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ORIGINAL PAPER

# Integration of invasive *Opuntia* spp. by native and alien seed dispersers in the Mediterranean area and the Canary Islands

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**Abstract** The success of many alien plant species depends on mutualistic relationships with other species. We describe the assemblage of seed dispersers on three species of alien *Opuntia* invading Mediterranean and Macaronesian habitats, and examine the quality of such plant-animal interactions. We identified vertebrates consuming *O. maxima*, *O. dillenii* and *O. stricta* fruits by direct observation and collecting droppings and pellets. Phenology of the alien species, as well as that of coexisting native species, was monitored for an entire year. Germination tests of ingested and non-ingested seeds were performed both in the greenhouse and in the field. Seed coat thickness and viability were also measured for all treatments. A great variety of taxa, including reptiles, birds and mammals actively participate in the seed dispersal of *Opuntia*. Phenology of *Opuntia* fruits in Menorca and Tenerife overlaps with only a few native fleshy-fruited plants present in the study areas, which suggests an advantage for the invader. Most seeds germinated during the second year of the experiment, independently of the effect produced by the dispersers' guts. We found great variation in the germination percentage of *Opuntia* after gut passage and in the effects of ingestion on seed coat thickness. Seed viability was somewhat reduced after gut passage compared to manually depulped seeds. Our results show how different *Opuntia* species are integrated into native communities by means of mutualistic interactions, with both native and alien dispersers. Although with heterogeneous effects, either type of disperser potentially contributes to the spread of these alien cacti in the recipient areas.

**Keywords** Alien species · Frugivores · Plant invasion · Seed germination · Seed viability

## Introduction

Mutualistic relationships, especially those involving plants and their pollinators and seed dispersers, are particularly important to secure species spread

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(Richardson et al. 2000; Mitchell et al. 2006). This biotic facilitation seems to be as important as the biotic resistance of the native communities to invasion, and could speed the impact of alien species on the recipient ecosystems. The biotic resistance hypothesis (Elton 1958) and the enemy-release hypothesis (Keane and Crawley 2002) have been the central paradigms in the study of biological invasions until recently. The former states that invasion risk decreases when local communities increase resource use, whereas the latter argues that the establishment of invasive species is enhanced by the absence of their natural enemies (herbivores, predators or pathogens), outside their original distribution ranges. Thus, in recent times, the influence of the biotic interactions in determining species success in the introduced communities has been one of the major topics in invasion biology.

Global scenarios of biodiversity predict that Mediterranean ecosystems will be exposed to more severe biological invasions in comparison with other ecosystems (Sala et al. 2000). In particular, island ecosystems are especially vulnerable due to the intrinsic traits of many island biotas, such as the existence of unsaturated communities and the proportionally lower native diversity (Hulme et al. 2008 and references therein). As a consequence, the relatively high proportion of alien species on islands, especially plants, most likely exerts additional pressures upon already threatened island endemics (Hulme 2004), although extinction caused by competition from exotic plants is much less frequent than animal extinctions caused by exotic species predation or pathogen action (Sax et al. 2007; Sax and Gaines 2008).

There are some studies assessing the risk posed to island ecosystems by plant invaders (see Lloret et al. 2004; Gritti et al. 2006; Hulme et al. 2008; Vilà et al. 2008), and the strategies they use to spread and become established (Bourgeois et al. 2005; Lloret et al. 2005; Lambdon and Hulme 2006; Traveset et al. 2008a). In the case of some invasive plants (e.g. *Opuntia* spp.), one of the key factors is that they take advantage of the assemblage of seed dispersers present in the invaded community. But even more important than the identification of the frugivores consuming alien fruits is the evaluation of such interactions and the effects of vertebrate guts on the seeds in terms of viability or germination capacity. There are few detailed studies of the relative contribution of different frugivore species (native and non-native) consuming alien plants (but see Renne et al. 2002; Cordeiro et al. 2004).

Many alien cacti species have been reported in Europe, the genus *Opuntia* being the one with the most species recorded. Spain, in particular, is the European country with most cacti species recorded (Essl and Kobler 2008). Although vegetative multiplication involving short-distance dispersal processes is common in the genus, sexual reproduction is also very important if we consider mid and long-distance events facilitated by seed dispersers that consume their fruits. When evaluating the role of human beings in species establishment, it has been found that deliberately introduced species show higher naturalization percentages than accidentally introduced taxa (Ööpik et al. 2008), and this may be true in the case of *Opuntia*.

The assemblage of seed dispersers in places where *Opuntia* species are native is very diverse. In island systems, such as the Galápagos, seed dispersal in this genus is associated with finches and possibly also with mockingbirds, tortoises, iguanas, native rodents and introduced black rats (Racine and Downhower 1974; Grant and Grant 1981). In mainland environments, such as the Chihuahuan Desert in North America, this process depends on species such as coyotes, common pigs, mule deer and northern ravens (Mandujano et al. 1997). Other species like jackrabbits, eastern cottontails and several small mammals have been also recorded as seed dispersers of *Opuntia* species in their native American range (Timmons 1941; Baskin and Baskin 1977; Montiel and Montaña 2000). Moreover, large mammals such as the white-tailed deer, pronghorn, bighorn sheep and bison consume the fruits of *Opuntia* (Janzen 1986). Even ants in the genus *Pogonomyrmex* have been found to act as main dispersers of *Opuntia* seeds in the San Luís Potosí highlands in México (Vargas and González 1992).

Where *Opuntia* spp. have been introduced, different seed dispersers have been identified: crows, baboons and elephants in South Africa (Hoffmann et al. 1998; Dean and Milton 2000; Reinhardt and Rossouw 2000), wild boars and thrushes in the Spanish Mediterranean region (Gimeno and Vilà 2002), and lizards and northern ravens in the Canary Islands (Valido 1999; Nogales et al. 1999). In the

Arabian Peninsula, baboons are important dispersers of the naturalized *O. dillenii* and *O. maxima* (Miller and Cope 1996).

