ORIGINAL PAPER

A recipe for weed disaster in islands: a super-generalist native pollinator aided by a 'Parlourmaid' plant welcome new arrivals in Fiji

Sarah E. Hayes · Marika Tuiwawa · Mark I. Stevens · Michael P. Schwarz

Abstract In isolated islands with low pollinator diversity, it has been suggested that native pollinators should evolve into super-generalists that could facilitate the spread of exotic plant species that might otherwise rely on specialist pollinators. Consequently, in the absence of exotic pollinators isolated islands may still be particularly vulnerable to a wide variety of introduced plants. Fiji has a highly abundant and diverse introduced plant fauna, as well as a variety of introduced bee species, but has extremely low endemic bee fauna diversity. We examined bee–plant pollination networks in lowland regions of Viti Levu (Fiji) where there is only one endemic bee species, *Homalictus fijiensis*. We show that this bee is a super-generalist for introduced plants, and whilst introduced bee species can show high intensities of floral visits, they do not substantially increase the breadth of weeds receiving bee visits. Surprisingly, one introduced plant species, *Sphagneticola trilobata*, receives high visitations from introduced bee species, even though it spreads vegetatively. We regard this species as a 'Parlourmaid' weed that likely augments the spread of exotic bees without gaining pollination benefits. Our results indicate a 'twofold' promotion of invasive species, namely, super-generalist native pollinators can promote the spread of diverse introduced plants, and Parlourmaid plants provide resources that can promote the spread of introduced pollinators.

S. E. Hayes (✉) · M. P. Schwarz
School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia
e-mail: sarah.e.hayes1@gmail.com

M. Tuiwawa
South Pacific Regional Herbarium, University of the South Pacific, PO Box 1168, Suva, Fiji

M. I. Stevens
South Australian Museum, GPO Box 234, Adelaide, SA 5001, Australia

M. I. Stevens
School of Pharmacy and Medical Sciences, University of South Australia, Adelaide, SA, Australia

Introduction

Island ecosystems tend to have much lower species diversity than continental regions, but tend to have high levels of species endemism, and the reasons for this have been well explored in island biogeography studies (e.g. Gillespie and Roderick 2002; Kier et al. 2009). When islands are geographically well separated

from mainland regions, immigration rates for new species are expected to be low, and if island size is small then extinction rates are expected to be high (MacArthur and Wilson 1963). Combined, these two factors predict comparatively low species diversity, but high levels of endemism, though of course many further factors have been incorporated in island biogeography theory since the 1960s (e.g. Heaney and Patterson 1986; Heaney 2000; Lomolino 2000; Losos and Ricklefs 2009; Warren et al. 2015). The consequences of low species diversity in islands is especially important for understanding plant–pollinator networks and how these shape natural ecosystems, support agricultural industries, as well as influence the spread of exotic weeds.

Olesen and colleagues argued that if pollinator diversity in islands is very low, intra-specific competition within pollinator species should select for wide host breadth, leading to 'super-generalist' pollinators (Olesen et al. 2002). This argument has also been posited for other kinds of species interactions, such as host-predator networks (e.g. Gillespie et al. 2017). The presence of super-generalist species in island ecosystems can have potentially major consequences for understanding the dynamics of invasion biology. For example, if potential weeds require specialized pollinators, they may not be able to colonize new habitats unless those pollinators are already present or co-introduced. On the other hand, if island pollinators have evolved into super-generalists they may be pre-adapted to utilize a wide variety of novel plant species and consequently augment their pollination. The concept of 'invasional meltdown' by Simberloff and Von Holle (1999) refers to this interaction between weeds and introduced pollinators that facilitate the establishment of both. However, native pollinators have also been found to visit introduced plants, and can therefore be responsible for the spread of these plants (see Olesen et al. 2002).

Fiji has an extremely low diversity of endemic bee species with only four described species forming a monophyletic clade in the halictic genus *Homalictus* (Groom et al. 2013). Of these, only one species, *H. fijiensis*, occurs at elevations below 800 m asl (Michener 1979) where it is highly abundant. A recent study (Staines et al. 2017) shows that this species is able to collect pollen via pollen larceny from the introduced solanaceous weed *Solanum torvum* which otherwise requires buzz pollination (Liu and

Pemberton 2009). This pollen larceny by a non-buzz pollinator also seems to effect pollination of *S. torvum* (Staines et al. 2017) and suggests an unusual extension of host breadth that has consequences for the spread of weeds that otherwise have specialized pollinator needs.

Whilst *Homalictus* species are the only native bees in Fiji, eight bee species have been introduced. One of these is the purposefully introduced honeybee, *Apis mellifera*, which is commercially used for honey production but which has also become an unmanaged feral species. The remaining introduced species include the allodapine bee *Braunsapis puangensis* (Apidae, Xylocopinae) (Groom et al. 2015; da Silva et al. 2016), a buzz-pollinating anthophorine bee *Amegilla pulchra* (Apidae, Anthophorinae) (Groom et al. 2014), and five megachilid species from the genera *Megachile* and *Heriades* (Megachilidae) (Davies et al. 2013). Surprisingly, there are very few studies that have examined floral host use by native Fijian *Homalictus* bees (e.g. Staines et al. 2017; Crichton et al. 2018), and only two studies that have examined the floral hosts of introduced bee species. Prasad and Hodge (2013) found that on Viti Levu *B. puangensis* was a common visitor to the pantropical weed *Sphagneticola trilobata*, but although this weed produces abundant flowers, it predominantly spreads vegetatively and seed set is low (Qi et al. 2014). *Amegilla pulchra* is also now widespread on Viti Levu, and although it is a buzz pollinator, Groutsch et al. (2018) did not record it visiting any plants with poricidal anthers, such as the widespread weed *S. torvum*. It was also found to be largely restricted to garden ornamental plants that appear to have low risk of becoming naturalized weeds.

