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Indirect interactions between invasive and native plants via pollinators

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Abstract In generalised pollination systems, the presence of alien plant species may change the foraging behaviour of pollinators on native plant species, which could result in reduced reproductive success of native plant species. We tested this idea of indirect interactions on a small spatial and temporal scale in a field study in Mauritius, where the invasive strawberry guava, *Psidium cattleianum*, provides additional floral resources for insect pollinators. We predicted that the presence of flowering guava would indirectly and negatively affect the reproductive success of the endemic plant *Bertiera zaluzania*, which has similar flowers, by diverting shared pollinators. We removed *P. cattleianum* flowers within a 5-m radius from around half the *B. zaluzania* target plants (treatment) and left *P. cattleianum* flowers intact around the other half (control). By far, the most abundant and shared pollinator was the introduced honey bee, *Apis mellifera*, but its visitation rates to treatment and control plants were similar. Likewise, fruit and seed set and fruit size and weight of *B. zaluzania* were not influenced by the presence of *P. cattleianum* flowers. Although other studies have shown small-scale effects of alien plant species on neighbouring natives, we found no evidence for such negative indirect interactions in our system. The dominance of introduced, established *A. mellifera* indicates their replacement of native insect flower visitors and their function as pollinators of native plant species. However, the pollination effectiveness of *A. mellifera* in comparison to native pollinators is unknown.

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Introduction

Alien species may utilise biotic interactions to successfully invade natural communities (Orians 1986; Mack et al. 2000), and a general knowledge of such new associations among species is fundamental to understanding invasion processes (Parker et al. 1999). One type of indirect interactions between flowering plants occurs when two plant species compete for a common pollinator, with negative consequences for the reproductive success of one or both species (Waser 1983; Campbell and Motten 1985). For example, pollinators may neglect certain flowering species because neighbouring plants offer larger amounts of nectar (Chittka and Schürkens 2001), or pollinators may transfer large quantities of heterospecific pollen that interfere with fertilisation by conspecific pollen (Campbell and Motten 1985; Feinsinger 1987). Such situations are possible when alien plant species invade new communities and start interacting indirectly with native species through shared pollinators (e.g., Richardson et al. 2000; Stout et al. 2002; Ghazoul 2004). Alien plant species can also increase the floral display in a community and, by attracting more pollinator species, facilitate pollination of neighbouring resident species (e.g. Thomson 1982; Rathcke 1983; Feldman

et al. 2004; Ghazoul 2006). For example, Johnson et al. (2003) showed that plant species providing large quantities of nectar increased the local abundance of pollinators, and as a consequence, the co-occurring, non-rewarding orchid *Anacamptis morio* (L.) Bateman, Pridgeon & Chase experienced higher pollination success.

Ecological studies on entire pollinator assemblages suggest that generalisation is a common feature of most plant–pollinator systems (Waser et al. 1996; Vázquez and Aizen 2004; Bascompte et al. 2006). Generalisation results in pollinators sharing floral resources, which is an assumption for indirect interactions to occur among flowering plants. Little is known about the role of indirect interactions in determining community composition of flowering plants (Levin and Anderson 1970; Waser 1978), and this question has only recently been addressed experimentally (Chittka and Schürkens 2001; Moeller 2004; Lopezaraiza et al. 2007). Indirect interactions may become particularly important when exotic plant species invade native habitats and cause shifts in native pollination systems.

Many island habitats are severely degraded through the invasion of alien plant species. Negative effects of invasive plants include the displacement of native plant species by strong competition for resources with exotic plants (Smith 1985; Simberloff 1995; Daehler 2003). In addition, island pollination systems are usually generalised (Olesen et al. 2002; Dupont et al. 2003) because only a subset of mainland pollinators has colonised island habitats in the past. This selective colonisation has resulted in relatively depauperate faunas compared to mainland pollinator communities (MacArthur and Wilson 1967; Feinsinger 1987). Therefore, introduced generalist pollinators and plants that attract a wide range of pollinators have a higher chance of successfully establishing within island pollination systems (Simberloff and von Holle 1999; Richardson et al. 2000). The role of indirect interactions in these systems, however, has not been studied intensively, and results are conflicting (e.g. Aigner 2004; Moragues and Traveset 2005).

