



Seed predation of two alien *Opuntia* species invading Mediterranean communities

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Abstract

Invasibility depends on the interaction of the introduced species with the abiotic and biotic factors of the recipient community. In particular, the biotic resistance posed by native herbivores has been claimed to be of great importance in controlling plant invasion. We investigated fruit and seed predation of two exotic *Opuntia* species within and between Mediterranean communities in order to determine how patterns of predation matched patterns of invasion. Predators were small mammals, presumably mice, which could consume more than 50% of the seeds produced. Predators could be equally effective in consuming fruit and single seeds. *O. maxima* fruits were slightly preferred to *O. stricta* fruits, but predators did not distinguish between seeds. Seed predation was more intense in invaded than in non-invaded communities. However, there was a high spatial variation in seed predation that did not always match patterns of invasion, suggesting that seed predation alone is not a good predictor of community invasibility to *Opuntia*. According to these results invasibility to *Opuntia* is limited in some (but not all) communities by native mice. Seed losses by predation were high for both species. However, we estimated that more than 75% of seeds dispersed by birds to non-invaded areas are not predated.

Introduction

Currently much emphasis is being placed on research into the factors controlling the establishment of alien species in natural and seminatural ecosystems in order to assess which ecosystems are more prone to invasion. Invasibility is the intrinsic property of ecosystems that determines the survival rate of an introduced species in a recipient ecosystem (Lonsdale 1999). The survival rate of an introduced plant species in a new region depends on species survival after maladaptation, environmental stochasticity (e.g. drought, fire) and the biotic resistance posed by native species. The role of natural enemies, such as generalist herbivores has been claimed to be one of the main mechanisms that reduces seedling establishment and controls plant invasion (Elton 1958; Crawley 1986). In particular, seed predators are considered to be the natural enemies that might exert the most ef-

ficient control of invasion because they increase seed loss (Crawley 1992). Postdispersal seed predation has been described to occur to introduced plants (Holmes 1990; Bossard 1991; Bossard and Rejmanek 1994). Postdispersal seed predators are usually generalist vertebrates that eat seeds that have been scattered on the ground by dispersal agents.

Studies on both native and alien plant species have shown that patterns of seed predation are very variable within and between sites because they depend on the types of predators and their response to habitat structure and plant cover (Janzen 1971; Hulme 1998). For example, seed predation of the alien *Acacia* in the South African fynbos decreases with vegetation cover (Holmes 1990). Similarly, mice and quails eat almost 50% of the European *Cytisus scoparius* seeds in disturbed areas of Californian shrubland and pine woodlands but not in undisturbed areas (Bossard 1991). Therefore, the spatial variability of seed predation

must be considered when predicting community differences in invasibility.

In this paper we focus on the role of seed predators as a component of the invasibility of Mediterranean communities to two prickly-pear cacti species (*Opuntia* spp). For this purpose fruit and seed transplant experiments within olive groves and in different vegetation types were performed to assess the magnitude of fruit and seed predation and to answer the following questions: 1) What are the main agents of seed predation? 2) Are there differences in seed predation between species? 3) Are there differences in seed predation within and between communities? And finally, 4) Do these differences match spatial patterns of invasion?

Material and methods

Study plant species description

Opuntia spp. (Cactaceae) are non-columnar cacti from Central America that were introduced to Europe by the Spanish conquerors during the end of the 15th century and the beginning of the 16th century (Barbera et al. 1992). *Opuntia* spp. have been used for consumption, livestock, foraging, fencing, the production of a red dye that was obtained from a cochineal insect host (*Dactylopius coccus*), and as ornamentals. *Opuntia* spp. are CAM plants with a very high efficient use of water, which might explain their success in invading Mediterranean and semiarid areas (Cortázar and Nobel 1990).