Collectively, these recent studies indicate a huge gap in our understanding of pollination networks involving bees in Fiji, despite the alarming number of weedy plant species in this archipelago (Parham 1958). The introduction of exotic plants into Fiji has been estimated to have increased the number of floral species in that region by ~ 50%, with a resulting exclusion of native species in many habitats (Ash 1992). A recent study by Shay et al. (2016) of plant–pollinator networks in another Pacific archipelago, the Ogasawara islands, indicated that a very high percentage of insect visitors to flowers were non-native species, suggesting that introduced pollinators could have major impacts on pollination networks in the

Pacific region. At present, there are no studies that allow us to estimate the potential effects of exotic pollinators on Fijian terrestrial ecosystems or on the spread of weedy plants.

Here we examine plant–pollinator networks for the only native lowland bee in Fiji, *Homalictus fijiensis*, and three introduced bee species in lowland regions of the major Fijian island of Viti Levu. We address two main questions: (1) does our data further support super-generalism in *H. fijiensis*, and (2) are the introductions to Fiji of three exotic bee species, *Apis mellifera*, *Braunsapis puangensis* and *Amegilla pulchra*, likely to augment the further spread of angiosperm weed species in Fiji?

Methods

Transect sites and bee–plant observation methods

Visitation data and specimens were collected on the main Fijian island of Viti Levu, in the South West Pacific (SWP). We observed plant–bee interactions at three sites, all of which were at elevations below 800 m asl, such that the only endemic bee species present was *H. fijiensis*. Main sites are shown in Fig. 1 and details listed in Table 1. The geographical coordinates and elevations for each transect within the sites are given in Online Resource 1, Table 1.

Transect positions included vegetation bordering roadside/tracksides, which consisted predominantly of introduced flora. Roadsides were surveyed over a period of 3 weeks during April between 0900 and 1700 hours, the main hours of bee extra-nidal activity (Rebola 2015), during all weather conditions. Floral visitation observations were carried out using transects 100 m in length and 6 m wide, along un-sealed roads/tracks. Transect width was split into 3 m on each side of the road/track. Each transect was separated by at least 100 m. Transects were walked slowly with observation time dependent upon density of flowering plants available, to a maximum duration of 20 min. For each transect, two observers simultaneously walked on opposite sides of the road/track for the length of the transect in the same direction. When a roadside did not permit a 100 m transect (e.g. it was intersected by a stream or steep cliffside), the road was walked haphazardly and continuously for up to a maximum of 20 min (Nielsen and Bascompte 2007; Spengler et al. 2011; Ploquin et al. 2013).

During the survey, each observer observed the flowering plants within the 3 m width of the transect, and up to 1 m in front of them (Lopezaraiza-Mikel et al. 2007). When an observer saw a bee land on a

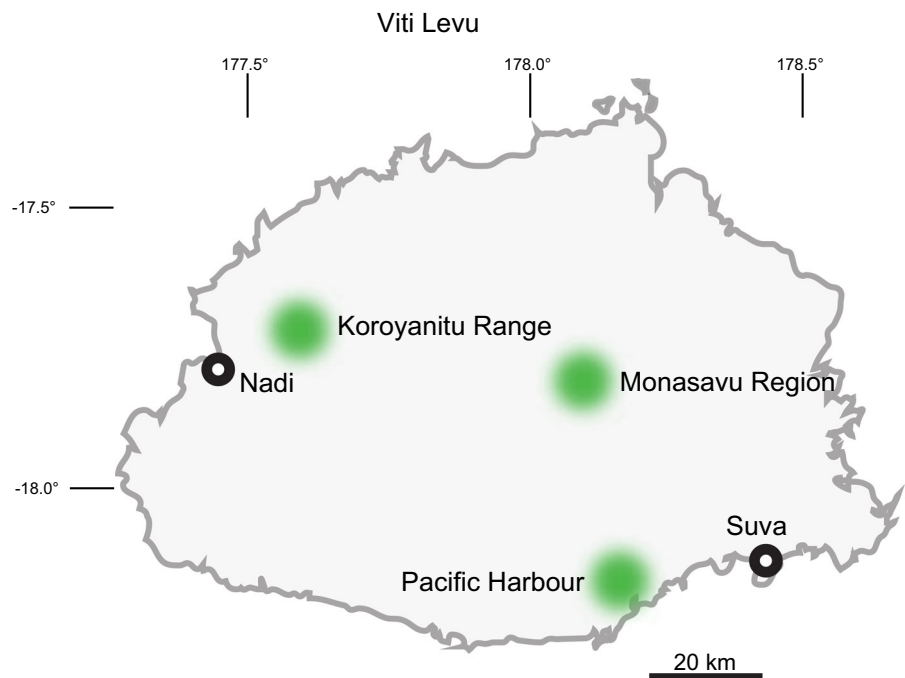**Fig. 1** Map indicating transect locations on the island of Viti Levu, Fiji

