



Interspecific pollen transport between non-native fennel and an island endemic buckwheat: assessment of the magnet effect

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Abstract Non-native plant species can disrupt plant–pollinator interactions by altering pollinator foraging behavior, which can in turn affect levels of interspecific pollen transfer between native and non-native plant species. These processes may be amplified in cases where introduced plant species act as magnet taxa that enhance pollinator visitation to other plant species. We investigated these interactions on Santa Cruz Island (Santa Barbara Co., California) between non-native fennel (*Foeniculum vulgare*), a widespread and abundant invader, and the endemic Santa Cruz Island buckwheat (*Eriogonum arborescens*), which broadly overlaps fennel in its local distribution and blooming phenology. A fennel flower removal experiment revealed that this invader acts as a magnet species by increasing insect visitation to adjacent buckwheat flowers. Analysis of the amount of pollen carried on the bodies of insect pollinators (i.e., pollen transport) revealed that 96% of visitors to buckwheat flowers carried fennel pollen and 72% of visitors to

fennel flowers carried buckwheat pollen. Pollen transport analyses and visitation rate data further suggest that members of three bee genera (primarily *Augochlorella*) may be responsible for the majority of fennel pollen deposited on the stigmas of buckwheat flowers (i.e., pollen transfer) and vice versa. Lastly, fennel pollen transport appeared to occur at a larger spatial scale than the magnet effect that fennel plants exert on floral visitors to neighboring buckwheat plants. The ability of fennel to act as a magnet species, coupled with the fact that it is widespread invader with known allelopathic capacities, suggests that future studies could evaluate if the transfer of fennel pollen adversely affects native plant reproduction in areas where fennel is introduced.

Keywords Conspecific pollen loss · Heterospecific pollen deposition · Magnet plant effect · Pollination

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Introduction

Plant invasions can compromise ecosystem structure and function (Levine et al. 2003; Vilà et al. 2011). These ecological effects include the disruption of mutualistic interactions between plants and pollinators (Traveset and Richardson 2006; Morales and Traveset 2009). For example, the presence of non-native plants can alter the rate at which pollinators visit flowers of native plants (Litt et al. 2014). Non-native plant

species can also compete for access to shared pollinators, decreasing floral visitation to native plants (Campbell and Motten 1985). Alternatively, highly attractive, non-native plant species can act as magnet species, drawing pollinators into their vicinity and facilitating increased floral visitation to neighboring native plants (Thomson 1978). Whether a non-native plant attracts pollinators away from, or towards, co-occurring native plants depends on a number of factors, including the density of the plant species in question, the spatial scale considered, the relative value of floral rewards, and the capacity of pollinators to switch hosts in response to the presence of the magnet species (Muñoz and Cavieres 2008; Masters and Emery 2015; Albrecht et al. 2016; Hernandez-Castellano et al. 2020). Such interactions represent a special case (i.e., between native and non-native species) of those that involve co-flowering plant species that share pollinators. Levin and Anderson (1970), for example, first proposed how such interactions depend on the host constancy of pollinators and the relative abundance and spatial interspersal of the plant species in question.

Even in cases when non-native, magnet species increase visitation to neighboring native plants, fitness impacts on native plants may be dependent on context. Pollinators drawn in by non-native, magnet species may deposit greater quantities of conspecific pollen onto native plants, yet pollinators may also alternate between visiting native and non-native plants, resulting in interspecific pollen transfer (hereafter IPT; Morales and Traveset 2008). IPT may impact the reproductive fitness of native plants via two mechanisms: the deposition of undesirable, potentially alleopathic, heterospecific pollen onto their floral stigmas, and the loss of their own pollen through deposition on non-native plants (Bell et al. 2005; Morales and Traveset 2008).

The degree of IPT between native and non-native plant species depends on a number of factors. IPT is most likely to occur if the shared pollinator assemblage includes species capable of transferring ecologically important amounts of pollen between native and non-native plant species (Morales and Traveset 2008). Non-native plant species visited by a broad range of pollinators (and perhaps especially by floral generalists) are more likely to serve as magnet species and to interfere with plant-pollinator interactions than those that attract relatively few pollinator species (Memmott

and Waser 2002). Host plant switching by pollinators can decrease the amount of conspecific pollen available on the bodies of pollinators (Bell et al. 2005), and the degree of IPT scales positively with the likelihood of shared pollinators to engage in switching (Morales and Traveset 2008). Thus, understanding pollinator-mediated impacts of non-native plants on co-occurring natives requires quantifying not only patterns of floral visitation, but also patterns of pollen transport and deposition by pollinators shared between native and non-native plants. Impacts of non-native plants on these distinct processes may act synergistically or in opposition across multiple spatial scales, causing the final outcome of pollinator-mediated impacts to be difficult to predict.

Here, we investigate how invasion by non-native fennel (*Foeniculum vulgare* Mill.) disrupts pollination mutualisms. Native to the Mediterranean region, fennel is a summer-blooming perennial that produces flowers attractive to a broad range of pollinators (Bosch et al. 1997; Chaudhary 2006; Shilpa et al. 2014; Skaldina 2020). Fennel is a common and widespread invader that produces large amounts of floral resources, yet surprisingly little is known about its impact on pollination mutualisms, as pollination studies involving fennel have not studied how it impacts other plant species. Fennel is an abundant invader in coastal California (Bossard et al. 2000), including Santa Cruz Island (Santa Barbara Co.) where we conducted fieldwork for this study. Fennel was purposefully introduced to Santa Cruz Island in the late 1800s (Junak et al. 1995) but greatly increased in abundance over the past few decades following island-wide removal of ungulates (in the 1990s) and pigs (in the 2000s) (Power et al. 2014). The numerical dominance of fennel on Santa Cruz Island and its attractiveness to a diversity of insects at this location (Thorp et al. 1994) highlight the importance of understanding more about pollinator-mediated interactions between this invader and native plant species. To assess the impact of fennel on pollinator visitation and IPT, we focused on Santa Cruz Island buckwheat (*Eriogonum arborescens* Greene), which is a medium-sized perennial shrub that is endemic to the northern Channel Islands. *Eriogonum arborescens* and *F. vulgare* are often interspersed (Fig. 1a), and the two species broadly overlap in their blooming phenology (April to September), which extends much later into

