Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds

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Summary

1. Post-dispersal predation of vertebrate-dispersed seeds has received little attention in the Mediterranean region. We investigated the spatial variation in post-dispersal seed predation of vertebrate-dispersed plants and its potential implications for plant diversity in fleshy fruited plant communities of southern Spain.

2. An experiment was conducted in forests and open scrubland at mid- and high elevations to explore: (a) the possibility of differential seed predation by rodents and granivorous ants; (b) the spatial variation, between and within habitats, in post-dispersal seed predation and predator abundance; and (c) whether the spatial distribution of predation covaries among plant species.

3. Rodents and granivorous ants proved to be important predators of vertebrate-dispersed seeds, and showed significant variation in their preferences for different seed species. Granivorous ant preferences depended on seed size, as seeds heavier than 20 mg were hardly ever removed. Rodents were indifferent to seed size.

4. Sites safe from predators were more frequent at mid-elevations. In contrast to other temperate communities, successional status (open scrubland *vs* forest) did not determine the probability of predation, probably because ants are more important as seed predators in the early successional stages of Mediterranean habitats than in other temperate communities. The large-scale variations in the occurrence of safe sites for the seeds depended on resource abundance rather than on predator abundance.

5. We found a significant interaction in seed predation rates between microhabitat and seed species at mid-elevations, but not in high-elevation habitats, implying stronger covariance across plant species in the microhabitats adequate for recruitment (e.g. with lower predation risk) at high elevation. This pattern may contribute to the differential plant diversity at mid- and high elevations in Mediterranean fleshy fruited plant communities. Theoretical models predict that seed predators may contribute to the maintenance of species diversity if the spatial distribution of safe sites from predators is uncorrelated across plant species, as it was at mid-elevations.

Key-words: Ant seed predation, fleshy fruited plants, large-scale variation, Mediterranean scrublands, rodent seed predation, small-scale variation

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Introduction

Small-scale (within-habitat) studies of the spatial patterns of seed dispersal (Willson & Traveset 2000), post-dispersal seed predation (Crawley 2000), and seedling survival (Schupp 1995) are the norm. Basic information about patterns of post-dispersal predation at the community level is scarce (Hulme 1997; Kollmann *et al.* 1998). We know little about the relationship between the abundance of predators and the intensity of post-dispersal seed predation (Manson & Stiles 1998); the preferences of predators towards different seed species (Jensen 1993; Kollmann *et al.* 1998); the relative importance of different types of predators (Hulme 1997; Hulme & Borelli 1999; Kelrick *et al.* 1986; Whelan *et al.* 1991); and how all these factors vary in space (Kollmann *et al.* 1998). Addressing these questions is essential to understanding the role of seed predators in plant population and community dynamics (Alcántara *et al.* 2000; Crawley 2000; Manson & Stiles 1998; Ostfeld *et al.* 1997).

Seed dispersal by animals may affect the plant species composition and the relative abundances of dominant

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shrubs and trees in Mediterranean ecosystems because fleshy fruited plant species are often dominant (Herrera 1992; Herrera 1995). However, post-dispersal seed predation may also influence their population and community dynamics (Davidson 1993; Hulme 1996; Hulme 1998; Janzen 1971; Louda 1989; Pickett *et al*. 1987; Rey & Alcántara 2000). Mediterranean scrublands may produce $60–1400 \times 10^3$ ripe fruits ha^{-1} (Jordano 2000), which can be an important seed resource for granivores.

Rodents and ants are post-dispersal seed predators of fleshy fruited plants in southern Spain (Hulme 1992; Hulme 1997). A differential impact of these predators on the spatial pattern of seed survival is expected as these animals prefer different seed species and microhabitats (Hulme 1997; Kelrick *et al*. 1986; Parmenter *et al*. 1984; Terborgh *et al*. 1993). The abundance and species composition of rodent and ant communities change on large spatial scales, so their impact on different plant communities may also change. Variation in the abundance and activity patterns of rodents and ants on larger spatial scales may be related to the successional stage of the vegetation (Kollmann 1995; Whelan *et al*. 1991; Wolff & Debussche 1999), or to variations in abiotic conditions (e.g. temperature, rainfall; Grodzinski 1985; Retana & Cerdá 2000). However, variations in seed predation at large spatial scales remain largely unexplored, particularly in the Mediterranean scrublands.