Main site location	Sampling dates	Site habitat description	Total transects walked
Koroyanitu mountain range	19-April-2016 to 21-April-2016	Small villages amongst grassland and subsistence farmland	11
Monasavu Dam region	23-April-2016 25-April-2016	Farmland and small villages, interspersed with forested mountains	10
Pacific Harbour region	27-April-2016	Farmland and small villages, interspersed with forested mountains	6

flower within the observation area, the bee was captured using a sweep net or else visually recorded if it could be confidently identified. The plant species being visited was identified according to plant species guides (Whistler 1995; Thaman 2012) and photos were taken of the plant's morphological characteristics. After each bee was captured, it was transferred into an individual vial containing 99% ethanol. Each individual captured, and each individual recorded as a visual observation, was classified as a bee–flower interaction and recorded as frequency data to be used as a single weight for the network analysis. If an individual bee was seen to be visiting the same individual flowering plant repeatedly during a transect walk, this was recorded as one interaction only.

Statistical analysis

Statistical analyses were carried out using SPSS version 23 for Windows, the Bipartite package version 2.06.1 (Dormann et al. 2008) and the Vegan package version 2.3-4 (Oksanen et al. 2016), both implemented in R version 3.3.0, and EstimateS version 9.1.0 (Colwell 2013). The function *plotweb* in Bipartite was used to provide a visual overview of the network. The functions of *dfun*, and *H2* in Bipartite were used to explore specialisation in terms of d' (Blüthgen et al. 2006), and niche partitioning ($H2'$) (Blüthgen et al. 2006). The function *specieslevel* in Bipartite was used to look at the degree (number of host species) of each bee and plant species and species strength (dependency of plant species on bee species). Then for C score (often interpreted as competitive exclusion) and robustness (robustness of system to loss of species) of the network, function *networklevel* in Bipartite was used. We also examined nestedness for transects with

and without *Sp. trilobata*, and an overall network including all transects regardless of *Sp. trilobata* presence or absence, by calculating WNODF (Almeida-Neto and Ulrich 2011) values using *nestednodf* in the Vegan package. This function measures nestedness for both plants and bees separately and for the interaction matrix as a whole. The significance of row, column and whole-matrix values was assessed using the *oecosimul* function in Vegan with 1000 randomized simulations. For *oecosimul* we used the *r00_both* algorithm which keeps the total matrix count sum constant, but shuffles cells and individuals among cells.

EstimateS was used to estimate the Shannon–Weiner diversity index and Chao1 diversity index (Chao et al. 2005) of bee species in the overall network using rarefaction analyses with 95% confidence intervals.

Mann–Whitney U tests were conducted in SPSS to determine whether there were significant differences in frequencies of *H. fijiensis*, *Ap. mellifera* and *B. puangensis* interactions with plants for data gathered during light rain or no rain, overcast conditions or sunny conditions, or whether there were differences between a 100 m transect or haphazard 20 min walk. We did not include data from *Am. Pulchra* in this test as the observed number of interactions was too small to allow for statistically meaningful results. Nonparametric correlation and Pearson's χ^2 correlation analyses were carried out for abundances of all bee species to explore covariance in their abundances.

Results

Analyses showed that there were no significant differences in visitation frequencies between different weather conditions including; light rain versus no rain, overcast conditions versus sunny conditions, or whether a 100 m transect versus haphazard 20 min walk was used (Online Resource 1, Table 2). All flowering species that were visited by bees, were flowering for the entire sampling period.

A total of 27 transects were conducted (Table 1) and the total observation time was 540 min. The total number of bee–flower interaction events was 174, with the highest number of interactions from *Ap. mellifera* (N = 81 interactions), followed by *H. fijiensis* (62), *B. puangensis* (24) and *Am. pulchra* (7). The percentage of transects that each species was recorded in was: *Ap. mellifera* (59.26%), *H. fijiensis* (44.44%), *B. puangensis* (33.33%) and *Am. pulchra* (7.41%), and the percentage of observations recorded for each bee species within each site is listed in Table 2.

Visitation frequency and host species

A network graph indicating the relative proportion of visits by each bee species to each plant over the entire sampling period is given in Fig. 2. A table providing species and family name, and origin and status information for plant species present within the network, is provided in Online Resource 1, Table 3. The majority of bee–flower interactions involved *Sphagneticola trilobata* (with 53 visits), visited by *Ap. mellifera*, *H. fijiensis* and *B. puangensis*. The smallest number of bee–flower interactions (1 visit only) involved *Mimosa pudica* and *Trichospermum calyculata*, both visited by *B. puangensis* (Fig. 2). The most common host plant species for each bee is as follows; *Ludwigia octovalis* for *H. fijiensis* (with 12 visits), *Sp. trilobata* for both *Ap. mellifera* (34 visits) and *B. paungensis* (15 visits), and *Stachytaypheta uvticifolia* for *Am. pulchra* (6 visits). Ten of the 19

plant species in the transects had visitation by only one pollinator species, whereas all four bee species visited *Triumfetta rhomboidea* (Table 3).

