

Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem

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Abstract

Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem.— In recent decades, the abundance and distribution of certain big game species, particularly red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), have increased in south central Spain as a result of hunting management strategies. The high density of these ungulate species may affect the abundance of epigeous invertebrates. We tested the relationships between big game abundance and biodiversity, taxon richness, the biomass of invertebrates and their frequency on nine hunting estates and in comparison to ungulate exclusion areas. Ungulate exclusion itself affected invertebrate richness, since lower values were found in the open plots, whereas the highest differences in invertebrate diversity between fenced and open plots was found in areas with high wild boar density. Where wild boar densities were high, the number of invertebrates decreased, while where they were low, red deer had a positive effect on invertebrate abundance. Fenced plots thus seemed to provide refuge for invertebrates, particularly where wild boar were abundant. This study supports the idea that the structure of fauna communities is damaged by high density populations of ungulates, probably due to decreased food availability owing to overgrazing, modified conditions of ecological microniches and direct predation. However, the effects depended on the group of invertebrates, since saprophytic species could benefit from high ungulate abundance. Our findings reflect the need to control ungulate population density under Mediterranean conditions in south–western Europe and to implement ungulate exclusion plots.

Key words: Biodiversity, Invertebrates, Overabundance, Red deer, Wild boar

Resumen

Efecto de la densidad de ungulados silvestres sobre los invertebrados en un ecosistema Mediterráneo.— En las últimas décadas, la abundancia y distribución de determinadas especies de caza mayor, especialmente el ciervo rojo (*Cervus elaphus*) y el jabalí (*Sus scrofa*), han aumentado en la zona centromeridional de España como resultado de las estrategias de gestión cinegética. La alta densidad de estas especies de ungulados puede afectar a la abundancia de los invertebrados epigeos. Estudiamos la relación entre la abundancia de las especies de caza mayor y la biodiversidad, la riqueza de taxones, la biomasa de invertebrados y su frecuencia en nueve fincas de caza, y se comparó con las zonas de exclusión de ungulados. De por sí, la exclusión de ungulados afectó a la riqueza de invertebrados, ya que se encontraron valores más bajos en las parcelas abiertas, mientras que las mayores diferencias en la diversidad de invertebrados entre parcelas abiertas y cercadas se encontraron en zonas con una alta densidad de jabalíes. Donde la densidad de jabalíes era alta, el número de invertebrados disminuyó, mientras que donde era baja, el ciervo rojo tuvo un efecto positivo en la abundancia de invertebrados. Así, las parcelas cercadas parecían ofrecer refugio a los invertebrados, sobre todo donde los jabalíes eran abundantes. Este estudio apoya la idea de que las poblaciones con una alta densidad de ungulados perjudican a la estructura de las comunidades faunísticas, probablemente debido a la disminución de la disponibilidad de alimentos como consecuencia del sobrepastoreo, la modificación de las condiciones de los micronichos ecológicos y la depredación directa. Sin embargo, los efectos dependieron del grupo de invertebrados, ya que las especies saprofitas podrían

beneficiarse de la alta abundancia de ungulados. Nuestros resultados reflejan la necesidad de controlar la densidad de las poblaciones de ungulados en condiciones mediterráneas en el suroeste de Europa y de establecer parcelas de exclusión de ungulados.

Palabras clave: Biodiversidad, Invertebrados, Sobreabundancia, Ciervo rojo, Jabalí

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Introduction

The soil invertebrate community participates actively in ecological processes that are essential for substrate soil fertility and plant succession (Hedlund & Öhrn, 2000; Osler & Sommerkorn, 2007). Sources of soil disturbance and their effect on invertebrates, including the use of pesticides, phytosanitary treatment and other measure, have been thoroughly studied in agricultural ecosystems (Vickery et al., 2009; Raebel et al., 2012). However, knowledge of the factors affecting invertebrate communities in forest ecosystems is scarce (McIntyre, 2000).

Ungulate density and range has increased throughout Europe and North America over the last century (Clutton-Brock & Albon, 1992; Côté et al., 2004; Gordon et al., 2004; Sarasa & Sarasa, 2013) as a result of the extirpation of large predators (Breitenmoser, 1998), changes in silviculture and agriculture, and the intensification of game management (Apollonio et al., 2010). This increase in wild ungulate populations may have a strong impact on soil nutrient status and biota due to grazing, rooting, trampling and dunging, and changes in plant community due to herbivory can also affect invertebrate community structure (see Spalinger et al., 2012), but specific studies on these relationships are scarce. High densities of either livestock (Rosa-García et al., 2009) or wild ungulates (Côté et al., 2004; Mohr et al., 2005) are known to affect epigeous invertebrate communities, which are useful bioindicators (Gerlach et al., 2013) and important food resources for many species of birds, including the red-legged partridge, a key prey for many predators and the most important game bird in Spain (Wilson et al., 1999). Previous studies on the effect of ungulates on invertebrates have been conducted in areas in which ungulates are invasive (Cuevas et al., 2010, 2012) and in temperate climates, focusing on deciduous forests (Côté et al., 2004; Mohr et al., 2005; Mizuki et al., 2010). However, few studies have reported the effect of native ungulates on invertebrate soil diversity in semiarid areas, such as Mediterranean habitats (Gebeyehu & Samways, 2006). Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are the principal wild ungulate species in Southern European Mediterranean habitats, reaching very high abundances when intensive hunting management is performed (Vicente et al., 2007), ranging between 0.04 to 66.77 deer/km² (mean = 19.51; n = 22 populations) (Acevedo et al., 2008). In fact, the red deer is considered by some authors to be among the most invasive species in the world (Lowe et al., 2000) and its negative effect on some arthropod taxa such as Orthoptera or other phytophagous insect has been reported in subalpine grasslands (Gómez et al., 2004; Spalinger et al., 2012).

