Diverse responses of shrub-associated arthropods to ungulate removal

Respuestas diversas de los artrópodos asociados al matorral a la exclusión de ungulados

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ABSTRACT

This paper experimentally examines the relationship between ungulates and arthropods associated with two common shrub species (*Astragalus granatensis* Lam. and *Genista versicolor* Boiss.) in the high mountains of Sierra Nevada (SE Spain). During two years we studied the effect of ungulate removal on the abundance, biomass, and diversity of arthropod families and beetle species. In general, our results have shown that ungulates significantly affected the arthropods living in the two studied shrub species. Ungulates affected arthropod community traits, this effect being evident mainly on arthropod and beetle diversity. However, we cannot draw conclusions about the positive or negative effect of browsing in our study area, because at each taxonomic level (arthropod families vs. beetle species) arthropods responded to ungulates in a different way. In addition, the effect of ungulates on arthropods and beetles differed between sites, years and sampling periods. Moreover, there were also complex responses of arthropods at family and species levels in relation to temporal variability, pointing out the necessity of conducting long-term studies to accurately determine the actual effect of grazing on arthropod communities.

RESUMEN

En este trabajo examinamos experimentalmente la relación que existe entre los ungulados y los artrópodos asociados a dos especies de matorral (*Astragalus granatensis* Lam. y *Genista versicolor* Boiss) muy abundantes en la alta montaña de Sierra Nevada (SE España). Durante dos años, estudiamos el efecto de la exclusión de ungulados en la abundancia, biomasa y diversidad de coleópteros y de familias de artrópodos. En general, nuestros resultados muestran que los ungulados tienen efectos sobre los artrópodos asociados a las dos especies de matorral, afectando principalmente a la diversidad tanto de artrópodos como de coleópteros. Sin embargo, no podemos sacar conclusiones sobre si el efecto de los ungulados es positivo o negativo, ya que cada nivel taxonómico respondió de una forma diferente. Además, también hubo diferencias en el efecto de los ungulados dependiendo del tipo de matorral, el mes o el año en el que se realizó el muestreo. En conclusión, debido a la complejidad de las respuestas cuando combinamos la variabilidad temporal con las diferencias obtenidas a nivel taxonómico, consideramos que son necesarios estudios a largo plazo para determinar el efecto real de los ungulados en la comunidad de artrópodos.

INTRODUCTION

Grazing by ungulates has a strong impact on the performance of many plant species and the structure and diversity of several plant communities (Huntly, 1991; Diaz *et al*., 1992; Tscharntke, 1997; Olff & Ritchie, 1998; Oba *et al*., 2000). Consequently, these mammalian herbivores can affect the diversity and composition of plant-associated insect communities (Hunter, 1992; Dennis *et al*., 1996; Tscharntke, 1997; Rambo and Faeth, 1999; Suominen *et al*., 1999a, b).

Different hypotheses have been proposed to explain the effect of ungulates on arthropod community. First, ungulates can affect arthropods by plant-mediated interactions, such as competition (Baines *et al*., 1994; Tscharntke, 1997; Gómez & González-Megías, 2002) and changes in plant palatability and quality (Danell & Huss-Danell, 1985; Faeth, 1986; 1988; Wiens et al., 1991; Hudson & Stiling, 1997; Karban & Baldwin, 1997; Master & Brown, 1997). Second, ungulates can affect some arthropods by accidentally, ingesting them while consuming plant tissue (Auerbach, 1991; Zamora & Gómez, 1993; Baines *et al*., 1994; Fernández-Haeger *et al*., 1996; Tscharntke, 1997; Gómez & González-Megías, 2002). Third, ungulates may alter arthropod communities by changing vegetation structure and thereby physically modifying the shared habitat (Abensperg-Traun et al., 1996; Bestelmeyer & Wiens, 1996; Dennis *et al*., 1997; Seymour and Dean, 1999). Finally, ungulates can provide new resources to arthropods, like excrements and carrion, allowing the presence of specialised species that live on this type of resources (Gardner *et al*., 1995; Abensperg-Traun *et al*., 1996; Bestelmeyer & Wiens, 1996; Dennis *et al*., 1997; Suominen *et al*., 1999a,b). Due to this diversity of mechanisms, arthropod response to ungulates may be positive (Abensperg-Traun *et al*., 1996; Elligsen *et al*., 1997; Seymour & Dean, 1999; Suominen *et al*., 1999b), negative (Dennis *et al*., 1996, 1997; Strand & Merritt, 1999; Suominen *et al*., 1999a) or neutral (Dennis *et al*., 1996; Rambo & Faeth, 1999).