The main goal of this study is to identify seed dispersers of introduced *Opuntia* spp. in introduced Mediterranean and Macaronesian habitats, focusing on the quality of such mutualistic interactions. The specific aims and predictions are:

1. To determine the assemblage of *Opuntia* spp. seed dispersers. We expect that the most generalist species in each study area will include fruits and seeds of these alien species in their diets (Nogales et al. 1999; Richardson et al. 2000; Renne et al. 2002; Valido et al. 2003). The probability of interactions with various guilds of seed dispersers (alien or native) is expected to be high due to the fact that we study alien species introduced into many different ecosystems (mainland, and continental and oceanic islands).
2. To describe the phenology of the native fleshy-fruited plants and the *Opuntia* species. We expect that in areas where *Opuntia* fruits for longer periods than at other sites, the probability of having a larger assemblage of dispersers is higher.
3. To evaluate the quality of the interactions (by examining seed coat thickness, viability and germination), which may depend both on the identity of the disperser and the plant species. We predict heterogeneous responses to ingestion by the different vertebrate species (Traveset and Verdú 2002).

## Methods

### The *Opuntia* species

*Opuntia* spp. are non-columnar Cactaceae that were introduced into Europe from America at the end of the fifteenth century and the beginning of the sixteenth century (Barbera et al. 1992). They are included in the list of the 100 most problematic invasive species around the world (http://www.issg.org/database). *Opuntia* spp. have been used for consumption, livestock forage, fencing, production of a red dye obtained from the cochineal beetle (*Dactylopius coccus*), and as ornamental plants. *Opuntia* spp. are CAM plants with a highly efficient use of water, which adds to their success in invading Mediterranean and semiarid areas (García de 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* have their leaves reduced to spines, which prevents water loss. The species in this study have flowers 5–10 cm in diameter, which are sessile and solitary and their fruits are berries of 4-8 cm. Vegetative multiplication is common in the genus; usually cladodes break off and root next to the parental plant and form conspicuous patches.

Of the three study species, *Opuntia maxima* often presents a height of around 3 m, whereas *O. dillenii* and *O. stricta* do not attain more than 2 and 1 m, respectively. The recruitment of sexually derived *Opuntia* spp. seedlings is reported to be a very rare event in native areas (Nobel 1988; Mandujano et al. 1998). However, in introduced areas, seedling recruitment can be greater than vegetative reproduction by cladodes (Vilà and Gimeno 2001). Fruit production is high in all three species and these are rich in water and sugars (Bravo-Hollis 1978). Each fruit contains on average 100-200 seeds, which are hard coated, flat and round, measuring approx. 4 mm in diameter (Vilà and Gimeno 2003). Nowadays, *O. maxima* is a cultivated species absent in wild conditions in Mexico, its original distribution area.

### Study areas

We conducted the study on two islands, an islet and in two mainland locations (Fig. 1). On each of the islands (Tenerife and Menorca) we performed the observations and collected material in two areas of approximately 0.5 ha. On the islet of Benidorm we sampled over 0.5 ha whereas in Cap de Creus, the area studied was approximately 1 ha at each of the two study sites (Port de la Selva and Selva de Mar).

#### *Tenerife, Canary Islands*

Tenerife is the largest (2,034 km$^2$) of the Canary Islands, an archipelago of volcanic origin. Fieldwork was carried out in *Teno Bajo* (28°21′18.83″N; 16°54′19.13″W), at the northwest of a strongly

