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Breeding system and pollen limitation in two supergeneralist alien plants invading Mediterranean shrublands

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Abstract. Many widely known invasive plants are well integrated into native plant–pollinator networks. Typically, these invaders have entomophilous flowers which are visited by a diverse array of pollinators. The type of breeding system and the role that pollination services play in the reproductive success of invasive plants have, however, received little attention. We studied the breeding system and pollen limitation of two entomophilous invasive plants, *Carpobrotus* affine *acinaciformis* and *Opuntia stricta*, in different Mediterranean coastal localities in north-eastern Spain. Both species are, to some degree self-compatible; however, because of frequent visitation, open pollination increased the seed set in both species by at least 50%. Whereas *O. stricta* showed no pollen limitation, some populations of *C.* aff. *acinaciformis* had a lower seed set in open-pollinated flowers than in flowers where supplementary hand-pollination ensured out-crossing. This local pollen limitation in *C.* aff. *acinaciformis* could be due to the low efficiency of its visitors (mainly beetles) or its hybrid status. On the basis of previous studies on *Carpobrotus* sp. hybrid complexes, we suggest that the variability among sites in the seed set of open-pollinated flowers is caused by different degrees of hybrid introgression. Not withstanding, we found the *C.* aff. *acinaciformis* seed sets studied were higher than those reported in other regions. Further research is needed to assess the invasion potential of these hybrids in Mediterranean shrublands.

Introduction

Many introduced alien plants establish and spread successfully, thus becoming invaders (Richardson and Pyšek 2000; Pyšek *et al*. 2004). Classic authors (e.g. Baker 1955, 1967, 1974; Stebbins 1957) have pointed out that an ideal weed, and therefore an ideal invasive plant, has asexual reproduction, is self-compatible and/or is pollinated by generalist insects. Recent studies on invasive plant traits have found that the most widespread and locally abundant invasive plants have asexual reproduction, are wind-pollinated and/or are capable of self-pollination (Daehler and Carino 2000; Lloret *et al*. 2005). Indeed, self-pollinated invasive plant species are more widespread than species requiring pollen vectors (van Kleunen and Johnson 2007). However, many well known invasive plants are entomophilous, receiving high numbers of flower visits by a diverse array of pollinators (Campbell 1989; Brown and Mitchell 2001; Chittka and Schürkens 2001; Bjerknes *et al*. 2007; Bartomeus *et al*. 2008*a*). In fact, many entomophilous invasive plants are well integrated in the plant–pollinator network of the introduced community (Memmot and Waser 2002; Lopezaraiza-Mikel *et al*. 2007). Except for species with highly specialised pollination systems, such as *Ficus* spp., pollinator limitation does not appear to be a major barrier for the spread of invasive plants (Richardson *et al*. 2000). However, invasive plants are often visited by different pollinators in invaded areas than in their native range (Forster 1994; Stout *et al*. 2006) and these new pollinator interactions may have a different efficiency compared with pollinator interactions in the plant's native region. Although entomophilous invasive plants can attract a wide array of flower visitors, it is important to ascertain how efficient these visitors are (Larson *et al*. 2006; Jakobsson *et al*. 2007) and how important pollination service is for seed production in the invasive plant.

Some invasive plants, despite having flowers visited by insects, are self-compatible, e.g. the garlic mustard (*Alliaria petiolata* (Bieb.)) in North America (Cavers *et al*. 1979), *Miconia calvescens* (DC.) in Tahiti (Meyer 1998) and several invasive species in South Africa (Rambuda and Johnson 2004). However, there is little knowledge about whether pollen limitation occurs in invasive species. In native plants, pollen limitation is spatially variable (Ashman *et al*. 2004; Knight *et al*. 2005) and few studies have shown this to be the case also for invasive species. *Cytisus scoparius* (L.), a European plant invading western North America, is pollen limited in localities with low visitation rates, but not at sites where the visitation rate is high (Parker 1997; Parker and Haubensak 2002). Similarly, the skunk vine (*Paederia fetida* (L.)) invading native habitats in Florida is pollen limited in certain populations, depending on the composition of the pollinator community (Liu *et al*. 2006). These studies suggest that the effect of pollinators on seed production in invasive plants is highly context specific. In addition, interpopulation variation in the breeding system

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seems to be common (Dieringer 1999; Lee *et al*. 2000). This is especially true when populations arise from a few founder individuals and are subject to bottleneck events that constrain the local variability in the breeding system (Sakai *et al*. 2001).