In general, population dynamics of arthropods occur in peaks of abundance concentrated in few months or even days (Speight *et al*., 1999). This means that the diversity and composition of the arthropod community associated with a specific plant-community may change at short (days or months) and long-periods (years). In addition, an arthropod community may respond to the same disturbance in different ways depending on habitat variability (e.g., productivity; Bestelmayer & Wiens, 1996). Both phenomena might be more important in habitats where there is a high temporal variability in temperature and precipitation regimes, as occurs in Mediterranean systems and high mountains (Mani, 1968; Blondel & Aronson, 1999). In these types of habitats, an accurate understanding of the effect of ungulates on arthropod communities thus requires the consideration of temporal variability in the ecological factors affecting insects.

This paper examines the relationship between ungulates and the arthropods associated with two common plant species in the high mountains of Sierra Nevada (SE Spain). Specifically, we assess (1) how removal of ungulates affects the abundance and biomass of arthropods, homoptera, and beetles, (2) how removal of ungulates affects diversity of arthropods (at the family level) and beetles (at the species level) and (3) the effects of temporal variability on the relationship between ungulates and arthropods.

METHODS

Study area

The study was done in Sierra Nevada National Park (Granada, SE Spain) above the timberline, between 2200 and 2300 m a.s.l. Two plant communities, composed mainly of dwarf shrubs, can be identified at this altitude. One community, occurring in calcareous soil series, is dominated by *Astragalus granatensis* (Leguminosae), whereas the second community is dominated by the shrub *Genista versicolor* (Leguminosae) and is associated to siliceous soil series. After snowmelt, these areas are used by domestic (sheep and goats) and wild ungulates (Spanish Ibex, *Capra pyrenaica*). The intensity of grazing (about 1.6 animal/ha, González-Megías, 2001) was the same in both plant communities.

We selected one site in each plant community, “Collado de las Sabinillas” on the calcareous soil and “Prados del Aire” in the siliceous soil. At each site, the Andalusian government established, in 1995, an exclusion area (> 4500 m^2) to protect endemic plant species. We selected two plots at each site, one inside the excluded area (“ungrazed”, hereafter) and another outside the exclusion (“grazed”). The fences exclude ungulates but not lagomorphs or other small herbivorous mammals. Both plots in each community were located less than 10 m one to each other in order to avoid as much as possible differences in soil characteristics, slope or aspect.

Arthropod sampling design

We sampled in 1997 and 1998 the arthropod fauna living in the foliage of the dominant shrub species in each site, *Genista versicolor* (*Genista* hereafter) at Prados del Aire and *Astragalus granatensis* (*Astragalus* hereafter) at Collado de las Sabinillas (see González-Megías et al. 2003 for additional details), using the beating method (Sutherland, 1996). Once per month, we sampled 10 shrubs in each of the four plots. Shrubs were tapped for 20 seconds with a wooden stick, catching all dislodged invertebrates in a 20x10 cm^2 beating tray held beneath. The content of the tray was included in a plastic bag and transport to the laboratory. We sampled the arthropod fauna four times in 1997 (June, July, August and September) and five times in 1998 (April, June, July, August and September). These periods coincided with the activity of ungulates every year. We chose the beating method instead of other methods, such as sweep nets, suction samples or direct searching, because all these alternative methods were assumed to be less suitable for our purpose. Sweep net and suction methods have been recommended to collect samples from low vegetation, but they are not efficient techniques to remove invertebrates from the foliage (Sutherland, 1996). In addition, direct searching requires prior identification knowledge of those invertebrates expected to be found. Moreover, although direct searching is likely to locate the more visually and active species, small and cryptically coloured invertebrates are likely to be under-estimated (Sutherland, 1996).

