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Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands

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Abstract

Invasive plant species are often considered as potential competitors of native species due to their usually greater capacity for colonization and expansion, but we still have scarce information on whether invasives can also compete for pollination services with natives. In the present study, we hypothesized that the showy flowers of the highly invasive *Carpobrotu* spp. can compete with native species (*Cistus monspeliensis*, *Cistus salviifolius*, *Anthyllis cytisoides* and *Lotus cytisoides*) with which it shares habitat and flowering time, influencing pollinator visitation. To test this, we censused insects visiting the flowers of native species in the field and recorded the number of flowers visited in adjacent areas with and without the presence of *Carpobrotus*. We also assessed the presence of exotic pollen on stigmas of native species and evaluated its effect on reproduction. We detected potential competition for pollinators only in one native species (*L. cytisoides*), a facilitative effect in two other species (*C. salviifolius* and *A. cytisoides*), and a neutral effect in a fourth one (*C. monspeliensis*). Moreover, such effects appear not to be consistent in time. The presence of *Carpobrotus* pollen on native stigmas was almost negligible, and hand-pollination experiments showed that such exotic pollen does not interfere significantly with native pollen, not affecting seed set. Our results indicate that the role of the invasive *Carpobrotus* in promoting or constraining the natural pollination dynamics is likely to have species specific effects on the native flora.
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1. Introduction

An increasing number of studies have demonstrated that invasive alien species are important competitors with native species for resources such as nutrients, water or light (e.g. Wardle et al., 1994; Weihe and Neely, 1997; Mack and D'Antonio, 1998) or simply for space (Newsom and Noble, 1986). Such competition often negatively affects the population growth of native species (e.g. Huenneke and Thomson, 1995; Randall, 1996; Williamson, 1996; Mack and D'Antonio, 1998; Gordon, 1998; Zavaleta et al., 2001). In contrast, little informa-

tion exists on the extent to which invasives compete for pollinator services with the native flora, with likely harmful consequences for the latter. The only three systems studied so far consist of the invasive *Lythrum salicaria* and the native congener *L. alatum* (Grabas and Laverty, 1999; Brown and Mitchell, 2001; Brown et al., 2002), the invasive *Impatiens glandulifera* inducing pollinators from native species such as *Stachys palustris* in central Europe (Chittka and Schürkens, 2001) and the invasives *Cakile maritima* and *Carpobrotus* spp. that coexist with the native *Dithyrea maritima* in southern California (Aigner, 2004). Many flowering plants depend upon pollinators for successful reproduction, and consequently the abundance and behaviour of pollen vectors may be an important ecological factor influencing seed production (reviewed in Burd, 1994).

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Invaders, especially those with showy flowers, can potentially influence either the quantity or the quality, or both, aspects of pollination. Many surveys of pollination systems reveal an inherent pollinator preference for large flowers and for long floral periods (Campbell, 1989; Ohara and Higashi, 1994; Schemske and Ågren, 1995; Connor and Rush, 1996). The *quantitative component* of pollination is a function of the number of insect visits, the number of flowers visited, and the amount of pollen deposited on the stigmas. By having 'more attractive' (larger or more rewarding) flowers, an invader may significantly reduce the number of pollinator visits to natives (Brown et al., 2002; Parker and Haubensak, 2002). Alternatively, although pollination facilitation between species appears to be rare (or has been rarely documented; Feldman et al., 2004 and references therein), an invasive species might facilitate the arrival of pollinators to native flowers, increasing visitation rates and, ultimately, reproductive success. The *qualitative component* of pollination, on the other hand, depends upon traits such as pollen source (e.g., distance from male donors to female targets), pollinator efficiency (the capacity of pollinators to deposit pollen in the adequate place) and ''purity'' of the pollen (i.e., whether it is conspecific or it is mixed with pollen grains from other species). Interspecific pollen transfer, in particular, can lead to strong competitive effects when pollen availability, stigma receptivity, or pollinator movements are limited (Waser, 1978; Campbell and Motten, 1985; Caruso and Alfaro, 2000; Brown et al., 2002).