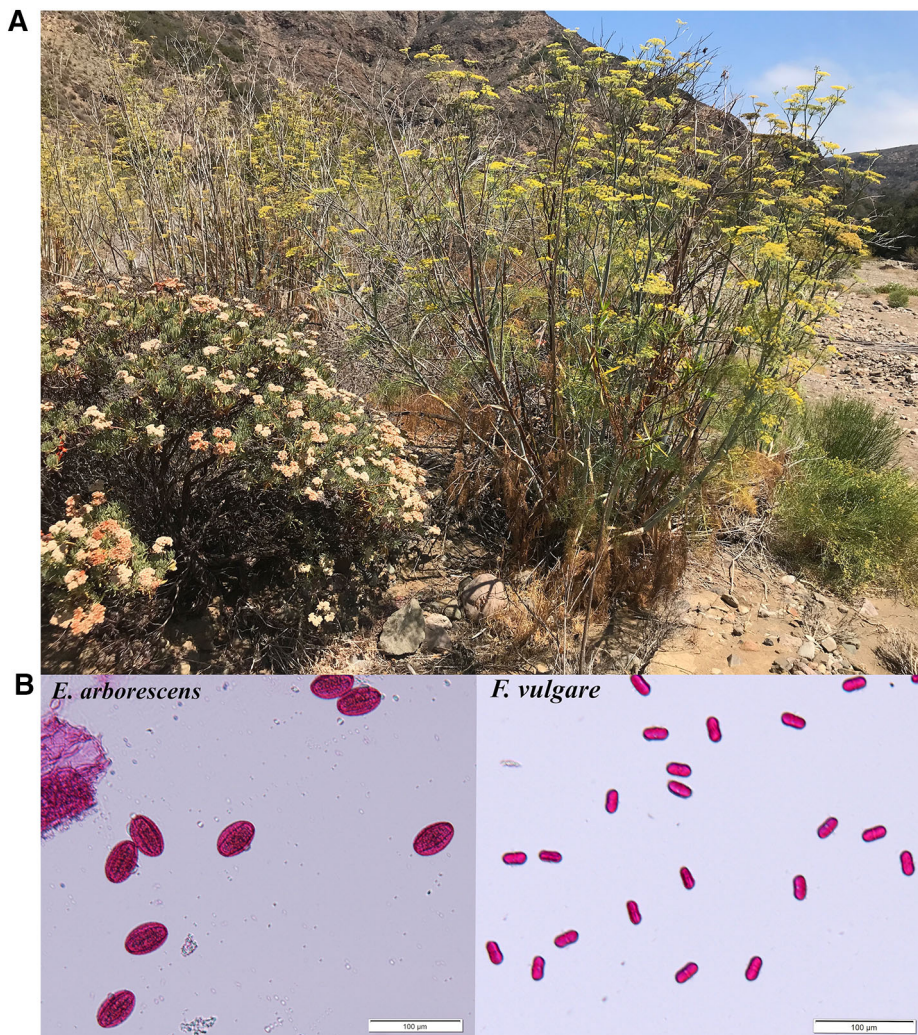


Fig. 1 The two focal plant species considered in this study: Santa Cruz Island Buckwheat (L; *Eriogonum arborescens*) and non-native fennel (R; *Foeniculum vulgare*). **a** Both individuals

in this picture are in bloom. **b** Santa Cruz Island Buckwheat pollen and fennel pollen grains at 100 µm magnification

the summer compared to most other plant species on Santa Cruz Island.

To assess how invasion by fennel affects pollinator visitation and IPT, we combined pollinator surveys, a fennel flower-removal experiment, and analysis of the pollen loads on visiting insects. These approaches allowed us to evaluate the following questions. (1) Does fennel act as magnet species? That is, does fennel flower removal decrease pollinator visitation to neighboring buckwheat relative to controls? (2) To what extent does pollinator sharing occur between fennel and buckwheat? (3) Is fennel pollen transported to buckwheat to a greater extent compared to the

converse? The results of this study argue for additional investigations into how the transfer of fennel pollen impacts native plant reproduction and more generally illustrate how plant invasions can alter pollinator foraging behavior in ways that increase the likelihood IPT.

Methods

Fieldwork was conducted on Santa Cruz Island, Santa Barbara Co., CA from June to September 2018. Santa Cruz Island (249 km² and 30 km offshore) is the

largest of the eight California Channel Islands and supports nearly 500 species of native plant species (Junak et al. 1995). All aspects of this study were conducted along the middle and lower reaches of Cañada del Puerto, which drains the largest watershed on the island. The lower reaches of this drainage form an open wash where fennel and buckwheat are among the two most abundant perennial plant species present. Fennel and buckwheat are spatially interspersed and comparable in their abundance at the study sites (Fig. 1a). We conducted flower-removal experiments and pollinator visitation surveys on ten spatially matched pairs of control and removal plots (individual plots were 10 × 10 m). “Appendix 1” lists GPS coordinates for these plots. Control and removal plots were paired based on proximity (with distances between plots within each pair ranging from 20 to 150 m) and the presence of roughly similar densities of fennel and buckwheat. Plots, on average, supported 11 ± 4 buckwheat plants and 17 ± 6 fennel plants (mean $\pm$ SE; all plots pooled). Each pair of plots was at least 35 m apart from the next closest pair.

Pollen transport data were collected at 18 additional locations (coordinates listed in “Appendix 2”) that were spatially interspersed among the plots used in the flower-removal experiment. Pollen transport data consisted of insects collected from buckwheat and fennel inflorescences. The local densities and relative proportions of buckwheat and fennel were similar to those on the removal experiment plots and representative of the study area in general. The area encompassing the paired plots and the locations where pollen transport data were collected was large enough so that the collection of insects to quantify pollen transport seems unlikely to have influenced visitation on control and removal plots. A map of all locations where data were collected is provided in “Appendix 3”.

Flower-removal experiment

To determine the effect of fennel flowers on insect visitation and heterospecific pollen deposition on buckwheat flowers, we experimentally removed fennel flowers and then compared insect visitation and pollen deposition on buckwheat plants in removal plots and those in control plots where fennel flowers were left intact. Plots within each pair were first randomly assigned to experimental group (i.e., control or removal). In removal plots, we cut off all of the

flowers on fennel inside the plots and also in a 3-m buffer zone outside of the boundary of each plot. To remove fennel flowers, we clipped the stalks 0.25–0.5 m below the flowers and then removed clipped flowers from the vicinity of the site. This method left intact most of the above-ground biomass of individual fennel plants, therefore minimally impacting the three-dimensional structural complexity of the habitat within each plot. Within our plots (i.e., excluding the 3-m buffer area), fennel flower removal resulted in a moderate reduction in the total extent of floral cover summed across fennel and buckwheat (mean = 17%, range = 6–36% at the time of removal). Flower removal continued as needed throughout the duration of the study to ensure that at no point in time did we allow fennel floral buds to go into bloom inside removal plots and their accompanying buffer.

To quantify how fennel flower removal affects floral visitation on buckwheat, we conducted pollinator surveys across all plot pairs as follows. One round of surveys was conducted 2–24 h prior to fennel flower removal (late July–early August), and three rounds of surveys were conducted after fennel flower removal: 8–13 August, 13–17 August, and 23–27 August. Pollinator surveys were conducted on sunny days between 0830–1700 h, with a majority of surveys conducted between 1000–1530 h. For each survey, we counted insects visiting buckwheat flowers for a total of 30 min per plot. Buckwheat plants within matched plots were observed over two, 15-min observation periods, with the researcher alternating between control and removal plots. The plot surveyed first within a pair was randomly selected. In the first three surveys, we counted floral visitors on three randomly selected buckwheat plants (excluding small buckwheat individuals below a threshold size) for 5 min each within each plot. In the final round of surveys, we counted insect visitation on two, randomly selected buckwheat plants for 7.5 min each on eight of the plot pairs because an inadequate number of individuals were in full bloom.

We estimated floral visitation rate (visits/min) by counting the number of times an insect landed on the blooming portions of a focal buckwheat plant. Cases in which an insect flew up and then landed again on the same plant were counted as different visits. Given that both focal plant species have minute flowers (2–3 mm in diameter) that grow in dense umbel-shaped clusters,

it was not possible to determine how many individual flowers visitors contacted on a given visit. The floral area covered per visit thus extended over a variable portion of each contiguous ‘insect-walkable’ cluster of inflorescences (e.g., Lanterman and Goodell 2018). A total of 5610 insect visits over 2400 min was recorded on buckwheat flowers in the flower-removal experiments (Table 1). Insects were identified to the lowest possible field-identifiable taxonomic category [i.e., to the level of species or genus for common bee (Hymenoptera: Anthophila) taxa, and to the level of family or order for all other visitors (Table 1)]. *Augochlorella pomoniella* (Cockerell), which was the most common bee species in our study, could not be reliably separated in the field from females of *Agapostemon texanus* (Cresson), which was a rare visitor by comparison. For this reason, we combine these species into a unique category: large green Halictinae (LGH).