We studied the breeding system and pollen limitation of two entomophilous invasive species, *Carpobrotus* affine *acinaciformis* (L.) and *Opuntia stricta* (Haw.), in different populations situated in north-eastern Spain. Vegetative reproduction is important in both species for the persistence of their populations, whereas seedling recruitment is essential to expand their area of distribution into new areas (Vilà and D'Antonio 1998, for *C.* aff. *acinaciformis*; Gimeno and Vilà 2002, for *O. stricta*). Both species are entomophilous supergeneralist species (Bartomeus *et al*. 2008*a*) and studies conducted in other regions have found that they are, at least to some degree, self-compatible (Suehs *et al*. 2004*b*, for *C.* aff. *acinaciformis*; Spears 1987, for *O. stricta*). *C.* aff. *acinaciformis* is particularly interesting with respect to its reproductive biology, as different levels of introgression between *C. edulis* (L.) and *C. acinaciformis* (L.) in different localities could affect its breeding system (Suehs *et al*. 2004*a*). Our hypotheses are that (1) pollinators contribute largely to the seed set of the two studied species and, therefore, (2) the two species are not pollen limited, although (3) the breeding system and pollen limitation, may vary among sites.

Materials and methods

Study area

Our study area was located in coastal Mediterranean shrublands in the Natural Park of Cap de Creus, Catalonia, north-eastern Spain. This area is characterised by relatively cool, wet winters and warm dry summers; the mean temperatures of the coldest (January) and hottest (August) months in 2005 were 6°C and 23°C, respectively, and the annual precipitation was 450 mm (www.meteocat.com accessed May 2006). Our study involved the two most abundant invasive plants in the Natural Park, namely *Carpobrotus* aff. *acinaciformis*, growing in coastal communities, and *O. stricta*, located on hilly stony slopes.

For each species, we selected three representative invaded sites of 50 × 50 m, situated at least 3 km apart. Cover of the invasive plants ranged from 15 to 35%, typifying an initial invasion stage. *C.* aff. *acinaciformis* and *O. stricta* coexisted with 17 and 16 coflowering species, respectively.

Study species

Carpobrotus aff. *acinaciformis* (Aizoaceae) are crawling, mat-forming, succulent herbs, with fast clonal growth (Vilà and D'Antonio 1998). Native to South Africa, the species is invasive in almost all Mediterranean-type regions. It was introduced to Spain for gardening and soil fixation at the beginning of the 20th century. It causes smothering, thereby reducing the regeneration of native flora and it changes the soil pH and nutrient regimes. This invader competes aggressively with native plant species (D'Antonio and Mahall 1991; D'Antonio 1993). In the study area, *C.* aff. *acinaciformis* may form hybrids between *C. edulis* and *C. acinaciformis*. Therefore, we follow the nomenclature proposed by Suehs *et al*. (2004*a*) and refer to this species as the hybrid complex *C.* aff. *acinaciformis*. These putative hybrids have flowers that are solitary, 8–10 cm in diameter and range in colour from white to yellow. The flowers are open, suggesting a generalist pollination system (Vilà and D'Antonio 1998). Flowering in Spain lasts from March to June (Sanz-Elorza *et al*. 2006). Fruits are fleshy, indehiscent and edible and are ~3.5 cm in diameter. Each fruit produces hundreds of seeds embedded in sticky, sweet, jelly-like mucilage.

The breeding system of *Carpobrotus* sp. hybrids and putative parents has been analysed in other Mediterranean communities. *C. edulis* is slightly agamospermic and self-compatible (Vilà *et al*. 1998; Suehs *et al*. 2004*b*). In California, *C. edulis* hybridises with *C. chilensis* (N.E.Br.) (Vilà and D'Antonio 1998) and hybrids are also self-compatible. In France, *C. edulis* hybridises with *C. acinaciformis*, resulting in the complex *C.* aff. *acinaciformis* forming stands with different levels of introgression. *C.* aff. *acinaciformis* is slightly self-compatible (Suehs *et al*. 2004*b*). In the study area, our focal populations had a phenotype resembling *C.* aff. *acinaciformis* in southern France (Suehs *et al*. 2004*a*), and there were patches of pure *C. edulis* phenotypes nearby.

