Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*)

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ABSTRACT

The role of herbivores in controlling plant population abundance and distribution is unclear. We experimentally determine the effect of damage by wild boars (*Sus scrofa*) in recruitment rate and spatial pattern of a Mediterranean tree, the holm oak (*Quercus ilex*). We monitored oak establishment in the Sierra Nevada of southeastern Spain during 4 years (1999–2002) in four plots, two fenced and two unfenced that were used as controls. In addition, we planted 1-year-old seedlings in all microhabitats, both in fenced and control plots, to experimentally determine the effect of wild boar on their microhabitat-dependent survival. Despite seedling abundance being similar inside and outside the fences, sapling abundance diminished up to 50% in unfenced plots compared to fenced plots. Wild boars also seemed to modify the spatial distribution of seedlings and saplings. Whereas seedlings were most abundant under pines both in fenced and control plots, sapling abundance was highest under pine trees in fenced plots, but similarly abundant under pines or shrubs in control plots. This change in spatial pattern was due to the effect of wild boars killing seedlings when looking for food under pines. The effects of the different mortality factors were not additive. Where ungulates are absent, recruitment is high and occurs under oaks and especially under pines. Where wild boars are present, recruitment diminishes and occurs mostly under shrubs and pines. Wild boars arrest population growth and modify the spatial pattern of recruitment.

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1. Introduction

Herbivores affect the reproduction, growth and survival of their host plants (Crawley, 2000; Strauss and Zangerl, 2002; Baraza et al., 2006). Unfortunately, most studies on plant–herbivore interactions are short-term and do not quantify the long-term fate of plant populations after experimentally controlling for herbivore abundance or activities (Maron and Crone, 2006). Consequently, the role played by herbivores in controlling the abundance and spatial pattern of plant populations is still unclear (Münzbergová and Herben, 2005; Maron and Crone, 2006; Halpern and Underwood, 2006).

Seedlings represent one of the most vulnerable stages in the life cycle of most plant species (Harper, 1977), and mortality at this stage is very high in many plant species (Kitajima and Fenner, 2000). Damage by animals is one of the greatest hazards affecting seedlings (Crawley, 2000; Kitajima and Fenner, 2000). Herbivores act as severe mortality factors for many plant species, greatly reducing the number of recruits (Hulme, 1994; Maron, 1997; Edwards and Crawley, 1999; Gómez et al., 2003; Asquith and Mejia-Chang, 2005; Del-Val et al., 2007). Consequently, the regeneration of some long-lived, woody perennials is thought to be arrested by the action of herbivores restricting seed production at consecutive life stages (Crawley and Long, 1995; Hulme, 1996; Asquith and Mejia-Chang, 2005; Maron and Crone, 2006).

Many recent studies have shown that seed and seedling predators, besides hampering the number of recruits, can also strongly influence the population dynamics of their host plants by altering their spatial patterns of recruitment (Crawley, 2000; Muller-Landau et al., 2002; Maron and Crone, 2006). This effect occurs mainly when the impact of herbivores varies spatially among microhabitats (Rey and Alcántara, 2000; Gómez et al., 2003; Gómez, 2005), and is magnified when in addition herbivores over-damage the recruits dispersed to or established in high-quality microsites (Callaway, 1992; Crawley and Long, 1995; Rousset and Lépart, 2000; Gómez, 2005). Under these circumstances, it is thought that the spatial distribution of many plant species inhabiting heterogeneous landscapes is a direct consequence of the activity of their major herbivores (Jordano and Herrera, 1995; Schupp, 1995; Schupp and Fuentes, 1995; Rey and

Alcántara, 2000). However, despite its crucial importance, few studies have experimentally demonstrated the role that herbivores play in shaping the spatial distribution pattern of plant populations (i.e., Fine et al., 2004; Gómez, 2005).