This study is aimed at exploring spatial variation in post-dispersal predation on seeds of Mediterranean fleshy fruited plants. The main questions addressed are: (a) is the large-scale spatial variation in post-dispersal seed predation related to the abundance and activity of rodents and ants?; (b) are different plant species consumed differentially by rodents or ants?; (c) are some seeds protected against predators in certain microhabitats?; and (d) are the patterns of seed predation among microhabitats the same for different plant species?. Answering questions (c) and (d) will help place the study of post-dispersal seed predation within the framework of theoretical models predicting the coexistence of a larger number of species when there is high spatial variation in recruitment rates (Crawley 2000).

Materials and methods

STUDY SITES

The study was undertaken in two areas of the Sierras Béticas of Jaén Province in south-east Spain. We chose one area at mid-elevation (700 m a.s.l.) located in Sierra Sur de Jaén, and one at high elevation (1500 m a.s.l.), *c*. 130 km to the north-west, located in Sierra de Segura. These Sierras share the same types of plant communities, soil types and topography. Within each area we chose an open scrubland and a forest site. The site representing open scrubland vegetation at

mid-elevation contains 18 fleshy fruited species, many of them among the dominant woody plants: *Olea europaea* var. *sylvestris*, *Crataegus monogyna*, *Rosa canina*, *Rhamnus lycioides*, *Phillyrea latifolia*, *Pistacia terebinthus* and *Quercus coccifera*. The site representing mid-elevation forest has 20 fleshy fruited species and is dominated by *Pinus halepensis* and *Quercus faginea*, with understorey consisting mainly of *Smilax aspera*, *Hedera helix*, *C. monogyna*, *P. latifolia*, *Pistacia lentiscus*, *Juniperus oxycedrus* and *Rosmarinus officinalis*. The site representing open scrubland vegetation at high elevation contains 12 fleshy fruited species and is dominated by *Berberis hispanica*, *C. monogyna*, *Rosa* spp., *Rubus ulmifolius* and *Juniperus communis*. Finally, vegetation in the site representing high-elevation forest has nine fleshy fruited species, and comprises the same species occurring in open scrubland but under a canopy of *Pinus nigra* ssp. s*alzmannii*.

In the high-elevation area, monthly temperatures average between 4·0 °C in January and 21·4 °C in July, and the mean annual precipitation is 835 mm, most of which falls in autumn–winter (69%) and spring (23%). In the mid-elevation area, monthly temperatures average between 8·6 °C in January and 27·4 °C in July, and the mean annual precipitation is 584 mm, most of which falls in autumn–winter (72%) and spring (20·5%).

ABUNDANCE OF RODENTS AND ANTS

Ants were sampled once every 2 weeks at each study site using 50 evenly distributed pit-fall traps over each study site. Pit-fall traps were active during 24 h. The ants were counted and identified in the laboratory, and subsequently assigned to a diet type based on personal observations; literature references (Espadaler & Gómez 1996; Wolff & Debussche 1999); and advice of specialists (X. Cerdá and A. Tinault, personal communication). Only the frequency of capture of granivorous ants is considered here.

The abundance (frequency of capture) of rodents was estimated using live traps. At each study site we used 30 trapping stations, each consisting of two traps with the doors oriented in opposite directions. These stations were spaced 10 m from each other and distributed along two sets of three parallel transects. One-night trapping sessions were conducted in March and July 1997. The traps were activated at dusk and checked at dawn. Trapped rodents were released immediately following identification.

SEED RAIN

As a part of a long-term study, in October 1996 we began monitoring the fleshy fruited seed rain at each study site using seedfall traps. We used $26 \times 33 \times 5$ cm aluminium trays covered with wire mesh to prevent seed removal. Traps were located under the most prominent scrub and/or tree species and in open interspaces

Table 1. Microhabitats and seed species (where appropriate) used in the experiment in each study site

Forest	Scrubland
High elevation	
Crataegus monogyna	*Crataegus monogyna*
Rosa sp.	*Rosa* sp.
Berberis hispanica	*Berberis hispanica*
Open	Open
Mid-elevation	
Crataegus monogyna	*Crataegus monogyna*
Hedera helix	*Rosa* sp.
Smilax aspera	*Olea europaea*
Open	Open

(termed microhabitats). When possible, eight trays were placed under each microhabitat at each study site. A total of 224 trays were set (high altitude region, $n = 60$ in forest, $n = 44$ in scrubland; mid-altitude region, $n = 70$ in forest, $n = 50$ in scrubland). Only results of the total seed density and species fallen at each site from October 1996 until April 1997 (the starting point of the post-dispersal seed predation experiments) are considered here.