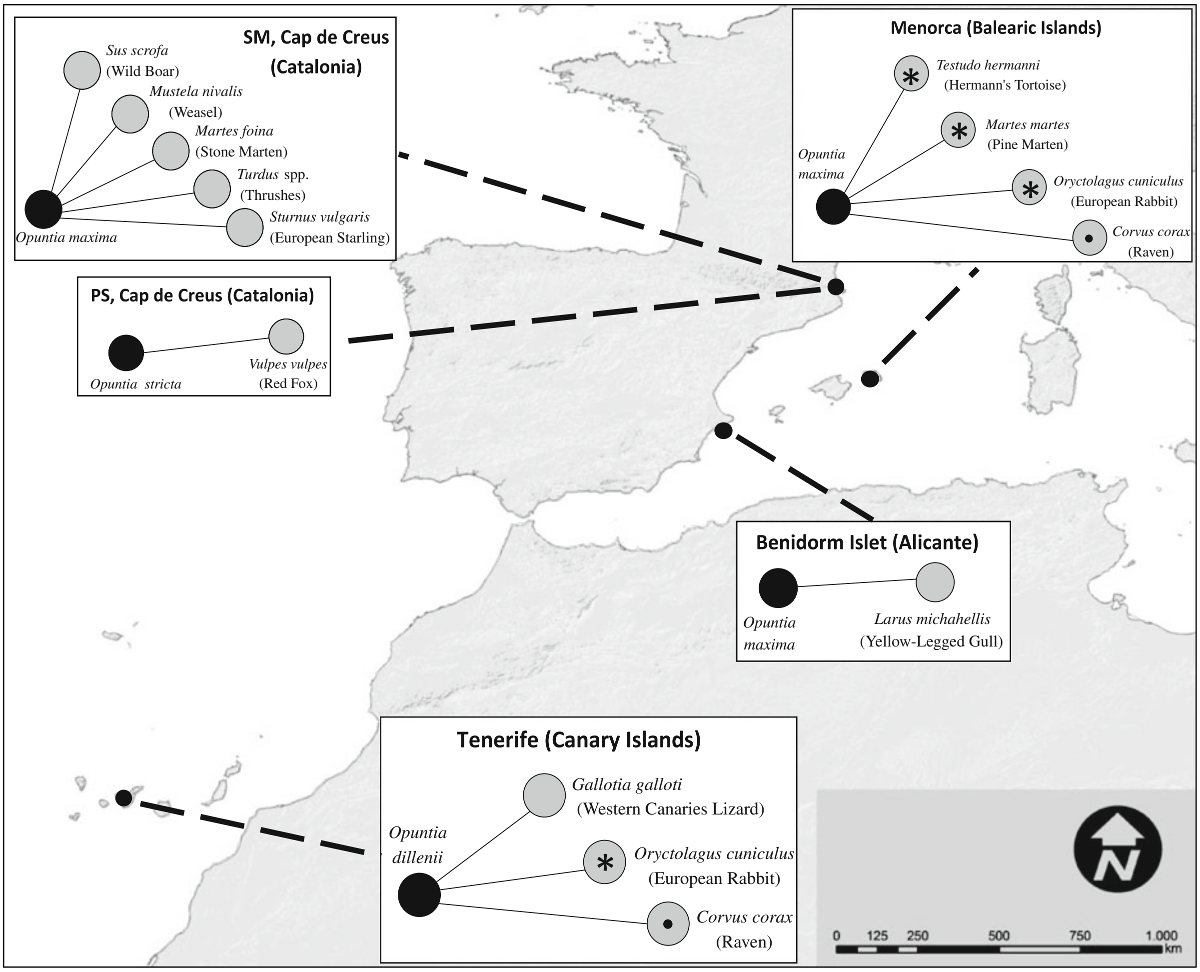


**Fig. 1** Sites, *Opuntia* species and seed dispersers included in this study. Plant species are indicated as *black nodes* and seed dispersers as *grey nodes*. The raven (*Corvus corax*), important in the past but quite rare nowadays is indicated with a *black dot*. Non-native seed disperser species are marked with an *asterisk* (*). The nomenclature of the different taxa cited in this work follows Fauna Ibérica (http://iberfauna.mncn.csic.es) and Flora Ibérica (http://www.floraiberica.org). *SM* Selva de Mar; *PS* Port de la Selva

eroded massif with deep seaward ravines (Walter and Schmincke 2002). The climate is xeric, with an annual mean temperature of *c.* 21°C and 200–300 mm of mean annual rainfall. The study sites are located in rocky coastal habitats, bearing a high number of endemic plants. The vegetation consists of low and sparse xerophytic shrubs, the predominant species being *Rubia fruticosa, Plocama pendula, Euphorbia* spp., *Withania aristata, Periploca laevigata* and the alien *Opuntia dillenii* (Valido et al. 2003). This alien has a density of *c.* 1200 indiv./ha in most of the invaded area. Our density estimation included both young and adult individuals.

### *Menorca, Balearic Islands*

Menorca is the second largest (702 km$^2$) of the Balearic Islands, an archipelago of continental origin. Fieldwork was carried out in S'Albufera d'Es Grau Natural Park (39°56′24.98″N; 4°15;6.31″E), also near the coast. The climate here is typically Mediterranean, with an annual mean temperature of *c.* 17°C and a mean annual rainfall of 573 mm. The study site was located in Mediterranean shrubland mixed with abandoned fields. The vegetation is dominated by *Pistacia lentiscus*, *Olea europaea*, *Phyllirea* spp., *Ampelodesmos mauritanica* and herbaceous species such as *Daucus carota*, *Foeniculum vulgare* and *Scolymus hispanicus* (Fraga et al. 2004). The alien *O. maxima* attains a high density (*c*. 200 indiv./ha) mainly around old houses. Our density estimation included both young and adult individuals.

### *Benidorm islet, Alicante*

The islet of Benidorm is a small (6.5 ha) limestone outcrop located approximately 3 km off the coast of the city of Benidorm (38°30′N, 0°08′E) in the province of Alicante (SE Iberian Peninsula). Mean annual rainfall is ca. 300 mm and annual temperature fluctuates between 12°C in January–February and 27°C in July–August. Vegetation is composed of halonitrophilous annual species and small shrubs typical of an arid Mediterranean island, such as *Lycium intricatum*, *Withania frutescens*, *Ephedra fragilis*, *Salsola oppositifolia* and *Atriplex prostata* with some scattered wild olives *Olea europaea* and abundant exotic vegetation, mostly *O. maxima*. Although some *Opuntia* removal has been carried out on the islet, the density of *O. maxima* is still very high (40% of coverage).

### *Cap de Creus, Catalonia*

The study was conducted in Cap de Creus Natural Park (NE Iberian Peninsula). The climate is Mediterranean, with cool, wet winters and warm dry summers. Mean temperatures of the coldest (January) and hottest (August) months are 4 and 21°C, respectively. Mean annual precipitation is 600 mm. The soils are acidic loamy sands. The vegetation is mainly dominated by old terraced olive-groves and vineyard, colonized by sclerophyllous shrublands and afforested pine woodlands. We studied *O. maxima* in Selva de Mar (SM, hereafter) and *O. stricta* in Port de la Selva (PS, hereafter). The two sites (3°13E, 42°18N) are old olive-groves, 3 km apart. In SM the understorey vegetation is dominated by *Lavandula stoechas* and *O. maxima* (2.3% of coverage). In PS the understorey vegetation is dominated by *Brachypodium retussum*, other grasses and *O. stricta* (5.5% of coverage). As on the islands, in the Spanish mainland, *Opuntia* species are very common in highly disturbed areas close to old houses and in abandoned fields, not always behaving as an invasive species.

### Identification of the assemblage of seed dispersers and plant phenology

In each study area we performed both direct censuses vertebrate activity on *Opuntia* plants and collected animal droppings except on Benidorm islet, where gull pellets were collected weekly during fruit ripening to extract *O. maxima* seeds.

We observed *O. dillenii* plants in Tenerife for 139 h, *O. maxima* plants in Menorca for 25 h and *O. maxima* and *O. stricta* in Cap de Creus for 10 h each. Differences in censusing time were due to the differences in manpower and fruit phenology. For example, in Cap de Creus and Menorca, *O. maxima* fruits are on the plant for less than 3 months while on Tenerife *O. dillenii* fruits are present all year long. In Tenerife, rabbit and lizard droppings (previously known to consume *Opuntia* fruits) were collected every 3 months over a complete year (Table 1). In Menorca, droppings of the potential dispersers (rabbits, tortoises and pine martens) of *O. maxima* were also collected every 3 months for a complete year (Table 1). On the two islands, native seeds were quantified in the collected droppings. In Cap de Creus, droppings of wild boars, red foxes, weasels, stone martens, starlings and thrushes were collected weekly during fruit ripening. Despite ravens occasionally consuming *Opuntia* fruits on Tenerife and Menorca (Nogales et al. 1999; O. García, pers. comm.), we could not obtain any pellets from this species, probably because it is currently rare.

