



University of Zurich
Zurich Open Repository and Archive

Winterthurerstr. 190
CH-8057 Zurich
<http://www.zora.unizh.ch>

Year: 2007

Positive indirect interactions between neighboring plant species via a lizard pollinator

Hansen, D M; Kiesbüy, H C; Jones, C G; Müller, C B

Hansen, D M; Kiesbüy, H C; Jones, C G; Müller, C B. Positive indirect interactions between neighboring plant species via a lizard pollinator. *Am. Nat.* 2007, 169(4):534-42.

Postprint available at:
<http://www.zora.unizh.ch>

Posted at the Zurich Open Repository and Archive, University of Zurich.
<http://www.zora.unizh.ch>

Originally published at:
Am. Nat. 2007, 169(4):534-42

Positive indirect interactions between neighboring plant species via a lizard pollinator

Abstract

In natural communities, species are embedded in networks of direct and indirect interactions. Most studies on indirect interactions have focused on how they affect predator-prey or competitive relationships. However, it is equally likely that indirect interactions play an important structuring role in mutualistic relationships in a natural community. We demonstrate experimentally that on a small spatial scale, dense thickets of endemic *Pandanus* plants have a strong positive trait-mediated indirect effect on the reproduction of the declining endemic Mauritian plant *Trochetia blackburniana*. This effect is mediated by the endemic gecko *Phelsuma cepediana* moving between *Pandanus* thickets, a preferred microhabitat, and nearby *T. blackburniana* plants, where it feeds on nectar and pollinates the plants. Our findings emphasize the importance of considering plant-animal interactions such as pollination at relatively small spatial scales in both basic ecological studies and applied conservation management.

Natural History Miscellany

Positive Indirect Interactions between Neighboring Plant Species via a Lizard Pollinator

Dennis M. Hansen,^{1,*} Heine C. Kiesbüy,^{1,†} Carl G. Jones,^{2,‡} and Christine B. Müller^{1,§}

1. Institute of Environmental Sciences, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland;
2. Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey JE3 5BP, Channel Islands and Mauritian Wildlife Foundation, Grannum Road, Vacoas, Mauritius

Submitted April 10, 2006; Accepted October 12, 2006;
Electronically published January 29, 2007

Online enhancements: appendix figures.

ABSTRACT: In natural communities, species are embedded in networks of direct and indirect interactions. Most studies on indirect interactions have focused on how they affect predator-prey or competitive relationships. However, it is equally likely that indirect interactions play an important structuring role in mutualistic relationships in a natural community. We demonstrate experimentally that on a small spatial scale, dense thickets of endemic *Pandanus* plants have a strong positive trait-mediated indirect effect on the reproduction of the declining endemic Mauritian plant *Trochetia blackburniana*. This effect is mediated by the endemic gecko *Phelsuma cepediana* moving between *Pandanus* thickets, a preferred microhabitat, and nearby *T. blackburniana* plants, where it feeds on nectar and pollinates the plants. Our findings emphasize the importance of considering plant-animal interactions such as pollination at relatively small spatial scales in both basic ecological studies and applied conservation management.

Keywords: plant-animal interactions, mutualism, community ecology, facilitation, indirect effects, conservation biology.

Among plants, the nuptials cannot be celebrated without the intervention of a third party to act as a marriage priest, and that the office of this third person is to unite the representatives of different households. ... Now the marriage priests who officiate in the vegetable kingdom are insects in search of honey; the winds, or anything which by accident, or design, may carry the pollen from one flower to another. (J. T. Rothrock, *American Naturalist*, volume 1, 1867)

Most ecological interactions between species are influenced by several co-occurring species because organisms live embedded in interaction networks. Accordingly, theoretical and empirical ecological work has expanded from single- or two-species studies to larger community frameworks of food webs and indirect interactions (e.g., Wootton 1994; Polis and Winemiller 1995; Morin 1999). Most experimental work on indirect interactions between three or more species has focused on either negative effects mediated by natural enemies (Charnov and Bonsall 2000) or indirect effects occurring along food chains (Schmitz et al. 2000). However, it is equally possible that neighboring species in a community can influence each other positively (Callaway 1997). For example, species can interact positively by providing services or nesting opportunities in return for food or protection against herbivores and predators or by other ways of trading resources (Ollerton 2006).

Pollination biology has provided countless examples of such direct trade in mutualistic interactions (Proctor et al. 1996). However, little is known about the effect of indirect interactions between plants in pollination biology. There are very few studies addressing this specifically; good examples include how neighboring flowering plants affect each other's reproduction negatively (e.g., Waser 1978; Brown and Mitchell 2001; Chittka and Schurkens 2001) or positively (Moeller 2004; Ghazoul 2006) through the specific behavior of shared pollinators. Landscape- or habitat-level differences in pollinator-mediated plant reproductive success have also been investigated in relation to availability of nesting sites, habitat corridors, or habitat

* Corresponding author; e-mail: dhansen@uwinst.unizh.ch.

† E-mail: heine@kiesbuy.com.

‡ E-mail: carl.jones@intnet.mu.

§ E-mail: cbm@uwinst.unizh.ch.

islands for pollinators (Steffan-Dewenter et al. 2001; Townsend and Levey 2005; Artz and Waddington 2006).

