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Post-dispersal seed removal in four Mediterranean oaks: species and microhabitat selection differ depending on large herbivore activity

Received: 26 December 2010 / Accepted: 24 January 2012 / Published online: 22 February 2012
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Abstract *Quercus* forest regeneration is limited by different factors, post-dispersal predation being one of the most critical stages. We analysed seed removal of four coexisting *Quercus* species (*Q. ilex*, *Q. suber*, *Q. faginea* and *Q. pyrenaica*) in a Mediterranean forest located in Southern Spain. Marked and weighed acorns from each of the species were placed in experimental units with or without exclusion of large herbivores and in two microhabitat types (*Q. ilex* shade or open). Acorn removal was monitored for 120 days in order to test the effect of exclusion of large herbivore and microhabitat type on seed removal rates and species selection. Interestingly, the results of microhabitat and species selection differed depending on the presence of large herbivores. Removal was faster in sites without exclusion, where most seeds ($\approx 85\%$) disappeared during the first 9 days. In these sites, no differences in seed removal were found between different microhabitats, but seeds of two species, those with higher seed mass (*Q. suber* and *Q. pyrenaica*) were most preferred. However, under exclusion of large herbivores, seed removal was affected by the microhabitat, this being greater in *Q. ilex* shaded microhabitats, which showed a higher structural diversity. Also, species selection was completely different under exclusion of large herbivores, and seeds of *Q. ilex* and *Q. faginea* were removed faster. These results highlight the importance of large herbivore activity on seed removal and its effect on microhabitat and species

selection. Therefore, specific selection by seed consumers may modify seedling recruitment and may have an important influence on the relative abundance of coexisting *Quercus* species.

Keywords Post-dispersal consumption · Exclusion · Natural regeneration · Seed mass

Introduction

Post-dispersal acorn predation is presumed to be one of the main factors limiting seedling establishment in Mediterranean oak forests (Herrera et al. 1995; Gómez et al. 2003; Pulido and Díaz 2005), where seed predation percentages could reach 100% (Gómez et al. 2003; Pérez-Ramos and Marañón 2008). Acorns are an important food source for many predators as they have a large mass, with high carbohydrate and nutrient content (Jensen 1985; Vázquez 1998). In Mediterranean environments, the most frequent acorn predators are rodents (*Apodemus* sp.), wild ungulates such as deer (*Cervus elaphus*, *Capreolus capreolus*) or wild boar (*Sus scrofa*), domestic cattle and many birds like magpies (*Pica pica*) and the European jay (*Garrulus glandarius*) (Shaw 1968; Siscart et al. 1999; García et al. 2002; Gómez et al. 2003; Pons and Pausas 2007b). A small fraction of acorns could be hoarded by small mammals, birds or even dung beetles (Gómez 2004b; Pérez-Ramos et al. 2007; Puerta-Piñero et al. 2010), and, if they are not recovered later, they have some chance of germinating and emerging. Thus, these species may act both as predators and dispersers (Pulido and Díaz 2005; Pérez-Ramos et al. 2007). However, ungulates usually consume acorns at once (Bonafant and Muñoz 2007; Muñoz et al. 2009), and they may also exploit hoards of acorns collected by small mammals (Focardi et al. 2000). Thus, the possibility of dispersal is null in these cases.

Ungulates such as wild boar and deer depend on acorn production in order to compensate for reduced

Electronic supplementary material The online version of this article (doi:10.1007/s11284-012-0927-7) contains supplementary material, which is available to authorized users.

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above-ground biomass availability during the autumn (Massei et al. 1997; Focardi et al. 2000). Therefore, large herbivores may have a strong impact on seed and seedling predation in *Quercus* forests, especially when herbivores are present at high densities (e.g. Gómez et al. 2003; Pérez-Ramos and Marañón 2008). For this reason, exclusion of large herbivores by fences has been proposed as a measure to increase seedling recruitment in grazed oak woodlands (Smit et al. 2001). Large herbivores may also affect the population of other seed predators negatively (i.e. mice, Smit et al. 2001; Pérez-Ramos and Marañón 2008) and also vegetation structure (i.e. decreasing leaf area index). As seed removal by rodents has been found to increase with the leaf area index (Pérez-Ramos et al. 2008), the intensive herbivore activity may also have an indirect effect on seed removal by other species (Smit et al. 2001).