In Fig. 2 the most commonly visited plant was *Sp. trilobata*, which comprised 42% of all flower visits by *Ap. mellifera*, 63% for *B. puangensis*, but only 6.5% for *H. fijiensis* and 0% for *Am. pulchra*. Interestingly, the spread of this plant is almost entirely vegetative (Thaman 1999; Qi et al. 2014), such that bee visits are unlikely to influence local abundance of this weed (but see discussion below). To examine how the presence of this plant may influence pollinator visitation and the spread of weeds via pollination services, we constructed a pair of network graphs which showed the relative proportion of visits by each bee species to each plant, within transects including *Sp. trilobata* (Fig. 3a), and transects without *Sp. trilobata* (Fig. 3b).

*Sphagneticola trilobata* present and absent networks

In the *Sp. trilobata* present network (Fig. 3a), *Ap. mellifera* exhibited the greatest number of bee/plant interactions (34), with 100% of its interactions on the *Sp. trilobata*. *H. fijiensis* accounted for 18 of the bee/plant interactions, spending 22.2% of its time on *Sp. trilobata*, and the rest of its time on six other species indicating that this bee species has the widest host range within this network. *Braunsapis paungensis* had a plant visitation of 17, spent 88.2% of its time on *Sp. trilobata*, and then the rest of its time on two other plant species. *Amegilla pulchra* had seven plant visitations, and was never recorded visiting *Sp. trilobata*.

In the *Sp. trilobata* absent network (Fig. 3b), *H. fijiensis* exhibited the widest host range within this network (9) but had only 44 bee/flower interactions, compared to *Ap. mellifera* with the greatest number of bee/flower interactions (47) but a smaller host range of seven. *Braunsapis paungensis* made a total of seven

Table 2 Percentage (%) of observations that were recorded in each site for each species

Site	Percentage (%) of observations			
	Apis	*Homalictus*	*Braunsapis*	*Amegilla*
Koroyanitu mountain range	61	22	14.63	2.44
Monosavu Dam	51.28	28.21	20.51	0
Pacific Harbour	29.09	56.36	3.63	10.91

Fig. 2 Bipartite plant–pollinator network construction of quantitative observation network. Plant species are given in the upper boxes, and bee species in the lower boxes. Lines represent weighted interaction frequencies between bee and plant species. Grey boxes indicate native plants and bee species, black boxes indicate introduced species
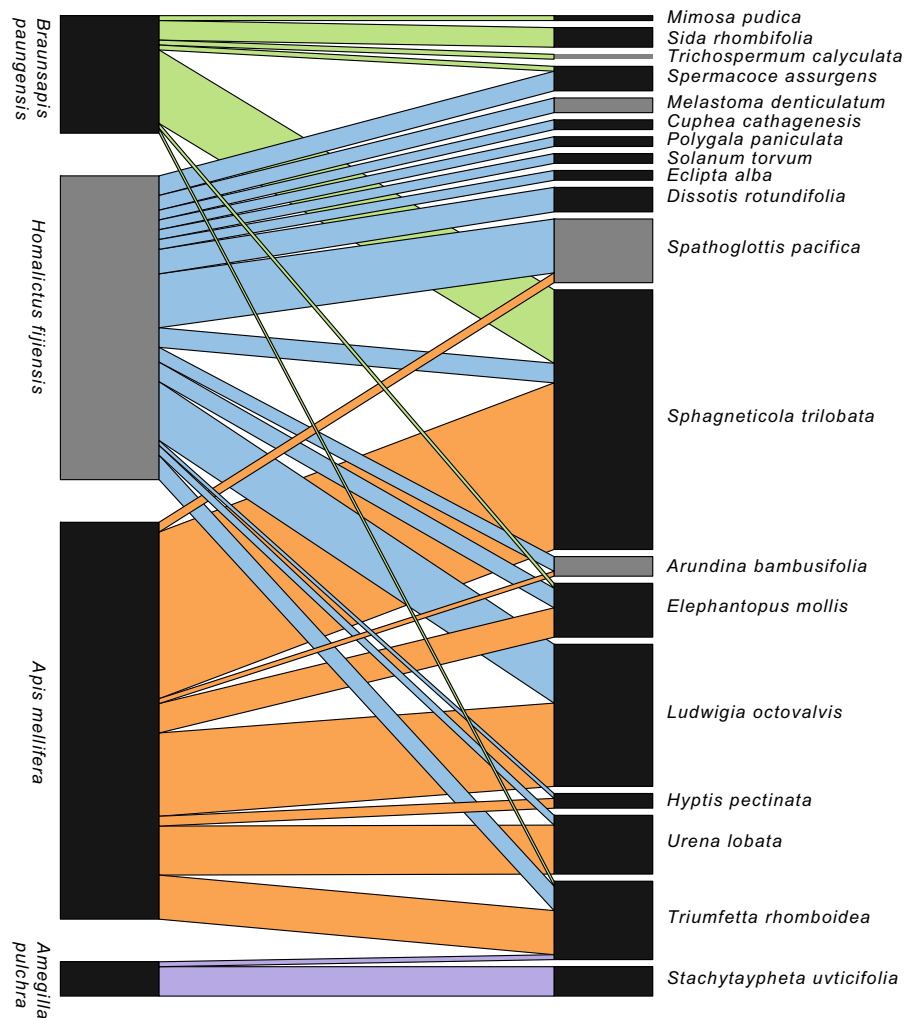
visits, with a host range of four, and *Am. pulchra* also made seven visits, but with a host range of only two.