To determine the amount of fennel pollen deposited on *E. arborescens* stigmas, we sampled buckwheat flowers on control and removal plots in 6 of the 10 plot pairs once between 14 and 29 August with plots from the same pair always sampled on the same day. On each plot, we collected receptive (i.e., fully extended) stigmas from four flowers (two flowers each from two different buckwheat plants). We placed all three

stigmas from a single flower together in a drop of glycerin jelly mixed with fuchsin dye on microscope slides (Kearns and Inouye 1999). Based on a reference collection of pollen collected from the vicinity of the study area, we classified and counted pollen grains present on the stigmas of a flower as buckwheat, fennel, or other (Fig. 1b). This effort was simplified by (1) the small size of the floral stigmas of *E. arborescens* flowers (which limited the total number of pollen grains present), and (2) the fact that no other common plant species were in bloom while the removal experiments were being conducted. The peak bloom of buckwheat and fennel occurs in summer when most plant species are no longer flowering. Island morning glory (*Calystegia macrostegia macrostegia* (Greene) Brummitt) and jimsonweed (*Datura wrightii* Regel) were also in bloom while this experiment took place, but these species were relatively uncommon compared to buckwheat and fennel in the vicinity of our study plots.

In addition to measuring pollinator visitation rates and pollen deposition, we also estimated the abundance of buckwheat and fennel blooms on each plot (1) to test for relationships between visitation rates and local-scale (i.e., patch- and plot-level) flower abundance, and (2) to assess the extent to which the removal of floral resources itself might affect pollinator visitation in

Table 1 Insect visitation (number and percent of all visits) to buckwheat flowers by taxonomic grouping before and after removal on all control and treatment plots

	Pre-removal				Post-removal			
	Control		Treatment		Control		Treatment	
	n	%	n	%	n	%	n	%
All bees	466		448	79.29	2391	88.39	1455	82.95
		80.21						
LGH	287		249	44.07	1436	53.09	944	53.82
		49.40						
<i>Colletes</i>	16		81	14.34	268	9.91	181	10.32
		2.75						
<i>Hylaeus</i>	161		89	15.75	599	22.14	272	15.51
		27.71						
Other bee spp.	2		29	5.13	88	3.25	58	3.30
		0.35						
All wasps	52		36	6.37	158	5.84	114	6.50
		8.95						
<i>V. pensylvanica</i>	13		6	1.06	48	1.77	50	2.85
		2.24						
All Diptera	63		78	13.81	156	5.77	185	10.55
		10.84						
Bombyliidae	45		63	11.15	87	3.22	121	6.90

Post-removal statistics represent the sum of all three post-removal surveys. “LGH” = large green halictinae

place of, or in addition to, the removal of any magnet effect exerted by fennel (Braun and Lortie 2019). For the first objective, during each survey, we measured the approximate area of floral coverage for each of the three observed buckwheat individuals using the length and width of individual plants as well as estimates of the percentage of flowers in bloom during each survey. We used the average percent coverage and the total number of buckwheat individuals on a plot to estimate the plot-level area of buckwheat floral coverage for each of the four survey periods in the flower-removal experiments. We also recorded the approximate number of fennel inflorescences in bloom, as well as estimated the average area of floral coverage per inflorescence, on all plots during the pre-removal survey and on control plots during the first and third post-removal surveys. Fennel floral cover was not recorded during the second post-removal survey because of its close temporal proximity to the first post-removal survey. The elapsed time between the first and second post-removal surveys was four days on average, compared to an average of 14 days between the pre-survey and first post-survey and 10 days between the second and third post-surveys. Since fennel floral cover during the second post-removal survey was comparable to that of the first, we assigned the same values of fennel floral cover to the first and second post-removal surveys in our analyses.

All statistical analyses were conducted in R v. 3.6.3 (R Development Core Team 2020). To compare insect visitation on buckwheat flowers from the fennel flower-removal experiment, we constructed two linear mixed-effects models, one for the pre-removal survey, and one for the set of post-removal surveys. In both models, the number of visits to each observed buckwheat individual was the dependent variable; independent variables included the treatment status (control versus removal) of the plot, the spatial extent of floral coverage on the observed buckwheat individual, and the total plot-level spatial extent of floral coverage (i.e., combining all focal and non-focal buckwheat individuals, as well as fennel when applicable). Both models included plot identity as a random-intercept term to account for multiple sampling in the same plot (i.e., multiple buckwheat individuals in both models, repeated sampling in post-removal models). The model for post-removal surveys additionally included survey round (first, second, third) as an independent variable. We used generalized linear mixed models (GLMMs) with a

Poisson distribution (link = log) to compare pollen deposition on buckwheat flowers from removal versus control plots. In these models, the dependent variable is the number of grains of pollen from buckwheat, fennel, or non-focal species (i.e., neither buckwheat nor fennel). Treatment status was the independent variable, and random-intercept effects included buckwheat individual identity, plot identity, and the date of sample collection.

Pollinator sharing between fennel and buckwheat

To assess the potential for pollinator sharing between buckwheat and fennel, we conducted pollinator visitation surveys on nine control plots. Each plot was surveyed on two occasions between 13 and 28 August during sunny days between 1100–1530 h. For each survey on each plot, we counted all insects observed visiting the flowers on a single buckwheat plant and a single fennel plant growing within 10 m of each other. Each individual plant was observed over two, 5-min observation periods, with the same observer alternating between observing buckwheat and fennel. The plant observed first during each survey was randomly selected. We estimated pollinator visitation rate (visits/min) using the methods described in the previous section (*Flower-removal experiment*).

To analyze data on pollinator sharing, we first calculated the percent similarity (PS; from Hansen (2000) as in Morales and Traveset (2008)) of pollinators visiting fennel and buckwheat; the PS estimate was based on the visitation rate data from the

Table 2 Mean ($\pm$ SE) insect visitation rate (visits/min) by taxonomic grouping observed on inflorescences of Santa Cruz Island Buckwheat (*Eriogonum arborescens*) and fennel (*Foeniculum vulgare*)

	<i>E. arborescens</i>	<i>F. vulgare</i>
LGH	2.22 $\pm$ 1.44	0.14 $\pm$ 0.19
<i>Colletes</i>	0.05 $\pm$ 0.07	0.07 $\pm$ 0.22
<i>Hylaeus</i>	0.23 $\pm$ 0.32	0.03 $\pm$ 0.07
Other bee spp.	0.03 $\pm$ 0.05	0.03 $\pm$ 0.07
<i>Vespula pensylvanica</i>	0.02 $\pm$ 0.04	0.81 $\pm$ 0.71
Other wasp spp.	0.02 $\pm$ 0.03	No visits recorded
Bombyliidae (Diptera)	0.12 $\pm$ 0.13	0.01 $\pm$ 0.02
Other Diptera	0.02 $\pm$ 0.04	0.07 $\pm$ 0.15

Visitation rate measurements were averaged across control plot (n = 9) surveys

pollinator surveys (Table 2). To visualize differences in the pollinator assemblages on fennel and buckwheat, we performed a non-metric multidimensional scaling (NMDS) ordination using package ‘*vegan*’ (Oksanen et al. 2012) in R. We also used the *adonis* function in ‘*vegan*’ to perform PERMANOVAs (Anderson 2001) to test for differences in the composition of the pollinator assemblages as well as their visitation rates on fennel and buckwheat. Both the ordinations and PERMANOVAs were based on Bray–Curtis distances from the community matrix of visitation data from the pollinator survey (Table 1), where each entry in the matrix is the plot-level presence or absence of a pollinator taxon (i.e., not abundance-weighted) or average visitation rate of a pollinator taxon (i.e., abundance-weighted) on either buckwheat or fennel in a given plot.

