Influence of the honeybee and trait similarity on the effect of a non-native plant on pollination and network rewiring

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Running headline: Plant invasions: the role of the honeybee and trait similarity

Summary

1. Introduced entomophilous non-native plants usually become well integrated into the diet of generalist pollinators. This integration can affect the entire recipient plant-pollinator network. Effects vary from facilitative to competitive, and understanding the factors that govern such variability is one of the fundamental goals in invasion ecology.

Species traits determine the linking patterns between plant and pollinator species. Therefore, trait similarity among plants or among pollinators might modulate how they affect each other.

2. We conducted a flower removal experiment to investigate the effects of the non-native entomophilous legume *Hedysarum coronarium* on the pollination patterns of a Mediterranean shrubland plant-pollinator network. Specifically, we explored whether effects were influenced by similarity with the resident plant species in flower morphology (papilionate *vs*. non-papilionate), and whether effects on the pollinator community were influenced by similarity in functional group with its main visitor species (bees *vs.* non-bees). In addition, we explored whether *Hedysarum* had an effect on the identity of interactions. For this purpose, we calculated the interaction rewiring; i.e., the number of plant-pollinator interactions that were gained or lost after invasion.

3. *Hedysarum* was well integrated into the diet of 15 generalist pollinators having the honeybee as its main visitor species. Such integration did not affect visitation rates, normalized degree (i.e., proportion of pollinators they are visited by) and niche overlap (i.e., proportion of plant species they share pollinators with) of plants, irrespective of their flower morphology. Only the proportion of honeybee visits to resident plants decreased with invasion. On the other hand, *Hedysarum* reduced visitation rates and niche overlap of pollinators, mainly those of bee species. Finally, we observed that changes in the foraging behaviour of the honeybee were positively associated with the interaction rewiring involving the rest (92 taxa) of pollinators.

4. In conclusion, pollinators show a plastic use of floral resources, responding to the presence of non-native plants. When the non-native attracts highly competitive pollinators such as the honeybee, plasticity is especially significant in pollinators that are functionally close to that competitive pollinator. The result is an interaction rewiring due to pollinators avoiding competition with the honeybee. Though this plasticity might not quantitatively affect the pollination of plants, consequences on their reproduction and the functioning of the network can derive from the interaction rewiring.

Key-words: *Apis mellifera, flower morphology, Hedysarum coronarium, plant invasion, plant-pollinator communities, pollinator functional group*

Introduction

Many entomophilous and obligate out-crossing non-native plants become well integrated into the diet of resident pollinators (Vilà et al. 2009). Many of these pollinators are super-generalist species such as the honeybee (*Apis mellifera* L.) or bumblebees (*Bombus* spp.) (Olesen, Eskildsen & Venkatasamy 2002; Stout, Kells & Goulson 2002; Gross et al. 2010). The new plant-pollinator interactions established do not occur in isolation but rather are embedded in complex interaction networks (Montoya, Pimm & Solé 2006), and thus the effect of non-natives can expand to the entire recipient plant-pollinator network (Lopezaraiza-Mikel et al. 2007, Bartomeus, Vilà & Santamaría 2008, Padrón et al. 2009, Ferrero et al. 2013).

The effects of non-native entomophilous plants on both pollinators and the pollination of plants (Bjerknes et al. 2007; Montero-Castaño & Vilà 2012) vary from facilitative to competitive, being highly context dependent. Understanding the factors that govern such variability would allow us to predict the impact of non-native plant species on recipient communities, which is one of the fundamental goals of invasion ecology (Simberloff et al. 2013).

The linking patterns of plant-pollinator interactions are determined by several factors. First of all, a match between plant traits (e.g. corolla size, shape and colour, type of reward offered) and pollinator traits (e.g. body size, tongue length) is required for interactions to be established (Stang, Klinkhamer & van der Meijden 2006; Santamaría & Rodríguez-Gironés 2007; Olesen et al. 2011; Encinas-Viso, Revilla & Etienne 2012; Bartomeus 2013). Consequently, the similarity among species in some traits can determine how plant and pollinator species affect each other (Lázaro, Hegland & Totland 2008; Morales & Traveset 2009; Campbell et al. 2010; Gibson, Richardson & Pauw 2012; Carvalheiro et al. 2014). For instance, observations on pairs of co-flowering non-native and native species have found that similarity in flower morphology can reduce pollinator visitation rates to native species (Morales & Traveset 2009). However, this trend has not been found when considering the entire native plant community (Morales & Aizen 2006; Vilà et al. 2009). In the case of non-native plants with flower morphologies not accessible to all pollinators, such as papilionate flowers (Córdoba & Cocucci 2011), we would expect them to compete more strongly for pollinators with resident species which share similar flower morphology.

