

## Effect of *Carpobrotus* spp. on the pollination success of native species. Interspecific pollen transfer as a mechanism of competition

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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 *Carpobrotus* spp. can compete with native species (*Cistus monspeliensis*, *Cistus salvifolius*, *Anthyllis cytisoides*, *Anthyllis barba-jovis*, *Lotus cytisoides*, and *Senecio leucanthemifolius*) with which it shares habitat and flowering time, influencing pollinator visitation. To test this, we censused insects visiting the flowers of the native species in the field and also the number of flowers visited. The study was performed on sites where native species occur sympatrically with either *C. affine acinaciformis* or *C. edulis* ('mix' stands) and on sites isolated from this exotic species ('pure' stands). Over two years of study in two islands of the western Mediterranean: Mallorca (Balearic Islands) and Bagaud (Hyères Islands), and on the adjacent mainland to Bagaud, we found that *Carpobrotus* spp. shares pollinators with all these native species. While we detected potential competition for pollinators in three cases (for *Cistus monspeliensis* in Bagaud island, for *A. barba-jovis* in the French mainland, and for *Lotus cytisoides* in Mallorca) we also found there was a facilitative effect in tree other species (*Cistus salvifolius* and *Anthyllis cytisoides* in Mallorca island and *Senecio leucanthemifolius* in Bagaud island). For the rest of the species, the presence of the exotic did not appear to have any effect neither on the frequency of pollinator visits nor on the number of flowers visited. We found spatial variation in such potential effects on pollination success, as *C. monspeliensis* was affected in Bagaud but not in Mallorca, whereas the opposite occurred with *L. cytisoides*. Moreover, we observed temporal variation in the effect of *Carpobrotus* on native species: while in 2002 we found no much evidence of either facilitation or competition in Mallorca, in 2003 -with greater pollinator activity- we did find such evidence.

### 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 et al 1998, Guix et al 2000) or simply for space (Newsome & Noble 1986). Such competition often negatively affects the population growth of native species (Huenneke and Thomson 1995, Randall 1996, Williamson 1996, Mack et al 1998, Gordon 1998, Zavaleta 2001). In contrast, little information exists on the extent to which invasives compete for pollinator services with the native flora, with likely harmful consequences for the latter. The only two sys-

tems studied so far consist of the invasive *Lythrum salicaria* and the native congener *L. alatum* (Grabas and Lavery 1999, Brown and Mitchell 2001, Brown et al. 2002) and the invasive *Impatiens glandulifera* bribing pollinators from native species such as *Stachys palustris*, *Lythrum salicaria*, and *Epilobium hirsutum* in central Europe (Chittka and Schürkens 2001).

Invaders, especially those with showy flowers, can potentially influence either the quantity or the quality, or both, aspects of pollination. The *quantity component* is a function of the number of insect visits, the number of flowers visited, and the amount of pollen deposited on the stigmas, which ultimately determine the success of fruit and seed production. Such components will be negatively affected if the invader reduces the number of pollinator visits to natives (by having 'more attractive flowers'). However, it may also happen that an invader facilitates the arrival of pollinators to native flowers, which might not be visited otherwise, increasing visitation rates and, ultimately, the fitness of native plants. The *quality component* of pollination, on the other hand, depends upon traits such as pollen source (for instance, distance from males to females), "purity" of the pollen (i.e., whether it is mixed with other types of pollen or is monospecific), and pollinator efficiency (the capacity of the pollinators to deposit pollen in the adequate place).

In this study, we examined the impact of *Carpobrotus affine acinaciformis* (L.) L. Bol. and *Carpobrotus edulis* (L.) N. E. Br., an invasive genus along the coast of the western Mediterranean Sea, on the pollination success of native species (estimated here as the frequency of insect flower visitors and the number of flowers visited, regardless the efficiency of pollination of the different insect flower visitors). *C. affine acinaciformis* was studied on the islands of Mallorca and Bagaud (Hyères Islands) and a continental site in southeast France, whereas *C. edulis* was studied only in Mallorca. Specifically, we compared pollinator service between populations of a total of six native species sympatric with *Carpobrotus* ("mix" populations) and adjacent populations that do not coexist with this invasive ("pure" populations). The questions addressed in this paper were: (1) Do native species and the exotic share any pollinator species? and (2) Is there a potential competitive or facilitative effect between the invasive and the native plants for pollinator services?

