PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Contrasting effects of invasive plants in plant–pollinator networks

Ignasi Bartomeus · Montserrat Vilà · Luís Santamaría

Abstract The structural organization of mutualism networks, typified by interspecific positive interactions, is important to maintain community diversity. However, there is little information available about the effect of introduced species on the structure of such networks. We compared uninvaded and invaded ecological communities, to examine how two species of invasive plants with large and showy flowers (*Carpobrotus affine acinaciformis* and *Opuntia stricta*) affect the structure of Mediterranean plant–pollinator networks. To attribute differences in pollination to the direct presence of the invasive species, areas were surveyed that contained similar native plant species cover, diversity and floral composition, with or without the invaders. Both invasive plant species received significantly more pollinator visits than any native species and invaders interacted strongly with pollinators. Overall, the pollinator community richness was similar in invaded and uninvaded plots, and only a few generalist pollinators visited invasive species exclusively. Invasive plants acted as pollination super generalists. The two species studied were visited by 43% and 31% of the total insect taxa in the community, respectively, suggesting they play a central role in the plant–pollinator networks. *Carpobrotus* and *Opuntia* had contrasting effects on pollinator visitation rates to native plants: *Carpobrotus* facilitated the visit of pollinators to native species, whereas *Opuntia* competed for pollinators with native species, increasing the nestedness of the plant–pollinator network. These results indicate that the introduction of a new species to a community can have important consequences for the structure of the plant–pollinator network.

Keywords *Carpobrotus affine acinaciformis* ·
Ecological networks · Generalization · Interaction strength ·
Invasive species

Introduction

The establishment and spread of introduced alien species modifies the structure and stability of ecological communities (Richardson and Pyšek 2000). The most well-known effects of invasive plant species on communities involve direct competition for nutrients, light, space or water, and the consequent loss of plant species diversity (Lodge 1993; Levine et al. 2003). In contrast, there is little information available about their effects on other trophic levels such as the bottom-up relationships. However, there is some evidence to suggest that invasive plants could cause disruptions to mutualistic interactions such as between plant and pollinators (Traveset and Richardson 2006).

A few studies on pollinator competition prompted by invasive plants have examined specific plant–pollinator interactions, in which visitation rates or diversity of pollinators were compared for particular native species present in

I. Bartomeus (✉)
Center for Ecological Research and Forestry Applications
(CREAF), Edifici C, Universitat Autònoma de Barcelona,
08193 Bellaterra, Barcelona, Catalonia, Spain
e-mail: nacho@creaf.uab.es

M. Vilà
Estación Biológica de Doñana, Centro Superior de Investigaciones
Científicas (EDB-CSIC), Avda/ María Luisa s/n,
Pabellón del Perú, 41013 Sevilla, Spain

L. Santamaría
Institut Mediterrani d' Estudis Avançats (IMEDEA),
C/ Miquel Marqués, 21, 07190 Esporles, Mallorca, Spain

invaded and uninvaded areas. Results of specific plant–pollinator interaction studies have yielded inconsistent results and so we cannot generalize that alien plants always affect the pollination success of native plants (Bjerknes et al. 2007). For example, the invader *Lythrum salicaria* reduces pollinator visitation and the seed set of its native congener *Lythrum alatum* under experimental conditions (Brown et al. 2002). Similarly, *Impatiens glandulifera* halves the seed set of the native *Stachys palustris* through pollinator competition (Chittka and Schürkens 2001). Although *Carpobrotus* spp. have no effect on the pollination of the rare plant *Dithyrea maritime* in southern California (Aigner 2004), in the Balearic Islands they have a competitive effect (i.e., fewer visits) on *Lotus cytisoides*, but a facilitative effect (i.e., more visits) on *Cistus salviifolius* and *Anthyllis cytisoides*, and no effect on *Cistus monspeliensis* (Traveset and Moragues 2005).

Although the above examples demonstrate some pollination changes regarding a focal plant species in the presence of a plant invader, it is important to understand how these changes affect the entire community's plant–pollinator interaction network. Mutualistic networks are extremely important for the diversity and stability of the community because they are involved in coevolution processes where multiple species rely on each other to succeed (Jordano 1987; Bascompte and Jordano 2007). Some animal-pollinated invasive plants may become integrated into plant–pollinator networks of the recipient community (Memmott and Wasser 2002) and may even be visited by endemic super generalist pollinators (Olesen et al. 2002). It is, therefore, essential to understand how invasive plants affect not only single plant–pollinator interactions but the whole plant–pollinator network. Only one study has examined how visitation rates differ between invaded and uninvaded sites. Lopezaraiza-Mikel et al. (2007) compared sites invaded by *I. glandulifera* with sites where *I. glandulifera* was experimentally removed. They found that the invader acted as a magnet species, invaded sites being more visited than those in which the invader was removed from the community.