Samples were analysed in the laboratory, where individuals were counted, measured (body length) and identified to family level (except for Acarina and Collembola). Although identification to family level has been indicated as an adequate taxonomic resolution to show the effect of ungulates on arthropod communities (Suominen *et al*., 1999b), beetles were sorted and sent to specialists for identification to species. This allowed us to compare the effect of ungulate exclusion at two taxonomic levels.

We measured every sampled plant of both species (height and two diameters) for calculating the volume of the plants.

Arthropods assemblage traits

We analysed the effect of ungulates on four arthropod assemblage traits: Abundance, biomass, diversity and composition. Abundance was expressed as the total number of individuals collected per census (i.e., summing the 10 plants), whereas biomass was expressed as cumulative weight of all individuals caught per census. The dry biomass (in mg) of the arthropods was estimated from body length using allometric equations (see Hódar, 1996).

The diversity of arthropods (family level) and beetles (species level) was assessed using four indices: i) Richness, (number of family or species) (Magurran, 1988); ii) Dominance, (the fraction of the collection that is represented by the most common family or species); iii) Shannon-Wiener (H') diversity index; and iv) Hurlbert's probability of intraspecific encounter (PIE). All these indexes were generated by a randomization process using EcoSim® (Gotelli & Entsminger, 2000).

Data analysis

Differences between browsing levels in arthropod abundance and biomass were analysed by means of contingency analyses, pooling the data of all plants per plot. We choose this procedure because, although it is more conservative and decreases power analysis, it avoids the risk of pseudoreplication (Zar, 1996; Underwood, 1997). Richness, Dominance, Shannon-Wiener index, and Hulbert's PIE were statistically compared among treatments using EcoSim v5.53®, which accounts for differences in the number of individuals sampled by rarefaction (Gotelli & Entsminger, 2000). Rarefaction uses iterative randomisation (1000 iterations) to generate an expected mean, variance and 95% confidence interval of the studied indexes for a sample of a given number of individuals (Gotelli & Entsminger, 2000). Thus, according to EcoSim, one sample has the same diversity (with α=0.05) as a second sample with an equal number of individuals if its diversity value falls inside the 95% confidence interval of the randomly-generated diversity index for the second sample (see Gotelli & Entsminger, 2000 for further details). Similarity of beetle assemblage composition between plots was calculated using the Morisita-Horn's coefficient (Magurran, 1988). This index ranges from 0 (denoting no similarity in community composition between sites) to 1 (denoting complete overlap). This index is considered to be one of the most robust measures of community similarity (Magurran, 1988).

RESULTS

Effect of ungulates on plants

Height of *Genista* plants was significantly larger in the ungrazed plot (28.7 ± 0.8 vs. 21.0 ± 0.8 cm; F= 50.0, df= 1,179, p= 0.0001). There was also difference between plots in *Genista* size, measured as volume (138,591.1 ± 15,443.4 vs. 116,423.6 ± 10,825.1 cm^3; F= 63.7, df= 1,179, p= 0.0001), plants being larger in the ungrazed plot. In contrast, there was no difference between plots neither in *Astragalus* plant height nor volume (p>0.05 for all cases).

Arthropod communities

A total of 1,657 arthropods were collected in 1997 and 2,313 in 1998, belonging to 16 orders and 44 families. Coleoptera (20.3% of total arthropods abundance in 1997 and 17.3% in 1998) and Homoptera (18.79% in 1997 and 26.0% in 1998) represented more than 40% of the individuals both years. Beetles were represented by 35 species (Appendix 1), the most abundant being the Apionidae seed predators *Exapion compactum* (71.8%) and *Exapion* nov. sp (15.3%) at Prados del Aire, and the curculionid species *Sitona tenuis* Rosenh.(40.21%) at Collado de las Sabinillas.

Effect of ungulates on arthropods

Abundance

In 1997, the abundance of arthropods at Prados del Aire was significantly higher in the grazed than in the ungrazed plot (G = 10.7, df = 2, p= 0.005). On the contrary, the abundance of Homoptera was higher in the ungrazed plot (G = 6.6, df = 1, p = 0.01; Table I). In 1998, the abundance of arthropods (G = 12.9, df = 1, p = 0.002) and beetles (G = 7.5, df = 1, p = 0.02) were higher in the ungrazed plot at Prados del Aire (Table I).