Network and Species level statistics

For the overall network, the highest individual specialisation (d') on plant species was found for *Am. pulchra* (d' = 0.86), followed by *B. puangensis* (0.43), *H. fijiensis* (0.38) and then *Ap. mellifera* (0.33). The floral host richness estimated using the Chao1 index, was highest for *H. fijiensis* (Chao1 = 9.7) and lowest for *Am. pulchra* (Chao1 = 0.69) (Fig. 4). The floral host diversity estimated using the Shannon–Weiner estimate, was highest for *H. fijiensis* (SW = 2.02) and lowest for *Am. pulchra* (SW = 0). Species strength was highest for *H. fijiensis* (10.06), followed

by *Ap. mellifera* (4.24), *B. puangensis* (3.64), and then *Am. pulchra* (1.06).

A WNODF value of 4.15 was obtained, with a significant nestedness (P = 0.01). Nestedness for bees and plants was also found to be significant (P = 0.01 for both). A $H2'$ value of 0.43 was found for the overall network. The C score value of bee and plant species was 0.40 and 0.33, respectively. Therefore, the network matrices were tightly packed and nested in a way that each species interacts with species that are more generalist than itself, and niche partitioning of the network was moderate, indicating an overall moderate interconnection. Competitive displacement between species is low to moderate. Robustness was estimated at 0.63 for the entire network, a moderately

Table 3 Quantitative observation network plant species degree (number of pollinator species as visitors), and which species of bee visit the plant

Species	Degree	Bee species visitor
Triumfetta rhomboidea	4	*Apis, Homalictus, Braunsapis* and *Amegilla*
Elephantopus mollis	3	*Apis, Homalictus* and *Braunsapis*
Sphagneticola trilobata	3	*Apis, Homalictus* and *Braunsapis*
Spermacoce assurgens	2	*Homalictus* and *Braunsapis*
Urena lobata	2	*Apis* and *Homalictus*
Plectranthus amboinicus	2	*Apis* and *Homalictus*
Spathoglottis pacifica	2	*Apis* and *Homalictus*
Arundina bambusifolia	2	*Apis* and *Homalictus*
Ludwigia octovalvis	2	*Apis* and *Homalictus*
Stachytaypheta uvticifolia	1	*Amegilla*
Mimosa pudica	1	*Braunsapis*
Cuphea cathagenesis	1	*Homalictus*
Polygala paniculata	1	*Homalictus*
Solanum torvum	1	*Homalictus*
Sida rhombifolia	1	*Braunsapis*
Melastoma denticulatum	1	*Homalictus*
Dissotis rotundifolia	1	*Homalictus*
Eclipta alba	1	*Homalictus*
Trichospermum calyculata	1	*Braunsapis*

Apis refers to *A. mellifera*, *Homalictus* refers to *Homalictus fijiensis*, *Braunsapis* refers to *B. puangensis* and *Amegilla* refers to *A. pulchra*

high value that indicates network resilience against extinction.

Sphagneticola trilobata *present network*

The highest individual specialisation (d') on plant species was found for *Am. pulchra* ($d' = 1.0$), followed by *H. fijiensis* (0.54), *Ap. mellifera* (0.43) and then *B. puangensis* (0.14). The host breadth of each species was as follows; one for *Ap. mellifera*, two for *Am. pulchra*, three for *B. puangensis*, and seven for *H.fijiensis*. Species strength was highest for *H.fijiensis* (5.87), followed by *Am. pulchra* (2.00), *B. puangensis* (1.48) and then *Ap. mellifera* (0.64).

We obtained a WNODF value of 0.92 which was significant ($P = 0.005$). Nestedness for plants was significant ($P = 0.003$) but was non-significant for bees ($P = 0.652$). We also obtained an H2′ value of 0.84 for the *Sp. trilobata* present network. This indicates that for the *Sp. trilobata* present transects, network matrices were not as tightly packed or nested as for the *Sp. trilobata* absent transects (as shown in results below), and hence lower interconnection within the network. The C score for bee and plant species within this network was found to be 0.54 and 0.47, respectively. This is concordant with competitive displacement among bee and plant species. However, it is also possible that these results reflect plant-specific preferences; for example the high visitation rates of *Ap. mellifera* to *Sp. trilobata* could reflect colony-level recruitment. The robustness value of bee species to the loss of plant species is 0.74, whereas the robustness value of plant species to the loss of bee species is 0.55.

Sphagneticola trilobata *absent network*

Amegilla pulchra showed a decrease of 0.16 in specialisation compared to its specialisation in the *Sp. trilobata* present network ($d' = 1.0$), but still had the highest individual specialisation ($d' = 0.84$) on plant species. *Braunsapis puangensis* showed a large increase in specialisation when *Sp. trilobata* was absent (0.71). *Apis mellifera* and *H. fijiensis* both showed a decrease in specialisation to (0.33) and (0.27), respectively, with *H. fijiensis* being the least specialised in this network. The host breadth of each species was as follows; seven for *Ap. mellifera*, nine for *H. fijiensis*, four for *B. puangensis*, and two for *Am. Pulchra*. Species strength was highest for *H. fijiensis* (5.12), followed by *Ap. mellifera* (3.65), *B. puangensis* (2.16), and then *Am. pulchra* (1.06).