Spatial acorn location is not at random, with acorns being located at certain microhabitats, because of processes such as seed rain or secondary dispersion by the animals (García and Houle 2005). As consumers do not move randomly, the microhabitat where seeds are located may determine their removal probabilities. For example, seed removal probability by rodents is greater in microhabitats near trees or shrubs, as they focus their activity on these areas (Ouden et al. 2005; Russo et al. 2006; Pons and Pausas 2007a; Pérez-Ramos and Marañón 2008). On the contrary, large herbivores such as wild boar are more active in open areas (Gómez et al. 2003). Furthermore, tree species composition could also affect removal probabilities as for example pine forests are found to be less visited by seed predators (Pons and Pausas 2007c; Gómez and Hódar 2008). Therefore, because the activity of seed predators is influenced by the vegetation, it would be expected to find a differential removal percentage depending on the structure and composition of vegetation.

Mixed forests with various coexisting *Quercus* species are common in Mediterranean ecosystems (Costa et al. 1997; VVAA 2009). Most of the Mediterranean *Quercus* species drop their seeds in autumn and winter. If different seed stock species are available at the same time, predators may differentially select acorns of some species (Shimada 2001; Pérez-Ramos and Marañón 2008), which may be related to species-specific chemical composition (Shimada and Saitoh 2003; Xiao et al. 2006) or seed size (Xiao et al. 2006; Pérez-Ramos et al. 2008). These differences in seed preference may have an influence on seedling recruitment. Few studies have evaluated seed removal for several coexisting species at the same time in Mediterranean environments (but see Pons and Pausas 2007c; Pérez-Ramos and Marañón 2008) with two to three coexisting *Quercus* species.

The spatial and temporal heterogeneity in seed availability and predator populations (Madsen and Löff 2005) as well as the high number of factors influencing these interactions make it difficult to extrapolate results from one area to another. Thus, it is necessary to obtain data on seed predation for different species and areas to reach conclusions about the importance of different factors.

From an applied perspective, the results on post-dispersal predation are also interesting. In some cases, restoration and artificial regeneration programmes utilise direct seeding as an effective tool (Pastor and Bonet 2007; González-Rodríguez et al. 2011). Therefore, the quantification of the factors that may influence seed removal could be important information towards increasing success in restoration programmes (Madsen and Löff 2005).

The aim of this study was to determine if seed removal rates of four Mediterranean oaks were affected differently under situations with or without large herbivore activity. We chose four oak species [*Q. ilex* L. subsp. *ballota* (Desf.) Samp., *Q. suber* L., *Q. faginea* Lam. and *Q. pyrenaica* Willd.] that coexist in the same area in a Mediterranean environment. Specifically, we tested the effects of exclusion of large herbivores and microhabitat type on seed removal rates and species selection. Our hypothesis was that both microhabitat and species selection may be different depending on the presence of large herbivores. If this is the case, different potential seed predators may modify the recruitment patterns and affect the relative abundance of *Quercus* species. The novel aspects of the present study are that it studied at the same time the seed removal of four coexisting species and evaluated the importance of herbivore exclusion. The attempt could be worthwhile to advance in the conservation and management practice in Mediterranean forest ecosystems.

Methods

Study area

The experiment was carried out in the Natural Park of “Sierra de Cardena y Montoro” (Córdoba, S Spain; 38°21’N, 3°12’W). The climate is characterised by continental variations and summer droughts with annual rainfall of between 570 and 970 mm and mean annual temperature of 15.3°C. Soils are mainly sandy. The experimental site consisted of an open forest of *Q. ilex* L. subsp. *ballota* (Desf.) with some sparse individuals of *Pinus pinaster* Aiton and *Cistus ladanifer* L. shrubs.

Potential predators present in the park are: wild boar (*Sus scrofa*), deer (*Cervus elaphus*), rodents (*Mus spretus*, *Apodemus sylvaticus*, *Sciurus vulgaris*) and birds such as the European jay (*Garrulus glandarius*) and the magpie (*Pica pica*). Rooting activity signals are frequent in the area, where the estimated density of wild boar is about 0.15 heads ha⁻¹ and 0.3 heads ha⁻¹ for deer (JM Quero, personal communication).