More recent work has explored the inherent structure of plant–pollinator networks. Plant–pollinator networks are not randomly organized; they have a nested structure (i.e., nestedness) meaning that there is a core of generalist plant and pollinator species, and an asymmetric dependence between them. Some specialized pollinators visit generalist plant species and vice versa, specific plant species are visited by generalist pollinators (Bascompte et al. 2003, 2006). The characteristics of plant–pollinator networks differ along environmental gradients such as humidity, insularity or latitude (Olesen and Jordano 2002; Ollerton and Cranmer 2002; Devoto et al. 2005). However, the effect of biotic controls on plant–

pollinator networks, such as the consequences of adding a new plant species (e.g., due to biological invasions) to the community have been far less explored. Moreover, no study has empirically investigated how network nestedness changes after a new species is introduced to a community.

We present here results of a field replicated comparative study on the effects of plant invasions on plant–pollinator interaction networks. Our hypothesis is that an introduced generalist invasive plant will establish many interactions with resident pollinators and consequently some interactions with native plant species will be lost. In principle this would increase network nestedness as a greater number of pollinator species interact with fewer plant species in the community. To test this hypothesis, we studied *Carpobrotus affine acinaciformis* and *Opuntia stricta*, which have invaded Mediterranean coastal communities. Both species have showy, large flowers but contrasting phenologies that could result in different effects on plant–pollinator networks. *Carpobrotus* flowers in spring, when most native species flower. In contrast, *Opuntia* flowers in early summer, when a few late-flowering natives bloom. Mediterranean communities tend to have more flowers than insects in early spring, whereas in late spring there are more insects than flowers. Thus, in early spring one would expect plants to compete for pollinators, whereas in summer pollinators would compete for flowers (Shmida and Dafni 1989; Petanidou and Lamborn 2005). We expected *Carpobrotus* to have a higher impact on the pollination network than *Opuntia*. Specifically, we asked:

1. Which pollinators visit invasive plants, as compared to native plants?
2. Do pollinator diversity, composition and visitation rates differ between invaded and uninvaded communities?
3. Does the structure of the plant–pollinator network (i.e., composition, strength of plant species, and nestedness of plant–pollinator interactions) change between invaded and uninvaded communities?

Materials and methods

Study area and study species

Our study area was in coastal Mediterranean shrublands in the Natural Park of Cap de Creus (Catalonia, northeastern Spain). This area is characterized by cool wet winters and warm dry summers. 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 (http://www.meteocat.com). Our study involved a

pollinator survey of the native flora and the two most abundant invasive plants in the park.

Carpobrotus (Aizoaceae) are crawling succulent herbs with fast clonal growth (Vilà and D'Antonio 1998). They are native to South Africa and are present in almost all Mediterranean regions of the world. They were introduced in Spain for gardening and soil fixation at the beginning of the twentieth century. In the study area *Carpobrotus* may be hybrids between *C. edulis* and *C. acinaciformis.* We will therefore follow Suehs et al. (2004) nomenclature and refer to them as the hybrid complex *Carpobrotus affine acinaciformis*. These putative hybrids have flowers that are solitary and 8–10 cm in diameter, range in color from yellow to purple and have a generalist pollination system (Vilà and D'Antonio 1998). Flowering lasts from March to June (Sanz-Elorza et al. 2006).

Opuntia stricta (Cactaceae) is a succulent perennial spiny plant introduced to Spain from Central America in the sixteenth century. It grows on sunny sandstone hillsides and is commonly cultivated as an ornamental. It can reach 1.5 m high and has big yellow flowers (5–10 cm in diameter). Flowering takes place from June to July (Sanz-Elorza et al. 2006).

Field sampling

In spring 2005, we delineated three sites per study species and established two paired 50 x 50-m plots in each site, one invaded and the other uninvaded separated on average by 300 m. Paired sites were at least 3 km apart from each other. To exclude possible indirect effects of the invasive plants on pollinator presence due to changes in plant species diversity (Kunin 1997) we chose areas that exhibited

initial stages of invasion and selected pairs of plots with similar plant species diversity, dominant species and vegetation cover. Plant species diversity was calculated using the Shannon index ($Sh = -\Sigma|Pi \log_{10} Pi|$; where Pi is the frequency of occupation of species i). Plant community cover was determined by the point-intercept method in four parallel 50-m transects (Table 1). Variation in plant species richness was not significant (invaded vs. uninvaded: 10.3 ± 0.7 vs. 12 ± 2.3, $t = -2.5$, $P = 0.13$ for *Carpobrotus* sites; 10.3 ± 1.3 vs. 10.3 ± 0.8, $t = 0.1$, $P = 0.9$ for *Opuntia* sites). Field work was conducted on sunny days with little wind and with temperatures higher than 15°C. Sites were sampled every 2 weeks during the entire flowering period of both species: 6 times from April to May for *Carpobrotus* sites and 4 times from June to early July for *Opuntia* sites.

Within each site, insect pollinator counts were made along two parallel 50-m permanent transects. To avoid oversampling of the most abundant plant species we limited our observations to a total of six observation areas per flowering species. In each observation area we focused only on one flowering species. The observation areas were approximately 30 x 30 cm and were located along transects at 2-m intervals. To reduce any temporal bias in observations along transects, we started each day's sampling at a different random initial point along each transect. In each observation areas, we counted the number of flowers, and recorded and identified all insects that visited the flowers within 1 min of observation. We captured unknown visitors during a maximum of 3 additional minutes for later identification. Voucher specimens were deposited at the CREAF. We only recorded an insect as a visitor if it touched the reproductive organs of the flower.