Opuntia stricta (Cactaceae) is a succulent, perennial, spiny plant introduced to Spain from Central America in the 16th century. *O. stricta* can dominate the vegetation of rocky outcrops, physically displacing native species. It is commonly cultivated as an ornamental and invades sunny sandstone hillsides and abandoned orchards (Vilà *et al*. 2003). Plants can become 1.5 m tall and flowers are 5–10 cm in diameter and yellow with abundant pollen. Flowering in Spain takes place from June to July (Sanz-Elorza *et al*. 2006). Fruits are obovoid and contain dozens of 4–6-cm-long, 2.5–4-cm-diameter seeds (Gimeno and Vilà 2002). The genus *Opuntia* has very heterogeneous breeding systems. Autogamy is rare, although most species are self-compatible and some need out-crossing for a successful seed set (Reyes-Agüero *et al*. 2006). It has been documented that levels of self-pollination could vary among populations (Bianchi *et al*. 2000). In Florida, where *O. stricta* is native, the species presents a high level of self-pollination and no pollen limitation (Spears 1987).

Pollinator sampling and pollination treatments

During spring 2005, *C.* aff. *acinaciformis* and *O. stricta* were sampled for a total of 36 min per site during their entire flowering season. In total, 276 flowers of *C.* aff. *acinaciformis* and 174 of *O. stricta* were observed, pooling the four observation periods conducted at each site. For details of the insect sampling protocol see Bartomeus *et al*. (2008*a*). By using this visitation data, we calculated pollinator diversity and the number of visits at each site.

To investigate the breeding system and whether the plants were pollen limited we assigned the following pollination treatments in each of our six focal populations, following protocols from Kearns and Inouye (1993) and Neal and Anderson (2004):

(1) spontaneous self-pollination – bagged flowers with 0.2-mm-pore bags to avoid any pollen transfer;
(2) facilitated self-pollination – hand-pollination with pollen from each own flower (flowers remained bagged before and after the hand-pollination treatment);

(3) anemogamy – bagged flowers with 2.5-mm-pore bags that permit the passing of pollen but exclude the majority of pollinators (Bartomeus *et al.* 2008*a*);
(4) forced out-crossing – hand-pollination with pollen added from other populations to ensure that pollen belongs to different individuals (flowers remained bagged before and after the hand-pollination treatment to ensure no pollen transfer or removal); and
(5) open pollination – flowers that were not manipulated; hand-pollination was performed with cotton swabs on fully receptive stigmas.

To ensure pollen viability, only fresh pollen, collected 15 min before hand-pollination, was used. Clean cotton swabs were completely covered by fresh pollen collected in Petri dishes and directly applied on the stigma surface.

In all, 40 flowers were randomly assigned to each treatment at each site. At the end of the experiment, some fruits had disappeared as fruits were consumed by frugivores (17.16% in *C.* aff. *acinaciformis* and 27.66% in *O. stricta*). However, overall there was not much variation between sample sizes among treatments and sites (*C.* aff. *acinaciformis*: 498 fruits; number of fruits per treatment and site (mean ± s.e.): 33.13 ± 1.82; *O. stricta*: 435 fruits; number of fruits per treatment and site: 28.93 ± 1.83). After maturation, fruits were collected, opened in the laboratory and seeds were counted. We investigated the effect of the pollination treatments and site on seed set (i.e. number of seeds per fruit) as a response variable with generalised linear mixed models (GLMM). The number of fruits collected per treatment was unbalanced and the number of seeds counted was strongly left-skewed and could not be normalised by transformations. Thus, we implemented models with Poisson error distribution and a logit link function, as recommended by Crawley (2002). The logit link function ensures that all the fitted values are positive whereas the Poisson error takes into account the fact that the data are integers and have variances that are equal to their means (Crawley 2002). We generated models with the glmmPQL function of the MASS library in the R statistical software (Development Core Team 2007). The explanatory variables pollination treatment and site were included as fixed factors. Site was included as a random effect to account for spatial autocorrelation in the data. To reveal *post hoc* pair-wise differences among treatment levels, we repeated the analysis grouping non-significant factor levels that did not differ from one another by model simplification (Crawley 2002). As the signification of the simplified model did not change, we retained the new grouping factors in the model, assuming no significant differences inside groups. This simplified model presented no significant interactions between group and site. However, some pollination treatments showed a significant interaction with site in the non-simplified model proposed (see Results section). For those treatments, we investigated differences in seed set within each site by using a generalised lineal model (GLM) for each site. In this analysis, treatment was the only fixed factor and we used again a Poisson error distribution.