Experimental design

Approximately 500 acorns from each species with no apparent damage were collected from the Natural Park of “Sierra de Cardena y Montoro” in October 2009.

Acorns were stored at 2–5°C in a cold chamber until November 2009. The acorns to be used in the experiment were selected by the flotation method. A sub-sample of acorns for each species was used to determine fresh weight and then oven-dried at 70°C for at least 48 h. Seed dry mass was determined after removing the pericarp from the cotyledons. Linear regression equations between acorn fresh mass (A_{FM}) and seed dry mass (S_{DM}) were established for each species in order to obtain a precise enough estimate of seed dry mass from acorn fresh mass ($R^2 > 0.88$; $n = 25$ acorns per species).

Two hundred acorns from each species were weighed and individually marked in the pericarp surface with an awl. In November 2009, 800 acorns (200 for species) were randomly distributed across 50 experimental units with this factor combination: (1) presence or absence of large herbivore exclusion and (2) microhabitat type (open areas or below *Q. ilex* tree, hereafter *Q. ilex* shade). Exclusion consisted of a fenced area of 2 ha, where large herbivores such as wild boar and deer had been excluded for at least 10 years. The 50 experimental units were distributed as follows: 20 experimental units outside the exclusion (10 in *Q. ilex* shade and 10 in open microhabitats) and 30 experimental units inside the exclusion (15 in *Q. ilex* shade and 15 in open microhabitats). The approximate minimum distance between different experimental units was about 10 m. At each experimental unit, acorns were divided into four groups 1 m apart. In each group there was one acorn per species (in all there were 4 acorns per species at each experimental unit). Each group position was marked with a stick 40 cm high, 20 cm away from acorns, in order to avoid attraction effects. In all, 800 acorns were monitored.

Data collection

At each experimental unit, the distance to the closest pine (*Pinus pinaster*), oak (*Q. ilex*) and shrub (*Cistus ladanifer*) was measured with a distance metre (Leica disto TM, Leica Geosystems AG, Switzerland). For the microhabitat characterisation, a circle of 10-m diameter was virtually drawn around each experimental unit. Different habitat categories, including physical structures relevant to rodents (Pons and Pausas 2007c), were recorded: bare soil, herbaceous layer, trunks, litter (> 1 cm depth), shrub, stones and artificial burrows. Then, in each circle (experimental unit), the percentage of each category was determined by visual estimate. A structural diversity index was computed as the Simpson's diversity index ($1 - \sum c_i^2$, where c_i was the proportion of each habitat category).

Monitoring of the acorns was carried out periodically (after 2, 9, 16, 24, 31, 64 and 120 days). At each census, acorn presence or absence was noted, as well as holes made by insects, post-dispersal predation signals (bites)

and germination of acorns. Acorns with post-dispersal predation signals in situ represented a very low percentage of the total (1%) so that they were not distinguished from the removal ones in the analysis.

In order to describe the experimental unit characteristics better, food availability (amount of acorns) was estimated at each census in each experimental unit. This variable was calculated by randomly placing three squares (25 × 25 cm) and counting available acorns inside them. We estimated the food availability as the mean of the three squares giving a value of number of acorns per m² for each experimental unit.

Statistical analysis

Microsite characterisation

Differences in habitat characteristics between the two types of microhabitats (open and *Q. ilex* shade) were studied by one-way ANOVA, using “microhabitat type” as categorical variable and as dependent variables: distance to the closest pinus, structural diversity index and the most relevant variables of structural habitat (% litter, % bare soil, % herbaceous layer, % shrub). Differences in food (acorn) availability between experimental units with or without exclusion were analysed by repeated measures ANOVA.

Large herbivore exclusion effect

Seed removal rates were highly different between exclusion and non-exclusion sites. As in the non-exclusion sites removal was very high during the first month (90.6%), we used 9-day data to calculate the mean early seed removal percentage for each species at an experimental unit in the exclusion and non-exclusion sites. Removal percentages between exclusion and non-exclusion sites were compared with ANOVA.

Seed removal under large herbivore exclusion

Data from experimental units located inside the exclusion were analysed in order to study seed removal by small consumers (not including deer and wild boar). Removal percentages after 64 days were used; as in the first 9 days, the seed removal percentage was very low (only 10%), and in the last census almost 100% of the acorns had disappeared (Fig. S1, Supplementary material).