Fig. 3 Bipartite plant–
pollinator network
construction of quantitative
observation network
including, **a** *Sphagneticola
trilobata* present,
b *Sphagneticola trilobata*
absent. Plant species are
given in the upper boxes,
and bee species in the lower
boxes. Grey boxes indicate
native plants and bee
species, black boxes
indicate introduced species
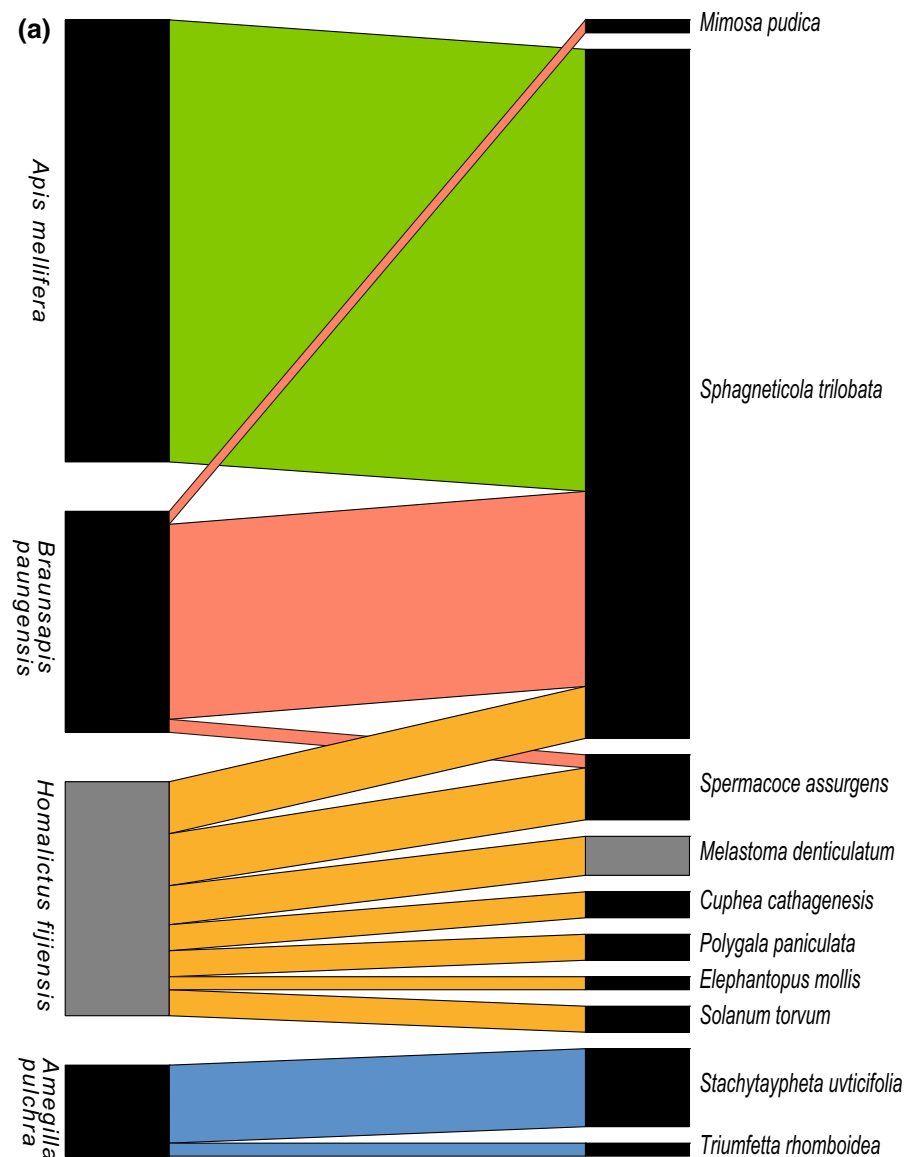
A WNODF value of 1.26 ($P = 0.330$ and a H2′ value of 0.45 was found when *Sp. trilobata* was absent. This indicates that the network matrices are packed or nested in a way that each species interacts more with species that are more generalist than itself. Interestingly nestedness for plants was non-significant ($P = 0.500$), whereas for bees it was significant ($P = 0.003$). Niche partitioning was found to be lower than the *Sp. trilobata* present network (H2′ = 0.84), where there was a higher level of overlap between pollinators' use of host species. The C-score for both bee and plant species within this network was found to be 0.36. This indicates a lower competitive displacement, or lower differences in floral preference, within bee and plant species, as compared to the *Sp. trilobata* present network. The robustness value of bee species to the loss of plant species is 0.84, whereas the robustness value of plant species to the loss of bee species is 0.65. These values are higher than what was found for the *Sp. trilobata* present network.