Seed rain was analysed at two scales. A first analysis explored the large-scale variation considering two factors: region and habitat. The second analysis explored the small-scale variation in seed rain among microhabitats within each study site. Both analyses were performed by fitting generalized linear models with Poisson distribution and log-link function (Visual GLZ module of STATISTICA; StatSoft, Inc. 2000), and using the total number of seeds fallen at each seedfall trap as the dependent variable.

POST-DISPERSAL REMOVAL EXPERIMENTS

We conducted experiments involving three main factors: type of predator (rodents and ants); microhabitat (three shrub species plus open interspaces); and seed species. The seed species used in the experiments were chosen among those occurring at each study site. Each seed was tested under conspecifics, under other two shrub species and in open interspaces (Table 1).

The experimental units consisted of exclosures allowing seed removal by rodents or invertebrates. To allow only invertebrates, we used closed Petri dishes with three 0·5 cm holes perforated around the dish. Throughout the survey period none of these exclosures showed signs of the activity of potential seed predators other than ants. Preliminary assays conducted in December 1996, when ants were inactive, proved that these exclosures did not lose seeds due to rainfall or wind. To allow seed removal by rodents while preventing the activity of ants and birds, we used a modification of the methods of Herrera *et al*. (1994) and Alcántara *et al*. (2000). Exclosures consisted of 20 seeds glued to the sides of a 10 × 10 cm square made of plastic mesh

nailed to the ground. Seeds were glued by one side onto the plastic squares, and we considered that a seed had been consumed whenever it disappeared from the square (which frequently appeared as gnawed), or was still on the square but gnawed.

The experiment followed a randomized-block design with microhabitat as blocking factor, and type of predator and seed species as within-block effects. The following design was repeated in the four study sites. Four blocks (replicates) were randomly selected within each microhabitat, each block consisting of an individual plant (in the case of shrub microhabitats) or a square 2 × 2 m in an open interspace (four blocks per microhabitat × four microhabitats = 16 blocks in each study site). In each block we placed all the combinations of exclosure by seed species (three seed species per block × two exclosures per species = six exclosures per block). The experiment was set up simultaneously in all study sites in March 1997, when the seed rain corresponding to yearly fruit production stopped. The first survey was conducted 24 h later. As predation levels were extremely low, the next survey was conducted 1 week later and once every 2 weeks thereafter until October 1997. This time span was chosen to match the experiment with the period of ant activity and larger abundance of rodents in the region (personal observations). Furthermore, rodent activity in the region is not expected to be higher during the winter season. The experiment was analysed using two approaches. The first deals with the occurrence of sites safe from predators. To estimate the probability that predators did not detect an exclosure (that it was located in a safe site), we used the experimental block as sampling unit. We consider that predators detected a block if at least one seed of any of the three species in the block had disappeared. The use of blocks as sampling units is a more conservative estimate than the use of individual exclosures. Thus, if predators liked the seeds used at one study site but rejected those used at another, the frequency of exclosures without predation would differ between study sites, not because of different probability of detection, but for different suitability of the seeds. Using the block as sampling unit does not involve this problem, as at least one seed species was significantly removed by predators at every study site. We assume that when an exclosure was detected in a block, the other exclosures in the block were also detected, as these were placed 1·5 m apart. The second approach explores the small-scale variation in seed predation. The dependent variable was the arcsin-transformed percentage of seeds that disappeared from the exclosures (predation rate). Data were analysed as a randomized-block ANOVA where the block was considered as random effect nested within microhabitat. Seed species and microhabitat were also considered as random factors. The within-block effect was the seed species. Analysis of the experiment was conducted independently for each type of predator and study site. All these analyses were conducted using the

Table 2. Seed-collecting ant species present in each study site

Species	Diet type	Mid-elevation		High elevation	
		Forest	Scrubland	Forest	Scrubland
Aphaenogaster gibbosa Latr.	O (G, Z, PM)		+		
Aphaenogaster iberica Em.	O (G, Z, PM)			+	+
Aphaenogaster senilis Mayr.	O (G, Z, PM)		+		
Aphaenogaster subterranea Latr.	O (G, Z, PM)		+		
Myrmica aloba Forel.	O (G, Z)			+	+
Messor barbarus L.	G, PM		+		
Messor bouvieri Bond.	G, PM		+		
Messor capitatus Latr.	G, PM		+		(*)
Messor structor Latr.	G, PM		+		
Pheidole pallidula Nyl.	O (Z, G)	+	+	+	+
Tetramorium semilaeve André.	O (G, Z, S)			+	+

First letter under diet type indicates main diet; subsequent letters indicate alternative diets. Diet types: G = granivorous; O = omnivorous (main food items in brackets); PM = plant matter; S = sucrose-rich liquids (aphid excretions and nectar); Z = zoonecrophagous.