Table I.—Mean abundance (total number of individuals per sampled period) and biomass (total weight of individuals per sampled period, in mg) per year (mean ± 1 SE) of arthropods and beetles in grazed and ungrazed plots during 1997 and 1998. For each year, values with different letters indicate significant differences according to a contingency analysis.
Tabla I.—Medias de abundancia (número total de individuos por período de muestreo) y biomasa (peso total de los individuos por periodo de muestreo, en mg) por año (media ± 1 ES) de artrópodos y coleópteros en parcelas pastoreadas y no pastoreadas durante 1997 y 1998. Para cada año, valores con letras diferentes señalan diferencias significativas según un análisis de contingencia.

	Prados del Aire		**Collado de las Sabinillas**	
	Ungrazed	Grazed	Ungrazed	Grazed
Abundance				
Arthropods				
1997	58.50 ± 12.07[a]	84.75 ± 21.44[b]	95.75 ± 18.32	97.75 ± 9.20
1998	101.00 ± 24.25[a]	74.40 ± 17.66[b]	119.00 ± 20.39	94.60 ± 22.10
Coleoptera				
1997	25.00 ± 6.51	31.00 ± 5.92	7.50 ± 0.87	6.00 ± 2.48
1998	29.60 ± 10.97[a]	18.60 ± 6.09[b]	5.00 ± 1.09	6.60 ± 2.62
Homoptera				
1997	8.50 ± 3.93[a]	3.25 ± 1.60[b]	25.25 ± 2.63	27.25 ± 5.59
1998	23.60 ± 12.04	25.60 ± 12.34	38.60 ± 15.37[a]	23.60 ± 6.95[b]
Biomass				
Arthropods				
1997	73.63 ± 5.24	72.12 ± 4.12	257.62 ± 15.33[a]	334.04 ± 11.54[b]
1998	128.02 ± 6.91	100.57 ± 6.05	218.65 ± 13.43[a]	282.03 ± 12.98[b]
Coleoptera				
1997	46.23 ± 0.07	48.18 ± 0.05	61.82 ± 3.71	52.68 ± 7.34
1998	43.38 ± 0.04	37.08 ± 0.09	49.62 ± 4.71	52.71 ± 3.66
Homoptera				
1997	8.71 ± 0.03	3.23 ± 0.04	13.26 ± 0.06	12.26 ± 0.06
1998	25.51 ± 0.02	35.39 ± 0.03	20.04 ± 0.003	10.34 ± 0.06

At Collado de las Sabinillas, by contrast, there was no difference between plots in the abundance of arthropods, beetles or Homoptera, but in 1998 the abundance of Homoptera was higher in the ungrazed plots (G = 9.5, df = 1, p = 0.002).

Biomass

Whereas we did not find between-plot differences in biomass at Prados del Aire, at Collado de las Sabinillas the biomass of arthropods was higher in the grazed plot both years (G = 5.1, df = 1, p = 0.02 in 1997 and G = 4.1, df = 1, p = 0.04 in 1998; Table I).

Diversity and composition

Arthropod and beetle diversity was also affected by the exclusion of ungulates. At Prados del Aire, both years arthropod diversity was higher in ungrazed plots and beetle diversity in the grazed plot (Table II). There was no difference in the composition of beetle assemblages, *Exapion compactum* and *Exapion* nov. sp. being the most abundant species in both plots. At Collado de las Sabinillas, arthropod and beetle diversity were higher in the grazed plot both years (Table II). In this case, the weevil *Sitona tenuis* was two times more abundant in the ungrazed plot (54.17% vs. 20.83% of the total abundance of beetles) in 1997.

Table II.—Between-treatment (grazed vs ungrazed) differences in arthropod and beetle diversity according to four different indices. For each year, values with different letters indicate significant differences according to a randomisation procedure (see Methods).
Table II.—Diferencias entre tratamientos (pastoreados vs. no pastoreados) en diversidad de artrópodos y de coleópteros según cuatro índices distintos. Para cada año, valores con letras diferentes señalan diferencias significativas según un procedimiento de aleatorización (ver Métodos).

