Community structure of pollination webs of Mauritian heathland habitats

Christopher N. Kaiser-Bunbury[a,*], Jane Memmott[b], Christine B. Müller[a,1]

[a]*Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*
[b]*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*

Abstract

Pollination webs have recently deepened our understanding of complex ecosystem functions and the susceptibility of biotic networks to anthropogenic disturbances. Extensive mutualistic networks from tropical species-rich communities, however, are extremely scarce. We present fully quantitative pollination webs of two plant–pollinator communities of natural heathland sites, one of which was in the process of being restored, on the oceanic island of Mauritius. The web interaction data cover a full flowering season from September 2003 to March 2004 and include all flowering plant and their pollinator species. Pollination webs at both sites were dominated by a few super-abundant, disproportionately well-connected species, and many rare and specialised species. The webs differed greatly in size, reflecting higher plant and pollinator species richness and abundance at the restored site. About one fifth of plant species at the smaller community received <3 visits. The main pollinators were insects from diverse taxonomic groups, while the few vertebrate pollinator species were abundant and highly linked. The difference in plant community composition between sites appeared to strongly affect the associated pollinator community and interactions with native plant species. Low visitation rate to introduced plant species suggested little indirect competition for pollinators with native plant species. Overall, our results indicated that the community structure was highly complex in comparison to temperate heathland communities. We discuss the observed differences in plant linkage and pollinator diversity and abundance between the sites with respect to habitat restoration management and its influence on pollination web structure and complexity. For habitat restoration to be successful in the long term, practitioners should aim to maintain structural diversity to support a species-rich and abundant pollinator assemblage which ensures native plant reproduction.
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Introduction

The majority of flowering plant species rely on interactions with pollinators for reproduction, while flower visitors benefit from these interactions by obtaining food in the form of pollen or nectar. Such mutualistic relationships are rarely mutually exclusive, but flowering plants interact often with a range of pollinator taxa, suggesting that generalisation is

*Corresponding author. Current address: Ecosystem Management, Institute of Terrestrial Ecosystems, Swiss Federal Institute of Technology (ETH) Zurich, Universitaetstrasse 16, 8092 Zurich, Switzerland. Tel.: +41 44 632 89 45; fax: +41 44 632 15 75.
    E-mail address: ch.kaiser@env.ethz.ch (C.N. Kaiser-Bunbury).
    [1]Deceased 7 March 2008.

the dominant feature of most pollination systems (Moldenke, 1975; Waser et al., 1996; but see Johnson and Steiner, 2000, 2003; Blüthgen et al., 2007). Such community-wide patterns in plant–pollinator networks can be explored through the application of a food web approach (Memmott, 1999; Dicks et al., 2002; Olesen and Jordano, 2002), which provides important information on ecosystem stability (Bascompte et al., 2006), the consequences of disturbance (e.g. extinctions; Memmott et al., 2004), the restoration of degraded ecosystems (Hobbs and Norton, 1996; Montalvo et al., 1997) and the role of introduced species in such ecosystems (e.g. Olesen et al., 2002; Morales and Aizen, 2006; Lopezaraiza-Mikel et al., 2007; Aizen et al., 2008; Bartomeus et al., 2008). While food webs traditionally describe predator–prey interactions, they can also be used to study networks of mutualistic interactions, such as pollination, where food is 'traded' for 'services' (Jordano, 1987). Community structure can be characterised by standard food web statistics such as the mean number of links of each interaction partner in a network (linkage; Paine, 1980) and the ratio of observed to possible interactions in a networks (connectance; Martinez, 1992), and visualised in quantitative flower visitation webs (hereafter referred to as pollination webs; cf. Memmott, 1999). Such webs provide complex yet tractable depictions of species richness and evenness (relative abundance), interaction frequency, and ecosystem structure and function.

Despite recent advances in the analysis of pollination webs, most webs describe temperate, arctic or high altitude habitats, largely due to practical constraints. Tropical and subtropical plant–pollinator communities are often extremely species rich, and as a result, constructing networks describing entire assemblages remain a considerable challenge. Consequently, most pollination studies in diverse ecosystems have focused on subsets of communities such as taxonomic groups of pollinators, or phenologically or spatially restricted plant species (e.g. Kanstrup and Olesen, 2000; Kato and Kawakita, 2004). A few comprehensive studies have compiled data on the reproductive biology of most flowering plant species within a tropical or subtropical forest community (Percival, 1974; Kato, 1996, 2000; Momose et al., 1998). However, these studies primarily report qualitative information on species diversity, community composition and flowering phenology. To make use of the more comprehensive community web approach, quantitative data on visitation frequency within well-defined spatial boundaries are required. In this study, we present two fully quantitative pollination webs of entire flowering plant communities on the oceanic island of Mauritius with the aim of investigating the structure and function of tropical plant–pollinator interactions at the community level.

The vast majority of island ecosystems have undergone multiple species extinctions and introductions (e.g. Simberloff, 1986, 1995; Cheke, 1987; Whittaker, 1998). Resident mutualistic associations, such as pollination, are likely to be affected by both the loss of biodiversity and the presence of alien species (Kearns et al., 1998; Ghazoul, 2004; Traveset and Richardson, 2006). Quantitative pollination webs are an ideal tool for understanding the effect of such changes in a community setting. Shifts in interaction frequency or pairwise dependency caused by the arrival of alien species and their consequences may only be fully understood within the wider network of interactions. Pollination webs are starting to be used to explore the impact of introduced species on native mutualistic associations (e.g. Memmott and Waser, 2002; Olesen et al., 2002, Morales and Aizen, 2006), and some used a fully quantitative approach to explore community-wide patterns of plant and animal invasion (Lopezaraiza-Mikel et al., 2007; Aizen et al., 2008).