In this paper, we experimentally investigate the effect of ungulates on the recruitment rate and spatial pattern of the holm oak *Quercus ilex* L. (Fagaceae) in the Sierra Nevada mountains (Granada province, SE Spain). Ungulates can affect several holm oak life cycle stages, from seed dispersal to saplings (Cuartas and García-González, 1992; García-González and Cuartas, 1992; Baraza, 2004; Focardi and Tinelli, 2005; Muñoz and Bonal, 2007). However, most damage is inflicted on seeds and seedlings (Focardi et al., 2000; Leiva and Fernández-Alés, 2003; Gómez, 2004; Pulido and Díaz, 2005). Our study addresses four specific questions: (1) Which mortality factors act at seedling stage of holm oak life cycle? (2) Is there a habitat-dependent survival of oak seedlings? (3) Does the selective action of different mortality agents alter the abundance and spatial distribution of oak recruits? (4) Is there a long-term effect of ungulates on the recruitment rate and spatial pattern of holm oak?

2. Materials and methods

2.1. Study system

Holm oak is a Mediterranean evergreen, which is shade-tolerant during its early life cycle stages (Retana et al., 1992; Espelta et al., 1995; Puerta-Piñero et al., 2007). Holm oak acorns are dispersed in the study area during autumn (late October through November) mainly by European jays (*Garrulus glandarius*) (Gómez, 2003) and to a lesser extent by woodmice (*Apodemus sylvaticus*) (Gómez et al., 2008). Acorns are usually transported far from adult oaks and buried under shrubs or under other trees (Gómez, 2003; Gómez et al., 2008). Like most oaks, holm oak does not form a persistent seed bank in the soil. Acorns are depredated after dispersal by wild boars (*Sus scrofa*) and woodmice (Gómez, 2004).

2.2. Study site

The study site is located in Trevenque (Sierra Nevada Protected Area, SE Spain), between 1550 and 1700 m a.s.l. The climate is continental Mediterranean, characterized by cold winters and hot summers with severe summer drought (July–August). Rainfall is concentrated mainly in autumn and spring, with an annual rainfall of 825 mm (mean 1990–1998; data from a climatic station located in the study site). The study site is composed of a mosaic of oak–pine woodlands (small stands of large oak trees and many reproductive resprouts, intermingled with single adult pines) coexisting with plantations (medium to large patches planted with non-native pines).

Two 2 ha fenced plots and two 2 ha unfenced (control) plots were established in 1999. All plots being roughly 100 m apart. Fences were established in 1990 to avoid the entrance of wild ungulates, mainly wild boars and Spanish ibex (*Capra pyrenaica*). These two ungulates are fairly abundant in the study area, although no information on their density is available. In each plot, the following microhabitats were defined: (1) "holm oak", under the canopy of adult and juvenile Holm oaks; (2) "pine", under the canopy of adult and juvenile pines (mostly *Pinus sylvestris* and *P. nigra*); (3) "shrub", under the canopy of shrub species >150 cm tall, mainly *Prunus ramburii* and *Crataegus granatensis*; and (4) "open", without tree or shrub cover, on bare soil with areas of fine gravel and cobble, sparse herbaceous vegetation (mainly annuals and short-lived perennials), and deep soil with a thick cover of herbs. These microhabitats cover 90% of the study site (Gómez, 2004).

2.3. Spatial pattern of recruitment depending on ungulate presence

All naturally established young saplings (less than 150 cm tall) and current-year seedlings were counted in twenty 5 m × 2 m transects per year in each of the above-described microhabitats and plots from 1999 to 2002 (960 transects in total, 9600 m² monitored). Transects were not fixed and were located in different places within the plots every year. The censuses were conducted several months after natural seedling emergence to allow analyzing the effect of wild boars and summer drought on survival. Damage intensity (percentage of current-year shoots damaged by Spanish ibex) was quantified for each sapling.

2.4. Experimental study of seedling survival

In autumn 1998, several thousand ripe acorns were collected from at least 20 trees located in the woodland adjacent to the study plots. Acorns were pooled to avoid problems related to inter-individual differences in acorn traits and stored in a cold room (2–4 °C) for several weeks. In December 1998, acorns were planted individually in cylindrical pots (7 cm wide × 20 cm deep) located in a fenced plot situated 0.5 km from the study plots and at the same altitude (1650 m a.s.l.). Acorns germinated in February–March and seedlings emerged in late May and June, typical of natural conditions. The seedlings were kept all summer in the nursery and, when they were 6 months old, 800 seedlings were randomly selected, root pruned to a root length of 20–25 cm, and transported to the study plots. In November 1999, when they started their second year, we planted 100 seedlings per plot × microhabitat combination. All seedlings still had the acorns attached.