The succulent stems are formed as a sequence of flattened segments, the cladodes, which tend to have an elliptical base that supports the greatly enlarged, flattened upper portion. *Opuntia* has spines as leaves, the flowers 5–10 cm in diameter, are sessile and solitary and the fruits are berries of 4–8 cm (Castroviejo et al. 1990). Vegetative reproduction is common. Usually cladodes break off and root next to the parental plant and form conspicuous patches of ramets (patches hereafter). The two study species were *Opuntia maxima* that presents an average height of 3 m and *O. stricta* that does not attain more than one meter. The recruitment of sexually derived *Opuntia* spp. seedlings has been reported to be a very rare event in native areas (Nobel 1988; Mandujano et al. 1998). However, in both studied introduced sites, seedling recruitment is larger than vegetative reproduction by cladodes (Vilà and Gimeno 2001). The phenology of

the two species is similar. The flowering and fruiting seasons occur from May to July.

Fruit production is high in *Opuntia* spp. Fruits are berries rich in water and sugars (Bravo-Hollis 1978). Each fruit contains on average 176 ± 8 seeds for *O. maxima* and 110 ± 6 for *O. stricta* ($n = 32$). The seeds are hard coated, flat and round and measure 0.41 ± 0.007 cm and 0.42 ± 0.005 cm in diameter ($n = 20$), respectively. When fruits ripen, they fall to the ground and are consumed by dispersers and predators. The seeds are dispersed by wild boars and by winter migratory birds such as thrushes (*Turdus philomelos*) and starlings (*Sturnus vulgaris*).

We distinguished between fruit and single-seed predation. We examined two components of fruit predation: the probability of fruit detection (= probability of the fruit being encountered and seeds consumed) and the probability of seed exploitation (= seeds predated/total number of seeds per fruit). Predated seeds were those with a hole in them. We recognized that a fruit was detected when it had been bitten and the seed predator had left a pile of chaff next to the fruit. Single-seed predation refers to the exploitation of single seeds dropped on the ground by bird dispersers. We have observed that seeds from wild boar scats are also predated within one month after deposition. However, seed predation after dispersal by wild boars was too difficult to simulate experimentally.

Study sites and species abundance

The study site was located in the Parc Natural del Cap de Creus (Catalonia, Spain). Like other European Mediterranean regions, during the last few decades Cap de Creus has experienced great changes due to tourism, an increment of disturbances (fire, housing development), crop abandonment and a concentration of population along the coast line (Debussche et al. 1998). The climate is Mediterranean with cool, wet winters and warm dry summers. Mean monthly temperatures of the coldest (January) and hottest (August) months are 4 °C and 21 °C, respectively. Mean annual precipitation is 600 mm. The soils are acidic loamy sands (Vilà 1996). The vegetation is mainly dominated by old terraced olive and vineyard groves, colonized by sclerophilous shrublands and a forested pine woodlands (Franquesa 1989). On average, more than 9% of the Park is occupied by terraced olive groves, which have been abandoned since the sixties due to the tourist boom (Folch 1988).

We studied fruit and seed predation of *Opuntia maxima* in Selva de Mar (SM) and *O. stricta* in Port de la Selva (PS). The two study sites (3°13' E, 42°18' N) are invaded old olive groves, three km apart. In SM the vegetation is dominated by *Lavandula stoechas* (31%) and *Olea europaea* (27%). In this site there are 592 ± 154 ($n = 12$) *O. maxima* patches/ha that cover 2.3% of the ground. In PS the vegetation is dominated by *Brachypodium retussum* (27%) and other grasses (22%), in this site olive trees represent 20% of the vegetation cover. Density of *O. stricta* in PS is 2020 ± 640 ($n = 14$) patches/ha and cover 5.5% of the ground.

Differences in fruit detection and seed predation between communities were also studied in the most common communities of the Park: olive groves, pinion pine (*Pinus pinea*) woodlands and shrublands. An extensive survey revealed that 29.3% of the areas invaded by *O. maxima* are abandoned olive orchards and that pine woodlands are the least (2.8%) invaded community type. In contrast, a 36.3% of the area invaded by *O. stricta* are pine woodlands (Vilà *et al.* unpubl. data). There were three replicates of each community type at three independent localities (Mont-Roses, Taula dels Lladres and Sant Sebastià) that were more than 2 km apart. In each locality, each community type was located more than 100 m from the other type. These communities were selected at a distance of at least 1 km from the previously described invaded olive orchards sites and any reproductive *Opuntia* plant to avoid differences in predator attraction due to differences in seed abundance. Using the point intercept method conducted with 8 randomly placed 25 m long transects we estimated that in olive groves olive tree cover was on average (\pm s.e.) $20.8 \pm 0.7\%$ and grass cover was $26.7 \pm 9.4\%$. In pine woodlands the pine canopy cover was $71.4 \pm 18.5\%$. The shrublands presented a dense vegetation cover, dominated by *Erica arborea* ($35.2 \pm 6.3\%$) and *Lavandula stoechas* ($18.8 \pm 6.6\%$).