In Mauritius, only about 2% of the island is covered with native forest, which is itself heavily degraded (J. Mauremootoo, pers. commun.). *In situ* restoration of degraded habitats in Mauritius consists primarily of hand-weeding introduced plant species in plots across a range of different habitat types. Over the past 20 years the weeding has resulted in a gradual regeneration of native flora within restored plots. However, there is little information on whether the pollinator community has also been restored, which is essential if the restoration is to be sustainable. We compiled and compared quantitative pollination webs of two communities, one managed site where restoration is in progress and one heavily degraded, unrestored site. The objective of this study was to characterise the structure of two complete tropical plant–pollinator webs, both of which contain birds and reptile pollinators in addition to insects. Once constructed, we discuss the likely impact of invasive species on network structure and the likely success of the restoration effort on native plant–pollinator interactions.

Materials and methods

Study area and sites

Our study was conducted in the Black River Gorges National Park of Mauritius (20°42′ S, 57°44′ E; 6754 ha; Fig. S1a). The area comprises the last remnants of *Erica/Phylica*-heath plant community, a formerly widespread vegetation type (Strahm, 1994). In Mauritius, it now occurs in only two small area of in total $<0.8\,km^2$ at Plaine Champagne and Pétrin. The habitat is characterised by dwarf forest and a high diversity of woody flowering plant species (Strahm, 1994).

Since 1986, the National Parks and Conservation Service and the non-governmental Mauritian Wildlife Foundation have established 10 Conservation Management Areas (CMAs; total area 44 ha) across all major Mauritian habitat types with the aim of restoring small areas of native flora. Each CMA is fenced, and introduced plants are hand-weeded twice a year. For this study we selected two sites, one restored and one unrestored (henceforth called restored and control sites, respectively) within an area of the same vegetation type. The restored site was Pétrin CMA (6.2 ha), which was first weeded in 1994. Pétrin CMA represents the last sample of an original heath community in Mauritius. The control site was of equal size in an unmanaged area, 0.54 km from the restored site. Both sites are situated on the Pétrin heathland plateau, which is surrounded by pine plantation. We selected the sites based on three criteria; (1) they represented a homogeneous heath community with similar native species diversity and abundance; (2) they are part of a continuous habitat type with the same abiotic conditions (e.g. altitude, aspect, climate, slope, soil, etc.); (3) a distance of 0.54 km between the sites was considered sufficient for their pollinator communities to be mostly independent. The majority of pollinator species were small flies, moths and beetles, which tend to have relatively short foraging distance. Thus, although, we do anticipate that large-distance foragers such as birds and honey bees may occasionally cross the distance between the sites, we believe that their effect is negligible in the community context. The major difference between the plant communities of the restored and control site was the dominance of invasive alien plants at the control site. In parts, strawberry guava *Psidium cattleianum* Sabine (Myrtaceae) and other introduced woody plant species form a continuous, almost monospecific stand with a maximum height of 1–1.5 m depriving the heath community at the control site of the characteristic open structure of the restored site.

At both study sites, we marked out a rectangular study area (330 × 100 m) in which we set up 23 parallel 100 m transects, at intervals of 15 m (Fig. S1b). Transects were divided into five 20 m sections. Sampling was conducted along these transects using a stratified, random approach.

Plant communities

To determine plant species abundance, we surveyed the plant communities in March 2003 by recording every individual of all woody flowering species in the study areas. For *P. cattleianum* plants at the control site, we counted the number of individuals >30 cm in height in 10 random 1-m^2 plots along each transect to obtain an estimate of its abundance.

To produce a quantitative measure of flower density over time, we conducted random flower counts in cubic meters along all 23 transects at each study site. Flower counts were carried out every 2 weeks from September 2003 to March 2004 (see Appendix I). Floral abundance, the mean number of flowers per cubic meter, was calculated for each species by dividing the total number of flowers by the total number of cubes sampled for each site ($n = 3450$).

Pollinator communities

Plant–animal interactions were recorded for all woody plant species that flowered between 15th September 2003 and 15th March 2004. In each 2-week period, we identified species, which were either flowering or were expected to start flowering within the next week. Pollinator observations were conducted on each plant species for four 30-min observation sessions, totalling 2 h of observation per species per 2-weeks. We recorded the identity of all flower visitors that touched the sexual parts of flowers, the number of flowers observed, and the number of visits by each pollinator, and expressed pollinator activity as visitation rate, i.e. the number of visits/flower/h to account for differences in number of observed flowers and observation time. Each visitor approaching a flowering plant was considered a new individual and was thus recorded as a separate visit (see Appendix I for further details).

Pollination webs

Quantitative pollination webs were illustrated as bipartite visitation graphs (Jordano, 1987). In such webs, a line between two vertices represents an interaction between the animal and the plant species. Here, floral abundance data were collected following a stratified sampling scheme along transects, and data on flower visitation were obtained with local observations. To scale the data gathered by the two sampling techniques, we expressed the visitation rate to a plant species as a function of its floral abundance in the study site. We define quantitative visitation rate of *i* on *j* as the total number of visits/flower/h of animal species *i* multiplied by the floral abundance of the plant species *j* visited by *i*. That is, each visit was weighted by the floral abundance of the interaction partner. We used the total number of visits of each animal species as a measure of abundance of a visitor species. The overall pollination webs of the entire season were drawn by programmes written in Mathematica™ (Wolfram Research Inc., Champaign, IL, USA) and the webs for individual insect orders were drawn by a programme written in Microsoft Visual Basics (Microsoft Corporation 2004, Redmond, WA, USA).

Structure of pollination webs

Pollination webs are characterised by a number of parameters. We calculated the following descriptive statistics for each web: number of plant species (P), number of flower visitor species (A), species richness ($R = P + A$), web size (i.e. total number of potential interactions, $S = P \times A$), total number of interactions recorded (I), and the total number of visits recorded (V). We also measured network connectance, $C = 100 \times (I/S)$, which is the fraction of realised interactions in the network (Jordano, 1987). During the season, network composition and size can fluctuate because plants and animals can 'join' or 'leave' the network (Basilio et al., 2006), thus C based on the overall community could overestimate the level of generalisation. Therefore, we calculated the overall connectance based on the mean connectance for each fortnightly period (see Medan et al., 2006). We also determined mean linkage for animal (l_a) and plant species (l_p), i.e. mean number of interactions per species, and the linkage of the most-connected animal and plant species (l_{max}).