	Prados del Aire				**Collado de las Sabinillas**			
	1997		1998		1997		1998	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Arthropods								
Richness	26[a]	33[b]	28[a]	29[b]	23[a]	18[b]	26	23
Hurlbert's PIE	0.89[a]	0.91[a]	0.87[a]	0.89[b]	0.82[a]	0.77[b]	0.85[a]	0.82[b]
Dominance	0.19[a]	0.18[b]	0.19[a]	0.22[b]	0.35	0.34	0.27	0.30
Shannon-Wiener	2.57[a]	2.70[b]	2.38[a]	2.55[b]	2.22[a]	1.79[b]	2.29[a]	2.14[b]
Beetles								
Richness	10[a]	7[b]	8	8	10[a]	12[b]	9[a]	12[b]
Hurlbert' PIE	0.37[a]	0.48[b]	0.34[a]	0.61[b]	0.71[a]	0.92[b]	0.70[a]	0.84[b]
Dominance	0.79[a]	0.70[b]	0.80[a]	0.53[b]	0.54[a]	0.20[b]	0.55[a]	0.41[b]
Shannon-Wiener	0.91[a]	0.99[a]	0.76[a]	1.20[b]	1.67[a]	2.30[b]	1.58[a]	2.07[b]

Temporal variability in arthropod abundance and diversity

Arthropods and beetles showed different responses to the exclusion of ungulates among months even from the same year (Figure 1). The effect of ungulate exclusion on arthropod and beetle abundance was negative, positive, or neutral depending on the month (Figure 1). For beetles, at Collado

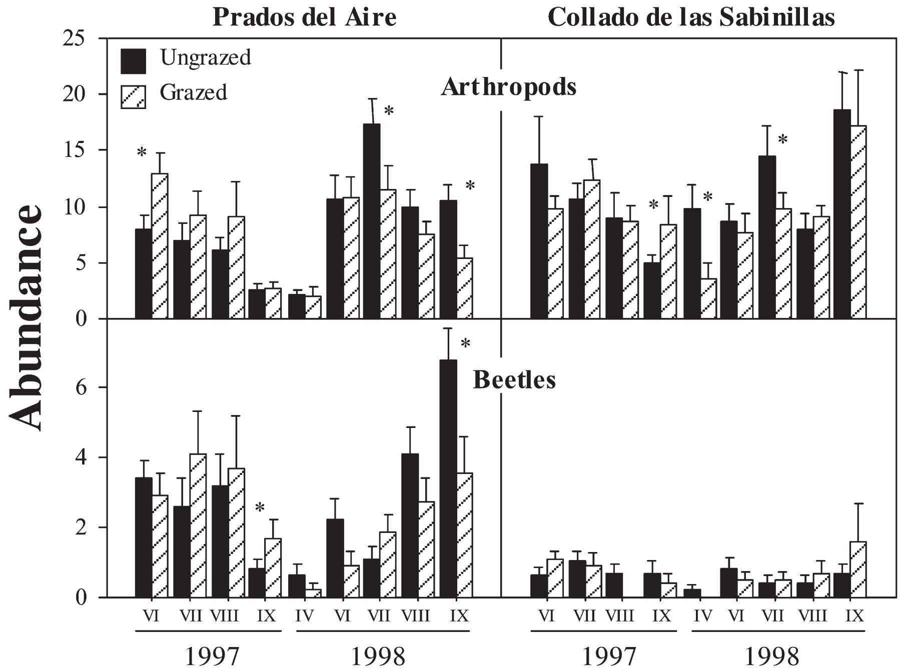

Fig. 1.—Temporal variability in the effect of ungulate exclusion on arthropod and beetle abundance (mean ± 1 SE) at the study sites. * $p < 0.05$ after a contingency analysis.
Fig. 1.—Variabilidad temporal en el efecto de la exclusión de ungulados sobre la abundancia de artrópodos y coleópteros (media ± 1 ES) en las zonas de estudio. * $p < 0.05$ tras un análisis de contingencia.

de las Sabinillas this variability was not evident because there were not differences in abundance between treatments (Figure 1).

A similar variability was found when analysing beetles diversity (Figure 2). There was between years and among months variability in the response of beetle diversity to ungulates (Figure 2).