Indirect interactions can be classified into those that mediate changes in population densities of the different species involved in trophic consumer-resource interactions (density-mediated or trophic effects; Abrams 1995) and those caused by changes in behavior or other traits between species that are not necessarily trophically dependent (trait-mediated indirect interactions; Abrams 1995). In recent reviews, Werner and Peacor (2003) and van Veen et al. (2006) pointed out the ubiquity and importance of trait-mediated indirect interactions in many different ecosystems, and Schmitz et al. (2004) reviewed the important role of trait-mediated indirect interactions along trophic chains. However, in all reviews, the emphases are again on negative indirect interactions.

In our study, we investigated the role of trait-mediated indirect interactions on a very small spatial scale in a mutualistic pollination system. Specifically, we studied the pollination biology of the endemic plant *Trochetia blackburniana* (Malvaceae) in Mauritius, where preliminary observations had shown that this species was often visited by the endemic blue-tailed day gecko *Phelsuma cepediana* (Gekkonidae). In the study area, dense patches of palmlike *Pandanus* plants (Pandanaceae) are favored microhabitats of this gecko. In our system, then, the trait that is being modified is the behavioral response of *Phelsuma* geckos to the presence of *Pandanus* patches and how the resulting higher density of geckos in and near these patches may confer an indirect positive effect to any gecko-pollinated plants in the vicinity of *Pandanus* patches. That is, our specific hypothesis is that *T. blackburniana* plants growing close to *Pandanus* patches will have a higher gecko visitation rate than plants growing farther away from *Pandanus* patches and that this will result in a correlated higher reproductive success for *T. blackburniana* plants near *Pandanus* patches.

Material and Methods

Study Site and Study Species

Our study site was Le Pétrin, an upland heath on the island of Mauritius covering some 25 ha in the Black River Gorges National Park, at 670 m above sea level. Le Pétrin is one of the last remnants of a once much more widespread upland heath and marsh that was cleared as late as 1970–1980 and replaced with exotic pine plantations. The upland heath is characterized by poor soils, leading to a low shrubby vegetation of 1–2 m in height, with stunted trees of no more than 5 m in height, interspersed with patches of *Pandanus* plants (Vaughan and Wiehe 1937). Our *Trochetia blackburniana* study plants were all

located within a central area of Le Pétrin, covering approximately 15 ha.

Trochetia blackburniana belongs, together with five other species, to a genus endemic to Mauritius and La Réunion. Four out of the five Mauritian *Trochetia* species are endangered and occur in only one or a few small relict populations. Only *T. blackburniana* is still relatively widely distributed, albeit in many small, localized populations. Much of its former habitat has been lost, and most of the surviving populations are found in habitats that are rapidly being degraded by invasive species. *Trochetia blackburniana* is a bush, some 1–4 m in height, commonly with a very open, candelabra-like growth form (fig. 1a) and large, bell-shaped (3 cm × 2.5 cm) flowers (fig. 1d–1h). Flowers are protandrous, and the stamens are fused into a tube, with the anthers located at the top. When entering the female phase, the staminal tube falls off, and the style and stigma are revealed underneath (figs. A1, A2 in the online edition of the *American Naturalist*). Because of this dichogamy, levels of autogamy are very low, with only 6.4% fruit set (D. M. Hansen and C. B. Müller, unpublished data), and *T. blackburniana* thus depends almost obligatorily on pollinators to set fruit. The five carpels in each fruit contain a total of 15–30 ovules. *Trochetia blackburniana* has a high level of self-compatibility. Almost all hand-pollinated flowers set fruit, and the resulting seed set is high: selfed flowers have 77% seed set, and outcrossed flowers have 87%–90% seed set (D. M. Hansen and C. B. Müller, unpublished data). Individual flowers last 4–7 days and produce a lot of clear to yellow-orange nectar (fig. A3 in the online edition of the *American Naturalist*). Nectar standing crop at noon is 5–83 μL (mean \pm SD = $30.9 \pm 17.6 \mu\text{L}$), with 10%–41% sugar content, dominated by hexose sugars (D. M. Hansen and C. B. Müller, unpublished data). An endemic specialist nectarivorous bird, the olive white-eye *Zosterops chloronothos*, has previously been documented as a main flower visitor of *T. blackburniana* (Cheke 1987; Staub 1988; Hansen et al. 2002). However, this bird is critically endangered and still declining (Nichols et al. 2004) and is now locally extinct in most areas where *T. blackburniana* is found, including Le Pétrin. Therefore, we were unable to assess its current importance in the pollination of *T. blackburniana*.

Pandanus is the main genus, in terms of distribution and species number, in the Pandanaceae, a large family of trees, shrubs, and climbers that occurs throughout the Old World tropics and subtropics (Cox 1990). For its size, Mauritius harbors a remarkably large number of endemic *Pandanus* species. Before the destructive human impacts, *Pandanus* patches, called *Pandanetums*, were an important structuring feature of the upland plant communities (Vaughan and Wiehe 1937, 1953). However, five out of the 19 endemic species are now extinct, and most of the