In addition to these qualitative descriptors, we computed quantitative equivalent, which account for the magnitude of an interaction (here quantitative visitation rate) and were based on the Shannon measure of entropy H. Following Bersier et al. (2002), we calculated (1) unweighted plant (lu_p) and animal linkage (lu_a), (2) weighted plant (lw_p) and animal linkage (lw_a), and (3) quantitative connectance (C_q), which is weighted by the quantitative visitation rate of each taxon. In addition, quantitative interaction evenness (ε) was calculated as: $\varepsilon = \Sigma(p_i \times \log_2(p_i))/\log_2(N)$, where p_i is the proportion of the total quantitative visitation rate (N) represented by interaction i (see Tylianakis et al., 2007). In contrast to unweighted linkage, weighted linkage gives individual weight to each taxon respective of its total interaction strength and, thus, better captures the functional importance of taxa in the pollination web. Plant and animal linkage are equivalent to the measures of generality and vulnerability in food webs. The descriptors were calculated for the 13 2-week webs covering the entire main flowering season of both sites.

Data analysis

On the community level, floral and plant abundance of native species may be affected by the presence of invasive plants, which in turn can affect pollinator diversity and behaviour. Thus, to describe the relationship of floral and plant abundance between sites, to test whether visitation rate of a plant species is dependent on its abundance, and to test whether plant species linkage is related to the total number of visits received we used linear mixed effects models. The fixed effect 'Site' was entered first in the model to minimise potential site effects before calculating other main effects, and to account for dependences within plant species, plant identity was included in the model as a random effect. Floral and plant abundance and quantitative visitation rate were ln-transformed to reach normality. All analyses were conducted with the statistical package R 2.1.1 (R Development Core Team, 2005; libraries used: MASS, nlme)

Results

Plants

Overall, 105 flowering plant species were recorded in the plant survey, of which 87 species (92.6% of all individuals) flowered between August 2003 and March 2004 (Appendix II). The remaining 18 species flowered during the winter months from April to August, two of which (*Philippia brachyphylla* and *Phylica nitida*) accounted for 78% of all winter-flowering individuals. The restored site contained 74 flowering plant species and the control site 64 species, and 51 plant species (95.6% of all individuals) occurred at both sites. Thirty-three of the flowering species (37.9%) were either endangered or critically endangered following the IUCN Red List criteria. Zero plant species at the restored site and eight plant species at the control site were introduced. The introduced plant species accounted for 15.4% of the total floral abundance in this community, but only 7.5% of all flower visits were observed on these species. Of the eight introduced plant species at the control site only five were visited by pollinators. All introduced species produced abundant fruits despite their relatively low visitation rate.

Both sites were dominated by a few common plant species (Fig. 1, S2–S6; Appendix II). At the restored site, the three most abundant flowering species accounted for 30% of all plant individuals while introduced plants accounted for 82.8% of all plant individuals at the control site, but only for 9.5% of all species (Fig. 2). The abundance of plant species that occurred at both sites was significantly higher in the restored compared with the unrestored site (paired $t = 3.48$, $p = 0.001$, $df = 50$). Floral abundance was dependent on the length of the flowering period of the given plant species ($F_{1,45} = 12.1$, $p < 0.0001$) and on plant species abundance ($F_{1,45} = 33.6$, $p < 0.0001$), both traits which are likely to be affected by increased competition for space and resources with invasive plants. Plant abundance of species that occurred at both sites was positively related to visitation rate ($F_{1,48} = 4.95$, $p = 0.031$). Similarly, there was a positive relationship between
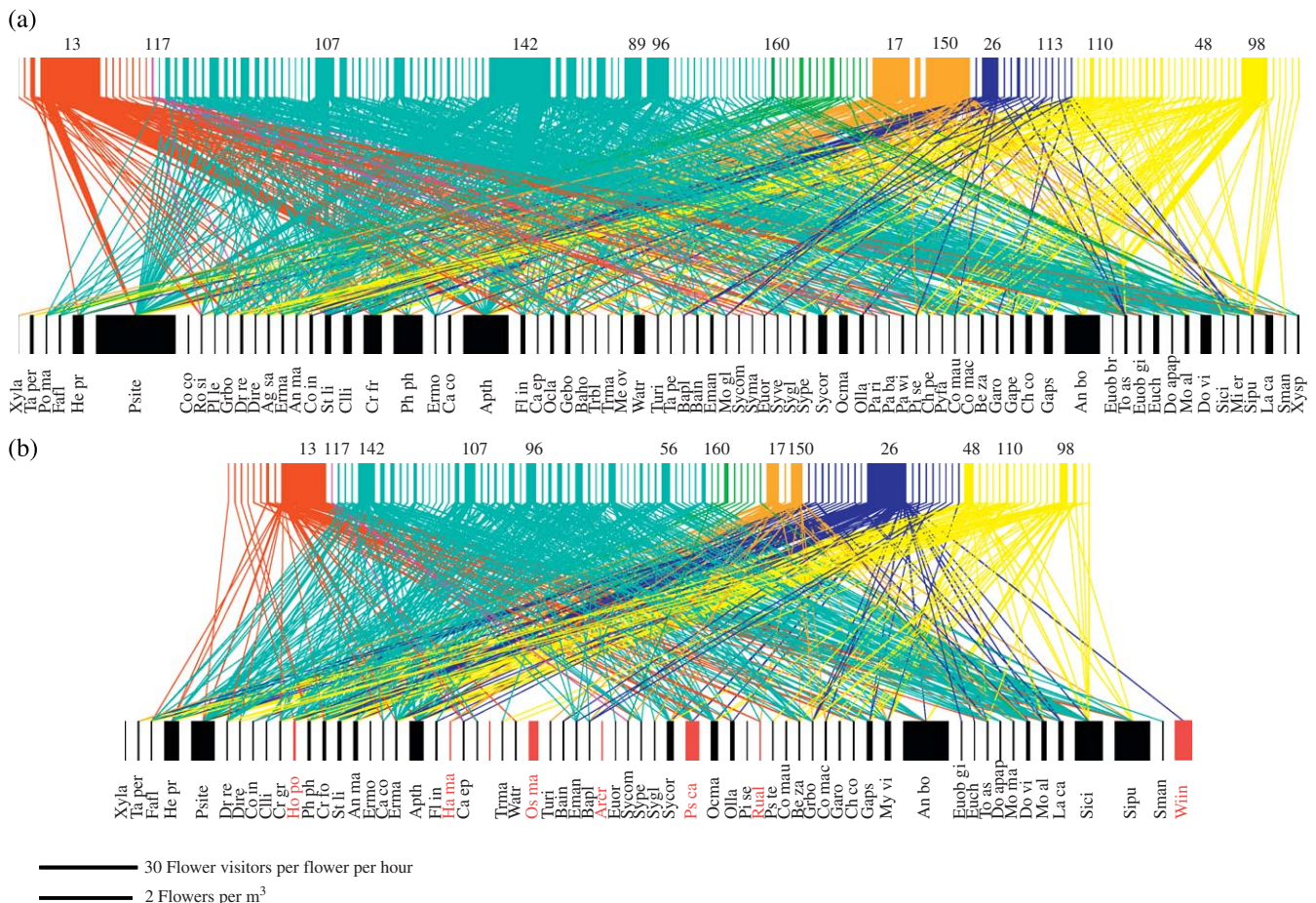
Fig. 1. Quantitative pollination webs of plant–pollinator communities at (a) the restored and (b) the control site. Visitor species are shown as rectangles at the top and plant species are shown at the bottom (red rectangles depict introduced plant species). The width of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantitative visitation rate between an interacting pair of species. Webs are drawn to the same scale. Full names to plant species abbreviations are presented in Appendix II. Animal species codes are only given for a selection of abundant pollinators referred to in the text. For all pollinator species codes see Appendix III. Red: Hymenoptera, pink: Gekkonidae, light blue: Diptera, dark green: Aves, light green: Hemiptera, orange: Formicidae, dark blue: Coleoptera, and yellow: Lepidoptera. 13. *Apis mellifera*, 17. *Brachymyrmex* sp, 26. *Chaetocnema* sp, 48. *Dysauxes florida*, 56. *Fannia pusio*, 89. *Melanostoma annulipes*, 96. *Musca domestica*, 98. *Nacoleia* sp 1, 107. *Pachycerina crinicornis*, 110. *Panara naso*, 113. *Pelecophora intemipta*, 117. *Phelsuma cepediana*, 142. *Stomorhina lunata*, 150. *Technomyrmex albipes*, 160. *Zosterops mauritianus*.

