

# Consistent pattern of habitat and species selection by post-dispersal seed predators in a Mediterranean mosaic landscape

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**Abstract** There is still little information on effects of habitat degradation on post-dispersal seed predation at the landscape scale. The aim of this study was to determine the influence of habitat degradation and seed species on the variability of post-dispersal seed-predation rate. Experimental seed removal was investigated in six Mediterranean woody plant species, four trees (*Pinus sylvestris*, *Quercus ilex*, *Acer opalus* ssp. *granatense*, and *Sorbus aria*) and two shrubs (*Berberis vulgaris* and *Crataegus monogyna*), in an extensively used mosaic landscape on the Sierra Nevada massif (SE Spain). Seed depots were distributed over 2 years in five differently degraded landscape units, each one with three plots: shrubland; native forest; and dense, cleared and fenced reforestation stands. Predation was the highest in native forest, shrubland, and fenced reforestation, and the lowest in dense and cleared reforestation stands, being

partially due to a positive correlation between shrub cover and post-dispersal seed predation. However, the main factors driving post-dispersal seed predation were intrinsic to seeds, as species preference explained most of the variance in our model for predation. The plant-species ranking was *Quercus* > *Pinus* > *Sorbus* > *Berberis* > *Acer* > *Crataegus*, the dominant tree species being the most depredated. These findings are novel because they suggest for the first time that species-selection patterns by post-dispersal seed predators tended to remain constant through both study years in all habitats comprising a mosaic landscape, whether native forest, reforestation stands or successional shrubland.

**Keywords** Degraded habitats · Field experiment · Land use change · Logistic regression · Predator preference · Sierra Nevada

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## Introduction

Post-dispersal seed predation is a limiting factor for natural regeneration of many forest ecosystems worldwide (Crawley 1992; Davidson 1993; Hulme 1993). In terms of plant populations, seed predators limit the abundance of seed banks and determine their spatial distribution, thereby having demographic consequences such as local extinction of species

(Crawley 1992; Hulme 1996). From a community perspective, preferences of post-dispersal seed predators can modify composition and abundance of species inhabiting forests and shrublands (Hulme 1996; García et al. 2005).

There are two main sources of variability on post-dispersal seed predation: intrinsic to seeds, such as size, nutrient content, coat thickness, or toxic defences (Vander Wall 1994; Hulme 1994; Hulme and Hunt 1999; García et al. 2005); or extrinsic, such as the structure of the habitat where seeds are dispersed, the variability of fruit production, or changes in predator pressure (Myster and Pickett 1993; Rey et al. 2002; Schnurr et al. 2004). In relation to spatial factors, most studies have analysed the variability of predation rates between microhabitats of the same landscape unit (Schupp and Fuentes 1995; Rey et al. 2002; Fedriani and Manzaneda 2005; García-Castaño et al. 2006). These field studies have provided strong evidence of a patchy structure of seed predation at a microhabitat scale within a given landscape unit. However, information on variability of post-dispersal seed predation within habitats differing in composition and structure in a given landscape is still scarce (but see García et al. 2005).

Most predation studies at the landscape scale have been conducted under the habitat-fragmentation paradigm. The size reduction of the fragment and the edge effect have been related to predation pressure, which proved to be increased (Santos and Tellería 1994, 1997; Kollmann and Buschor 2003; Fleury and Galetti 2006; García and Chacoff 2007) or reduced (through changes in seed-predator abundances; Wyatt and Silman 2004; Hanson et al. 2006) with fragment size. This conceptual approach of intact forest fragments immersed in a degraded matrix is based on the classical biogeographical island theory of MacArthur and Wilson (1967). However, Mediterranean landscapes do not correspond to a “fragment-matrix” structure of suitable habitats surrounded by inhospitable matrices, but rather they are mosaics composed of adjacent patches with different degrees of degradation and suitability for species (Wiens 1995; Duelli 1997). The type of degradation may affect the pattern of seed predation through the different availability of food and protection that predators can find in each habitat (Torre and Diaz 2004), very often related to shrub cover (Simonetti 1989). Despite the commonness of mosaic landscapes

around the world as a result of human impact (Turner et al. 2001), there are no explicit studies addressing the variability in post-dispersal seed predation in the overall landscape units of a mosaic landscape. This knowledge is relevant for the understanding of the recruitment limitations in a degradation framework (Mendoza et al. 2008).

