

A new native plant in the neighborhood: effects on plant–pollinator networks, pollination, and plant reproductive success

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Abstract. Ecological communities are dynamic entities subjected to extinction/colonization events. Because species are connected through complex interaction networks, the arrival of a new species is likely to affect various species across the community, as observed in plant biological invasions. However, plant invasions usually represent extreme scenarios in which the community is strongly dominated by the alien species, confounding the effects of a change in species composition with a massive increase in floral resource availability. Our study addresses changes in plant community composition involving native species, a common phenomenon under the current climate change scenario in which plants are modifying their distribution ranges. We experimentally manipulated patches of a natural scrubland community by introducing a native plant (henceforth colonizing plant). To avoid introducing a disproportionate amount of floral resources we adjusted the number of flowers of the colonizing plant to the amount of floral resources locally available in each patch. We had two objectives: (1) to analyse the effects of the arrival of a new plant on the pollinator community, the rearrangement of plant–pollinator interactions and the structure of the plant–pollinator network; (2) to evaluate potential consequences for pollination and the reproductive success of resident plant species. The colonizing plant acted as a magnet species, attracting bumble bees and facilitating interactions to other plants through spill-over. The introduction of the colonizing plant also affected the structure of plant–pollinator networks (colonized networks were more generalized and more nested than control networks) and modified the arrangement of plant and pollinator species into modules. Ultimately, these changes resulted in higher heterospecific (but not conspecific) pollen deposition and had contrasting effects on the reproductive success of two resident plant species (higher fruit set and lower seed set, respectively). Our study shows that relationships between plants and pollinators are rapidly rearranged in response to novel situations (even when the new plant is not overly dominant), with important functional consequences on pollination and plant reproductive success. Our study establishes a link between network structure and pollination and plant reproductive success, which may be mediated by differences among pollinator species in foraging behavior.

Key words: *Cistus albidus*; *Cistus salviifolius*; *field experiment*; *Lavandula stoechas*; *plant colonization*; *plant community*; *plant–pollinator interactions*; *Thymus vulgaris*.

INTRODUCTION

Ecological communities are dynamic entities subjected to changes in species composition through extinction and colonization events. These changes may occur more or less gradually over long periods of time, due to

ecological processes such as competition/facilitation (Tilman 2004) and shifts in environmental conditions (e.g. climate change; Chen et al. 2011), or more rapidly as a result of ecological disturbances and human-induced biological introductions (Paine 1966, Shea and Chesson 2002).

The species of a community interact among themselves generating complex interaction networks. Thus, the extinction/colonization of a given species will not only affect the interactions involving this species but may also have cascading effects on other species

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interactions, either by causing a redistribution of interactions (rewiring) or by modifying the strength of interactions (Poisot et al. 2015, Tylianakis and Morris 2017). In turn, these changes may have important consequences on the reproduction of certain species and ultimately on community structure and ecosystem functioning (Bergstrom et al. 2009). Network analysis has been intensively used in the last decade to study interactions among plants and pollinators at the community level. In general, plant–pollinator networks are heterogeneous, asymmetric, nested and modular (Jordano et al. 2003, Bascompte et al. 2003, Bascompte et al. 2006, Olesen et al. 2007). Network topology and network stability are intimately related (e.g. Tylianakis et al. 2010), and theoretical approaches suggest that the loss of keystone species/interactions may result in secondary extinctions and network fragmentation (Memmot et al. 2004, Santamaría et al. 2015, Traveset et al. 2017).

Human-induced translocations of exotic plants provide scenarios of relatively rapid incorporation of new species into ecological networks. Invasive plants are usually pollinator-generalist and are readily visited by native pollinators (Traveset and Richardson 2006). This scenario may cause pollinators to change their foraging decisions, potentially leading to changes in network structure (Ghazoul 2004, Aizen et al. 2008), and ultimately modifying pollen transfer patterns, with potential consequences on the reproductive success of native plants (Lopezaraiza-Mikel et al. 2007, Morales and Traveset 2009, Vanbergen et al. 2018). In some cases, invasive plant species may compete for pollinators with native species (Brown et al. 2002, Bartomeus et al. 2008). In other cases, invasive plants may act as magnet species, attracting pollinators to the community and promoting higher visitation rates to other plants via spill over (Moragues and Traveset 2005, Bartomeus et al. 2008, Molina-Montenegro et al. 2008).

However, plant invasions usually represent extreme scenarios in which the local community is strongly dominated by an alien species that often produces large amounts of floral resources compared to the native species (e.g. Chittka and Schürkens 2001). Therefore, it is difficult to discern whether changes in plant–pollinator interactions are attributable to changes in plant composition per se or to a massive increase in floral resource availability. In this study, we are interested in changes in plant community composition involving native species. We experimentally manipulate patches of a natural scrubland community by introducing a native plant (simulating a range expansion) and then assess the ability of the plant–pollinator community to rearrange its interactions and the short-term ecological consequences on the reproduction of resident plants. Importantly, we control for the amount of floral resources introduced. We have two objectives: (1) to analyse the effects of the arrival of a new species on the pollinator community, plant–pollinator interactions and the structure of the plant–pollinator network; and (2) to evaluate the

consequences of these changes on pollination (pollen deposition on the stigmas) and plant reproductive success (fruit and seed set).

We work in natural communities dominated by the shrub *Cistus salviifolius* in which we introduce the co-flowering congeneric *C. albidus*. *C. albidus* usually occurs at lower altitudes than *C. salviifolius* (Bolós et al. 2005). Therefore, our manipulation mimics an elevational shift, a common phenomenon under the current climate change scenario (Kelly and Goulden 2008). Additionally, our manipulation is plausible because both plants coexist in other areas (Trabaud and Oustric 1989, Bosch 1992, Bosch et al. 2009). *C. albidus* produces more pollen and nectar per flower than *C. salviifolius* and attracts more and larger pollinators (Bosch 1992). Consequently, we envision three possible outcomes. First, *C. albidus* could draw pollinators away from *C. salviifolius* and/or other resident plant species. Depending on the magnitude of this effect, it could result in reduced pollination and reproductive success. Studies on plant invasions have shown that interspecific competition for pollinators often results in decreased connectivity of native species (Aizen et al. 2008, Kaiser-Bunbury et al. 2011). Thus, under this scenario we would expect an overall decrease in generalization. Second, *C. albidus* could act as a magnet species and attract new pollinators. Then, *C. albidus* could share them with the local community, thus acting as a facilitator. This spill-over effect could enhance pollination and reproductive success of the resident plant species. However, given that *C. albidus* produces large amounts of pollen and attracts large pollinators, which carry and deposit large amounts of pollen (Bosch 1992, Willmer and Finlayson 2014), this scenario could also result in increased heterospecific pollen deposition. Under this scenario, we would expect an increase in generalization (Valdovinos et al. 2009) and network nestedness (Traveset et al. 2013), as well as a decrease in network modularity (Santos et al. 2012, Albrecht et al. 2014). Alternatively (third scenario), *C. albidus* could attract new pollinators but not share them with the other plants, with no effects on pollination and reproductive success of the resident community. This scenario would favour the appearance of a new network module dominated by *C. albidus*.

