

The tolerance of island plant–pollinator networks to alien plants

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Summary

1. Invasive alien plant species pose a severe threat to native plant communities world-wide, especially on islands. While many studies focus on the direct impact of alien plants on native systems, indirect effects of plant invaders on co-flowering natives, for example through competition for pollination services, are less well studied and the results are variable.

2. We used six temporally and taxonomically highly resolved plant–pollinator networks from the island of Mahé, Seychelles, to investigate the indirect impact of invasive alien plant species on remnant native plant communities mediated by shared pollinators. We employed fully quantitative network parameters and information on plant reproductive success, and pollinator diversity and behaviour, to detect changes in plant–pollinator networks along an invasion gradient.

3. The number of visits to and fruit set of native plants did not change with invasion intensity. Weighted plant linkage and interaction evenness, however, was lower at invaded sites than at less invaded sites. These patterns were primarily driven by shifts in interactions of the most common pollinator, the introduced honey bee *Apis mellifera*, while weak interactions and strong native interactions remained unchanged.

4. *Synthesis.* The implications of these findings are twofold: first, quantitative network parameters are important tools for detecting underlying biological patterns. Secondly, alien plants and pollinators may play a greater role in shaping network structure at high than low levels of invasion. We could not show, however, whether the presence of invasive plants result in a simplification of plant–pollinator networks that is detrimental to native plants and pollinators alike.

Key-words: Indian Ocean, indirect interactions, inselbergs, interaction connectance, invasion ecology, invasive alien species, plant communities, pollination webs, Seychelles Islands

Introduction

The introduction of alien species into native ecosystems constitutes one of the major threats for the persistence and integrity of ecosystem functioning (Mack *et al.* 2000; Sala *et al.* 2000). Pollination interactions play a vital role in the reproduction of most plant species, and empirical studies have shown that alien plant species alter pollination of neighbouring, mostly native, plants through shared pollinators (reviewed in Traveset & Richardson 2006; Bjerknes *et al.* 2007). The effects of indirect interactions between plant species range from mutually benefi-

cial (Moeller 2004; Moragues & Traveset 2005; Molina-Montenegro, Badano & Cavieres 2008), to neutral (Aigner 2004; Jones 2004; Kaiser-Bunbury & Müller 2009) and competitive (reviewed in Mitchell *et al.* 2009). Alien plants can compete for pollination with native plants through changes in pollinator visitation and shifts in quantity and quality of pollen delivered to flowers, thus affecting plant reproductive success of native species (Chittka & Schürkens 2001; Brown, Mitchell & Graham 2002; Kandori *et al.* 2009) or causing shifts in foraging behaviour of native pollinators (Ghazoul, Liston & Boyle 1998; Cunningham 2000; Ghazoul 2004). So far, however, no clear and consistent general pattern has emerged (Traveset & Richardson 2006) and thus it is difficult to predict the consequences of invasion on native flora and fauna (Strayer *et al.* 2006). A recent synthesis found an overall slightly negative impact on plant fitness and pollinator visitation rate resulting

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from shared pollinators between native and alien plant species (Morales & Traveset 2009). Most of the present studies investigate small systems consisting of few plant species and their pollinators, providing detailed insights on the underlying biological processes of pair-wise interactions. Here, we use a network approach to study the effects of plant invasion on plant–pollinator interactions and native plant fitness on the community level.

In recent years, the study of pollination interactions at the community level has flourished and a variety of tools have been developed that has greatly furthered our understanding of complex network structure and dynamics (Bascompte & Jordano 2007). One characteristic property of pollination networks is the nested structure of their interactions, which means that most pollination networks consist of (i) a core of generalist species that interact closely with each other and (ii) a few specialized species that tend to interact with the most generalized species (Bascompte *et al.* 2003). Since asymmetry of interactions, which was previously noted by Petanidou & Ellis (1996), creates a high degree of redundancy in pollination networks, it has been suggested that this feature contributes substantially to the persistence of specialized species and the robustness of networks (Memmott, Waser & Price 2004; Kaiser-Bunbury *et al.* 2010). While the level of sophistication of network tools and their usage has advanced rapidly, from purely qualitative network parameters based on presence/absence links (e.g. Vázquez 2005; Jordano, Bascompte & Olesen 2006) to quantitative parameters based on a measure of interaction strength (e.g. Bersier, Banašek-Richter & Cattin 2002; Blüthgen, Menzel & Blüthgen 2006), their descriptive and predictive power of real-world processes and biological mechanisms lags behind (Blüthgen *et al.* 2008; Vázquez, Chacoff & Cagnolo 2009). For instance, studies on the impact of alien invasive species on plant–pollinator networks have provided novel insight into the mechanisms by which these species integrate into native pollination systems (Memmott & Waser 2002; Olesen, Eklundsen & Venkatasamy 2002; Morales & Aizen 2006; Aizen, Morales & Morales 2008). At the community level, however, we lack information on the impact of alien species on native plant fitness and pollinator fauna. While some smaller-scale experimental studies exist (Lopezaraiza-Mikel *et al.* 2007), there is, to our knowledge, no such work that combines a broad pollination network approach with the evaluation of biological processes underlying the changes in network topology. Our study used quantitative network parameters as a tool to detect changes in plant–pollinator communities caused by plant invasion and linked these changes to pollinator visitation rate and plant reproductive success.

Islands are particularly well suited for studying the effects of invasive species on plant–pollinator interactions. Most islands have experienced many introductions since human colonization (Kueffer *et al.* 2010) and, together with habitat destruction and exploitation, invasive alien species have devastated native island floras and faunas world-wide (Whittaker & Fernández-Palacios 2006). Due to their small size and isolation, biotas of oceanic islands are typically depauperate compared to continental ones (MacArthur & Wilson 1967). In community

studies, small system sizes facilitate both the inclusion of all species and data collection over prolonged periods, minimizing the risk of sampling bias. Moreover, island plant–pollinator networks are characterized by predominantly generalized interactions (Bernardello *et al.* 2001; Rathcke 2001; Dupont, Hansen & Olesen 2003; Kaiser-Bunbury, Memmott & Müller 2009). In island systems where many plant species interact with many pollinator species and vice versa, most flowers are white, green or generally dull in colour and morphologically unspecialized with bowl-shaped corollas offering floral rewards to a wide range of flower visitors (Carlquist 1974; Webb & Kelly 1993; Anderson *et al.* 2001; Kaiser 2006). Alien colonizing plant species that have similar flower shapes and colours to the native plants are likely to attract the native pollinator community and thereby interfere with native plant–pollinator networks. Collectively, these conditions inherent to islands provide an ideal basis for our work, as alien plants have the potential to interfere with mutualistic interactions, and recommendations for conservation may be directly applicable to habitat restoration.