Seedling survival was recorded monthly during the first year and every 3 months during the second year. When possible, we noted the causes of seedling mortality. Holm oak, like many species of oaks, readily resprouts after shoot damage due to browsing or drought. For this reason, we collected all seedlings still left in the study area at the end of the experiment, to determine whether live tissue persisted in the roots. We assumed that seedlings were dead if the main root, after cross-sectioning, was completely dry.

2.5. Data analysis

The natural spatial patterns of seedlings and saplings were analyzed using Generalized Linear Models (Proc GENMOD, SAS, 1997) with a Poisson distribution of errors. In these models, we included fencing, microhabitat and year (only for seedlings) as fixed main factors. Cumulative mortality of experimental seedlings, estimate as the proportion of seedlings surviving at the end of the experiment, was analyzed with a binomial Nominal Model (Proc CATMOD, SAS, 1997). Differences in seedling survivorship were explored using a Cox's Proportional Hazards semiparametric model (Proc PHREG, SAS, 1997) using maximum partial likelihood as estimation method (Allison, 1995). To handle ties in survival times, we used the EXACT method that assumes a true but unknown ordering for the tied event times (Allison, 1995). The effects of the different mortality agents were analyzed by a multinomial Nominal Model (Proc CATMOD, SAS, 1997) using maximum likelihood estimations (Stokes et al., 1995). In this model, we included fencing and microhabitat as main factors and plots nested into fencing.

3. Results

3.1. Effect of ungulates on recruitment rate and spatial pattern

The abundance of natural current-year seedlings varied among microhabitats, but not between years or between fencing

Table 1
Summary of the Generalized Linear Models for seedling and sapling abundance depending on ungulate exclusion and microhabitat

Source	Seedling abundance			Sapling abundance		
	d.f.	χ^2	P	d.f.	χ^2	P
Fencing	4	4.29	0.369	1	19.05	0.0001
Microhabitat	12	31.24	0.0001	3	96.44	0.0001
Fencing × microhabitat	11	2.99	0.996	3	9.34	0.096
Year	4	7.07	0.853			
Fencing × year	12	11.25	0.508			
Microhabitat × year	36	9.93	0.999			
Deviance	88	148.69		307	289.09	

Year was not included in the model testing sapling abundance.

Table 2
Effect of microhabitat and fencing in seedling survivorship and seedling cumulative survival after 2 years of experiment

Source	d.f.	Survivorship		Cumulative survival	
		L–R χ^2	P values	Wald χ^2	P values
Fencing	1	19.12	0.00001	5.22	0.01
Microhabitat	3	197.76	0.00001	53.40	0.0000
Fencing × microhabitat	3	13.96	0.003	19.44	0.0002
Plot (fencing)	2	30.39	0.00001	24.60	0.0000
Model	11	283.37	0.00001	278.61	0.00001

Seedling survivorship was analyzed by a Cox's proportional hazards semiparametric model, whereas cumulative survival was analyzed by a nominal model.
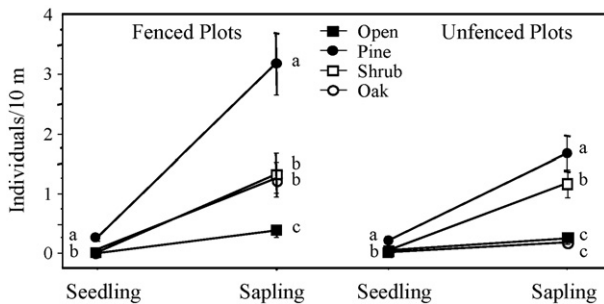

Fig. 1. Between-microhabitat difference in holm oak seedling (data averaged from the period 1999 to 2002) and sapling density (individuals/10 m²) in fenced and unfenced plots. Means with different letters are statistically different at $P < 0.05$ within each microhabitat × fencing combination.

treatments (Table 1). Seedlings were significantly more abundant under pines than under any of the other three microhabitats (Fig. 1). In fact, 67% of the seedlings ($N = 89$) were located under pines, whereas 17% were under oak, 12% under tall shrubs and 3% in open sites. This pattern was similar both in fenced and unfenced plots, the microhabitat × fencing interaction being not significant (Table 1).