Species preference was assessed by two analytical approaches: log-rank survival curves and electivity index. Log-rank survival curves were constructed following the Kaplan–Meier procedure (Kaplan and Meier 1958). This analysis considers both seed permanence time and status (present or absent) at the last survival assessment.

An electivity index was calculated (Pons and Pausas 2007c) for each species and experimental unit as

$$E_i = (d - p)/(d + p)$$

where d is the number of acorns removed and p the number of acorns not removed in the census at day 64. The electivity index ranges from -1 to 1 , with negative values indicating avoidance and positive values indicating selection. Differences in the electivity index across species were compared by one-way ANOVA, considering species as the factor and the electivity index as a dependent variable.

Within each species, microhabitat selection (*Q. ilex* shade and open areas) was analysed by one-way ANOVA (where the seed removal percentage per experimental unit was the dependent variable and the microhabitat the independent factor).

Seed removal without large herbivore exclusion

Statistical analyses for the seed removal without exclusion of large herbivores were the same as those with exclusion (see above). The only difference was that we use data of removal at 9 days and not at 64 days (as for the exclusion) because at this time all acorns had been removed (Fig. S1, Supplementary material), and no effect of microhabitat and species selection could be de-

Table 1 Mean, standard deviation and range of estimated seed dry mass for each species

	Seed dry mass (g)	
	Mean \pm SD	Min–max
<i>Quercus ilex</i> sp. <i>ballota</i>	1.45 \pm 0.45	0.61–2.99
<i>Q. suber</i>	2.26 \pm 0.90	0.36–4.90
<i>Q. faginea</i>	1.05 \pm 0.29	0.47–1.80
<i>Q. pyrenaica</i>	3.68 \pm 0.7	1.45–5.48

Seed dry mass was obtained by predictors based in seed fresh mass (linear regressions, $R^2 > 0.88$; $n = 25$ acorns per species). Seed dry mass was determined after removing the pericarp from the cotyledons

Table 2 Mean \pm standard deviation of some characteristics of the two microsites considered (open and *Q. ilex* shade) in large herbivores exclusion and non-exclusion sites

	Non-exclusion		Exclusion	
	Open	<i>Q. ilex</i> shade	Open	<i>Q. ilex</i> shade
Closest pine distance (m)	5.8 \pm 1.7A	8.9 \pm 2.7B	8.8 \pm 3.7a	9.0 \pm 3.2a
Structural diversity index ^a	0.47 \pm 0.15A	0.41 \pm 0.15A	0.47 \pm 0.15a	0.59 \pm 0.13b
Litter and branches (%)	24.8 \pm 18.4A	24.0 \pm 22.6A	17.1 \pm 20.2a	38.1 \pm 19.5b
Herbaceous layer (%)	3.0 \pm 3.5A	3.5 \pm 2.1A	28.3 \pm 31.6a	17.3 \pm 25.0a
Bare soil (%)	60.6 \pm 21.0A	64.0 \pm 23.4A	17.4 \pm 21.1a	21.7 \pm 18.9a
Shrub (%)	9.8 \pm 10.5A	6.1 \pm 12.3A	17.4 \pm 21.1a	12.7 \pm 18.1a
Acorn availability (seeds m ⁻²) ^b	1 \pm 2A	28 \pm 29B	1 \pm 2a	62 \pm 46b

Different letters indicate significant differences ($P < 0.05$) in experimental units with exclusion (lower case letters) or without exclusion (capital letters) between *Q. ilex* shade and open sites

^a Structural diversity index was calculated as the Simpson's diversity index ($1 - \sum c_i^2$, where c_i was the proportion of each habitat category)

^b Mean acorn availability was calculated during November to mid January 2010

tected. Therefore, early removal percentage (9 days) was used as a variable that indicated the selection preferences on microhabitat and species (Table 1).

All statistical analyses were performed using STATISTICA 8.0 (Statsoft, Inc.).