We used six fully quantitative pollination networks to investigate the impact of invasive plant species on co-flowering native plants and their associated pollinator communities in an island setting. We hypothesized that alien plants compete with native species for pollination and negatively affect their reproductive success. We asked: (i) Does pollinator visitation frequency of native plants decrease with increasing invasion? (ii) Do changes in pollinator foraging behaviour result in a decline in fitness among native plants? More generally, we investigated the mechanisms by which alien plants impact upon plant–pollinator networks and affect the tolerance of native communities to future invasion.

Materials and methods

STUDY SITES

Our study was conducted on Mahé, the largest granitic island of the Seychelles, Indian Ocean (4°40' S, 55°26' E; Fig. 1). Mahé belongs to the oldest oceanic island group in the world, being a remnant of Gondwanaland from which it split *c.* 70 million years ago. The islands' great age, coupled with their geographical isolation, has resulted in a unique biota which has arisen more by evolution than immigration (Dalziel 1995), and *c.* 35% of the native Seychelles flora are endemic to the islands (Stoddart 1984).

While habitat clearance and alien species have permanently changed the character of most native communities on the Seychelles, the vegetation on granitic inselbergs – steep-sided monolithic outcrops – has remained largely intact. Inselbergs have strikingly different microclimatic and edaphic conditions from their surroundings. Consequently, they harbour unique plant communities characterized by an outstanding degree of endemism, which, locally, can be as high as 96% of the species (Fleischmann *et al.* 1996). Inselberg plant communities are characterized by shrubs and small trees, including palms and screw palms. Average canopy height is 1–2 m with a few trees that attain a maximum height of 4–5 m. Dominant plant species include native *Pandanus* spp., *Memecylon eleagni*, *Paragenipa wrightii*, *Canthium bibracteatum*, and four species of endemic palms *Deckenia nobilis*, *Nephrosperma vanhoutteanum*, *Phoenixophorium*

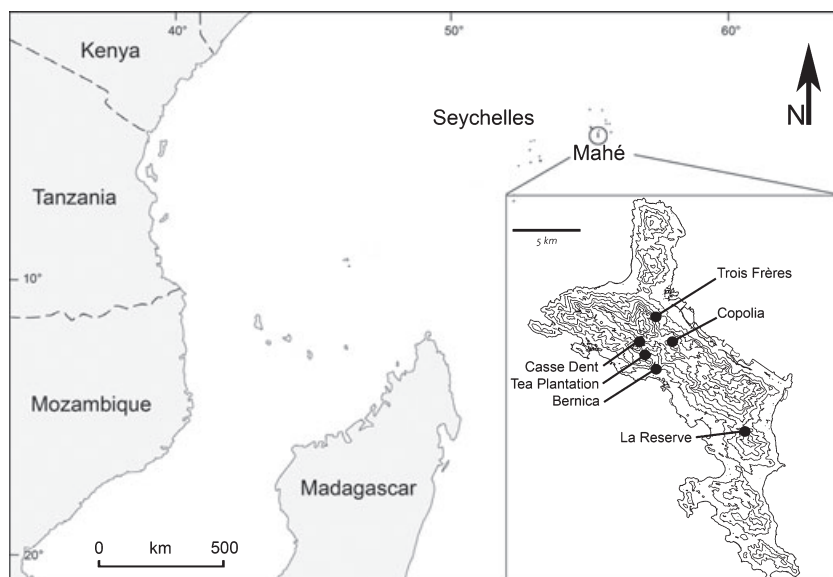


Fig. 1. Map of the study sites on the main island of Mahé, Seychelles. All six sites represent mid-altitude inselberg vegetation with a high degree of plant endemism.

borsigianum and *Roscheria melanochaetes* (Robertson 1989; Friedman 1994). There are no flowering herbs in the communities. The inselbergs create refuges for endemic plants formerly found in habitats now dominated by alien species. Inselbergs, nevertheless, are exposed to the encroachment of alien plants, resulting in a series of communities scattered across the island with a varying degree of invasion. As the disturbance history for inselbergs across Mahé is similar (L. Chong-Seng, pers. comm.), we assume that the varying degree of invasion on inselbergs is primarily a function of intensity and duration of exposure to alien plants from the surrounding habitat. Nevertheless, it is important to note that we analysed different inselbergs with potentially different disturbance histories instead of a purely temporal invasion gradient.

We collected fully quantitative pollination networks from six mid-altitude inselberg communities (Fig. 1 inset; Table 1) between September 2007 and April 2008. Full-season networks covered the entire flowering season (eight consecutive months) and temporal networks refer to 1-month networks. Temporal monthly networks can be treated as semi-independent units because the methodology and techniques of data collection were the same for each network and the flower community differed between months. The sites were located on average 4.47 km (± 3.41 SD) apart, and the habitat at each site was clearly separated from the surrounding habitat by steep rock faces. None of the sites were actively managed or modified. We selected the sites based on the following criteria: (i) they represented mid-altitude inselberg communities with broadly the same mix of native plant species; (ii) the distance between the sites was considered sufficient for their pollinator communities to be largely independent; and (iii) the degree of plant invasion varied, ranging from sparsely invaded sites to those dominated by alien plants. Although it is possible that a few long-distance foragers such as birds, hawkmoths and large bees crossed between sites, it is relatively unlikely that these flower visitors carried large amounts of pollen between conspecifics at different sites. At all study sites, we established between two and four parallel 100-m transects which covered c. 80% of each inselberg habitat (Table 1). Transects were divided into 25 m sections for a stratified, random sampling of plant, seedling and floral abundance. Pollinator observations were not restricted to transects but scattered across the entire inselberg depending on the availability of flowering plants.

INSELBERG PLANT AND POLLINATOR COMMUNITIES

We determined the degree of plant invasion and native plant species composition of each inselberg community by: (i) surveying each community prior to the study between 2 and 8 September 2007; and (ii) recording monthly floral abundance between September 2007 and April 2008, the period during which on average 79% (range 74–82%) of inselberg species flowered. For the plant survey, every three paces along each transect (walked by the same researcher) we recorded all individuals > 1 m in vertical height that occurred on both sides of the transects. Thus, at each point a total area of 3 m² was surveyed (3 m length on each side \times 0.5 m width). Seedlings and saplings at all sites were recorded between 21 and 27 April 2008 in 1 \times 1 m quadrats every three paces on alternating sides of the transect.