+, Species collected in traps; *, species observed in the study site but not collected in pit-fall traps.

Visual GLM module of STATISTICA (StatSoft, Inc. 2000).

Our interpretations of this experiment depend on the assumption that seed predation rates are proportional to seed removal rates. The available literature suggests that this assumption is largely valid in the case of seeds of fleshy fruited plants (see e.g. Hulme 1997; Hulme & Borelli 1999; Kollmann *et al*. 1998; Webb & Willson 1985).

Results

ABUNDANCE OF RODENTS AND ANTS

Apodemus sylvaticus was the only rodent species captured in the traps. The frequency of rodent capture was similar in forests at both elevations (0·035 and 0·042 captures per trap per night at mid- and high elevation, respectively), and lower than in scrublands. The latter were also similar between elevations (0·145 and 0·135 captures per trap per night at mid- and high elevation, respectively).

Eleven species of harvester ants were found (Table 2). At mid-elevation the frequency of capture was higher in scrubland (98% of traps) than in forest (74% of traps). Similarly, more species were present in the scrubland (eight species) than in the forest (one species). At high elevation, the frequency of capture was more similar among habitats (84 and 89% of traps in scrubland and forest, respectively), as was the number of species (five and four in scrubland and forest, respectively).

LARGE-SCALE VARIATION IN SEED RAIN AND FREQUENCY OF SAFE SITES

The mean number of seeds arriving on the ground differed significantly between regions (Wald $\chi^2 = 13·93$, $P < 0·001$) but not habitats (Wald $\chi^2 = 0·05$, $P = 0·82$). The effect of region was independent of habitat (Wald
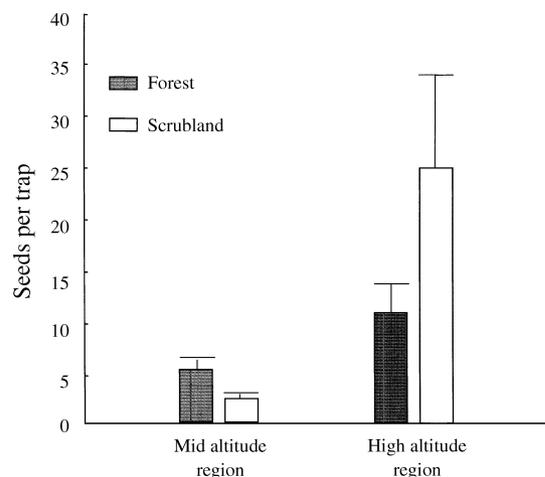

Fig. 1. Seed rain variation between study sites. Means and standard error bars are shown. Each tray had an area of 26×33 cm.

$\chi^2 = 3·82$, $P = 0·06$). Thus both forest and scrubland habitats had a considerably higher seed rain in the high-altitude region than at mid-altitude (Fig. 1).

No site was safe from predators at high elevation, as all our experimental blocks were detected by ants and rodents. However, at least a few sites were safe from rodents at mid-elevations. Ants did not discover 6·3 and 12·5% of the blocks in the forest and scrubland, respectively, and rodents left 18·8% of the blocks untouched in both forest and scrubland. The blocks that remained undetected were not consistently placed under particular microhabitats.

SMALL-SCALE AND SPECIES-SPECIFIC VARIATION IN SEED PREDATION

The seed rain was variable among microhabitats in all study sites (high altitude, Wald $\chi^2 = 464·7$ in forest, Wald $\chi^2 = 879·38$ in scrubland; mid-altitude, Wald