The aim of the present study was to determine how seed species and different composition and structure of landscape units (derived from different habitat degradation or change in land use) affect post-dispersal seed predation patterns. For this purpose, we experimentally evaluated seed removal in the different landscape units composing the mosaic landscape in Mediterranean mountains, each one with a characteristic species composition and structure: native forest (the least degraded landscape unit), pine reforestation stands, and post-fire successional shrublands (these two latter coming from the degradation of the former). Our working hypothesis was that the composition and structure of the landscape unit (the spatial pattern) will affect the post-dispersal seed-predation rate (the process, *sensu* Turner 1989). Different plant-species composition and structure of landscape units may impose diverging abundance and/or activity of predators, eventually determining different post-dispersal seed-predation rates. In particular, we sought to determine: (1) whether post-dispersal seed predation varied more depending on seed species or the type of landscape unit, and (2) whether there was inter-annual variability in the two criteria (species *versus* landscape-unit selection). The examination of the effects of seed-species identity, different landscape units and their interaction during 2 consecutive years will contribute to identify seed predation patterns and their potential effects on the regeneration dynamics of shrubs and trees in this Mediterranean mosaic landscape.

## Methods

### Study area

The present study was conducted during 2004–2005, at Sierra Nevada National Park, surrounding the Trevenque Peak area (37°5' N, 3°28' W, Granada Province, SE, Spain). The climate is Mediterranean mountain type, with hot dry summers and cold,

snowy winters, and rainfall (818.1 mm year<sup>-1</sup>, average during 1990–2006) heaviest in autumn and spring. The bedrock is calcareous, and the predominating soils are regosols and cambisols (Delgado et al. 1989). The study area is composed of a mosaic landscape with five different landscape units located between 1,600 and 1,900 m a.s.l.: native forest, dense, cleared, and fenced reforestation stands, and shrubland. The first represents low degradation, whereas the reforestation stands and the shrubland constitute two contrasting types of degraded habitats. The native forest is mainly composed of *Pinus sylvestris* var. *nevadensis* Christ. mixed with other trees such as *Taxus baccata* L. or *Acer opalus* ssp. *granatense* Boiss. (mean tree density 114 trees ha<sup>-1</sup>), and a dense shrubby understorey composed of different fleshy-fruited shrub species (*Berberis vulgaris* ssp. *australis* Boiss., *Crataegus monogyna* Jacq., *Juniperus communis* L. and *Lonicera xylosteum* L.). Dense reforestation stands contain *Pinus sylvestris* L. and *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco with mean densities of 1,041 individuals ha<sup>-1</sup>. Fenced stands are reforestations with herbivore exclosure since 1982 and the same tree density as dense stands. In cleared reforestation stands timber was harvested in 2000 reducing tree densities to 521 individuals ha<sup>-1</sup>. Shrubland is a post-fire area from a reforestation burnt in 1983 and currently dominated by *Crataegus monogyna* Jacq., *Prunus ramburii* Boiss., *Salvia lavandulifolia* Vahl. and *Erinacea anthyllis* Link., with widely scattered trees (21 individuals ha<sup>-1</sup>). Despite the fact that *Quercus ilex* is an abundant species conforming to the sapling bank in all the studied landscape units, this species rarely appear conforming to the adult canopy (Mendoza 2008). Each landscape unit was represented by three randomly chosen plots of similar size (mean 0.53 ha) with an average distance of 688 m between the three plots of the same landscape unit. Plot areas were calculated by GIS using GPS data (Leica SR 500; Leyca Geosystems, Switzerland). The selected patches of the five different landscape units occupied an area of about 3 km<sup>2</sup> and were representative of the study area (Fig. 1).

### Study species

To quantify the predation rate, we used seeds of six woody species based on two arguments. First, these