We studied indirect interactions between an invasive and an endemic flowering plant species on the oceanic island of Mauritius. Mauritius has experienced multiple plant and animal invasions (Cheke and Hume 2008), which have reduced the population sizes of many native plant species (Page and d'Argent 1997). As on other islands, we observe generalised pollination systems (predominantly flies; Kaiser 2006) and a paucity of pollinator species (Hansen et al. 2002). We experimentally studied the impact of the abundant flowers of the highly invasive strawberry guava *Psidium cattleianum* Sabine (Myrtaceae) on the reproductive success of the endemic plant *Bertiera zaluzania* Gaertner f. (Rubiaceae) on a small local scale. *B. zaluzania* was selected because it is a typical representative of the Rubiaceae family, which contains 59 native species in

Mauritius, 29 of which are listed as endangered or critically endangered according to IUCN criteria (Mauritian Wildlife Foundation, unpublished database). In addition, *B. zaluzania* co-flowers with *P. cattleianum*, and both plant species have white, easily accessible flowers, leading us to assume that they will share generalist pollinators. We thus hypothesised that (1) the removal of *P. cattleianum* flowers around *B. zaluzania* changes the visitation rate of pollinators to *B. zaluzania*, (2) pollinators visiting *B. zaluzania* without surrounding *P. cattleianum* flowers carry less heterospecific pollen compared to those visiting *B. zaluzania* surrounded by *P. cattleianum* flowers and (3) the change in visitation rate to *B. zaluzania* ultimately results in an altered reproductive success for *B. zaluzania*.

Materials and methods

Study sites

Our study was conducted at Plaine Champagne, a part of the central upland plateau of the 6,754-ha Black River Gorges National Park in Mauritius (20°42′ S, 57°44′ E). The study site is a remnant area of approximately 9 ha covered by a diverse heathland community that was formerly widespread throughout the upland plateau. During the last century, the area has been heavily invaded by alien plant species, such as *P. cattleianum*, *Ligustrum robustum* Blume (Oleaceae) and *Wikstroemia indica* Mey (Thymelaeaceae), which now dominate this habitat (Page and D'Argent 1997; CN Kaiser-Bunbury, personal observation). The field work was carried out between November 2003 and May 2004, which covered the second half of the main flowering season with approximately 75% of native and 90% of introduced plant species flowering and fruiting during this period.

Study species and floral traits

The introduced strawberry guava *P. cattleianum* is one of the most invasive weeds in the upland forests of Mauritius, with a peak flowering season in the upland region from November to December. *P. cattleianum* is a hermaphroditic perennial and displays open white flowers with a diameter of about 3.5 cm and several hundred anthers. Flowers of *P. cattleianum* produce no nectar, as inferred by sampling nectar with 5-µl glass microcapillaries from a total of 35 flowers on 11 plants on six non-consecutive days.

The endemic plant species, *B. zaluzania*, is a morphologically hermaphroditic, but functionally dioecious, perennial shrub of about 2 m height, which protrudes above the lower thicket of *P. cattleianum*. Heterostylous male and female flowers are morphologically different. Female flowers of *B. zaluzania* stay viable for a maximum of 1 day, often with the

stigma being observed to wilt at around noon. Flowers of *B. zaluzania* are displayed in inflorescences of up to 150 flowers, each flower about 1.5 cm in diameter. Flowering of *B. zaluzania* occurs from November to January and fruiting from March to April. Fruits contain up to 300 seeds each. Flowers produced on average 2.8 ± 0.4 SE µl nectar with a sugar concentration of 16.3 ± 0.4 SE %, as determined from 45 newly opened flowers (20 female and 25 male) between 7 and 9 A.M. with a hand-held refractometer (Eclipse 45-81, Bellingham and Stanley). Functional male and female flowers produced similar nectar quantities ($F_{1, 43} = 3.078$, $P = 0.086$) with similar sugar concentrations ($F_{1, 43} = 1.331$, $P = 0.23$). We found no pollen grains on the anthers of seven functionally female plants, while those of seven male plants contained $16,315 \pm 6,455$ SD pollen grains per anther. The number of pollen grains was determined by light microscopy using a counting chamber.