Fig. 3 continued
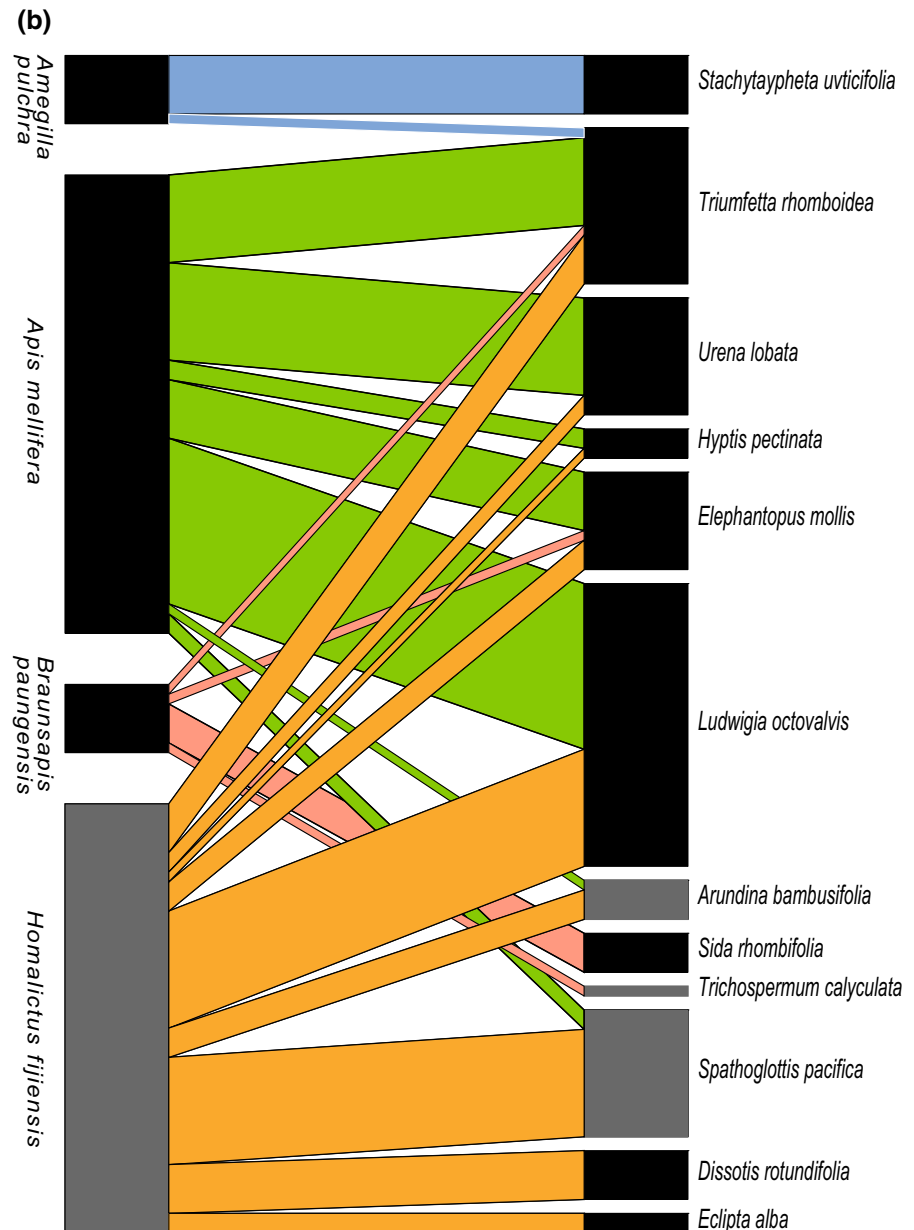
Correlation between endemic and introduced bee species

Bivariate correlation analyses and Pearson's χ^2 analyses showed that the visitation frequency of *H. fijiensis* within each transect did not significantly vary with the visitation frequency of *B. puangensis* (Spearman's ρ correlation coefficient: 0.039, $P = 0.885$), *Ap. mellifera* ($\rho = -0.059$, $P = 0.783$), or when *B. puangensis*, *Ap. mellifera* and *Am. pulchra* were combined ($\rho = 0.183$, $P = 0.393$). In addition, the presence of *H. fijiensis* was not associated with the presence of any of the three exotic bee species combined (Pearson's χ^2: 2.579, $P = 0.108$).

Discussion

We were surprised to find that of the total of 174 observed bee–plant interactions, only 21 were with
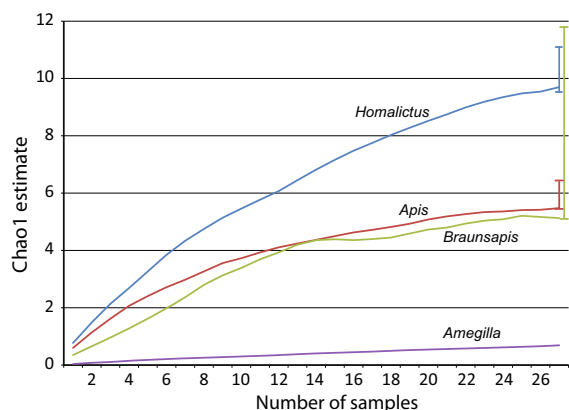
Fig. 4 Graph of Chao1 estimates (host plant species richness) for all bee species in the observation network. 95% confidence intervals (CI) were estimated at 27 rarefaction samples, and the slight differences in horizontal positioning of CI bars are only to increase figure clarity. *Amegilla pulchra* is disregarded in the 95% CI analysis as the sample size was too small for meaningful estimation

indigenous plants, comprising only four species (Fig. 2), and the majority of all interactions were focussed on the introduced species *Spahneticola trilobata* which reproduces vegetatively. Therefore, the vast majority of plant species that were involved in interactions were introduced plant species, and majority of plant species present in roadside angiosperm communities were introduced. This discrepancy between indigenous and introduced plant species was less exaggerated for bee species, where 62 of the interactions involved the endemic *H. fijiensis* and 81 interactions involved the introduced *Ap. mellifera*. Of the four native plant species, only one species, *Trichospermum calyculatum*, did not receive visits from *H. fijiensis* (and was instead visited by *B. paungensis* only), *M. denticulatum* was only visited by *H. fijiensis*, whereas the other two native plant species *Sp. pacifica* and *A. bambusifolia*, were visited by both *Ap. mellifera* and *H. fijiensis*.