MATERIALS AND METHODS

Study area and site selection

The study was conducted in Montseny Natural Park (Barcelona, NE Spain) in 2016, and comprised an area of 32 km² between 432 and 818 m a.s.l. (Appendix S1: Table S1). The climate in the area is sub-Mediterranean, with a mean annual temperature of 13.8 °C and a mean rainfall of 649 mm.

The area is occupied by a matrix of dense Mediterranean holm oak (*Quercus ilex*) forests with scattered patches of Mediterranean scrubland. We selected 18 of

these patches (henceforth plots) measuring $\sim 500 \text{ m}^2$ (range: 200–900 m^2) (Appendix S1: Fig. S1). All plots were dominated by *Cistus salviifolius* and included some subdominant species such as *Lavandula stoechas* and *Thymus vulgaris*. Distance between nearest plots was $\sim 900 \text{ m}$ (range 387–2,487 m). This distance is assumed to encompass the foraging range of most pollinator species (Greenleaf et al. 2007). All plots were surrounded by dense forest ($>95\%$ of the landscape cover within a 250 m radius). To further isolate plots, before the beginning of the flowering period we removed all flowering plants within a 50 m buffer from the periphery of each plot.

Introduction of *Cistus albidus*

Plots were distributed between the two treatments (colonized, control) based on plant community composition, flowering phenology and geographical distribution (Appendix S1: Table S1, Fig. S1). As a result, plots of the two treatments did not differ in flower abundance, flower richness, flower diversity (t -test, $|t| < 0.93$, $P > 0.36$ in all three cases), flower composition (PERMANOVA, pseudo- $F_{1,16} = 0.71$, $P = 0.74$) or spatial distribution (test on spatial homogeneity of group dispersion, $F_{1,16} = 0.40$, $P = 0.54$).

Potted *C. albidus* individuals with open flowers were introduced in nine of the 18 plots (colonized plots) when *C. salviifolius* started to bloom (mid-April). *C. albidus* pots (~ 15 per plot) were intermixed with *C. salviifolius* individuals. The remainder of the plots ($n = 9$) were left unmanipulated (control plots).

C. salviifolius and *C. albidus* flowers are actinomorphic and have a similar structure. However, *C. albidus* flowers are pink (as opposed to white in *C. salviifolius*), slightly larger, and produce approximately twice as much pollen and nectar (Bosch 1992). To avoid the potentially confounding effect of a massive increase in floral resources, we matched *C. albidus* floral resources (pollen and nectar) to those of the local *C. salviifolius* population in each colonized plot. Therefore, the number of introduced *C. albidus* flowers (~ 80 flowers/plot, range: 56–104) was approximately half the number of *C. salviifolius* flowers (~ 150 flowers/plot, range: 106–195 flowers/plot). To allow pollinators to adjust to the new flower context, pollinator surveys were conducted 3 d after the introduction of *C. albidus*. Early in the morning, before starting the pollinator surveys, we further adjusted the number of *C. salviifolius* and *C. albidus* flowers to the desired 2:1 ratio by either adding or removing *C. albidus* flowers.

Pollinator surveys

Pollinator surveys were conducted between 24 April and 5 May. Each plot was surveyed by 2–3 observers throughout a day, from 09:30 until 14:30. This period encompasses the entire life span of individual

C. salviifolius and *C. albidus* flowers (Bosch 1992). We sampled 2–3 plots per day. Sampling dates did not vary between control and colonized plots (Wilcoxon test, $W = 41$, $P = 1$).

Early in the morning, before starting the pollinator survey, all open flowers in the plot were counted. Pollinator surveys consisted of several rounds (~ 11 rounds/plot, range 6–20 rounds) in which we recorded all pollinators contacting the reproductive organs of the flowers. Some pollinators were captured for later identification in the laboratory. Usually, all flowers in the plot were surveyed in each round. However, when a plant species was very abundant, subsets of flowers were surveyed. On the other hand, to record a sufficiently large number of interactions in rare plant species, these were surveyed more frequently. We define visitation rate as the number of pollinators visiting a plant species divided by the number of flowers surveyed, and interaction frequency as the visitation rate of a pollinator species to a plant species multiplied by the flower abundance (number of open flowers) of that plant species. We use interaction frequency as a measure of interaction strength (e.g. Vázquez et al. 2005). We define abundance of a pollinator species as the sum of the frequencies of all interactions in which this pollinator species is involved.

We recorded 188 pollinator species. Most of them were rare (166 species accounted for less than 1% of total pollinator abundance). To facilitate comparison across plots and because similar pollinators are expected to have similar effects on pollination, pollinator species were grouped into 17 functional groups based on taxonomic, morphometric and abundance criteria (Gómez et al 2010). The 17 pollinator groups were: (1) honey bees (*Apis mellifera*); (2) bumble bees (mostly *Bombus terrestris*); (3) short-tongued small bees ($<10 \text{ mm}$ long) (STSB); (4) short-tongued large bees ($>10 \text{ mm}$ long) (STLB); (5) long-tongued small bees (LTSB); (6) long-tongued large bees (LTLB); (7) hoverflies; (8) bee flies; (9) flies; (10) ants; (11) butterflies; (12) wasps; (13) true bugs; (14) grasshoppers; (15) small ($<5 \text{ mm}$ long) beetles; (16) medium-sized (5–10 mm long) beetles; (17) large ($>10 \text{ mm}$ long) beetles. Unless otherwise indicated, analyses were conducted using pollinator functional groups.