The genus *Carpobrotus* is especially invasive along the coast of the western Mediterranean Sea (Suehs et al., 2004a,b). In this study, we examined the impact of two species, *Carpobrotus acinaciformis* (L.) L. Bol. (which is actually a dubious taxon due to the high capacity to hybridize with other *Carpobrotus* species and that is why it is also cited as *C. affine acinaciformis*; Suehs et al., 2001) and *Carpobrotus edulis* (L.) N. E. Br., on quantitative and qualitative components of pollination success of four native species. Specifically, we compared pollinator services between invaded and adjacent non-invaded stands. The questions we addressed were: (1) do native species and the exotic share pollinators? (2) is there a potential competitive or facilitative effect between the invasive and the native plants for pollinator services? (3) how commonly does heterospecific pollen transfer occur and does it affect seed set in native species?

2. Methods

2.1. The species and study sites

The *Carpobrotus* taxa (Aizoaceae) are immediately recognizable in the field by their trailing habit and long,

robust internodes. Flowers are solitary, actinomorphic and up to 120 mm in diameter. Stamens and petals are numerous (400–600 and 120–130, respectively), and the 8–18 pistils are centrally arranged and spread to a star shape at maturity (Wisura and Glen, 1993). *C. edulis* is the only member of its genus that has distinctly yellow flowers, while *C. affine acinaciformis* typically has magenta flowers. Both taxa are considered a serious threat to several protected plant species in the Balearic Islands (e.g. Vilà and Muñoz, 1999; García, 1999) as well as to others in other Mediterranean islands (Suehs et al., 2001).

Two of the native species studied belong to the Cistaceae family (*Cistus monspeliensis* L. and *Cistus salviifolius* L.), having actinomorphic white flowers with numerous yellow stamens, while the other two are in the Fabaceae (*Anthyllis cytisoides* L. and *Lotus cytisoides* L.), bearing typical zygomorphic yellow flowers that require pollinator tripping. The study took place on Mallorca, the largest island in the Spanish Balearic archipelago (Western Mediterranean). We selected two localities with calcareous substrate where *Carpobrotus* was present: Cala Figuera, a rocky coast habitat at the southwest, and Son Serra de Marina (Son Serra, hereafter), a dune environment at the north (Fig. 1).
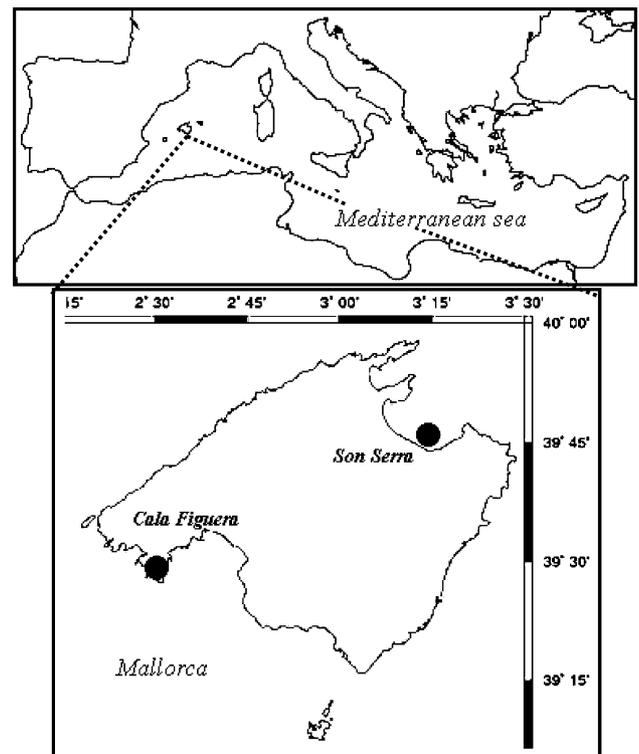

Fig. 1. Map of the Mediterranean Sea and of Mallorca Island with the experimental localities shown.