A high abundance of wild boar has also been reported to have a strong impact on edaphic fauna through disturbance (Herrero et al., 2006; Giménez-Anaya et al., 2008), rooting, and the direct consumption of meso- and macroinvertebrates (Cuevas et al., 2010). However, despite the large increase in the densities of wild boar and deer, little is known about the

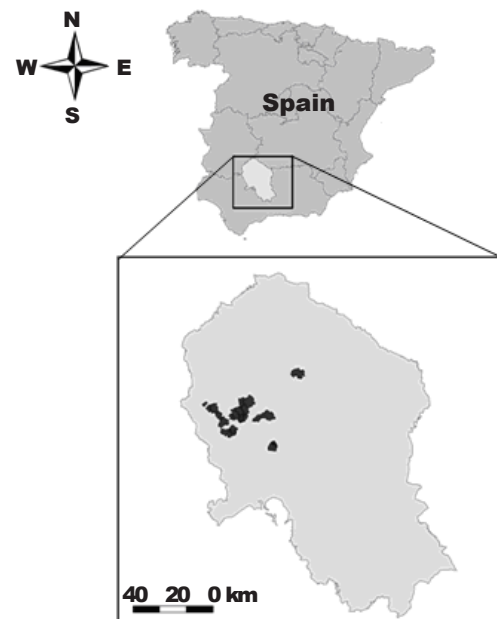


Fig. 1. Map of Spain showing the location of the sampling sites (Córdoba province in light grey).

Fig. 1. Mapa de España que muestra la ubicación de los sitios de muestreo (provincia de Córdoba en gris claro).

ecological impact of their overabundance on Mediterranean ecosystems (Barrios-García & Ballari, 2012; Carpio et al., 2014b) and particularly on the epigeous invertebrate assemblage, essential elements in the diet of many birds (Holland et al., 2006).

The aim of this study was to determine the impact of wild boar and red deer on diversity, richness and biomass of epigeous invertebrates in a semiarid Mediterranean environment from south central Spain, within the native distribution range of these two ungulate species.

Material and methods

Study area

Data were collected on 9 different hunting estates, which had an average area of 2,470 hectares (range 1,480–3,600 ha), located in southern Spain. The altitude ranged from 400 to 800 m.a.s.l. The dominant vegetation included tree species such as holm oak (*Quercus ilex*) and cork oak (*Quercus suber*), pine plantations (*Pinus pinea* and *Pinus pinaster*), shrub species such as *Cistus* spp., *Erica* spp., *Pistacia* spp., *Phyllirea* spp. and *Rosmarinus officinalis*, and scattered pastures and small areas of crops (Vicente et al., 2007). These savannah-like landscape units are called 'dehesas'. The study sites are mainly devoted to recreational hunting for wild boar and red deer.

Estimating red deer and wild boar abundance

Deer population size was estimated at hunting estate level, the estates being considered as discrete management units. Two spotlight counting events between September and October 2011 were used to estimate the deer population size at each estate. Transects (mean length = 20.3 km \pm 2.34 SE) were driven at 10–15 km/h (Carpio et al., 2014a). The distance from the observer to the centre of a deer group was measured, and compass bearings were taken to determine the angle between deer, or deer groups, and the transect line. The distance between the observer and the deer was measured with a Leica LRF 1200 Scan telemeter (Solms, Germany) (range 15–1,100 m; precision \pm 1m/ \pm 0.1%). The abundance of the deer populations was estimated by distance sampling (Buckland et al., 2004, Distance 5.0 software). Half-normal, uniform and hazard rate models for the detection function were fitted against the data using cosine, hermite polynomial and simple polynomial adjustment terms, which were fitted sequentially. The selection of the best model and adjustment term were based on Akaike's Information Criterion (AIC). The best relative fit of the model and adjustment term for distance-sampling was the hazard-rate cosine based on the lowest AIC score. However, this census method suffers significant variations depending on the type of game mode that is practiced (hunts or stalking).

Two 4 km transects per site were sampled for signs of wild boar activity following the guidelines of Acevedo et al. (2007). Each transect consisted of 40 segments of 100 m in length and 1 m in width. Every 100 m segment was divided into 10 sectors of 10 m in length. Sign frequency was defined as the average number of 10-m sectors containing droppings per 100-m transect (Carpio et al., 2014b), and a single average value of wild boar abundance was calculated per estate.

Experimental plots

We used five ungulate proof fences in each one of the nine hunting states. These fenced plots (hereafter FP) were constructed three to five years prior to data collection and they were constructed from steel. Each FP was 0.5 ha, with a mesh size of 150 mm \times 100 mm in order to prevent the ungulates access, although they were accessible to other animals (Carpio et al., 2014b). Two pitfall traps were randomly placed in each FP, resulting in a total of 90 traps where ungulates were excluded. Another two pitfall traps were placed 100m outside of each FP as controls (Open Plots, OP), resulting in 180 pitfall traps in total.

We conducted two surveys of invertebrates. The pitfall traps consisted of plastic receptacles, with a capacity of 0.75 litres and an opening diameter of 12 cm, buried at ground level (Paschetta et al., 2013). These were half filled with a solution of salts (to preserve the specimens caught) and soap (to break the water surface tension). The trapped invertebrates were collected 14 days after the traps

had been set (Allombert et al., 2005). The contents of the receptacles were passed through a sieve. The invertebrates were preserved in 100 ml plastic containers with 70% alcohol and later identified by stereomicroscope in the laboratory. Specimens were identified to order level (Barrientos & Abelló, 2004), as in some previous studies on the diet of farmland birds (Holland et al., 2006).