The qualitative component of pollination (and the effect of heterospecific pollen on seed set of native species) were examined only in Mallorca and results are presented in another paper (Mora-gues, E. & Traveset, A. in prep.)

## 2 METHODS

### 2.1 Study species and study sites

The *Carpobrotus* taxa studied are robust, trailing succulents with finger-shaped leaves and a mat-forming habit. Flowers are solitary, actinomorphic and up to 120 cm in diameter (Blake 1969, Wisura and Glen 1993). Stamens and petals are numerous (400-600 and 120-130, respectively), and the 8 to 18 pistils are centrally arranged and spread to a star shape at maturity (Blake 1969, Wisura and Glen 1993). *C. edulis* (L.) N. E. Br is the only member of its genus to have distinctly yellow flowers, while *C. affine acinaciformis* (L.) L. Bol. typically has magenta flowers (Suehs et al. in press). Both taxa are considered a serious threat to several locally threatened or protected plant species in both France (Suehs et al. 2001) and the Balearic islands of Spain (Vilà and Muñoz 1999).

The native species studied include *Lotus cytisoides* L., *Cistus monspeliensis* L., *Cistus salvifolius* L., *Anthyllis barbajovis* L., *Anthyllis cytisoides* L., and *Senecio leucanthemifolius* Poir. *C. monspeliensis*, *C. salvifolius*, and *S. leucanthemifolius* all have actinomorphic flowers, while *L. cytisoides* and the two *Anthyllis* species are Fabaceae, and have typical zygomorphic flowers that require pollinator tripping. *S. leucanthemifolius*, *A. cytisoides* and *L. cytisoides* all have yellow flowers, while *A. barbajovis* and both *Cistus* species have white flowers.

The study took place on the eastern Spanish island of Mallorca and in southeast France. For each country we selected two localities where *Carpobrotus* spp. was present. In Mallorca, the localities were: Son Serra (sandy environment situated at the north of the island) and Cala Figuera (rocky coast at the southwest). The French localities were Bagaud Island (Hyères Islands) and the adjacent

mainland at Brégançon, both of which are very similar as regards their typical shrubland communities and siliceous substrate.

## 2.2 Censuses of flower visitors

Observations on insect flower visitors were carried out during the springs of 2002 in France and those of 2002-2003 in Spain, on stands of native species sympatric with a *Carpobrotus* population ("mix") and occurring isolated from *Carpobrotus* populations ("pure"), as well as for *Carpobrotus* itself. The species studied in each locality at both regions are shown in Table 1.

Table 1. Study species and stands in both countries.

	FRANCE		SPAIN	
	Bagaud Is. (Hyères Islands)	Brégançon (Mainland)	Son Serra (Mallorca)	Cala Figuera (Mallorca)
Exotic species	<i>C. affine acinaciformis</i>		<i>C. edulis</i>	<i>C. affine acinaciformis</i>
	<i>Cistus monspeliensis</i>	Anthyllis barbajovis	<i>Cistus salvifolius</i>	<i>Cistus monspeliensis</i>
Native species	<i>Lotus cytisoides</i>		<i>Lotus cytisoides</i>	<i>Anthyllis cytisoides</i>
	<i>Senecio leucanthemifolius</i>			

During the flowering peak, censuses of 15 min were made on a minimum of 15 individuals of each species in each stand. Observations took place between 9 am and 6 pm, on sunny and not windy days, and were randomly performed in the two stands (mix vs. pure). In each census we recorded: (1) the number of insects visiting flowers, (2) the insect species identification (at least to the order level, when species or genus was unknown), and (3) the number of open flowers observed in each censused individual. Simultaneous observations were also made on *Carpobrotus* in order to determine which insects groups were shared between the exotic and the native species.