Indirect effects between plant species: experimental design

We selected 20 single-standing, female *B. zaluzania* target plants surrounded by dense stands of *P. cattleianum*. The target plants were assigned randomly to two experimental groups of ten plants each. In one group (treatment), all *P. cattleianum* flowers and buds within a circle of 5 m radius were removed before flower initiation of *B. zaluzania*. In the other group (control), *P. cattleianum* flowers and buds around *B. zaluzania* were not removed. Treatment and control plants were spatially interspersed in the habitat. No other plant species were flowering within this 5-m radius. The removal of approximately 10,000 *P. cattleianum* flowers in an area of 78.5 m^2 around the target plant was considered sufficient to reveal effects on the productive success of *B. zaluzania* through changed foraging behaviour of pollinators on a small spatial scale (see Goverde et al. 2002). Given that *P. cattleianum* is the only flowering plant species in the experimental plots and their flower removal is the only modification within the 5-m radius, we assumed that changes in visitation rate and reproductive success of *B. zaluzania* would be associated with the floral manipulation. However, for logistical reasons, we could not test directly for shifts in pollinator behaviour between *P. cattleianum* and *B. zaluzania* as a result of competition for pollination.

To determine the reproductive success of *B. zaluzania*, we counted buds and inflorescences of target plants at the beginning of the experiment and then counted the developing fruits 2 weeks after wilting of the last flower in January 2004. Eight weeks later, in March 2004, we collected a total of 705 ripe fruits from all target plants, measured their weight and size and recorded the number of seeds in a sub-sample of these collected fruits ($n = 532$). We defined fruit set as the proportion of buds developing into fruits and seed set as the mean number of seeds per fruit.

Seed set provides indirect information on pollination efficiency; as in fruits with multiple seeds, the number of pollen grains deposited on the stigma is usually directly related to the number of seeds produced by the fruit (Silander and Primack 1978; Campbell 1986).

Pollinator activity

Pollinator observations on *B. zaluzania* were conducted on nine sunny days, every 2–3 days, between 28th November and 22nd December 2003. Flower visitors to randomly chosen *B. zaluzania* plants (five plants of the treatment group and six plants of the control group) were recorded. Total observation time was 32 half-hour 'observation units'. All observations were carried out evenly distributed between 7 A.M., when the first flowers opened, and dusk at 6 P.M. When accurate visitor identification was not possible by sight, insects were caught for later identification after a foraging bout. For each half-hour observation unit, we counted the number of flowers observed in order to calculate visitation rate, which was defined as the number of visits per flower per hour. Flower visitors were only recorded when they touched the receptive parts of the flowers. *P. cattleianum* flowers and buds were counted in ten quadrats (0.25 m^2) placed randomly within each circle around *B. zaluzania* control plants to estimate the number of guava flowers and buds within the experimental patch.

Pollen load on insects

As an indicator of heterospecific pollen transfer, we estimated pollen loads by collecting 35 flower visitors before they entered flowers of *B. zaluzania*. The insects were collected from the target plants but not during pollinator observations. Each insect was wiped with a 0.25-cm^2 piece of fuchsin gel (Kearns and Inouye 1993) to collect pollen from the head, the ventral and dorsal sides of the thorax and the abdomen. The gel was melted onto a microscope slide and covered with a glass cover slip. Pollen grains were identified and counted using light microscopy.

Data analysis

We analysed differences among treatments using analysis of variances (ANOVAs; statistical package R 2.1.1; R Development Core Team 2005). To fulfil the assumptions of normality and homoscedasticity of residuals, we transformed the response variables 'visitation rate' reciprocal, 'fruit set' arcsine-square-root, 'seed set' log$_{10}$ and both 'pollen loads' and 'number of pollen grains' from *B. zaluzania* and *P. cattleianum* log$_{10}$, following the sugges-

tions of Box–Cox transformation tests (Quinn and Keough 2002). To test for differences between the number of pollen grains from different plant species carried by flower visitors, we used a two-way ANOVA with individuals and treatment as factors. Non-parametric tests were used when assumptions of normality and homoscedasticity of residuals could not be met by data transformation. The relationship between fruit and seed set was analysed with a linear model, accounting for different treatment effects by entering treatment as a factor in the analysis. We used a linear regression to test whether fruit set of the control group of *B. zaluzania* was affected by the number of *P. cattleianum* flowers within the 5-m radius. All means± standard errors displayed in the figures were calculated from untransformed data.