We studied the diversity and structure of invertebrate orders larger than 0.02 mm (mesofauna and macrofauna) present in our study area, excluding microfauna (less than 0.02 mm) (Swift et al., 1979). We therefore studied the most important groups in the diet of red-legged partridge chicks (Holland et al., 2006; Aebischer & Ewald, 2012). We excluded pitfall traps containing necrophagous insects (11% of placed traps) and also those in which more than 50% of individuals belonged to the order Hymenoptera (13% of placed traps) owing to the proximity of ant nests as these could exert a repellent effect on other arthropods (Blum, 1978).

For each sampling point, we calculated the invertebrate dry weight (B), taxon richness (S) and the Shannon index (Shannon, 1948).

To obtain the dry weight, the contents of the pitfall traps were dehydrated in an oven at 80°C for 24 h. A precision scale (0.001 g) was used. We calculated the values for each variable from the average of the two pitfall traps in each pair of sampling periods (OP and FP).

Vegetation structure

The vegetation structure was described by creating a buffer area of a 25 m radius around each pitfall trap and the percentage of grass, scrub and woodland cover was estimated by eye, following similar protocols for general habitat-species studies (Morrison et al., 1992). All the estimates of vegetation structure were performed by the same observer (A.J.C).

The amount of plant biomass was assessed from cuttings in an area of 25 cm² of herbaceous vegetation. Two sampling points were randomly selected in both the fenced and the open plots. The sampled vegetation was dried in a drying oven with hot air circulation at 60°C until a constant weight was obtained. An electric balance (precision: 0.01 g) was used.

Statistical analysis

The relationships between ungulate abundance (separately for red deer and wild boar, respectively) on invertebrate richness, dry mass, the Shannon index and absolute frequency (number of invertebrates per sample) were tested using generalized linear mixed models (GLMMs). With regard to the absolute frequency models, the analyses were carried out separately for each of the four taxonomic groups into which the samples had been pooled. The taxonomic categories were 'Hymenoptera' ($n = 1,120$), 'Insecta' other than Hymenoptera (16 orders, $n = 1,743$), class 'Arachnida' (including orders Araneida, Acari, Opiliones, Scorpionida, Pseudoescorpionida and

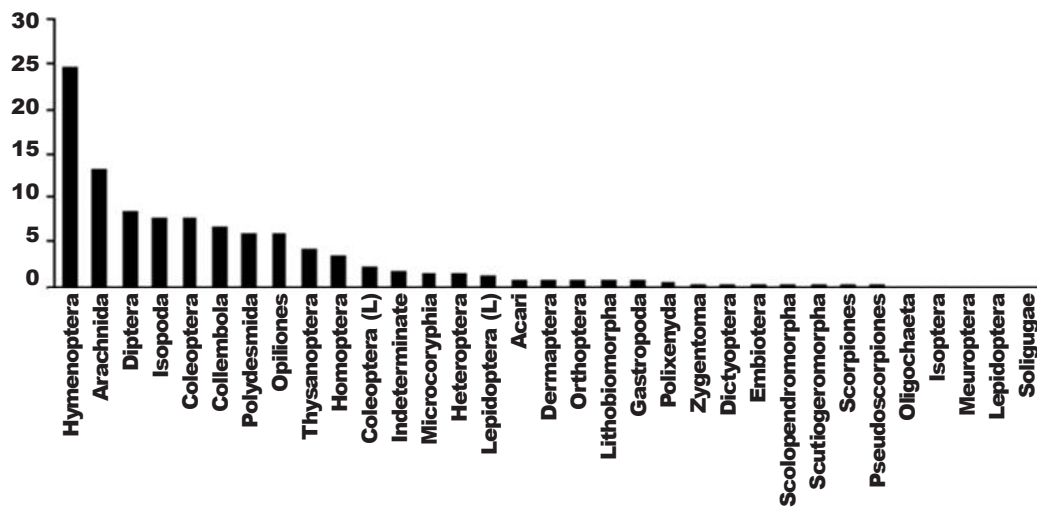


Fig. 2. Percentage of trapped invertebrates belonging to each order as regards the total.

Fig. 2. Porcentaje de invertebrados atrapados pertenecientes a cada orden con respecto al total.

Solifugae; six orders, $n = 906$), and 'others' (including the subphylum Myriapoda, order Isopoda, and classes Oligochaeta and Gastropoda; nine taxa, $n = 787$).

Treatment (two levels: open vs. fenced plots) was included in the model as the factor, whereas red deer and wild boar abundances, in addition to the vegetal biomass (g) and percentage of grass, shrub and tree covers, were included as co-variables. We also included the interaction between the treatment and the abundances of ungulates and the interaction between deer and wild boar density. The estate was included (nine levels) as a random factor. Since every plot was sampled twice, the sampling dates were included in the model as repeated measures.

A normal distribution function and an identity link were used for dry mass, and the Shannon index, and a Poisson function and log-link function were used for

richness and absolute frequency models. Rather than using criteria based on parsimony to select the 'best model' (which favour precision vs. bias) we used the full models: (i) because our models had high degrees of freedom (nine explanatory variables) and there was no need to guard against over-fitting, (ii) to protect from the bias of regression coefficients, and (iii) to preserve the accuracy of confidence intervals while using other non-collinear factors for control purposes (multiplicity adjustment, while our understanding of the underlying biological processes led us to believe that the important variables to control for had been included). The assumptions of normality, homogeneity and independence in the residuals were assessed in models with normal distribution function (Zuur et al., 2009). Statistical analyses were performed using InfoStats and SAS 9.0 statistical software. The significant p -value was set at $p = 0.05$.

Table 1. Mean and standard deviations for the variables quantifying invertebrate abundance: OP. Open plots; FP. Fenced plots.