Second, pollinators adapt their foraging behaviour to the abundance and quality of available floral resources (Mustajarvi et al. 2001) in order to optimize their food intake (Armbruster & Herzig 1984). Therefore, the arrival of a highly rewarding non-native plant can alter the foraging behaviour of pollinators by modifying the floral environment (Memmott & Waser 2002; Vilà et al. 2009). Pollinators would respond in accordance with their body size, sociability, preferred food resource, flying distances, etc. (Greenleaf et al. 2007; Bommarco et al. 2010). Pollinator taxa sharing some of these ecological characteristics might behave similarly and might thus belong to the same functional group due to their functional redundancy (Hagen *et al.* 2012). We would expect the effect of non-native plants to be higher in those pollinators belonging to the same functional group than those visiting them.

Finally, the linking patterns of plant-pollinator interactions are also influenced by interspecific competition among taxa (Carstensen et al. 2014). Some highly competitive pollinator species are able to displace other pollinators by depleting floral resources (e.g. Roubik 1980, Paini 2004) and/or by physical disturbance (Gross & Mackay 1998). Therefore, the arrival of a highly rewarding non-native plant can also alter the foraging behaviour of pollinators by altering the behaviour of one or more highly competitive species able to displace other pollinators.

Through the above mentioned mechanisms, invasion not only alters the frequency of plant-pollinator interactions, but can also entail their reshuffling, with gains or losses of exclusive pair-wise interactions in recipient communities (Bartomeus *et al.* 2008). The turnover of interactions when co-occurring species interact differently over time or space is known as interaction rewiring (Burkle & Alarcón 2011; Poisot et al. 2012; Trojelsgaard et al. 2015). Interaction rewiring can have important consequences on networks. They way interactions are shaped; i.e., their topology, affects networks' functioning and persistence to species loss (Kaiser-Bunbury et al. 2010; Tylianakis et al. 2010; Ramos-Jiliberto et al. 2012). Even if topological properties are conserved after invasion (e.g. Vilà et al. 2009, but see Aizen, Morales & Morales 2008), the functional role of particular species may change (Campos-Navarrete et al. 2013; Nielsen & Totland 2014).

We present a flower removal field experiment, conducted during two consecutive years, to investigate the effect of a highly rewarding non-native legume species on the pollination patterns of the entire plant-pollinator network. Specifically, we address the following questions: (a) how is a non-native entomophilous plant species with a floral morphology that restricts pollinator visitation integrated into the diet of the resident pollinator community? (b) is the effect of the non-native plant on the visitation of the resident plants dependent on the similarity in flower morphology between the non-native and resident species? (c) is the effect of the non-native plant on the foraging behaviour of pollinators dependent on the functional similarity between the non-native's main visitor and the pollinators?; and finally (d) is there an interaction rewiring and is it influenced by the foraging behaviour of the non-native's main visitor and its functional closeness to the rest of pollinators?

Materials and methods

Non-native species and study area

Hedysarum coronarium L. (Leguminosae) is a short-lived N-fixing perennial (Sulas et al. 2000) with either erect (0.8 m average height) or prostrate growth (Bustamante et al. 1998). Its inflorescences are racemes with up to 30 pink flowers rich in pollen and nectar (Rodríguez-Riaño, Ortega-Olivencia & Devesa 1999) that bloom during April and May. Its papilionate and restrictive flowers (Córdoba & Cocucci 2011) are self-compatible but present high out-crossing rates (Louati-Namouchi, Louati & Chriki 2000, Yagoubi & Chriki 2000). *Hedysarum* is mainly pollinated by bees, and in particular the honeybee which is its main pollinator in the study area and in other areas as well (Satta et al. 2000; Montero-Castaño, Vilà & Ortiz-Sánchez 2014) (Fig. 1).