Results

Pollinator activity

A total of seven visitor species were recorded on flowers of *B. zaluzania* (Table 1). The honey bee *Apis mellifera* L. (Apidae) was by far the most common visitor, with 95% of all visitations, and it visited flowers of both treatment and control plants. Other species were observed visiting flowers only nine times, and none of the observed visitors occurred at both treatment and control plants (Table 1). The overall visitation rate to control (1.01 ± 0.48 SE visits per flower per hour, hereafter, mean±SE) and treatment (0.65 ± 0.30) plants of *B. zaluzania* was not significantly different ($F_{1,\,9}=0.09$, $P=0.76$). Visitation rates in the morning and the afternoon were also similar ($U=35.0$, $n=16$, $P=0.92$). On *P. cattleianum* flowers, we observed mainly honey bees and single individuals of other insect species foraging for pollen (Bombyliidae fly *Villa unifasciata* and pollen-feeding beetle *Chaetocnema* sp., Kaiser 2006).

Pollen loads on insects

Overall, flower visitors to *B. zaluzania* (20 *A. mellifera*, six *V. unifasciata*, three *Allograpta nasuta*, three *Chaetocnema* sp., two Curculionidae and one *Pristomerus* sp.) carried significantly fewer conspecific pollen grains than pollen of *P. cattleianum* and unidentified plant species (*Bertiera*, 2.17 ± 0.47; *Psidium*, 65.7 ± 40.3; other, 17.2 ± 6.72; $F_{individuals}$ $2,68=2.21$, $P=0.003$, $F_{treatment}2,\,68=14.42$, $P<0.001$). The total number of pollen grains carried by flower visitors to treatment and control groups was not significantly different ($F_{1,\,33}=3.12$, $P=0.086$). Flower visitors to treatment plants carried significantly fewer conspecific pollen grains than visitors to control plants (1.20 ± 0.47 vs. 3.46 ± 0.8; $F_{2,\,68}=8.278$, $P=0.007$). The pollen loads from other plant species were similar between groups ($F_{1,\,33}=3.658$, $P=0.065$; Fig. 1a). Honey bees, the most common flower visitors, carried significantly fewer pollen grains when visiting treatment *B. zaluzania* compared to those visiting control plants ($F_{1,\,18}=5.118$, $P=0.036$; Fig. 1b).

Reproductive success

Treatment plants of *B. zaluzania* produced a mean fruit set of 53.0 (±5.9)% (range, 10% to 81%; $n=10$) and control plants a mean fruit set of 51.3 (±2.4)% (range, 39% to 63%; $n=9$; due to a fungal infestation, one plant of the control group lost all its buds and flowers and was therefore excluded from further analyses). Fruit set was not statistically different for treatment and control plants ($F_{1,\,17}=0.52$, $P=0.48$). Similarly, seed set of 84.0 (±12.0) of treatment plants did not differ statistically from seed set of 82.5 (±7.76) of the control plants ($F_{1,\,17}=0.028$, $P=0.87$). Overall, fruit and seed set were positively correlated ($F_{1,\,16}=6.47$, $P=0.02$, $R^2=0.29$), but there was no effect of treatment ($F_{1,\,16}=0.09$, $P=0.77$). *P. cattleianum* plants produced on average 10,383 (±790) flowers and buds