Fruit predation

A fruit enclosure experiment was conducted to find out the main agents of fruit predation between microsites within olive groves. The microsites were selected according to the vegetation cover most representative of this community type: beneath olive trees, beneath adult *Opuntia* and in open areas. Each experimental unit comprised two enclosure treatments that were used to identify and quantify the predators. The

enclosure treatments were:

1. Invertebrate access only: a fruit was placed inside a 5 mm wire mesh cage (15 cm \times 15 cm \times 15 cm). Fruits were therefore available to invertebrates only.
2. Small mammal and invertebrate access: a fruit was placed in the centre of a 2-cm wire mesh cage (15 cm \times 15 cm \times 15 cm) to prevent it being accessible to a bird beak. We are familiar with the aspect of fruits consumed by birds (fruits smashed into pieces) and none of our fruits inside the cage had this aspect. Fruits were available to small mammals (mice and voles) and invertebrates but not to large mammals (rabbits, feral pigs) (Vilà and Gimeno, unpubl. data).

In November 1998 six experimental units with *O. maxima* fruits were placed in each of the three microsite types in SM and eight experimental units with *O. stricta* fruits in three microsite types in PS. Each experimental unit was placed at least 5 m apart from the next. Enclosure treatments within an experimental unit were randomly placed in a 1.5 m \times 1.5 m area. The fruits came from randomly selected plants from the same site where the experiment was performed. In total we collected 36 fruits of *O. maxima* in SM (3 microsite types \times 2 enclosure treatments \times 6 replicates) and 48 fruits of *O. stricta* in PS (3 microsite types \times 2 enclosure treatments \times 8 replicates). Fruits were visited at irregular times during 5 months and we recorded if the fruits had been bitten and their seeds predated. In April 1999, when the fruits were already dry, we collected them and counted the number of intact and predated seeds. We are confident that our estimation of the proportion of seeds predated is correct, because the number of seeds/fruit in intact fruits was not significantly different from the sum of predated and not predated seeds/fruit ($F_{1, 38} = 0.27$, $p = 0.61$). To evaluate the effect of the enclosure treatment and microsite on the percentage of predated seeds per fruit we applied a two-way ANOVA for each species after arcsin transformation of the data.

In October 1999 we set up another experiment to check for differences in fruit predation between species in different community types. Because the first experiment demonstrated that loss attributable to invertebrates was null, we only carried out the test for small mammal access, namely fruit inside a 2 cm wire mesh cage as described above. In total we used 108 fruits (3 localities \times 3 community types \times 2 species \times

6 experimental units). Fruits were visited at irregular times over 5 months to check for seed predation. In March 2000 we collected the fruits that had been preyed upon to count the number of intact and predated seeds.

A log-linear model (Zar 1984) was applied to compare if fruit detection was affected by: locality, community type, species and the combination of these variables. We chose to ignore higher-order interactions because of the difficulty of interpretation. Differences in the percentage of predated seeds per fruit according to community and species were compared by a two-way ANOVA after arcsin transformation of the data.