Table 1 Characteristics of *Carpobrotus affine acinaciformis* and *Opuntia stricta* sites in invaded and uninvaded plots[a]

Site	Plot	Sampling period	Target invader	Target invader cover (%)	Total cover (%)	Dominant native species	Dominant species cover (%)	Shannon index	No. flowering species	Sørensen index
BAT	Uninvaded	April–May			180	*Lavandula stoechas, Thimelea hirsute*	70.5	1.06	9	0.95
	Invaded	April–May	*Carpobrotus*	46.5	167	*T. hirsute, L. stoechas*	39.5	1.13	10	
MED	Uninvaded	April–May			162	*Rosmarinus officinalis, Cistus monspeliensis*	35.5	1.07	11	0.72
	Invaded	April–May	*Carpobrotus*	39.0	140	*Cistus salvifolius, R. officinalis*	23.0	1.13	14	
FAR	Uninvaded	April–May			149	*C. monspeliensis, R. officinalis*	36.5	1.18	11	0.87
	Invaded	April–May	*Carpobrotus*	25.5	139	*C. salvifolius, R. officinalis*	29.0	1.24	12	
SEL	Uninvaded	June–July			147	*L. stoechas, Sedum sediforme*	52.5	0.95	12	0.75
	Invaded	June–July	*Opuntia*	12.5	134	*L. stoechas, Psoralea bituminosa*	24.5	0.94	11	
FRA	Uninvaded	June–July			120	*Daucus carota, Aetheorrina bulbosa*	35.0	1.05	10	0.64
	Invaded	June–July	*Opuntia*	24.5	132	*D. carota, A. bulbosa*	23.5	1.04	11	
MIQ	Uninvaded	June–July			130	*A. bulbosa, P. bituminosa*	40.0	0.91	9	0.80
	Invaded	June–July	*Opuntia*	15.0	118	*D. carota, A. bulbosa*	27.5	1.08	9	

[a] See text for details on methods

Our sampling protocol allowed us to standardize the time spent observing each plant species compared to classic transect walks. Each species was sampled for a total of 36 min per site. In total, each site was surveyed for pollinators for more than 6 h.

To ascertain whether differences in pollinator activity were due to differences in flower abundance, we estimated the number of flowers of each plant species in the vicinity of each transect. Each sampling day when pollinator sampling was finished, we determined the total number of flowers or inflorescences (flower units hereafter) per plant species in 1-m^2 areas located at 1-m intervals along the transects. The total number of flower units in paired invaded and uninvaded plots did not differ for either species (Wilcoxon test, paired comparisons: for *Carpobrotus*, $P = 0.3$–0.5; for *Opuntia*, $P = 0.2$–0.5). We therefore assumed pollinator activity in invaded and uninvaded plots was independent of differences in native floral abundance.

Plant-pollination network analysis

With the data collected we constructed a plant–pollinator interaction network for each of the 12 plots. Networks were represented as two-dimensional matrices, in which rows represented the plants and columns the pollinator species. We constructed two matrices per plot, one in which cell values represented the presence or absence of the interaction and another in which cells were the frequency of visits observed for each plant–pollinator interaction.

To test whether the two invasive species received a number of visits comparable to average visitation on a particular native species within each invaded plot, we compared the visitation frequency received by the invader with a normal distribution fitted to the number of visits to native species, with a Z-statistic.

To explore whether invaded and uninvaded plots differed in pollinator assemblage, we calculated the Sørensen similarity index [$S = (2 \times C)/(2C + A + B)$; where C is the number of pollinator species that were common in both plots, A is the number of pollinators only present in invaded plots, and B is the number of pollinators present only in uninvaded plots]. S ranges from 1 (identical assemblages) to 0 (maximally dissimilar assemblages).

Differences between invaded and uninvaded plots in pollinator species richness, frequency of visits of the main pollinator orders, and frequency of visits to native plants were compared with paired t-tests. To account for the limited power associated with the low sample size ($n = 3$ networks per treatment), we also report marginally significant differences ($\alpha = 0.1$). The limited sample size is largely justified by the considerable effort involved in the simultaneous characterization of several whole plant–pollinator networks in an area where a reference pollinator collection does not

exist. Statistical analyses were carried out using STATISTICA (StatSoft 2001).

We tested whether invasion influenced pollinator visitation rates (i.e., number of visits per flower) to native species with a generalized linear mixed model [GLMM; PROC MIXED in SAS (SAS Institute 2001)]. The model was visitation rate = presence of the invader (yes or no) + plot + plant family + plant species nested within family + error. We considered family and plot random factors, and species and presence or absence of the invader fixed factors. In this way, we could test whether the invaders affected the visitation rates of native plant species while accounting for the clustering of plants according to taxonomy and plot.