**Fig. 1** Map of the study area representing a mosaic landscape with adjacent patches composed of habitats with different degrees of degradation. Each letter represents a different habitat type: A = native forest, B = shrubland, C = cleared reforestation stands, D = dense reforestation stands and E = fenced reforestation stands

species were representative of the woody community appearing in the native forest of the study area, including four trees (*Pinus sylvestris* var. *nevadensis* Christ., *Quercus ilex* L., *Acer opalus* ssp. *granatense* Boiss and *Sorbus aria* L.) and two shrubs (*Berberis vulgaris* ssp. *australis* Boiss. and *Crataegus monogyna* Jacq; hereafter, all of them will be called by their genus name). *Pinus* and *Quercus* are the dominant tree species, whereas *Berberis* and *Crataegus* are the dominant shrubs. *Quercus*, *Sorbus*, *Berberis* and *Crataegus* are dispersed by vertebrates (Herrera 1992; Gómez 2004a), whereas *Pinus* and *Acer* are wind-dispersed. The sample thus included both anemochorous and zoochorous species, in addition to a broad array of different mechanical or toxic defences (Kollmann et al. 1998; García-Castaño 2001; García et al. 2005). Second, the size range of the seeds of the selected species (Table 1) was representative of the size range of the whole community available for seed predators. All fruits, cones and acorns were collected in the same study area in the autumn preceding each experimental trial. Seeds were extracted and stored at 4°C until the field experiments.

**Table 1** Seed characteristics of the six species used in predation experiment

Species	Weight (g)	Length (cm)	Toxins
<i>Acer opalus</i>	0.042 ± 0.006	0.731 ± 0.384	–
<i>Berberis vulgaris</i>	0.019 ± 0.004	0.593 ± 0.048	Oxyacanthine, chelidonic acid, isoquinoline alkaloid
<i>Crataegus monogyna</i>	0.742 ± 0.017	0.563 ± 0.069	–
<i>Pinus sylvestris</i>	0.012 ± 0.001	0.514 ± 0.029	–
<i>Quercus ilex</i>	5.078 ± 1.554	3.346 ± 0.378	Tannins
<i>Sorbus aria</i>	0.022 ± 0.009	0.576 ± 0.039	–

Means are given ±1 SD. For each measurement, 100 seeds were used. Information in toxicity is taken from the literature (Kollmann et al. 1998; Johnson et al. 1993)

Previous studies in the same study area (Castro et al. 1999; García et al. 2000; Gómez 2004a, b) have reported, by field observation and trapping, that the community of seed predators is composed of *Apodemus sylvaticus* (woodmouse) and *Sus scrofa* (wild boar). *S. scrofa* only consume acorns of *Quercus* spp, whereas *A. sylvaticus* predaes seeds of the six species used in our experiment. Consumption of seeds by birds on the ground is rare in our study area (no data recorded on bird censuses and focal observations for 3 years; unpublished data). Ants were not considered as seed predators because they were inactive at the moment the experiment was performed.

### Experimental design

Seed predation was quantified by recording removal of seeds of the six species offered simultaneously to predators in the field. Each experimental unit, a seed depot, was composed of two squares (20 × 20 cm) of plastic mesh pegged to the soil, a distance of 2 m one from each other. To each square of plastic mesh, two seeds of five species (*Acer*, *Pinus*, *Sorbus*, *Crataegus* and *Berberis*) were glued in random position with a low-odour thermoplastic adhesive (wind and rain resistant). Also, one *Quercus* acorn was placed next to the mesh (see Herrera et al. 1994; Alcántara et al. 2000; García et al. 2005 for a similar procedure). This procedure was intended to mimic natural seed dispersal; *Quercus* acorns were partially buried, imitating activity of *Garrulus glandarius* (jay), while the rest of seeds were mixed with litter (3–5 mm depth), simulating dispersal by wind or birds.

Seed depots were included in sampling stations. In reforestation stands, the only kind of microhabitat

present was “under pine canopy”, due to the high density and uniform distribution of planted pines. Therefore, sampling stations were composed of two meshes. By contrast, the native forest and shrubland had greater horizontal structural heterogeneity. Because it has been demonstrated that the predation rate changes between microhabitats of the same landscape unit (Hulme 1994; Manson and Stiles 1998; Russell and Schupp 1998), we considered this source of heterogeneity in forest and shrub habitats. Thus, in each landscape unit, sampling stations were composed of four seed depots, each one on the four dominant microhabitats. In the native forest, these were: under pine trees, under the two most abundant fleshy-fruited shrubs and open areas. In shrubland, these were: under the canopy of *Crataegus*, *Prunus* and *Salvia*, and open areas. Each sampling station was randomly placed within plots maintaining a distance of at least 5 m from each other. In another attempt to sample the structural heterogeneity of each type of landscape unit, we measured shrub cover using a 2-m radius circle centred in the seed depot and recorded the percentage of the surface area covered by shrubs. The overall design was a factorial experiment with four factors: landscape unit, species, year and shrub cover. The landscape-unit factor had five levels, with three replicated plots per each one: native forest, dense, cleared, fenced-reforestation stands and shrubland. We established 15 sampling stations per plot, making a total of 45 sampling stations per level of landscape unit. Seeds were exposed to predators at the end of winters of 2004 and 2005 (March) and monitored after 30 days. This is the moment just when seed dispersal by wind and by zoochorous animals are getting finished, but before the beginning of the seedling emergence