Results

Carpobrotus aff. *acinaciformis* and *O. stricta* were mainly visited by insects from the orders Coleoptera and Hymenoptera. In total, 23 and 17 taxa visited *C.* aff. *acinaciformis* and *O. stricta*, respectively (Appendix 1). At one of the study sites of *C.* aff. *acinaciformis* (C1), we found a higher number of flower visits and flower-visiting taxa than at the other two sites (Table 1). In *O. stricta*, we found a comparable number of visitor species at the three study sites, although one site (O1) received fewer flower visits (Table 1). Hymenoptera represented 39.49 ± 1.67% of visitor species per site and made up 29.52 ± 4.38% of the visits to *C.* aff. *Acinaciformis*. However, for *O. stricta*, Hymenoptera represented 67.22 ± 8.06% of visitors per site and made up 70.74 ± 10.62% of the visits.

All fruits collected contained seeds. The number of seeds per fruit could be explained by the pollination treatment both in *C.* aff. *acinaciformis* and in *O. stricta*, when site id was included in the model. After model simplification, we found two significantly different treatment groups in *C.* aff. *acinaciformis* (Group 1: forced out-crossing + open pollination + anemogamy; Group 2: facilitated self-pollination + spontaneous self-pollination) and three groups in *O. stricta* (Group 1: forced out-crossing + open pollination; Group 2: anemogamy + facilitated self-pollination; Group 3: spontaneous self-pollination) (Table 2). These groups reflect the pair-wise differences between treatments. In different groups, treatments were significantly different; however, within the same group treatments were not significantly different. Both species had the highest seed set when pollen from other plants was added (forced out-crossing) or when its flowers were open pollinated. In *C.* aff. *acinaciformis*, anemogamy also resulted in a high seed set, whereas in *O. stricta*, anemogamy reduced the seed set to half. Although both species are self-compatible, facilitated and spontaneous self-pollination reduced the seed set significantly compared with open-pollinated flowers. In *O. stricta*, spontaneous self-pollination achieved the lowest seed-set values (Fig. 1).

Overall, for both plant species, we found no differences in seed set among sites (Table 2), indicating that the seed production in each pollination treatment did not vary consistently within sites. For *O. stricta*, we did not find any significant interaction between pollination treatment and site. However, for *C.* aff. *acinaciformis* some pollination treatments showed an interaction with site before model simplification, indicating particular differences of those treatments between sites (GLMM: forced out-crossing × site estimate = 0.27, s.e. = 0.09, $t_{486} = 2.85$, *P*-value = 0.005; anemogamy × site estimate = –0.26, s.e. = 0.09, $t_{486} = 2.84$, *P*-value = 0.005; all

Table 1. Number of visitor species and visits received by *Carpobrotus* aff. *acinaciformis* and *Opuntia stricta* at each site

Site	No. of visitors	No. of visits
Carpobrotus aff. *acinaciformis*		
Site C1	19	64
Site C2	10	36
Site C3	11	33
Opunita stricta		
Site O1	12	24
Site O2	12	49
Site O3	10	57

Table 2. Minimum adequate mixed model of *Carpobrotus* aff. *acinaciformis* and *Opuntia stricta*

Different levels of pollination treatments are grouped by model simplification. In *C.* aff. *acinaciformis*, Group 1 includes forced out-crossing, open pollination and anemogamy, whereas Group 2 includes facilitated and spontaneous self-pollination. In *O. stricta*, Group 1 includes forced out-crossing and open pollination treatments, Group 2 anemogamy and facilitated self-pollination and Group 3 spontaneous self-pollination. The estimates and statistical tests are related to the differences of each group with respect to Group 2 in *C.* aff. *acinaciformis* and Group 3 in *O. stricta* (Crawley 2002)