Stigma pollen loads

To evaluate pollination, we measured pollen deposition on the stigmas of *C. salviifolius* (present in all plots), *L. stoechas* (present in seven control and seven colonized plots), *T. vulgaris* female morph (henceforth *T. vulgaris* F, six control and six colonized plots) and *T. vulgaris* hermaphroditic morph (henceforth *T. vulgaris* H, six control and five colonized plots). For each of these species/morphs (henceforth focal plants) we tagged 10 size-representative individuals distributed across the plot. Early in the morning, before pollinators were active, we marked 6 newly-opened (unvisited)

flowers on each tagged individual. In *L. stoechas* the probability that a flower will set a fruit depends on its position within the inflorescence (Muñoz and Devesa 1987). For this reason, in this species we marked only central flowers located in the most basal part of the inflorescences.

At the end of the pollinator survey, and just before *C. salviifolius* flowers started losing their petals and closing their sepals, we collected the stigmas of two marked flowers of each of the 10 tagged individuals per focal plant. By working with newly-opened flowers and collecting them at the end of the day, we ensured that pollen deposition was directly attributable to the visitation patterns observed during the pollinator survey. Stigma collection was done with extreme caution to avoid accidental pollen self-deposition. Stigmas were placed individually on a layer of fuchsine-stained gelatine (Beattie 1971) in Eppendorf tubes and kept at 4°C until processed. The remaining 4 marked flowers per individual were left for later assessment of fruit and seed set.

Collected stigmas were mounted on glass slides, and pollen grains were identified and counted (all pollen grains in *L. stoechas*, *T. vulgaris* F and *T. vulgaris* H; ca. 75% of the stigma surface in *C. salviifolius*) at 300X by the Palynological Service of Universitat Autònoma de Barcelona (<http://sct.uab.cat/lap/>).

Fruit- and seed-set

L. stoechas and *T. vulgaris* flowers remain open and receptive for 3–4 d (Muñoz and Devesa 1987, Arnan et al. 2014). For this reason, and to extend the potential effects of *C. albidus* on pollinator visitation and reproductive success of focal plants, potted *C. albidus* were left in the field for three days following the pollinator surveys.

We collected the fruits of the four marked flowers left on each tagged individual at the beginning of the fruit-ripening period (*C. salviifolius* and *T. vulgaris*: 1 month after bloom; *L. stoechas*: 4 months after bloom). In the laboratory, we opened these fruits and counted viable and unviable seeds. Small, pale-coloured seeds without endosperm were considered unviable.

Data analyses

Pollinator community.—To compare the pollinator community of control and colonized plots we analysed overall pollinator species abundance, richness, diversity (Shannon index) and composition, and the abundance of each pollinator functional group. Pollinator abundance data were log-transformed to meet model assumptions. Because pollinator abundance and flower abundance were highly correlated ($r = 0.91$), abundance data were analysed with ANCOVAs, with treatment (control and colonized plots) as fixed factor and flower abundance as a covariate. In the analysis of pollinator functional group abundance, we applied the Benjamini-

Hochberg method for multiple test comparisons. Pollinator species richness (log-transformed) and diversity were analysed with *t*-tests, and pollinator species composition with PERMANOVA (Bray-Curtis dissimilarity index).

Plant–pollinator interaction patterns.—We compared overall visitation rates at the plot level and in focal plants (*C. salviifolius*, *L. stoechas*, *T. vulgaris* F and *T. vulgaris* H). We used Wilcoxon tests because data were not normally distributed and could not be appropriately transformed. In addition, we compared pollinator group composition of each focal plant between control and colonized plots with PERMANOVA (Bray-Curtis dissimilarity index). To detect which pollinator groups differed between control and colonized plots, we calculated the contribution of each pollinator group to the observed dissimilarity with a SIMPER analysis.

Network structure.—We built a plant–pollinator network for each plot with the interaction frequency data. To characterize overall network generalization, we calculated H_2' (Blüthgen et al. 2006), plant generality (weighted mean number of pollinator species visiting a plant species) and pollinator generality (weighted mean number of plant species visited by a pollinator species) (Bersier et al. 2002). We also characterized specialization of focal plant species and pollinator functional groups using d' (Blüthgen et al. 2006). We conducted *t*-tests to compare the values of these metrics between control and colonized plots. Comparisons of pollinator functional group d' were conducted with Wilcoxon tests followed by Benjamini-Hochberg corrections.

For each network we calculated nestedness using the Weighted Nestedness metric based on Overlap and Decreasing Fill (*WNODF*) (Almeida-Neto and Ulrich 2010). To assess the significance of nestedness in each network we built a null model in which 1,000 networks were generated by setting the probability of interaction between two species proportional to their relative abundances (Vázquez et al. 2007). Then, the observed value was compared with the 95% confidence interval of the null distribution. Nestedness values of control and colonized networks were compared with a *t*-test. Finally, to analyse the effect of *C. albidus* on network nestedness we calculated the contribution of *C. albidus* to the observed nestedness (Saavedra et al. 2011).

We calculated the modularity of each network using Consensus Modularity (Gómez et al. 2014). This script uses the *QuanBiMo* algorithm (Dormann and Strauss 2013) and returns a number of modules (nQ), a modularity index (Q), and its significance by comparison to a null model. The number of modules and the modularity index of control and colonized networks were compared with *t*-tests or Wilcoxon tests depending on data distribution. To synthesise the modularity patterns observed, we pooled together the data of all control and all

colonized local networks to build a control metanetwork and a colonized metanetwork.

Pollination and plant reproductive success.—To study the functional consequences of the introduction of *C. albidus* we compared pollination (amount of conspecific and heterospecific pollen grains deposited on the stigmas) and plant reproductive success (fruit and seed set) of focal plants in control and colonized plots.

We conducted generalized linear mixed models on the number of conspecific pollen grains deposited on the stigmas (Poisson family for *C. salviifolius* and, due to the high frequency of zeros, negative binomial family for *L. stoechas*, *T. vulgaris* F and *T. vulgaris* H), with treatment (control vs colonized) as fixed factor and plot and individual plant (nested within plot) as random factors. We used a similar procedure to analyse heterospecific pollen grain deposition with zero-inflated negative binomial family models. Heterospecific pollen grains could belong to *C. albidus* or to resident species. To discriminate between these two types of heterospecific deposition we analysed heterospecific pollen composition with PERMANOVA (Bray-Curtis dissimilarity index). Rare pollen species (<1% of total pollen grains) were grouped into a single category (*other*), and a dummy variable ($\alpha = 0.01$) was added to allow model convergence. To detect which heterospecific pollen types differed between control and colonized plots, we calculated the contribution of each heterospecific pollen type to the observed dissimilarity with a SIMPER analysis.