Pollen transport

To estimate pollen transport (i.e., the amount of pollen carried on the bodies of insect visitors and therefore potentially available for deposition) between buckwheat and fennel by different types of insects, we collected pollinators on fennel and buckwheat flowers between 16 July and 22 August and then sampled pollen from these specimens using methods described by Alarcón (2010). Insects collected for pollen transport estimates were netted from flowers between 0700–1800 and directly transferred into a 10 ml vial, to minimize the loss of pollen on the insect body. We attempted to collect all insects observed visiting the focal fennel or buckwheat plant as we encountered them, with one exception. For safety reasons (involved with working on an island), we refrained from collecting the western yellowjacket (*Vespula pensylvanica* Saussure). Collected insects were placed in a cooler in the field and then transferred to a freezer within a few hours after collection. Using a dissecting microscope, we swabbed each insect body with a 2×2 mm cube of glycerin jelly mixed with fuchsin dye. When swabbing for pollen, the portions of each specimen where pollen might have become unavailable for pollination (e.g., scopae on bees) were avoided (Kearns and Inouye 1999; Alarcón 2010). After melting the glycerin cube onto a glass microscope slide, we then used a compound microscope to identify and quantify pollen grains on each slide. Based on a reference collection of pollen collected

from the vicinity of the study sites, we classified and counted pollen grains present from each flower as buckwheat, fennel, or other up to a total of 1000 grains. Only 15% of all insect individuals had > 1000 pollen grains swabbed from their bodies. Floral visitors were categorized as in Table 3.

We analyzed pollen transport data in two ways. First, we used Kruskal–Wallis tests to compare the number of buckwheat or fennel pollen grains carried (i.e., number of pollen grains of the two focal plant species swabbed from each individual) by the major groups of insect visitors (bees, flies, and wasps) and then among common groups of bees (LGH, *Colletes*, *Hylaeus*, *Halictus*). Pollen transport estimates for both buckwheat and fennel pollen were calculated separately for buckwheat visitors and fennel visitors. Second, we evaluated differences in the presence of the opposing plant species’ pollen (i.e., buckwheat versus fennel) on insect visitors by constructing a GLMM with a binomial distribution (link = logit). In this model, data collected from each sampling location on each date constituted a replicate, the response variable was the ratio of insects that carried pollen of the opposing species to those that did not, the independent variable was the identity of the plant species from which insects were collected (buckwheat versus fennel), and date was included as a random-intercept term.

Results

Flower-removal experiment

The experimental removal of fennel flowers reduced insect visitation on neighboring buckwheat flowers, relative to that observed on control plots. Prior to flower removal, insect visitation on buckwheat flowers did not differ between control and removal plots (linear mixed-effects model $t_{16.7} = 0.06$, $P = 0.96$) and was only positively related to the spatial extent of floral coverage of the observed buckwheat individual (Fig. 2a; $t_{44} = 2.60$, $P = 0.013$). However, after removal, insect visitation was 35% higher on control plots relative to removal plots ($t_{16.3} = 3.43$, $P = 0.0034$), and was positively related to floral coverage of observed buckwheat ($t_{151.4} = 2.57$, $P = 0.011$), negatively related to plot-level, total floral coverage ($t_{33.5} = 2.66$, $P = 0.012$), and higher in the

Table 3 Pollen grains found on insect taxa when collected from (a) Santa Cruz Island Buckwheat or (b) fennel. IQR = interquartile range. “% zero” = the percentage of individuals within the insect group that did not have any of the specific (buckwheat or fennel) pollen grains on their body

(a) Buckwheat insects		Buckwheat pollen			Fennel pollen		
Insect	n	Median	IQR	% zero	Median	IQR	% zero
All insects	235	19	5–67	8.94%	30	11–74.5	3.83%
Bees	160	28	6.75–116.75	8.75%	36	13.75–86.5	3.13%
LGH	48	169	45.75–534.25	2.08%	65	21.75–310.25	4.17%
<i>Colletes</i>	19	64	36–210.5	5.26%	45	16–63.5	0.00%
<i>Hylaeus</i>	80	12.5	4–26	12.50%	23	10–64	2.50%
<i>Halictus</i>	2	50	–	0.00%	51	–	0.00%
Wasps	24	13	3.75–36.25	8.33%	14	3.75–46.5	12.50%
Diptera	51	12	4–26	9.80%	26	8–58	1.96%
(b) Fennel insects		Buckwheat pollen			Fennel pollen		
All insects	134	3	0–8	28.36%	309	73–1000	0.00%
Bees	103	3	0–8	28.16%	549	154–1000	0.00%
LGH	24	7.5	2.25–41.75	25.00%	1000	429–1000	0.00%
<i>Colletes</i>	8	2.5	0.75–3.75	25.00%	470	320.25–772	0.00%
<i>Hylaeus</i>	32	2	0–6.25	28.13%	143.5	76.75–239	0.00%
<i>Halictus</i>	24	2	0–7	29.17%	1000	652.25–1000	0.00%
Wasps	7	0	0–3.5	57.14%	44.5	8.00–44.5	0.00%
Diptera	24	3	1–9.5	20.83%	182	21.75–182	0.00%

third post-removal survey round than in the first two survey rounds ($t_{152} = 6.63$, $P < 0.0001$). Higher visitation in the third survey may have been due to the declining availability of floral resources produced by both buckwheat and fennel. Concentration of floral visitors onto fewer available floral resources may have explained why visitation rate was both negatively related to plot-level floral coverage, and higher in the third post-removal survey, at which time overall floral resource availability declined relative to the first two surveys. Bees accounted for much of the difference between treatments in post-removal visitation (Fig. 2b and Table 1; $t_{16.5} = 3.36$, $P = 0.0038$); other insects did not appear to respond to fennel-flower removal (Table 1; see “Appendix 4” for a complete accounting of these statistical analyses).

Although experimental removal of fennel flowers reduced insect visitation on buckwheat flowers, patterns of pollen deposition on buckwheat flowers did not differ between the two experimental groups. With respect to heterospecific pollen deposition, flowers in the two experimental groups had similar incidences of fennel pollen, with fennel pollen being observed on the stigmas of 11 of 28 flowers in the control group and 12 of 28 flowers in the removal group. Individual

buckwheat flowers from plants in the control group had 1.29 ± 0.39 (mean $\pm$ SE) fennel pollen grains on their stigmas, whereas sampled flowers from plants in the removal group had 1.21 ± 0.54 fennel pollen grains (Poisson GLMM $z = -0.52$, $P = 0.61$). Flowers from plants in the control group also had 0.79 ± 0.20 non-focal pollen grains (i.e., neither buckwheat nor fennel), whereas flowers from plants in the removal group had 0.86 ± 0.16 non-focal pollen grains ($z = 0.25$, $P = 0.80$). With respect to conspecific pollen transfer, flowers from plants in the control group had 8.68 ± 2.60 buckwheat pollen grains on their stigmas, whereas flowers from plants in the removal group had 5.29 ± 1.25 buckwheat pollen grains ($z = -1.45$, $P = 0.15$). In addition to analyses conducted on absolute pollen grain counts, analyses conducted on ratios ($x:(\text{total}-x)$) using binomial GLMM (link = logit) yielded patterns of significance that were similar to those based on absolute counts.