Monthly floral abundance was determined by conducting flower counts in cubic metres randomly located as five 1-m³ cubes on alternating sites along each 25-m transect section ($n = 20$ cubes per 100-m transect). The cubes were placed at the closest patch of flowers to the transect, and flowering plants within the distance of 2 m perpendicular to the transect were included in flower counts. We counted the number of floral units in flower (referred to as 'flowers' hereafter) in each cube. One floral unit was defined as one individual flower or a cluster of flowers in the case of palm inflorescences. Floral abundance, the mean number of flowers per cubic metre, was calculated for each species by dividing the total number of flowers by the total number of cubes sampled at each site (for further details on sampling methods see Kaiser 2006; Kaiser-Bunbury, Memmott & Müller 2009).

We defined two measures of invasion intensity at each site: (i) the ratio of alien to native plant abundance; and (ii) the ratio of alien to native floral abundance (Table 1). The former was used to investigate changes in plant-specific traits along the invasion gradient, e.g. fruit set which may be affected not only by pollinator diversity but also by competition for light and nutrients with invasive plants. Network parameters, however, are strongly associated with pollinator behaviour, which in turn is most likely to be influenced by the availability of native and alien floral resources in the community (e.g. Hegland & Totland 2005; Stang, Klinkhamer & van der Meijden 2006; Bjerknes *et al.* 2007). Thus we used the ratio of alien to native floral abundance to investigate the impact of invasion on pollination network structure.

Table 1. Characteristics of the six study sites on Mahé, Seychelles, with information on total flower observation times, native and alien plant abundances and invasion gradients (ratio of alien : native plant and floral abundances) across sites

Sites	Location	Size (ha)	Altitude (m a.s.l.)	No. transects	Total length transects (m)	Observation time (h)	Plant abundance natives (aliens) [m^{-2}]	Ratio plant abundance aliens : natives	Ratio floral abundance aliens : natives
Bernica	55°26'51–53" E, 4°40'8–16" S	~1.7	320	4	400	181.5	2.51 (0.08)	0.03	0.056
Copolia	55°27'23–28" E, 4°40'7–12" S	~1.3	570	4	400	263.5	2.65 (0.30)	0.11	0.049
Casse Dent	55°26'11–15" E, 4°39'16–17" S	~0.7	490	2	175	158.75	2.41 (0.42)	0.17	0.058
Trois Frères	55°26'48–53" E, 4°38'10–14" S	~1.3	460	4	400	213.75	1.57 (0.48)	0.31	0.255
La Reserve	55°30'13–17" E, 4°42'35–37" S	~1.0	300	4	400	164	1.43 (0.93)	0.65	0.154
Tea Plantation	55°26'21–27" E, 4°39'40–42" S	~1.4	420	3	400	187.5	1.04 (1.01)	0.97	0.553

Pollinator observations were conducted on each plant species which flowered between September 2007 and April 2008. After an initial phase during which observation sessions lasted for 15 min, we changed the standard observation unit to 30 min (plus 2 min settling time) to reduce the level of disturbance. We aimed to observe pollinators for 3 h/plant species/site/month, but bad weather periods and sudden stops of flowering reduced the total observation time/species/month to 2.83 ± 0.87 h (total number of observation sessions at all sites $n = 2476$ resulted in 1169 h of observation; Table 1). We recorded the identity of all flower visitors which touched the reproductive parts of flowers and the number of flowers observed. Each visitor approaching the observed plant was considered as a new individual and was thus recorded as a separate visit. We used the total number of visits of each animal species as a measure of abundance of a pollinator species.

NETWORK PARAMETERS

We constructed plant–pollinator interaction matrices for full-season networks at each site and calculated quantitative parameters for each network. For the network parameters, we used visitation frequencies as a surrogate for interaction strength (Vázquez, Morris & Jordano 2005; Bascompte, Jordano & Olesen 2006; Sahli & Conner 2007; Vázquez *et al.* 2007) and expressed mean visitation frequency per hour ('interaction frequency') as the total number of visits/flower/hour of animal species i multiplied by the floral abundance of the plant species j visited by i (Kaiser-Bunbury, Memmott & Müller 2009). That is, each visit was quantified based on the floral abundance of the interaction partner in each full-season or temporal network.

The approach of 'timed observations' used in this study contrast the methods of 'transect walks' used in most pollination network studies. During transect walks, data on visitation are collected according to the relative abundance of plant species (or flowers) in the system, i.e. visits to abundant plant species are disproportionately more likely to be recorded than visits to rare plant species. This sampling design might increase the risk of overestimating the degree of specialization of rare plant species, and abundant plant species may appear more generalized in relation to other, less abundant species in the system. Standardizing observation time could reduce this risk as long as the observation time of each plant species is sufficiently long to record the majority of its pollinator species.

Quantitative parameters are weighted measures that incorporate the interaction frequency of individual mutualists. These metrics are more robust to sampling differences than their qualitative counterparts (Banašek-Richter, Cattin & Bersier 2004), making them more conservative when comparing habitats. We calculated four quantitative parameters of well-described qualitative equivalents (see below and Table 2), i.e. weighted linkage for plants (lw_p ; also called weighted vulnerability) and pollinators (lw_a ; weighted generality), quantitative connectance (C_q ; weighted connectance), and interaction evenness (IE) (Bersier, Banašek-Richter & Cattin 2002; Tylianakis, Tscharnke & Lewis 2007; Kaiser-Bunbury, Memmott & Müller 2009). Weighted linkage and quantitative connectance, in contrast to qualitative linkage (the number of interaction partners of each species) and connectance (the number of realized interactions over the number of possible interactions in a network), gives individual weight to each taxon respective of their total interaction frequency and therefore better captures the functional importance of a taxon in the community. Interaction evenness was derived from the Shannon index and is defined as $IE = p_{ij} \log_2 p_{ij} / \log_2 S$, where S is the total number of plant–pollinator interactions in the network and p_{ij} is the proportion of interactions between plant i and pollinator j (Tylianakis,

Table 2. Summary statistics of plant–pollinator networks at the six study sites. Qualitative network parameters include ratio of animal to plant species, full network size, connectance, and mean and maximal plant and animal linkage. Overall connectance (C) is based on the connectance of each monthly network

Statistics	Bernica	Copolia	Casse Dent	Trois Frères	La Reserve	Tea Plantation
Number of native plant species (aliens) (P)	16 (2)	21 (2)	17 (3)	17 (4)	10 (6)	18 (2)
Number of pollinator taxa (A)	57	65	47	55	49	54
Number of visits (V)	12 117	7283	6381	6674	10 323	6968
Number of interactions (I)	193	213	152	178	153	163
Ratio A/P	3.17	2.83	2.35	2.62	3.06	2.70
Network size (S)	1026	1495	640	1155	784	1080
Connectance (C)	27.4	18.5	26.4	23.0	29.8	26.7
Maximal plant linkage (l_{\max})	36	22	24	21	21	22
Maximal animal linkage (l_{\max})	16	17	14	17	14	14
Mean plant linkage (l_p)	10.7 ± 1.75	9.2 ± 1.18	8.9 ± 1.39	8.9 ± 1.16	10.2 ± 1.45	8.5 ± 1.38
Mean animal linkage (l_a)	3.3 ± 0.42	3.3 ± 0.42	3.2 ± 0.39	3.2 ± 0.44	3.1 ± 0.43	3.0 ± 0.38

Tscharntke & Lewis 2007; Vázquez, Chacoff & Cagnolo 2009). Interaction evenness is a measure of the uniformity of interactions between different mutualists in the network, it shows how well-distributed interactions are among species within the community. Uneven networks, for example, show high skewness in the distributions of interaction frequencies.