Fruit set was calculated as the proportion of flowers (four marked flowers on 10 individuals per focal plant) that formed at least one seed. We used generalized linear mixed models (binomial family) on the proportion of flowers producing fruits (1: yes, 0: no), with treatment as fixed factor and plot and individual (nested within plot) as random factors. *C. salviifolius* flowers have a variable number of ovules, whereas *L. stoechas* and *T. vulgaris* flowers have four ovules. We tested differences between treatments in seed set (number of seeds/ fruit) with generalized linear mixed models (Poisson family) on seed number, with treatment as fixed factor and plot and individual (nested in plot) as random factors.

All analyses were conducted in R (R Core Team, 2018). We used the package *vegan* (Oksanen et al. 2018) for multivariate statistics, *Bipartite* (Dormann et al. 2008) for network analyses and *lme4* (Bates et al. 2015) and *glmmADMB* (Skaug et al. 2016) for linear models. All means are followed by \pm SE.

RESULTS

Pollinator community

The introduction of *Cistus albidus* did not alter pollinator abundance ($F_{1,15} = 0.21$, $P = 0.65$), species richness ($t_{14,7} = -0.41$, $P = 0.68$), diversity ($t_{15,7} = -0.26$, $P = 0.80$), or composition (pseudo- $F_{1,16} = 0.73$,

$P = 0.76$). However, bumblebee abundance increased 3.2-fold in colonized plots (control plots: 0.99 ± 0.40 individuals/ plot; colonized plots: 3.15 ± 1.10 ; $F_{1,15} = 12.06$, $P = 0.003$). These differences in bumblebee abundance persisted when visits recorded on *C. albidus* were excluded from the analysis (colonized plots: 2.57 ± 0.88 ; $F_{1,15} = 7.62$, $P = 0.015$), indicating that bumble bees attracted to the colonized plots visited not only *C. albidus* but also other plants in the community. There were no differences between treatments in the abundance of the other pollinator groups (Appendix S1: Table S2).

Plant–pollinator interaction patterns

C. albidus was visited mostly by honey bees (43% of the visits), followed by hoverflies (17%), short-tongued small bees (mostly *Lasioglossum* spp., 10%), short-tongued large bees (mostly *Andrena* spp., 5%), bumble bees (9%), and small beetles (7%) (Appendix S1: Fig. S2).

Visitation rate at the plot level did not differ between treatments (control plots: 0.29 ± 0.10 individuals/ 100 flowers; colonized plots: 0.26 ± 0.05 ; $W = 39$, $P = 0.93$), and visitation rates of the focal plants were also similar in the two treatments (all $W < 36$, $P > 0.43$). However, pollinator composition of *Lavandula stoechas* changed in colonized plots (pseudo- $F_{1,12} = 2.12$, $P = 0.04$). Bumble bees increased their visitation rate 1.7-fold (control plots: 0.015 ± 0.01 individuals/ 100 flowers; colonized plots: 0.026 ± 0.005 ; SIMPER, $P = 0.015$) and became the most important pollinator group of this plant in colonized plots (Fig. 1). Pollinator composition did not vary in *Thymus vulgaris* F (pseudo- $F_{1,11} = 0.67$, $P = 0.77$), *T. vulgaris* H (pseudo- $F_{1,9} = 0.58$, $P = 0.77$), or *C. salviifolius* (pseudo- $F_{1,16} = 0.32$, $P = 0.95$). Bumblebee visitation rate to *C. salviifolius* was 7-fold greater in colonized plots (marginally significant trend; control plots: 0.011 ± 0.008 individuals/100 flowers; colonized plots: 0.068 ± 0.03 ; SIMPER, $P = 0.086$), but bumble bees remained an infrequent visitor of *C. salviifolius* (Fig. 1).

Network structure

Network and species generalization.—Network specialization (H_2') decreased 0.80-fold from control to colonized networks (Table 1). Plant generality remained unaltered but pollinator generality increased 1.5-fold (Table 1). These differences became non-significant when we removed *C. albidus* from the networks of the colonized plots, indicating that the increase in generalization was primarily driven by the interactions involving the introduced plant (Table 1).

Species specialization (d') decreased 0.39-fold in *C. salviifolius* and 0.5-fold in *T. vulgaris* F (Table 1) but did not change in *L. stoechas* and *T. vulgaris* H (Table 1). In colonized networks *C. albidus* showed the lowest specialization ($d' = 0.10 \pm 0.04$) (Table 1).