**Table 1** Number of observed visits by animal species to *B. zaluzania*

	Flower visitors	No. of visits	Visitation rate
Treatment (185)	*Apis mellifera* L. (Hymenoptera)	104	0.98 ± 0.47[a]
	Pristomerus sp. (Hymenoptera)	1	0.009
	Villa unifasciata Macquart (Diptera)	3	0.021 ± 0.014
	Zosterops mauritianus Gmelin (Aves)	2	0.008
Control (163)	*Apis mellifera* L. (Hymenoptera)	66	0.63 ± 0.29[a]
	Allograpta nasuta Macquart (Diptera)	1	0.007
	Chaetocnema sp. (Coleoptera)	1	0.021
	Curculionidae (Coleoptera)	1	0.021

Observations were conducted for each 8 h (16 half-hour sessions) on treatment (*P. cattleianum* flowers removed) and control plants (no flowers removed). Numbers in brackets are total number of flowers observed. Mean (±SE) visitation rates (visits per flower per hour) were calculated by using the mean visits for each observation session and plant (treatment, $n=5$; control, $n=6$)

[a] $F_{1,\,9}=0.38$, $P=0.56$

Fig. 1 Mean number of pollen grains (±SE) from insects that visited flowers of treatment and control plants (**A**). The pollen loads of 35 insects were collected and sorted into three groups, *Bertiera zaluzania*, *Psidium cattleianum* and unidentified pollen (Others). Mean number of pollen grains (±SE) from *Apis mellifera* that visited flowers of treatment and control plants (**B**). The pollen loads of 20 honey bees that visited *B. zaluzania* were compared and grouped in *B. zaluzania*, *P. cattleianum* and other, unidentified pollen (Others). *Different letters on bars* indicate significant differences (*P*<0.05)
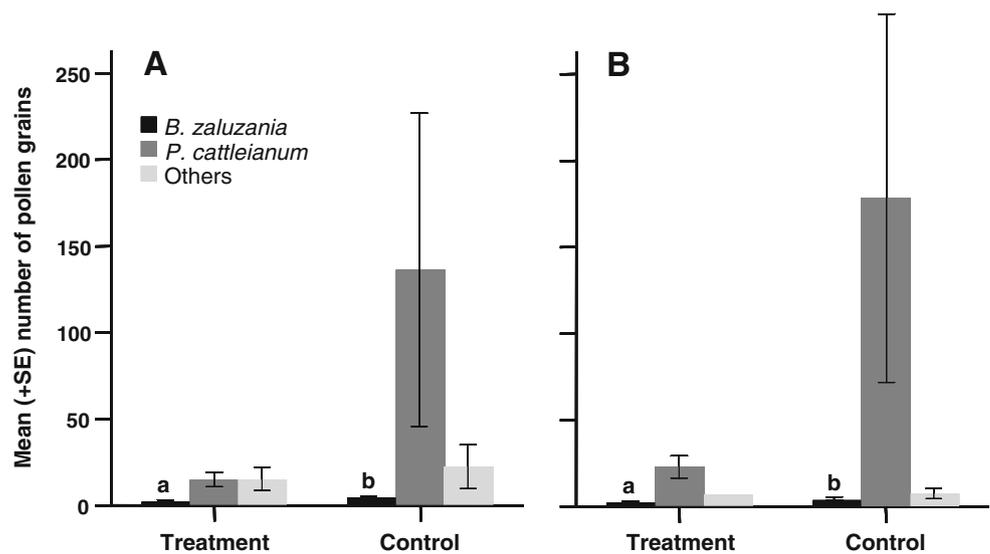
within the 5-m experimental radius around *B. zaluzania* control plants. There was no relationship between fruit set and the number of *P. cattleianum* flowers in the control group (R^2=0.01, df=8, *P*=0.79). No statistically significant differences between treatment and control plants were detected for other reproductive traits, such as fruit size and weight, number of inflorescences per plant or number of buds per inflorescence (Table 2).