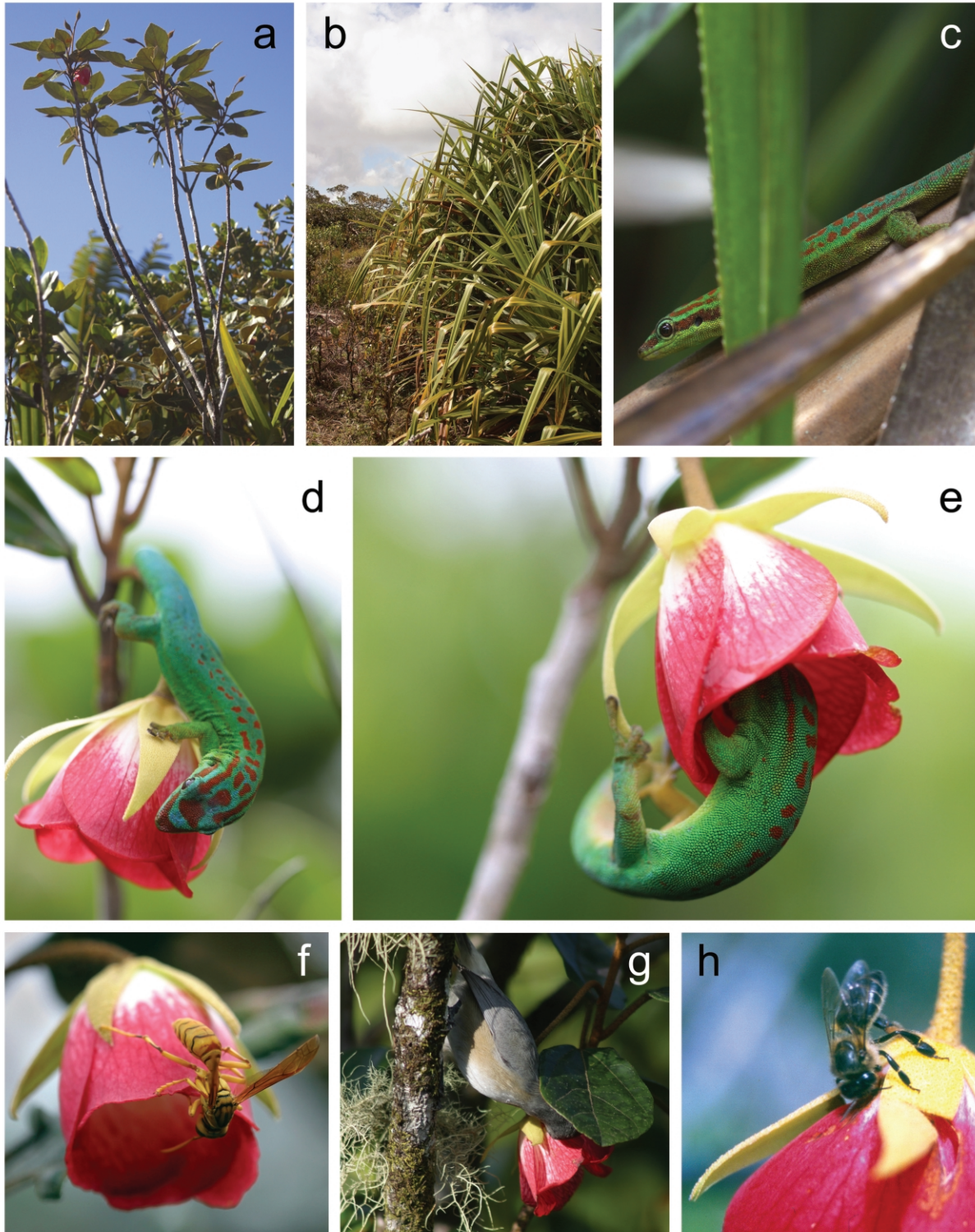


Figure 1: Study site and study species. *a*, Typical *Trochetia blackburniana* plant at Le Pétrin. *b*, Edge of a *Pandanus* patch, showing the difference between the relative openness of the heath at Le Pétrin and the dense thicket formed by *Pandanus* plants. *c*, Male *Phelsuma cepediana* gecko moving through the dense maze of spiky *Pandanus* leaves. *d*, Male *P. cepediana* approaching a flower of *T. blackburniana*. *e*, Nectar-feeding male *P. cepediana* in a *T. blackburniana* flower. *f*, Introduced wasp *Polistes hebraeus*. *g*, Endemic Mauritius gray white-eye *Zosterops mauritianus* nectar robbing by piercing a hole at the base of a flower. *h*, Introduced honeybee *Apis mellifera* stealing nectar through a hole pierced by *Z. mauritianus*. Photo *b* by C. N. Kaiser; all other photos by D. M. Hansen.

remaining species are critically endangered through destruction or altering of their habitat (Bossier and Guého 2003). The *Pandanus* patches in our study site were mainly composed of one or several of the following species: *Pandanus barklyi*, *Pandanus palustris*, *Pandanus rigidifolius*, and *Pandanus wiehi*. Because *Pandanus* patches are very variable in size and species composition but otherwise very similar in vegetation structure and leaf morphology, we here define a *Pandanus* patch as a dense stand of one or several *Pandanus* species covering a minimal area of 5 m \times 5 m (fig. 1b). All *Pandanus* species are dioecious and wind pollinated, and their large (2–10 cm), mostly colorful fruitlets are often dispersed by animals (Cox 1990).