Single-seed predation

We evaluated the predation that might occur following bird transport of seeds. We conducted an experiment that sought to simulate the dispersal of *Opuntia* seeds that come from bird scats and are deposited in different microsites within an olive grove. Seeds were individually cemented with glue to 25 cm long pieces of nylon fishing line with the opposite end of the line tied to a wire stake flag placed in the ground. The seeds were carefully lowered onto the ground. These seeds were collected from fresh fruits in the same area of study so as not to alter the seed pool of the study site. At each site and for each species we placed groups of 5 seeds in 10 microsites of each type (3 microsite types \times 5 seeds \times 10 replicates = 150 seeds). Seeds within a group were placed from 20 to 40 cm apart and groups of seeds were at least 5 m far from the closest one. The experiment was initiated in October 1998 and seed removal was supervised after 4, 10, 22, 37, 52, 78, 100 and 119 days. Microsite differences regarding the number of predated seeds at the end of the experiment were analysed with a χ^2 analysis. Heterogeneity in seed survival curves was tested by the Gehan-Wilcoxon test (Pyke and Thompson 1986).

A similar experiment was carried out in the three community types where we conducted the predispersal seed predation experiment. In each community there were 10 replicates of three seeds for each species (3 localities \times 3 community types \times 2 species \times 3 seeds \times 10 replicates = 540 seeds). All seeds used were collected from randomly selected fruits in invaded areas nearby. The test was initiated in February 1999 and it was checked for seed removal after seventy days. A log-linear model (Zar 1984) was ap-

plied to compare the effects of locality, community type, species and the combination of these variables on the proportion of predated seeds per fruit. As for fruit detection, we ignored second order interactions.

Results

Fruit predation

No seed predation was detected in the 5mm wire mesh cages. Only small mammals preyed upon *Opuntia* seeds. For *O. maxima* 83.3% of fruits beneath adult plants and 66.7% in the open were detected. Beneath olive trees all fruits were detected. For *O. stricta*, all the fruits in the open remained intact while 50.0% and 37.5% were detected beneath adult plants and olive trees, respectively.

Once a fruit was detected, a significant amount of seeds were predated ($53.9 \pm 6.7\%$ seeds/fruit for *O. maxima* and 13.3 ± 8.9 for *O. stricta*) (Figure 1). Rodents were responsible for seed predation. The presence of seed coats on site left after seed embryos had been eaten allowed us to distinguish seed predation by rodents from seed-predation by insects (Bond and Breytenbach 1985). Rodent activity was evident from the presence of piles of seed chaff next to the bitten fruit. Seed predation was not significantly different between microsites ($F = 3.95$, $p = 0.5$ for *O. maxima*, $t = 1.77$, $p = 0.1$, for *O. stricta*) (Figure 1).

Patterns of fruit detection between communities were characterised by considerable variation (Figure 2, Table 1). There was no fruit predation in pine woodlands and thus, this community type was not added to the analysis. There were no significant differences between fruit predation in shrublands and olive groves in Sant Sebastià but it was lower in shrublands in the other two localities. On average, *O. maxima* fruits were preferred to *O. stricta* fruits ($38.9 \pm 36.0\%$ detected versus $27.8 \pm 27.2\%$) but this was highly variable between localities.

Seed predation was higher in *O. stricta* ($86.5 \pm 4.1\%$) than in *O. maxima* ($72.3 \pm 3.0\%$) ($F = 5.69$, $p = 0.026$). There were no significant differences between olive groves and shrublands ($F = 1.87$, $p = 0.18$) (Figure 3). The interaction species \times community was not significant ($F = 0.32$, $p = 0.08$).

