation is mainly composed by taller species and some perennial grasses can be abundant.

The dehesa is grazed by a transhumant flock of 600 free-ranging sheep (about 2 sheep/ha), starting in December and lasting until the end of June when most herbaceous vegetation is dry. The main wild herbivore is a dense population of the native European rabbit. The dehesa is specifically managed for small game hunting as well as grazing and the traditional mowing.

Experimental design and sampling

In August 2001, five replicate blocks with three grazing treatments were placed at both low and high productivity areas, which were at least 900 m apart. The three grazing treatments were rab-

bit-grazed, control (free herbivore grazing) and non-grazed. We constructed 36-m² fenced her-bivore exclosure plots with a 1 m high chicken mesh (width 2.5 cm). The mesh in rabbit plots was lifted 20 cm above ground level to allow rabbit access but exclude sheep. Control plots had no fences to allow access to both herbivo-res. Non-grazed plots had complete fences to exclude both herbivores. In the non-grazed plots, the mesh was buried 30 cm into the soil forming a "L" shape to avoid rabbits burrowing underneath. Mowing was not carried out in any treatment.

To assess differences in productivity between sites, above ground net primary production and soil moisture and fertility were estimated. We measured above ground plant biomass in non-grazed plots at the season peak (April-May) after clipping seven samples of herbaceous vegetation (20 × 20 cm quadrats) at ground level in 2002, 2003 and 2004. We sorted litter from the samples, they were oven dried at 55º C for 48 h and weighed. Only data from 2002 were used, as litter accumulation may alter pro-ductivity in successive years.

In spring 2003, we took four random eight-cm deep soil samples in each block for soil analy-ses. Soil was passed through a 2 mm sieve to separate stones and litter and was air dried. Total soil N was determined using micro-Kjeldahl digestion and organic matter using the Walkley and Black (1934) method. We collected two random eight-cm deep soil samples at each block in winter, spring and summer of 2003 to determine soil moisture content. Samples were root cleaned and oven-dried at 100º C. They were weighed before and after drying, and the difference in weight was considered a measure of soil moisture for each season.

Rabbit and sheep density was measured by faecal pellet counts from January 2002 until December 2004. Three 1 × 1 m quadrats were placed in every grazed plot. The quadrats were monthly visited and completely cleared of faecal pellets before monitoring started. The use of pellet counts as a herbivore density indicator has been tested for ungulates (Fuller 1991) and European rabbits (Taylor and Williams 1956) and is considered an appropriate indirect cen-sus method. Pellet persistence can differ bet-ween habitats and seasons (Taylor and Williams, 1956), thus we estimated "pellet decay rate" throughout the seasons in low and high productivity areas in order to ensure that a period of one month between pellet clearance and count was adequate.

We recorded visual aerial cover of plant species at peak season (spring) in 2002, 2003 and 2004 in seven 20 × 20 cm quadrats per plot. This quadrat size has been commonly used to study Mediterranean annual herbaceous communities (Montalvo *et al.* 1993). Plant taxonomy follows Tutin *et al.* (1964-1981). We sorted species into groups: grasses, forbs, legumes, and composi-te. In more productive sites, we also sorted spe-cies into tall, short and perennials. Community parameters estimated per plot were: species richness (S); Shannon-Wiener diversity index (Shannon and Weaver 1949), ($H' = - \Sigma$ pi $\log_2$ pi) where pi is the proportion of species i; and Pielou's (1966) evenness index ($J' = H'/H'$ max) where H' is the Shannon-Wiener diversity index. We calculated spatial heterogeneity in species composition in each plot using Sorensen's dissimilarity index (Faith *et al.* 1987) ($D = 1 - 2W/(A+B)$), where W is the sum of the lower of the two shared abundances for each species in both quadrats, and A and B are the sums of abundances in the individual quadrats.

Data analyses

All response variables were tested for normality and homogeneity of variances and log $(x + 1)$ or square-root transformations were performed where needed. Student t-tests were used to assess significant differences in above ground primary production, soil fertility, and sheep pellet numbers between low productivity and high productivity sites. Repeated measures ANOVA was used to assess differences in soil moisture between high and low productivity

sites during spring, summer and winter. Differences in rabbit pellet number were analysed with a two-way ANOVA, using grazing treatment and productivity class as factors. Treatment effects on plant community parameters in individual years were analysed with ANOVAs, where grazing treatment was used as fixed factor and block as random factor. Repeated measures ANOVAs were used to estimate overall significance of treatment effects from year 2002 to year 2004 in fully factorial analysis with grazing treatment as between subject factor and year and year × grazing treatment interaction as within subject factors. Productivity was not included as a factor in the analyses of plant community parameters, but analysed them separately for more and less productive sites. This was decided due to differences in plant species composition and herbivore densities between both sites. Post-hoc tests (Tukey-test, $p < 0.05$) were used to test differences between treatments. The statistical package SPSS 12.0 (SPSS Inc., 1989-2003) was used for analyses.