The abundance of saplings was significantly affected not only by microhabitat but also by fencing (Table 1). Saplings were more abundant inside (1.54 ± 0.19 saplings/10 m²) than outside (0.82 ± 0.11) fences. In addition, saplings were more abundant under pines (Fig. 1). However, there was a marginally significant microhabitat × fencing interaction (Table 1). The abundance of saplings under pines was highest inside fences, but decreased outside fences to be similar than under shrubs and oaks (Table 1). In addition, the abundance of saplings under shrubs was significantly higher than under oaks or open sites only in unfenced plots (Fig. 1). The intensity of damage to sapling foliage by Spanish ibex was very low, since less than 5% of the tissue was damaged pooling all years and plots.
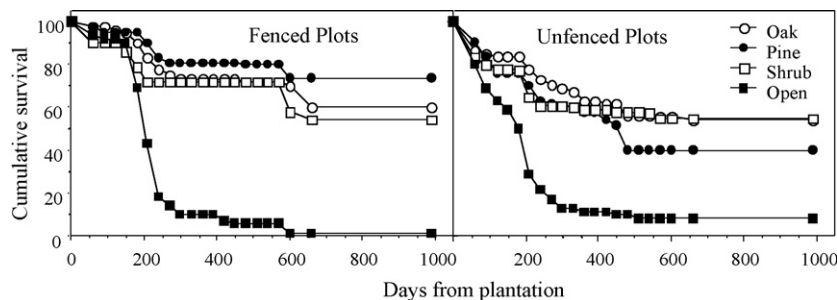
3.2. Experimental determination of seedling survival

A mean survivorship of $43.25 \pm 0.01\%$ ($\pm$binomial S.D.) of the 800 experimental seedlings was recorded at the end of the experiment (2 years). Survivorship was lower outside ($39.25 \pm 0.03\%$) than inside fences ($47.25 \pm 0.03\%$) ($\chi^2 = 5.22$, d.f. = 1, $P < 0.01$, likelihood ratio). In addition, there were also between-microhabitat differences in cumulative survivorship ($\chi^2 = 53.40$, d.f. = 3, $P < 0.0001$). While almost no seedling survived in the open ($4.5 \pm 4.0\%$), both inside and outside the fences, survival was higher than 50% in the other microhabitats (pine = $57.0 \pm 7.0\%$, oak = $57.0 \pm 7.5\%$, shrub = $54.5 \pm 4.3\%$).

There was a significant fencing × microhabitat interaction on survivorship (Table 2), indicating that the spatial pattern of survival was affected by fencing. Thus, the best microhabitat for seedling survival inside fences was under pine (Fig. 2). However, outside fences, the suitability of this microhabitat greatly decreased (Fig. 2).

We identified five causes of seedling mortality ($N = 460$ seedlings): drought, woodmice, wild boars, trampling by Spanish ibex and vole tunnels. Woodmice killed the seedlings by consuming the acorns attached to the root, usually cutting the stems before removing the acorns. Wild boars killed the seedlings by uprooting them before consuming the acorns and chewing the swollen roots, or accidentally, when looking for fungi and other buried food items. There was a significant effect of fencing on the intensity of mortality factors affecting seedlings (Table 3). In unfenced plots, wild boars killed about 60% of the seedlings and drought killed 25% (Fig. 3). Most seedlings killed by wild boars were under pines and oaks, whereas summer drought was especially severe in open sites. In fenced plots, by contrast, wild boars and trampling by ungulates were not present. However, as observed in Fig. 3, there was compensation in the intensity of the different mortality causes. Thus, the effect of drought and woodmice were much more severe inside than outside fences, since they killed approximately 60% and 20% of the seedlings,

Fig. 2. Product-limit survival functions for experimental holm oak seedlings planted in several microhabitats in fenced and unfenced plots. Shown are survival values resulting from life table estimations using LIFETEST procedure (SAS, 1997).