To assess how the flowering and fruiting periods of *Opuntia* overlapped with those of the other plant species in the Tenerife and Menorca communities, we monitored flower and fleshy-fruit crops in 10 plants per species every 2 months.

### Germination tests

From 2006 to 2008 we performed a greenhouse germination assay with the seeds obtained from the droppings and non-ingested seeds depulped by hand (control), following the protocol described by Traveset and Verdú (2002). Seeds from all areas except Benidorm islet were planted at Tagoro (Tenerife Island; 300 m a.s.l.). Control seeds came from a bulk of fruits taken from a minimum of 20 randomly chosen plants in each study area. Each seed was independently sown ≈ 5 mm deep in a 4 cm$^2$ pot

**Table 1** Seeds of *Opuntia* spp. found in droppings of the different dispersers in some study areas

| Study area | Disperser | Seed number per dropping or pellet (mean ± SE) | Percentage frequency in droppings or pellets | Number of droppings or pellets analysed | Percentage of undamaged seeds | Total seeds found |
|---|---|---|---|---|---|---|
| Tenerife (Canary Islands) | *Gallotia galloti* | 0.41 ± 0.03 | 21.1 | 1,235 | 72.3 | 501 |
| | *Oryctolagus cuniculus* | 0.12 ± 0.01 | 9.9 | 1,600 | 68.4 | 190 |
| Menorca (Balearic Islands) | *Testudo hermanni* | 27.13 ± 8.65 | 56.5 | 23 | 91.7 | 624 |
| | *Martes martes* | 26.18 ± 17.65 | 36.4 | 11 | 95.8 | 288 |
| | *Oryctolagus cuniculus* | 0.11 ± 0.01 | 7.1 | 1,600 | 93.5 | 168 |
| Benidorm Islet (Alicante) | *Larus michahellis* | 407.3 ± 18.97 | 100 | 55 | – | 18860 |

For Cap de Creus, we do not have detailed information about the collected seeds used in the germination experiments. On Benidorm islet, percentage of undamaged seeds was not estimated

using a standard substrate (50% turf: 50% gardening soil). Pots were watered every 2 days from October to March simulating the rainy season. Germination was monitored every 2 days. Germination was defined as the emergence of any part of the seedling from the soil surface. We used the accumulation of seed emergence every 5 days to calculate speed of germination.

The germination experiment for Benidorm seeds was carried out in Valencia; in this case, seeds were sown in groups of ten in a greenhouse located close to sea level, and were watered automatically twice a week and monitored for germination once a week. Seeds were chosen randomly from a common pool of seeds coming from fruits chosen randomly from at least 10 different plants. Control seeds were air-dried at room temperature before sowing, so that conditions were as similar as possible compared to seeds coming from pellets, and speed of germination was calculated on a weekly basis.

In addition, on the two islands and the islet we planted ingested and control seeds in the areas invaded by *Opuntia*, by placing the seeds 5–20 mm into the soil in autumn. The number of seeds planted was dissimilar due to differences in seed availability (specific numbers are indicated in the results section). Seed germination was followed up for 2 years. The potentially great effect of dispersers in separating seed from pulp has not been tested in the greenhouse or field experiments.

### Assessment of seed coat thickness and viability

Decreased seed coat thickness, due to scarification, following gut passage has previously been documented in other species (e.g. Traveset et al. 2001; Nogales et al. 2005) and this appears to influence seed germination (Traveset 1998, Traveset et al. 2008b). We measured coat thickness ($n = 5$ measures per seed; number of seeds per treatment are indicated in the results section) of seeds collected on Menorca and Tenerife, for each treatment and the controls. For this, we used a dissecting microscope connected to a computer using *Leica DFC* software and *ImageJ* program (http://rsbweb.nih.gov/ij). Seed length was also measured and used as a covariable in the statistical analysis when comparing coat thickness between ingested and control seeds.

Seed viability tests were carried out for each different treatment by staining them with 2,3,5-triphenyl tetrazolium chloride (TTC) (Scharpf 1970; Marrero et al. 2007) to estimate the possible bias caused by seed dormancy in the effect recorded during the germination experiments. Seeds were immersed for 36 h in TTC after soaking them for 48 h in water. A seed was considered to be viable if the embryo turned pink.

### Statistical analysis

We calculated 95% Bayesian credible intervals for seed viability percentages and also mean percentage ratios in the case of germination data. For Markov Chain Monte Carlo simulations (MCMC), we assumed that our data came from a binomial distribution and that the prior distribution of the parameter (e.g. percentage of germinated seeds) was a flat uniform probability distribution ranging between 0 and 1, because we had no previous information on the parameter. By using a flat prior distribution, all the inference is based on our set of data (i.e. on the likelihood), but a posterior probability distribution of the parameter is obtained. We ran three chains with 1,000 iterations for each chain. We tested the hypothesis of equal mean percentage germination ratios by checking whether the estimated credible intervals of the mean ratio included the value 1 or not. The advantage of using credible intervals is that we not only test the statistical significance of the null hypothesis but provide a measure of uncertainty.

Kolmogorov–Smirnov tests were performed to evaluate differences in germination rates between control and ingested seeds. In the case of seed coat thickness, we performed an ANCOVA analysis including seed length as a covariate and applied the Bonferroni correction to avoid spurious results, which were taken into account in the Least Significant Difference (LSD) post hoc analysis. We used SPSS v.15 and WinBUGS 1.4.3 for frequentist and Bayesian analyses, respectively.