3. Results

Differences in productivity and herbivore densities between upland and lowland sites

Lowland sites had significantly greater above ground primary production, soil organic matter and total soil nitrogen percentage than upland sites ($t = -3.6$, $p = 0.007$; $t = -7.2$, $p = 0.000$; $t = -7.4$, $p = 0.000$, respectively) (**Fig. 6.1a-c**). Soil moisture was also significantly higher in lowland sites in the three seasons (Season: $F = 377.03$, $p = 0.000$; Site: $F = 66.79$, $p = 0.000$; Season × Site: $F = 94.66$, $p = 0000$) (**Fig. 6.1d**).
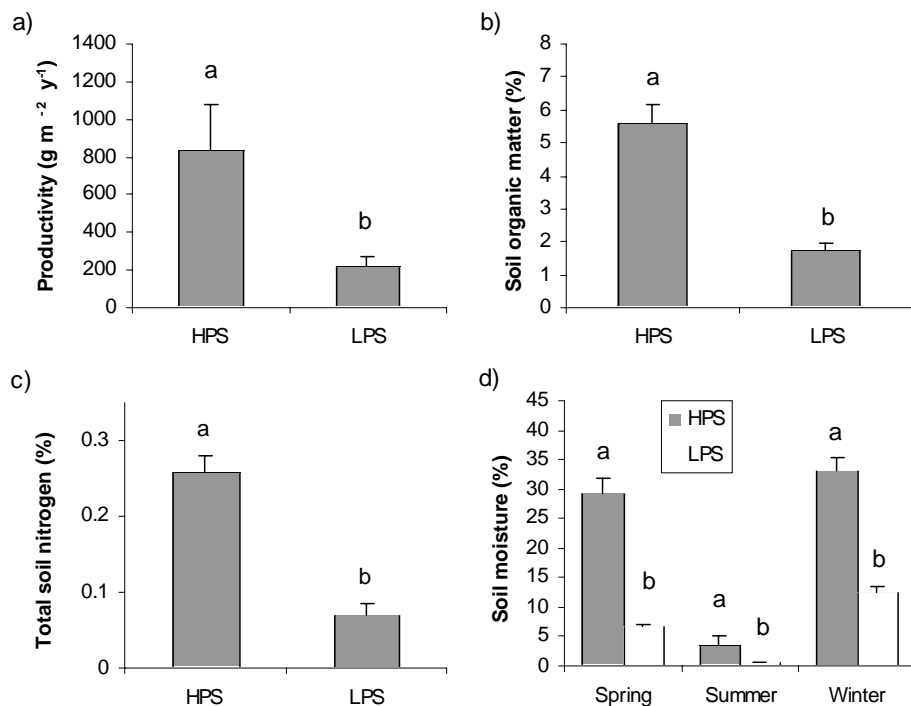
There was a significant interaction between pro-

Figure 6.1: Means (± SE) of above ground primary production and soil parameters for high productivity sites (HPS) and low productivity sites (LPS): a) above ground primary production, b) percentage of soil organic matter, c) percentage of total soil nitrogen, d) percentage of soil misture in spring, summer and winter. Different letters indicate statistical differences (t-student; p< 0.05).

ductivity and grazing treatment on rabbit grazing preference; in low productivity sites, rabbits showed preference for rabbit-grazed plots compared to control (free grazing) treatment, whereas in high productivity sites rabbits did not show preference for any treatment (productivity: F = 14.03, p = 0.000; grazing treatment: F = 7.50, p = 0.008; productivity x grazing treat-