We also compared similarities of the interaction scenarios (i.e., identities and frequencies of plant-pollination interactions) between invaded and uninvaded visitation matrices by constructing one similarity matrix estimated with Kulczynski's distance coefficient [$K = 1/2(W/A + W/B)$; where W is the sum of the minimum visits of the various species, this minimum being defined as the visits at the site where the species is the rarest and, A and B are the sums of the visits of all species at each site, respectively]. The index was calculated between all pairs of plots (Legendre and Legendre 1998; Vázquez and Simberloff 2003). This index was semi-metric, meaning that it accounted for differences in contribution to the coefficient between abundant species and rare species. We used the resulting pair-wise similarity matrix as input for non-metric multidimensional scaling (NMDS), an ordination technique used to provide a visual representation of the pattern of proximities among plots (Legendre and Legendre 1998; Vázquez and Simberloff 2003). To test differences in the array of interactions between plots we performed a Wilcoxon test for each pair of plots where all paired plant–insect interactions in the two plots, including empty cells, were used as input.

To explore in depth the similarity of plant–pollinator interactions, we calculated the number of common plant–pollinator interactions and the number of plant–pollinator interactions that occurred in only one of the paired plots (Ie). In invaded plots we could distinguish between exclusive pollinator–invasive species interactions (Ii) and exclusive pollinator–native species interactions (In). Therefore, in invaded plots: Ie = Ii + In.

We further analyzed the structure of the matrix with the index of matrix nestedness (N) and the importance of each plant species in terms of interaction strength. Matrix nestedness is an estimation of the network organization (Bascompte et al. 2003) and is calculated from temperature (T) as $N = (100-T)/100$. Values range from 0 (random structure) to 1 (maximum nestedness). To calculate T, we organized the matrix in rows of pollinators and columns of plants, ordering the entries from those presenting the most to the

least interactions. This maximally packed matrix was used to calculate the isocline of perfect nestedness for each matrix. The absence of a pair-wise interaction below the isocline or the presence of a pair-wise interaction above the isocline was then recorded as unexpected. Therefore, T is the measure of physical disorder calculated from the normalized measure of global distance from unexpected records to the isocline. To assess the significance of N for each matrix, we compared the observed value of N with a benchmark provided by null model 2 in Bascompte et al. (2003) in which each cell in the interaction matrix has the following probability $(Pri + Pci)/2$, where Pri is the fraction of interactions of row i and Pci is the fraction of interactions of the column i equivalent. We generated 1,000 random matrices with this null model. Analyses were conducted with the ANINHADO software (Guimaraes and Guimaraes 2006). T values for plants represented how far from the nested pattern each plant species was, and idiosyncratic T values were used to assess changes in the community. Differences in N between invaded and uninvaded plots for each invader species were compared with a paired t-test.

The strength of each plant species in the matrix is a measure of the dependence of pollinators on each particular plant species (Bascompte et al. 2006). Strength is defined as the sum of pollinator dependencies on a particular plant species. Dependence of a pollinator on a plant species is the fraction of all visits by a particular pollinator species to a particular plant ($Da,P = Va$-p/Va; where Da,P is the dependence of pollinator a on plant species p, Va-p is the number of visits of pollinator a to plant p and Va is the total number of visits of pollinator a to all plant species in the community). We tested for differences in the strength of plant species between invaded and uninvaded plots with a paired t-test. Furthermore, to test whether the two invasive plant species had a higher strength than native species, within each site we compared the invasive species strength with a normal distribution fitted to the strength of the native species by means of a Z-statistic.

Results

### Pollinators on invader versus native plant species

We observed a total of 23 and 17 insect taxa on *Carpobrotus* and *Opuntia*, respectively. Both species were visited by several species of Coleoptera (e.g., *Oedemera lurida* and *Oxythyrea funesta* on *Carpobrotus* and *Myrabilis quadripunctata* on *Opuntia*) and Hymenoptera (e.g., *Bombus terrestris, Anthidium sticticum* to *Carpobrotus* and *Xylocopa violacea, Apis mellifera* to *Opuntia*). The native plants were also visited by some Diptera and Lepidoptera. Almost no pollinators were exclusive to *Carpobrotus*, which were vis-

ited by 43.4% of the observed insect taxa. *Opuntia* was visited by 30.9% of the observed insect taxa. *X. violacea* (i.e., carpenter bees) exclusively visited *Opuntia* plants and were a frequent pollinator (19.5% of the total visits to *Opuntia*).

Both invader species received on average more visits than any native species (Z-tests: $P < 0.001$ in all sites). *Carpobrotus* received $27.8 \pm 7.2\%$ (mean $\pm$ SE) of the total visits observed. On average, native species in invaded plots received $7.61 \pm 1.23\%$ of the visits. *Opuntia* received $44.1 \pm 11.2\%$ of the observed visits, whereas on average, native species received $6.16 \pm 2.33\%$.