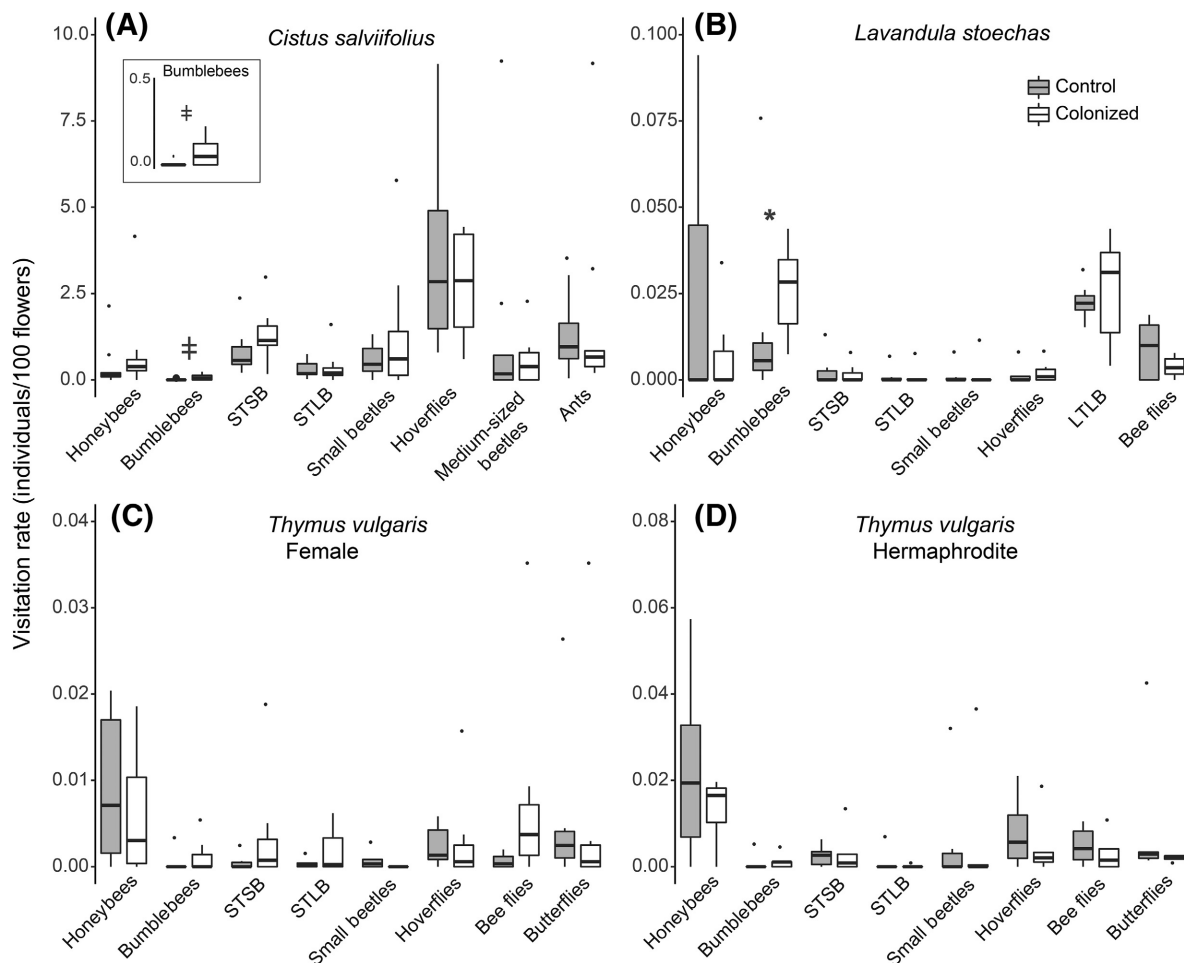


FIG. 1. Visitation rate (pollinator individuals per 100 flowers) of the main pollinator groups to focal plants in control (grey) and colonized (white) plots. Significant (*, $P < 0.05$) and marginally significant (\dagger , $P < 0.1$) differences from SIMPER analyses are indicated. STSB: Short-Tongued Small Bees, STL: Short-Tongued Large Bees, LTLB: Long-Tongued Large Bees.

Specialization (d') did not change in any pollinator functional group (Appendix S1: Table S3).

Network nestedness and modularity.—All control and colonized networks were significantly less nested than random webs (Appendix S1: Table S4). However, nestedness tended to increase from control to colonized networks ($WNODE$; control plots: 27.6 ± 2.3 ; colonized plots: 32.2 ± 1 ; $t = -1.85$, $P = 0.09$). *C. albidus* tended to be a positive contributor to network nestedness (individual nestedness contribution = 0.54 ± 0.39 ; Wilcoxon test on contribution greater than 0, $V = 36$, $P = 0.06$), and clearly belonged to the core of supergeneralist species (Fig. 2B). This core also included the four focal plants and *Euphorbia characias* in both control and colonized plots (Fig. 2A, B).

All control and colonized networks were significantly modular (Appendix S1: Table S5). Control and colonized networks had similar levels of modularity (Q index; control plots: 0.33 ± 0.04 ; colonized plots:

0.34 ± 0.03 ; $t = -0.16$, $P = 0.87$) and a similar number of modules (nQ ; control plots: 3.40 ± 0.29 ; colonized plots: 3.80 ± 0.15 ; $W = 34$, $P = 0.50$). However, module composition of the control and colonized metanetworks showed some important differences (Fig. 2C,D). The control metanetwork had three modules (Fig. 2C). Module *a* included *C. salviifolius* and other plant species visited by hoverflies, beetles (small, medium-sized and large) and short-tongued bees (small and large). Module *b* included *L. stoechas* and *T. vulgaris* (both morphs) and other plant species visited by bee flies, bumble bees, butterflies, honey bees and long-tongued bees (small and large). Module *c* included *Euphorbia characias* and other plant species visited by ants and flies (Fig. 2C). In the colonized metanetwork modules *a* and *c* were almost identical to modules *a* and *c* of the control metanetwork (Fig. 2D). However, the introduction of *C. albidus* caused module *b* to split into two modules. Module *b1* included *T. vulgaris* (both morphs) and *C. albidus*, with the honeybee as the most important pollinator, followed

TABLE 1. Measures of network specialization (H_2'), trophic level generalization (plant and pollinator generality) and species specialization (d') in control and colonized networks (N = 9 per treatment).

Metric	Control networks		Colonized networks		<i>t</i>	<i>P</i>
	Mean	SE	Mean	SE		
Network specialization (H_2')	0.51	0.02	0.41	0.03	2.68	0.018*
Plant generality	4.34	0.48	4.62	0.40	-0.45	0.66
Pollinator generality	1.97	0.15	2.96	0.24	-3.44	0.004*
Species specialization (d')						
<i>Cistus salviifolius</i>	0.33	0.07	0.13	0.05	2.31	0.036
<i>Lavandula stoechas</i>	0.56	0.07	0.43	0.06	1.37	0.20
<i>Thymus vulgaris</i> F	0.28	0.03	0.14	0.05	2.49	0.031
<i>Thymus vulgaris</i> H	0.23	0.06	0.27	0.12	-0.34	0.74
<i>Cistus albidus</i>	-	-	0.10	0.04	-	-

See Appendix S1: Table S3 for d' values of pollinator functional groups.

*Non-significant when *C. albidus* visits are removed from the analysis.

by bee flies and butterflies. *L. stoechas* was included in a separate module (*b2*) visited by bumble bees and long-tongued bees (small and large) (Fig. 2D).

Pollination and plant reproductive success

Pollination.—None of the four focal plants showed differences in conspecific pollen stigma loads between control and colonized plots (all $|z| < 1.54$, $P > 0.12$) (Fig. 3A–D). In contrast, heterospecific pollen deposition in two focal plants, *C. salviifolius* and *L. stoechas*, was greater in colonized plots ($z = 4.51$, $P < 0.001$ and $z = 2.59$, $P = 0.01$, respectively) (Fig. 3E,F). However, even in these two species, heterospecific pollen loads were a small fraction of overall pollen loads ($0.4 \pm 0.1\%$ and $2.4 \pm 1.1\%$, respectively).