ment: F = 5.11, p = 0.028) (**Fig. 6.2a**). Rabbit pellet density was higher in the low productivity sites but only in the rabbit only plots. Sheep pellet density differences between less and more productive sites were barely significant (t = -2.008, p = 0.054), with higher densities in high productivity sites (**Fig. 6.2b**).
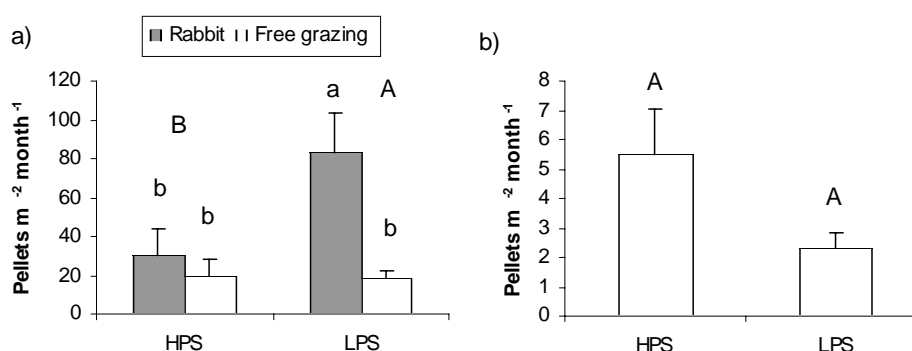

Figure 6.2: Rabbit and sheep visitation of the plots in high productivity sites (HPS) and low productivity sites (LPS), expressed as average number of faecal pellets per m^2 and month (± SE): a) number of rabbit faecal pellets, b) number of sheep faecal pellets. Different letters indicate statistically different pellet rates. Capital letters indicate differential pellet rates between HPS and LPS and lower case letters indicate differential pellet rates between grazing treatments (Tukey-test, p<0.05).

Effects of grazing on vegetation at high and low productivity sites

The herbaceous vegetation was highly diverse and over the three year study period 111 vascular species were identified in the plots. Forty-eight species were found in high productivity sites, twenty-three in low productivity sites, and forty sharing both sites.

In high productivity sites, grazing treatments had no significant effects on species richness, evenness and diversity (**Tables 6.1** and **6.2**). Spatial heterogeneity in species composition (Sorensen´s index) was significantly higher in the non-grazed treatment with respect to the grazed ones in 2003 and 2004 (**Fig. 6.3a**). Legumes were significantly higher in the control treatment in 2003 and 2004 (**Fig. 6.3b**).

Composites were significantly higher in the control treatment in 2003 (**Fig. 6.3c**). Tall species were significantly higher in the rabbit grazing treatment in 2004 (**Fig. 6.3d**). Year had significant effects in all plant community parameters except species richness and short species cover.

In low productivity sites, grazing treatments had no significant effects on either species richness, evenness or diversity (**Tables 6.1** and **6.2**). Spatial heterogeneity in species composition was significantly higher in the non-grazed treatment with respect to the grazed ones in 2002 (**Fig. 6.4a**). Legumes were significantly higher in the non-grazed than in the grazed plots in 2002 and 2003 (**Fig. 6.4b**). Year had significant effects on all plant community parameters except grasses and forbs.

Table 6.1: Results of two-way ANOVAs for plant community parameters and functional groups in each of the three years of grazing treatments in high and low productivity sites. Significant grazing effects are shown in Figures 6.3 and 6.4. * = p < 0.05; ** = p < 0.01; *** p < 0.001

Vegetation parameters		High productivity sites			Low productivity sites		
			Year			Year	
		2002	2003	2004	2002	2003	2004
		F	F	F	F	F	F
Species richness	df = 2	0.70	3.89	1.08	2.34	0.15	0.95
Evenness (J)	df = 2	2.32	0.01	4.00	0.84	1.79	0.05
Diversity (H´)	df = 2	0.46	1.61	2.80	1.06	1.49	0.11
Spatial heterogeneity	df = 2	3.12	7.90*	8.82**	7.14*	2.39	0.42
Grasses	df = 2	0.82	0.54	2.44	2.69	1.47	3.10
Legumes	df = 2	1.66	7.44*	7.46*	31.31***	6.79*	2.28
Composites	df = 2	0.53	4.83	2.44	0.57	0.27	2.15
Forbs	df = 2	0.01	1.79	1.39	3.71	2.47	2.73
Perennials	df = 2	0.47	1.69	0.37	Not estimated [a]		
Tall species	df = 2	0.10	1.32	6.33*	Not estimated [a]		
Short species	df = 2	0.001	3.04	3.12	Not estimated [a]		

[a] The abundance of perennials and tall species was too low in low productivity sites to allow statistical analyses of their responses to grazing treatments. Short species were abundant in low productivity sites but were only used in high productivity sites in order to assess the effect of grazing treatments on the subordinate-dominant light competitors.