Hedysarum is native of the southwestern part of the Mediterranean basin (Talavera et al. 1988), where it grows from sea level to low frost-free altitudes (Gutiérrez 1982). It has been introduced as a forage plant into other semiarid regions of the Mediterranean basin due to its high palatability and feeding value to cattle (Yagoubi & Chriki 2000). It is also used for erosion control, re-vegetation and high quality honey production (Flores et al. 1997; Satta et al. 2000). Currently it grows in many Mediterranean basin countries; from Turkey to Spain (Flores et al. 1997).

We conducted our study in Menorca (the northernmost of the Balearic Islands, Spain). *Hedysarum* was introduced to this island between the end of the 18th century and the beginning of the 19th century (Ortells & Campos 1983). Since 1860 it has been used in a traditional cyclical agro-farming system (Bustamante, Allés & Espadas 2007). In addition, *Hedysarum* has escaped from cultivated fields and has become naturalised (*sensu* Pyšek et al. 2004) in natural and semi-natural areas such as ditches, old-fields, field edges and ruderal areas (Fraga et al. 2004).

Experimental design and pollination censuses

We located three sites with early successional shrublands (Carreras, Pons & Canals 2007) where we established three pairs (one in each site) of invaded 20x20 m^2 plots. Paired plots were located at an average distance of 138.3 m (ranging from 95 to 164 m), so that they could potentially share the same pollinator community because most of pollinator flying distances fall within this range (Gathmann & Tscharntke 2002; Osborne *et al.* 2008; Mawdsley & Sithole 2009; Bommarco *et al.* 2010). Meanwhile, the average distance between pairs was 11.5 km (ranging from 600 m to 17.2 km) to assure their independence.

Despite *Hedysarum* being one of the most dominant species in the shrublands (cover ranging from 26.4% to 48.6% across plots), in each plot it coexisted with 8.33 ± 0.33 (mean ± SE, hereafter) native co-flowering species. Overall, ten native plant species also belonged to the family Leguminosae and represented on average 36.4 ± 7.3% of the plant species in each plot. The rest of the native plant species (17) belonged to seven different families and had open and accessible flowers (Appendix S1 in Supporting Information).

To investigate the effect of *Hedysarum* on recipient plant-pollinator networks, we manually removed all *Hedysarum* inflorescences from one randomly selected plot of each pair (removal plot, hereafter), while the other plot was not manipulated (invaded plot, hereafter).

We conducted pollination censuses in the same study plots in the springs of 2009 and 2010 throughout the entire flowering period of *Hedysarum* (April-May). In both years weather conditions fell within the average ranges for these months in the study area (AEMET).

Pollination censuses were conducted on sunny, warm (≥ 17 ºC) and non-windy days, from 10 a.m. to 6 p.m. During each observation period (15 min), we counted the number of floral units (hereafter flowers, according to Dicks, Corbet & Pywell 2002) under observation, the number and identity of pollinators and the number of visits of each pollinator species. A visitor was considered a pollinator if it entered a flower and touched its sexual parts. The pollinator species that could not be identified in the field were sorted into distinct morphospecies and caught for later identification by specialists. Voucher specimens are deposited at EBD-CSIC.

The observation schedule for each plant species and individual under observation was randomly established. We considered a plot to be properly surveyed when, according to its rarefaction curve, we found no new plant-pollinator interaction after six or more censuses (Appendix S2). In total, we conducted 1252 censuses (313 h). On average each plant species was observed for 5.79 ± 0.60 h per plot, ranging from 1 h to 23.25 h.

Statistical analyses

For each study plot we built plant-pollinator networks with the data gathered during the two study years (i.e. six networks: three invaded and three removal plots). A network is defined as a two dimensional matrix ($i*j$) describing the interaction between the flowering plant species (i) and the pollinator species (j) in the community. Each cell in the matrix (a_{ij}) can be 1 or 0 indicating whether the interaction between the plant species i and the visitor species j is observed or not, respectively. Quantitative networks were built following the same criteria, except that each a_{ij} value is the weight of the interaction between the plant species i and the pollinator j measured as the visitation rate (nº visits/flower/hour) (Jordano, Bascompte & Olesen 2003).