2.2. Experimental procedures and statistical analyses

2.2.1. Selfing rates of native species

Before assessing if native species share pollinators with *Carpobrotus* species, our concern was to determine if they are autogamous or whether they need pollinators in order to produce seeds. Before flower anthesis, we bagged flowering branches with white cloth bags that did not allow the passage of pollen, counting the number of floral buds within each bag. After flower senescence, we removed the bags and counted the number of developing fruits in them. On the same individuals, we marked branches that were used as control (open pollination). We used a total of 14 individuals of *A. cytisoides* (1106 control vs. 767 selfed flowers), 14 individuals of *C. monspeliensis* (115 control vs. 221 selfed flowers), 10 individuals of *C. salviifolius* (93 control vs. 96 selfed flowers) and 10 individuals of *L. cytisoides* (100 control vs. 100 selfed flower), although samples sizes were somewhat reduced due to vandalism. The experiment was carried out during the spring of 2001. *A. cytisoides* and *C. monspeliensis* were studied at Cala Figuera (were *C. acinaciformis* is present) whereas *C. salviifolius* and *L. cytisoides* were studied at Son Serra, where they coexist with *C. edulis*.

We compared seed set between control and bagged flowers for each species by means of a paired *t* test. In the case of *A. cytisoides*, no analyses was performed as seed set for the selfing treatment was nil in all individuals. The software employed was STATISTICA v. 6.0 (Statsoft 2001).

2.2.2. Quantitative component of pollination: censuses of flower visitors

Observations on insect flower visitors were made during the springs of 2002 and 2003, on stands of native species sympatric with a *Carpobrotus* population ("mixed" stands) and on adjacent stands with no *Carpobrotus* present ("pure" stands).

During the flowering peak of each year, censuses of 15 min were made on a minimum of 15 individuals of each species (native and invasive) in each stand and locality. Observations took place between 9 am and 6 pm, on sunny and calm days, and were randomly performed in each stand. Pure and mixed stands were separated by at least 50 m from each other, depending upon locality. A total of 11.5 h of observations in the pure stands, and a total of 30 h in the mixed stands were made. In each census we recorded: (1) the number of insects visiting flowers; (2) the insect species identity (at least to the family level, when species or genus was unknown); (3) the number of open flowers in each censused individual.

As data could not be normalized with any transformation, we performed a generalized linear model (GEN-MOD), using a Poisson error distribution and a power link function. A separate analysis was done with each dependent variable: (1) number of insect visits; (2) number of flowers visited per census, using type of stand and year as fixed factors and number of open flowers at each census as a covariate.

2.2.3. Qualitative component of pollination
2.2.3.1. Pollinator efficiency.
We examined stigmas of native flowers on mixed stands to assess the presence of *Carpobrotus* pollen on them. We collected a total of 90 flowers from each native species (10/indiv., 9 indiv.) at three different distances from a *Carpobrotus* patch (close: <10 m; intermediate: 10–30 m and far: >30 m; 30 flowers/distance). Flowers were collected a short time before sunset, when pollinators' activity was practically finished, and inserted into small vials with alcohol (70%) to fix pollen grains settled on stigmas. In the laboratory, stigmas were extracted and placed in distilled water, and pollen grains were counted on them by means of a haemocytometer under a binocular microscope.

The low levels of exotic pollen found on native stigmas did not allow to perform a statistical analysis of the data.

2.2.3.2. Effect of heterospecific pollen on native seed set.
We examined this only on the two native species of *Cistus* because of the difficulty of working with the leguminous flowers. In each of five individuals of the two *Cistus*, we applied three different treatments: (1) hand-pollination with exotic *Carpobrotus* pollen (named hereafter aliengamy); (2) mixture of *Carpobrotus* and species' own pollen (always from other individuals) (hereafter, mixgamy); (3) legitimate native pollen also from conspecific individuals (xenogamy). A fourth group of flowers was used as a control (open pollination). Ten flowers per individual were used for each treatment and control. The experiments were performed during the 2003 spring. For the mixture treatment, we gathered fresh pollen from various *Carpobrotus* and *Cistus* individuals and we mixed them with a thin paintbrush in a small Petri dish before hand-pollinated targets. Exotic and native pollen of each *Cistus* species was also collected in separate Petri dishes. Pollen was added at anthesis time, when stigmas were fully receptive.