Results

Microhabitat characterisation

In the non-exclusion sites, in general, there were no differences in the characteristics of *Q. ilex* shaded and open areas (Table 2), only the distance to the closest pine was greater in the experimental units located in *Q. ilex* shade ($P < 0.05$). However, in the exclusion sites, the experimental units located in *Q. ilex* shaded areas presented a higher structural diversity index ($P < 0.05$) and higher percentage of litter and branches ($P < 0.01$) than open areas, but no differences were found in other characteristics (percentage of herbaceous plants, shrub and bare soil or distance to the closest pine) (Table 2).

Acorn availability (seeds m⁻²) in autumn was higher in oaks protected against large herbivores (62 \pm 46 seeds m⁻²) than those without exclusion (28 \pm 29 seeds m⁻²; $P = 0.04$) (Table 2), although a high variability did exist between trees. Acorn availability was near zero in open areas either with exclusion or without exclusion (Table 2). From November to mid-December, there was no variation in acorn availability with time (Fig. S2, Supplementary material), but there was a significant decrease in acorn availability afterwards. In the last census (April 2010) no seeds were found in any experimental unit (these data were not included in total average).

Effect of large herbivore exclusion

Seed removal was very high in the experimental units without exclusion of large herbivores, as, after 9 days, seed removal was very high (about 85%). After a month,

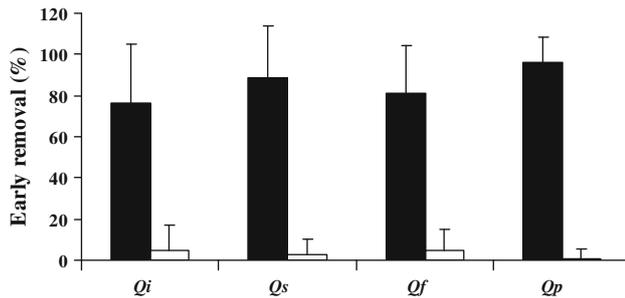


Fig. 1 Early removal percentage (after 9 days) for each species in the exclusion site (black bars) and in the non-exclusion site (white bars). *Qi*, *Quercus ilex* sp. *ballota*; *Qs*, *Q. suber*; *Qf*, *Q. faginea*; *Qp*, *Q. pyrenaica*. Data represent mean \pm standard deviation

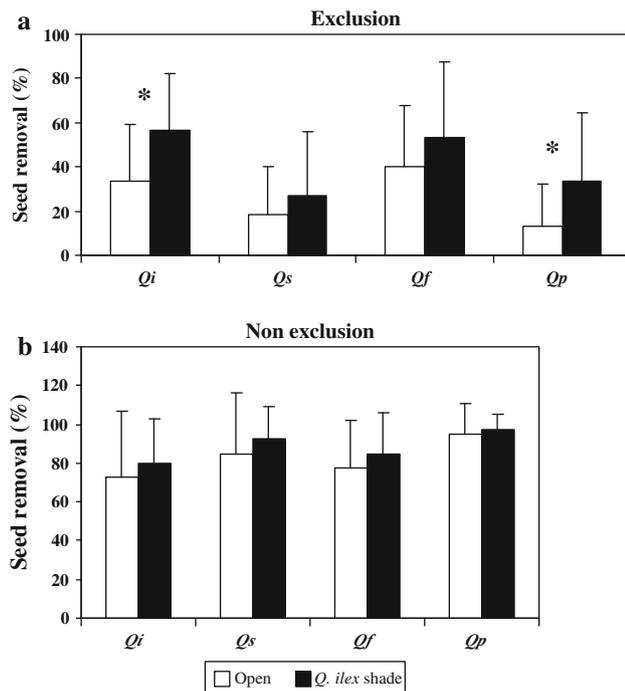


Fig. 2 Seed removal percentage in the site with exclusion of large herbivores (a) and without exclusion (b) for two microsites: open experimental units (white bars) and shaded oak experimental units (black bars). Asterisk indicates significant differences ($P < 0.05$) between the two types of microsite for each species (*Qi*, *Quercus ilex* sp. *ballota*; *Qs*, *Q. suber*; *Qf*, *Q. faginea*; *Qp*, *Q. pyrenaica*). Data for the exclusion were after 64 days and for non-exclusion after 9 days of the experiment

all seeds (100%) had been removed in the non-fenced sites (Fig. S1, Supplementary material). However, in those microsites located with exclusion of large herbivores, seed removal percentage after 9 days was very low (about 10%) (Fig. 1).