Table 6.2: Results of repeated measures ANOVAs for plant community parameters and functional groups throughout the three years of grazing treatments in high and low productivity sites. Significant grazing effects are shown in Figures 6.3 and 6.4. * = p < 0.05; ** = p < 0.01; *** p < 0.001

Vegetation parameters	High productivity sites			Low productivity sites		
	Grazing	Year	Grazing × Year	Grazing	Year	Grazing × Year
	df = 2	df = 2	df = 2	df = 2	df = 2	df = 2
	F	F	F	F	F	F
Species richness	0.34	0.16	0.86	1.07	23.56***	0.52
Evenness (J)	0.48	23.96***	1.62	0.32	8.74*	0.79
Diversity (H´)	0.19	6.73**	1.66	0.53	15.68**	0.32
Spatial heterogeneity	0.45*	6.18**	1.18	4.05*	4.07*	0.77
Grasses	0.49	33.35**	0.79	0.32	2.89	2.56
Legumes	0.96	18.20**	2.87*	7.86*	22.87***	0.77
Composites	0.58	12.15***	0.93	0.58	27.28***	1.49
Forbs	0.05	7.64**	0.74	2.83	1.80	0.52
Perennials	0.39	3.42*	1.49	Not estimated [a]		
Tall species	0.54	11.44***	1.92	Not estimated [a]		
Short species	0.45	1.26	0.91	Not estimated [a]		

[a] As in Table 6.1.

4. Discussion

Topography, soil fertility and primary productivity

The typical rolling dehesa landscape resulted in higher soil moisture, soil fertility and plant biomass in lowlands with respect to uplands. This leads to a considerable spatial and temporal heterogeneity in floristic composition and primary productivity and also in plant phenology, as pasture remains green for longer during the summer drought in the lower areas (see also Gómez-Sal *et al.* 1986). Topographic differences lead to further variations in nutrient quality of the herbaceous vegetation, higher quality forage being found in lowlands (Vázquez-de-Aldana *et al.* 2000). Therefore, at a local scale we found relatively fertile and humid pastures in lowland and infertile and dry pastures in upland areas.
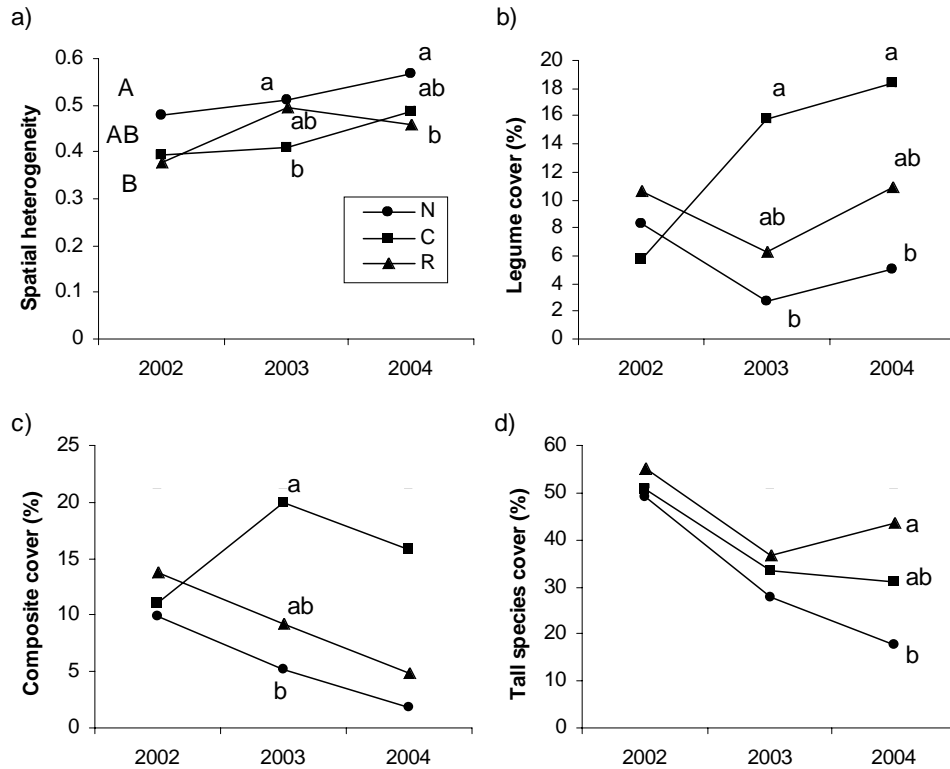
Figure 6.3: Temporal changes in high productivity sites throughout 2002, 2003 and 2004: a) spatial heterogeneity in species composition, b) legume cover, c) composite cover, d) tall species cover. R = rabbit-grazed treatment, C = free grazing treatment, N = non-grazed. Capital letters indicate effects detected using the repeated measures ANOVAs and lower case letters indicate effects detected using the two-way ANOVAs in particular years. Treatments or points with the same letter are not statistically different (Tukey-test, p<0.05). A > B > C and a > b > c. See Table 6.1 and 6.2 for F and p-values.