period (April–June) for all species. Thus, our experimental design was conducted in the moment when predators can alter the seed bank available to emerge in that year. Furthermore, in our study system there is no a permanent soil seed bank (Mendoza 2008), so the effect of seed predators is exerted on the seeds dispersed the same year.

For the overall 15 plots, the mean density of the exposed seeds was  $0.013 \pm 0.006$  seeds  $m^{-2}$  for *Quercus*, and  $0.025 \pm 0.013$  seeds  $m^{-2}$  for all other species. This value was consistently lower than the natural seed rain for the studied species in the same areas (3–180 seeds  $m^{-2}$  depending on the species and the landscape unit; Mendoza et al. 2008), thereby avoiding attraction of predators due to increased seed density (García et al. 2007 and references therein).

We considered a seed to be depredated in two cases: when it was missing from the plastic mesh, or when it remained on the mesh but was gnawed and empty (García et al. 2005). We identified the predator when possible (rodent *versus* wild boar): gnaw marks on the seed coat and the presence of typical faeces were attributed to rodents, whereas visible disturbance in the soil due to rooting around the seed and characteristic faeces were assigned to *S. scrofa*.

#### Data analysis

For statistical analyses, we used the predation rate from each of the 15 sampling stations (composed of one seed depot in reforestation stands and of four in shrubland and native forest). Data were analysed with a logistic model (binomial generalized model) with a logit link function, because the probability of each individual seed to be depredated was binary. We used as response variable for the predation rate, calculated as the proportion of depredated seeds to the total number of exposed seeds per sampling station. The categorical predictors were species, year and landscape unit; and the continuous predictor was shrub cover. Interactions of shrub cover with the other predictors were not included in the model due to the lack of biological sense (as shrub cover was the same for each seed depot where seeds of six species were exposed during both years). Plot was removed as the predictor since we found no significant differences between the plots of the same landscape unit. We used the  $R_L^2$  measure of explained variance (Menard 2000; Quinn and Keough 2002). Explained variance

was calculated using the rate of the Wald  $\chi^2$  of each factor to the whole model  $G^2$  variance (Zar 1999).  $P$ -value as well as explained variance were the criteria used to determine the significance of the predictors. JMP v. 7.0 (SAS Institute Inc. 2007) was used for data analysis. Contrast tests were performed in order to establish significant differences in levels within a predictor variable.

#### Results

Out of the total number of cases in which the predator was identified, 98.5% of the predation was found to be by rodents, and only 1.5% by wild boars (consistently acorn consumption), thus identifying rodents as the principal seed predators in our study system.

All the main effects considered (species, landscape unit, year and shrub cover) were strongly significant separately (Table 2). The interactions between the first three main effects were significant in all cases except for the interaction between landscape unit and year.

The fenced reforestation stand was the landscape unit with the highest predation pressure ( $61.2\% \pm 42.6$  SD), followed by the shrubland ( $53\% \pm 41.4$  SD) and the native forest ( $48.3\% \pm 38.7$  SD), the lowest being in cleared ( $34.16\% \pm 39.8$  SD) and dense reforestation stands ( $24.4\% \pm 36.1$  SD; Fig. 2). The lack of significance between the interaction of landscape unit and year indicated that this habitat selection pattern of seed predation remained constant during both study years (Fig. 2). Shrub cover had a significant effect over predation rate, although the variance explained by this effect was very low (Table 2). Habitats with higher percentages of shrub cover—shrubland ( $36.6\% \pm 3.6$  SD of shrub cover), native forest ( $32.9\% \pm 5.3$  SD) and fenced reforestation stands ( $25.5\% \pm 4.1$  SD)—had higher predation rates than in the landscape units where the shrub cover was scant, as in cleared reforestation stands ( $13.5\% \pm 2.8$  SD) and, particularly, dense reforestation stands ( $1.9\% \pm 0.9$  SD).