Phelsuma cepediana is an endemic diurnal gecko that is common in the remaining upland native plant communities of Mauritius. It is a medium-sized gecko (males = 116–136 mm; females = 77–119 mm total length) with a broad diet of insects, nectar, and fruits (Vinson and Vinson 1969; D. M. Hansen, personal observation). At Le Pétrin and elsewhere in Mauritius, we have observed *P. cepediana* visiting many native and endemic plant species for nectar, including *T. blackburniana* (Hansen et al. 2006; fig. 1d, 1e). We have no formal density measures of *P. cepediana* in different microhabitats because small arboreal lizards are very difficult to census, but during our work in Le Pétrin, we always saw many more *P. cepediana* in *Pandanus* patches than in any other microhabitat (fig. 1c). Even a small patch of *Pandanus* plants forms a dense, impenetrable matrix of spiky, serrated leaves. Hiding in such patches may protect *P. cepediana* from sudden attacks by its main predator, the Mauritian kestrel *Falco punctatus*, a bird feeding almost exclusively on *Phelsuma* geckos (Groombridge et al. 2001), and from other endemic Mauritian birds that prey on *Phelsuma* geckos (Cheke 1987). Furthermore, *Pandanus* patches provide good egg-laying sites, and the dense shade they offer may be important for *Phelsuma* thermoregulation.

Pollinator Observations and Fruit Set

First, it was necessary to establish whether *Phelsuma* visitation rates to *T. blackburniana* plants were indeed affected by proximity to *Pandanus* patches and to investigate whether any other animals visited the flowers. Second, we recorded fruit set for the observed *T. blackburniana* plants. Between March and July 2003, we spent 37 observation periods (mean \pm SE = 62.4 \pm 2.4 min/period) in Pétrin observing flowering *T. blackburniana* plants. Another flower-visiting endemic Mauritian gecko, *Phelsuma ornata*, in a habitat similar to our study site, was shown to move distances of 0–15 m on average within a 24-h period (Nyhagen et al. 2001). Therefore, we chose to observe *T. blackburniana* plants within the following two distance cate-

gories: near (<10 m) or away from (>20 m) *Pandanus* patches. The mean number of flowers observed per period was 12.0 \pm 1.36 near *Pandanus* patches and 15.0 \pm 1.33 away from *Pandanus* patches. In total, 17 observation periods were spent away from and 20 were near *Pandanus* patches. Many hours of preliminary observations, both close-up and farther away from the plants, revealed no flower visitors smaller than introduced honeybees but did show that birds and geckos in particular were shy when human observers were too close (D. M. Hansen, personal observation). Hence, observations were done from a distance of at least 8 m using 10 \times 32-mm binoculars. All observed flower visitors were identified and recorded. To investigate levels of fruit set in relation to animal visitation, we recorded the total number of flowers per plant of all 96 observed plants for the entire flowering season (March–September) and the resulting number of fruits in October 2003, again noting whether the *Trochetia* plants grew near (n = 27 plants) or away from (n = 69 plants) *Pandanus* patches.

Gecko Exclusion Experiment

To test the hypothesis that proximity of *Pandanus* patches leads to higher gecko visitation rates and a subsequently higher fruit set in *T. blackburniana* plants, we performed an exclusion experiment from June to August 2004. We selected 45 experimental plants, to which control plants or parts of plants were assigned. This resulted in a total of 45 pairs that were each assigned a pair ID and used as a random factor in the statistical analysis. Of the 45 experimental plants, 19 grew near (<10 m) and 26 grew away from (>20 m) *Pandanus* patches. To be able to control for possible effects of plant size on reproductive success, we measured the height of all experimental and additional control plants to the nearest centimeter. On the experimental plants of each pair, geckos were excluded from one to three major branches with two to 25 buds (mean \pm SE = 7.0 \pm 0.59). Exclusion was done by wrapping 30–40 cm of a branch with brown tape and coating this tape with silicon-based car grease. The greased branches and plants were isolated from surrounding vegetation by at least 50 cm because we had observed *P. cepediana* jumping a maximum of 20–30 cm horizontally. Excluded buds on each experimental plant were paired with a similar number of control buds (mean \pm SE = 7.2 \pm 0.68) on nonexcluded branches of the same plant or adjacent plants (within 5 m) of similar size (total additional control plants n = 19; nine near and 10 away). The 19 experimental plants that grew near *Pandanus* patches occurred in five distinct groups, each of which grew within separate clusters of *Pandanus* patches at least 150 m apart (two to seven experimental *T. blackburniana* plants and between five and

eight *Pandanus* patches per cluster). The 26 experimental plants that grew away from *Pandanus* patches were selected in five separate groups covering an area similar to the five clusters of *Pandanus* patches. These 10 groups were assigned a cluster ID that was used as a random factor in the statistical analysis.

After 5–7 weeks, in August 2004, developing fruits were counted and harvested. Because of previously observed high levels of fruit and seed predation by introduced rats and lepidopteran larvae throughout the *T. blackburniana* population in Pétrin (D. M. Hansen, personal observation), we harvested unripe fruits. It is easy to discern developing fruits because the previously flexible peduncle goes rigid and the fruit orients itself upward within a week of fertilization. In contrast, a flower that is not fertilized will rapidly wilt and fall off shortly after anthesis. The unripe fruits were cut open with a scalpel to score the number of developing seeds and the total number of ovules. Only fruits where we could clearly discern between small, unfertilized ovules and larger, developing seeds were included in the seed set analysis.