Composition of heterospecific pollen loads in *C. salviifolius*, *L. stoechas* and *T. vulgaris* F changed between control and colonized plots (all $F > 4.4$, $P < 0.003$). These changes were mediated mainly by *C. albidus* pollen (Fig. 3E–H), but heterospecific deposition of *T. vulgaris* H, *L. stoechas*, and other (non-focal plants) pollen also increased (SIMPER, *p*-values between 0.001 and 0.06).

Plant reproductive success.—The introduction of *C. albidus* affected the reproductive success of two of the four focal plants. In colonized plots, the fruit set of *T. vulgaris* F increased 1.32-fold ($z = 2.36$, $P = 0.018$) (Fig. 3K), whereas seed set of *L. stoechas* tended to decrease 0.83-fold ($z = -1.77$, $P = 0.077$) (Fig. 3N).

DISCUSSION

The experimental introduction of *Cistus albidus* had important consequences for local plant–pollinator communities. First, it caused an increase in bumblebee abundance that, importantly, did not only involve visitation to *C. albidus*, but also to other plants. Second, it affected the structure of plant–pollinator networks. The pollinator trophic level and some focal plant species became more generalized, resulting in a generalization increase at the network level. The introduction of *C. albidus* also increased network nestedness and modified the arrangement of plants and pollinators in modules. Ultimately, all these changes resulted in higher heterospecific pollen deposition and contrasting effects on the reproductive success of some focal plants. Overall, these results fall within our second envisioned scenario, in which *C. albidus* acts as a magnet species, facilitating interactions to other plants through spill-over and promoting generalization.

Effects on the pollinator community and plant–pollinator interaction patterns

Bumble bees increased their abundance three-fold in colonized plots, resulting in increased visitation to *Lavandula stoechas* and, to a certain extent, *C. salviifolius*. Because *C. albidus* was introduced three days before the surveys, this result implies that bumble bees were able to locate the introduced plant in a relatively short period of time. Bumble bees have long foraging ranges (up to 3 km) and are known to select patches with high floral rewards (Goulson 2010). In our study, bumble bees visited recently-opened *C. albidus* flowers early in the morning when anthers were fully loaded with pollen. Later in the day, as *C. albidus* pollen was rapidly depleted, bumble bees switched to visiting *L. stoechas* for nectar collection.

Effects on network structure

The introduction of *C. albidus* fostered generalization of the overall network (decrease in H_2') and at the pollinator trophic level (increase in pollinator generality). These changes were mostly a consequence of new interactions involving *C. albidus*, but generalization also increased in two of the four focal plants, *C. salviifolius* and *Thymus vulgaris* F. Several studies have analysed the effects of plant invasions on the structure of plant–pollinator interactions. In some cases, invasive species increase generalization (Valdovinos et al. 2009), but other studies have found opposite results (Aizen et al. 2008, Kaiser-Bunbury et al. 2011). These discrepancies may be explained by the level of dominance of the invasive species in terms of floral resources. At high levels of dominance, competition for pollinators and decrease in generalization are expected to occur (Ratchke 1983, Bjerknes et al. 2007, Muñoz and Cavieres 2008). Because