## Results

### Seed disperser assemblages

No bird species were directly observed consuming *Opuntia* fruits in Cap de Creus, Tenerife, and Menorca, despite the c. 174 h of direct censusing. However, the analysis of droppings gave us better information on the assemblages of native and non-native frugivores that disperse *Opuntia* seeds (Fig. 1). A minimum of 12 species (2 reptiles, 3 birds and 7 mammals) consumed and dispersed seeds of *Opuntia* spp. While bird and mammal dispersers were distributed over all study areas, reptiles were only present in insular environments (Tenerife and Menorca). Lizards in the Canaries, tortoises and pine martens on Menorca and gulls on Benidorm islet were the dispersal agents that moved the greatest number of seeds (Table 1).

Regarding phenology of the studied *Opuntia* species, their flowering season occurs from May to July (when the spring bloom of most native species has ceased) and the fruiting season from September to December for *O. maxima*, although *O. dillenii* in Tenerife and *O. stricta* in Cap de Creus (PS) have a longer period with ripe fruits. The long persistence of *O. dillenii* fruits is partially due to the fact that vertebrate fruit consumers do not deplete the large crops that this plant produces in the study areas (M. Nogales, pers. obs.). The fruiting peak of this species on this island coincides with that of the endemic shrub *P. pendula* (Rubiaceae), which is dispersed by lizards and birds.

On Tenerife and Menorca, where we conducted the phenology survey, we recorded a different pattern of fruit consumption throughout the year. Lizards and rabbits on Tenerife showed a maximum consumption of *Opuntia* during the spring (164 excreted seeds; $n = 300$ droppings) and summer (92 excreted seeds; $n = 400$ droppings), respectively, although the fruits were available almost all year round. On this island, *O. dillenii* was the third most frequent species ($n = 691$) of the 2835 seeds found in the droppings, after the natives *P. pendula* ($n = 4420$) and *R. fruticosa* ($n = 1840$). On Menorca, in contrast, both fruit availability and consumption of *Opuntia* were more seasonal and *Phillyrea* spp. (42 excreted seeds; $n = 400$) and *O. europaea* (29 excreted seeds; $n = 400$) were found in rabbit droppings, although in lower proportions than *Opuntia* seeds (84 excreted seeds; $n = 400$), which we attribute to the short overlapping fruiting periods: the fruiting peak of *O. maxima* takes place in September, when the fruiting period for these native species begins. Thus, we did not confirm our second prediction in which areas where *Opuntia* fruits for longer periods were expected to have larger assemblages of dispersers. *O. dillenii* has ripe fruits available almost all year round and only lizards and rabbits were found dispersing its seeds; whereas *O. maxima* has shorter fruiting periods in areas such as Menorca or Cap de Creus (SM), showing larger assemblages of vertebrates consuming its fruits.

### Seed germination

Lizards enhanced the germination of *O. dillenii* seeds compared to control seeds on Tenerife (Fig. 2 and Table 2). Furthermore, the lizard digestive effect partially broke the characteristic dormancy of *Opuntia* seeds during their first year (Control: 0.87% and *Gallotia*: 5.65%; $G_1 = 9.29$, $P = 0.002$). When data were analysed over 2 years, however, no statistically significant differences were observed in germination rate between controls and lizard defecated seeds

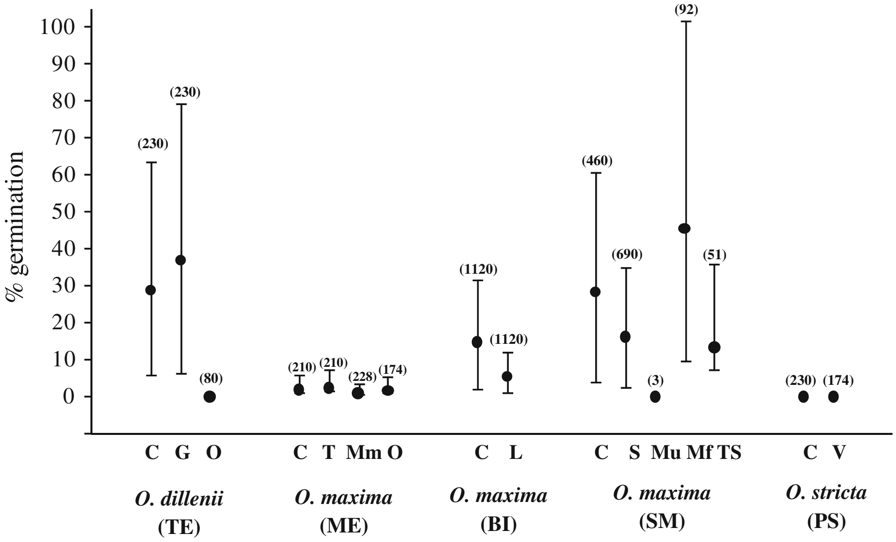


**Fig. 2** Mean (± 95% Bayesian credible intervals) germination percentages for control seeds (C) and seeds dispersed by different animal species (G, *Gallotia galloti*; O, *Oryctolagus cuniculus*; T, *Testudo hermanni*; Mm, *Martes martes*; L, *Larus michahellis*; S, *Sus scrofa*; Mu, *Mustela nivalis*; Mf, *Martes foina*; TS, *Turdus*/*Sturnus*; V, *Vulpes vulpes*) in each study site (TE, Tenerife; ME, Menorca; BI, Benidorm islet; SM, Cap de Creus (Selva de Mar); PS, Cap de Creus (Port de la Selva)). Number of seeds sown in *parenthesis*

($Z = 1.07$, $P = 0.20$). As occurs in other species of *Opuntia*, both control and lizard defecated seeds germinated more frequently during the second year (2005: 3.26% and 2006: 29.13%; $G_1 = 7.06$, $P = 0.008$).