Statistical Analyses

Measured variables are all presented as means \pm SE. Visitation rates to *T. blackburniana* in relation to proximity of *Pandanus* patches were analyzed by ANOVA after a $(x + 1)^{-2}$ transformation to obtain normal distribution of residuals. Fruit set data from the first season were analyzed with a generalized linear model using a quasi-binomial error structure, with proximity to *Pandanus* as an explanatory variable. For the analysis of fruit set in the second experimental season, because of the overall unbalanced design and many zero values and to account for the spatial structure of clusters, we fitted a generalized linear mixed-effects model (GLMM in GenStat 9.1 with a fixed fitting; Breslow and Clayton 1993) using a binomial error structure. Proximity to *Pandanus* patches and exclusion treatment versus control plants were fixed effects; pair ID nested in cluster ID were random effects. We obtained complete seed set data for only a very small subset of pairs. Hence, the analysis of seed set was done by comparing average seed set at the pair level with an ANOVA, with proximity to *Pandanus* patches and exclusion treatment versus control plants as explanatory variables. Apart from the GLMM, all analyses were done using R, version 2.3.1 (R Development Core Team 2006).

Results

Pollinator Observations and Fruit Set

At *Trochetia blackburniana* flowers, we observed *Phelsuma cepediana* (fig. 1d, 1e), the introduced wasp *Polistes he-*

braeus (fig. 1f), the endemic bird Mauritius gray white-eye *Zosterops mauritianus*, and the introduced honeybee *Apis mellifera*, all of which were foraging for nectar. The latter two almost exclusively foraged for nectar through holes pierced in the corolla and are therefore unlikely to be efficient pollen vectors (fig. 1g, 1h). When *P. cepediana* entered the flowers, it did so either from above, climbing down the peduncle, or by reaching out to grab and enter the flower while still clinging onto the branch (fig. A1b, A1c; fig. A4 in the online edition of the *American Naturalist*). In doing so, pollen was deposited either just behind the head or on the gecko's throat and chest. There was a significant difference in visitation rate between visitor species ($F = 34.459$, $df = 1, 140$, $P < .001$) and a significant effect of proximity to *Pandanus* patches ($F = 22.271$, $df = 1, 140$, $P < .001$). Most important, there was a significant interaction between flower visitor species and distance ($F = 16.197$, $df = 3, 140$, $P < .001$), which resulted from the much higher mean visitation rate of *P. cepediana* when *T. blackburniana* grew near *Pandanus* patches compared to that for plants farther away (fig. 2a). The resulting fruit set of observed *T. blackburniana* plants in September 2003 was significantly increased when plants grew near *Pandanus* patches ($F = 29.004$, $df = 1, 94$, $P < .001$; fig. 2b).

Gecko Exclusion Experiment

Gecko exclusion had significant effects on the fruit set of *T. blackburniana* (fig. 3); there was a highly significant negative effect of gecko exclusion on the fruit set of *T. blackburniana* ($df = 1$, Wald/ $df = 42.88$, $P < .001$) and a significant difference in fruit set near and away from *Pandanus* patches ($df = 1$, Wald/ $df = 9.07$, $P = .003$). However, there was no significant interaction between proximity and gecko exclusion ($df = 1$, Wald/ $df = 0.32$, $P = .574$), meaning that fruit set on excluded branches was decreased both near and away from *Pandanus* patches.

This is probably due to the fact that the exclusion experiment was carried out in the peak flowering time of *T. blackburniana*, which is also a time when *P. cepediana* is very active. Thus, even away from *Pandanus* patches, we get a significant effect on fruit set by excluding geckos. There was no difference in seed set of fruits developing from excluded and control flowers or from fruits near and away from *Pandanus* patches ($F = 0.2806$, $df = 2, 33$, $P = .757$). Overall average seed set was $43.8\% \pm 0.04\%$. Compared with the 70%–80% seed set from hand pollination, it seems that *T. blackburniana* is pollen limited—even in control plants that grow near *Pandanus* patches.

There was no significant difference in mean height of experimental and control plants near and away from