In terms of species, the most depredated was *Quercus* ( $77.4\% \pm 35.6$  SD), followed by *Pinus* ( $73.3\% \pm 34.1$  SD), and *Sorbus* ( $69.2\% \pm 35.5$  SD; Fig. 2). *Berberis* ( $30.1\% \pm 30.7$  SD) showed medium predation values, whereas *Acer* ( $10.4\% \pm 16.9$  SD) and *Crataegus* ( $5.5\% \pm 14.2$  SD) registered very low

**Table 2** Results of the generalized linear model examining the significance of habitat, species identity, year, and the interactions among main factors on the seed predation rate

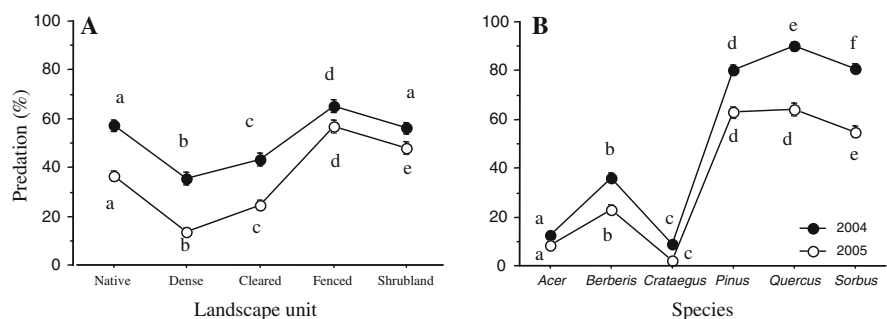
Model effects	DF	Wald $\chi^2$	<i>P</i>	Explained variance (%)
Species	5	4,040.18	<b>&lt;0.0001</b>	68.62
Year	1	127.91	<b>&lt;0.0001</b>	2.17
Landscape unit	4	95.93	<b>&lt;0.0001</b>	1.63
Shrub cover	1	26.25	<b>&lt;0.0001</b>	0.44
Landscape unit $\times$ species	20	214.36	<b>&lt;0.0001</b>	3.64
Species $\times$ year	5	43.55	<b>&lt;0.0001</b>	0.74
Landscape unit $\times$ year	4	8.31	0.08	0.14
Landscape unit $\times$ species $\times$ year	20	62.67	<b>&lt;0.0001</b>	1.07

Binomial was the probability distribution, and logit the link function. Explained variance is calculated as the proportion of whole model variance ( $G^2$ ) fitted by each factor (Wald  $\chi^2$ )

Whole model test:  $G^2 = 5,887.77$ ;  $R_L^2 = 0.447$ ; DF = 60;  $P < 0.0001$

Bold indicates significant effects in the model

**Fig. 2** Mean predation percentages among the landscape units (a) and the species (b), differing between the 2 study years. Bars show  $\pm 1$  SE. Each point represents the mean predation percentage for the five landscape units or the six study species, respectively



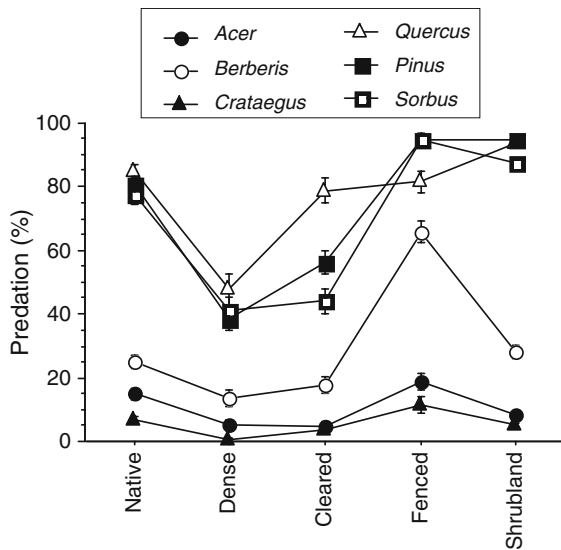
predation rates (Fig. 3). Again, this pattern of species preferences tended to be constant through time, although *Quercus* and *Sorbus* had not significantly different predation rates in 2005 (reflected in the significant interaction between species and year). The predation rates differed significantly between years, being higher in 2004 than in 2005 for all cases (Fig. 2).