In order to explore both quantitative and qualitative alterations in pollination patterns, for each plant and pollinator species we calculated visitation rate, normalised degree and niche overlap in each network (Table 1). These response variables, respectively, inform about the intensity and number of interactions established by each species, and about how these interactions are distributed. The proportion of honeybee visits (the main pollinator of *Hedysarum* in the study area) was also calculated for each plant species. Interaction rewiring was calculated for plant species shared between paired invaded and removal plots. Based on our experimental design, all pollinator species were assumed to be shared between invaded and removal paired plots (Table 1). We estimated two values of interaction rewiring: one considering all the interactions between shared species and the other excluding singletons (i.e., interactions that were only observed once), which represent interactions that are rare and difficult to detect and, thus, could potentially overestimate rewiring (Chacoff et al. 2012).

To explore the effect of *Hedysarum* on the pollination of resident plant species and whether their similarity in flower morphology with *Hedysarum* influenced such an effect, we built linear and generalised mixed models with the effect of treatment (invaded *vs*. removal), flower morphology (papilionate *vs*. non-papilionate) and their interaction as fixed effects. Site was included as a random factor in the models. The response variable visits (V_p), standardised by the number of flowers and hours of observation, was log-transformed and analysed through a linear mixed model. For the response variables normalised degree (D_p) and niche overlap (NO_p) we built generalised mixed models with binomial as error distribution family. The proportion of honeybee visits was logit-transformed according to Warton & Hui (2011) and analysed through a linear mixed model.

To explore the effect of *Hedysarum* on the foraging behaviour of pollinator species and whether their functional similarity to the main visitor of *Hedysarum* (i.e. the honeybee) influenced such an effect, we built linear and generalised models with the effect of treatment (invaded *vs*. removal), functional group (bees *vs*. non-bees) and their interaction as fixed effects. The functional group of bees included all bee species observed and the short tongued bumblebee *Bombus terrestris*. The functional group of non-bees included wasps, dipterans and coleopterans. Though the functional group of bees includes a wide variety of taxa, they all have larger flying ranges, visitation rates and capacities to reach low accessible floral resources than the non-bees, and are functionally closer to the honeybee. In addition, this functional classification is a compromise between the information available about the ecology of the observed taxa and an acceptable representation of functional groups across invaded and removal plots for allowing robust statistical analyses.

For the log-transformed response variable visits (V_a), we built a linear model with the logarithms of the number of flowers and hours of observation included as offsets. For the response variables normalised degree (D_a) and niche overlap (NO_a) we built generalised models with binomial as error distribution family. We also calculated the three response variables for the honeybee and analysed them through paired Wilcoxon tests.

Finally, we explored whether interaction rewiring of pollinators excluding the honeybee was influenced by changes in the foraging behaviour of the honeybee or by their functional similarity with the honeybee. We defined the changes in the foraging behaviour of the honeybee as the difference in the proportion of visits to a given plant species that the honeybee achieved in invaded and removal paired networks. For those plant species present in more than one site, data were pooled for all invaded and all removal plots where present. We built a generalised linear model with the change in foraging behaviour of the honeybee, the functional group of the pollinators involved (bees *vs*. non-bees) and their interaction as fixed factors. The binomial was the error distribution family. The analysis was repeated for the response variable interaction rewiring calculated excluding singletons.

The calculation of the network parameters and the analyses were performed in R (R Development Core Team 2014). Network parameters were calculated with the library *bipartite*. Linear and generalised mixed models were conducted with the libraries *nlme* and *lme4*, respectively. *Post hoc* multiple comparisons were conducted by building our own contrast matrices and analysing them with the library *multcomp*.

Results

We observed a total of 28 flowering plant species from eight different families. The eleven papilionate species, including *Hedysarum*, represented 41.8 ± 7.6% of the species in all study plots. Plants were visited by 93 pollinator species belonging to 38 families of Coleoptera (19.4%), Diptera (38.7%) and Hymenoptera (41.9%) (Appendix S1). All pollinator species are considered native to the study site.

Integration of Hedysarum into the diet of resident pollinators

Hedysarum was visited by a total of 15 pollinator species: 11 hymenopterans (including 7 Apidae) and four coleopterans, which represented 16.1% of the total community of pollinators. With the exception of the bees *Andrena ovatula* (Kirby, 1802) and *Synhalonia hungarica* (Friese, 1895), which represented only the 0.7% of its visits, all pollinators that visited *Hedysarum* were also observed visiting other plant species. Pollinators visiting *Hedysarum* were on average more generalised than pollinators visiting only natives (D_a = 0.24 ± 0.07 and 0.09 ± 0.01, respectively; Z = -5.081, p-value < 0.001).