Pollinator structure in invaded versus uninvaded communities

In total we found 53 and 55 different pollinator taxa in invaded and uninvaded *Carpobrotus* and *Opuntia* sites, respectively. There were differences in the composition of invaded and uninvaded plots measured with S; $S = 0.52 \pm 0.02$ for *Carpobrotus* sites and $S = 0.54 \pm 0.04$ for *Opuntia* sites. However, the presence of an invasive species did not affect pollinator species richness (invaded vs. uninvaded: 29.33 ± 3.71 vs. 20.33 ± 1.21, $t = 2$, $P = 0.18$ for *Carpobrotus* sites; 23.67 ± 1.20 vs. 21.00 ± 2.00, $t = 1.02$, $P = 0.29$ for *Opuntia* sites). We only found significantly more Coleoptera visits ($t = -5.46$, $P = 0.03$) in *Carpobrotus*-invaded plots compared to uninvaded plots. This difference was principally due to the frequency of visits to the invasive species and to Asteracea and Cistacea. There was no detectable difference in the insect orders observed in *Opuntia*-invaded and uninvaded sites, probably because of the large variability among plots (Fig. 1; paired t-tests: $P > 0.10$).
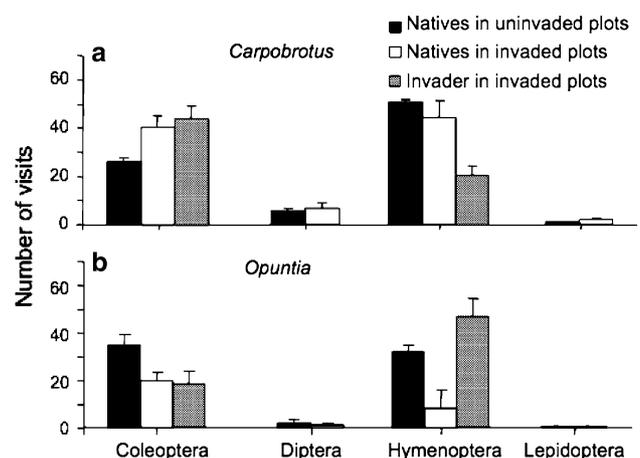

Fig. 1 Total number of visits (mean $\pm$ SE) for the different orders of insect pollinators observed in **a** *Carpobrotus affine acinaciformis*- and **b** *Opuntia stricta*-invaded and uninvaded plots. In invaded plots, visits to the plant invader and to native plant species are indicated

The frequency of visits to the invasive and native species as a whole did differ. There were marginally more visits in invaded than in uninvaded *Carpobrotus* plots (159.33 ± 22.26 vs. 83.33 ± 6.76, $t = 2.97$, $P = 0.10$). In the invaded plots, visitation rates increased significantly in more than 70% of the native species (GLMM test: fixed effects—presence of the invader, $F_{1,29} = 6.23$, $P = 0.02$; species within families, $F_{14, 1} = 18.01$, $P = 0.18$; random effects—plot, $Z = 0.93$, $P = 0.35$; family, $Z = 1.21$, $P = 0.23$) In contrast, the overall number of visits to *Opuntia* plots did not differ between invaded and uninvaded plots (95.33 ± 10.14 vs. 70.67 ± 4.10, $t = 2.51$, $P = 0.13$). However, visitation rates decreased in more than 60% of the native species in invaded plots (fixed effects—presence of the invader, $F_{1,27} = 4.91$, $P = 0.04$; species within families, $F_{14, 1} = 14.99$, $P = 0.20$; random effects—plot, $Z = 1.41$, $P = 0.16$; family, $Z = 1.25$, $P = 0.21$).

Plant–pollinator network in invaded vs. uninvaded communities

The greater number of visits in *Carpobrotus*-invaded vs. uninvaded plots resulted in a marginal increase in the number of plant–pollinator interactions (67.67 ± 6.34 vs. 39.33 ± 16.37, *t*-test = 3.47, $P = 0.07$). Nevertheless, paired *Carpobrotus*-invaded and uninvaded plots shared 57.66 ± 8.01% species interactions. Invaded plots had marginally more exclusive interactions than uninvaded plots (*t*-test = 3.46, $P = 0.07$). Most of the exclusive interactions, almost 70% in invaded plots, involved native plants. In fact, pollinators as a whole interacted with more plant species in *Carpobrotus*-invaded plots than in uninvaded plots (invaded, 2.33 ± 0.09 interactions/pollinator species; uninvaded, 1.94 ± 0.07 interactions/pollinator species; *t*-test = 4.64, $P = 0.04$). *Opuntia*-invaded and uninvaded plots shared even fewer common interactions (31.43 ± 3.56%). There were no significant differences in the total number of exclusive interactions between invaded and uninvaded plots (*t*-test = 0.24, $P = 0.4$). However, almost 50% of the exclusive interactions in invaded plots were due to interactions with *Opuntia* (Fig. 2).