Discussion

We found the removal of introduced *P. cattleianum* flowers to have no detectable effect on the number of visitors to native *B. zaluzania* or on the overall amount of pollen carried by the visitors. However, the amount of *B. zaluzania* pollen carried by visitors to control plants was higher than that on visitors to treatment plants. We detected no difference in fruit and seed set between treatment and control plants. We conclude that the reproductive success of *B. zaluzania* is unlikely to be affected by small-scale indirect interactions between co-occurring *B. zaluzania* and

P. cattleianum. However, we acknowledge that our findings refer to a small spatial scale, and thus, further evidence is required on indirect interactions between plants on a larger spatial and temporal scale. We know of only one study that investigated comparably small-scale fragmentation effects on pollinator visitation frequency (Goverde et al. 2002). The authors describe a sharp decline in visitation frequency to *Betonia officinalis* by the bumblebee *Bombus veteranus* in fragmented plots in comparison to control plots. Other studies on a larger scale have shown neutral effects similar to the results presented in this study (e.g. Aigner 2004), but findings of positive (e.g. Moeller 2004; Ghazoul 2006) and negative effects (e.g. Brown and Mitchell 2001) have also been reported.

The absence of small-scale indirect interactions between the invasive *P. cattleianum* and the rare, declining *B. zaluzania* could be encouraging, as this suggests that the presence of invasive *P. cattleianum* flowers may not constitute an additional threat to *B. zaluzania* and potentially to other native plant species through indirect competitive effects via pollinators. Presumably, the primary impact of *P. cattleianum* on native plant species is direct

Table 2 Comparison of floral and reproductive traits of *B. zaluzania* when flowers of *P. cattleianum* were experimentally removed (treatment) vs. when *P. cattleianum* flowers were present (control)

Trait	Means±SE		*F*	*df*	*P* value
	No *P. cattleianum* flowers	With *P. cattleianum* flowers			
Buds per plant	45±4.1	50.34±5.64	0.61	1,19	0.44
Flowers per plant	1,049±163	979±172	0.26	1,19	0.61
Inflorescences per plant	23.6±3.6	19.3±3.0	0.84	1,19	0.37
Fruits per plant	560±116	524±118	0.05	1,18	0.83
Fruit weight	0.47±0.03	0.52±0.02	3.86	1,18	0.06
Fruit size	9.8±0.34	10.3±0.23	1.58	1,18	0.22

competition for nutrients, space and light (Huenneke and Vitousek 1990). This competition has contributed to a decline in population size and relative abundance of *B. zaluzania* throughout the upland of Mauritius (Page and D'Argent 1997). The removal of *P. cattleianum* flowers and buds around *B. zaluzania* treatment plants may cause compensatory vegetative growth of *P. cattleianum* (e.g. Järemo et al. 1996), which could have drained nutrients. The increased competition for soil nutrients and water may explain the trend towards production of lighter fruits by treatment plants compared to control plants that we observed. However, detailed soil nutrient analyses would be necessary to support this hypothesis.

Surprisingly, little is known about the reproductive biology of *P. cattleianum*, but the congeneric *P. firmum* of Brazil is self-compatible and visited by a variety of bee species (Proença and Gibbs 1994). During the initial invasion process of *P. cattleianum* in Mauritius, honey bees may well have played a crucial role in its success. Honey bees were introduced to Mauritius approximately 300 years ago (Staub 1993), and the presence of the invasive *P. cattleianum* could have facilitated the establishment of feral honey bees in natural sites and vice versa. Consequently, the original pollinator community may have undergone displacement and local extinction through competition with the highly abundant honey bees for floral resources (e.g., Paton 1993; Butz Huryn 1997; Paini 2004). Indeed, displacement of native pollinators by honey bees is common in many degraded ecosystems, including oceanic islands (Hansen et al. 2002; Dupont et al. 2004). There is evidence that mutualists can enhance the competitive abilities of invaders (Simberloff and von Holle 1999; Richardson et al. 2000; Morales and Aizen 2002). A study in California and on Santa Cruz Island showed that the invasion of yellow starthistle *Centaurea solstitialis* is facilitated by interactions with the non-native *A. mellifera* (Barthell et al. 2001). The combined invasion of plants and mutualistic partners will ultimately also benefit the animal mutualists (see Traveset and Richardson 2006 and references therein).