Table 3. Within-site variation in post-dispersal seed predation

	High elevation		Mid-elevation	
	Forest	Scrubland	Forest	Scrubland
Rodents				
B(M)	$F_{12,24} = 2·47$	$F_{12,24} = 1·51$	$F_{12,24} = 1·67$	$F_{12,24} = 0·63$
M	$F_{(3,5·95)} = 1·11$	$F_{(3,6·49)} = 0·98$	$F_{3,7·4} = 0·73$	$F_{(3,5·38)} = 0·10$
S	$F_{(2,6·00)} = 13·54$	$F_{(2,6·00)} = 16·47$	$F_{(2,6·00)} = 7·43$	$F_{(2,6·00)} = 1·46$
M × S	$F_{6,24} = 0·38$	$F_{6,24} = 1·36$	$F_{6,24} = 4·14$	$F_{6,24} = 7·94$
Granivorous ants				
B(M)	$F_{12,24} = 0·68$	$F_{12,24} = 1·59$	$F_{12,24} = 1·66$	$F_{12,24} = 1·46$
M	$F_{(3,5·91)} = 2·74$	$F_{(3,7·36)} = 0·62$	$F_{(3,5·93)} = 0·64$	$F_{(3,6·97)} = 1·63$
S	$F_{(2,6·00)} = 4·12$	$F_{(2,6·00)} = 4·60$	$F_{(2,6·00)} = 75·27$	$F_{(2,6·00)} = 21·55$
M × S	$F_{6,24} = 0·57$	$F_{6,24} = 2·17$	$F_{6,24} = 0·88$	$F_{6,24} = 2·70$

Summary of ANOVAs testing the effects of microhabitat (M) and seed species (S) on the percentage of seeds removed from exclosures. Both effects are considered random. Block (B) is considered as a random effect nested within microhabitat. Separate analyses are conducted for each study site and type of predator. Significant effects ($P < 0·05$) are indicated in bold type.

$\chi^2 = 103·66$ in forest, Wald $\chi^2 = 128·2$ in scrubland; $P < 0·001$ in all cases), with open interspaces typically receiving few seeds and fruiting shrubs receiving many seeds, especially from conspecifics.

Results of the analyses of seed predation rates from our experimental design are shown in Table 3 and Figs 2 and 3.

Rodents

Predation rates in habitats at high elevation depended only on the seed species. In the forest site, predation was high for all species, but *Rosa* seeds were consumed more than the others. Predation rates in the scrubland site were slightly lower than in the forest, especially for *Crataegus* seeds, which were consumed less than the other species. In habitats at high elevation, predation did not depend on the microhabitat, either as a main effect or as an interaction with seed species. There was a significant interaction between microhabitat and seed species in both habitats at mid-elevation, indicating that the risk of predation in different microhabitats was not correlated among seed species. In the forest site, *Crataegus* and *Smilax* seeds were hardly consumed and therefore predation on these seeds did not vary with microhabitat; however, *Hedera* seeds received more attention from rodents, especially under *Smilax* vines. In the scrubland site, the low level of predation on *Crataegus* seeds did not vary among microhabitats; however, *Olea* seeds were consumed more under *Olea* and *Crataegus* bushes, while *Rosa* seeds were consumed more in open interspaces and under *Rosa* bushes.