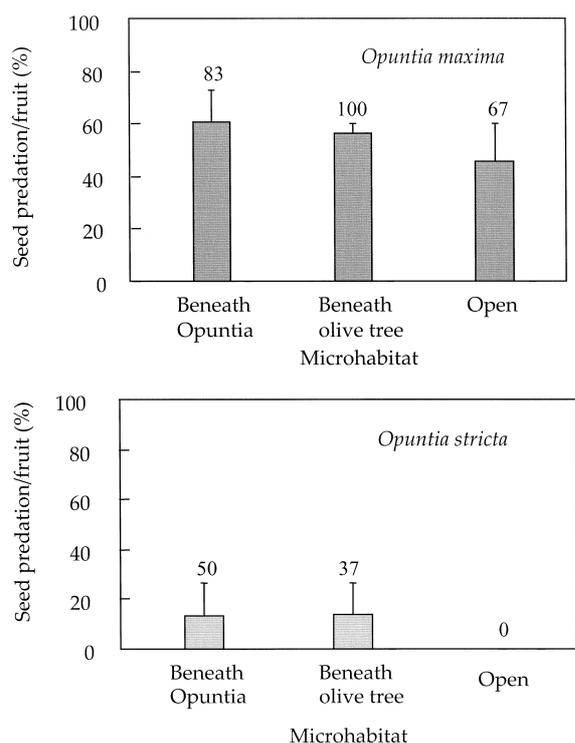


Figure 1. Percentage of seeds predated per fruit by small mammals for *O. maxima* and *O. stricta* in three microsites within invaded olive groves. Values on top of the bars represent the percentage of detected fruits inside the enclosures. (See text for a detailed explanation of fruit transplant enclosures). Error bars represent \pm SE.

Table 1. Log-linear analysis of the effect of locality, community type and *Opuntia* species on the percentage of fruits detected.

Source of variation	df	χ^2	p-value
Locality (L)	2	233.01	0.000*
Community (C)	1	10.99	0.001*
Species (S)	1	10.99	0.001*
L \times C	2	68.78	0.000*
L \times S	2	19.83	0.000*
C \times S	1	0.02	0.88

Single-seed predation

Single-seed predation was very intense during the first 40 days in which 56% seeds of *O. maxima* and 28% of *O. stricta* disappeared. At the end of the experiment 74% of *O. maxima* seeds and 55% of *O. stricta* seeds had been predated (Figure 4).

There were significant differences in the percentage of *O. maxima* single-seed predation between microsites ($F = 6.63$, $p = 0.005$). Single-seed predation

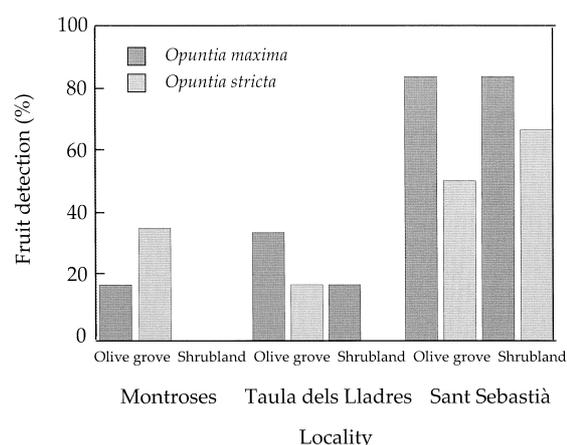


Figure 2. Fruit detection of *O. maxima* and *O. stricta* in different localities and community types. None of the fruits placed in pine woodlands were detected.

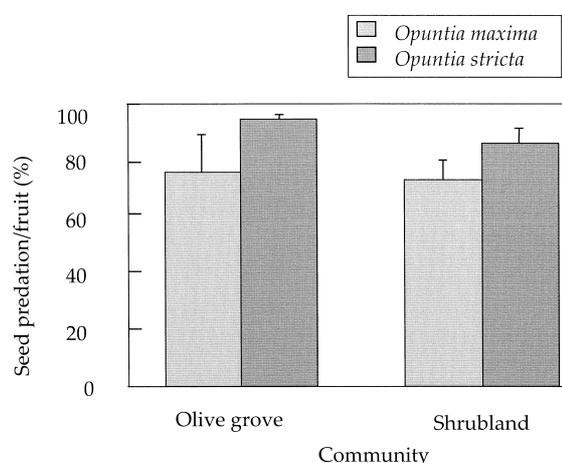


Figure 3. Percentage of seeds predated per fruit by small mammals for *O. maxima* and *O. stricta* in olive orchards and shrublands. None of the fruits placed in pine woodlands were detected. Error bars represent \pm SE.

was lower beneath olive trees (52.5%) than in open areas (80.0%) ($p = 0.017$) and beneath *O. maxima* (92.5%) ($p = 0.002$). The temporal pattern of single-seed predation was also different between microsites ($\chi = 14.91$, $p = 0.0006$, $df = 2$, Gehan-Wilcoxon test). Seeds were predated slower beneath olive trees than at the other microsites. In contrast, for *O. stricta* there were not significant differences between microsites regarding the patterns of seed predation ($\chi = 4.29$, $p = 0.12$, $df = 2$, Gehan-Wilcoxon test) and the percentage of predated seeds at the end of the experiment ($F = 0.83$, $p = 0.45$) (Figure 4).