Pollinator sharing between fennel and buckwheat

Table 2 lists floral visitors on fennel and buckwheat in terms of their visitation rates. Bees (especially LGH

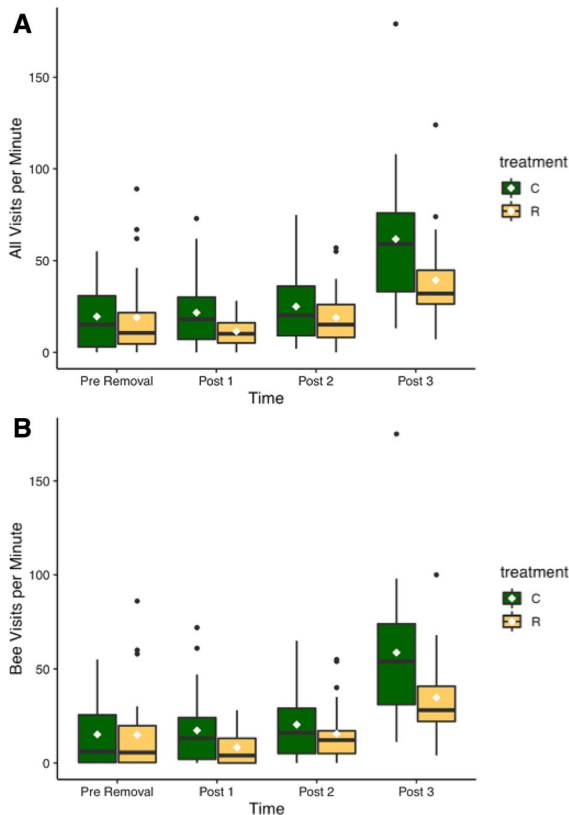


Fig. 2 Visits per minute made by **a** all insects and **b** bees to individual buckwheat plants on control (C, dark-colored boxes) and removal (R, light-colored boxes) plots before (Pre Removal) and after (Post 1, Post 2, Post 3) fennel removal. Boxes indicate central 50% of data; bold horizontal lines represent medians, and white diamonds are means. Whiskers extend from the quartiles to $1.5 \times$ the interquartile range (or the most extreme values, whichever is closest to the median). Points are outliers

and *Hylaeus*) were the most frequent visitors on buckwheat flowers, whereas the western yellowjacket was the most frequent visitor on fennel flowers. The degree of assemblage-level pollinator sharing (based on PS (percent similarity) values) between buckwheat and fennel was 15.76% when calculated as the PS of the rates of visitation by putative pollinator taxa. Ordinations based on the community matrix of visitation data revealed that the composition of the pollinator assemblages based on observed presence/absence on fennel and buckwheat differed from one another (Fig. 3a; PERMANOVA $F_{1,15} = 7.30$, $P = 0.008$). We also detected differences in the pollinator assemblages between fennel and buckwheat in an ordination based on visitation rates of pollinators (Fig. 3b; PERMANOVA $F_{1,15} = 9.58$, $P = 0.002$).

The most frequently observed floral visitors that were shared between buckwheat and fennel were bees (Table 2; especially LGH, *Colletes*, and *Hylaeus*).

Pollen transport

Pollen transport data revealed that 96% (226/235) of insects collected on buckwheat flowers carried fennel pollen, whereas 72% (96/134) of insects collected on fennel flowers carried buckwheat pollen. Major pollinator groups collected from buckwheat flowers differed in terms of the amount of fennel pollen on their bodies (Kruskal–Wallis Test: $\chi^2_2 = 10.08$, $P = 0.0065$; Table 3a), with bees carrying the most fennel pollen (median = 36 grains) per individual followed by flies (median = 26 grains) and wasps (median = 13 grains). Comparisons among bee genera revealed additional differences across taxa (Kruskal–Wallis Test: $\chi^2_3 = 12.61$, $P = 0.0056$; Table 3a), with LGH (all 48 individuals were *Augochlorella pomoniella*) carrying the most fennel pollen on their bodies (median = 65 grains) per individual, followed by *Colletes* (median = 45 grains) and then *Hylaeus* (median = 23 grains). In contrast, major pollinator groups (excluding *Vespula*) collected from fennel flowers did not differ in terms of the amount of buckwheat pollen on their bodies (Kruskal–Wallis Test: $\chi^2_2 = 2.285$, $P = 0.32$; Table 3b). Comparisons among bee genera, however, did reveal differences across taxa (Kruskal–Wallis Test: $\chi^2_3 = 7.72$, $P = 0.052$; Table 3b) with LGH (22 individuals were *Augochlorella pomoniella* and two were *Agapostemon texanus*) carrying the most buckwheat pollen (median = 7.5 grains) per individual followed by *Colletes* individuals (median = 2.5 grains) and *Hylaeus* (median = 2 grains). Pooled across all taxa, a greater proportion of insects collected from buckwheat carried fennel pollen than vice versa (binomial GLMM $z = 5.74$, $P < 0.0001$).

Discussion

The flower-removal experiment revealed that bees reduced their visitation to buckwheat in response to the removal of fennel flowers (Fig. 2b). Given that fennel increased pollinator visitation to the local floral neighborhood above levels expected based on its proportional contribution to local floral abundance,

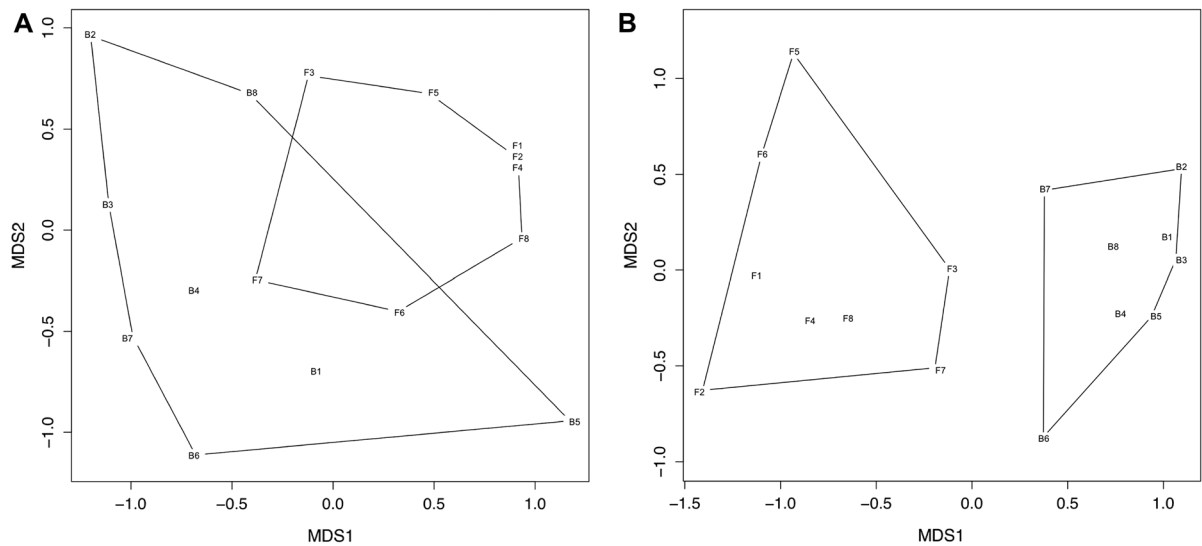


Fig. 3 NMDS ordinations based on the community matrix of insect visitation on native Santa Cruz Island Buckwheat (*Eriogonum arborescens*) and non-native fennel (*Foeniculum vulgare*). **a** Pollinator composition based on presence or absence