Table 3
Summary of the multinomial nominal model testing the effect of fencing and microhabitat on the intensity of the different mortality factors of seedlings

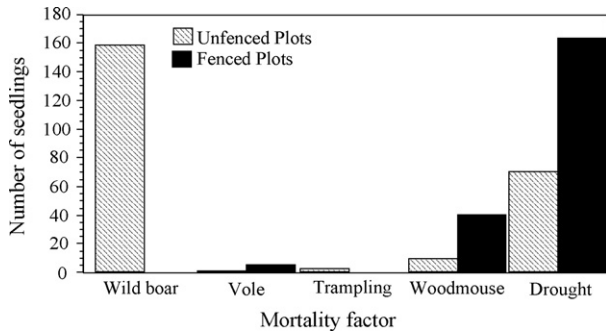| Source	d.f.	Wald χ^2	P values
Fencing	4	10.18	0.037
Microhabitat	12	12.35	0.418
Fencing × microhabitat	12	4.70	0.967
Plot (fencing)	8	16.23	0.039
Model	36	419.74	0.0001

Fig. 3. Effect of fencing on holm oak seedling mortality by wild boars.

respectively. This compensation occurred because wild boars killed seedlings before the effect of summer drought and many seedlings escaping wild boars in fenced plots were subsequently killed by drought.

4. Discussion

Our study suggests that ungulates highly affect holm oak recruitment at the study site. Despite current-year seedling abundance being similar inside and outside fences, sapling abundance diminished up to 50% in unfenced plots compared to fenced plots. High seedling or sapling survival due to ungulate exclusion may ultimately have little effect on adult population size if mortality at subsequent life stages is compensatory (Maron and Crone, 2006). Nevertheless, the main population bottleneck in the holm oak life cycle occurs during seed and seedling stages, since sapling survival is very high (Pulido and Díaz, 2005). Thus, once established, saplings are likely to reach maturity due to their strong ability to resprout, lowering the likelihood of compensatory mortality.

Holm oak recruitment is limited by wild boar damage to acorns and seedlings. Wild boars consume a large proportion of the acorn crop (Gómez, 2004) and injure and kill many newly established and older seedlings (this study). In contrast, browsing of sapling oaks by Spanish ibex was very rare at the study site. Although many studies have reported severe negative effects of post-dispersal seed and seedling predators on recruitment (Crawley, 2000; Hulme, 1997; Castro et al., 1999; Edwards and Crawley, 1999; Gómez et al., 2003; Asquith and Mejia-Chang, 2005; Del-Val et al., 2007), to infer from those data an effect on plant populations is risky since plant populations can often be limited by microsite conditions rather than by seed availability (Andersen, 1989; Eriksson and Ehrlén, 1992; Turnbull et al., 2000). It is necessary, in contrast, to quantify directly the effects of herbivores on plant population recruitment and growth (Maron and Crone, 2006). Our study, by having excluded ungulates for more than 10 years, suggests that these mammalian herbivores can actually limit holm oak recruitment and abundance in the study site. We need to take into account a potential caveat of our experimental design. Our

experimental plots were only 100 m apart. Since ungulates can move much higher distances everyday than 100 m, it is possible that ungulates travelled throughout the experimental plots. This could lead to an improper replication of the ungulate effect. However, we do not think that this issue affected our main results since our personal observations suggest that damage by wild boars to oaks seedlings and saplings are frequent in the entire study area.

Our plantation experiment has also shown that the effects of different mortality factors were not additive. In fact, there was compensation in the intensity of each mortality factor in fenced plots with respect to unfenced ones. When excluding wild boars, the effect of drought, voles and woodmice highly increased. However, the compensation was not total, since these three mortality factors could not account for all the mortality suffered by seedlings in unfenced plots. Nevertheless, the existence of compensation between different mortality factors suggests caution when inferring the importance of different mortality agents exclusively from observational studies.