Single-seed predation was significantly different between localities and communities (Table 2). The

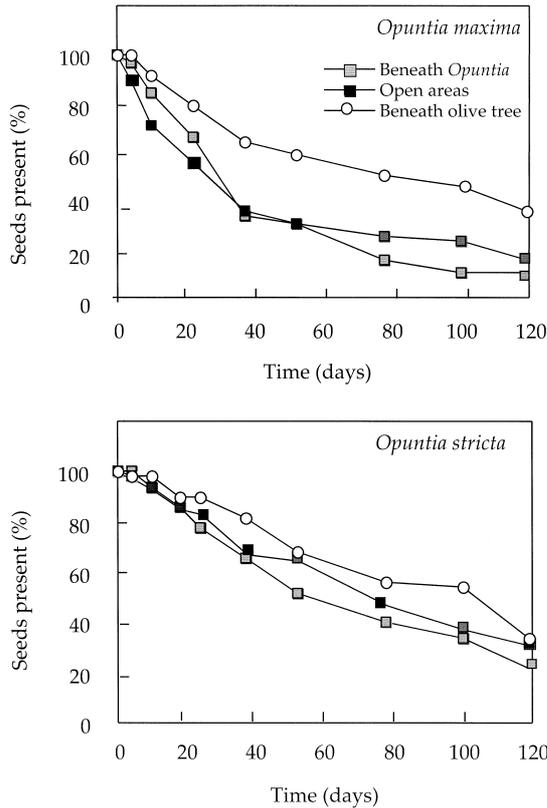


Figure 4. Single-seed predation over time for *O. maxima* and *O. stricta* in three microsites within invaded olive groves.

Table 2. Log-linear analysis of the effect of locality, community type and *Opuntia* species on the percentage of single-seed predation.

Source of variation	df	F	p-level
Locality (L)	2	98.93	0.000*
Community (C)	2	182.73	0.000*
Species (S)	1	2.77	0.96
L × C	4	65.93	0.000*
L × S	2	6.40	0.04
C × S	2	1.30	0.52

percentage of single-seed predation was the lowest in pine woodlands (13.8% for *O. maxima* and 10.0% for *O. stricta*) and the highest in shrublands (56.7%). On average, there were no significant differences between species (Figure 5).

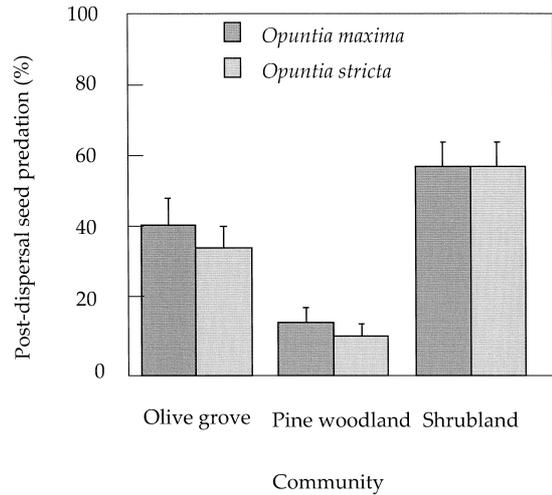


Figure 5. Single-seed predation for *O. maxima* and *O. stricta* in different community types. Error bars represent \pm SE.

Discussion

Our results demonstrate that predators are small mammals. Although we did not carry out trapping tests we believe that the mouse *Apodemus sylvaticus* (Muridae) was the main predator. This species is a generalist granivore very commonly found foraging the ground in Mediterranean vegetation (Herrera 1984; Verdú and García-Fayos 1996; Hulme 1998). This mouse tends to form chaff piles like the ones we saw around *Opuntia* fruits. In invaded areas, mice can consume more than 80% of the seeds produced by *Opuntia*.