of pollinators. Ordination stress equals 0.09. **b** Pollinator composition based on the visitation rates of pollinators. Ordination stress equals 0.09. Points are labelled by plot and plant (B = buckwheat, F = fennel)

fennel acts as a magnet species (sensu Thomson 1978) that enhances visitation to surrounding plant species. The level of pollinator sharing (based on PS (Morales and Traveset 2008) between the magnet, non-native fennel and native buckwheat was 15.76%, with members of only three bee genera (*Colletes*, *Hylaeus*, and *Augochlorella* (which made up nearly all of the LGH category)) commonly visiting flowers of both plant species (Table 2). The level of observed pollinator sharing in our study was comparable to that documented for other pairs of plant species, especially when the focal plants being considered differ with respect to their main pollinators (Morales and Traveset 2008). On the other hand, we found that most pollinator individuals collected on both fennel and buckwheat carried pollen of the opposing plant species. Examination of pollen transport thus revealed that the actual degree of pollinator sharing was much higher than that estimated from standardized pollinator observations. These results in turn suggest that visitation observations alone may underestimate the intensity of pollinator-mediated interactions between native and non-native plant species.

Like our study, other removal experiments have reported that non-native plants can facilitate visitation to native plants (Moragues and Traveset 2005), but this outcome appears to be less common than cases

where visitation to natives either increases after removal of non-natives (Moragues and Traveset 2005; Baskett et al. 2011) or exhibits no response to non-natives (Bartomeus et al. 2010; Albrecht et al. 2016; Moragues and Traveset 2005). Effects on visitation can also change from facilitative to competitive with increasing invader density (Muñoz and Cavieres 2008).

Fennel and buckwheat pollen found on buckwheat stigmas appeared unaffected by decreased bee visitation caused by the removal of fennel flowers in both their absolute quantity (an average of < 2 and < 7 grains per flower, respectively) and relative proportion (an average of 15% and 72% of all pollen present, respectively). Thus, the spatial scale of the export of fennel pollen to buckwheat appears to be greater than the magnet effect on visitation, given that fennel pollen was still found on buckwheat stigmas within removal plots. While the presence of non-native plants often increases heterospecific pollen receipt by natives (e.g., Dietzsch et al. 2011; McKinney and Goodell 2010), non-native plants sometimes fail to affect pollen receipt by natives despite influencing patterns of floral visitation (e.g., Jakobsson et al. 2008; Hernandez-Castellano et al. 2020). Given the low average stigmatic pollen load of buckwheat, stigma saturation may have occurred at floral visitation rates

lower than the lowest rates observed in our study. The control plots in our study did vary in fennel density, but all plots were located in areas with a relatively even representation of fennel and buckwheat plants. Had we performed our study in areas with higher fennel abundance, we may have observed different levels of fennel pollen deposition (i.e., across experimental groups) on buckwheat flowers.

The ubiquity and preponderance of fennel pollen on the bodies of pollinators (Table 3) may help to explain our finding that the local-scale removal of fennel flowers did not decrease the transfer of fennel pollen onto buckwheat. When the majority of individuals in the total pollinator pool in the environment carry fennel pollen, there is a high probability that a given pollinator arriving on buckwheat flowers from outside of the boundaries of our study plot would transfer fennel pollen. In the present study, it seems likely that fennel flower removals carried out over a larger spatial scale would have been needed to depress heterospecific pollen deposition onto buckwheat. The most frequent visitors to buckwheat flowers are medium-sized bees that likely forage over areas considerably larger than those encompassed by our study plots. Thus, it appears that the spatial scale at which fennel exports its pollen to buckwheat is greater than that of the magnet effect it exerts on the assemblage of their shared pollinators. This finding corroborates those of previous studies reporting that the impact of non-native plants on neighbors depends upon the spatial scale considered (Albrecht et al. 2016; Hegland 2014) and emphasizes the importance of quantifying both potentially facilitative and competitive effects of non-natives at multiple spatial scales (Braun and Lortie 2019; Thomson 2019).

The pollen transport data revealed that a higher proportion of pollinators visiting buckwheat carried fennel pollen compared to the converse situation. Given the small amount of fennel pollen present on buckwheat stigmas, it seems most likely that the large amount of fennel pollen found on the bodies of buckwheat floral visitors (Table 3) originated from fennel flowers they previously visited during the same foraging bout, rather than from fennel pollen previously deposited on buckwheat flowers. Levels of interspecific pollen export and receipt may commonly be asymmetrical for plant species that share pollinators (Tur et al. 2016), indicating that directionality may exist in the flow of pollen among species. Our

findings further suggest that pollinator behavior that contributes to directionality in pollen flow may play a more important role in IPT between non-native and native plant species than previously appreciated. For instance, the most frequent visitor of buckwheat, *A. pomoniella*, consistently carried large quantities of fennel pollen while foraging on buckwheat, and relatively small quantities of buckwheat pollen while foraging on fennel (Table 3), which this species visits at low frequencies. Thus, *A. pomoniella* may export large quantities of non-native fennel pollen to buckwheat despite the fact that it visited buckwheat at a much higher rate (over an order of magnitude higher; Table 2). More generally, this finding cautions that the directionality of pollen flow may enable non-native plant species to exert strong heterospecific pollen pressure on neighboring native plants even when the observed degree of pollinator sharing appears to be low.

Although we did not collect *V. pensylvanica* for pollen transport analysis, this species can act as a competent pollinator for some plant species (Jacobs et al. 2010; Thomson 2019) and could potentially be an important agent of pollen transport and transfer in our system as well given that it was the most commonly observed visitor on fennel. However, since *V. pensylvanica* infrequently visits buckwheat (Table 2), its exclusion is unlikely to have large effects on the pollen transport dataset of floral visitors collected from buckwheat. On the other hand, given that it exhibited qualitatively opposite patterns of visitation relative to *A. pomoniella* (i.e., visiting fennel at high frequencies and buckwheat at low frequencies), *V. pensylvanica* could potentially contribute to directional pollen flow from buckwheat to fennel. Thus, without data from *V. pensylvanica*, we are unable to conclusively determine whether net pollen transport is stronger from fennel to buckwheat (as suggested by our data on non-*Vespula* floral visitors) or vice versa. However, the lack of data on *V. pensylvanica* is unlikely to alter our qualitative conclusion that directionality of floral host choice exhibited by key floral visitors (e.g., *A. pomoniella*) likely plays an important role in heterospecific receipt from the perspective of buckwheat.

The present study documented the potential for substantial IPT in this system resulting in both heterospecific pollen deposition and putative conspecific pollen loss, but we did not assess if these

phenomena impacted the reproductive success of buckwheat. Santa Cruz Island buckwheat produces minute flowers, which grow in dense, spherical clusters. These traits made it difficult to perform experiments testing how fennel pollen might affect buckwheat fruit set or seed set. The presence of only a few fennel pollen grains on buckwheat stigmas, however, could nonetheless affect buckwheat reproduction. Plant species, like buckwheat, that possess short styles, small stigmas and a lower pollen:ovule ratio can be more impacted by the presence of heterospecific pollen compared to species that have larger stigmas, longer styles and a higher pollen:ovule ratio (Lanuza et al. 2021). Additionally, Morales and Traveset (2008) and Murphy and Aarssen (1995) emphasize that even small amounts of heterospecific pollen deposition can negatively affect reproduction when pollen grains are allelopathic. Fennel pollen clearly has the potential to be allelopathic, given that other portions of this plant have demonstrated allelopathic properties (Colvin and Gliessman 2011; Nourimand et al. 2011; Ravlic et al. 2016).