## Discussion

### Species selection

In our predation model, species identity explained most of the variability in the predation rate (Table 2). This agrees with many other studies showing that the predation risk depends more on structural and biochemical characteristics of species than on the place where a seed is dispersed (Crawley 1992; Barnea et al. 1993; Hulme 1997; García-Castaño 2001). Our predation experiment revealed that

rodents selected certain species, establishing a strong preference ranking: *Quercus* > *Pinus* > *Sorbus* > *Berberis* > *Acer* > *Crataegus* (Fig. 2). Species preference may be determined by intrinsic seed factors, such as the presence of toxins, nutrient contents or a thick coat (Kollmann et al. 1998; Rey et al. 2002), as well as seed size (Martínez et al. 2007; Mendoza and Dirzo 2007). In the case of *Berberis*, the relatively low predation rate found may be influenced by the presence of several toxins such as oxyacanthine, chelidonic acid and isoquinoline alkaloid (Kollmann et al. 1998). The lowest predation rate of *Crataegus* is presumably because of the very thick seed coat of this species (García-Castaño 2001; García et al. 2005). That is, for similar sizes, seeds with proportionally thicker coats are better defended, so they are less profitable for predators (in terms of higher seed-husking cost, Hulme 1993) than those with an embryo plus endosperm fraction surrounded by a thinner coat. Therefore, the absence of either a thick coat or toxins in *Pinus* and *Sorbus* may be one reason



**Fig. 3** Differences in seed predation among habitats of the six study species. Bars show  $\pm 1$  SE. Each point represents the mean predation percentage of the three patches of each habitat. Data were pooled for both study years. Contrast tests were performed to compare the predation among types of landscape unit (different letters indicate significant differences). *Acer*: native (a); dense (b); cleared (c); fenced (a); shrubland (b). *Berberis*: native (a); dense (b); cleared (b); fenced (c); shrubland (a). *Crataegus*: native (a); dense (b); cleared (a); fenced (c); shrubland (a). *Quercus*: native (a); dense (b); cleared (a); fenced (a); shrubland (c). *Pinus*: native (a); dense (b); cleared (c); fenced (d); shrubland (d). *Sorbus*: native (a); dense (b); cleared (b); fenced (c); shrubland (d)

for their high predation values. *Quercus* was the most depredated species, presumably because it was also the heaviest seed of the six species and contained a high percentage of lipids, therefore representing a valuable resource for predators (Gómez 2004b). Also, this species was depredated by all the predators in the area (wild boar as well as rodents) so the predation risk was increased.

#### Landscape unit selection

Classical approaches to landscape degradation based on a “fragment-matrix” concept that assumed that intact fragments were surrounded by an unattractive matrix, differences in predation being determined by fragment size or edge effect (Burkey 1993; Orrock et al. 2003; Tallmon et al. 2003). On the contrary, in a mosaic-landscape approach, there is no place for an unattractive matrix, because the landscape is composed of adjacent patches diverging in their

degradation type (Wiens 1995). In fact, within our mosaic landscape, we found a pattern that related landscape units to post-dispersal seed predation over both studied years, indicating that the predation process can be affected by the composition and structure of habitats differing in the type of degradation. This was in part explained by the abundance of shrubs, although the effect did not explain much variance in the model (Table 2). Presumably, shrubs offer shelter and food to rodents, the main predators, thereby increasing their abundance and activity (Simonetti 1989; Fedriani and Manzaneda 2005; Muñoz 2005; Mortelliti and Biotani 2006). Following this trend, the native forest (the least-degraded landscape unit) as well as shrubland showed heavy predation pressure (Fig. 2). These results can be explained by the fact that in these landscape units the shrub cover was denser, and the microhabitats were highly heterogeneous. On the contrary, dense and cleared reforestation stands had the lowest values of seed predation. The low shrub cover in these landscape units resulted in less availability of safe sites for rodents (Muñoz 2005), and therefore these landscape units were unattractive for seed predators. Fencing dramatically boosted predation rates in reforestation stands most likely due to an increase in the shrub understorey. Also, the existence of indirect interactions between rodents versus ungulates and wild boars may be responsible for an increase in the rodent populations due to fencing (Focardi et al. 2000; Smit et al. 2001; Shepherd and Ditzgen 2005; Muñoz and Bonal 2007). Although in our model the shrub cover explained only 0.44% of the total variance, this may be attributed to operational sampling restrictions (same shrub cover for the six species on each sampling station and for both years).