Although *Hedysarum* received 54% of the visits observed in invaded plots, when standardised by the number of flowers, its visitation rate was low and similar to that of the resident papilionate species and lower than that of non-papilionate species (Fig. 2a). On average, *Hedysarum* had a normalised degree higher than papilionate species but similar to that of non-papilionate species (Fig. 2b). *Hedysarum* also had an averaged niche overlap higher than papilionate species but lower than non-papilionate species (Fig. 2c). *Hedysarum* was mostly visited (92.7 ± 4.2%) by the honeybee. On average, the proportion of honeybee visits to *Hedysarum* was higher than that to resident plant species, whether papilionate or not (Fig. 2d).

Effect of Hedysarum on the pollination of resident plants and the influence of flower morphology similarity

There were no significant differences in pollinator visits, normalised degree or niche overlap of resident plants between invaded and removal plots. Flower morphology had a significant effect on these variables, with papilionate species showing lower values for the three response variables than the non-papilionate ones. The interaction between treatment and flower morphology was not significant for any of the response variables, indicating that *Hedysarum* did not affect the pollination of resident plants, irrespective of their similarity in flower morphology (Table 2, Figs 2a, b and c).

The abovementioned results obtained for the entire pool of pollinators contrasted with those considering only the honeybee. The proportion of honeybee visits was lower in invaded than in removal plots, regardless of flower morphology. Once again, the interaction between treatment and flower morphology was not significant (Table 2, Fig. 2d).

Effect of Hedysarum on the foraging behaviour of pollinators and the influence of functional similarity

Pollinator visitation rates differed between invaded and removal plots but did not differ between functional groups. The interaction between the two variables was not significant, indicating that *Hedysarum* did not more strongly affect the visits conducted by bees, i.e., those taxa functionally closer to the honeybee, than those conducted by non-bee pollinators. Bees conducted less visits in invaded than in removal plots; while a similar but not significant trend was observed for the non-bees functional group (Table 2, Fig. 3c). No significant trend was observed for honeybee visits (N = 6, V= 6, p-value = 0.250) (Fig. 3c).

The normalised degree of pollinators did not differ between invaded and removal plots, neither between functional groups. The interaction between the two variables was not significant (Table 2, Fig. 3a). The honeybee also showed a similar normalised degree in invaded and removal plots (N = 6, V = 1, p-value = 0.500) (Fig. 3b).

The niche overlap of pollinators differed between invaded and removal plots and between functional groups. In addition, the interaction between the two variables was also significant: while both functional groups had lower niche overlap in invaded than in removal plots, bees were more strongly affected than non-bee pollinators (Table 2, Fig. 3b). No significant trend was observed for honeybee niche overlap (N = 6, V = 0, p-value = 0.250) (Fig. 3b).

Effect of Hedysarum on interaction rewiring and the influence of honeybee foraging behaviour

In the experiment, 29.7 ± 4.4% of the interactions among shared species were observed both in invaded and removal paired plots. Meanwhile, 34.3 ± 8.8% and 36.7 ± 4.4% of the interactions were exclusive to invaded and removal plots, respectively. The contribution to exclusive interactions was similar across plant species, as for all of them at least half of their interactions were exclusive to either invaded or removal plots. In the case of pollinators, their contribution to exclusive interactions was highly diverse across species. Most pollinators were only involved in exclusive interactions; few of them showed high fidelity and were only involved in interactions shared between invaded plots. All the intermediate contributions were also observed.

Interaction rewiring was influenced by changes in foraging behaviour of the honeybee. That is, for a given plant species, the greater the difference between invaded and removal plots in honeybee visits, the higher the proportion of rewired interactions (Chisq= 5.185, p-value = 0.023) (Fig. 4). We observed this relationship irrespective of the functional group of the pollinators involved (Chisq = 0.001, p-value = 0.983). The interaction between the two explicative variables (i.e. functional group and changes in the foraging behaviour of the honeybee) was also not significant (F = 0.203, p-value = 0.652). Results did not qualitatively differ when singletons were excluded from the analysis.