After hand-pollination, we marked the persistent floral stem of each pollinated flower with a different coloured label for each treatment. At the end of the experiment, all fruits were collected and weighted. The tiny (1.0–1.5 mm) seeds within each fruit were counted and weighted. For *C. monspeliensis*, the final number of flowers from which we could obtain seed set data for each treatment was: $n = 38$ (aliengamy), $n = 46$ (xenogamy), $n = 44$ (mixgamy) and $n = 37$ (control). For *C. salviifolius*, many fruits aborted and fell down at an early stage, and in this case we could gather data from only two individuals: $n = 6$ (aliengamy),

$n = 11$ (xenogamy), $n = 3$ (mixgamy) and $n = 12$ (control); thus, results on this species need to be taken with caution.

Variation in both number of seeds per fruit and fruit weight among treatments was tested by performing a General Linear Model with a normal distribution for each species and for each dependent variable, using treatment and individual as the independent variables. As all treatments were applied to each individual, we considered a repeated measures design with individual as subjects and treatment as a fixed factor.

3. Results

3.1. Dependency of native plant species upon pollination vectors

The bagging experiments revealed very low selfing rates in the native species; they were even nil in the case of *A. cytisoides*. Fruit set in bagged flowers was consistently lower than in control ones (Table 1), implying that the four native species do need pollination vectors for their reproductive success.

3.2. Effect of Carpobrotus flowers on insect flower visitation to native species

In Cala Figuera, both insect and flower visitation rate to *A. cytisoides* were higher in the mixed than in the pure stand (0.004 for insect visitation and $\chi^2 = 8.75$, $P = 0.008$ for flower visitation), and this was consistent between years ($\chi^2 = 0.34$, $P = 0.56$ and $\chi^2 = 0.03$, $P = 0.87$, respectively; interaction not significant; Fig. 2). In contrast, non-significant differences were observed in *C. monspeliensis* between stands ($\chi^2 = 1.70$, $P = 0.19$ for insect visitation, and $\chi^2 = 0.58$, $P = 0.45$ for flower visitation, respectively), although differences existed between years ($\chi^2 = 59.93$, $P < 0.001$ and $\chi^2 = 15.80$, $P < 0.001$, respectively) (Fig. 2). In Son Serra, both variables differed significantly between stands for *C. salviifolius* ($\chi^2 = 8.80$, $P = 0.003$ for insect visitation and $\chi^2 = 6.00$, $P = 0.005$ for flower visitation), being greater in the mixed than in the pure stand (Fig. 2) and between years ($\chi^2 = 10.94$ and 11.203, respectively, $P < 0.002$). Such

differences were only significant in 2003, and that is why the interaction stand × year was significant ($P < 0.01$). The other species at Son Serra, *L. cytisoides*, showed also inconsistent results: considering both years, stands were not found to differ significantly ($\chi^2 = 0.42$, $P = 0.52$), but years did differ ($\chi^2 = 5.43$, $P = 0.02$) and there was a significant interaction ($\chi^2 = 4.02$, $P = 0.04$) because both variables were much higher for the pure than for the mixed stand only in 2003. This year, thus, a potential competitive effect between the exotic and this native plant was detected (Fig. 2).

3.2.1. Insect guilds visiting the flowers of native species
The main insect orders that visited native species were Hymenopterae, Dipterae and Coleopterae (Table 2). Ants (the family Formicidae) were also observed on the flowers of three of the species. Hymenopterans (mainly bees) were dominant in all native species, although beetles were also quantitatively important. A high fraction of insect species were shared between native plants and *Carpobrotus* (over 50%; Table 3).