Germination of *O. maxima* seeds from Menorca, including all gut treatments (tortoises, martens and rabbits), was rather low and probably hindered detection of statistical differences among them (Fig. 2). Regarding *O. maxima* from Benidorm islet, seeds ingested by gulls showed a lower percentage of seed germination (Fig. 2 and Table 2) and germination rate ($Z = 1.46$, $P = 0.028$) than control seeds.

Finally, percentage germination of *O. maxima* seeds from Cap de Creus (SM) was rather variable depending on the different gut treatments (Fig. 2). Seeds ingested by stone martens enhanced germination whereas seeds ingested by wild boars and birds germinated in lower percentages than control seeds. No statistically significant differences were noted between seeds eaten by wild boars and birds (Table 2). Regarding germination rate, there was a non-significant trend for control seeds to germinate somewhat earlier than those dispersed by stone martens, and seeds ingested by wild boars somewhat earlier than those dispersed by stone martens (Control vs. *Sus*: $Z = 0.80$ $P = 0.54$; Control vs. *Martes*: $Z = 1.34$ $P = 0.056$; *Sus* vs. *Martes*: $Z = 1.34$ $P = 0.056$). Lastly, no germination was recorded in the following cases: (a) control and fox ingested seeds of *O. stricta* in Cap de Creus (PS), (b) rabbit ingested seeds of *O. dillenii* and (c) weasel ingested seeds of *O. maxima* in Cap de Creus (SM).

Large differences were noted between the germination of control seeds of the different species of *Opuntia*, and between *O. maxima* populations (Table 3 and Fig. 2). Control seeds of *O. dillenii* on Tenerife, *O. maxima* in Cap de Creus (SM) and on Benidorm islet showed the maximum germination (28.8, 28.4 and 14.7%, respectively).

Germination in the field was low and seeds germinated only on Menorca, where a total of 16 seeds germinated [1.5% from a total of 1100 seeds planted (8 *O. maxima* control seeds of 600 planted, 2/250 from tortoises, 2/125 from pine martens and 4/125 from rabbits)], and in Cap de Creus (PS) only 2 *O. stricta* control seeds of 200 planted germinated.

## Seed coat thickness and viability

On Tenerife, lizards and rabbits were not found to have a statistically significant effect on seed coat

**Table 2** Mean percentage germination ratios of *Opuntia* spp. seeds and 95% Bayesian credible intervals to test for equality (ratio = 1) of germination percentage between control and treatment or between pairs of treatments in each study area

| Study area | Compared treatments | n1 | n2 | Mean % ratio | 95% CrI |
|---|---|---|---|---|---|
| Tenerife | Control and *Gallotia* | 230 | 230 | 0.785 | 0.586–1.002 |
| Menorca | Control and *Testudo* | 210 | 210 | 0.996 | 0.186–3.011 |
|  | Control and *M. martes* | 210 | 228 | 3.887 | 0.455–16.433 |
|  | Control and *Oryctolagus* | 210 | 174 | 1.850 | 0.270–6.326 |
|  | *Testudo* and *M. martes* | 210 | 228 | 5.249 | 0.625–20.025 |
|  | *Testudo* and *Oryctolagus* | 210 | 174 | 2.339 | 0.361–7.188 |
|  | *M. martes* and *Oryctolagus* | 228 | 174 | 0.830 | 0.067–3.096 |
| Benidorm Islet | **Control and *Larus*** | **1,120** | **1,120** | **2.748** | **2.086–3.620** |
| Selva de Mar | **Control and *Sus*** | **460** | **690** | **1.790** | **1.420–2.221** |
|  | **Control and *M. foina*** | **460** | **92** | **0.631** | **0.482–0.821** |
|  | **Control and *Turdus/Sturnus*** | **460** | **51** | **2.416** | **1.210–4.807** |
|  | ***Sus* and *M. foina*** | **690** | **92** | **0.355** | **0.264–0.464** |
|  | *Sus* and *Turdus/Sturnus* | 690 | 51 | 1.359 | 0.671–2.710 |
|  | ***M. foina* and *Turdus/Sturnus*** | **92** | **51** | **3.889** | **1.884–7.623** |

*Mustela* treatment was not included in Cap de Creus (Selva de Mar) due to the limited sample size, nor were *Oryctolagus* on Tenerife or *Vulpes* in Cap de Creus (Port de la Selva), due to the lack of germination

Number of seeds sown in each case is shown (n1 and n2). Those cases in which the ratios did not include the value 1 are indicated in bold

**Table 3** Mean percentage germination ratios and 95% Bayesian credible intervals for pairs of *Opuntia* species in all study areas (**TE**, Tenerife; **ME**, Menorca; **BI**, Benidorm islet; **SM**, Cap de Creus (Selva de Mar) to test for equality (ratio = 1) between pairs

| Compared species | n1 | n2 | Mean % ratio | 95% CrI |
|---|---|---|---|---|
| ***O. dillenii* (TE) and *O. maxima* (ME)** | **230** | **210** | **20.34** | **6.51–55.12** |
| ***O. dillenii* (TE) and *O. maxima* (BI)** | **230** | **1,120** | **1.974** | **1.511–2.470** |
| *O. dillenii* (TE) and *O. maxima* (SM) | 230 | 460 | 1.015 | 0.771–1.292 |
| ***O. maxima* (ME) and *O. maxima* (BI)** | **210** | **1,120** | **0.129** | **0.035–0.287** |
| ***O. maxima* (ME) and *O. maxima* (SM)** | **1,210** | **460** | **0.066** | **0.018–0.148** |
| ***O. maxima* (BI) and *O. maxima* (SM)** | **1,120** | **460** | **0.517** | **0.421–0.625** |

*O. stricta* in Cap de Creus (PS) was not included due to the lack of germination

Number of control seeds sown in each case is shown (n1 and n2). Those cases in which the mean percentage ratio did not include the value 1 are indicated in bold

thickness. In contrast, on Menorca, a statistically significant decrease in seed coat thickness was detected in seeds ingested by tortoises and pine martens compared to *O. maxima* control seeds (Fig. 3).