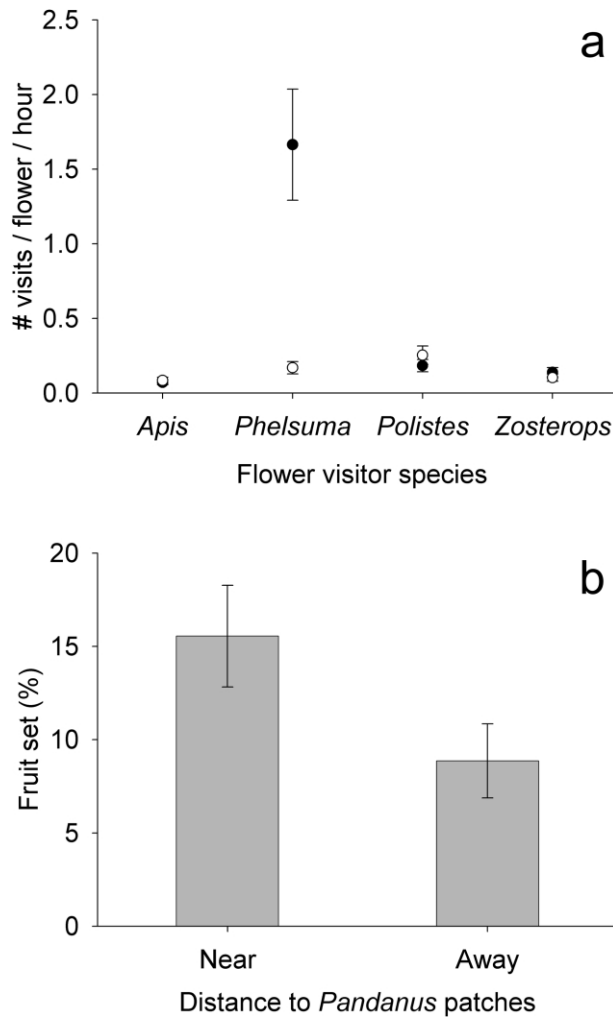


Figure 2: a, Visitation rates (mean \pm 1 SE) of all flower visitors at *Trochetia blackburniana* flowers that grow near (filled circles) and away from (open circles) *Pandanus* patches. The visitation rate of only the gecko *Phelsuma cepediana* is dramatically increased near *Pandanus* patches. b, Subsequent fruit set (mean \pm 1 SE) is significantly higher for *T. blackburniana* plants growing near *Pandanus* patches compared to that of plants growing farther away.

Pandanus patches (near = 159.0 ± 8.9 cm; away = 155.2 ± 10.7 cm; $t = 0.27$, $P = .788$).

Discussion

We found a strong positive correlation between proximity of *Trochetia blackburniana* plants to *Pandanus* patches and *Phelsuma* visitation rates, which was mirrored in the resulting fruit set of *T. blackburniana*. The gecko exclusion experiment confirmed this pattern, providing evidence of a positive trait-mediated indirect interaction between two unrelated plant species via a pollinator of only one of them.

Thus, plant community structure combined with pollinator behavior on a very small spatial scale are strong determinants for the reproductive success of *T. blackburniana*. It should be noted that the overall lower fruit set illustrated in figure 2, compared to that in figure 3, is due to the former being based on the whole flowering season, from March to September, while the latter is based on 5 weeks in the peak flowering season, when the geckos are most active as flower visitors. Hence, the pattern of high fruit set near *Pandanus* is much clearer when based on flowers that are open during the peak flowering season of *T. blackburniana*.

Of course, there could be other explanations for the observed difference in reproductive success between *T. blackburniana* plants close to and away from *Pandanus* patches. One possibility would be corresponding differences in soil nutrients. However, in another study at Le Pétrin (C. N. Kaiser and C. B. Müller, unpublished data), an analysis of soil samples from six transects of 100 m, spaced 60–75 m apart, revealed no significant differences in nutrient levels between transects. Several of our observed plants ($n \approx 50$) and experimental/control plants ($n = 22$), as well as many of the *Pandanus* patches (together forming two of the five clusters used in our analysis), grew within this area. Furthermore, if there would have been differences in soil nutrients between near and away that affected growth and vigor of *T. blackburniana* plants, we would not have expected to find a uniform plant size distribution across the population at Le Pétrin, nor would we have expected to find such a strong effect

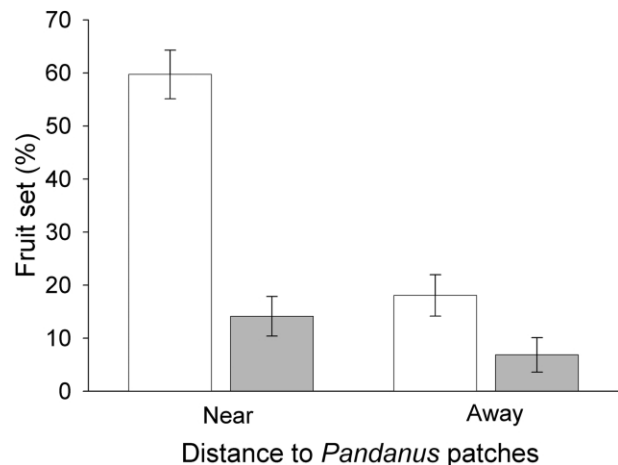


Figure 3: Fruit set (proportion of flowers developing into fruits; mean \pm 1 SE) of experimental *Trochetia blackburniana* plants is correlated to proximity of *Pandanus* patches. Open bars refer to the fruit set of control flowers and shaded bars to the fruit set of flowers from which geckos were excluded.

on *T. blackburniana* reproductive success by the simple experiment of excluding nonflying pollinators (i.e., geckos) near *Pandanus* patches.

Our study is a good example of how trait-mediated indirect interactions can not only structure predator-prey or competitive interactions but also play a significant role in mutualistic interactions. Other studies have also shown pollinator-mediated positive indirect interactions between plant species on a small spatial scale (Thomson 1978; Dafni 1983; Laverty 1992; Johnson et al. 2003; Moeller 2004; Ghazoul 2006), but in all of these cases, the facilitation results from shared pollinators seeking rewards in two or more plant species that were often closely related. In our system, the positive indirect effect between two plant species is mediated by an animal that seeks floral rewards in—and acts as pollinator of—only one of them. Moreover, our results highlight the significance of the community context when considering conservation management of endangered plant species.