For ease of comparison to other published pollination networks, we also present qualitative network parameters (see Table 2). We calculated number of plant species (P), number of flower visitor taxa (A), web size ($S = P \times A$), total number of visits (V) and interactions recorded (I), and mean and maximal (l_{\max}) linkage for animal (l_a) and plant species (l_p). We also present network connectance, $C = 100 \times (I/S)$ based on the mean connectance for each time period (Medan *et al.* 2006).

DATA ANALYSIS

All analyses were run with the statistical software R 2.9.1 (R Development Core Team 2005), mixed effect models were fitted with the function lmer (library: lme4; Bates & Maechler 2009), and model design and selection procedure followed recommendations by Zuur *et al.* (2009).

We compared the abundance patterns of native and alien adults, seedlings and saplings between sites with a linear mixed model. Seedling and sapling abundance (log-transformed) were entered as response variables in separate models and the explanatory variables adult abundance (log-transformed) and origin of the species were entered as main and interaction fixed effects. The models included species and site as crossed random effects.

POLLINATOR DIVERSITY AND INTERACTION FREQUENCY

To assess the effect of alien flowering plants on pollinator diversity and the degree of competition for pollinator visitation between native and alien plants, we determined the ratio in floral abundance of alien to native plants (invasion level) for each time period and site. We fitted two linear mixed models with a Gaussian distribution: (i) the number of pollinator species at each site and time period ($n = 48$) was entered as response variable and floral abundance and invasion level were entered as fixed effects. Floral abundance was included in the model as it was previously shown to affect pollinator species richness (Rathcke 1983; Thompson 2001; Ebeling *et al.* 2008). To

account for potential temporal and spatial non-independence we included site and time period as crossed random factors into the models. (ii) We applied a log ($Y + 0.001$) transformation to interaction frequency and used the data as response variable in the model. Floral abundance and invasion level were fitted as fixed effects, and only main effects were included into the final model. Interaction frequency for each plant species was pooled for time periods to reduce the number of observations with no visits. We fitted one complete model with all native plant species and individual models for each of the seven most common native plants. In the complete model, plant species ($n = 30$) and site ($n = 6$) were entered as crossed random effects. In the models for individual plant species, time period ($n = 8$) and site were included as crossed random effects. To obtain P -values for mixed models we ran Markov Chain Monte Carlo (MCMC) for 10 000 iterations using the function 'pvals.fnc' in the library 'languageR' (Baayen 2008). MCMC is a type of Bayesian Gibbs Sampling approach which varies parameter values randomly and estimates likelihood to build up a distribution from which point estimates and credible intervals are derived.

POLLINATION SUCCESS

We recorded pollination success of native plants as the proportion of fertilized flowers, i.e. fruit set. We recorded fruit set from a total of 31 native plant species. Of those, 16 species occurred at two or more sites in sufficient number of individuals (> 3 flowering females). Seven native plant species occurred at four or more sites in sufficient numbers for randomization, so individual between-site comparisons were restricted to these plant species. Of the 16 species, 12 (75%) are either self-incompatible hermaphrodite, dioecious, or consecutively monoecious, and of the seven most common species, five (71.5%) are dependent on a vector to deliver pollen between flowers for reproduction.

We marked a total of 29 107 buds on 594 branches or inflorescences nested in 406 plants. Due to the different number of trees (or shrubs) per species per site, the data on fruit set were unbalanced. Also, for the calculation and analyses of fruit set we needed to account for the number of flowers on each plant. We therefore analysed fruit set patterns with a generalized mixed effect model, using a binomial distribution, with floral abundance and invasion intensity as fixed effects, and species, tree and inflorescence identity as nested and site as crossed random effects. This method is robust for unbalanced data and, by using the 'cbind' command to calculate fruit set we weighted the sample sizes by the number of flowers recorded on

each tree. We also ran the same model without species as a random effect for each of the seven most common native plant species. To control for differences in population size and the amount of species-specific reward offered, we included species floral abundance at each site in the model.

QUANTITATIVE NETWORK PARAMETERS

First, we tested for correlations between plant invasion and lw_p , lw_a , C_q , and IE of the six full-season networks. We ranked the six sites according to their degree of invasion (ratio of alien : native floral abundance) and analysed the quantitative network parameters with nonparametric Spearman-rank correlations. In a second step, we used linear mixed models to analyse changes in lw_p , lw_a , and C_q of all 48 temporal networks across the invasion gradient, using the ratio of alien : native floral abundance as continuous explanatory variable and time period and site as crossed random effects.

Further, we used IE to detect shifts in interaction patterns within a network resulting from the presence of alien flowers in the system. We calculated IE for those 30 temporal networks in which alien flowers were present. We then calculated the standardized change in IE ($\bar{IE} = (IE_{full} - IE_{native})/IE_{full}$) as the difference in IE between complete networks (all plant species present; IE_{full}) and native sub-networks (IE_{native}) across the invasion intensity gradient. The relationship between \bar{IE} and invasion intensity was nonlinear, so we ran a piecewise linear regression to determine the position of the best-fitted breakpoint ($x = 0.3776$) and then ran individual linear mixed models for data points each side of the breakpoint. Site and time period were included in the models as non-nested random factors. A decline in IE can be due to shifts in the proportion of strong and weak interactions in the networks. To determine whether shifts in IE were due to changes in total and relative frequency of weak or strong interactions, we ran several linear mixed models with total and relative interaction frequency of weak interactions (log-transformed) and strong interactions for the two most common pollinator species (*Apis mellifera* and *Lasioglossum mahense*) as response variable and invasion intensity as fixed effect. Site and time period were included in the models as crossed random effects. We defined a weak interaction as an interaction between a plant and a pollinator species with ≤ 3 visits in each temporal network, and such weak interactions accounted for 51.8% of all mutualistic interactions. Finally, to test for the loss of native interactions as a consequence of increasingly uneven networks with invasion, we used a linear mixed model with site and time period as non-nested random factors to investigate the relationship between qualitative connectance of native sub-networks (log-transformed) and changes in IE.