DISCUSSION

Our results have shown that ungulate exclusion significantly affected the arthropods living in the two studied shrub species. However, we found between-site differences in the exclusion of ungulates on arthropods and beetles. Although there was no clear effect of ungulates on the abundance

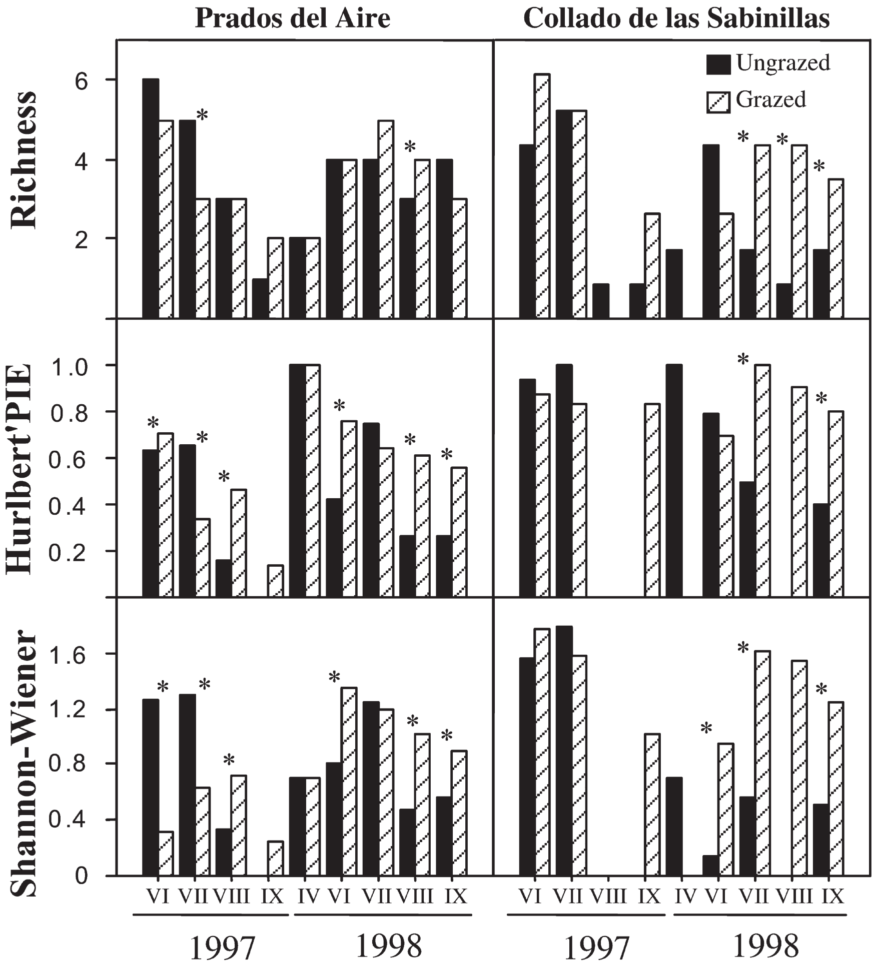

Fig. 2.—Temporal variability in the effect of ungulates exclusion on beetle diversity at the study sites. * $p < 0.05$ after a randomisation procedure (see Methods).
Fig. 2.—Variabilidad temporal en el efecto de la exclusión de ungulados sobre la diversidad de coleópteros en las zonas de estudio. * $p < 0.05$ tras un procedimiento de aleatorización (ver Métodos).

and biomass of beetles and arthropods, this effect was spatially and temporally consistent on arthropod and beetle diversity. Arthropod diversity was affected by ungulates both years in both plant communities but in a different way: whereas there was a positive effect of ungulate exclusion on arthropod diversity at Prados del Aire, this effect was negative at Collado de las Sabinillas. Nonetheless, there was a common effect of ungulates on beetle diversity in both areas, since the diversity of beetles was always higher in the ungrazed plots. This spatial variability may be a consequence of the differential response of host plant species to browsing effects. *Genista* plants are highly consumed by ungulates, meanwhile *Astragalus* is a thorny and less palatable shrubs. This suggests that most ungulate effects on arthropod community on Collado de las Sabinillas are indirect effects such as the addition of new resources (excrements, carrions) or the trampling effects. Another source of variation would be the high differences in the composition of plant and arthropod communities between areas (Morisita Horn values less than 0.02). This spatial variability between sites under the same intensity of browsing has been found in other studies (Abensperg-Traun *et al*., 1996; Suominen *et al*., 1999a)