The two-dimensional representation of the NMDS presents a stress of 0.001 for *Carpobrotus* and 0.05 for *Opuntia*, showing a high correspondence with the input data (similarities of the interaction identities). *Carpobrotus*-invaded plots were distinctly separated from uninvaded plots (Fig. 3) and tended to cluster together along dimension 2. In two out of three sites, interaction identities differed significantly between paired native versus non-native plots (Wilcoxon test: site BAT, $Z = 5.08$, $P < 0.0001$; site MED, $Z = 3.86$, $P < 0.001$). In contrast, although *Opuntia*-invaded plots also showed a consistent segregation from uninvaded plots along dimension 2 of the
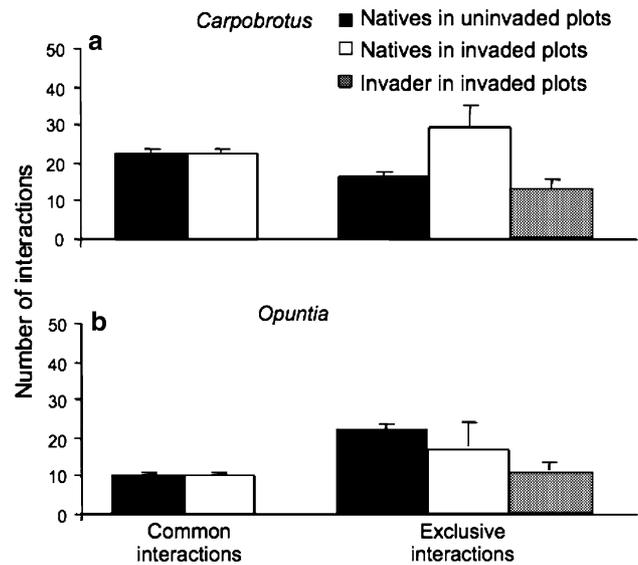
Fig. 2 Mean (±SE) number of common interactions and exclusive plant–pollinator interactions in **a** *C.* aff. *acinaciformis*- and **b** *O. stricta*-invaded and uninvaded plots. In invaded plots, the exclusive interactions with the plant invader and with the native plant species are indicated

MDS, these differences were not significant in the identity of interactions (Wilcoxon test: $P > 0.1$ in all sites).

The structure of the plant–pollinator network was significantly nested ($P < 0.05$) in half of the plots when compared with the benchmark of 1,000 random matrices for each plot with the null model 2 (Table 2). All *Opuntia*-invaded plots were significantly more nested than expected by random outcome, but none of the uninvaded plots were (Table 2). Nestedness did not differ between invaded and uninvaded plots for *Carpobrotus* (uninvaded vs. invaded: 0.82 ± 0.002 vs. 0.77 ± 0.001, $t = 1.34$, $P = 0.3$). However, *Opuntia*-invaded plots were marginally more nested than uninvaded plots (0.83 ± 0.0007 vs. 0.73 ± 0.0002, $t = -3.49$, $P = 0.07$).

The strength of each native plant species was not significantly different between invaded and uninvaded plots (*t*-test: $P > 0.05$ in all plots). The invasive plants had high strength values in all plots and on average these were significantly higher than the strength value of native plant species (Table 2).

Discussion

Our work, along with that of Lopezaraiza-Mikel et al. (2007), is unique in empirically testing how an invasive plant species can affect plant–pollinator networks. While Lopezaraiza-Mikel et al. (2007) looked at the effect of a zygomorphic invasive plant, we investigated two actinomorphic species with different floral phenologies. The two
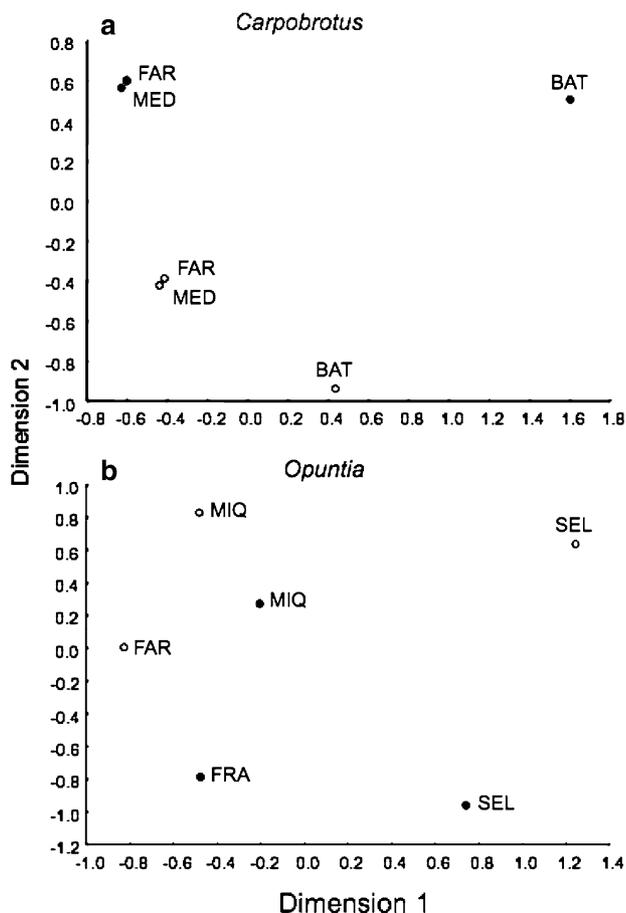
Fig. 3 Representation of similarities of the plant–pollinator identity interactions in **a** *C.* aff. *acinaciformis-* and **b** *O. stricta*-uninvaded (*close circles*) and invaded (*open circles*) plots, generated in two dimensions by multidimensional scaling analysis. See Table 1 for study site names and characteristics

invaders we studied had larger flowers than any of the co-occurring native species and attracted significantly more pollinator species than any native. However, the consequences for plant–pollinator networks differed between species. *Carpobrotus*-invaded plots received a larger number of visits, mainly from Coleoptera, resulting in an increasing number of plant–pollinator interactions. Although *Opuntia*-invaded plots received a similar number of visits as uninvaded plots, most visits were to the invasive species, thus reducing the visits to native plants. We examined the consequences of the presence of the two invaders from the perspective of the native plants, the pollinators, and the plant–pollinator network as a whole.