Seed losses by predation are very similar between species and they were higher in invaded than in non-invaded areas. If we had conducted our study only in invaded areas, our conclusions would have been different. Fruit predation was higher in the sites invaded by *O. maxima* than in the sites invaded by *O. stricta*. The proportion of predated seeds within a single fruit can be estimated by the average proportion of detected fruits multiplied by the average proportion of predated seeds in the detected fruit. According to this calculation, in invaded olive groves, 45% of *O. maxima* seeds were predated while only 4% of *O. stricta* were. However, these differences could be density dependent. Indeed, plant density at the *O. stricta* stand (2020 ± 640 patches/ha) was higher than in the *O. maxima* stand (592 ± 154 patches/ha) and these differences could have an effect on mice satiation. Differences could also be related to variation in predator activity between old olive groves. As we also con-

ducted fruit and seed transplant experiments in non-invaded areas, we are certain that species differences between communities are not biased by density dependent factors. *Opuntia maxima* fruits were preferred to *O. stricta* fruits but predators did not distinguish between seeds. Differences in fruit preference could be due to the larger fruit size and sweeter taste of *O. maxima* compared to *O. stricta* (Vilà & Gimeno, pers. obs.). Other studies have shown that differences in fruit quality in exotic species act as cues for fruit preference, but other criteria are also relevant (Vilà and D'Antonio 1998).

As for native species, the spatial variability in seed predation is high and it is very common to find non-consistent spatial rates of seed predation (Wilson and Whelan 1990). The interaction locality \times community found for *Opuntia* highlights this generalisation. Furthermore, spatial patterns of seed predation do not match patterns of invasion. For example, we expected that microhabitats and communities which tended to be the least invaded had the highest predation and vice versa. However, this trend was not consistent. For example, despite the high fruit and seed predation beneath *Opuntia*, seed predation is not strong enough to mask patterns of seed rain and abundance of seedlings found in this microhabitat (> 36% of the total). Fruit predation is the lowest in open areas, but few seedlings (< 10%) recruit in this microhabitat (Vilà and Gimeno 2001). Similarly, patterns of fruit and seed predation between communities do not always match patterns of invasion. For instance, predation is the lowest in pine woodlands for both species. Pine woodlands are the most invaded communities by *O. stricta* but the least invaded communities by *O. maxima* (Vilà et al., unpubl. data). Although further studies should investigate the ultimate ecological factors (e.g. shading, predator abundance, plant cover, presence of other plant species producing consumable seeds) that explain patterns of seed predation at different spatial scales, these results indicate that predation rates alone are a weak predictive tool to determine differences in invasibility between communities.

For long-lived perennials losses due to seed predation do not necessarily have an impact on population recruitment (Andersen 1989). Furthermore, although native generalist herbivores consume alien plants, natural enemies seem to play a low biotic resistance to plant invasions than previously thought (Maron and Vilà 2001). The role of seed predation by vertebrates in controlling *Opuntia* invasion remains unknown. Several studies have shown that seed pre-

dation by mice and voles translates into reduced seedling recruitment (Maron and Simms 1997; Ostfeld et al. 1997). However, the role of seed predation in *Opuntia* invasion will depend on whether seedling recruitment is seed or safe-site limited. If it is seed limited, seed reduction will decrease the seed bank and ultimately seedling recruitment. In contrast, if it is safe-site limited, seed removal from unsuitable sites will have a minimal effect on seedling recruitment.

Overall, although seed predation is intense, *Opuntia* continues to invade tree stands by cladode and seedling recruitment (Vilà and Gimeno 2001). Mathematical models have found that an impact higher than 90% seed loss in alien species is needed to reduce population growth (Noble and Weiss 1989; Hoffmann and Moran 1998; Parker 2000). These studies indicate that once the exotic species has established itself, the ability of seed predators to suppress the exotic plant population may be limited. Furthermore, our results suggest that the potential for seed predation might be even lower in founder populations because more than 75% of seeds dispersed to non-invaded areas escaped from predation. To have a broad picture of community invasibility to *Opuntia*, future studies should focus on differences between communities as regards dispersal patterns, seed load and microhabitat effects on seedling recruitment.

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