The ability of fennel to act as a magnet species, coupled with its known allelopathic capacities, suggest that future studies could evaluate the extent to which native plant reproduction may be impacted by the receipt of fennel pollen. Given the abundance of fennel on Santa Cruz Island (Power et al. 2014), pollinator-mediated effects of fennel on buckwheat and other unique components of this island's flora (Junak et al. 1995) perhaps deserve special consideration. The potential for negative affects resulting from IPT also seem worth investigating in other portions of fennel's expansive introduced range. These effects might be particularly important in regions with abundant, super-generalist pollinators, such as the western honey bee (*Apis mellifera* L.), which is among the most common visitor on fennel in other systems (Chaudhary 2006; *personal obs.*).

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Appendix 1

GPS coordinates for paired control and removal plots on Santa Cruz Island.

Plot	LAT	LONG
2 Control	34.01118	– 119.68977
2 Removal	34.01122	– 119.69038
4 Control	34.01139	– 119.69183
4 Removal	34.01152	– 119.69225
5 Control	34.01099	– 119.69656
5 Removal	34.01115	– 119.69634
6 Control	34.01068	– 119.69737
6 Removal	34.01047	– 119.69750
7 Control	34.00974	– 119.69774
7 Removal	34.01019	– 119.69727
8 Control	33.99738	– 119.72720
8 Removal	33.99789	– 119.72679
9 Control	33.99704	– 119.72903
9 Removal	33.99762	– 119.72884
10 Control	33.99949	– 119.73544
10 Removal	33.99976	– 119.73565
11 Control	33.99918	– 119.73835
11 Removal	34.00029	– 119.73942
12 Control	34.01192	– 119.69320
12 Removal	34.01170	– 119.69447

Appendix 2

GPS coordinates for the locations where insects were collected for pollen transport analyses. (P = Prisoner's, FS = Field Station, and C = Cabins).

Location	LAT	LONG
P-1	34.01054	– 119.69741
P-2	34.00830	– 119.69832
P-3	34.00817	– 119.69798
P-4	34.00691	– 119.70004
P-5	34.00567	– 119.70230
P-6	34.00556	– 119.70303
FS-1	33.99697	– 119.72897
FS-2	33.99755	– 119.72709

Location	LAT	LONG
FS-3	33.99797	– 119.72761
FS-4	33.99765	– 119.72859
FS-5	33.99769	– 119.72916
FS-6	33.99770	– 119.72990
C-1	33.99961	– 119.73545
C-2	33.99966	– 119.73590
C-3	33.99910	– 119.73695
C-4	33.99893	– 119.73786
C-5	33.99950	– 119.73860
C-6	33.99958	– 119.73880

Appendix 3

Maps of fennel removal experimental plots and sites used to estimate pollen transfer potential in three locations: (a) Prisoner's, (b) Field Station and (c) Cabins along the La Cañada wash on Santa Cruz Island. Removal experimental plots are denoted with blue squares (C = control plot, R = removal plot) and pollen transfer potential sites are denoted with red circles. (P = Prisoner's, FS = Field Station, and C = Cabins).

(a)



(b)



(c)



Appendix 4

Statistical output of linear mixed-effects models examining impacts of fennel-removal treatment on insect visitation to buckwheat (dependent variable). Independent variables for both pre-removal and post-removal models included the treatment status (control versus removal) of the plot, the spatial extent of floral coverage on the observed buckwheat individual, and

the total plot-level spatial extent of floral coverage (i.e., combining all focal and non-focal buckwheat individuals, as well as fennel when applicable). Plot identity was included as a random-intercept term to account for multiple sampling in the same plot. The model for post-removal surveys additionally included survey round (first, second, third) as an independent variable.

Model	Fixed Effects	<i>t</i>	<i>P</i>	Slope $\pm$ SE
All visitors, pre-removal:	Treatment	− 0.06	0.96	− 0.318 $\pm$ 5.809
	Plot floral area	− 0.48	0.64	− 0.404 $\pm$ 0.840
	Bush area	2.60	0.013	6.343 $\pm$ 2.438
All visitors, post-removal:	Treatment	− 3.43	0.0034	− 14.032 $\pm$ 4.091
	Plot floral area	− 2.66	0.012	− 1.466 $\pm$ 0.551
	Bush area	− 2.57	0.011	4.614 $\pm$ 1.794
	2nd survey	1.39	0.17	5.269 $\pm$ 3.780
	3rd survey	6.63	< 0.0001	29.568 $\pm$ 4.460
Bees, pre-removal:	Treatment	− 0.03	0.98	− 0.157 $\pm$ 5.657
	Plot floral area	− 0.06	0.95	− 0.049 $\pm$ 0.821
	Bush area	1.83	0.07	4.532 $\pm$ 2.484
Bees, post-removal:	Treatment	− 3.36	0.0038	− 13.656 $\pm$ 4.062
	Plot floral area	− 2.71	0.010	− 1.475 $\pm$ 0.544
	Bush area	2.16	0.032	3.786 $\pm$ 1.753
	2nd survey	1.34	0.18	4.926 $\pm$ 3.688
	3rd survey	6.75	< 0.0001	29.447 $\pm$ 4.360
LGH, pre-removal:	Treatment	− 0.22	0.83	− 0.941 $\pm$ 4.337
	Plot floral area	0.003	0.99	0.002 $\pm$ 0.626
	Bush area	1.21	0.23	2.152 $\pm$ 1.782
LGH, post-removal:	Treatment	− 1.55	0.14	− 7.040 $\pm$ 4.530
	Plot floral area	− 1.40	0.17	− 0.723 $\pm$ 0.517
	Bush area	1.02	0.31	1.350 $\pm$ 1.329
	2nd survey	0.89	0.37	2.444 $\pm$ 2.733
	3rd survey	3.29	0.0013	11.136 $\pm$ 3.389
Non-bees, pre-removal:	Treatment	− 0.17	0.87	− 0.165 $\pm$ 0.980
	Plot floral area	− 2.43	0.025	− 0.347 $\pm$ 0.143
	Bush area	3.69	0.00060	1.720 $\pm$ 0.467
Non-bees, post-removal:	Treatment	− 0.41	0.68	− 0.407 $\pm$ 0.996
	Plot floral area	− 0.03	0.98	− 0.004 $\pm$ 0.131
	Bush area	2.02	0.05	0.824 $\pm$ 0.408
	2nd survey	0.40	0.69	0.338 $\pm$ 0.856
	3rd survey	0.08	0.93	0.084 $\pm$ 1.018