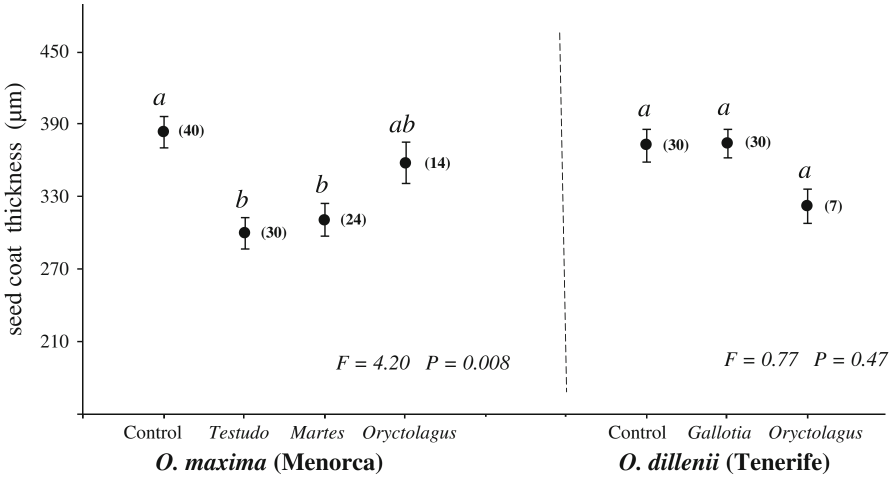
Seeds consumed by vertebrates were less viable compared to control seeds. On Tenerife, percentage viability was 66% (95%CrI = 48–81%) in control seeds vs. 52% (95%CrI = 35–68%) in seeds defecated by lizards. The trend was the same on Menorca: 95% (87–99%) in control seeds vs. 62% (39–83%) from rabbits, 59% (42–75%) from tortoises and 31% (16–50%) from pine martens.

## Discussion

### Assemblage of seed dispersers of *Opuntia* spp.

The three species of *Opuntia* were found to be dispersed by a great array of vertebrates in the different study areas, including reptiles (i.e. lizards and tortoises), birds (i.e. gulls and passeriforms) and mammals (i.e. wild boar, weasels, martens, foxes and rabbits). As expected, all these species are highly generalist in their diets, which facilitates the inclusion of these fleshy-fruited aliens. Most *Opuntia* dispersers

**Fig. 3** Mean (±SE) seed-coat thickness for *O. maxima* in Menorca and *O. dillenii* in Tenerife. *Letters* indicate statistically significant differences within each alien species after Bonferroni correction. Number of seeds measured in *parenthesis*



were native, although alien frugivores were also found to consume their fruits and spread the seeds. Introduced dispersers, in particular, can facilitate the expansion of other alien organisms with the potential to promote an "invasional meltdown effect" (Simberloff and Von Holle 1999; Traveset and Richardson 2006). In the Canary Islands, native frugivores such as the endemic lizards of the genus *Gallotia* are known to play an important role as dispersers of a number of fleshy-fruited plant species in lowland habitats (Valido and Nogales 1994; Valido et al. 2003). Birds were not detected in the seed dispersal assemblage of *Opuntia* in the islands, although we know that ravens (*Corvus corax*) were important consumers of its fruits in the past, on both Tenerife (Nogales et al. 1999) and Menorca (O. García, personal communication), and some passeriforms consume *Opuntia* fruits in different areas of Tenerife (A. González-Castro, unpublished data). By contrast, in the mainland area, the thrushes (*Turdus*) and starlings (*Sturnus*) were found to consume *O. maxima* fruits. The interaction between sea gulls (*Larus*) and *Opuntia* on Benidorm islet seems to be rather specific, although these seabirds may have had a fundamental contribution to the great local expansion of the cactus. Gulls and ravens have indeed been documented as dispersers of fleshy-fruited plants on different islands/islets (Nogales et al. 1999, 2001 and references therein). Due to their long flying distances, such dispersers in the Canary Islands have greatly contributed to the relatively rapid and wide expansion of some *Opuntia* species originally planted by humans. This process has been reported in South Africa, where densities of *Opuntia* around telephone posts or fences are higher than in open areas due to the location of crow nests (Dean and Milton 2000).

Besides the identity of seed dispersers, it is important to consider the fruiting phenology of the different *Opuntia* species in order to understand how 'valuable' their fruits are relative to those of other species available at each particular site. For example, on Tenerife, the availability of *O. dillenii* fruits throughout the year contrasts with the short period (only a few months) that *O. maxima* fruits are available on Menorca. In the Galápagos Islands, the prolonged and asynchronous ripening of *Opuntia* fruits has been interpreted as a way to ensure seed dispersal by iguanas and tortoises, which are active all year round, as well as to reduce seed predation by finches which selectively feed beneath those trees with rapid rates of fruit-fall (Racine and Downhower 1974). The same might actually happen in Tenerife, where lizards are also active during all months of the year. In Cap de Creus (SM) and Menorca, the fruiting period of *O. maxima* overlaps with a few native plants, which possibly promotes rapid fruit consumption due to low availability of other fruit species. In contrast, in Cap de Creus (PS), *O. stricta* fruits remain on the plant for most of the winter and there is an overlap with many native species. On Benidorm islet, fruits ripen mostly in autumn (September–October), when gulls have finished their breeding season but are still present. During this period, up to 32 migratory passerines could benefit from the opening action of gulls on the fruits, promoting easier access to the pulp. This has been observed with resident warblers (*Sylvia melanocephala*) and lizards (*Podarcis hispanica*) (J. Santamaría-Reos, unpublished data).