	Estimate	s.e.	d.f.	*t*-value	*P*-value
Carpobrotus aff. *acinaciformis*					
Intercept	5.86	0.16	492	37.13	<0.001
Treatment					
Group 1	0.95	0.16	492	5.43	<0.001
Site	–0.02	0.08	1	–0.15	0.90
Opunita stricta					
Intercept	2.56	0.37	427	6.86	<0.001
Treatment					
Group 1	1.96	0.38	427	5.04	<0.001
Group 2	1.30	0.41	427	3.17	<0.001
Site	0.14	0.17	1	0.85	0.55

other treatment interactions were non-significant). We then compared seed set among treatments in Group 1 (i.e. forced out-crossing, open pollination and anemogamy) for each site. Significant differences among pollination treatments emerged only within sites C2 and C3. At site C2, open-pollination treatment was different from the forced out-crossing and anemogamy treatments (GLM estimate for forced out-crossing = 0.17, s.e. = 0.07, $t_{79} = 2.56$, *P*-value = 0.01; GLM estimate for anemogamy = –0.16, s.e. = 0.07, $t_{79} = –2.27$, *P*-value = 0.03; Fig. 1). At site C3, open pollination was significantly different only from forced out-crossing (GLM estimate for forced out-crossing = 0.39, s.e. = 0.09, $t_{114} = 4.17$, *P*-value < 0.001; GLM estimate for anemogamy = –0.17, s.e. = 0.11, $t_{114} = –1.69$, *P*-value = 0.93; Fig. 1).

Discussion

Both *Carpobrotus* aff. *acinaciformis* and *O. stricta* were visited by a wide array of flower visitors contributing to their seed set. For both species, we found significant differences in seed set among the pollination treatments tested. In the case of *C.* aff. *acinaciformis*, some differences among pollination treatments varied among sites.

Forced cross-pollination in *C.* aff. *acinaciformis* resulted in the highest seed set in two of three sites. The fact that site C1 presented a lower seed set could be attributed to differences in the degree of hybrid introgression among the different plant populations. It is unlikely to be due to differences in the resource availability of each site because site did not show a consistent effect along other pollination treatments. In Southern France, on average, the seed set in the cross-pollination treatments had intermediate values (ranging from 800 to 1200 seeds per fruit) compared with those for *C. acinaciformis* (~500 seeds) and *C. edulis* (~1300 seeds) (Suehs *et al.* 2004*b*). Consequently, *C. acinaciformis* increases its seed set when crossed with *C. edulis* (Suehs *et al.* 2004*a*). Therefore, the spatial variability in seed set found in our study area could be a result of different levels of introgression among sites. It will be crucial to characterise *C.* aff. *acinaciformis* phenotypes to assess differences in the invasion potential of hybrids in Cap de Creus Natural Park, where the invasion has advanced by at least 10 ha in the last 5 years (information provided by Natural Park officers).

Recent studies have reported that insects visiting *C.* aff. *acinaciformis* carry high amounts of *C.* aff. *acinaciformis* pollen (Bartomeus *et al.* 2008*b*; Jakobsson *et al.* 2008). Thus, we expected that plants would not be pollen limited. Nevertheless, open-pollinated *C.* aff. *acinaciformis* flowers set fewer seeds than cross-pollinated flowers at sites C2 and C3, as revealed in the GLM performed for each site. In parallel, we observed lower pollinator diversity and fewer flower visits at these two sites. Almost 60% of the visits to flowers of *C.* aff. *acinaciformis* were by beetles that, despite being abundant, spend long periods of time on single flowers (Bosch 1992),