Tabla 1. Media y desviaciones estándar de las variables que cuantifican la abundancia de invertebrados: OP. Parcelas abiertas; FP. Parcelas cerradas.

	March collection		April collection		March + April	
	OP	FP	OP	FP	OP	FP
Shannon index	1.56 ± 0.36	1.75 ± 0.28	1.57 ± 0.37	1.65 ± 0.32	1.56 ± 0.36	1.66 ± 0.31
Taxon richness	7.06 ± 2.31	8.13 ± 1.89	7.3 ± 2.24	8.22 ± 2.41	7.11 ± .45	8.32 ± 2.15
Weight arthropods	0.15 ± 0.18	0.13 ± 0.11	0.08 ± 0.08	0.16 ± 0.18	0.12 ± 0.15	0.14 ± 0.15
Absolute frequency	36.44 ± 5.1	37.8 ± 3.07	43 ± 4.91	56.09 ± 5.67	39.22 ± 3.5	47.05 ± 3.4

Table 2. Full model on the effects of ungulates on invertebrate richness, dry mass and Shannon diversity index (* $p < 0.05$).

Tabla 2. Modelo completo sobre los efectos de los ungulados en la riqueza, el peso seco y el índice de diversidad de Shannon de los invertebrados ($p < 0,05$).*

	Taxon richness		Dry mass		Shannon index	
	<i>F</i>	β	<i>F</i>	β	<i>F</i>	β
Treatment (T)	7.8*	1.21	1.62	0.42	0.07	1.01
Deer density (Dd)	0.01	2.18	0.44	-2.76	0.03	0.63
Wild boar abundance (Wba)	0.01	-3.36	0.54	-0.95	0.03	-0.82
Shrub	0.1	0.0017	0.05	0.0006	1.10	0.0009
Dd * Wba	0.01	0.59	0.28	3.67	0.01	0.36
T * Dd	0.61	-3.25	0.63	1.76	1.57	-0.81
Plant biomass	0.17	-0.15	0.01	0.0052	4.31	0.03
Wooded	1.1	0.017	0.05	-0.0017	3.1	0.0045
Grass	0.43	-0.0004	3.62	1.9	1.65	-0.0001
T * Wba	1.78	4.92	1.33	-2.23	4.3*	1.17

Results

The best relative fit of the model and adjustment term for distance–sampling was the hazard–rate cosine based on the lowest AIC score. The average red deer density, expressed as the number of deer per 100 ha, ranged from 25 to 68 (average 39 ± 14 SD). The coefficients of variation of distance–sampling estimates ranged from 2.95% to 38.86%. The abundance indices for wild boar ranged from 0.04 to 0.47 (average $0.26 \pm$ SD 0.15).

We identified 5781 invertebrates, 3,201 of which were captured in FP and 2,580 in OP (table 1). They were spread over 33 taxa (17 insect orders, six Arachnida orders, six Myriapoda orders, one Crustacean order, one Gastropoda class, one Oligochaeta class and a group corresponding to indeterminate individuals; fig. 2).

The invertebrate dry mass was marginally significant and positively associated with the percentage of grass cover (table 2, $F_{1,123} = 3.62$, $p = 0.059$), whereas invertebrate richness differed statistically between treatments, with the values for the OP being lower than those for the FP ($F_{1,123} = 7.8$, $p < 0.05$). The Shannon Index was statistically related to the interaction between treatment and wild boar abundance, meaning that the differences in arthropod diversity were only evidenced when high wild boar densities occurred ($F_{1,123} = 4.31$, $p < 0.05$; table 2). This was mainly due to an increase in the diversity index in the FP with high densities of wild boar (fig. 3), with diversity remaining similar in the OP.

Table 3 shows the models concerning the relationships between invertebrate numbers on the surface (absolute abundance) and ungulate densities, both

overall and separately for each taxonomic group: Insecta (no Hymenoptera), Hymenoptera, Arachnida and 'others'. The percentage of shrubs was statistically and negatively related to both Hymenoptera counts and the total amount of arthropods. Interestingly, the interaction between deer and wild boar abundances was statistically related to the total invertebrate counts (fig. 4A) and the number of invertebrates included in the 'others' group (fig. 4B). Independently of red deer abundance, when high wild boar densities occurred the number of invertebrates decreased, although at low wild boar abundance a positive association between red deer density and the number of invertebrates was recorded. Those invertebrates included in the 'others' group were more frequent in areas with high abundance of both red deer and wild boar. A positive relationship between red deer density and the absolute frequency of trapped invertebrates was also found (fig. 5A, 5B).

Discussion

Our main results were that (i) higher values of invertebrates richness were found in ungulate exclusion areas, and (ii) the high densities of wild boar had a particularly negative effect on invertebrates diversity. These findings support the negative relationships between high wild boar abundance and invertebrates in Mediterranean ecosystems, which may be considered to be arthropod hotspots (Hernandez–Manrique et al., 2012).