plant abundance and linkage (restored: $R^2 = 0.14$, $F_{1,72} = 12.09$, $p = 0.001$; control: $R^2 = 0.17$, $F_{1,62} = 12.90$, $p = 0.001$).

The majority of flowering species produced open (23.0%), cup-shaped (33.3%) or brush (18.4%) flowers, which were easily accessible to a wide range of flower visitors. The dominating petal colours were white (36.8%), cream (27.6%), and pale pink (19.5%). The main exceptions were *Trochetia blackburniana* Bojer (Malvaceae; red flowers), *Syzygium mauritianum* Guého & Scott (Myrtaceae; red) and *Roussea simplex* Sm. (Rousseaceae, yellow) with showy, conspicuous, and brightly coloured flowers, which offered large amounts of nectar. These plant species were also among the few that were visited by vertebrate pollinators.

Pollinators

Overall, there were 161 animal species visiting flowers (Appendix III; 79 spp. were identified to species level accounting for 74.2% of all interactions, genus: 32 spp./23.5%, subfamily: 12 spp./3.7%, family: 36 spp./1.7%, order: 3 spp./0.1%; see Figs. S2–S6) from 65 families within 5 invertebrate and 2 vertebrate orders. Seventy-four species occurred at both sites, of which 23 species were introduced. Of all pollinator species, 45 were endemic or native to Mauritius (restored vs control = 40 spp.vs 32 spp.), 35 were introduced (33 spp.vs 26 spp.), and no origin could be determined for 81. Of all visits, the latter group accounted for only 9%, native and endemic species carried out 28%, and introduced
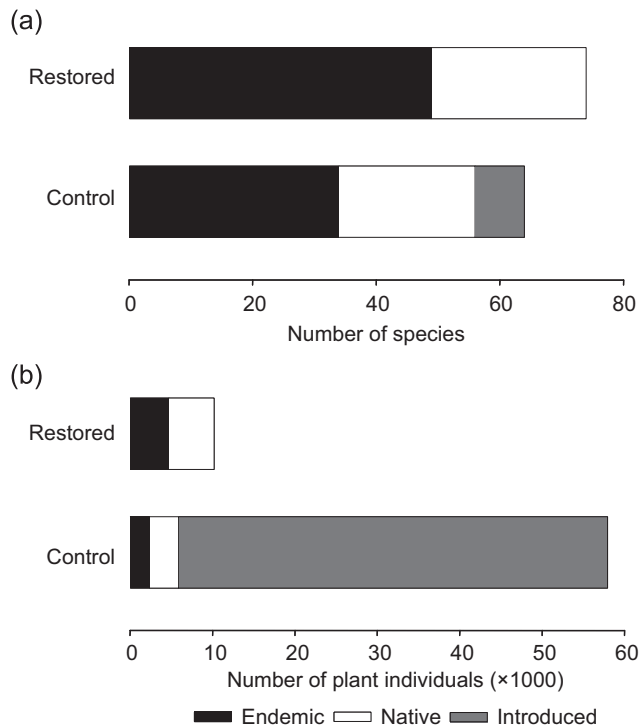
(a)

(b)

Fig. 2. Endemic, native and introduced plant species (a) richness and (b) abundance at both site.

animals accounted for 63%. Overall, 77 species were observed only once or twice, and only 14 species were recorded on flowers >100 times.

During 35 h of nocturnal observations, we observed 19 (11.8%) pollinator species visiting a total of 19 plant species across the entire season. At the restored site, 18 pollinator species visited 18 plant species, and at the control site 6 pollinator species visited 7 plant species. Nocturnal interactions accounted for 4.6% and 2.1% of interactions in the restored and the control site, respectively.