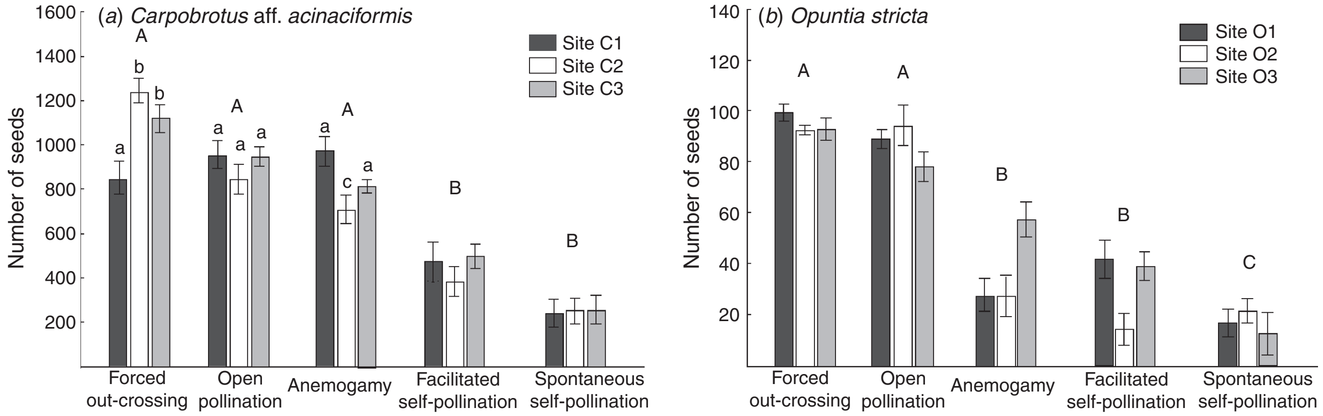

Fig. 1. Mean number (±s.e.) of seeds per fruit produced by *Carpobrotus* aff. *acinaciformis* (*a*) and *Opuntia stricta* (*b*) at three sites (C1, C2 and C3 for *C. acinaciformis* and O1, O2 and O3 for *O. stricta*) for the following pollination treatments: forced out-crossing (hand-pollination with pollen from other localities); open pollination; anemogamy (wind pollination); facilitated self-pollination (hand-pollinated stigmas with the pollen of the same flower); and spontaneous self-pollination (bagged flowers). Different capital letters indicate significant differences among treatments, following model simplification into groups. Different lowercase letters indicate differences among sites within Group 1 treatments (A) as revealed by the generalised linear model for each site.

potentially reducing effective cross-pollination and mainly contributing to self-pollination. This pattern has also been observed in California, where thrips are involved in self-pollination in the congener *C. chilensis* (Vilà *et al*. 1998). As reported by Suehs *et al*. (2006), the production of aborted pollen can be high within hybrids. In the populations studied, on average 30% of pollen was abnormal and deformed (I. Bartomeus, pers. obs.) and this could also decrease the quality of the pollen deposited on stigmas, especially in self-pollination processes.

Opuntia stricta had the highest levels of seed set in cross-pollination and open pollination at all three sites. This indicates that pollinators are very efficient and that the species is not pollen limited. In its native range, *Opuntia* sp. is strongly associated with bee pollination, and coevolution with at least two genera has been suggested, namely *Diadasia* (Apidae) and *Lithurge* (Megachilidae) (Grant *et al*. 1979; Reyes-Agüero *et al*. 2006). Although neither of these two genera is present in the study area, *O. stricta* is visited by many bee species, including a large number of visits from honeybees (*Apis mellifera*) and carpenter bees (*Xylocopa violacea*). Both bee species are large pollinators that are capable of providing proper pollination to *O. stricta* flowers. These flowers require bees bigger than 1.5 cm long in order to be efficiently pollinated (Grant and Hurd 1979). In the Mediterranean region, *O. stricta* flowers late in the season when flowering of most of the other bee-pollinated species (e.g. *Rosmarinus officinalis* (L.), *Lavandula stoechas* (L.)) is over; hence, *O. stricta* could represent an important resource for large bees later in the season.

Both species were self-compatible; however, self-pollination treatments reduced the number of seeds to 50% compared with open-pollinated flowers. On the basis of previous studies, we expected a high degree of self-pollination in *O. stricta* (Spears 1987). On the contrary, in all three populations we found low self-pollination, which increased when facilitated mechanically. Other *Opuntia* species also showed different levels of self-fertility among populations (Bianchi *et al*. 2000).

The present study is the first to test anemogamia in *C.* aff. *acinaciformis* and *O. stricta.* Although probably pollinators smaller than 2 mm could not be excluded, they were not seen. Wind-pollinated flowers of *C.* aff. *acinaciformis* had as much seed production as open pollinated flowers. *C.* aff. *acinaciformis* flowers do not fit into a typical wind-pollination scenario (Proctor *et al*. 1996). Nevertheless, these flowers have an open-bowl shape, with exposed stigmas and a high production of small pollen (Blake 1969). Invaded sites are very windy and, as demonstrated in other entomophilous species, wind can contribute to pollen dispersal (Dafni and Dukas 1986; Bullock 1994). The anemogamy treatment was not significantly different from facilitated self-pollination treatments in *O. stricta.*