Implications for the native plants

In general, pollinator limitation does not appear to be a major barrier for the spread of introduced plants (Richardson et al. 2000). Many invasive plants are pollination generalists, with attractive nectar and pollen-rich flowers that

constitute an easy resource (Campbell 1989). In our study, *Carpobrotus* received more visits than any native species; still, the average number of interactions (3–4 pollinator species/plant species) was within the range reported by Olesen et al. (2002) for oceanic islands. In invaded plots, the general trend was for an increased visitation rate to most native plant species. Only a few specialized species with zygomorphic flowers, such as Labiatae (*Lavandula stoechas*) and Papilonaceae (*Lathirus clymenum*) received fewer visits in invaded than in uninvaded plots. These results seem to contradict the "floral market" hypothesis (Chittka and Schürkens 2001), which suggests that animals choose between products (plant species) on the basis of their quality (nectar and pollen). According to this hypothesis showy, resource-rich invasive plants with higher reward levels might receive higher visitation rates, thus decreasing visitation rates to the natives. Instead, *Carpobrotus* appears to have a facilitative effect on the visitation to natives. Similar observations were made by Fleishman et al. (2005), who found that the higher the total amount of resources available in the community, the more pollinators are attracted to all plants. Whether this enhanced pollinator visitation translates to a positive effect on the native species seed set is not known. In these circumstances the pollen transport web might be dominated by the invader as found in Lopezaraiza-Mikel et al. (2007), and invasive pollen could be deposited on native stigmas interfering with fecundity. Preliminary results show that *Carpobrotus* pollen is indeed transported on pollinator's bodies, but few pollen grains reach native stigmas suggesting that the ultimate impact on natives is low (I. Bartomeus et al., unpublished data).

We expected *Carpobrotus* to have a higher impact on competition for pollinators than *Opuntia* because there were more species with flowering phenologies overlapping with *Carpobrotus* than with *Opuntia*. However, we found the contrary: when *Opuntia* overlaps with late spring flowering native species, we found that it tended to monopolize the available pollinators, depriving native plant species of their service. This result suggests that the "floral market" hypothesis best fits situations where resources are scarce for pollinators. Overall, assuming that visitation rates are good surrogates for pollination efficiency (Vázquez et al. 2005; Sahli and Conner 2006), these two invasive plants could have contrasting effects on native plant reproduction: enhancement by *Carpobrotus*, but reduction by *Opuntia*.

Implications for the pollinator community

Although pollinator diversity in Mediterranean communities is not well known (Petanidou and Ellis 1993), this region is a well-established hotspot of bee diversity and speciation (Michener 2000). Despite current concern about the homogenization of pollinator diversity (Kearns et al.

Table 2 Plant-pollination network parameters for *Carpobrotus affine acinaciformis*- and *Opuntia stricta*-invaded (_*i*) and uninvaded (_*ni*) plots. Strength values are for the invader and for native plants (mean ± SE) in invaded and uninvaded plots. The normalized *Z*-value and the associated probability (*PZ*) for the invader strength to be higher than natives are given. The temperature (*T*), nestedness (*N*) and the associated probability for *T* (*PT*) to occur by random has been tested using null model 2 according to Bascompte et al. (2003)

Site	Species	Strength	Z-value	PZ	T	N	PT
BAT	*Carpobrotus*	11.21					
	Natives_ni	3.4 ± 0.74	2.70	0.007	13.29	0.87	0.1
	Natives_i	2.1 ± 1.06	3.87	0.0001	23.07	0.77	0.001
MED	*Carpobrotus*	4.12					
	Natives_ni	1.93 ± 0.60	1.21	0.22	16.53	0.83	0.05
	Natives_i	2.84 ± 0.87	0.50	0.62	17.29	0.83	0.01
FAR	*Carpobrotus*	5.01					
	Natives_ni	2.41 ± 0.73	1.18	0.23	26.52	0.73	0.2
	Natives_i	1.85 ± 0.40	2.61	0.009	27.75	0.72	0.1
SEL	*Opuntia*	7.76					
	Natives_ni	2.12 ± 0.79	2.51	0.012	29.38	0.71	0.2
	Natives_i	2.15 ± 0.98	2.01	0.044	14.96	0.85	0.01
MIQ	*Opuntia*	10.28					
	Natives_ni	2.97 ± 1.13	2.63	0.0085	25.53	0.74	0.08
	Natives_i	1.78 ± 0.90	3.84	0.0001	20.91	0.79	0.01
FRA	*Opuntia*	7.10					
	Natives_ni	3.0 ± 1.16	1.24	0.215	27.32	0.73	0.1
	Natives_i	2.1 ± 0.74	2.42	0.015	14.29	0.86	0.01

1998; Steffan-Dewenter et al. 2005), the two invasive plants we studied did not reduce the diversity of pollinators. This may be a transient pattern, because our study was conducted in the early stages of invasion, and so native plant diversity and composition are only slightly affected. Given that pollinators tend to show a high degree of floral constancy (Kevan and Baker 1983), in sites at more advanced stages of invasion, in which native plant diversity has been reduced (Lockwood and McKinney 2001; Vilà et al. 2006), pollinator diversity is more likely to be affected (Steffan-Dewenter and Tscharntke 2001). Additionally, we do not know the effects that the invaders might have on pollinator fitness and behavior, such as altering nesting sites (Graves and Shapiro 2003). To date, evidence for the impact of invasive plants on native pollinator population size and dynamics remains speculative (Traveset and Richardson 2006).