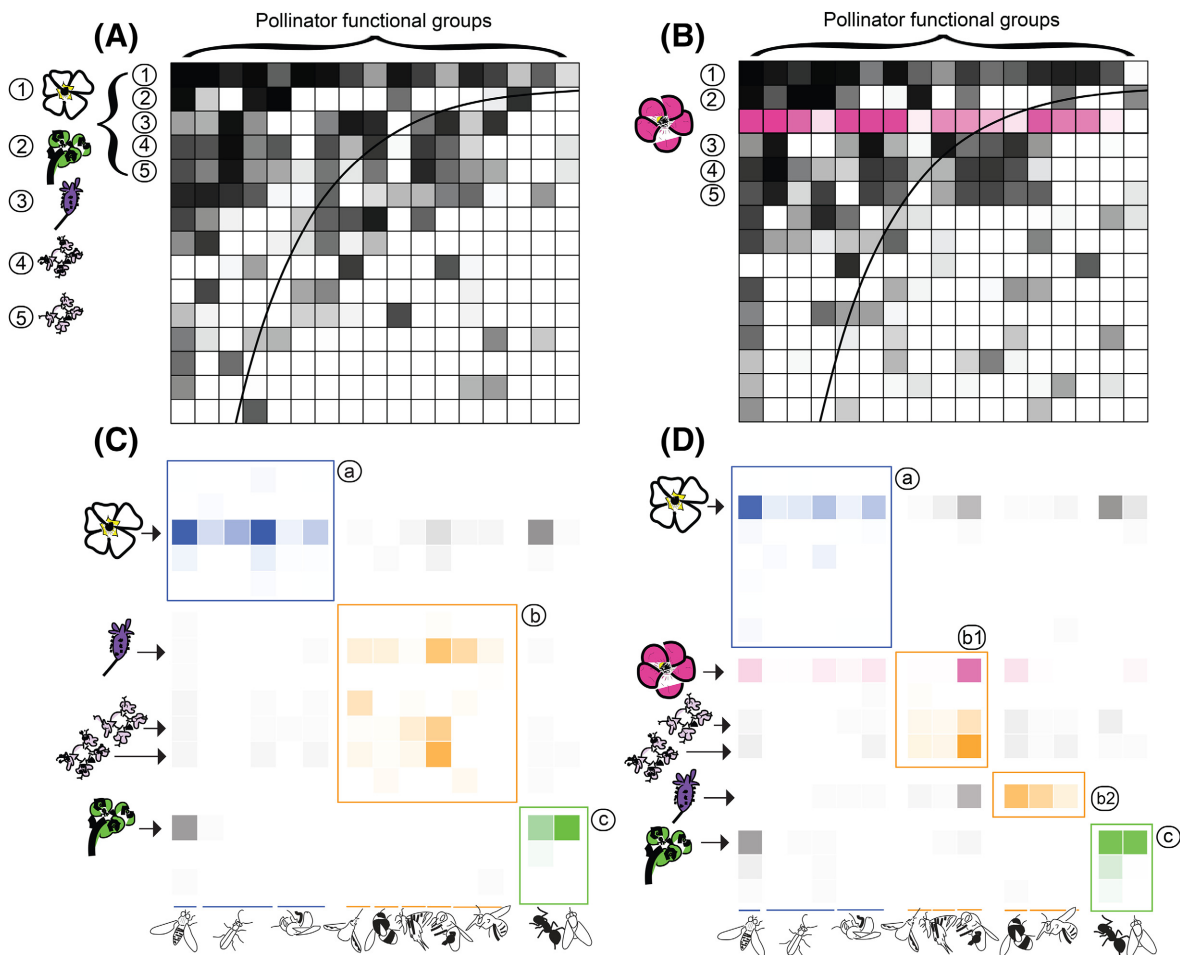


FIG. 2. Nested (A, B) and modular (C, D) matrices of control (A, C) and colonized (B, D) metanetworks ($N = 9$ local networks per treatment). Colour intensity denotes interaction frequency. In nested matrices (A, B), the solid line represents the isocline of perfect nestedness, and plants forming the core of supergeneralist species are indicated by numbers (1. *Cistus salviifolius*, 2. *Euphorbia characias*, 3. *Lavandula stoechas*, 4. *Thymus vulgaris* H, 5. *Thymus vulgaris* F, plus *Cistus albidus* [pink flower in B]). In modular matrices (C, D) interactions within each module are coloured differently (blue, orange, green), and pollinator groups are, from left to right in C: hoverflies, beetles (small, medium-sized and large), short-tongued bees (small and large), bee flies, bumble bees, butterflies, honey bees, long-tongued bees (small and large), ants and flies. *Cistus albidus* interactions are shown in pink. For clarity, only the 15 most-connected plant species and the 14 most-connected pollinator groups are shown.

invasive plants usually produce large amounts of floral resources and become strongly dominant, it is not surprising that competition for pollinators and negative effects on generalization are a common outcome in plant invasion studies (Morales and Traveset 2009). By contrast, we worked with native species and deliberately maintained the levels of introduced floral resources similar to those of resident species. At these low levels of dominance, facilitation and increased generalization are expected (Ratchke 1983, Ghazoul 2006, Muñoz and Cavieres 2008).

C. albidus generated new strong interactions and was an important component of the core of supergeneralist species, thus contributing to an increase in

network nestedness. New species are more likely to be incorporated into local communities when they interact with resident generalist species, resulting in reduced effective competition and ultimately enhancing the number of coexisting species (Bastolla et al. 2009, Thébault and Fontaine 2010). Ultimately, generalization and network nestedness are expected to foster stability against perturbation events such as plant and pollinator extinctions (Waser et al. 1996, Thébault and Fontaine 2010).

Contrary to our expectations, the introduction of *C. albidus* did not result in decreased network modularity, but it had important effects on the arrangement of plant–pollinator interactions, causing a module of the

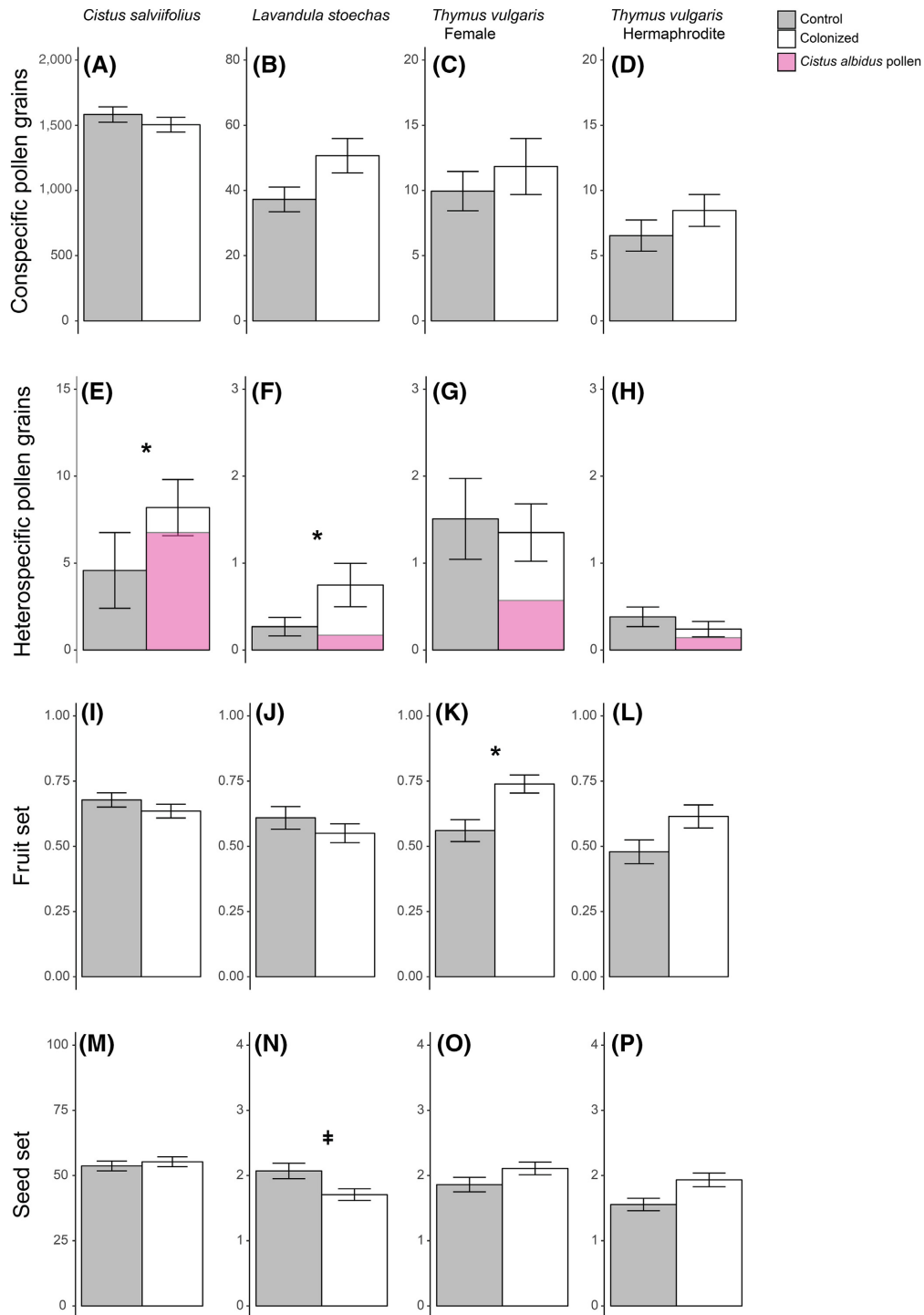


FIG. 3. Conspecific (A–D) and heterospecific (E–H) pollen grains deposited on the stigmas, and fruit set (% of flowers that developed into fruits) (I–L) and seed set (number of seeds per fruit) (M–P), of focal plants in control (grey) and colonized (white) plots (mean \pm SE). Significant (*, $P < 0.05$) and marginally significant (#, $P < 0.1$) differences are indicated.

control metanetwork to split into two in the colonized metanetwork. This result was mediated by the increase in the interaction frequency between bumble bees and

L. stoechas. Because modules are considered coevolutionary units (Olesen et al. 2007), module reorganization at the regional level could imply changes in the selective

pressures of local, isolated plant populations, with potential consequences on evolutionary dynamics.