Habitat preferences by herbivores

Rabbits and sheep did not show a clear significant preference for different productivity sites. According to Ritchie and Olff (1999), we expected high productivity sites to be intensely used by sheep and rabbits, while rabbits would mainly use low productivity sites. Several constrains appear when we apply this model to the studied ecosystem. The study period was wetter than usual and low productivity areas were probably productive enough to support sheep and rabbit grazing. Additionally, herbivores may avoid too productive sites, as they can find it difficult to get an effective bite from the dense and tall vegetation (van de Koopel *et al.* 1996). Furthermore, predation may limit small herbivores (Krebs *et al.* 1999) as the selection of fora-

ging habitats represents a trade-off between nutritional gain and minimization of predation risk (Lima and Dill 1990). Rabbits are often restricted to the proximity of warrens and areas of dense scrub cover to avoid predators (Palomares and Delibes 1997). In dehesa environments, warrens are mainly located in uplands, as in lowlands they tend to flood during the rainy season (personal observation). Moreover, as a consequence of traditional mowing of lowlands, most scrub cover is limited to uplands. Grasslands of high productivity sites were relatively more distant from potential rabbit refuges than those of low productivity sites. Only two of the five high productivity blocks presented an intense rabbit use and they were located in an area close to warrens and scrub

cover, whereas the other three were located in open grasslands farther from cover. Predation risk, rather than productivity or food quality, may be influencing foraging habitat selection for rabbits. However, when warrens or cover are close to productive sites, rabbits use them frequently, as rabbit minimise the risk of predation whilst foraging high quality abundant food.

In low productivity sites, rabbits favoured the rabbit-grazed plots. In these plots we observed many more rabbit latrines than in the plots grazed by sheep-plus-rabbits. This preference of rabbits for the rabbit-grazed plots could be explained because rabbits may feel more secure from avian predators inside fences; or it may be a competitive strategy with sheep. The first option seems to be more likely, as rabbit preferences were maintained in blocks less visited by sheep. This choice was not evident in high productivity sites, where rabbits did not show any specific inclination for grazing treatment. It is likely that the risk of predation by avian and terrestrial predators is perceived differently in open grasslands (high productivity sites) with tall herbaceous vegetation than in areas where warrens and scrub cover are abundant (low productivity sites) (see also Moreno *et al.* 1996).

Herbivore effects on plant community

Rabbit and sheep grazing did not influence plant species richness, evenness and diversity in either high or low productivity sites. We expected in the grazed treatments a reduction in species richness at low productivity sites and an increase at high productivity sites. Why did herbivores not affect plant diversity in our study? Several factors may have contributed to this result.

Firstly, the Mediterranean region has evolved under centuries of domestic herbivore grazing and soil disturbance (Le Houérou 1981). Furthermore, high densities of the native wild European rabbit have been historically described in the Iberian Peninsula (Flux 1994). Thus, the lack of grazing effects found in our system agrees with Milchunas´ (1988) generalised model of plant diversity and grazing intensity. This model predicts that semi-arid grasslands with a long history of large herbivore grazing are resistant to change as a result of the lack of disturbance intolerant species in the local flora. Ritchie and Olff (1999) also point out that "the evolutionary history of grazing may be crucial in predicting ecosystem responses to multiple herbivore species when production is limited by water, particularly on nutrient-poor soils".
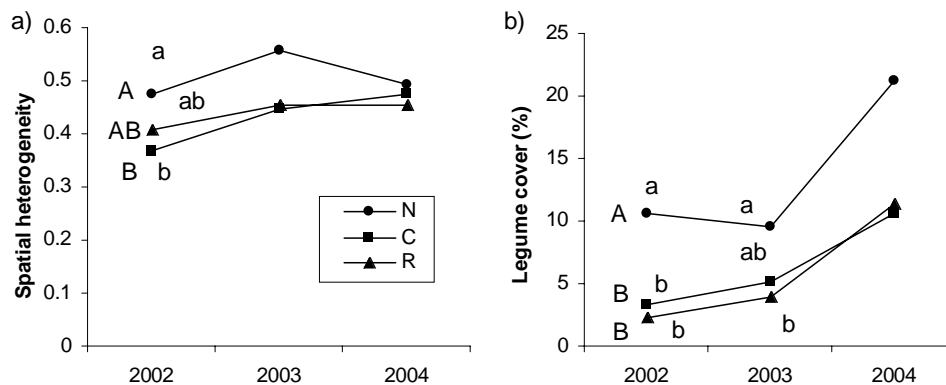