## 2.3 Statistical analyses

To compare the number of insect visits and the number of flowers visited per census between pure and mix stands, we performed two-way analyses of variance for Mallorca data, using type of stand and year as the independent variables, and the number of flowers observed as a covariate. For France, data were available only for 2002, so we carried out a one-way analysis of variance, also controlling for the number of flowers observed in each census.

# 3 RESULTS

## 3.1 Effect of *Carpobrotus* on insect flower visitation to native species

The two species simultaneously studied in France and Spain showed different results in the two regions. *Cistus monspeliensis* in Bagaud island had a higher number of insect visits and flowers visited in the pure than in the mix stand, suggesting a potentially competitive effect of *Carpobrotus* on this species. In Mallorca, in contrast, no significant differences were observed between stands either in 2002 or 2003 (Figs. 1 and 2). For *Lotus cytisoides*, we did not find significant differences between stands in Bagaud and we observed inconsistent results in Mallorca: while in 2002 no significant differences were observed in frequency of insect visits and number of flowers visited, in 2003 these variables were higher in the pure than in the mix stand, suggesting also a possible competitive effect between the exotic and the native plant (Figs. 1 and 2).

For *Cistus salvifolius*, the effect of stand, year, and the interaction between these two factors were all significant, either on the frequency of insect visits or on the number of flowers visited. In this case, the presence of *Carpobrotus* flowers appeared to increase these two variables, and thus had a potentially facilitative effect, but only in 2003 (Fig. 2).

As in the case of *C. salvifolius*, we obtained significant differences between stands in the number of insect visits and flowers visited for *Anthyllis cytisoides*. Both dependent variables were higher in the mix stand than in the pure one, and this was consistent between years (Fig.2).

For the other species of *Anthyllis* (*A. barbajovis*, from the mainland), the opposite occurred: both the number of insect visits and flowers visited were significantly greater in the pure stand than in the mix one (Fig. 1).

In *Senecio leucanthemifolius*, the number of insect visits was significantly higher in the mix stand, suggesting a facilitative effect of *Carpobrotus*. However, such higher frequency of visits did not translate into a higher number of flowers visited (Fig. 1).

### 3.2 Insect guilds visiting the flowers of native species

The main insect orders that visited native species were Hymenopterae, Dipterae and Coleopterae. Ants (the family Formicidae) were also observed, although only in Mallorca. In France, bees and wasps were the main (or only) visitors of all studied species. In Mallorca, the diversity of insects visiting the flowers of native species was higher than in France. Hymenopterans were dominant, although Coleopterans (beetles) had also an important role as pollinator vectors, at least quantitatively. Dipterans (flies of different sizes) were mainly observed at the southern population of Mallorca (Cala Figuera), on *A. cytisoides* and on *C. monspeliensis* (Table 2).

Table 2. Minimum number of species for each insect order observed. (\*) The family Formicidae is considered separately because of the special behaviour of ants on flowers. CA: *Carpobrotus affine acinaciformis*; CE: *Carpobrotus edulis*; AC: *Anthyllis cytisoides*; CM: *Cistus monspeliensis*; LC: *Lotus cytisoides*; CS: *Cistus salvifolius*; AB: *Anthyllis barbajovis*; SL: *Senecio leucanthemifolius*

			Hymenoptera	Diptera	Coleoptera	Formicidae*			
FRANCE	SPAIN	Cala Figuera (Mallorca)	AC	2	1	1	0	4	
			CA	CM	3	2	3	1	10
					5	3	4	1	
		Son Serra (Mallorca)	CE	LC	2	0	1	2	5
				CS	4	0	5	1	10
					6	0	6	3	
	Brégançon (Mainland)	CA	AB		3	0	0	0	3
					3	0	0	0	
						5	1	1	0
		Bagaud (Hyères Is.)	CA	CM	5	1	1	0	7
				LC	4	1	1	0	6
				SL	3	1	1	0	5
			7	2	2	0			

When examining the insect species shared between the native and the exotic species, we found that this was a high fraction (over 50% in Mallorca and 100% in France; Table 2). In Mallorca, the two *Cistus* species were found to share a higher number of insect species with *Carpobrotus* than the two leguminous species in the genus *Lotus* and *Anthyllis*.