Effects on pollen deposition

Although *C. albidus* acted as a facilitator of certain interactions to focal plants, it did not affect conspecific pollen loads, a result that is consistent with the fact that overall (all pollinators) visitation rates did not change for any of the four focal plants. It is important to note that to avoid introducing large amounts of *C. albidus* pollen we adjusted the number of *C. albidus* flowers to the existing floral resources in each plot. The impact of the arrival of a new plant on both conspecific and heterospecific pollen deposition patterns of resident plants is likely to increase if the newcoming plant becomes dominant over time, as seen in many instances of exotic plant introductions (Morales and Traveset 2008, Dietzsch et al., 2011).

On the other hand, we found a significant increment in heterospecific pollen deposition in two of the four focal plants. Most of this heterospecific deposition involved *C. albidus* pollen. *C. albidus* produces large amounts of pollen (Bosch 1992) and was the most generalized plant species in the network, sharing the most abundant pollinators with focal plants and thus acting as a hub-donor (*sensu* Tur et al. 2016). However, changes in heterospecific deposition were also mediated by pollens of other plants in the community. This result is consistent with the above-mentioned increase in generalization and suggests changes in pollinator floral fidelity (Morales and Traveset 2008).

Effects on plant reproductive success

Under a scenario of *C. albidus* facilitating interactions to resident plants, we envisioned either a positive effect on reproductive success by means of increased conspecific pollen deposition, or a negative effect by means of increased heterospecific pollen deposition. However, we found no changes in conspecific pollen deposition and the increase in heterospecific pollen deposition was too low to result in stigma clogging (Ashman and Arceogómez 2013). Consequently, we hypothesize that the observed changes in the reproductive success of focal plants were mediated by changes in the quality of the conspecific pollen deposited (Aizen and Harder 2007).

The seed set of *L. stoechas* trended towards a decrease in colonized plots. This plant species was mostly visited by honey bees in control plots and by bumble bees in colonized plots. Honey bees and bumble bees show important differences in foraging behaviour. Compared to the honeybee, bumble bees visit more flowers per individual plant (Arnan et al. 2014), a behaviour that results in increased geitonogamy (Karron et al. 2009), potentially lowering seed set (de Jong et al. 1993). To establish whether bumble bees also visited more flowers per individual in *L. stoechas*, we conducted an independent

pollinator survey in the same study area in which we measured the number of flowers visited by bumble bees and honey bees on *L. stoechas* individuals. Bumble bees visited more than twice (117 ± 26.7) as many flowers as honey bees (52.7 ± 10.7) (GLMM, $z = 33.7$, $P < 0.001$) per individual. This result suggests that the shift in the major pollinator of *L. stoechas* resulted in increased deposition of geitonogamous pollen, ultimately leading to reduced reproductive success. An *ad hoc* analysis of *L. stoechas* fruits of the tagged plants of the control and colonized plots confirmed that seed set was negatively correlated to bumblebee visitation (proportion of bumblebee visits: GLM, $F_{1,12} = 5.1$, $P = 0.04$; $r = -0.55$; bumblebee visitation rate: GLM, $F_{1,12} = 3.4$, $P = 0.09$; $r = -0.47$).

On the other hand, fruit set of *T. vulgaris* F increased in colonized plots. Again, because we found no differences in conspecific pollen loads between control and colonized plots, we hypothesize that this change in reproductive success was mediated by changes in conspecific pollen quality. *T. vulgaris* F pollinator-generalization increased in colonized plots and various studies have found a positive relationship between pollinator diversity and plant reproductive success (Gómez et al. 2007, Perfectti et al. 2009, Albrecht et al. 2012). Different pollinator species have different foraging behaviours, notably in terms of distances flown between consecutively-visited plants (Herrera 1987a, 1987b), resulting in different outcrossing distances. Therefore, pollinator diversity entails genetic diversity of pollen loads and increased chances of reaching optimal outcrossing distances (Waddington 1983, Waser and Price 1991), potentially leading to increased reproductive success (Niesenbaum 1999, Paschke et al. 2002).

CONCLUDING REMARKS

We show that the arrival of a native plant into a natural community may affect the pollinator community, plant–pollinator interactions, network structure, pollination and plant reproductive success even when the new plant is not overly dominant. Our experiment simulates a process that is becoming increasingly frequent under the current scenario of climate change in which some plants are rapidly modifying their distribution along elevational gradients (e.g. Kelly and Goulson 2008), leading to changes in the flowering “theater”. Our results demonstrate that ecological relationships between plants and pollinators are rapidly rearranged in response to novel situations, and the observed changes in plant reproductive success suggest that these shifts in interaction patterns may have long-term evolutionary consequences. In addition, our study establishes a relationship between network structure and function (see also Gómez et al. 2011, Gómez and Perfectti 2012). In our study, the relationship between network structure and pollination and plant reproductive success appears to be mediated by differences among pollinators in foraging behavior

(abundance of pollinators that differ in number of flowers visited per individual plant, outcrossing distances) leading to changes in pollen quality. Pollen quality, as opposed to pollen quantity, is increasingly being signaled as a factor limiting plant reproductive success (Aizen and Harder 2007, Arceo-Gómez and Ashman 2014). Therefore, we encourage pollination ecologists to further explore the link between pollinator foraging behavior, plant–pollinator network structure and the quality component of pollination (e.g. Valverde et al. 2019) to improve our understanding of the relationship between interaction patterns and plant reproductive success.

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SUPPORTING INFORMATION

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