The higher abundance of invertebrates in the FP may be caused by a local attraction effect, since invertebrates might seek refuge in fenced patches

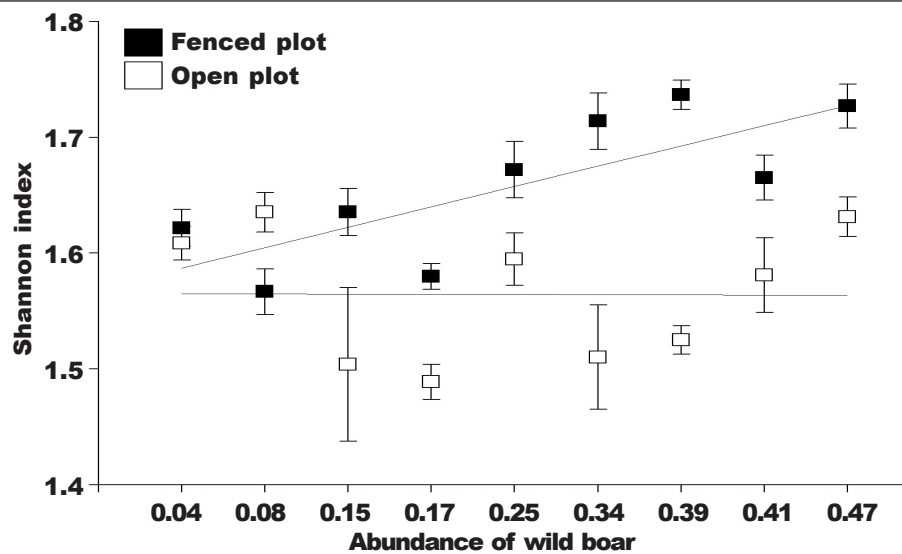


Fig. 3. Shannon index as a function of wild boar abundance index per estate (mean ± SE).

Fig. 3. Índice de Shannon en función del índice de abundancia de jabalíes por finca (media ± EE).

in which they actively look for the conditions inside the plots where no wild board predation (Grayson & Hassall, 1985) or overgrazing occurs. Overgrazing is known to cause a decrease in the food that is available to the edaphic fauna (Dennis et al., 2001, 2008;

Rosa–García et al., 2009, 2010) and suitable places for egg production, laying and incubation. Moreover, inside the fenced plots, the invertebrates would avoid disturbance from wild boar and red deer, which strongly affect soil compaction/structure through trampling and

Table 3. Full models on the effects of ungulates on the number of invertebrates (Insecta, Hymenoptera, Arachnida, others and total, respectively): ** $p < 0.01$; * $p < 0.05$.

Tabla 3. Modelos completos sobre los efectos de los ungulados en el número de invertebrados (Insecta, Hymenoptera, Arácnida, otros y total, respectivamente): ** $p < 0,01$; * $p < 0,05$.

	Insecta		Hymenoptera		Arachnida		Others		Total	
	F	β	F	β	F	β	F	β	F	β
Intercept	1.1	0.44	1.57*	1.48	0.14	1.78	1.17	-10.2	2.86**	3.18
Treatment (T)	0.43	0.14	0.22	0.16	0.22	0.27	0.025	-1.26	0.39	0.21
Deer density (Dd)	2.2	2.10	0.36	-0.75	0.004	0.47	5.99*	80.53	5.19*	3.75
Wild boar abundance (Wba)	0.26	0.17	0	0.095	0.009	-0.45	3.33	50.54	2.13	1.65
Shrub	0.5	0.025	7.31**	-0.13	0.02	0.012	2.12	-1.96	9.88**	-0.17
Dd * Wba	0.96	-2.82	0.023	0.49	0.005	0.39	5.36*	-177.4	4.29*	7.59
T * Dd	2.31	-0.63	0.003	-0.061	0.14	-0.67	0.14	-9.1	0.42	-0.79
Plant biomass	0.58	0.049	0.07	-0.026	0.06	-0.04	1.17	2.51	0.37	0.19
Wooded	2.5	-0.084	0.43	-0.049	0.02	0.017	0.004	0.12	0.31	-0.086
Grass	0.54	0.001	0.78	-0.002	0.16	-0.001	0.06	-0.015	0.43	-0.002
T * Wba	2.32	0.88	0.07	-0.22	0.09	0.022	0.45	13.98	0.89	0.94

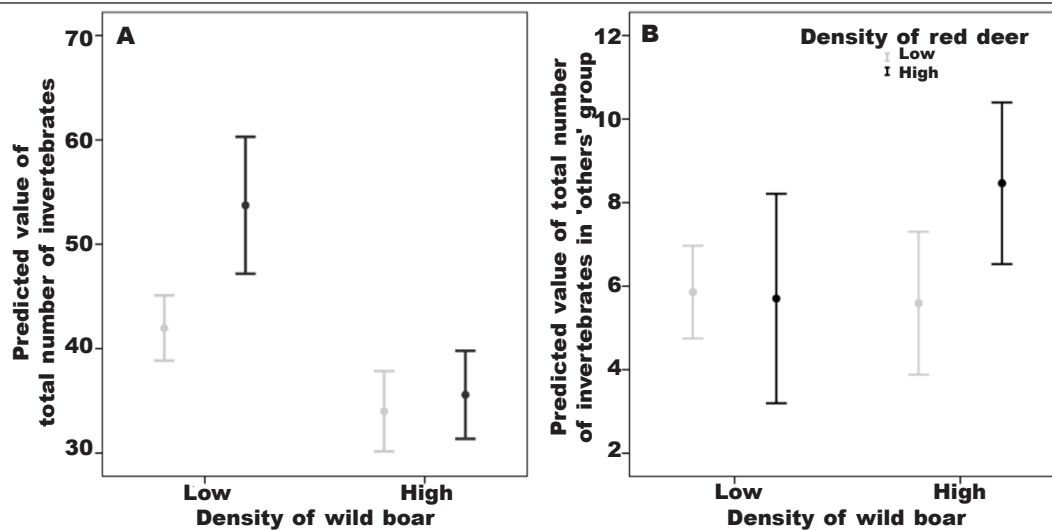


Fig. 4. Total number of invertebrates (A) and number of invertebrates included in 'others' group (B) as a function of interaction of wild boar and red deer abundance index groups (categorized according to the median \pm 95% CI of the abundance indexes).