Results

We observed pollinators of 23 endemic, seven native and seven alien plant species belonging to 14, seven and seven families, respectively, across all sites. The most abundant and flower-producing alien plant species were *Cinnamomum verum*, *Alstonia macrophylla*, *Chrysobalanus icaco* and *Psidium cattleianum*. All species have white or pale-green and -yellow flowers, 95% of which offer floral rewards in easily accessible open flowers to a wide variety of flower visitors. Only two endemic plants exist that offer floral resources to a specialized pollinator community; *Colea seychellarum* (Bignoniaceae; main visitor: endemic sunbird *Nectarinia dussumierii*) and *Glionnetia sericea* (Rubiaceae; native and alien hawkmoths such as *Agrilus*

convolvuli and *Cenophodes tamsi*). Both plant species have long tubular corollas and legitimate access to nectar is only possible with a long bill or proboscis. The relative abundance of alien plants was lowest at Bernica (ratio of alien to native plants = 0.03) and highest at Tea Plantation (0.97; Table 1). The abundance patterns of seedlings and saplings across all sites did not differ from that of the adult plant abundance (adult abundance \times origin; seedlings: $t = 0.85$, $P = 0.46$; saplings: $t = 2.95$, $P = 0.081$).

In total, we recorded 97 pollinator taxa (see Table 1 for site differences), of which 34 were identified to species (accounting for 74.8% of visits) and seven to family level. The remaining pollinators were identified to morphospecies level. Pollinators encompassed insects from six orders, two bird species (*N. dussumierii* and the alien fody *Foudia madagascariensis*, together responsible for 2.1% of all visits), and two endemic lizard species (the skink *Mabuya sechellensis* and the gecko *Phelsuma astriata*, 2% visits). Amongst the insects, the hymenopterans (excluding ants) were the second most species-rich group (16 spp.), accounting for the majority of visits (62.8%). Remaining visits were made by 42 species of Diptera (15.8%), 16 species of Coleoptera (9.8%), six species of Lepidoptera (0.3%) and 13 other taxa (7.2%). The origin of 54 pollinator taxa could be identified, of which 13 are endemic, 30 native, and 11 alien, accounting for 6%, 39.7%, and 43.8% of visits, respectively. Alien flower visitors included the honey bee (*A. mellifera adansonii*), wasps (e.g. *Polistes olivaceus*), birds (*Foudia madagascariensis*) and ants (e.g. *Technomyrmex albipes*).

The most abundant and active flower visitors were the alien honey bee *A. mellifera* (Apidae) and the native solitary bee *Lasioglossum mahense* (Halictidae) which were responsible for 33.5% and 23.3% of all visits, respectively. Both species appeared to be equally generalized in invaded and less invaded sites: *A. mellifera* and *L. mahense* interacted with 24 and 23 native and seven and six alien species, respectively. If we compare, however, the percentage of interaction frequency to alien plants, 73.7% and 29.7%, respectively, of all *A. mellifera* visits at the heavily invaded sites Tea Plantation and Trois Frères, were to alien flowers, while only 3.3% and $< 1\%$ of *L. mahense* visits were to alien flowers at these two sites (Fig. 2a). At the two least invaded sites Bernica and Copolia, both *A. mellifera* and *L. mahense* species spent similar proportions of their visits on alien flowers (mean 1.2% and 2.4%, respectively; Fig. 2a). Half of these shifts by honeybees from native to alien flowers were at the expense of visits to endemic palms (*Deckenia nobilis*, *Phoenixophorium borsigianum* and *Nephrosperma vanhoutteana*), which suffered a 39.5% decline in interaction frequency between the least and the most invaded sites by all pollinators combined. Further, 75% of visits to alien plants were by alien pollinators, 51.5% of which are carried out by *A. mellifera*, and only 4.6% by *L. mahense*.

POLLINATOR DIVERSITY AND INTERACTION FREQUENCY

Neither pollinator diversity nor interaction frequency to all native plant species changed significantly across the invasion

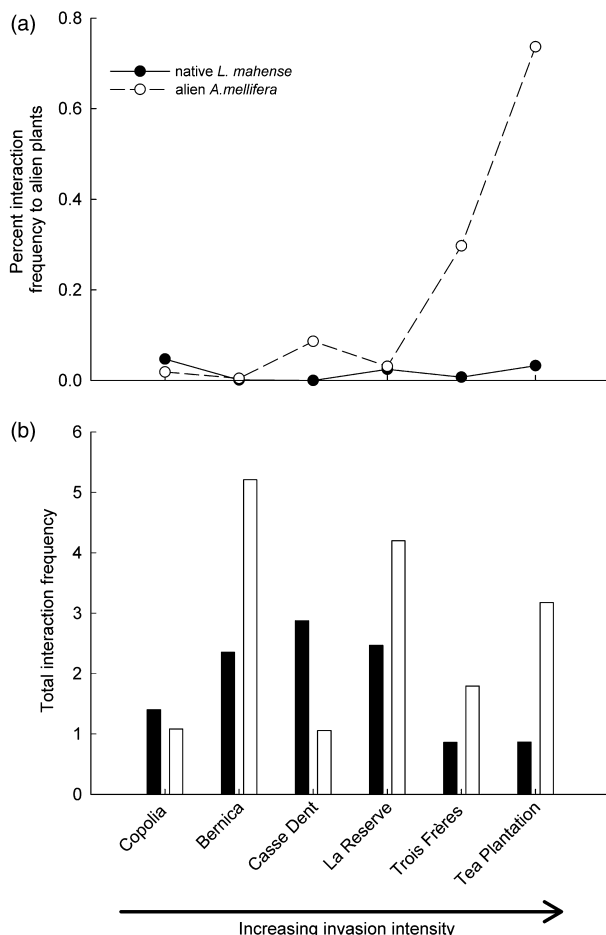


Fig. 2. (a) Percentage of interaction frequency to alien plants by the two most abundant and generalized pollinator species, the native solitary bee *Lasioglossum mahense* (full circles) and the introduced honey bee *Apis mellifera* (empty circles). (b) Total interaction frequency of *L. mahense* (black bars) and *A. mellifera* (empty bars). The sites are arranged by increasing invasion intensity from left to right (based on ratio of alien : native floral abundance). *Apis mellifera* shifted its visits from native plants to alien plants with increasing invasion intensity, but there was no consistent change in total interaction frequency of the two pollinator species along the invasion gradient.

gradient after accounting for floral abundance ($t = -1.82$, $P(\text{MCMC}) = 0.080$; $t = -1.48$, $P(\text{MCMC}) = 0.16$). Interaction frequency to the seven most common native plant species (*Paragenipa wrightii*, *Memecylon eleagni*, *Erythroxylum sechellarum*, *Canthium bibraceatum*, *Nephrosperma vanhoutteanum* and *Pheonicophorium borsigianum*) remained constant in the presence of alien flowering plants (combine model: $t = -1.34$, $P(\text{MCMC}) = 0.23$; individual models: $P(\text{MCMC}) > 0.1$).