In *Carpobrotus*-invaded plots there were more visits by Coleoptera than in uninvaded plots. Coleoptera is a very generalist group of pollinators and little is known about their importance in Mediterranean plant pollination. Honey bees, which are maintained for honey production in several places in the Cap de Creus area, were not especially abundant neither in the *Carpobrotus*-invaded plots nor on *Carpobrotus* flowers (only 1.4 ± 0.1% of total visits). They were nonetheless present, visiting principally Labiatae flowers such as *Lavandula stoechas* and *Rosmarinus officinalis*. In *Opuntia*-invaded plots the presence of honey bees was high, especially on *Opuntia* flowers (11.1 ± 3.7% of total visits). In our study super-generalist pollinators are not

the main pollinators supporting invasive plants (Olesen et al. 2002).

In *Opuntia*-invaded networks, *Xilocopa violacea* [usually considered a generalist pollinator (Westrich 1990)] visited *Opuntia* flowers exclusively. The absence of *X. violacea* from uninvaded networks confirms that insects can easily learn to choose and exploit new resources (Dukas and Bernays 2001; Weiss and Papaj 2003) and that, depending on the scale of observation, interactions that appear to be specialized can be interpreted as facultative or local specializations. Unraveling the pollination ecology of invasive plants in introduced and native ranges is a future challenge. A study on this has shown that although the identity of pollinators visiting the invader might differ between introduced and native habitats, flower visitation rates might not be significantly different at home than abroad (Stout et al. 2006).

Implications for the plant–pollinator network

Invasion can also affect the identity of plant-pollination interactions. In *Carpobrotus* paired sites, the similarity of interaction scenarios reflected on the MDS showed few differences within uninvaded plots, especially between those with a similar floral composition, and a large separation with their paired invaded plots. In contrast, for *Opuntia* differences between invaded and uninvaded sites were not significant.

Generalization among plants and pollinators is a common pattern in mutualistic interactions, with strict special-

ists (i.e., one-to-one interaction) being the exception rather than the norm (Waser et al. 1996; Vázquez and Aizen 2004). In addition, asymmetric specialization predominates as reflected by the nestedness of the plant–pollinator networks (Bascompte et al. 2003). Our results indicate that although the nested plant–pollinator structure is very stable (Bascompte et al. 2003; Jordano et al. 2003) it can be modified with introduced species that have not coevolved in the system. Nestedness increased in *Opuntia* plots, probably because while no important links disappeared, invasive plants interacted with many pollinators, attaining a central role in the plant–pollinator network. Furthermore, the high strength value and the central role invasive species played in the plant–pollinator networks suggest that invasion could have long-term consequences, and the dependence of pollinators on the invader may not be reversible. Manipulation experiments are needed to test this prediction.

Conclusion

Both *C.* aff. *acinaciformis* and *O. stricta* are insect-pollinated invasive plant species that in our study behaved as super generalists, occupying a central role in the community and reducing the protagonism of pollinator interactions with native species. However, they had contrasting effects on the relationships between plant and pollinators. Because these invasive species attract a wide diversity and abundance of pollinators, the spatial and temporal scale at which this attraction operates can result in either positive or negative effects on the visitation to native plants. In our study, visitation rates to native plants were enhanced in plots that had been invaded by *Carpobrotus* and reduced in plots invaded by *Opuntia. Carpobrotus* attracted pollinators which increased visitation to natives, whereas *Opuntia* diverted pollinators away from the native species in the community. This altered the structure of the plant–pollinator networks and resulted in an increase in nestedness in *Opuntia*-invaded plots.

Invasive plants are considered to be the third major cause of pollinator diversity loss through changes in native flora (Kearns et al. 1998). However, few studies have tested this hypothesis except in agroecosystems (but see Steffan-Dewenter and Tscharntke 2001). We envision that the outcomes of biological invasions on plant–pollinator interactions will be context specific, and will depend on the invader identity and abundance, the overlap in phenology of the invader and the native plants in a local community, the flower similarity between the invader and native species as well as the indirect effects of the invader on native plant composition and diversity. For example, Vázquez et al. (2007), found that a large proportion of the variation in the observed plant–pollinator structure was explained by differences in species abundance. Consequently, the impact of an invader will depend not only on qualitative traits but also on their dominance in the community. More experimental studies on different invasion scenarios are needed to disentangle the mechanisms involved in the impact of invaders on plant–pollinator networks.

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