Granivorous ants

Predation rate in the forest site at high elevation did not vary among seeds or microhabitats. There were differences among seed species in the scrubland site at high elevation, mainly due to less predation of *Crataegus* seeds. Similarly, predation depended only on the seed species in the forest site at mid-elevation, where *Hedera* seeds were especially consumed. Finally, predation in the scrubland site at mid-elevation depended mainly on the seed species, so that *Rosa* seeds were
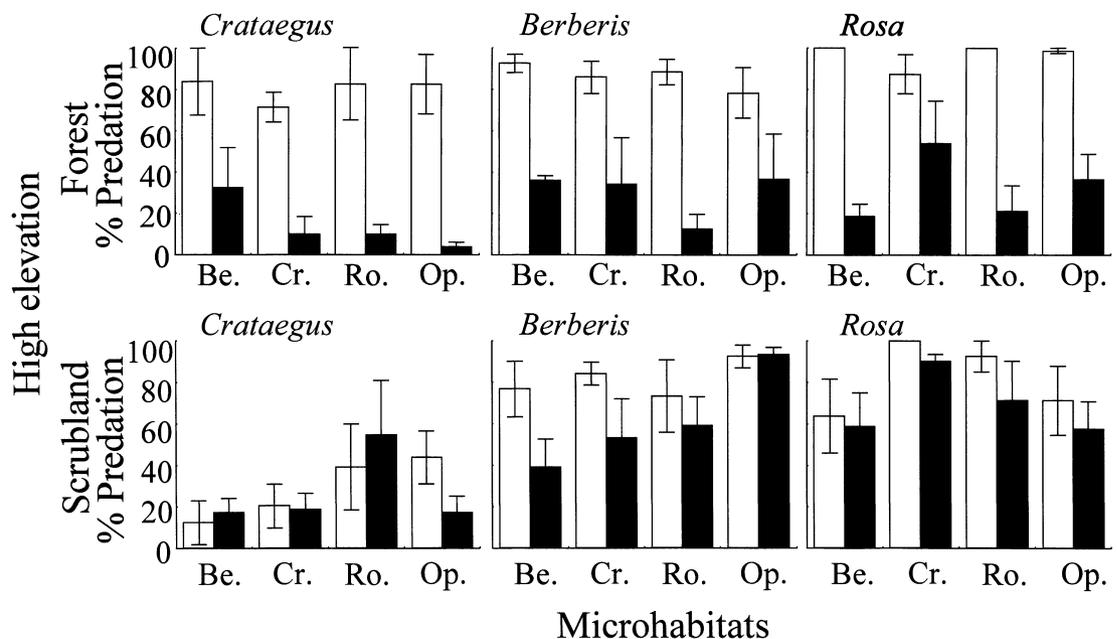
Fig. 2. Variation in the percentage of predation by rodents (open bars) and granivorous ants (shaded bars) on seeds of fleshy fruited plants. Results obtained in forests and scrublands located at high-elevation (1500 m a.s.l.) in mountains of southern Spain. Results for each seed species are shown in different panels. The *x*-axis in all cases represents the microhabitats where seeds were placed: *Berberis hispanica* (Be.), *Crataegus monogyna* (Cr.), open interspaces (Op.), *Rosa* sp. (Ro.).
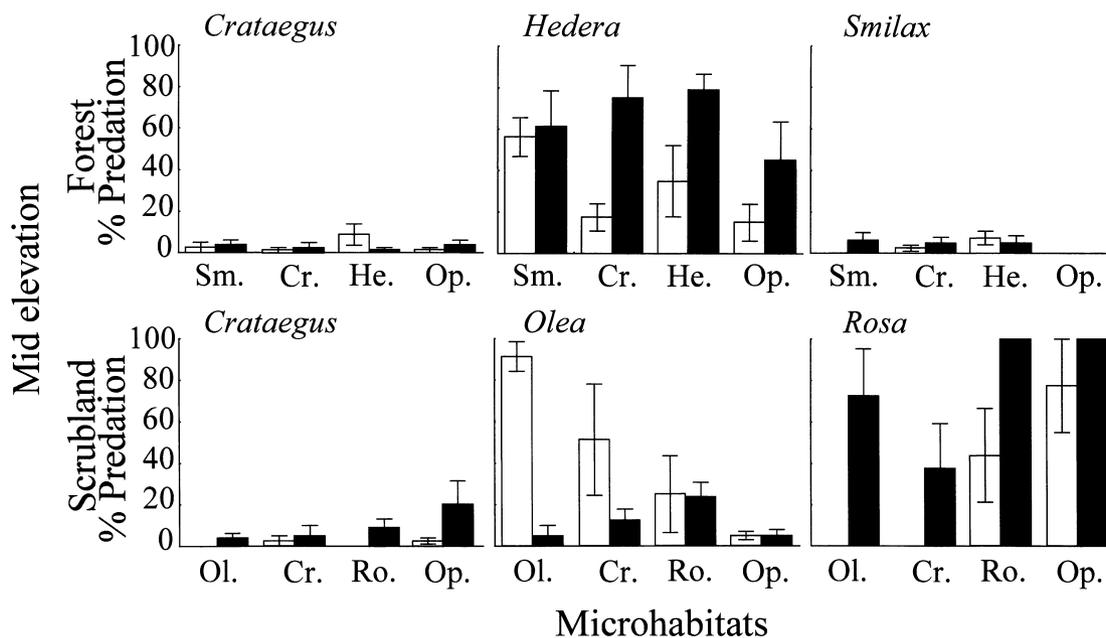
Fig. 3. Variation in the percentage of predation by rodents (open bars) and granivorous ants (shaded bars) on seeds of fleshy fruited plants. Results obtained in forests and scrublands located at mid-elevation (700 m a.s.l.) in mountains of southern Spain. Results for each seed species are shown in different panels. The *x*-axis in all cases represents the microhabitats where seeds were placed: *Crataegus monogyna* (Cr.), *Hedera helix* (He.), *Olea europaea* (Ol.), open interspaces (Op.), *Rosa* sp. (Ro.), *Smilax aspera* (Sm.).

consumed more than the other species. However, there was a slightly significant interaction between seed species and microhabitat. This was caused by differences between microhabitats in predation on *Rosa* seeds, while the low predation on *Crataegus* and *Olea* seeds did not vary among microhabitats.