REPRODUCTIVE SUCCESS

The lack of change in pollinator interaction frequency to native plants in the presence of invasives corresponded with their pollination success. Fruit set of the 16 most common native plant species did not change with invasion intensity ($Z = 0.89$, $P = 0.37$). Fruit set of the seven most common native plant species, however, increased slightly with invasion intensity

based on the ratio of native to alien flowers ($Z = 2.17$, $P = 0.030$), but not with invasion intensity based on the ratio of native to alien plants ($Z = 1.87$, $P = 0.24$) in the inselberg communities. Analysing the seven most common plants individually, fruit set remained constant across the invasion level apart from one endemic species, *Paragenipa wrightii*, which showed a slight increase in fruit set with invasion intensity ($Z = 3.96$, $P < 0.0001$; all other $P > 0.05$; Fig. 3). The power of our analysis allowed us to detect a fruit set effect size of 21% using the conservative value of $n = 6$ sites (critical value = 0.05, statistical power > 0.8), and it is possible that smaller differences in fruit set across sites might have been detected had data been available from more than six sites. There are, however, difficulties in unambiguously attributing such small differences to the degree of invasion on account of other random variables that might also influence fruit set and confound causal attribution of effects to the main explanatory variable.

QUANTITATIVE NETWORK PARAMETERS

In the full-season networks, lw_p decreased significantly with invasion ($S = 68$, $P = 0.017$) across the six inselberg sites, and lw_a , C_q and IE were not significantly affected by the presence of alien flowers in the network ($S = 38$, $P = 0.92$; $S = 62$, $P = 0.10$; $S = 54$, $P = 0.29$, respectively; Fig. 4). Similarly, lw_p decreased with invasion across all 48 temporal networks ($t = -2.55$, $P(\text{MCMC}) = 0.024$) but lw_a and C_q were independent of invasion (all network parameters log-transformed; lw_a : $t = -1.36$, $P(\text{MCMC}) = 0.22$; C_q : $t = 0.19$, $P(\text{MCMC}) = 0.83$). Each temporal network contained between three and 13 plants species (mean 8 spp.) and 8–28 pollinator species (mean 19 spp.).

Interaction evenness ranged from 0.77 ± 0.06 SD at Copolia to 0.66 ± 0.11 SD at Casse Dent, with an overall mean $IE = 0.72 \pm 0.11$ SD. Standardized IE (\bar{IE}) across temporal networks plotted against invasion intensity showed a clear nonlinear distribution (Fig. 5). At low levels of invasion, \bar{IE} was not affected by the presence of alien flowers in networks ($t = -1.09$, $P(\text{MCMC}) = 0.28$). When the ratio of alien to native flowers in a community exceeded a threshold value of $c. 0.5$ (33% of all flowers in the community belong to alien plants), \bar{IE} declined with increasing invasion ($t = -3.74$, $P(\text{MCMC}) = 0.0028$; Fig. 5). Further, the coefficient of variation of IE between temporal networks with and without alien flowers increased linearly with invasion intensity ($n = 6$, $P = 0.048$, $R^2 = 0.663$) suggesting greater fluctuations in IE in more heavily invaded sites. Qualitative connectance of native sub-networks was unaffected by a change in IE due to invasion (log-transformed; $t = -2.43$, $P(\text{MCMC}) = 0.12$) suggesting that the decline in IE did not disproportionately reduce the number of native interactions in the networks.

A decline in IE can be due to shifts in the proportion of strong and weak interactions to all plant species in the networks. There was no relative change in the interaction frequency of weak interactions with invasion intensity ($t = 1.39$, $P(\text{MCMC}) = 0.216$) but the total interaction frequency of the weak interactions decreased with invasion

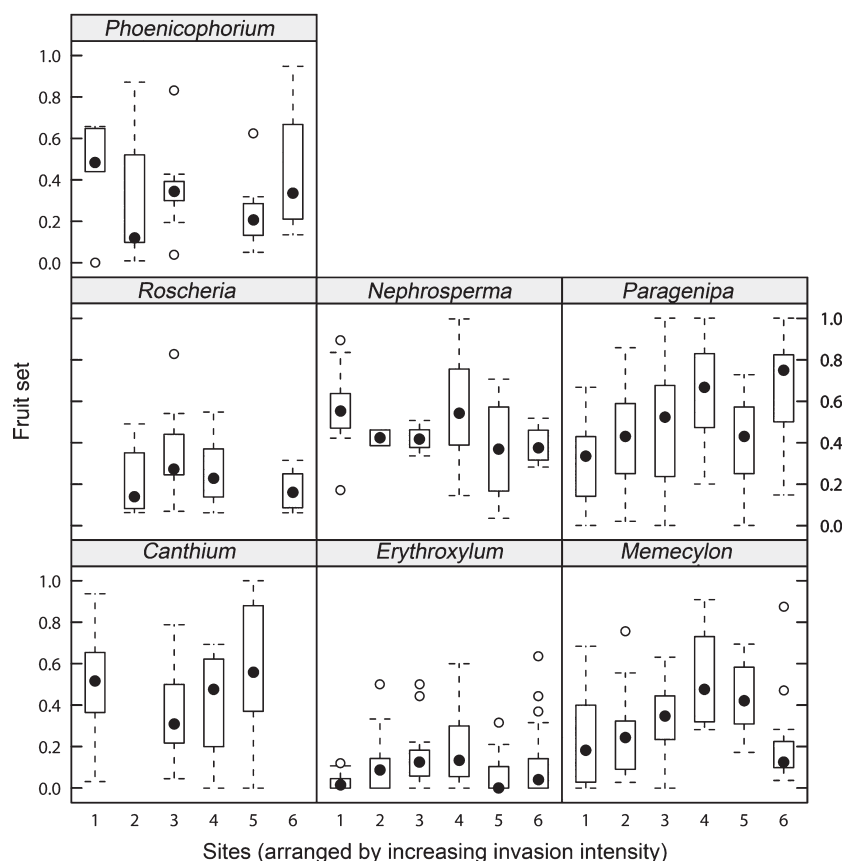


Fig. 3. Fruit set of the seven most common native plant species along the invasion gradient. Site 1 (Bernica) is the least and site 6 (Tea Plantation) the most invaded (ratio alien : native plant abundance; see Table 1). Box-plots show the median and 25th and 75th percentiles, and the whiskers indicate the maximum value or 1.5 times the interquartile range of the data. Individual empty circles represent outliers. Only *Paragenipa wrightii* ($P < 0.0001$) showed a significant trend towards higher fruit set at invaded sites.