Microhabitat and species selection

Seed predators showed a different behaviour between sites with and without exclusion. In relation to micro-

Table 3 Mean \pm standard deviation of electivity index for each species in the non-exclusion site (after 9 days) and in the exclusion site (after 64 days)

	Non-exclusion	Exclusion
<i>Quercus ilex</i> sp. <i>ballota</i>	0.52 \pm 0.57B	-0.10 \pm 0.56a
<i>Q. suber</i>	0.77 \pm 0.49AB	-0.55 \pm 0.51b
<i>Q. faginea</i>	0.62 \pm 0.45AB	-0.06 \pm 0.62a
<i>Q. pyrenaica</i>	0.92 \pm 0.24A	-0.53 \pm 0.54b

Different letters indicate significant differences ($P < 0.05$) across species for non-exclusion (capital letters) and with exclusion (lower case)

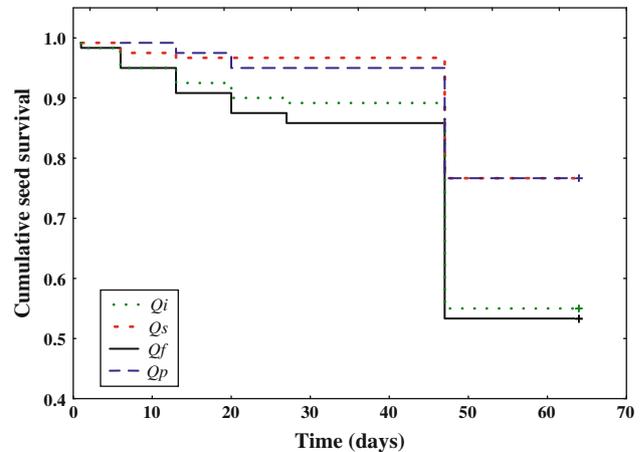


Fig. 3 Probability curve (Kaplan–Meier) of cumulative survival in the exclusion site for each species from the beginning of the experiment. An acorn is considered as “surviving” if it has not been removed. *Qi*, *Quercus ilex* sp. *ballota*; *Qs*, *Q. suber*; *Qf*, *Q. faginea*; *Qp*, *Q. pyrenaica*

habitat selection, for the non-exclusion, there were no differences in seed removal percentages between open and *Q. ilex* shaded areas for any of the four studied species (for all species $P > 0.15$). However, for the sites with exclusion of large herbivores, seed removal was higher in *Q. ilex* shaded areas, and these differences were significant for *Q. ilex* ($P = 0.02$) and *Q. pyrenaica* seeds ($P = 0.04$) (Fig. 2).

With respect to species selection, the results also differ between the sites with and without exclusion. In the non-fenced sites, there were significant differences in the electivity index (after 9 days) among species. The two species with bigger acorns (*Q. suber* and *Q. pyrenaica*) showed a higher electivity index and therefore the acorns were removed faster (Table 3). In the sites with exclusion of large herbivores, the seed electivity index (after 64 days) also differed among the four species, but, in this case, the other two species (*Q. ilex* and *Q. faginea*) had a significantly higher electivity index (Table 3). Therefore, these two species had a lower probability of seed survival (i.e. the acorns of these species were removed faster; see probability curve of cumulative survival, Fig. 3).

Discussion

Seed removal was very high for all species and sites 4 months after starting the experiment (almost 100% of the seeds had disappeared). As expected, the highest removal percentages were found in the non-fenced sites, these being about 85% after 9 days of the experiment. In accordance with these results are the data on acorn availability, which were also lower in the areas with non-exclusion, showing the importance of wild boar and deer as acorn consumers in this early establishment phase (Gómez et al. 2003; Gómez 2004b; Pulido and Díaz 2005). Gómez (2004b) found that 98% of *Q. pyrenaica* acorns were consumed in not fenced sites after 90 days. Moreover, large herbivores may cause this direct effect on seed losses, but also an indirect effect in the long term: decreasing vegetation cover (lower leaf area index), which can negatively affect rodent populations.