References

- Alarcón R (2010) Congruence between visitation and pollen-transport networks in a California plant-pollinator community. *Oikos* 119:35–44. <https://doi.org/10.1111/j.1600-0706.2009.17694.x>
- Anderson, MJ (2001) A new method for nonparametric multivariate analysis of variance. *Austral Eco* 26:32–46
- Albrecht M, Ramis MR, Traveset A (2016) Pollinator-mediated impacts of alien invasive plants on the pollination of native plants: the role of spatial scale and distinct behaviour among pollinator guilds. *Biol Invasions* 18:1801–1812. <https://doi.org/10.1007/s10530-016-1121-6>
- Bartomeus I, Vilà M, Steffan-Dewenter I (2010) Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *J Ecol* 98:440–450. <https://doi.org/10.1111/j.1365-2745.2009.01629.x>
- Baskett CA, Emery SM, Rudgers JA (2011) Pollinator visits to threatened species are restored following invasive plant removal. *Int J Plant Sci* 172:411–422. <https://doi.org/10.1086/658182>
- Bell JM, Karron JD, Mitchell RJ (2005) Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. *Ecology* 86:762–771. <https://doi.org/10.1890/04-0694>
- Bosch J, Retana J, Cerdá X (1997) Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* 109:583–591. <https://doi.org/10.1007/s004420050120>
- Bossard CC, Randall JM, Hoshovsky MC (eds) (2000) Invasive plants of California's wildlands. University of California Press, Berkeley
- Braun J, Lortie CJ (2019) Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspect Plant Ecol Evol Syst* 36:33–40. <https://doi.org/10.1016/j.ppees.2018.12.003>
- Campbell DR, Motten AF (1985) The mechanism of competition for pollination between two forest herbs. *Ecology* 66:554–563
- Chaudhary O (2006) Diversity, foraging behaviour of floral visitors and pollination ecology of fennel (*Foeniculum vulgare* Mill). *J Spices Aromat Crop* 15:34–41
- Colvin WI, Gliessman SR (2011) Effects of fennel (*Foeniculum vulgare* L.) interference on germination of introduced and native plant species. *Allelopath J* 28:41–51
- Dietzsch AC, Stanley DA, Stout JC (2011) Relative abundance of an invasive alien plant affects native pollination processes. *Oecologia* 167:469–479. <https://doi.org/10.1007/s00442-011-1987-z>
- Hansen TF, Armbruster WS, Antonsen L (2000) Comparative analysis of character displacement and spatial adaptations as illustrated by the evolution of *Dalechampia* blossoms. *Am Nat* 156:S17–S34. <https://doi.org/10.1086/303413>
- Hegland SJ (2014) Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Funct Ecol* 28:561–568
- Hernández-Castellano C, Rodrigo A, Gómez JM, Stefanescu C, Calleja JA, Reverté S, Bosch J (2020) A new native plant in the neighborhood: effects on plant–pollinator networks, pollination, and plant reproductive success. *Ecology* 101:1–13. <https://doi.org/10.1002/ecy.3046>
- Jacobs JH, Clark SJ, Denholm I, Goulson D, Stoate C, Osborne JL (2010) Pollinator effectiveness and fruit set in common ivy, *Hederahelix* (Araliaceae). *Arthropod-Plant Interact* 4:19–28
- Jakobsson A, Padrón B, Traveset A (2008) Pollen transfer from invasive *Carpobrotus* spp. to natives—a study of pollinator behaviour and reproduction success. *Biol Conserv* 141:136–145. <https://doi.org/10.1016/j.biocon.2007.09.005>
- Junak S, Ayers T, Scott R, Wilken D, Young D (eds) (1995A) A flora of Santa Cruz Island. Santa Barbara Botanical Garden, Santa Barbara
- Kearns CA, Inouye DW (1999) Techniques for pollination biologists. University Press of Colorado, Niwot, CO
- Lanternman J, Goodell K (2018) Bumble bee colony growth and reproduction on reclaimed surface coal mines. *Restor Ecol* 26(1):183–194
- Lanuza JB, Bartomeus I, Ashman T-L, Bible G, Rader R (2021) Recipient and donor characteristics govern the hierarchical structure of heterospecific pollen competition networks. *J Ecol* 109:2329–2341. <https://doi.org/10.1111/1365-2745.13640>
- Levin DA, Anderson WW (1970) Competition for pollinators between simultaneously flowering species. *Am Nat* 104:455–467
- Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc B Biol Sci* 270:775–781. <https://doi.org/10.1098/rspb.2003.2327>
- Litt AR, Cord EE, Fulbright TE, Schuster GL (2014) Effects of invasive plants on arthropods. *Conserv Biol* 28:1532–1549. <https://doi.org/10.1111/cobi.12350>
- Masters JA, Emery SM (2015) The showy invasive plant *Ranunculus ficaria* facilitates pollinator activity, pollen deposition, but not always seed production for two native spring ephemeral plants. *Biol Invasions* 17:2329–2337. <https://doi.org/10.1007/s10530-015-0878-3>
- Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proc R Soc B Biol Sci* 269:2395–2399. <https://doi.org/10.1098/rspb.2002.2174>
- Moragues E, Traveset A (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. *Biol Conserv* 122:611–619. <https://doi.org/10.1016/j.biocon.2004.09.015>
- McKinney AM, Goodell K (2010) Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol Invasions* 12:2751–2763. <https://doi.org/10.1007/s10530-009-9680-4>
- Morales CL, Traveset A (2008) Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *CRC Crit Rev Plant Sci* 27:221–238. <https://doi.org/10.1080/07352680802205631>
- Morales CL, Traveset A (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol Lett* 12:716–728. <https://doi.org/10.1111/j.1461-0248.2009.01319.x>

- Muñoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *J Ecol* 96:459–467. <https://doi.org/10.1111/j.1365-2745.2008.01361.x>
- Murphy SD, Aarssen LW (1995) Reduced seed set in *Elytrigia Repens* caused by allelopathic pollen from *Phleum-Pratense*. *Can J Bot* 73:1417–1422. <https://doi.org/10.1139/b95-154>
- Nourimand M, Mohsenzadeh S, Teixeira Da Silva JA, Sahar-khiz MJ (2011) Allelopathic potential of fennel (*Foeniculum vulgare* Mill.). *Med Aromat Plant Sci Biotechnol* 5:54–57
- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2012) vegan: community ecology package. R package version 2.0–4. <http://CRAN.R-project.org/package=vegan>
- Power PJ, Stanley T, Cowan C, Roberts JR (2014) Native plant recovery in study plots after fennel (*Foeniculum vulgare*) control on Santa Cruz Island. *Monogr West North Am Nat* 7:465–476. <https://doi.org/10.3398/042.007.0136>
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ravlić M, Baličević R, Nikolić M, Sarailić A (2016) Assessment of allelopathic potential of Fennel, Rue and Sage on weed species Hoary Cress (*Lepidium draba*). *Not Bot Horti Agrobi* 44:48–52. <https://doi.org/10.15835/nbha44110097>
- Shilpa P, Sowmya K, Srikanth C (2014) Pollinator diversity and foraging activity on fennel, *Foeniculum vulgare* Mill. and African marigold, *Tagetes minuta* L. *Pest Manag Hortic Ecosyst* 20:236–239
- Skaldina O (2020) Insects associated with sweet fennel: beneficial visitors attracted by a generalist plant". *Arthropod-Plant Inter* 14:399–407. <https://doi.org/10.1007/s11829-020-09752-x>
- Thomson JD (1978) Effect of stand composition on insect visitation in two-species mixtures of *Hieracium*. *Am Midl Nat* 100:431–440
- Thomson DL (2019) Effects of long-term variation in pollinator abundance and diversity on reproduction of a generalist plant. *J Ecol* 107:491–502. <https://doi.org/10.1111/1365-2745.13055>
- Thorp RW, Wenner AM, & Barthell JF (1994) Flowers visited by honey bees and native bees on Santa Cruz Island. In: 4th California Islands Symposium, pp 351–36
- Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol Evol* 21:208–216. <https://doi.org/10.1016/j.tree.2006.01.006>
- Tur C, Sáez A, Traveset A, Aizen MA (2016) Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in South Andean plant communities. *Ecol Lett* 19(5):576–586. <https://doi.org/10.1111/ele.12594>
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>

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