The species-specific predation rates by ants or rodents were not correlated across sites with the species-specific seed rain (Spearman's rank correlation, $r = 0.16$, $P = 0.62$; $r = 0.41$, $P = 0.18$, for ants and rodents, respectively; $n = 12$ in both cases), indicating that variation in predation rates among seed species was probably not frequency-dependent.

Discussion

DIFFERENTIAL PREDATION BY RODENTS AND ANTS ON DIFFERENT SEED SPECIES

Clear preferences between seeds of different fleshy fruited plants have been shown for rodents (Hulme 1997; Jensen 1993; Kollmann *et al*. 1998; Webb & Willson 1985; Willson & Whelan 1990). Moreover, Kollmann *et al*. (1998) showed that the rankings of preference among seeds may be quite constant in time and in distant localities. Our study further strengthens these findings. The ranking of predation by rodents found in southern Spain (*Crataegus* < *Berberis* < *Rosa*) fits the pattern found by Kollmann *et al*. (1998) in Germany and England. Despite this consistency, it remains unclear which seed traits determine the ranking in rodent preferences. Some species may be preferred for their absolute benefit (seed mass) or benefit/

cost ratio (Alcántara *et al*. 2000; Blate *et al*. 1998; Hulme 1997), whereas seed coat thickness and chemical composition may determine the consumption of others (Blate *et al*. 1998; Kollmann *et al*. 1998).

Little is known about whether granivorous ant communities show preferences between the seeds of different fleshy fruited plants. If they show any preference, it would be expected to be based on seed size (Hulme 1992; Inouye *et al*. 1980; Levey & Byrne 1993); however no pattern of preference has been discerned yet (Hulme 1997). The present study indicates that some ant communities may show preferences among seed species and, when a preference occurred, smaller seeds were mostly consumed. In general, granivorous ants hardly removed seeds larger than 20 mg (*Olea*, *Crataegus* and *Smilax*), but removed important numbers of smaller seeds (*Rosa*, *Berberis* and *Hedera*). If such predation resembles that occurring under natural conditions, small-seeded fleshy fruited plants may be strongly affected by granivorous ants (e.g. species of *Ficus*, *Juniperus*, *Lonicera*, *Rhamnus*, *Rubus* or *Vaccinium*).

Contrasting seed preferences between rodents and ants might complicate the patterns of post-dispersal seed survival. Our experimental design would allow us to directly compare predation levels caused by rodents against those caused by ants. Such comparisons are tempting; however, their statistical accuracy and interpretation are not clear when exclosure methods are necessarily very different. Therefore our results comparing types of predators must be viewed with caution. In general, ants and rodents showed similar preferences among seeds within each site, except in the scrubland at mid-elevation, where ants removed more

Rosa seeds than rodents did, while the opposite happened to *Olea* seeds. Another interesting result is the pattern of predation suffered by *Rosa* seeds at different sites. *Rosa* seeds were removed in all experiments, but the main predator was different at every site: rodents and ants removed similar proportion of seeds in the high-elevation scrubland; rodents were the main predators in the forest at high elevation; and ants in the scrubland at mid-elevation.

Summarizing, our results on the probability of seed predation and removal rates show that rodents and ants are important seed predators of Mediterranean fleshy fruited species, and differentially consume the seeds of different species. Ant preferences appear to be based on seed size, while other factors affect rodents' preferences. Both predators show some overlap in their preferences, resulting in strong predation on the small seeds of *Rosa* and *Berberis*.

LARGE-SCALE VARIATIONS IN PREDATOR ABUNDANCE AND AVAILABILITY OF SITES SAFE FROM PREDATORS

The frequency of microsites safe from predators is expected to depend primarily on the abundance of predators. Mediterranean ant communities vary along gradients of vegetation cover, possibly due to correlated changes in temperature (Retana & Cerdá 2000). Open habitats have greater diversity of ant species and total densities of ants on the ground. Our results resemble this pattern, as both the probability of capture and the number of species of granivorous ants was slightly higher in scrublands than in forests, especially in scrublands at mid-elevation where the climate is hotter. On the other hand, *A. sylvaticus* was captured more frequently in scrublands than in forests, but there were no differences between elevations.