Based on floral traits, such as a tubular corolla with readily accessible nectar, relatively high nectar sugar concentration and modest nectar volume, we speculate that the original pollinators of *B. zaluzania* might have been flies or short-tongued solitary bees. In fact, in another study on a restored area nearby (~6 ha, all exotic plant species removed), Kaiser (2006) reported five Diptera species (*Chrysomya megacephala* Fabricius, *Episyrphus* sp. near *circularis* Hull, *Ischiodon aegyptius* Wiedemann, *Pachycerina crinicornis* Thomson and *Stomorhina lunata* Fabricius), an endemic gecko species (*Phelsuma cepediana* Merrem) and an introduced Hymenoptera species (*Polistes hebraeus* Fabricius) visiting *B. zaluzania*. These findings suggest that *B. zaluzania* in our study site experienced a depauperate pollinator

assemblage and an over-dominance of honey bees that might have resulted in competition between honey bees and native pollinators. The study may have shown a different pattern if the main pollinator of *B. zaluzania* was not *A. mellifera*, as this pollinator was introduced to Mauritius and did not co-evolve with the target plant.

Fruit and seed set of *B. zaluzania* in our study was comparable to that of other closely related plant species in the same family on the Mascarene Islands (Pailler et al. 1998a, b). Therefore, our findings suggest that honey bees are adequate pollinators of *B. zaluzania*. However, when comparing native pollinators with introduced honey bees, other aspects of pollination quality have to be accounted for, such as the abilities to maintain genetic diversity and pollen flow among small, declining plant populations (e.g., Paton 1993). We found pollen grains of *B. zaluzania* and *P. cattleianum* on individual honey bees visiting *B. zaluzania*, indicating that honey bees switched between visits to *B. zaluzania* and *P. cattleianum* and acted as shared pollinators. However, if *P. cattleianum* pollen clogs *B. zaluzania* stigmas, this should have been reflected in differences in fruit and seed sets between treatment and control plants. Differences in pollen loads (large amounts of *P. cattleianum* pollen on honey bees from control plants and comparatively low overall loads on honey bees from treatment plants) and higher *B. zaluzania* pollen load on insects visiting control plants compared to those visiting treatment plants also suggested a certain degree of segregation in the pollinator assemblage into pollen and nectar foragers (see Wilson 1971). Butz Huryn (1997) reviewed studies on honey bee pollen loads and showed that they intensively utilise only a small proportion of plant species. She pointed out that if only small amounts of pollen are removed, little effect on the flora can be expected. This was recently supported by a study by Jakobsson et al. (2008) who showed that, although pollen transfer between a South African invasive in the Mediterranean region and the native congenerics occurs, the effect on the reproduction of the native species is comparatively small. Such mechanisms may explain the unchanged reproductive success of *B. zaluzania* when surrounding *P. cattleianum* flowers were removed. Alternatively, the manipulated area of 78.5 m^2 may have been too small to reveal marked foraging changes of pollinators. Honey bees are capable of flying relatively long distances (Schulke and Waser 2001) and, when foraging, respond to large-scale changes in habitat structure (Menzel et al. 1997; Steffan-Dewenter et al. 2002). However, in other studies, it has been shown that foraging behaviour of pollinators can change in response to floral abundance at small spatial scales (Kunin 1997; Goverde et al. 2002; Ghazoul 2006; Lopezaraiza et al. 2007).

Our results demonstrate that the presence of the invasive *P. cattleianum* flowers has no effect on the foraging

behaviour and the efficiency of shared honey bee pollinators and that the subsequent reproductive success of the native *B. zaluzania* is not changed for plants in close proximity to *P. cattleianum* flowers. Honey bees may have replaced the original pollinators of *B. zaluzania,* and indirect effects may have occurred in the past. At present, there is little evidence that indirect interactions between invasive *P. cattleianum* and a simultaneously flowering native plant species via pollinators amplify the presumed direct competitive effects of this successful invader. Given the absence of indirect interactions mediated by shared pollinators in our study (mainly *A. mellifera*) and contrasting findings in other experimental studies, we suggest studying whole plant–pollinator network studies and conducting research on a greater spatial and temporal scale to elucidate the indirect impact of invasive plant species on an entire plant community of native plant species. This approach promises to establish better how indirect interactions contribute to the structure of flowering plant communities that need to be preserved.

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