Table 3. Number of insect species observed on the native species at each locality and in each region, and absolute and relative number of species that are shared between each native plant and the invasive.

			Total diversity of flower visitors	Insects shared between native and invasive	% Insect shared
SPAIN	Son Serra (Mallorca)	<i>C. salvifolius</i> MIX	10	8	80
		<i>C. salvifolius</i> PURE	12	9	75
		<i>L. cytisoides</i> MIX	9	5	55.55
		<i>L. cytisoides</i> PURE	7	3	42.86
	Cala Figuera (Mallorca)	<i>A. cytisoides</i> MIX	9	4	44.44
		<i>A. cytisoides</i> PURE	7	5	71.43
		<i>C. monspeliensis</i> MIX	14	10	71.43
		<i>C. monspeliensis</i> PURE	15	10	66.67
	Bagaud (Hyères Is.)	<i>C. monspeliensis</i> MIX	6	6	100.00
		<i>C. monspeliensis</i> PURE	6	6	100.00
		<i>L. cytisoides</i> MIX	3	3	100.00
		<i>L. cytisoides</i> PURE	6	6	100.00
FRANCE	Brégançon (Mainland)	<i>S. leucanthemifolius</i> MIX	3	3	100.00
		<i>S. leucanthemifolius</i> PURE	4	4	100.00
		<i>A. barbajovis</i> MIX	3	2	66.67
		<i>A. barbajovis</i> PURE	3	3	100.00

#### 4 CONCLUSIONS

This study revealed that the presence of *Carpobrotus* in an area has the capacity to alter the pollination success, at least its quantitative component, of the native species that flower at the same time as this exotic. The flowers of this invasive plant appeared to be able to decrease the number of insect visits, and subsequently the number of flowers visited, to some native plant species. This was found for half of the studied natives: *C. monspeliensis* and *A. barbajovis* in France, and *L. cytisoides* in Mallorca, which evidences a potentially **competitive** effect between the invasive and the natives. Alternatively, the flowers of *Carpobrotus* showed to increase the ‘attraction’ of insects to natives, indicating a potentially **facilitative** effect. This was observed with *C. salvifolius* and *A. cytisoides* in Mallorca and with *S. leucanthemifolius* in Bagaud, although in the latter case, a higher number of insects to flowers did not imply a higher number of flowers visited. Still, another possibility is that the presence of *Carpobrotus* flowers has a **neutral** effect on the pollinator attraction to native species. This was found in *C. monspeliensis* (in Mallorca) and in *L. cytisoides* (in Bagaud). Besides spatial variation, the effect of *Carpobrotus* flowers on the insect flower visitation to natives may vary temporally. Data gathered in Mallorca over two years showed significant differences in half of the species examined in this island; both in *L. cytisoides* and *C. salvifolius*, the effect of *Carpobrotus* was significant in 2003 but not the previous year. This indicates that this type of studies needs to consider more than one field season to be able to generalize on the degree to which exotic species influence the pollination success of native plants. Insect composition and abundances can vary much from year to year, and so can vary their effect on plant pollination. The identification of insect taxa showed that a large proportion of them are shared between the native species and the exotic *Carpobrotus* spp. Hymenopterans appeared to be the most abundant flower visitors, mainly in France but also in Mallorca. In this island, beetles and flies were also quantitatively important.