Fig. 4. Número total de invertebrados (A) y número de invertebrados incluidos en el grupo otros (B) en función de la interacción de los índices de abundancia de jabalíes y de ciervos rojos (agrupados según la mediana \pm IC del 95% de los índices de abundancia).

rooting activities (Massei & Genov, 2004; Bueno, 2011). This could alter the establishment of a range of invertebrate species with different ecological requirements (Thiele-Bruhn et al., 2012), thus reducing the diversity of invertebrates. Our study supports previous findings in other environments showing that the overabundance of wild boar damages the structure of fauna communities (Côté et al., 2004; Allombert et al., 2005; Mohr et al., 2005; Albon & Brewer, 2007; Cuevas et al., 2012; Wirthner et al., 2012). However, in our study, the principal predictor of the invertebrate dry mass was the percentage of pasture cover, probably because pasture cover benefits certain abundant species more than others, and the ungulate effect is not appreciated in terms of invertebrate biomass.

Moreover, the differences on invertebrates diversity (Shannon Index) between fenced and open areas were higher in hunting states with higher wild boar density. In other words, the values of Shannon Diversity Index were much higher in ungulate proof areas than in open areas characterized by high wild boar densities. This may be due to the less favourable habitat in the surroundings as a consequence of overgrazing and rooting activity, possibly attracting more invertebrates to undisturbed patches (Gardiner & Hassall, 2009). Indeed, the wild boar diet includes not only vegetation but also many meso- and macro-invertebrates (Cuevas et al., 2010). Therefore, high wild boar densities may cause an intense disturbance of edaphic fauna, and invertebrates from the area tend to aggregate more in FP than in areas with lower wild boar abundance.

Interestingly, the interaction between deer and wild boar abundances was statistically related to the total counts of invertebrates and the number of invertebrates included in the 'others' group. Independently of red deer abundance, when wild boar densities were high, the number of invertebrates decreased, indicating that the wild boar, at high densities, have an overall negative impact on invertebrates. However, when wild boar abundance was low, a positive association between red deer density and the number of invertebrates was evident. We observed a positive relationship between red deer density and the absolute frequency of trapped invertebrates and the 'others' category, which must be explained in terms of the interaction between red deer and wild boar abundances (also significant, see discussion below). In contrast, as figure 5A shows, the high absolute frequency of invertebrates was recorded at intermediate values of red deer density, which is in agreement with previous studies that suggest a positive effect of moderate grazing pressure (Gómez et al., 2004).

Our results further suggest that Isopoda and Myriapoda groups, the most abundant taxa found in the 'other' group, could benefit from high red deer abundances (fig. 5B). These groups have phytophagous but also important saprophytic diets and may therefore benefit from the removal of bushes and the presence of the layer of grass, which provides an increased amount of organic plant matter, and therefore an increased source of food (Bugalho & Milne, 2003; Côté et al., 2004). Furthermore, ungulate faeces attract invertebrates that consume the dung and gain moisture from it or consume microbes within it (Stewart, 2001).

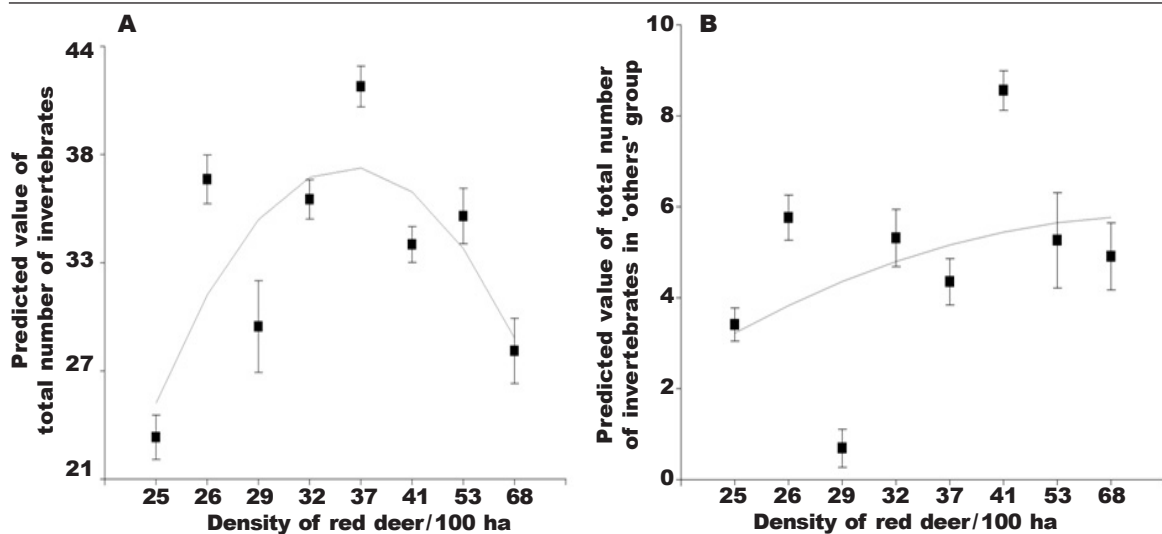


Fig. 5. Total number of invertebrates (A) and number of invertebrates included in 'others' group (B) as a function of red deer density per estate (mean \pm SE).

Fig. 5. Número total de invertebrados (A) y número de invertebrados incluidos en el grupo otros (B) en función de la densidad de ciervos rojos por finca (media \pm EE).