A small part of seed removal can be associated with dispersal and therefore it may contribute to seedling establishment (Pérez-Ramos et al. 2007). However, a large proportion of seed removal is related to seed predation (Gómez et al. 2003), and therefore, post-dispersal seed removal could be a strong limitation for oak natural regeneration in this conserved area as well as it has been found in other areas for different *Quercus* species (Shaw 1968; Kollmann and Schill 1996; Gómez et al. 2003; Gómez 2004b; Pérez-Ramos et al. 2010).

In areas without exclusion, acorn spatial location did not affect the probability of escaping from animal removal, probably because large herbivores did not prefer any specific microhabitat and also due to their greater mobility. Similarly, Gómez et al. (2003) did not find any microhabitat effect on *Q. pyrenaica* seed predation in an area without exclusion, where wild boar predation may mask rodent preferences. Moreover, in the non-exclusion site, there were no differences in the characteristics of open and *Q. ilex* shaded areas (Table 2), and ungulates may not select any microhabitat. Another explaining factor could be the fact that seed removal after 9 days was very high (85%), due to the high preference of acorns by large herbivores (Gómez and Hódar 2008). On the other hand, seed consumers in the non-exclusion sites showed a greater preference for *Q. suber* and *Q. pyrenaica*. This is an unexpected result as *Q. ilex* acorns are usually more often consumed because of their better nutritional characteristics (Pons and Pausas 2007b). Given that in this experiment the seed mass of *Q. suber* and *Q. pyrenaica* was higher than in the other species, this could be the reason for animal preference. Several studies have found that larger seeds have a greater probability of being removed (Gómez 2004a; Pérez-Ramos et al. 2008). Pérez-Ramos et al. (2008) found that the species with bigger seeds (*Q. suber*) were removed faster and in a higher proportion than those of *Q. canariensis* (with smaller seeds). However, larger seeds have many advantages for establishment such as high germination and emergence rates, plant growth or

survival probabilities (Moles and Westoby 2004; Baraloto et al. 2005; Urbietta et al. 2008; González-Rodríguez et al. 2010). Gómez (2004a) proposed conflictive selective forces acting on seed size.

Interestingly, different trends with respect to microhabitat and species selection were found in the exclusion sites. In these sites, the probability of removal (in *Q. ilex* and *Q. pyrenaica*) was greater in sites located under oak cover. These microsites may be safer sites for micromammals because of their greater structural diversity and higher litter and branch percentage. Thus, the risk of seed predation is greater in denser vegetation areas, where rodents focus their activity (Herrera et al. 1995; Alcántara et al. 2000; Pulido 2002). On the other hand, as acorn availability was higher in sites located under oaks, this may cause an attraction effect on predators. However, this selection relative to the microsite is not general for the four species, as two of the species studied in the present experiment (*Q. suber* and *Q. faginea*) did not show any significant differences in seed removal between open and *Q. ilex*-shaded sites. This could be explained by the activity of other seed predators, for example European jays (*G. glandarius*), which usually take acorns from open areas (Pons and Pausas 2007a), thus having an opposite preference to rodents.

The other difference in seed removal between the sites with or without exclusion of large herbivores was the species selection. In the exclusion site, seed consumers (rodents and birds) preferred *Q. ilex* and *Q. faginea* acorns, which were the species with the smallest seeds. This selection would probably be owing to differences in nutrient content (León-Camacho et al. 2004), toughness of the acorn skin (Zhang et al. 2004) or toxic secondary compounds such as tannins (Shimada and Saitoh 2003). In this sense, *Q. suber* seeds show a high proportion of phenolic compounds in their skin, and have a bitter taste that is not attractive for predators (Cantos et al. 2003). Other authors have found that some rodents are able to detect seed dormancy, thus avoiding seeds close to germination (Smallwood et al. 2001). This can explain why species with an earlier germination like *Q. pyrenaica* might be avoided by seed consumers. On the other hand, although all species are present in the natural park and coexist in some areas, in the study site there are just *Q. ilex* and *Q. faginea* individuals, suggesting predator selection for this species (Janzen 1971).

Other factors considered in other studies that may explain the differences in removal probability could be for example the distance to pines, or the acorn availability. We did not find any effect of the distance to pines on removal rates. In other studies, pine forests have been found to be less visited by predators, which has been explained by the fact that they show more areas of bare soil, where small consumers may suffer a greater probability of being predated (Pons and Pausas 2007c). This effect was not observed in our study area, where pines are dispersed individuals, and both open and *Q. ilex*-shaded areas were at similar distances from pines.