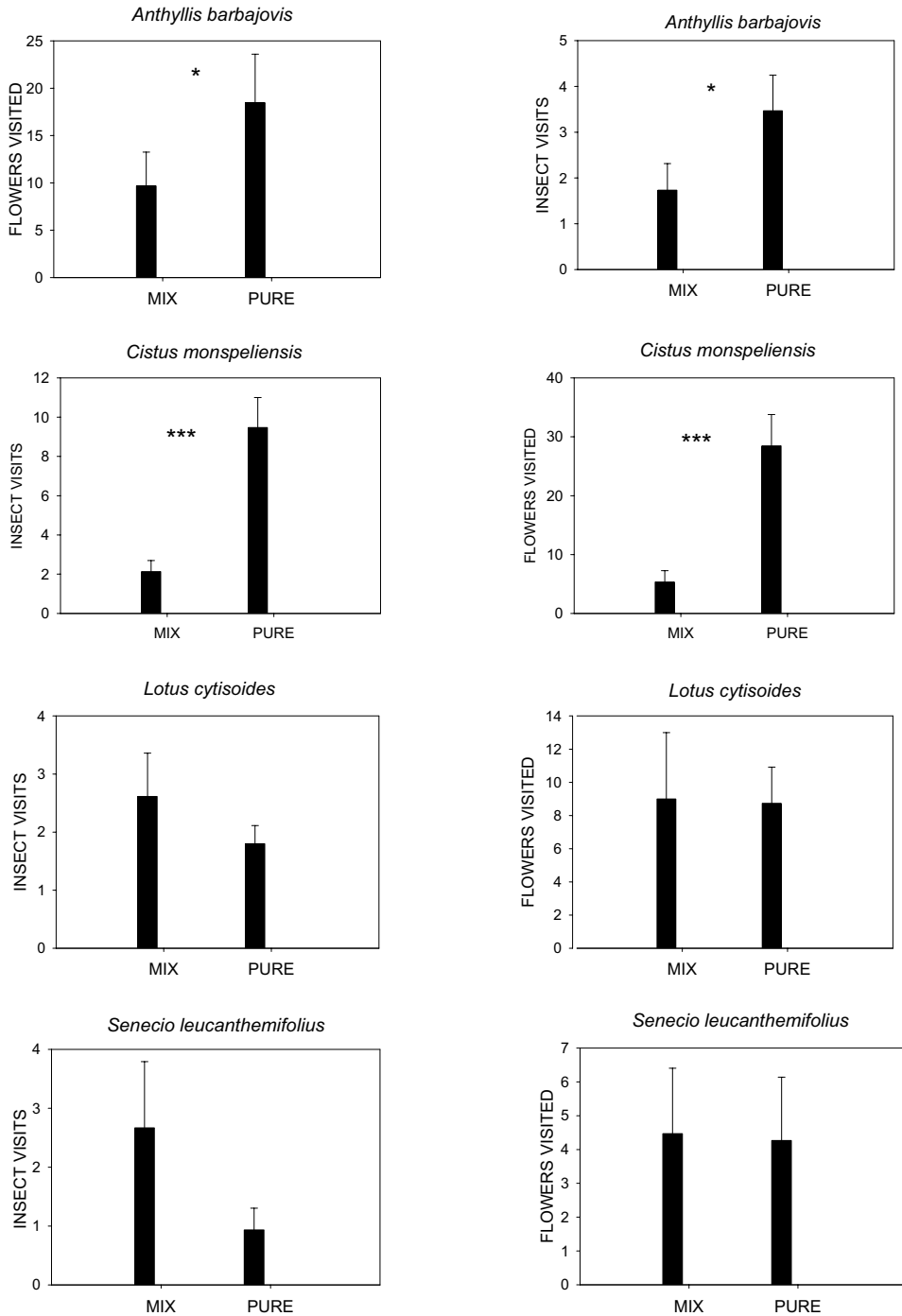


Figure 1: Mean number of insect visits per census and mean number of flowers visited per census for mix and pure populations of native species in France. Error bars indicate standard deviations and stars indicate significant differences at the  $p < 0.05$  (\*) and  $p < 0.001$  (\*\*\*) levels. (2002 data).