With regard to the Arachnida and Insecta category, we found no differences in abundance either inside or outside the fenced plots, although grass favoured the presence of the Araneida order (Rosa-García et al., 2009). The composition of the habitat and the development of pastures as a result of moderate deer grazing may benefit the presence of animals included in the Arachnida category (Dennis et al., 2001; Paschetta et al., 2013). On the other hand, our results show that the percentage of shrub cover has negative effects on the abundance of Hymenoptera. A study carried out by Azcarate & Peco (2012) in a Mediterranean ecosystem led them to conclude that the generation of a more heterogeneous environment at the smaller scales increased the species diversity of ants. However, the reasons for the negative influence of shrubs on Hymenoptera remain unclear and more research on the type of ecological relationships that exist between them are therefore necessary as few studies have focused on discovering these relationships in a Mediterranean environment.

General conclusions

This research has evidenced the relationships between ungulate abundance (in high density areas) and edaphic invertebrate abundance and richness under Mediterranean constraints. Overall, this study supports the notion that high density populations of wild boar may damage the structure of soil fauna communities as a result of a decrease in food availability owing to overgrazing, soil disturbance by rooting, and direct predation. The conservation applications of this study refer to wild boar population density control under Mediterranean

conditions where big game hunting has become an important industry. In particular, high densities of wild boar have a strong impact on invertebrates when compared to red deer, and a positive association was even noted in regard to the number of trapped invertebrates. Furthermore, since fenced plots evidenced a local scale effect, playing a role as refuges, the implementation of ungulate proof exclusion fences is desirable in order to maintain invertebrate communities, which would in turn enhance the food availability for many birds, including the red legged-partridge. However, more studies are needed to develop field protocols (e.g. the size and location of such fenced patches) and to assess population control effects on the invertebrate community.

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References

Acevedo, P., Vicente, J., Höfle, U., Cassinello, J., Ruiz-Fons, F. & Gortázar, C., 2007. Estimation

- of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. *Epidemiology and Infection*, 135: 519–527.
- Acevedo, P., Ruiz-Fons, F., Vicente, J., Reyes-García, A. R., Alzaga, V. & Gortázar, C., 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *Journal of Zoology*, 276: 37–47.
- Aebischer, N. J. & Ewald, J. A., 2012. The grey partridge in the UK: population status, research, policy and prospects. *Animal Biodiversity and Conservation*, 35.2: 203–212.
- Albon, S. D. & Brewer, M. J., 2007. Quantifying the grazing impacts associated with different herbivores on rangelands. *Journal of Applied Ecology*, 44: 1176–1187.
- Allombert, S., Stockton, S. & Martin, J. L., 2005. A Natural Experiment on the Impact of Overabundant Deer on Forest Invertebrates. *Conservation Biology*, 19: 1917–1929.
- Apollonio, M., Anderson, R. & Putman, R., 2010. *European Ungulates and their Management in the 21st Century*. Cambridge Univ. Press, Cambridge.
- Azcarate, F. M. & Peco, B., 2012. Abandonment of grazing in a Mediterranean grassland area: consequences for ant assemblages. *Insect Conservation and Diversity*, 5: 279–288.
- Barrientos, J. A. & Abelló, P., 2004. *Curso práctico de entomología*. Univ. Autónoma de Barcelona, Barcelona.
- Barrios-García, M. N. & Ballari, S. A., 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biological Invasions*, 14: 2283–2300.
- Blum, M. S., 1978. Biochemical defenses of insects. In: *Biochemistry of insects*: 465–513 (M. Rockstein, Ed.). Academic Press, New York.
- Breitenmoser, U., 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation*, 83: 279–289.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L., 2004. Introduction to distance sampling: estimating abundance of biological population. Oxford Univ. Press, Oxford.
- Bueno, C. G., 2011. Impacto de las perturbaciones del jabalí en los pastos supraforestales de los Pirineos Centrales. Ph. D. Thesis, Univ. de Zaragoza, Instituto Pirenaico de Ecología (CSIC).
- Bugalho, M. N. & Milne, J. A., 2003. The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint? *Forest Ecology and Management*, 181: 23–29.
- Carpio, A. J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F. S., 2014a. The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit? *Wildlife Biology*, 20: 161–166.
- Carpio, A. J., Guerrero-Casado, J., Tortosa, F. S. & Vicente, J., 2014b. Predation of simulated red-legged partridge nests in big game estates from South Central Spain. *European Journal of Wildlife Research*, 60: 391–394.
- Clutton-Brock, T. H. & Albon, S. D., 1992. Trial and error in the Highlands. *Nature*, 358: 11–12.
- Côté, S. D., Rooney, T. P., Trembley, J. P., Dussault, C. & Waller, D. M., 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35: 113–147.
- Cuevas, M. F., Mastrantonio, L., Ojeda, R. A. & Jaksic, F. M., 2012. Effects of wild boar disturbance on vegetation and soil properties in the Monte Desert, Argentina. *Mammalian Biology*, 77: 299–306.
- Cuevas, M. F., Novillo, A., Campos, C., Dacar, M. A. & Ojeda, R. A., 2010. Food habits and impact of rooting behaviour of the invasive wild boar, *Sus scrofa*, in a protected area of the Monte Desert, Argentina. *Journal of Arid Environment*, 74: 1582–1585.
- Dennis, P., Skartveit, J., McCracken, D. I., Pakeman, R. J., Beaton, K., Kunaver, A. & Evans, D. M., 2008. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology*, 45: 279–287.
- Dennis, P., Young, M. R. & Bentley, C., 2001. The effects of varied grazing management on epigeal spiders harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agriculture, Ecosystems and Environment*, 86: 39–57.
- Gardiner, T. & Hassall, M., 2009. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? *Journal of Insect Conservation*, 13: 97–102.
- Gebeyehu, S. & Samways, M. J., 2006. Conservation refugium value of a large mesa for grasshoppers in South Africa. *Biodiversity and Conservation*, 15: 717–734.
- Gerlach, J., Samways, M. & Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*, 17: 831–850.
- Giménez-Anaya, A., Herrero, J., Rosell, C., Couto, S. & García-Serrano, A., 2008. Food habits of wild boars (*Sus scrofa*) in a Mediterranean Coastal Wetland. *Wetlands*, 28: 197–203.
- Gómez, J. M., González-Megías, A. & Sanchez-Pinero, F., 2004. Effects of ungulates on epigeal arthropods in Sierra Nevada National Park (Southeast Spain). *Biodiversity and Conservation*, 13: 733–752.
- Gordon, I. J., Hester, A. J. & Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, 41: 1021–1031.
- Grayson, F. W. L. & Hassall, M., 1985. Effects of rabbit grazing on population variables of *Chorthippus brunneus* (Orthoptera). *Oikos*, 44: 27–34.
- Hedlund, K. & Öhrn, M. S., 2000. Tritrophic interactions in a soil community enhance decomposition rates. *Oikos*, 88: 585–591.
- Hernandez-Manrique, O. L., Numa, C., Verdu, J. R., Galante, E. & Lobo, J. M., 2012. Current protected sites do not allow the representation of endangered invertebrates: the Spanish case. *Insect Conservation and Diversity*, 5: 414–421.