With respect to the effect of a higher density of acorns, there are two possibilities: either a negative impact on removal percentage of acorns by a satiation effect on predators (Kelly and Sork 2002) or a positive effect on removal due to an attractor effect of a higher acorn availability. We observed the latter in open sites: where the acorn availability is very low (Fig. S2, Supplementary material), the removal percentage is also low. On the contrary, in *Q. ilex*-shaded areas, where the acorn availability is high, the acorn removal is also high. Therefore, the acorn availability may act as an attractor of seed predators. However, we do not know if the effect of a higher seed removal under *Q. ilex* shade microhabitat is due to the higher acorn availability or to more favourable conditions for predators (e.g. dense vegetation) (Pérez-Ramos et al. 2008).

Some of the disappeared seeds might not have been consumed. Almost all seeds are usually consumed in situ, but a small fraction could be buried by small consumers such as rodents or birds (Kollmann and Schill 1996; Santos and Tellería 1997; Pons and Pausas 2007a). Although a high proportion of the buried acorns may be relocated and eaten later (Kollmann and Schill 1996; Seiwa et al. 2002), a small fraction may escape predation. In this way, the small consumers may also act as important dispersers (Siscart et al. 1999; Pulido and Díaz 2005). Differences in seed predation rates have been related to seed production and fluctuations in consumer populations (Silvertown 1980; Wolff 1996; Pérez-Ramos et al. 2008). In our study, acorn production was high (data not shown), so it was possible that many buried acorns would not have been relocated because of a satiation effect on predators (Janzen 1971; Silvertown 1980; Espelta et al. 2009). However, Leiva and Fernández-Alés (2003) did not find any satiation evidence. With respect to consumer populations, the use of fences may have increased rodent density as it reduced competition with large seed consumers (deer and wild boar) (Pérez-Ramos and Marañón 2008), and, thus, their impact on recruitment will have been greater, even in the high seed production years.

In the non-fenced area, seedling recruitment may be strongly limited as wild boar and deer (presumed to be responsible for the highest removal percentages) do not act as dispersers because they consume seeds in situ. Moreover, wild ungulate abundance may cause a reduction in the population of species acting as predators–dispersers (i.e. rodents), especially in areas with low shrub abundance like in the study site (Muñoz et al. 2009).

Overall, the importance of these results is that the difference in species selection in sites with and without exclusion of large herbivores may modify recruitment and can have a strong influence on the abundance of the species coexisting in an area (Gómez et al. 2003).

Conclusions

Post-dispersal predation is an important limitation to natural regeneration of *Quercus* species in Mediterranean forests, at least in areas not excluded from large herbivores. In the non-excluded area, acorns were quickly removed, and consumers preferred species with larger seeds (*Q. suber* and *Q. pyrenaica*). The use of fences provides places to which wild boar and deer, responsible for these high removal rates, cannot have access. Interestingly, in the fenced area, acorn selection was different, and *Q. ilex* and *Q. faginea* seeds disappeared first, probably because of their higher nutritional value; also seed removal was higher in sites situated under oak cover. Therefore, seed selection by seed consumers is influenced by large herbivore activity; it may modify seedling recruitment and could have a strong influence on the abundance of coexisting species in Mediterranean ecosystems.

Acknowledgments This study was supported by a predoctoral fellowship FPI-MEC awarded to V. G-R, the coordinated Spanish MEC projects DINAMED (CGL2005-05830-C03-02/BOS) and INTERBOS (CGL2008-04503-C03-02), and FEDER funding. We thank Jose Manuel Quero, Pedro Lara, Fernando Puig and Bartolomé Arévalo for their facilities for seed collection and permission to conduct the field experiment in the Natural Park “Sierra de Cardeña y Montoro” (Córdoba, Spain). We are grateful to Andrés Cortés for field help. Ignacio M. Pérez-Ramos gave us useful advice on the experimental design and kindly revised a previous version of the paper. Pablo Ferreras gave us information related to the micromammals in the area. The suggestions of two anonymous reviewers improved this paper. Our research group is a member of the GLOBIMED network (<http://www.globimed.net>).

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