3.3. Presence of Carpobrotus pollen on stigmas of native species

We recorded exotic pollen on native stigmas only in the two species studied at Son Serra (*C. salviifolius* and *L. cytisoides*). For *C. salviifolius*, heterospecific pollen was found only occasionally: in 3 out of 90 flowers examined (and in all cases at a distance <10 m from any flowering *Carpobrotus*). The levels of heterospecific pollen were very low (only $0.59 \pm 0.39\%$ of all pollen grains recorded corresponded to *Carpobrotus*). For *L. cytisoides*, heterospecific pollen was also found occasionally in 2 out of 90 flowers observed (in this case at a distance >30 m), and again the proportion of *Carpobrotus* pollen grains was negligible ($1.14 \pm 0.86\%$).

3.4. Effect of heterospecific pollen on seed set of Cistus

In the case of *C. monspeliensis*, results revealed significant differences ($F_{3,105} = 18.24$, $P < 0.0001$) among treatments in the number of seeds/fruit (which was highly correlated with weight of seeds/fruit: $r = 0.89$,

Table 1
Percentage (mean ± SE) of flowers of each native species that set fruit in the control (open pollination) and in the autogamy treatment

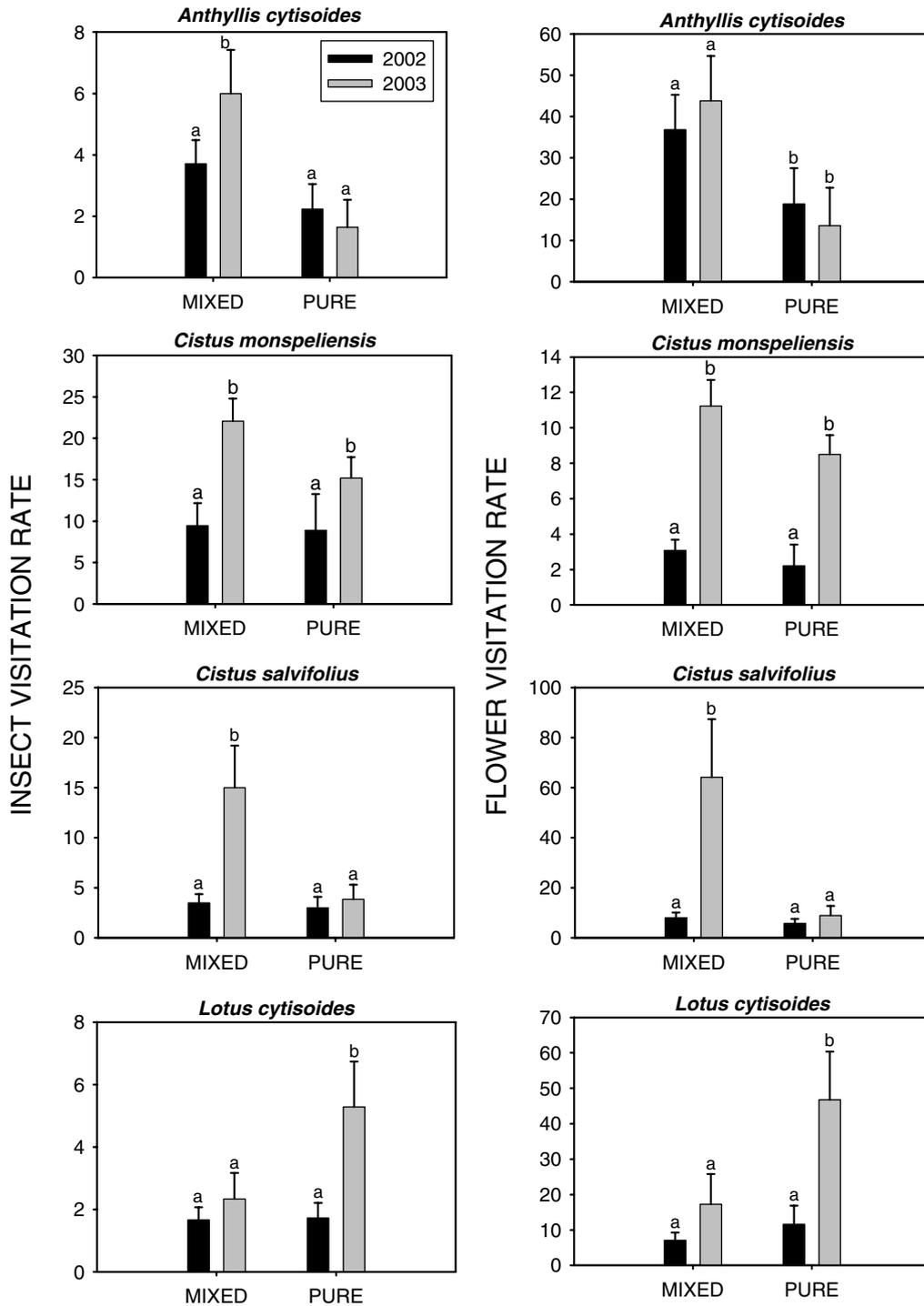|	Control flowers	Selfed flowers	n	df	t	P
A. cytisoides	0.65 ± 0.05	0.00 ± 0.00	14	–	–	–
C. monspeliensis	0.31 ± 0.04	0.17 ± 0.07	9	8	2.650	=0.029
C. salviifolius	0.65 ± 0.06	0.14 ± 0.05	9	8	7.065	<0.001
L. cytisoides	0.53 ± 0.11	0.08 ± 0.06	10	9	4.302	<0.001