- Herrero, J., García-Serrano, A., Couto, S., Ortuño, V. M. & García-González, R., 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *European Journal of Wildlife Research*, 52: 245–250.
- Holland, J. M., Hutchison, M. A. S., Smith, B. & Aebischer, N. J., 2006. A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. *Annals of Applied Biology*, 148: 49–71.
- Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M., 2000. *100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database*. The Invasive Species Specialist Group (ISSG). Auckland, New Zealand.
- Massei, G. & Genov, P., 2004. The environmental impact of wild boar. *Galemys*, 16: 135–145.
- McIntyre, N. E., 2000. Ecology of urban arthropods: a review and a call to action. *Annals of the Entomological Society of America*, 93: 825–835.
- Mizuki, I., Yamasaki, M., Kakutani, T. & Isagi, Y., 2010. Negligible impact of deer-induced habitat degradation on the genetic diversity of extant *Bombus diversus* populations in comparison with museum specimens. *Journal of Insect Conservation*, 14: 191–198.
- Mohr, D., Cohnstaedt, L. & Topp, W., 2005. Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. *Soil Biology and Biochemistry*, 37: 693–700.
- Morrison, M. L., Marcot, B. G. & Mannan, R. W., 1992. *Wildlife-habitat relationship. Concepts and applications*. Univ. of Wisconsin Press, Madison.
- Osler, G. H. R. & Sommerkorn, M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. *Ecology*, 88: 1611–1621.
- Paschetta, M., La Morgia, V., Masante, D., Negro, M., Rolando, A. & Isaia, M., 2013. Grazing history influences biodiversity: a case study on ground-dwelling arachnids (*Arachnida: Araneae, Opiliones*) in the Natural Park of Alpi Marittime (NW Italy). *Journal of Insect Conservation*, 17: 339–356.
- Raebel, E. M., Merckx, T., Feber, R. E., Riordan, P., Macdonald, D. W. & Thompson, D. J., 2012. Identifying high-quality pond habitats for Odonata in lowland England: implications for agri-environment schemes. *Insect Conservation and Diversity*, 5: 422–432.
- Rosa-García, R., Jáuregui, B. M., García, U., Osoro, K. & Celaya, R., 2009. Effects of livestock breed and grazing pressure on ground-dwelling arthropods in Cantabrian heathlands. *Ecological Entomology*, 34: 466–475.
- Rosa-García, R., Ocharan, F. J., García, U., Osoro, K. & Celaya, R., 2010. Arthropod fauna on grassland-heathland associations under different grazing managements with domestic ruminants. *Comptes Rendus Biologies*, 333: 226–234.
- Shannon, C. E., 1948. A mathematical theory of communication. *Bell System Technical Journal*, 27: 379–423.
- Sarasa, M. & Sarasa, J. A., 2013. Intensive monitoring suggests population oscillations and migration in wild boar *Sus scrofa* in the Pyrenees. *Animal Biodiversity and Conservation*, 36: 79–88.
- Spalinger, L. C., Haynes, A. G., Schutz, M. & Risch, A. C., 2012. Impact of wild ungulate grazing on Orthoptera abundance and diversity in subalpine grasslands. *Insect Conservation and Diversity*, 5: 444–452.
- Stewart, A. J. A., 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. *Forestry*, 74: 259–270.
- Swift, M. J., Heal, O. W. & Anderson, J. M., 1979. *Decomposition in terrestrial ecosystems*. Blackwell Scientific, Oxford, UK.
- Thiele-Bruhn, S., Bloem, J., Vries, F. Td., Kalbitz, K. & Wagg, C., 2012. Linking soil biodiversity and agricultural soil management. *Current Opinion in Environmental Sustainability*, 4: 523–528.
- Vicente, J., Höfle, U., Fernández-de-Mera, I. G. & Gortázar, C., 2007. The importance of parasites life histories and host density in predicting the impact of infections in red deer. *Oecologia*, 152: 655–664.
- Vickery, J., Feber, R. & Fuller, R., 2009. Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. *Agriculture, Ecosystems and Environment*, 133: 1–13.
- Wilson, J. D., Morris, A. J., Arroyo, B. E., Clark, S. C. & Bradbury, R. B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems and Environment*, 75: 13–30.
- Wirthner, S., Schütz, M., Page-Dumroese, D. S., Busse, M. D., Kirchner, J. W. & Risch, A. C., 2012. Do changes in soil properties after rooting by wild boars (*Sus scrofa*) affect understory vegetation in Swiss hardwood forests? *Canadian Journal of Forest Research*, 42: 585–592.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York, Springer.