Several non-exclusive hypotheses have been proposed to explain the positive or negative effects of ungulates on arthropod/beetle diversity. First, ungulates may provoke a habitat simplification affecting plant complexity, and thereby affecting arthropod community associated to these habitats (Lawton, 1983; Abensperg-Traun *et al*., 1996; Bestelmeyer & Wiens, 1996; Tscharntke, 1997; Waltz & Witham, 1997; Hayson & Coulson, 1998; Kruess & Tscharntke, 2002). *Genista* plants were effectively larger (in height and size) in the ungrazed plot than in the grazed one, where arthropod diversity was higher, which could suggest an effect of habitat complexity on arthropods. However, beetle diversity in both plant communities as well as arthropod diversity at Collado de las Sabinillas was higher in the grazed plot. Previous studies have shown a lower plant complexity on both excluded areas (Gonzalez-Megias, 2001; Gonzalez-Megias *et al*., 2003). For this reason, we presume that the effect of ungulates on arthropod and beetle diversity was not mediated by the alteration in plant complexity.

Second, ungulates, by consuming plant tissue, may affect arthropod diversity through direct and indirect effects. This is very important in our study because more than 87% of captured beetles were herbivores. There are some ways in which ungulate herbivory may affect insect abundance and diversity (Danell & Huss-Danell, 1985; Huntly, 1991; Sallabanks & Courtney, 1992; Meyer, 1993; Meyer & Root, 1993; Müller-Scharer & Brown, 1995; Martinsen *et al*., 1998). Thus, the effect can occur via exploitative competition, for using the same resources, such as leaves, shoots, flowers or fruits, a phenomenon widely reported (Sallabanks and Courtney, 1992; Baines *et al*., 1994; Tscharntke, 1997; Gómez & González-Megías, 2002). Our results have shown that *Sitona tenuis*, the most abundant species at Collado de las Sabinillas, was more abundant in the absence of ungulates at least in one of the years of study. Like ungulates, this weevil feeds mainly on leaves and current-year shoots. Exploitative competition has been also demonstrated between ungulates and *Timarcha lugens*, a crisomelid beetle that live in the same area (Gómez & González-Megías, 2002).

Although most beetles were herbivores, these insects were positively affected by ungulates, something already shown in other studies (Abensperg-Traun *et al*., 1996; Suominen *et al*., 1999a). In contrast, the abundance of Homoptera was negatively affected by ungulates in both sites. Although ungulates and homoptera belong to different functional groups, one being a plant-chewer and the other a sap-sucker, recent studies have demonstrated that herbivores do not need to belong to the same guild to exert strong effects one on each other (Strauss, 1987, 1991; Hunter, 1992; Schoener, 1993; Stewart, 1996; Roche & Fritz, 1997; Gómez & González-Megías, 2002). Herbivore damage can induce changes in the allelochemistry, productivity, architecture, phenology, and other attributes of most plant species (Karban & Baldwin, 1997), which affect the performance of other herbivores sharing the host-plant (Faeth & Wilson, 1997; Master & Brown, 1997), even if insects do not live on the same plant tissue (Inbar *et al*., 1995; Salt *et al*., 1996; Master & Brown, 1997; Fisher *et al*., 2000). Other authors have found a strong negative impact of browsing and cutting on sap-suckers as a consequence of a simplification of plant architecture (Morris, 1992; Völkl *et al*., 1993).

Cagnolo *et al*. (2002) found a high correlation between family of arthropods and species of beetles in the response to ungulates. In contrast, other authors have found a differential response to ungulates depending on the identity of the organisms or the taxonomic level considered (Abensperg-Traun *et al*., 1996; Dennis *et al*., 1997; Gardner *et al*., 1997; Tscharntke, 1997; Molina *et al*., 1999; Suominen *et al*., 1999b). Our results showed that the effect of ungulates on arthropod and beetle diversity was consistent at Collado de las Sabinillas but not at Prados del Aire, where arthropod diversity was higher in the ungrazed plot and beetle diversity in the grazed plot.