($t = -2.68$, $P(\text{MCMC}) = 0.0096$). For strong interactions of the two most common pollinator species, the total interaction frequency of *A. mellifera* was unaffected by invasion (log transformed; $t = -0.71$, $P(\text{MCMC}) = 0.537$) but the relative importance of *A. mellifera* in the networks increased with invasion (square root transformed; $t = 2.72$, $P(\text{MCMC}) = 0.0017$). The native *L. mahense* showed little change with invasion; both total interaction frequency (square root transformed) and the relative importance of *L. mahense* in the networks was similar across the invasion gradient ($t = -1.76$, $P(\text{MCMC}) = 0.084$; $t = -1.28$, $P(\text{MCMC}) = 0.14$).

Discussion

Plant communities on Seychelles Inselbergs are subject to a varying degree of invasion by several alien plant species, with potential implications for reproductive mutualisms among native plants and their pollinators. Our study showed, however, that these native communities appeared relatively tolerant to disruption of mutualistic interactions by invasive species. Specifically, the number of pollinator species and interaction frequency to native plants were mostly unaffected by invasion. Indeed, fruit set of most native plant species was not impacted by alien plants, to the extent that an effect size of 21% could be detected statistically given the most conservative power of the test. The abundance of seedlings and saplings further showed that recruitment of native plants was directly related to adult population size independent of the degree of

invasion. Our results thus stand in contrast to several other studies that demonstrate a disruption of native plant–pollinator interactions by alien plant species with negative consequences for native plant reproduction (Grabas & Lavery 1999; Chittka & Schürkens 2001; Brown, Mitchell & Graham 2002; Tscheulin *et al.* 2009). For example, the dandelion species *Taraxacum officinale* invasive to Japan negatively affects pollinator visitation rates and seed set on the native congeneric *T. japonicum* when the species occur together (Kandori *et al.* 2009). Another study tested the effects of alien *Carpobrotus* species on native co-flowering plants on the Balearic island of Mallorca (Moragues & Traveset 2005). The authors described species-specific competitive, neutral and facilitative effects on reproductive success of four native plant species through indirect interactions with pollinators (see also Bartomeus, Vilà & Santamaría 2008). These studies are limited in that they investigate a small number of plant species, and most community level studies have not been followed through to seed or fruit production but focus instead on the effect of alien plant species on pollination network structure (but see Vázquez & Simberloff 2002). Our study is a community level study which does investigate reproductive processes from flower visitation to fruit set. Other more extensive studies have also highlighted that, despite the integration of alien species in native plant–pollinator networks, the impact on native plant reproduction may be smaller and subject to higher temporal variation than initially anticipated (Larson, Royer & Royer 2006; Bartomeus, Bosch & Vilà 2008).

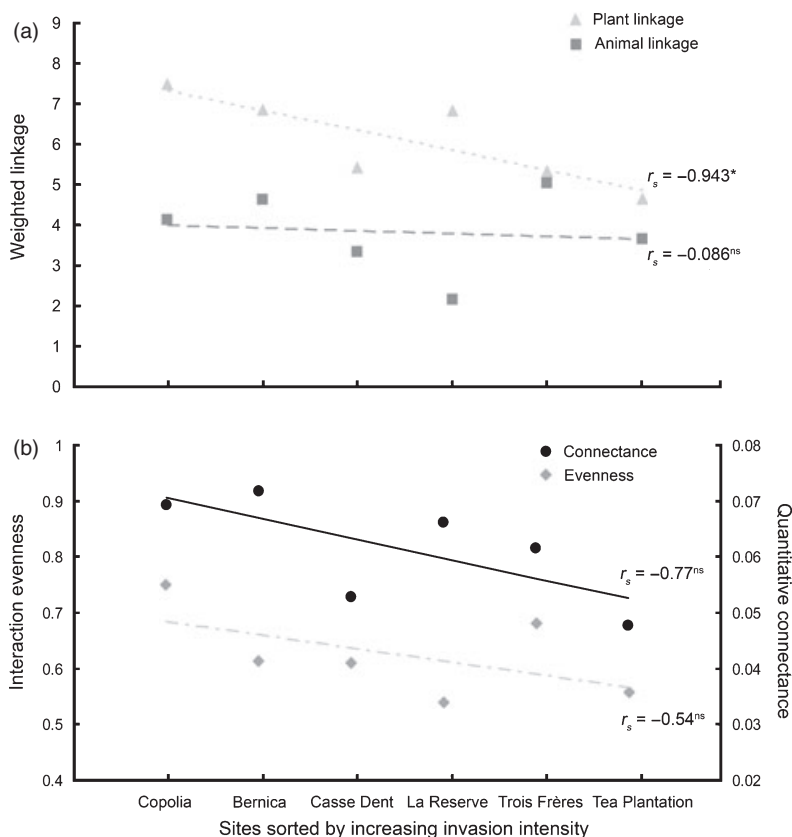


Fig. 4. Quantitative parameters of full-season networks plotted against the six inselberg sites sorted by the invasion intensity (ratio alien : native floral abundance). (a) Weighted plant linkage declines with invasion intensity (triangles and dotted line) while weighted animal linkage (squares and dashed line), (b) quantitative connectance (circles and full line) and interaction evenness (diamonds and dashed-dotted line) showed no significant change with across the plant invasion gradient.

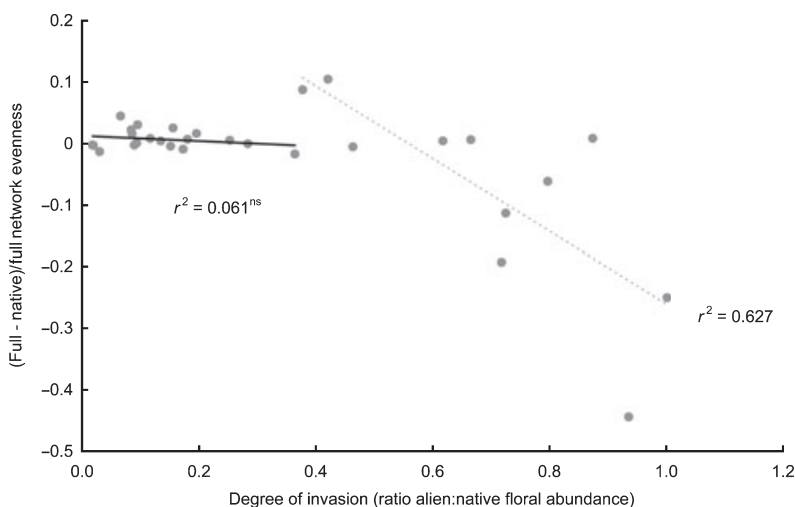


Fig. 5. Influence of alien flowers on interaction evenness (IE). For all monthly networks with alien flowers present ($n = 30$), we calculated the standardized change in interaction evenness $((IE_{full} - IE_{native}) / IE_{full})$ due to the presence of alien flowers, and plotted those against the ratio of alien to native floral abundance in the community. Low levels of invasion had little effect on interaction evenness, but an intermediate to high level of relative abundance of alien flowers in the networks resulted in a decline of interaction evenness.