The most species-rich group of flower visitors were the true flies (Diptera; 71 species; see Fig. S3) and, within this order, 26 species belonged to the families Muscidae (house flies) and Syrphidae (hover flies). Social and solitary bees, which represent a major group of flower visitors in most mainland pollinator communities were extremely species-poor in our study with only one species in the family Apidae (*Apis mellifera* L.) and one solitary species in the family Colletidae (*Paleorhiza* sp.) (see Fig. S2). The largest difference in number of visitor species between the sites was seen in the Lepidoptera (30 spp. at the restored vs 17 spp. at the control site; see Fig. S4). Dipterans were the most abundant flower visitors (41.7% of all visits) followed by hymenopterans (excluding Formicidae: 19.6%) and the Formicidae (14.2%) (see Fig. S6).

The honey bee (*Apis mellifera*) was overall the most abundant flower visitor in the study, accounting for

15.8% of all visits. At the restored site, honey bees and the widespread fly *Stomorhina lunata* Fabricius (Calliphoridae) were equally abundant (together 27.6% of all visits), followed by the introduced yellow-footed ant *Technomyrmex albipes* Smith (10.0%) and the native ant *Brachymyrmex* sp. (8.4%; both Formicidae). The ranking of flower visitor abundance was similar at the control site except that, after *A. mellifera* (19.4% of visits), the accidentally introduced flea beetle *Chaetocnema* sp. (Chrysomelidae; see also Fig. S5) was the second most abundant species (16.9%), followed by *S. lunata* (6.8%), *Brachymyrmex* sp. (5.2%), and *T. albipes* (4.6%). Honey bees interacted with 43 plant species at the restored and 28 species at the control site (51% vs 44%). Of these, only three species at both sites were visited by ≤3 pollinator species, including honey bees, suggesting that honey bees did not serve as pollinators for many specialised plant species.

Flower visitors of both vertebrate groups contributed to 0.7% of all visits at the restored site and 0.1% at the control site. Nevertheless, the single gecko species in the study area, the Blue-tailed Day Gecko *Phelsuma cepediana* Merrem, visited 12 plant species at the restored site and 3 species at the control site (16% vs 5%). Similarly, birds visited more plant species (8 vs 2) at the restored than the control site. Overall, there were 3 plant species where vertebrates, particularly *P. cepediana*, were the sole regular flower visitors (Fig. 1; Appendix IV). Of the 4 observed vertebrate flower visitors, the 2 generalist bird species, the Madagascar Fody *Foudia madagascariense* and the Red-whiskered Bulbul *Pycnonotus jocosus* were both introduced to Mauritius, and these were observed to forage for nectar on flowers at the restored site only once. In contrast, the endemic Grey White-eye *Zosterops mauritianus* and *P. cepediana* were regular flower visitors of 16 plant species at the restored site, 11 of which were not visited by vertebrates at the control site. Ten of 11 plant species visited by *P. cepediana* were also visited by *A. mellifera*, suggesting strong potential for resource competition between introduced and endemic pollinators. The two species were observed to interact on the same plant only during nine out of 65 observation sessions. While *P. cepediana* made 11 visits to plants where *A. mellifera* was present, it visited the same plants 33 times when *A. mellifera* was absent. *Apis mellifera* also avoided plants where *P. cepediana* was present (82 vs 128). In one case, we have observed aggressive behaviour of *A. mellifera* towards *P. cepediana* when feeding on the male flowers of *Pandanus barklyi*.

Structure of pollination webs

Pollination web descriptors on both plant–pollinator communities are presented in Table 1. Mean

quantitative evenness and connectance based on 13 2-weekly sub-webs were not significantly different between sites ($p > 0.1$, paired t-test; Table 2). Both web parameters showed no consistent patterns with regards to higher or lower values in the restored compared with the control site across the 2-weekly sub-webs. Floral abundance was almost twice as high at the restored as at the control site, and regarding quantitative visitation rate, the web of the restored site was 1.8 times larger.

Five percent of plant species at the restored site and 18.8% at the control site received $\leqslant 3$ visits. On average, at the control site there were 0.48 ± 0.19 (hereafter means $\pm$ SE unless otherwise stated) visits/flower/h to introduced plants compared with 0.59 ± 0.11 to native plants. In comparison, mean visitation rate to native plant species at the restored site was 0.70 ± 0.20 visits/flower/h. Visitation rates to all plant species at both sites are presented in Appendix II.

There were plant species at both sites that received no visitors during the study (Fig. 3a). On average, linkage of plant and animal species that occurred at both sites was higher at the restored than the control site (Table 3). Linkage of native plant species did not differ to that of introduced species (native: 8.91 ± 1.2; introduced: 4.6 ± 2.3; bootstrapped 95% CI 4.25–14.25). The majority of flower visitors were observed to visit only one or two plant species (Fig. 3b). At the same time, both pollinator communities contained few super-generalist species with a linkage > 20.

Mean quantitative plant and animal linkage showed a similar pattern compared with qualitative linkage. Both weighted and unweighted linkage of plants appear approximately two-fold larger than the respective linkage value for animals. Neither weighted nor unweighted linkage of plants and animals differed between sites (Table 2).

Table 1. Pollination web parameters of both study site.

Statistics	Restored	Control
Number of plant species (P)	74	64
Number of animal species (A)	135	100
Number of visits (V)	3961	3334
Number of interactions (I)	744	534
Ratio A/P	1.84	1.56
Network size (S)	9990	6400
Connectance (C)	13.23	15.57
Maximal plant linkage (l_{max})	39	38
Maximal animal linkage (l_{max})	45	34
Plant linkage (l_p)	10.2 ± 1.06	8.34 ± 1.15
Animal linkage (l_a)	5.52 ± 0.71	5.39 ± 0.71

We present the total number of plant (P) and animals species (A), visits (V), and interactions (I), as well as the ratio of animal per plant species, web size (S), connectance (C), maximal plant and animal linkage (l_{max}), and mean $\pm$ SE plant (l_p) and animal linkage (l_a).