Lizard pollination of *T. blackburniana* is an interesting phenomenon in itself because only a few studies so far have identified lizards as important pollinators of plants. Most of the known examples of lizard pollination occur on islands where a low diversity and a low abundance of invertebrates may force otherwise mostly insectivorous lizards to expand their diet to include fruit and nectar (Olesen and Valido 2003). Insular lizard species also often occur in extremely high densities compared to congeners in mainland habitats (Rodda and Dean-Bradley 2002), which in turn is likely to increase their relative importance in insular food webs. Another Mauritian gecko, *Phelsuma ornata*, has previously been shown to be an efficient pollen vector for several coastal plants (Nyhagen et al. 2001). Furthermore, Olesen et al. (2002) found *P. ornata* to be the most important endemic species in a pollination network on the Mauritian offshore islet of Île aux Aigrettes. An interesting point, which we were sadly unable to address in our study, is the potential role of colored nectar in *Phelsuma-Trochetia* interactions. A recent study by Hansen et al. (2006) demonstrated how the mysterious Mauritian colored nectar (Olesen et al. 1998) acts as a visual floral signal for *Phelsuma* geckos. Because the nectar color of *T. blackburniana* varies from clear to yellow-orange, interplant or seasonal differences in nectar color may play a structuring role in our system as well.

There is evidence that proximity to *Pandanus* patches affects gecko visitation rate and reproductive success in at least two other endemic Mauritian plants, *Labourdonnaisia callophylloides* (Sapotaceae; C. N. Kaiser and C. B. Müller, unpublished data) and the critically endangered *Rousetta simplex* (Rousseaceae; D. M. Hansen and C. B. Müller, unpublished data). Hence, our results lead to valuable management insights for ongoing conservation efforts to

save the highly endangered flora of Mauritius. Additionally, large numbers of *Phelsuma* geckos in *Pandanus* plants have also been noted in the neighboring island of La Réunion (L. Gigord, personal communication) and in Madagascar (M. Callmander, personal communication). Both these islands are also biodiversity hotspots with high levels of endemism and many endangered plant taxa, so our results may be applicable there as well.

Pandanus plants and thickets may be important for species-level and functional biodiversity in many habitats in the paleotropics, where they are being used by a wide variety of animals as nesting places, homes, or hideouts (e.g., birds and small marsupials in Australia [Braithwaite and Lonsdale 1987; Rowley and Russell 1993] and freshwater crabs in Taiwan [Schubart et al. 2003] and Madagascar [Cumberlidge et al. 2002]). Lehtinen (2002) documented a total of 41 species of reptiles and amphibians in Madagascar, including five *Phelsuma* species, that were frequently or obligatorily associated with *Pandanus* plants. For some of the above species, loss of *Pandanus* patches resulted in population declines (Braithwaite and Lonsdale 1987; Schubart et al. 2003), again demonstrating the importance of *Pandanus* patches for conservation management. Together with our results, these studies demonstrate that the habitat heterogeneity caused by dense *Pandanus* thickets can promote complex community interactions for a wide range of species across much of the paleotropics.

To conclude, trait-mediated indirect interactions have received much recent attention in community ecological studies of predator-prey and competitive interactions reviewed by Schmitz et al. (2004) and Werner and Peacor (2003). Here, we demonstrate an equal importance of trait-mediated indirect interactions in structuring a mutualistic pollination interaction. Moreover, given that lizard pollination is widespread on many islands, and given that islands harbor much of the world's endangered flora and herpetofauna, our results are relevant for the conservation of many endangered island plants and lizards. Our findings emphasize the importance of considering plant-animal interactions such as pollination at relatively small spatial scales in both basic ecological studies and applied conservation management.

Acknowledgments

We thank the National Parks and Conservation Service of Mauritius and the Mauritian Wildlife Foundation for their support; L. Reiter for help in the field; C. Kaiser for use of a photo; R. Callaway, E. Conti, T. Good, A. Hector, C. Kaiser, J. Krauss, R. Mitchell, L. Turnbull, and two reviewers for constructive comments; and S. Härrä, A. Hector, and C. Philipson for help with the statistical analyses.

The Swiss National Science Foundation (grant 631-065950 to C.B.M.) financed the study.