Discussion

The important role of the honeybee in the integration of Hedysarum into the recipient plant-pollinator network

Hedysarum was well integrated into recipient plant-pollinator networks, being visited by more species than the average for the resident plants. As pollinators seek to optimize their foraging behaviour (Olesen et al. 2008; Petanidou et al. 2008; Lázaro & Totland 2010), it might be advantageous for them to include abundant and high-rewarding species like *Hedysarum* in their diet. Particularly, the honeybee played an important role in such integration by performing most of the *Hedysarum* visits. The honeybee, like other generalised, abundant and ubiquitous pollinators (Goulson 2003), is able to include many plant species in its diet, even non-natives (Memmott & Waser 2002; Olesen et al. 2002; Morales & Aizen 2006; Padrón et al. 2009). In addition, plants with flowers arranged in inflorescences like *Hedysarum*, might be particularly attractive to the honeybee due to its flower constancy (Grüeter et al. 2011) and intense foraging behaviour with short flying distances between consecutive visits (Gross 2001). This behaviour would also explain the high percentage of honeybee visits observed in *Hedysarum*.

Despite *Hedysarum* integration, pollinator species visiting *Hedysarum* represented a low percentage of the total pool of pollinator species (16.1%) in the community compared to other non-native plant species invading other systems. Vilà et al. (2009) studied five non-native plant species and found that they were visited by 31 to 50% of the pollinator species in the community. However, the five non-native species studied had open and non-restrictive flower morphologies, allowing a wider range of pollinators to visit them. Meanwhile, non-natives with more restrictive flower morphologies like legumes, filter pollinators according to their ability to access rewards (Córdoba & Cocucci 2011). Non-native plants with restrictive flower morphologies might face similar limitations in introduced areas than in their native ranges. In fact, *Hedysarum* has a normalised degree in its native range comparable to that in the introduced communities on Menorca (Montero-Castaño et al. 2014).

The effect of Hedysarum on resident plant pollination was not influenced by similarity in flower morphology

The integration of *Hedysarum* into the recipient plant-pollinator networks did not have a larger effect on the pollination of plants exhibiting similar flower morphology to *Hedysarum* (i.e., those with papilionate flowers). Papilionate flowers are not accessible to all types of pollinators (Córdoba & Cocucci 2011). In fact, plants with papilionate flowers showed low visitation rates and normalised degree in both invaded and removal plots, obscuring the detection of an influence of *Hedysarum* presence. The expected influence of similarity in flower morphology on pollination between non-native and resident plants might be more easily observed for non-native plant species with minimally restrictive flower morphologies such as Composites, as reported by Morales & Traveset (2009).

Though *Hedysarum* did not have an overall effect on the average number or frequency of interactions involving resident plants (i.e. no quantitative effect), it affected the identity of some of those interactions (i.e. qualitative effect) as demonstrated by the lower proportion of honeybee visits observed in invaded networks. As has already been mentioned, *Hedysarum* was highly attractive to the honeybee, which reduced its presence on resident plants. Consequently, in invaded plots more resident floral resources were available to other pollinators. Honeybees can outcompete other pollinator species by depleting floral resources (Roubik 1983; Paini 2004; Valido, Rodríguez-Rodríguez & Jordano 2014) due to their abundance, generalised diet, communication skills, wide activity periods and systematic foraging behaviour (Huryn 1997, Gathmann & Tscharntke 2002, Steffan-Dewenter et al. 2002, Steffan-Dewenter & Kuhn 2003). Besides, honeybees have been shown to displace smaller species from flowers by physical disturbance (Gross & Mackay 1998).

Hedysarum affected the foraging behaviour of bees

As expected, *Hedysarum* affected the behaviour of pollinators and more noticeably those functionally closer to the honeybee. *Hedysarum* decreased the frequency (visitation rate), though not the number (normalised degree), of the interactions established by bees. Besides, *Hedysarum* altered the distribution of such interactions and more noticeably decreased the niche overlap of bees.

The decrease in the visitation rate of bees in invaded plots seemed to be the result of an indirect effect of *Hedysarum* through the alteration of the foraging behaviour of the honeybee, as suggested by the opposite trends observed for both groups. As we have previously discussed, the honeybee can be a strong competitor for other pollinator species; especially for functionally redundant species. Resource partitioning in time and space reduces competition and allows species coexistence (Westphal, Steffan-Dewenter & Tscharntke 2006). However, such partitioning might be blurred among species belonging to the same functional group due to shared phenotypic and behavioural traits (e.g. tongue length, preferred resources, periods of maximum activity, etc.).