Table 2. Mean $\pm$ SE quantitative pollination web parameters of both study sites.

Quantitative statistics	Restored	Control
Evenness (ε)	0.70 ± 0.027	0.70 ± 0.026
Connectance (Cq)	0.075 ± 0.007	0.082 ± 0.006
Unweighted plant linkage (lu_p)	3.32 ± 0.38	3.08 ± 0.39
Unweighted animal linkage (lu_a)	1.57 ± 0.08	1.60 ± 0.06
Weighted plant linkage (lw_p)	5.12 ± 0.47	4.44 ± 0.41
Weighted animal linkage (lw_p)	2.32 ± 0.22	2.20 ± 0.20

Means were calculated from 13 2-weekly webs in both the restored and the control site. We present interaction evenness (ε), connectance (Cq), unweighted plant (luq_p) and animal linkage (lu_a), and weighted plant (lw_p) and animal linkage (lw_a). Means of all parameters were not significantly different ($p > 0.1$, paired t-test) between sites, but weighted linkage (log-transformed) was significantly higher ($p < 0.001$, paired t-test) than unweighted linkage (log-transformed) for animal and plants at both sites.

Discussion

While a few extensive studies report qualitative information on plant–pollinator communities (e.g. Inoue et al., 1990; Kato et al., 1990; Petanidou, 1991, Kato, 2000), our study presents 2 of the most extensive, highly resolved and comprehensive fully quantitative plant–pollinator webs to date, which can be analysed with a food web approach. The pollination webs include all woody plant species that flowered between August 2003 and April 2004 independent of flowering time (diurnal or nocturnal), length of flowering period and range of pollinator species. The methodological setup of repeated 2-weekly sampling resulted in a high temporal and spatial resolution of the webs, minimising the chance of sampling bias.

By focusing on the community level there is loss of accuracy with respect to pollination efficiency of individual visitors. Not all flower visitors are pollinators, and the pollination efficiency of those that are varies with plant species (Schemske and Horvitz, 1984). Vázquez et al. (2005, and references within), however, advocated that visitation frequency of flower visitors is an appropriate surrogate for *per-capita* pollination efficiency, and pollinator efficiency plays a smaller role (see also Sahli and Conner, 2006).

Due to the scarcity of heath habitats in Mauritius and the intensity of the data collection, the study could not be replicated over several restored and control sites. As far as possible we statistically accounted for spatial and temporal dependencies of errors between sites and plant and animal species by using linear mixed-effect models and paired t-tests. Thus, the findings presented in this study suggest that the structural differences in the plant and pollinator communities are tied to habitat restoration in the Conservation Management Area.
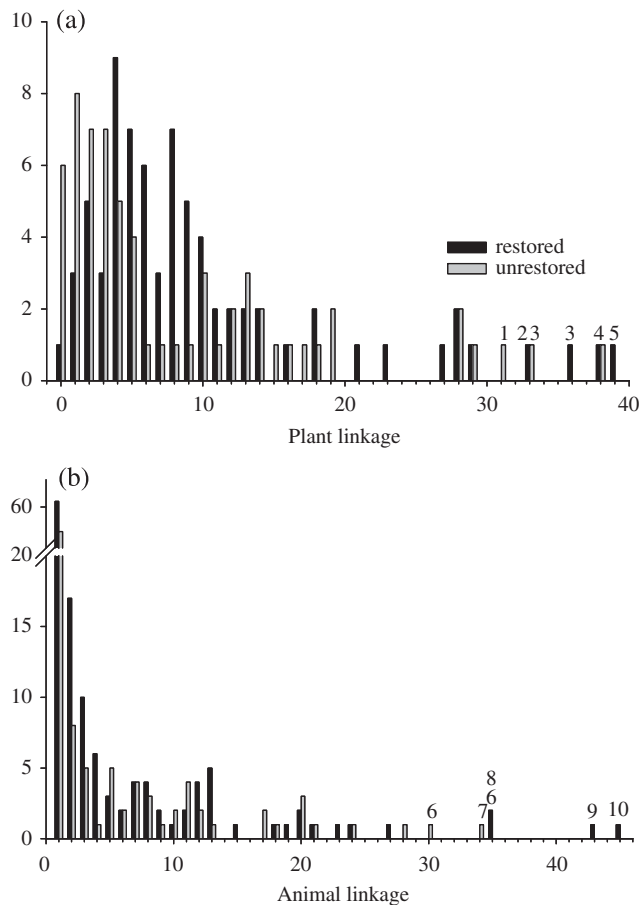
Fig. 3. Frequency of (a) plant linkage and (b) pollinator linkage in the restored and the control site. Each bar represents the count of species with a given linkage (number of taxa interacted with). The majority of pollinator species visited only one plant species, and few pollinators were extremely generalised. Pollinator species with a low linkage are less likely to be observed than species with a higher linkage. Species identity is given for highly generalised plant species: 1. *Sideroxylon cinereum*, 2. *Sideroxylon puberlum*, 3. *Stillingia lineata*, 4. *Psidia terebinthina* (both sites), 5. *Aphloia theiformis*; animal species: 6. *Stomorhina lunata*, 7. *Chaetocnema* sp., 8. *Pachycerina crinicornis*, 9. *Apis mellifera*, and 10. *Technomyrmex albipes*.

Table 3. Linkage of plant and pollinator species which occurred at both sites.

	Restored	Control
Plants		
Mean linkage$\pm$SE	11.57 ± 1.41	9.15 ± 1.36
Median	9	5
Paired t	2.93	
df	50	
p	0.005	
Pollinators		
Mean linkage$\pm$SE	9.06 ± 1.16	6.94 ± 0.92
Median	5.5	3
paired t	3.40	
df	71	
P	0.001	

(Oostermeijer et al., 2000). It has been shown that spatial isolation on the level of neighbouring plant species has resulted in reproductive decline for a variety of plants (Ghazoul, 2005; Knight et al., 2005; but see Feinsinger et al., 1986). Many pollinators respond to the relative abundance of plants and/or flowers in a density-dependent manner when foraging for floral resources (Smithson and Macnair, 1997; Fleishman et al., 2005). As most plant species in Pétrin produce inconspicuous, small flowers, invasion of introduced plant species, even if the actual abundance of native plants and their flowers remains unaffected in the short term, is likely to have a considerable effect on the foraging behaviour of pollinators, and eventually on the reproduction of self-incompatible native plants.