Literature Cited

- Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* 146:112–134.
- Artz, D. R., and K. D. Waddington. 2006. The effects of neighbouring tree islands on pollinator density and diversity, and on pollination of a wet prairie species, *Asclepias lanceolata* (Apocynaceae). *Journal of Ecology* 94:597–608.
- Bosser, J., and J. Guého. 2003. Pandanacées. Flore des Mascareignes. Vol. 190. Mauritius Sugar Industry Research Institute, Reduit.
- Braithwaite, C. J. R., and W. M. Lonsdale. 1987. The rarity of *Sminthopsis virginiae* (Marsupialia: Dasyuridae) in relation to natural and unnatural habitats. *Conservation Biology* 1:341–344.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. *Journal of the American Statistical Association* 88:9–25.
- Brown, B. J., and R. J. Mitchell. 2001. Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* (Berlin) 129:43–49.
- Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* (Berlin) 112:143–149.
- Chaneton, E. J., and M. B. Bonsall. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* 88:380–394.
- Cheke, A. S. 1987. The ecology of the smaller land birds of Mauritius. Pages 151–207 in A. W. Diamond, ed. *Studies of Mascarene Island birds*. Cambridge University Press, Cambridge.
- Chittka, L., and S. Schurkens. 2001. Successful invasion of a floral market. *Nature* 411:653.
- Cox, P. A. 1990. Pollination and the evolution of breeding systems in Pandanaceae. *Annals of the Missouri Botanical Garden* 77:816–840.
- Cumberlidge, N., C. B. Boyko, and A. W. Harvey. 2002. A new genus and species of freshwater crab (Crustacea, Decapoda, Potamoidea) from northern Madagascar, and a second new species associated with *Pandanus* leaf axils. *Journal of Natural History* 36:65–77.
- Dafni, A. 1983. Pollination of *Orchis caspia*: a nectarless plant which deceives the pollinators of nectariferous species from other plant families. *Journal of Ecology* 71:467–474.
- Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. *Journal of Ecology* 94:295–304.
- Groombridge, J. J., M. W. Bruford, C. G. Jones, and R. A. Nichols. 2001. Evaluating the severity of the population bottleneck in the Mauritius kestrel *Falco punctatus* from ringing records using MCMC estimation. *Journal of Animal Ecology* 70:401–409.
- Hansen, D. M., J. M. Olesen, and C. G. Jones. 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? *Journal of Biogeography* 29:721–734.
- Hansen, D. M., K. Beer, and C. B. Müller. 2006. Mauritian coloured nectar no longer a mystery: a visual signal for lizard pollinators. *Biology Letters* 2:165–168.
- Johnson, S. D., C. I. Peter, L. A. Nilsson, and J. Agren. 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84:2919–2927.
- Laverty, T. M. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* (Berlin) 89:502–508.
- Lehtinen, R. M. 2002. The use of screw pines (*Pandanus* spp.) by amphibians and reptiles in Madagascar. *Herpetological Bulletin* 82:20–25.
- Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301.
- Morin, P. 1999. *Community ecology*. Blackwell Science, Oxford.
- Nichols, R., L. Woolaver, and C. Jones. 2004. Continued decline and conservation needs of the endangered Mauritius olive white-eye *Zosterops chloronothos*. *Oryx* 38:291–296.
- Nyhagen, D. F., C. Kragelund, J. M. Olesen, and C. G. Jones. 2001. Insular interactions between lizards and flowers: flower visitation by an endemic Mauritian gecko. *Journal of Tropical Ecology* 17:755–761.
- Olesen, J. M., and A. Valido. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology & Evolution* 18:177–181.
- Olesen, J. M., N. Rønsted, U. Tolderlund, C. Cornett, P. Mølgaard, J. Madsen, C. G. Jones, and C. E. Olsen. 1998. Mauritian red nectar remains a mystery. *Nature* 393:529.
- Olesen, J. M., L. I. Eskildsen, and S. Venkatasamy. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distribution* 8:181–192.
- Ollerton, J. 2006. “Biological barter”: patterns of specialization compared across different mutualisms. Pages 411–435 in N. M. Waser and J. Ollerton, eds. *Plant pollinator interactions: from specialization to generalization*. University of Chicago Press, Chicago.
- Polis, G. A., and K. Winemiller. 1995. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York.
- Proctor, M., P. Yeo, and A. Lack. 1996. *The natural history of pollination*. Timber, Portland.
- R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rodda, G. H., and K. Dean-Bradley. 2002. Excess density compensation of island herpetofaunal assemblages. *Journal of Biogeography* 29:623–632.
- Rothrock, J. T. 1867. The fertilization of flowering plants. *American Naturalist* 1:64–72.
- Rowley, I., and E. Russell. 1993. The purple-crowned fairy-wren *Malurus coronatus*. 2. Breeding biology, social-organization, demography and management. *Emu* 93:235–250.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155:141–153.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.
- Schubart, C. D., H. C. Liu, and J. A. Cuesta. 2003. A new genus and new species of tree-climbing crab (Crustacea: Brachyura: Sesarmidae) from Taiwan with notes on its ecology, larval morphology and phylogeny. *Raffles Bulletin of Zoology* 51:49–59.
- Staub, F. 1988. Evolutionary trends in some Mauritian phanerogams in relation to their pollinators. *Proceedings of the Royal Society of Arts and Sciences of Mauritius* 5:7–78.
- Steffan-Dewenter, I., U. Munzenberg, and T. Tscharnkte. 2001. Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society B: Biological Sciences* 268:1685–1690.

- Thomson, J. D. 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. *American Midland Naturalist* 100:431–440.
- Townsend, P. A., and D. J. Levey. 2005. An experimental test of whether habitat corridors affect pollen transfer. *Ecology* 86:466–475.
- van Veen, F. J. F., R. J. Morris, and H. C. J. Godfray. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51: 187–208.
- Vaughan, R. E., and P. O. Wiehe. 1937. Studies on the vegetation of Mauritius. I. A preliminary survey of the plant communities. *Journal of Ecology* 25:289–343.
- . 1953. The genus *Pandanus* in the Mascarene Islands. *Botanical Journal of the Linnean Society* 55:1–33.
- Vinson, J., and J.-M. Vinson. 1969. The saurian fauna of the Mascarene Islands. *Mauritius Institute Bulletin* 6:203–320.
- Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934–944.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.

Natural History Editor: Henry M. Wilbur