Although there was variation between sites in the abundance of rodents and ants, this variation did not translate into variation in the intensity of predation (see also Díaz 1992, Hulme 1994; Hulme & Borelli 1999; Manson & Stiles 1998). Moreover, combining results on predator abundance, seed rain and sites safe from predators suggests that the large-scale variation in the occurrence of safe sites is related more to resource abundance than to predator abundance, as the localities with more seed rain had fewer safe sites despite having equal, or even lower, predator abundance. In any case, the probability of arriving at a microsite safe from predators was small in all the communities studied, especially in habitats at high elevation, where seed predation was extensive and did not vary among microhabitats. The few microsites safe from rodents occurred in habitats at mid-elevation. Accordingly, the percentage of predation by rodents on *Crataegus* and *Rosa* (the only species tested at both elevations) was greater in habitats at high than mid-elevation. This resembles the natural pattern of seed predation. Data from natural seed rains showed that

seed removal in the high-altitude region was almost double that in the mid-altitude region (Garrido *et al.* 1997; P.J.R. and co-workers, unpublished results), whereas the rates of predation differed between habitats only in the first region.

Studies comparing seed predation in early and late-successional habitats have failed to find a general pattern, and have frequently shown contradictory results (Hammond 1995; Holl & Lulow 1997; Janzen 1985; Kollmann 1995; Osunkoya 1994; Uhl 1987; Whelan *et al.* 1991). If we consider open scrubland habitats as a building phase and the forests as a mature phase in a secondary succession, our study on Mediterranean habitats does not confirm the pattern found by Kollmann (1995) showing that seed predation of fleshy fruited temperate plants increases consistently along a successional sere. A probable reason for this difference is the more important role of ants in post-dispersal seed removal in the Mediterranean region, in contrast with their minor role in other temperate communities (Hulme 1997; Hulme & Borelli 1999; Kollmann *et al.* 1998; but see Terborgh *et al.* 1993).

We are not aware of any other study comparing seed predation between localities at different elevations or, alternatively, at sufficiently different latitudes. Thus we cannot know the generality of the pattern found. Nevertheless, variation in the availability of safe sites may have important implications for different plant communities.

COVARIATION AMONG SPECIES IN SITES SAFE FROM PREDATORS: IMPLICATIONS FOR PLANT COMMUNITY DIVERSITY

The number of species of fleshy fruited plants in Mediterranean communities decreases with elevation (Herrera 1995). The plant communities we investigated fit this pattern, as sites at mid-elevation had almost twice as many fleshy fruited species as those at high elevation. Multiple factors may contribute to this pattern. Differences have been considered between elevations in the relative area they occupy; in the temporal stability of their habitats; or in the availability and types of seed dispersers they host (Herrera 1992; Herrera 1995; Rey 2001). Post-dispersal seed predation may also affect the composition of fleshy fruited plant communities in Mediterranean habitats. Models suggest that post-dispersal predators may exclude some species from the community if they show marked preferences towards specific plant species; on the other hand, post-dispersal seed predators may contribute to the maintenance of species diversity if the spatial distribution of sites safe from predators is uncorrelated across plant species (Crawley 2000; Pacala 1997).

According to the models, post-dispersal seed predators could contribute to differences in species diversity among elevations whenever covariance across plant species in the microhabitats adequate for recruitment (e.g. with smaller predation risk) increases with elevation.

In our analyses, a significant interaction between microhabitat and seed species would mean that different seeds suffer different predation in different microhabitats (low covariance). The interaction was significant for seed predation by rodents at mid-elevation habitats, and for predation by ants only in the scrubland site at mid-elevation. Therefore, as many studies have shown, there was variation among microhabitats in the probability of predation of some seed species (Hulme 1994; Manson & Stiles 1998; Russell & Schupp 1998; but see Verdú & García-Fayos 1996). In addition, our results agree with the pattern shown by models, so that where variation in predation among microhabitats was not correlated across species, there were more species. The lack of positive covariation may involve a negative correlation between species, like that which occurred between *Olea* and *Rosa* (Fig. 3). Alternatively, it may occur because predation does not vary among microhabitats in some species, especially in those with low predation rates (*Crataegus* and *Smilax*), while it varies in others (*Rosa, Olea, Hedera*).

Our study suggests a potential role of these consumers in some Mediterranean plant communities. In communities at high elevation, the scarcity of sites safe from predators and the significant spatial covariation of predation rates among seed species may allow the expression of a competitive hierarchy among the fleshy fruited plants. In these conditions, the species recruiting locally would depend on the particular combination of species that dispersers deposited there, and on differences among species in their competitive ability in terms of germination, seedling survival and growth. On the other hand, in communities at mid-elevation we detected a complex pattern of variation in species-specific rates of post-dispersal seed predation by rodents and granivorous ants, which further varied between microhabitats. This variability is superimposed on that created by dispersers, and may contribute to the greater richness of fleshy fruited plants in Mediterranean communities at mid- and low elevations.

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