The 8 introduced plant species at the control site accounted for almost 83% of all plant individuals in the area. Nonetheless, direct competition between introduced and native plants for flower visitations appears low. The combination of abundant invasive plant species and low attraction to pollinators appears to contrast an invasion scenario proposed by Aizen et al. (2008). The authors suggest that plant invasion and increase in attractiveness to pollinator is complimentary. In our study, introduced plant species showed low linkage: 3 species (*Ossaea marginata*, *Clidemia hirta*, and *Ardisia crenate*) received no visitors and only one visit was observed to a fourth, *Wikstroemia indica*. This implies that these introduced species rely little on the local pollinator community for reproduction, which is a common strategy to overcome pollen limitation by invasive alien plant species (Baker's rule; Baker, 1967). Similarly, Memmott and Waser (2002) and Olesen et al. (2002) described fewer flower visitors on introduced compared with native species in a plant community in central USA (but see Morales and Aizen, 2002, 2006). However, we may have recorded a transient pattern in Mauritius because invaders with attractive floral

Plants

Theoretical and empirical studies have shown that plant population density is positively correlated with plant fitness (e.g. Silander and Primack, 1978; Klinkhamer et al., 1989). We showed that plant abundance of most native species was higher at the restored than the control site, and that it was positively related to the number of pollinator species and visitation rate. Consequently, the relatively lower frequency of rare or locally rare plant species at the control site could have detrimental effects on the quality and quantity of pollen dispersal of those native plants in the degraded area

resources were less abundant at the control site than at other locations on the island, where they received many more visits by a range of pollinators (C. Kaiser-Bunbury, pers. obs.). Thus, invasion may have been still in the early stages, despite clear signs in the pollination web structure (see section below the "Structure of pollination webs").

Pollinators

In our study, dipterans were the most abundant flower visitors, a pattern commonly observed in pollination assemblages in high latitudes (e.g. Elberling and Olesen, 1999), high altitudes (e.g. Arroyo et al., 1982; Inouye and Pyke, 1988) and on islands (e.g. Anderson et al., 2001). Flies have been widely acknowledged as potential pollinators of many plant species (Kearns, 2001) and generalist species overcome their low efficiency as pollinators with their abundance, particularly when more efficient pollinators are absent (McGuire and Armbruster, 1991). Native and endemic pollinators accounted for only 28% of visits whereas introduced animals accounted for 63% (unknown origin 9%), which illustrates the dominance of introduced pollinators in the communities. While these numbers do not necessarily reflect the contribution of native or introduced flower visitors to pollination, they provide a possible explanation for the demise of native pollinator diversity in Pétrin.

All vertebrates were more abundant and more highly connected at the restored site compared with the control site. The role of lizards in pollination has been considered vital to the reproduction of many native Mauritian plant species (Nyhagen et al., 2001; Hansen et al., 2007), and on other islands, for example the Balearic Islands (Olesen and Valido, 2003, and references therein). The endemic blue-tailed day gecko *Phelsuma cepediana* is an important pollinator of several endangered plant species in Pétrin, e.g. *Trochetia blackburniana* (Hansen et al., 2006) and *Roussea simplex* (Hansen, 2005). Male *Phelsuma* geckos are territorial and their abundance is related to habitat composition and quality (Harmon, 2005). The low structural diversity and the lack of suitable habitat for geckos at the control site probably contributed to the low density of *P. cepediana* in the degraded habitat. Similarly, the foraging behaviour of the endemic grey white-eye *Zosterops mauritianus*, which was more frequently encountered at the restored site, appears to be linked to habitat composition and the availability of floral resources (Hansen et al., 2002; Kaiser et al., 2008). A similar relationship between pollinator occurrence and habitat composition was described from conservation areas in the Cape Floral Region (Pauw, 2007). There, soil type and succession stage of the vegetation, both

anthropogenically altered, reduced seed set of 6 native plant species that rely on the pollination by the oil-collecting bee *Rediviva peringueyi*, indicating a strong relationship between habitat structure and pollinator services.

The most abundant and highly linked flower visitor was the introduced honey bee *Apis mellifera*. Given that no artificial beehives were maintained within or close to the boundaries of the National Park for the duration of the study (National Parks and Conservation Service Mauritius, pers. commun.) it is likely that the majority of honey bees belonged to natural or naturalised populations. One reason for the high visitation frequency of honey bees may be their prolonged flight and foraging season, which result in an overlap in foraging time with most co-occurring pollinator species. Therefore, honey bees may be strong competitors for floral resources (e.g. Eickwort and Ginsberg, 1980; Dupont et al., 2004). At the same time, honey bees may be beneficial, by ensuring pollination for many plants. Due to their abundance and generalist foraging pattern, they can serve as pollinators to rare plant species, where the original pollinators may be extinct. In contrast to findings from Mediterranean plant–pollinator communities where honey bees are strongly associated with specialised plant species (i.e. plants with low linkage; Petanidou and Potts, 2006), honey bees in Pétrin were equally associated with common, generalised plant species and poorly visited, rare species, a pattern frequently observed in highly generalised taxa in pollination webs (interaction asymmetry; e.g., Bascompte et al., 2003; Vázquez and Aizen, 2004; Kaiser, 2006). We did not observe a disproportionate increase in honey bee linkage or abundance at the invaded site in contrast to findings by Aizen et al. (2008). Nevertheless, the honey bee and other introduced pollinator species such as the flies *Stomorhina lunata* and *Pachycerina crinicornis* and the bettle *Chaetocnema* sp. 1 can certainly be regarded as super-generalist with the potential to modify network structure (e.g. invasive generalist plant species affect nestedness; Bartomeus et al., 2008), but the role of habitat restoration in these processes remains unclear.