In an invaded community, invasive plant species face a new reproductive situation. How the invasive species adapt to this new situation is important in order to understand the mechanisms involved in the invasion process. Both species included in the present study have a generalist pollination syndrome that allows a wide range of pollinators to visit their flowers. Although both species have a certain degree of self-pollination, floral visitors contribute to seed production. Whereas in *O. stricta* the seed set is not limited by pollinators, in *C.* aff. *acinaciformis* open pollination did not reach the maximum potential seed set at two of three sites. It remains to be explored whether *C.* aff. *acinaciformis* pollen limitation is due to low visitor efficiency by beetles or due to its hybrid status, which results in a large amount of non-viable pollen. However, we found *C.* aff. *acinaciformis* seed set was higher than those reported in other regions. Further research is needed to assess the invasion potential of these hybrids in Mediterranean shrublands.

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Appendix 1. Visitors sampled visiting *Carpobrotus* aff. *acinaciformis* and *Opuntia stricta*, and the total number of visits recorded to both plant species

Previous plant–pollination analyses sampling all visitors to plant species at this site (Bartomeus *et al*. 2008*a*) showed that no visitors were exclusive to *C.* aff. *acinaciformis*, which was visited by 43.4% of the observed insect taxa and that *Opuntia stricta* was visited by 30.9% of the observed insect taxa, with only *Xylocopa violacea* an exclusive visitor of the invasive plant

Order	Family	Species	No. of visits
Carpobrotus aff. *acinaciformis*			
Coleoptera	Dasytidae	*Coleoptera*_sp. 1	1
Coleoptera	Dasytidae	*Coleoptera*_sp. 2	8
Coleoptera	Bruchidae	*Coleoptera*_sp. 3	2
Coleoptera	Chrysomelidae	*Cryptocephalus* sp.	3
Coleoptera	Mordelidae	*Mordella* sp.	1
Coleoptera	Mordelidae	*Mordellistema* sp.	7
Coleoptera	Oedemeridae	*Oedemera flavipes*	3
Coleoptera	Oedemeridae	*Oedemera lurida*	21
Coleoptera	Oedemeridae	*Oedemera nobilis*	2
Coleoptera	Scarabaeidae	*Oxythyrea funesta*	20
Coleoptera	Dasytidae	*Psilothix* sp.	22
Hymenoptera	Andrenidae	*Andrena* sp.	4
Hymenoptera	Megachilidae	*Anthidium sticticum*	5
Hymenoptera	Apoidea	*Apis melifera*	7
Hymenoptera	Apoidea	*Bombus terrestris*	14
Hymenoptera	Anthophoridae	*Eucera* sp	1
Hymenoptera	Megachillidae	*Megachille* sp.	1
Hymenoptera	Halictidae	*Halictus* sp.	1
Hymenoptera	Halictidae	*Halictus* sp.	3
Hymenoptera	Megachilidae	*Megachile* sp.	1
Hymenoptera	Megachilidae	*Osmia* sp.	2
Hymenoptera	Formicidae	*Plagiolepsis pigmaea*	2
Hymenoptera	Anthophoridae	*Xylocopa* sp.	1
Opuntia stricta			
Coleoptera	Dasytidae	*Coleoptera*_sp. 1	4
Coleoptera	Mordelidae	*Mordella* sp.	2
Coleoptera	Mordelidae	*Mordellistena* sp.	3
Coleoptera	Maloidea	*Myrabilis quadripunctata*	20
Coleoptera	Oedemeridae	*Oedemera flavipes*	2
Coleoptera	Oedemeridae	*Oxythyrea funesta*	6
Hymenoptera	Andrenidae	*Andrena* sp.	1
Hymenoptera	Megachilidae	*Anthidium* sp.	5
Hymenoptera	Megachilidae	*Anthidium sticticum*	2
Hymenoptera	Apoidea	*Apis melifera*	33
Hymenoptera	Apoidea	*Bombus terrestris*	18
Hymenoptera	Formicidae	*Camponotus aetiops*	7
Hymenoptera	Halictidae	*Halictus pirenaicus*	5
Hymenoptera	Colletidae	*Hylaeus nigritus*	2
Hymenoptera	Halictidae	*Lasioglossum* sp.	3
Hymenoptera	Scolidae	*Scolia* sp.	2
Hymenoptera	Anthophoridae	*Xylocopa violacea*	15