Fig. 2. Mean insect and flower visitation rates (number of insect visits and number of flowers visited per census of 15 min, respectively) in the mixed and pure stands for each native species. Standard error bars are shown. Different letters on bars indicate significant differences ($P < 0.001$ or $P < 0.05$).

$P < 0.0001$), being higher for xenogamy than for the rest of treatments, lowest for aliengamy and controls, and intermediate between these two groups for mixgamy (Tukeys' HSD test) (Fig. 3). Such results suggested, thus, the possibility of pollen limitation. Unexpectedly, aliengamy ('pure' *Carpobrotus* pollen) re-sulted in a similar number of seeds per fruit as the con-trols, which indicates no interference of exotic pollen on seed set. The correlation between number of seeds and fruit weight was rather low ($r = 0.30$, $P < 0.0001$). Fruit weight was similar among treatments ($F_{3,111} = 0.59$, $P = 0.62$).

Table 2
Species of each insect order observed visiting the flowers of the study native plants

			Hymenoptera	Diptera	Coleoptera	Formicidae[a]
Cala Figuera	CA	AC	*Apis mellifera*	Sarcophagidae	Cantharidae	–
			Lasioglossum sp.			
		CM	*Apis mellifera*	*Lucilia sericata*	*Psilothrix* sp.	*Crematogaster scutellaris*
			Lasioglossum sp.		Meliodae	unidentified sp.
			Polistes omisus		Oedemeridae	
Son Serra	CE	LC	*Dasycolia ciliate*	–	Cantharidae	*Plagiolepis pygmaea*
			Halictus sp.			unidentified sp.
		CS	*Dasycolia ciliate*	–	*Oedemera flavipes*	unidentified sp.
			Polistes omisus		*Psilothrix* sp.	
			Lasioglossum sp.		Meliodae	
			Halictus sp.		Cantharidae	
					Cetonidae	

CA, *Carpobrotus acinaciformis*; CE, *Carpobrotus edulis*; AC, *Anthyllis cytisoides*; CM, *Cistus monspeliensis*; LC, *Lotus cytisoides*; CS, *Cistus salviifolius*.
[a] The family Formicidae is considered separately because of the special behavior of ants on flowers.