Figure 6.4: Temporal changes in low productivity sites throughout 2002, 2003 and 2004: a) spatial heterogeneity in species composition and b) legume cover. Specifications as for Fig. 6.3. See Table 6.1 and 6.2 for F and p-values.

Secondly, it is likely that in semi-arid environments rabbits are less selective than we expected. Several British studies show rabbits as highly selective herbivores (Bhadresa 1977, Soane 1980). However, in semi-arid environments, Petterson (2001) found that although rabbits maintained some degree of selectivity, they were mostly generalists and ate a wide variety of food items. Rabbits practise caecotrophy, i.e. they reingest soft pellets produced in the colon that contain high proportions of proteins, minerals and vitamins (Hirakawa 2001). As high quality plants are rare in poor semi-arid environments, natural selection might have forced rabbits to feed on more abundant low quality plants. Sakaguchi *et al.* (1992) suggest that this specialisation may contribute to the success of rabbits in arid ecosystems. The existence of a small-sized herbivore with special adaptations can influence the outcome of plant herbivore interactions and may affect the adjustment of Ritchie and Olff´s model for Iberian Mediterranean ecosystems.

Thirdly, Mediterranean climatic conditions and the annual nature of the plant community could result in different responses than those predicted for temperate perennial communities. For plant communities in arid and semi-arid environments rainfall variability appears to be a potent determinant of system change (Westoby *et al.* 1989). Ellis and Swift (1988) proposed a non-equilibrium model for arid ecosystems where herbivory plays a relatively little role in determining changes in vegetation composition, which are mainly driven by abiotic factors. Different authors have demonstrated that an unpredictable environment is the usual cause of irregular fluctuations in floristic composition of these species-rich annual Mediterranean pastures (Peco *et al.* 1998). Grazing treatments can be masked by those of abiotic factors. However, the significant variation in cover of some functional groups between grazing treatments reveals that herbivory is playing some role in determining floristic composition in our system. In low productivity areas grazing by rabbits and

sheep decreased legume abundance. In contrast, in high productivity sites legume cover was significantly higher in the free grazing treatment. It seems likely that sheep grazing opens the canopy for these subordinate species. Legumes were positively selected by rabbits and sheep in low productivity sites and were the group most affected by grazing treatments. In Mediterranean semi-arid ecosystems, legumes possess significantly higher protein contents than grasses and other types of forbs (Vázquez-de-Aldana *et al.* 2000). The little annual response to a grazing treatment will be consistent in direction and thus, in the long-term, cumulative grazing effects would establish the direction of changes in plant composition, whereas rainfall variability would mainly influence short-term changes (O'Connor and Roux 1995). Higher diversity in grazed vs. ungrazed grasslands has been found for Mediterranean regions (Noy-Meir *et al.* 1998), particularly in the Central Iberian Peninsula (Montalvo *et al.* 1993). We acknowledge that the short duration of this study is potentially a significant limitation.

Recognition of the role of grazing animals in maintaining vegetation types and diversity has increase in Europe during the last decades (Noy-Meir 1998, van Wieren 1995). Although in our short-term study, rabbit and sheep grazing did not affect plant diversity at a local community scale, both herbivores are essential in keeping diversity and heterogeneity at a landscape scale. Large herbivores increase heterogeneity through dung pats, urine deposition, resting sites and seed dispersal (Olff and Ritchie 1998), while European rabbits may create heterogeneity also through soil disturbance by scratching and burrowing (Huntly and Reichman 1994). Furthermore, in most of the Iberian Mediterranean ecosystems, livestock and wild rabbits have shared a long common evolutionary history. More research about the interactions between European rabbits, a keystone species in the Iberian Peninsula, and free ranging livestock would help elucidate their grazing effects in the Mediterranean basin. The evolu-

tionary history of grazing by large and small herbivores should be taken into account in those studies assessing plant responses to herbivory.

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