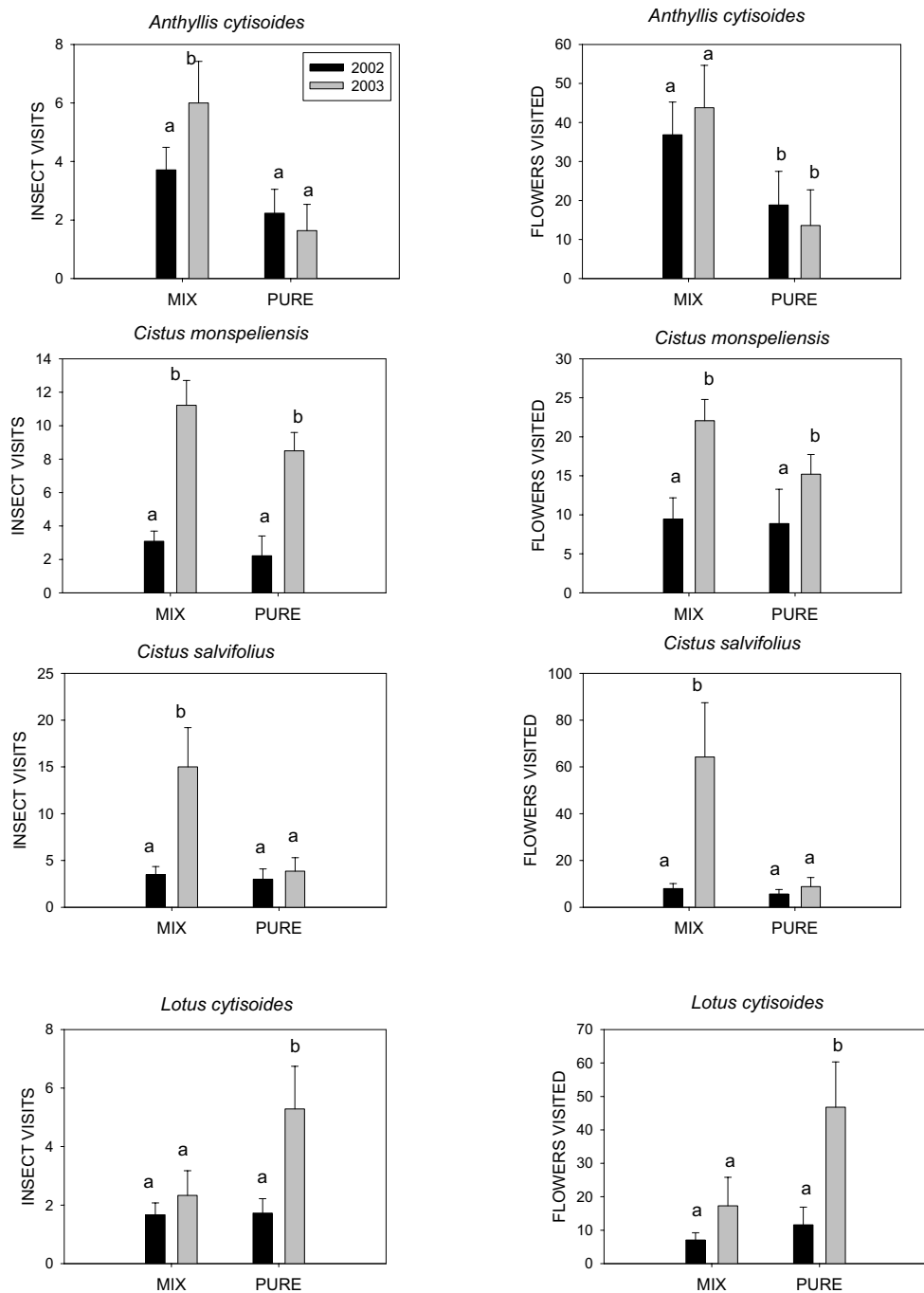


Figure 2: Mean number of insect visits per census and mean number of flowers visited per census for mix and pure populations of native species in Mallorca. Standard error bars are shown. Different letters on bars indicate significant differences ( $P < 0.001$  or  $p < 0.05$ ).

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