Structure of pollination webs

There were almost twice as many flowers at the restored than the control site, and the web of the restored site was 1.8 times larger with regards to quantitative visitation rate, indicating an overall higher complexity at the restored site. With an increase in the total amount of resources available in the community we observed a relative increase in attractiveness of all plants to pollinators, an observation previously described by Fleishman et al. (2005) (see also Morales and

Aizen, 2006). Also, mutualistic interaction strength declines at heavily invaded sites, which could be one explanation why the control site has substantially lower quantitative visitation rates than the restored site shown by the overall smaller web (Aizen et al., 2008). Both webs were characterised by a few abundant species, highly linked hubs, and by many rare species with weak interactions, indicated by higher weighted compared with unweighted linkages, similar evenness, and quantitative connectance at both sites. Qualitative connectance was twice as high as in highly diverse Mediterranean pollination web and two-thirds of the mean connectance in a temperate forest in Argentina, the only 2 published networks for which connectance was corrected for the extended sampling period (Basilio et al., 2006; Medan et al., 2006). However, since connectance is size-dependent, its use as an index of generalisation in tropical and temperate pollination systems is questionable (Kay and Schemske, 2004; but see Petanidou and Potts, 2006). Here, the quantitative linkage is independent of network size and should be preferred because it depicts biologically meaningful community-specific differences and reduces the risk of misinterpretation due to sampling bias (see Goldwasser and Roughgarden, 1997). For example, both plant and animal mean weighted linkage is higher than the unweighted linkage (Table 2) indicating that plants and animals in the webs tend to form generalist hubs, i.e. generalist pollinator species interact relatively strongly with generalist plant species and vice versa. This pattern appeared to be even slighlty stronger for plant species in the restored site compared with the control site (lw_p 5.12 vs. 4.44).

To our knowledge, however, there are no pollination web studies to date that present quantitative parameters allowing comparisons of general patterns across different ecosystems. Thus, comparisons can so far only be based on qualitative parameters. Animal species at both sites showed a similar degree of generalisation and plant species at the restored site interacted, on average, with almost 2 species more than plant species at the control site (see Table 1 and Appendix II). While mean plant linkage in our study lies well within the range of linkage values from the 29 plant–pollinator communities presented by Jordano et al. (2006), the mean pollinator linkage is high in comparison to the webs reported by the authors—only one artic pollinator community shows a higher degree of generalisation (see also Morales and Aizen, 2006). Thus, both pollinator communities reflect common feature of many island plant–pollinator communities (Barrett, 1996; Anderson et al., 2001), and even plant linkage in our webs is comparatively high when we consider that island plants tend to be less generalised than mainland species (Olesen and Jordano, 2002). One contributing factor to the high degree of generalisation could be the comparatively low ratio of animal to plant species (see Table 1; A/P ratio is

amongst the lowest of the networks presented by Jordano et al., 2006) resulting from a depauperate pollinator fauna in comparison to mainland communities (MacArthur and Wilson, 1967).

Plant species that interact with numerous pollinator species, and *vice versa*, may be important for the structure and stability of plant–pollinator communities. For example, generalised species have a high resource overlap, which may result in strong direct and indirect competition for floral resources (between pollinator species) or for pollination services (between plant species). In our study, the most dominant and generalised pollinators were introduced invertebrates. Those species showed substantial niche overlaps with native pollinators such as birds, geckos, butterflies, and flies, and consequently native pollinators may be displaced to less profitable sources of food (e.g. Hansen et al., 2002). An advantage of generalised systems is resilience against disturbances. The stability of plant–pollinator communities is thought to increase with a high degree of redundancy in pollinators because adverse events are unlikely to affect all species equally severely (Lawton, 1994; Memmott et al., 2004). At the control site, 43.8% of plant species received fewer than four visitors compared with 14.9% at the restored site, thus, if a high level of generalisation can 'secure' against the collapse of plant–pollinator webs, the control site may be more vulnerable to perturbations.

Implications for conservation

Both sites were relatively similar in terms of native plant species richness, but habitat composition at the control site was heavily altered by the presence of invasive species. The degradation of heath habitat in some areas of Pétrin by introduced plants had a strong effect on plant abundance and the diversity of plant and pollinator assemblages and interactions in these areas. The similar dominance of introduced generalist flower visitors at both sites indicated that, for common animal species, structural difference between plant communities had little effect on their foraging behaviour. Native pollinator species richness and density, however, were higher at the restored site, which may be a consequence of habitat restoration. For example, bird and gecko visitation was almost absent at the control site, and both groups of pollinators have been shown to be sensitive to changes in plant community composition (Hansen et al., 2007; Kaiser et al., 2008). The relationship between habitat composition and pollinator assemblages described in this study has implications for the conservation of degraded habitats in Mauritius, on other oceanic islands, and also in mainland ecosystems.

The diversity of a plant community may be related to the functional diversity of its pollinator community

(Fontaine et al., 2006), and species-rich floras support a higher diversity of pollinators (Kevan 1999). Differences in floral abundance affect foraging decisions of insects (Waser and Real, 1979; Feinsinger, 1987), and insects concentrate their foraging on dense patches of flowers (Thomson, 1981), which are more common in habitats where native plants do not compete with invasives for resources. To maintain pollinator diversity, one has to preserve structural diversity to provide food sources, nesting and oviposition sites, and resting or mating sites (Kevan, 1999).

Conclusion

Pollination web studies are useful tools to analyse plant–pollinator assemblages of different habitat types. In our study we collected data for pollination webs of 2 sites only and, thus, cannot deduce with certainty that the observed differences between sites are due to habitat restoration. However, we can state that both sites were similar in plant species richness but fairly distinct in plant and pollinator community composition, which suggests that habitat restoration may positively affect the functional ecosystem integrity of restored sites. Higher pollinator species richness and abundance at the restored site indicated a positive effect of habitat restoration on pollinator diversity, which may increase community stability and secure a higher rate of pollination success of native plant species. For habitat restoration to be successful in the long term, practitioners should thus maintain structural diversity to support a species-rich and abundant pollinator assemblage that ensures native plant reproduction, despite frequent biotic and abiotic perturbations.

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Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2009.04.001.

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