#### Habitat and temporal patterns of species-specific selection

Strong post-dispersal predation pressure (average for all species and landscape units both years = 44%) was found in the landscape mosaic of Sierra Nevada, similar to values found in other Mediterranean mountains such as Sierra de Cazorla (48%, Herrera et al. 1994), Sierra Sur de Jaén (47%, Alcántara et al. 2000), or temperate woodlands (51%, García et al. 2005). However, this pressure of post-dispersal seed

predation did not have the same magnitude between adjacent landscape units in a landscape mosaic. According to our results, predation pressure was higher in some landscape units (shrubland, native forest and fenced reforestation stands) than in others (dense and cleared reforestation stands). Although differences between landscape units were significant and only explained a low percentage of the total variance, there was no significant interaction between year and landscape unit (Table 2), reflecting that the landscape-unit pattern was consistent, at least during both study years. Despite this, the total intensity of predation rates shifted among years, potentially modifying recruitment opportunities (Eriksson and Fröberg 1996), especially for the preferred species (*Pinus* and *Quercus*). The year 2005 was more favourable for seed survival than 2004, when predation intensity was very high and only a few seeds were available to create a seed bank. This inter-annual variability in predation pressure may be related to temporal variation in fruit production and pine cones (Mendoza 2008). In the case of species-selection pattern, it was consistent over habitats and time; that is, in most cases, the same ranking of seed predation was maintained in each landscape unit every year except for *Quercus*, the most depredated species in all landscape units except in fenced reforestation stands (Fig. 3). This predation rate of *Quercus* undoubtedly decreased because of the exclusion (by fencing) of wild boar, one of the main acorn predators (Gómez et al. 2008). This is reflected in the significant interaction between landscape unit and species in the model. The existence of patterns on species preference among different habitats can be found in other systems such as temperate forests (Kollmann et al. 1998; Hulme and Borelli 1999) or Mediterranean woodlands (Hulme 1997; Rey et al. 2002).

#### Consequences for regeneration

Our results suggest the existence of species- and habitat-selection patterns in predation rate among degraded habitats through time. Seed predation differed between adjacent landscape units of similar size, and the intensity of predation depended more on seed characteristics than on the shrub coverage in each landscape unit. Thus, our experimental results support the contention that differences in the

composition and structure of this Mediterranean mosaic landscape (the pattern) may affect the post-dispersal seed-predation rate (the process) at the landscape scale. Because habitat use and diet selection by rodents can change across years depending on the availability of food resources, abundance of rodents and their predators, and climatic conditions (Schnurr et al. 2004; Caccia et al. 2006), long-term experiments integrating broad spatial and temporal scales are needed to give more support to the pattern found in this study.

Consistent patterns of species selection by seed predators can have demographic effects, as the systematically more-consumed species (i.e., *Quercus* or *Pinus*) suffer a significantly higher reduction in the number of propagules available for recruitment than the less-consumed species (Janzen 1971; Louda 1989; Davidson 1993; Hulme 1996; Rey and Alcántara 2000; García et al. 2005). As a consequence of these selection criteria, seed predators can affect the coexistence of different tree species (Hulme 1996; Wright 2002) by drastically reducing the seed survival of the two dominant tree species (*Pinus* and *Quercus*), in favour of the rarest tree species (*Acer*; see Paine and Beck 2007 for a similar abundance-dependent pattern). The impact of seed predators on both dominant tree species is exacerbated by the fact that neither *Pinus* nor *Quercus* have a seed bank and they have less supra-annual variability in seed production in comparison with other Mediterranean species (Herrera et al. 1998), probably because they are unable to saturate rodents by crop overabundance.

Notably, seed predators favoured the shrub species (*Berberis* and *Crataegus*), which were less attacked than were the tree species (*Quercus* and *Pinus*) in all landscape units. As shrub species are more abundant than tree species in terms of cover as well as number of individuals, this could potentially alter species composition and abundance of the woody community at the seedling stage. Consequently, post-dispersal seed predation can filter the species pool available for recruitment of the woody community in a similar way in all landscape units, irrespective of the degree of degradation, reducing the number of propagules of dominant tree species (*Pinus* and *Quercus*) and favouring a shrub-like landscape, which is the type of landscape unit where rodents can find both food and refuge. These findings are novel because they



indicate that although seed predation pressure differs between adjacent landscape units, the selective filtering on the seed bank of woody species due to post-dispersal seed predators, tends to be constant in all landscape units, whether native forest, reforestation stands, or successional shrubland.

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