An interesting result showed by our study is that the effects of ungulate exclusion on arthropods differed depending on the year and the sampling period. For example, at Prados del Aire ungulates affected positively arthropod abundance in 1997 but negatively in 1998. Moreover, this variability occurred not only between years but also among sampling periods. Since differences in species composition between years can provoke a mosaic of responses to the same perturbation (Schoonhaven *et al*., 1998; Speight *et al*., 1999), a temporal change in species composition in the study area might explain this temporal variability in our results. However, Curculionidae was the dominant family of beetles in both years (60% of relative abundance) and the similarity in beetle assemblage composition between years was very high, with values over 90% (Morisita-Horn index). Variability in habitat productivity has been proposed to be the cause of the differential response of the same insect community to grazing (Bestelmeyer & Wiens, 1996). Moreover, the variability in species abundance and diversity in Mediterranean areas and high mountain habitats have been explained as a consequence of the high annual and seasonal variability in habitat productivity (Mani, 1968; Wolda, 1987; Blondel & Aronson, 1999).

In conclusion, our results have shown that ungulates affect arthropod community traits, this effect being evident mainly on arthropod and beetle diversity. However, we cannot conclude about the positive or negative effect of browsing in our study area since at each taxonomic level (families of arthropods vs. species of beetles), arthropods responded to ungulates in a different way. Moreover, there were also complex responses of arthropods at family and species levels in relation to temporal variability, pointing out the necessity of conducting long-term studies to accurately determine the actual effect of grazing on arthropod communities.

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Appendix 1. Number of individuals for each species of Coleoptera collected in grazed and ungrazed plots at Collado de las Sabinillas (*Astragalus* plant community) and Prados del Aire (*Genista* plant community).

	Astragalus ungrazed	*Astragalus* grazed	*Genista* ungrazed	*Genista* grazed
Cantharidae				
Cantharidae sp.4	0	1	0	0
Cantharidae sp.5	1	0	0	0
Carabidae				
Philorhizus crucifer crucifer	0	2	0	0
Chrysomelidae				
Aphtona euphorbiae	0	1	0	0
Calomicrus circumfusus Marsham	0	2	0	0
Chaetocnema tibialis Ill.	1	1	0	0
Longitarsus albineus	0	1	3	0
Gonoctena olivacea	0	0	3	3
Galeruca interrupta	1	0	0	0
Coccinellidae				
Coccinella septempunctata L.	3	2	0	0
Adalia bipunctata L.	0	1	0	0
Scymnus suturalis Thunberg	1	0	0	0
Sidis helgae	0	0	0	4
Apionidae				
Exapion compactum	0	0	194	135
Exapion nov. sp.	0	0	19	51
Curculionidae				
Sitona tenuis Rosenh.	25	14	0	1
Curculionidae sp.7	0	0	1	1
Curculionidae sp.8	2	4	5	8
Curculionidae sp.11	0	3	0	0
Curculionidae sp.21	1	2	0	0
Curculionidae sp.38	1	0	0	0
Curculionidae sp.56	0	0	2	1
Curculionidae sp.59	1	0	0	0
Malachiidae				
Malachiidae sp.2	0	2	0	0
Malachiidae sp.3	0	1	3	1
Malachiidae sp.6	0	0	1	0

	Astragalus ungrazed	*Astragalus* grazed	*Genista* ungrazed	*Genista* grazed
Melyridae				
Dasytes nigropunctatus Küst.	4	4	0	0
Melyridae sp.1	0	0	7	7
Melyridae sp.3	1	0	5	3
Melyridae sp.7	1	0	0	0
Nitidulidae				
Meligethes sp.1	0	1	0	0
Ptinidae				
Ptinidae sp.3	1	1	0	0
Scarabaeidae				
Hymenoplia chevrolati Mulsant	0	1	0	0
Scolitidae				
Scolitidae sp.1	0	1	0	0
Tenebrionidae				
Lagria hirta L.	1	0	0	0
Larvae	0	1	1	1