Table 3
Number of insect species observed on each native species at each locality and at each stand (Mixed, with presence of *Carpobrotus*, Pure, with *Carpobrotus* absent) and absolute and relative numbers of species that are shared between each native plant and the invasive

Locality	Native plant species	Type of stand	Number of species visiting flowers	Insects shared between native and invasive
Son Serra	*C. salviifolius*	Mixed	10	8 (80%)
		Pure	12	9 (75%)
	L. cytisoides	Mixed	9	5 (55.6%)
		Pure	7	3 (42.9%)
Cala Figuera	*A. cytisoides*	Mixed	9	4 (44.4%)
		Pure	7	5 (71.4%)
	C. monspeliensis	Mixed	14	10 (71.4%)
		Pure	15	10 (66.7%)

In the case of *C. salviifolius*, we found no significant differences among treatments, either in the number of seeds per fruit ($F_{3,9} = 1.73$, $P = 0.23$) or in fruit weight ($F_{3,12} = 1.82$, $P = 0.20$). As in *C. monspeliensis*, these two variables were significantly correlated ($r = 0.70$, $P < 0.0001$). In contrast to that species, though, *C. salviifolius* showed no pollen limitation as the addition of xenogamous pollen did not increase the number of seeds produced per fruit. The mixgamy treatment tended to decrease that parameter, although the addition of *Carpobrotus* pollen alone had no effect on it (Fig. 3).

4. Discussion

All native species examined in this study strongly depended on pollinator vectors, as indicated by their low levels of selfing. Hence, any change in the frequency of insect visits or in the insects' foraging behaviour due to the presence of an exotic plant species in their 'environment' is likely to alter their reproductive success.

The consequences of competition for pollination services on seed set have been studied in a wide variety of systems and different outcomes have been found to vary from negative (reduced seed set; e.g. Brown et al., 2002 and references therein) to positive (increase seed set; e.g., Rathcke, 1988; Gross, 1996), or even neutral effects (e.g. Kunin, 1997; Caruso, 1999). All these possibilities were observed in our study system. Despite the greater nectar and pollen rewards of *Carpobrotus* flowers, a negative (competitive) effect on both insect and flower visitation rates was found only in *L. cytisoides*. On the contrary, the presence of *Carpobrotus* flowers appeared to facilitate insect visitation to flowers of two species: *C. salviifolius* and *A. cytisoides*. With such result, thus, we argue that pollination facilitation among plants may not be as rare as previously thought (Feldman et al., 2004). What is certainly more difficult, and was not the goal of this study, is to assess that an increased insect visitation rate translates into an increased population growth rate (e.g. Parker, 2000; Feldman et al., 2004). The possibility that *Carpobrotus* flowers had a neutral effect on
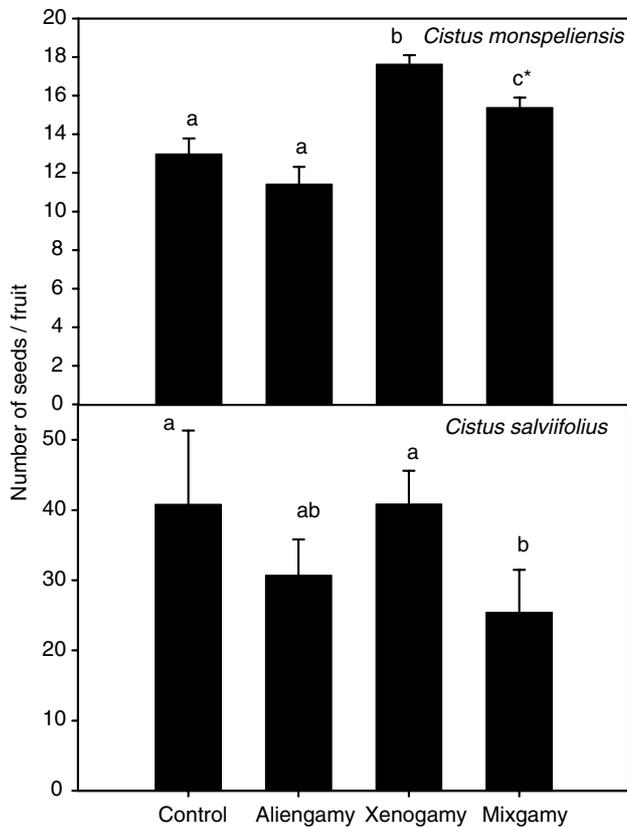
Fig. 3. Mean number of seeds per fruit for *Cistus monspeliensis* and *Cistus salviifolius* produced in the applied treatments (see text for details) and the control. Standard error bars are shown. Different letters on bars indicate significant differences (*P* < 0.001) (Tukey's HSD test). The * indicates a significant difference at *P* < 0.05 between c and b.

pollinator attractiveness to other species was found with the other species, *C. monspeliensis*.