To understand the mechanistic basis for apparent tolerance of native communities we need to explore the network patterns in more detail. While overall flower visitation and fruit set remained rather constant, it is possible that the identity of pollinators and patterns of interactions changed more substantially along the invasion gradient. Indeed, weighted plant linkage (a combined measure of the variety and strength of interactions for any one plant species with its pollinators) and IE (a measure of uniformity of interactions in a network) both decreased with increasing invasion intensity. In other words, following invasion the plant–pollinator networks became

effectively simpler and more heterogeneous, a pattern also found by Aizen, Morales & Morales (2008), yet still retained the key interactions such that fruit set remained similar. This has three implications. First, native plants become dependent on fewer pollinators and therefore more vulnerable to future declines in those pollinators (e.g. Memmott, Waser & Price 2004; Kaiser-Bunbury *et al.* 2010). Secondly, a simplification of pollinator diversity may reduce seed quality of native plants with potential detrimental long-term effects on the genetic diversity of the population (reviewed in Morales & Traveset 2008). And thirdly, the overall diversity of interactions declines

with uncertain implications for the functioning of the inselberg ecosystems (e.g. Fontaine *et al.* 2006). Thus, while native fruit set remains constant there are subtle changes in terms of community interactions. Further, the apparent tolerance of native inselberg communities could partly be a result of disturbance-related changes that occurred prior to the study. For example, some rare species may have gone extinct during initial disturbance and the plant and pollinator species that remain on inselbergs represent the subset of the original community that is more tolerant to plant invasion. While this may be true for pollinator species, it is unlikely to reflect a realistic scenario for native plant species as species composition has changed little since earlier description of inselberg communities (Proctor 1984).

Our work additionally suggests that IE, which has been directly linked to network robustness (Dunne, Williams & Martinez 2002; Tylianakis, Tscharnkte & Lewis 2007), may display split behaviour on either side of an invasion threshold. From the early stages of invasion up to the point at which around a third of all flowers belong to introduced plants there was little change in network structure, but beyond that point IE declined. A similar dichotomy with regard to the impact of invasive plants on pollinator interactions was shown by Aizen, Morales & Morales (2008). This pattern implies again some tolerance by native communities in terms of network restructuring in response to plant invasion. Furthermore, inselberg sites that were more invaded had much higher monthly variability in IE. Taken together, our results suggest that alien plant species, once present in sufficiently high numbers, can modify intrinsic network properties without showing obvious variation in pollinator richness, visitation patterns and fruit set on the community level. Up to now, it has only been shown at the species level that seed production of natives can depend on flower density of alien species (e.g. Muñoz & Cavieres 2008).

The IE results presented here may have arisen by abundant and generalized pollinator species strengthening existing links or by switching completely to other plant species. An alternative explanation is that weak interactions weaken further or disappear entirely (Aizen, Morales & Morales 2008). We showed that strong interactions explain declining IE with invasion. Given that there were no significant changes across sites in floral abundance, the observed decline in IE with increasing invasion is largely due to the shift by *A. mellifera* from native to alien flowers in invaded communities; it may not be primarily a function of changes in the abundance of flowers or pollinators, as proposed by Blüthgen *et al.* (2008). From the perspective of plants, alien species depended heavily on visits by alien pollinators. Nevertheless, even in highly invaded sites *A. mellifera* and other alien pollinators do continue to visit natives, and any shift in allegiances does not significantly impact upon fruit set of native plants across sites. *Apis mellifera* (and other ecologically equivalent alien pollinators) may therefore provide alternative pollinator services to native plants even where invasive plants are abundant, thereby affording insurance against loss of native pollinators.

It is clear that among these communities in the Seychelles there is a strong mutual dependency of alien plants and pollin-

ators. Such 'invader complexes' have been described elsewhere (Memmott & Waser 2002; Morales & Aizen 2002; Olesen, Eskildsen & Venkatasamy 2002; Morales & Aizen 2006; but see Aizen, Morales & Morales 2008), and our data suggest that interactions between aliens become increasingly pronounced at later stages of plant invasion. This pattern is also consistent with the results of a meta-analysis by Morales & Traveset (2009).

What conclusions can be drawn from our findings with regard to the viability of native inselberg communities? Plant–pollinator interactions and fruit set of native plants were little affected by alien plants in the communities when they occurred in low relative abundance. At low invasion intensity, it seems unlikely that rare or specialized pollinators are displaced as a result of indirect plant competition for pollination. Disruptions in mutualistic interactions are expected to set in with high levels of invasion intensity as shown by the decline in IE. The simultaneous increase in within-site temporal variation of IE supports previous studies that described plant–pollinator networks as very dynamic systems (Petanidou *et al.* 2008). This may partly be explained by the ability of pollinators to react quickly to resource availability on different spatial scales (Steffan-Dewenter *et al.* 2002; Dauber *et al.* 2009). While these disruptions do not implicitly reduce native plant fitness in our study, they could pose a threat to interaction diversity and system stability in more specialized systems with lower interaction redundancy (Memmott & Waser 2002; Memmott, Waser & Price 2004; Kaiser-Bunbury *et al.* 2010). Tylianakis, Tscharnkte & Lewis (2007) have shown that lower IE in food webs is associated with degraded habitat communities, a pattern also found in other biotic networks (Hawkins *et al.* 1999; Olesen, Eskildsen & Venkatasamy 2002; Bascompte, Jordano & Olesen 2006; Hejda, Pyšek & Jarošík 2009). The direct consequences of reduced IE (or increased interaction asymmetry) on the stability of mutualistic networks, however, are unknown. Our findings contribute to this debate insofar as they show that pollination interactions in invaded habitats become increasingly unevenly distributed, possibly due to changes in interaction frequency of a few pollinators that have strong interactions within the networks. We could not show whether these shifts result in a simplification of the network that is detrimental to native plants and pollinators alike. Most native mutualists persisted even in the heavily invaded sites, and the most important native pollinators remained faithful to the native plants. Our results highlight the importance of accounting for biological detail when interpreting underlying network structure, and raise the question of causality between anthropogenic disturbance of species interactions and ecosystem response.

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