Despite the fact that the normalised degree was not altered, niche overlap of bees decreased in invaded plots. That is, in invaded plots there was a reorganisation of plant-pollinator interactions. In invaded plots, bees able to visit papilionate species (including *Hedysarum*) were more interconnected among them than with those bees visiting non-papilionate species, and vice versa. Meanwhile, in removal plots, bees able to visit papilionate species also visited non-papilionate plants in order to fulfil their requirements, and consequently increased their niche overlap. The same trend was observed for non-bees. However, as only a few non-bee species are able to access papilionate flowers, the effect of *Hedysarum* was less significant.

The honeybee leads the interaction rewiring between invaded and removal networks

We observed that plant-pollinator interactions are highly plastic, suggesting a high lability of pollinators in resource use. Due to our experimental set up, we assume that paired invaded and removal networks share the same pollinator community. However, we cannot disregard potential differences in the abundance of some pollinators, mainly of the less mobile ones. Though that could slightly overestimate the lability of pollinators in resource use, the observed percentage of exclusive interactions to invaded or removal networks is consistent with the 30% found by other authors (Petanidou et al. 2008).

Plasticity of plant-pollinator interactions can have several non-exclusive explanations. First, it can be determined by the local floral environment. On the one hand, the abundance of floral rewards affects the probability of interactions (Vázquez et al. 2007), as stated by neutral theory (Hubbell 2001). On the other hand, neutrality can be diluted by magnet effects (Johnson et al. 2003; Molina-Montenegro, Badano & Cavieres 2008; Montero-Castaño & Vilà 2015) or conversely, by the monopolisation of visits by particular neighbours (Chittka, Gumbert & Kunze 1997; Kandori et al. 2009; Morales & Traveset 2009). Second, coexisting pollinator species can influence each other’s foraging behaviour; especially, when abundant and/or highly competitive species are involved, such as the honeybee (Valido et al. 2014).

Though both drivers may be acting in this study case, we have evidence for the second explanation, as the interaction rewiring was associated with the changes in honeybee foraging behavior between invaded and removal networks.

Floral resources seem to be a limiting factor in the study system. Therefore, for a given resident plant, the greater the differences in honeybee visits, the greater the differences in floral resources available to other pollinators and the higher the chance of finding different interactions between invaded and removal plots. This result sheds some light on the conditions under which rewiring occurs, which is an important topic ripe for empirical and theoretical consideration (Burkle & Alarcón 2011).

For instance, for a more realistic projection of the long-term response of plant pollinator networks to the arrival or removal of species, modellers are incorporating information on rewiring (e.g. Kaiser-Bunbury et al. 2010, Ramos-Jiliberto et al. 2012, Valdovinos et al. 2013). In fact, the incorporation of topological plasticity based on interaction rewiring, seems to increase network robustness to secondary extinctions (Ramos-Jiliberto et al. 2012).

Even if network topological properties are conserved after invasion, the effects that we have observed at the species level can have consequences on the reproduction of resident plant and pollinator species.

Pollination visitation patterns of resident plants were nor quantitatively altered, but the identity of visitor species differed between invaded and removal plots: the honeybee accounted for a higher proportion of visits to plants in removal than in invaded plots. Visitor species differ in their pollination effectiveness in terms of pollen removal, transport and deposition (Ne'eman *et al.* 2010) thus, implications on the reproductive success of resident plants would be expected. In terms of pollen quality, the honeybee is considered a low efficient pollinator as it usually increases geitonogamy (Westerkamp 1991; Garibaldi *et al.* 2013). Therefore, higher reproductive success of resident plants would be expected in invaded plots. Regarding to pollinator species, their pollination patterns were quantitatively and qualitatively altered, what would also have consequences on their fitness. However, the impacts and underlying mechanisms of changes on food resources on pollinators' fitness are poorly understood, preventing us to advance any predictions. In fact, the literature on the effect of invasions on pollinators show diverse and even contradictory impacts on pollinators (Montero-Castaño & Vilà 2012; Litt *et al.* 2014).