Such effect of *Carpobrotus* flowers on insect flower visitation to a particular native plant species may vary spatially and temporally. Preliminary observations made in southern France, specifically in Bagaud (Hyères Islands) (C. Suehs, unpublished data), suggested that *Carpobrotus* had a negative effect on *C. monspeliensis* and a neutral effect on *C. salviifolius*. On the other hand, our data from two years showed significant differences in two of the species examined; both in *L. cytisoides* and *C. salviifolius*, the effect of *Carpobrotus* was significant in 2003 but not the previous year. These results indicate, thus, that this type of study needs to consider more than one population and field season to generalize on the degree to which exotic species influence pollination success of native plants. The link between fluctuating pollination success and fluctuating reproduction may be mediated by the population dynamics of pollinators (Thompson, 2001). It is well known, for instance, that insect community composition and abundances can vary much from year to year, as well as their effect on plant reproduction (e.g. Aigner, 2004). Many factors

can indeed influence reproduction, adding variability to the relationship between visitation and fruit set (Parker and Haubensak, 2002). Such temporal unpredictability, of even the most effective pollinator, is what actually appears to favour generalization in most species (Waser et al., 1996).

A large proportion of the insect visitors are shared between the native species examined and the exotic *Carpobrotus* spp. Hymenopterans were the most abundant flower visitors at both localities, although beetles were also quantitatively important. As expected from their flower morphology, the two *Cistus* species shared a higher number of insect visitors with *Carpobrotus* than the two leguminous species.

The levels of heterospecific pollen on native stigmas were rather low (and only in *C. salviifolius* and *L. cytisoides*), suggesting that *Carpobrotus* does not reduce reproductive success of native plants through this mechanism of competition. In the case of *L. cytisoides*, the only species that potentially compete with *Carpobrotus* for insect visits, the low levels of heterospecific pollen found in its stigmas indicate that reproductive success (measured as number of seeds/fruit) is almost unaffected by such pollen interference. The question remains though whether the lower frequency of insect visits in mixed stands translates into a lower seed production. The *Carpobrotus* flowering boom occurs simultaneously with that of many native species, so pollinators are not resource limited. The low levels of heterospecific pollen found on native stigmas might be due to an abundant (not limiting) nectar and/or pollen of such natives, and perhaps also to a higher quality of those resources. Assessing this would certainly require information not gathered in this study.

The addition of exotic pollen on the stigmas of both *Cistus* species was shown to be irrelevant for pollination success. In both cases, the pollen grains of *Carpobrotus* appeared not to obstruct, either partially or totally, the stigma as the number of seeds produced per fruit was unaffected. Such findings contrast with those reported by Brown et al. (2002), probably because in that case the invasive and the native species were congeneric, which makes a pollen germination interference much more likely.

In summary, our results suggest that the invasive *Carpobrotus* spp. may influence the quantitative component of pollination, either positively (in *A. cytisoides* and *C. salvifolius*) or negatively (in *L. cytisoides*), although may also have no effect on it. Regarding the qualitative component of pollination, we found that the seed production of at least two *Cistus* species is not altered by the exotic pollen. As this invasive species has spread and is still spreading very rapidly along the Mediterranean coastal areas, it will be interesting to examine its impact on other native flora in future studies. From the conservation viewpoint, it should be kept in mind

that its influence on the pollination of native plants is likely to be species specific, that it may depend upon the ecological context (i.e. the environmental conditions prevailing at a given site), and that it can vary from year to year, along with fluctuations in other factors (insect abundance, composition, flower abundance of other native plants, etc.).

Acknowledgements

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