There was a clear spatial pattern in the natural holm oak recruitment both during seedling and sapling stages. Most seedlings emerge under pines, being less abundant under oaks and under shrubs and very scarce in open sites. In addition, this spatial pattern was quite similar in fenced and control plots, suggesting that ungulates did not affect the spatial distribution of recently emerged seedlings. Holm oak acorns are dispersed by European jays and woodmice (Gómez, 2003; Muñoz and Bonal, 2007; Pons and Pausas, 2007a,b; Gómez et al., 2008). However, at the study site, jays are much more effective dispersers than rodents, since the latter relocate and consume more than 98% of the cached acorns (Gómez, 2003, 2004; Gómez et al., 2008). Whereas birds hide the acorns mostly under pines (Gómez, 2003; Gómez et al., 2004), rodents prefer to cache them under oaks and shrubs (Gómez et al., 2008). Furthermore, fewer acorns under pines are lost to post-dispersal seed predators, like wild boars or woodmice, because these organisms spend less time in those places looking for acorns (Gómez, 2004). Finally, this microhabitat is especially suitable for the early stages of the life cycle of holm oak, like germination and emergence (Gómez, 2004; Gómez et al., 2004; Puerta-Piñero et al., 2007). All these several reasons probably act synergistically to produce the observed overabundance of oak seedlings under pines.

The abundance of oak saplings also varied significantly among microhabitats. However, we detected a spatial uncoupling between seedling and sapling stages, since the spatial pattern of saplings differed from that of seedlings. Saplings in unfenced plots were proportionally more abundant under shrubs than in open sites or under oaks, despite seedlings being similarly abundant in those microhabitats. In addition, although seedlings were very abundant under pines, sapling abundance in this microhabitat was also similar to that under shrubs in control plots. Between-stage differences in spatial patterns have been found in this oak species for other demographic stages, including seed dispersal and seedling establishment (Gómez, 2003, 2004). Thus, the probability of seedling emergence is high in open sites because acorn predation is low and germination is high, but few seedlings survive their first summer in that microhabitat because of summer drought. In contrast, seed predation is severe, but germination, emergence, and 1-year seedling survival and growth are very high under holm oak canopies (Gómez, 2004). Integrating those results with the current findings, it seems that the suitability of the different microhabitats for *Q. ilex* recruitment varies dramatically depending on the demographic stage considered. It is therefore necessary to consider the changes occurring in the distribution of recruits throughout the overall demographic process to get an accurate view of the spatial pattern of recruitment and the driving mechanisms (Schupp, 1995).

Our experiment has demonstrated that damage by ungulates, together with summer drought, were important factors producing the observed spatial patterns of saplings in holm oak. Thus, the experimental results have shown a severe effect of summer drought on seedlings located in open sites and intense wild boar damage to those located under oaks and pines. These two mortality factors have been proven crucial for seedling survival of many Mediterranean woody plants (Herrera et al., 1994; Castro et al., 1999; Rey and Alcántara, 2000; García, 2001; Gómez et al., 2003), including the studied species (Gómez-Aparicio et al., 2005; Puerta-Piñero et al., 2007). It is remarkable that wild boars killed most seedlings accidentally, while looking for acorns under oaks or fungi under pines. A consequence of the action of ungulates was that saplings were less abundant under pines and oaks as expected from seedling emergence in those microhabitats. It seems that the only microhabitat where seedlings can survive summer drought and, above all, damage by ungulates is under shrubs. Protection by shrubs against damage by herbivory and abiotic factors is also common in many tree species (Gómez et al., 2001; García and Obeso, 2003; Gómez-Aparicio et al., 2004; Baraza et al., 2006; Smit et al., 2006, 2007), including several oaks (Callaway and D'Antonio, 1991; Callaway et al., 1991; Callaway, 1992; Callaway and Davis, 1998; Rousset and Lépart, 1999, 2000; Gómez et al., 2003). In our system, the only microhabitat where sapling abundance was not affected by wild boars was under shrubs. Thus, this microhabitat seems to facilitate holm oak regeneration in the study site. This finding can have important consequences for the management of holm oak forests. Thus, we recommend that managers preserve the shrub layer to favour the regeneration of holm oaks in southern Spain.

In conclusion, our experiment suggests that holm oak recruitment can be herbivory limited in the study site. Where wild boars are absent, recruitment is high and occurs under oaks and above all under pines. Where wild boars are present, recruitment diminishes and occurs mostly under shrubs and pines. Wild boars act in this system not only by arresting population growth, but by modifying the spatial pattern of recruitment generated during preceding demographic stages.

Acknowledgements

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