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Data Accessibility

DData deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.77rn2 (Montero-Castaño & Vilà, 2016)

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Plant-pollinator networks.

Table S1.1. Flowering plant species present in the study plots.

Table S1.2. Pollinator species observed visiting flowering plants

Appendix S2. Rarefaction curves.

Figure legends

Figure 1. Non-native *Hedysarum* (left) and detail of an inflorescence being visited by a honeybee (right). Photographs by A. Montero-Castaño.

Figure 2. Effect of *Hedysarum* on the pollination patterns of resident plants. Mean ± 95%CI (a) visits (standardised per flower and hour and log-transformed), (b) normalised degree, (c) niche overlap and (d) proportion of honeybee visits to *Hedysarum* and resident papilionate and non-papilionate species in invaded and removal plots. Upper case symbols represent the significance levels for differences between invaded and removal plots according to the *post hoc* multilevel comparisons conducted for the models: ** $p < 0.01$, n.s = no significant.

Figure 3. Effect of *Hedysarum* on the foraging behaviour of pollinators. Mean ± 95%CI (a) visits (standardised per flower and hour and log-transformed), (b) normalised degree, (b) and (c) niche overlap of the honeybee, bees and non-bees in invaded and removal plots. Upper case symbols represent the significance levels for differences between invaded and removal plots; in the case of bees and non-bees functional groups, according to the *post hoc* multilevel comparisons conducted for the models: ˙ p-value = 0.05, ** $p < 0.01$, *** $p < 0.001$, n.s = no significant.

Figure 4. Relationship between interaction rewiring and changes in the foraging behavior of the honeybee. (a) Positive relationship between these two variables and (b) its bipartite network representation. Changes in the foraging behaviour of the honeybee are defined as the difference in the proportion of visits to a given plant species that the honeybee achieved in invaded and removal paired networks.

Shared species of the three pairs of networks studied are pooled and represented together. In (b) the size of the circles representing plant species indicates differences in the proportion of honeybee visits between invaded and removal plots. Grey lines represent rewired interactions (whether exclusive of invaded or removal plots) and black lines represent non-rewired interactions (i.e. those observed in both invaded and removal plots).

Tables

Table 1. Response variables estimated for both plant (*p*) and animal pollinator (*a*) species.

Parameter	Symbol	Definition
Visits	V_p	Number of visits a plant species receives
	V_a	Number of visits a pollinator species makes
Normalised degree	D_p	Proportion of the total number of pollinator species a particular plant species is visited by
	D_a	Proportion of the total number of plant species a particular pollinator species visits
Niche overlap	NO_p	Proportion of the total number of plant species a particular plant species shares pollinators with
	NO_a	Proportion of the total number of pollinator species a particular pollinator species shares visited plants with
Interaction rewiring		Proportion of the interactions involving plant species shared between paired invaded and removal plots that are exclusive to invaded or to removal plots

Table 2. Likelihood Ratio Tests (LRT) of the effects of treatment and flower morphology and their interaction on visitation rates, normalised degree and niche overlap for resident plant and pollinator communities. Significance levels: ˙ p-value ≈ 0.05, * < 0.05, ** < 0.01, *** < 0.001.

Resident community	**N**	**Response variable**	**Explicative variable**	**p-value**	
Plants	54	Visits (V_p)	Treatment	0.732	
			Flower morphology	< 0.001	***
			Treatment*Flower morphology	0.854	
	54	Normalised degree (D_p)	Treatment	0.892	
			Flower morphology	< 0.001	***
			Treatment*Flower morphology	0.973	
	54	Niche overlap (NO_p)	Treatment	0.187	
			Flower morphology	< 0.001	***
			Treatment*Flower morphology	0.562	
	54	Proportion honeybee visits	Treatment	< 0.001	***
			Flower morphology	0.845	
			Treatment*Flower morphology	0.403	
Pollinators	178	Visits (V_a)	Treatment	0.005	**
			Functional group	0.988	
			Treatment*Functional group	0.405	
	191	Normalised degree (D_a)	Treatment	0.828	
			Functional group	0.140	
			Treatment*Functional group	0.929	
	191	Niche overlap (NO_a)	Treatment	< 0.001	***
			Functional group	< 0.001	***
			Treatment*Functional group	0.002	**