## Quality of the *Opuntia* seed disperser interactions

The passage of seeds through the digestive tract seems an unnecessary requirement for germination in the genus *Opuntia* (Reyes-Agüero et al. 2006 and references therein). Nevertheless, endozoochorous dispersal seemingly provides some additional advantages to such taxa (e.g. habitat colonization, genetic variability, avoidance of long-term local extinction) (Mandujano et al. 1997). Endozoochorous dispersal may also be advantageous in separating pulp and seeds and this specific factor was not considered in the present study. Moreover, some researchers have found that rapid germination is important for seedlings to become established before the arrival of the dry season (Izhaki and Safriel 1990; Verdú and Traveset 2005; Nogales et al. 2006). This factor is noteworthy in some *Opuntia* species introduced in places with strongly arid conditions, such as *O. dillenii* in the xeric coastal zones of the Canary Islands. The enhanced seed germination rate of this species promoted by lizards may in fact be quite advantageous for plants that live in environments where rain is highly unpredictable. Previous germination tests with this species had shown a germinability of 13% for seeds ingested by ravens compared to 0% for controls (Nogales et al. 1999). It is possible that the higher figures for lizard-ingested seeds are due to greater seed scarification caused by longer passage times (Valido and Nogales 2003) compared to that of ravens (Nogales et al. 1999), although we would need to compare seeds from the same population to assess this properly.

In the case of *O. maxima*, we found a high variability in the germination percentage at the different study sites. In general, however, there was a similar germination pattern between controls and seeds passed through the particular frugivores at each site (see Fig. 2), indicating that ingestion does not enhance germination relative to manual depulping and that the main effect of frugivores of this plant could be seed dispersal and the separation of seeds from pulp. Some underlying factors, such as the maternal effect on germination, might be important in the outcome of the different dispersers. This effect is clearly appreciated in *O. maxima* on Menorca, where a generally low germination was recorded in control seeds and also in the interactions with its dispersers. However, at two of the three study sites (Menorca and Benidorm islet), *O. maxima* seeds were viable and a fraction of them germinated after passing through disperser guts. A relatively low germination proportion was previously recorded for those *O. maxima* seeds dispersed in the Canaries by ravens (Barquín et al. 1986; Nogales et al. 1999) and by the introduced Barbary ground squirrel (López-Darias and Nogales 2008), although in these experiments only the first year of germination was considered and possible seed dormancy was not taken into account. In Cap de Creus, viability of seeds dispersed by wild boars was the same as that of control seeds (Gimeno and Vilà 2002). The total lack of germination of *O. stricta* seeds again suggests the importance of the mother plant effect in control seeds (viability and germination performance) and the potentially different effects of the dispersers on the seeds.

Our germination experiments confirmed the previously reported dormancy period during the first year of life in the seeds of many *Opuntia* species (Reyes-Agüero et al. 2006 and references therein). However, the Benidorm islet population was an exception, where seedlings emerged mostly during their first year. In this regard, Mandujano et al. (1997) mentioned that despite the seed ingestion effect of the different dispersers, seeds of some *Opuntia* species (such as *O. rastrera*) have an obligate primary dormancy caused by embryo immaturity. In native areas of *Opuntia* species, and specifically in *O. rastrera*, practically all dispersers are birds and mammals (Montiel and Montaña 2000). The study by Mandujano et al. (1997) showed that coyotes, woodrats and common pigs, but not mule deer or northern ravens, decreased seed germination percentage with respect to control seeds, which further indicates the heterogeneity of responses to the different types of dispersers.

A decreased seed coat thickness (greater scarification) following gut passage has been documented in different studies (e.g. Traveset et al. 2001; Nogales et al. 2005), although the consequences of such changes in germination remain largely unknown (but see Traveset et al. 2008b). We detected a statistically significant decrease in seed coat thickness of ingested seeds of *O. maxima* on Menorca. Such a reduction, however, did not translate into greater germination, which might be due to the scarce germination percentage recorded in the different treatments analysed, possibly because of a maternal effect, or other unmeasured factors.

Although seed viability was reduced after passing through vertebrate guts, the invasion of *Opuntia* spp. on Menorca and Tenerife demonstrates that the number of viable seeds dispersed is enough to favour their spread into new habitats. In a previous study, high viabilities have been found for *O. maxima* seeds, either ingested by frugivores or not (Gimeno and Vilà 2002).

## Conclusions

Sexual reproduction can be crucial to both native and alien plant species during the upward colonization of steep areas. This is precisely the case on many oceanic islands (e.g. the western Canaries) where seed dispersal, especially mediated by vertebrate frugivores, is important in this process. On an island scale, another factor that has probably facilitated the wide invasion of *Opuntia*, at least in the Canaries, is the characteristic huge numbers of lizards (due to density compensation on islands) present in these arid island ecosystems, which seems to be found in other oceanic archipelagos (Olesen and Valido 2003). We found that lizards consume large amounts of *Opuntia* fruits, and are effective dispersers of this alien species in Tenerife, and thus their role as promoters of the invasion is probably substantial. In the Canary Islands, there is actually a complex of coinciding factors that favour the spread of *O. dillenii*. These are: (1) the presence of relatively large lizards that consume great amounts of its fruits, (2) the small overlap between the fruiting peak of the alien and that of most native fleshy-fruit plant species, (3) availability of fruits all year-round, and (4) the enhancement of germination rate promoted by seed ingestion by lizards. These factors together with vegetative multiplication explain the invasion of wide areas of xeric shrub habitats during the last 50 years, after the rotavating of relatively large land areas on the coast of the Teno massif (NW Tenerife). Previous studies in the Mediterranean (Vilà et al. 2003) and the Canary Islands (Arteaga et al. 2009) show how areas where agriculture has been abandoned are more likely to be invaded by alien species and similarly, disturbance factors determine introduced-species richness in the native areas. In a general sense, islands have been described to be more vulnerable to invasions than mainland areas (Gimeno et al. 2006; Vilà and Gimeno 2006).

In short, our findings show how different species of *Opuntia* can invade vast areas, aided by native and introduced dispersers present in different geographical zones, either in continental or insular ecosystems. The consideration of these dispersal events over the last few centuries contributes to the understanding of how the alien *Opuntia* species may have covered such extensive areas since they were introduced into Mediterranean and Macaronesian habitats. Our study contributes to the idea that any control programme of invasive plants would need to take into account their interactions with the local fauna (see, for example, Harris et al. 2009).

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