Homalictus fijiensis as a super-generalist

Our results indicate that *H. fijiensis* had the largest species richness of host plants, visiting 84% of plant species within the network and holding the highest plant species richness estimate (Chao1 index), and also showed resilience to the presence of the introduced bee species. *Homalictus fijiensis* has previously been assumed to be a super-generalist (Groom et al.

2013) because of theoretical expectations for low pollinator diversity in islands (Olesen et al. 2002), and recently Crichton et al. (2018) supported this assumption. Our results are concordant with these findings. Endemic super-generalisation on island ecosystems can be explained by low pollinator diversity and high plant diversity, leading to wide floral niches and super-generalisation, and several other studies have indicated endemic super-generalisation on other island ecosystems (Olesen et al. 2002; Padrón et al. 2009; Sugiura 2010; Traveset et al. 2013).

Super-generalism by *H. fijiensis* is not only suggested by the breadth of its host species, but also by its visits to two plant species that normally require buzz-pollination. Staines et al. (2017) showed that *H. fijiensis* is able to access pollen from *Solanum torvum* by chewing into anther tips and is likely to effect pollination in this plant. Although we observed few visits by *H. fijiensis* to *S. torvum*, we did observe visits by this bee to another introduced buzz-pollinated plant, *Dissotis rotundifolia*. We did not record bee behaviours during these visits, but given the pollen larceny of *S. torvum* by *H. fijiensis* recorded by Staines et al. (2017), a similar larceny of *D. rotundifolia* is possible. This possibility of pollen larceny is further suggested in that *D. rotundifolia*, like other Melastomaceae, does not produce nectar rewards and was not visited by introduced bees in our transects.

Homalictus fijiensis was found to have a higher specialisation of host plants than *Ap. mellifera*, which seems counterintuitive to our super-generalist finding. However, "specialisation" in this context (using d') is a measure of the deviation of a pollinator's actual visits from expected visits based on host plant availability (Blüthgen et al. 2006). Therefore, whilst *H. fijiensis* is a super-generalist, with the widest range of plant hosts, many of its host plants were not commonly visited in the network as a whole. This is supported in the *Sp. trilobata* absent network, where *Ap. mellifera* becomes more specialised than *H. fijiensis*, due to its most common host (and the host being commonly visited within the entire network) being absent.

Within plant–pollinator networks, visitation to alien plant species is not always preferred, but can be a result of relative abundance and richness of alien plant species (Williams et al. 2011). *Apis mellifera* usually concentrates visits to certain plant species, using colony recruitment towards species that have

higher reward:effort ratios (Beekman and Ratnieks 2000). Given that the majority of the plants identified within the network are introduced, our results are therefore interesting in that many host plants visited by *H. fijiensis* received few or no visits from *Ap. mellifera*. One possibility is that *Ap. mellifera* is able to recruit hive mates to plants with higher floral rewards and/or that it is able to outcompete or exclude *H. fijiensis* from. We found no significant correlation between the presence and visitation frequency of *Ap. mellifera* and *H. fijiensis*, and *B. paungensis* and *H. fijiensis*.

Interestingly, in our *Sp. trilobata* present transects, all *Ap. mellifera* and most *B. puangensis* visits were to this weed, whilst *H. fijiensis* had a much broader host breadth. *Homalictus fijiensis* may therefore be important for maintaining wide pollination services when *Sp. trilobata* is present. Further studies are needed to examine whether such floral breadth also occurs in areas with greater indigenous plant richness.

'Parlourmaid' plants, asymmetric facilitation and invader meltdown

Our network analyses indicate that the pan-tropical invasive weed *Sp. trilobata* received a high proportion of visits from *Ap. mellifera* and *B. puangensis*. This is interesting because *Sp. trilobata* predominantly spreads vegetatively. Qi et al. (2014) found that germination of seeds produced by *Sp. trilobata* are inhibited by the dense vegetative mats formed by this weed, so pollination is unlikely to influence further spreading in areas it has already invaded. *Sphagneticola trilobata* was introduced into Fiji in the 1970s and has rapidly become a major and ubiquitous weed in that region (Thaman 1999).

The high visitation rates of *Ap. mellifera* and *B. puangensis* to *Sp. trilobata* indicate floral preferences for these bees that are not matched by *H. fijensis*. Consequently, *Sp. trilobata* is likely to provide floral resources that disproportionately help the success of these two introduced bee species, whilst receiving few benefits in areas where it is already established. This is very different from the notion of 'invader meltdowns' where introduced plants and pollinators both benefit from their co-introductions. Instead, we can therefore think of *Sp. trilobata* as a 'Parlourmaid' species that 'welcomes guests into a house' whilst receiving only minimal benefits. This is a different situation from

invader complexes (D'Antonio and Dudley 1993), where both introduced plants and pollinators benefit from their interactions, but it may be similar to some one-way facilitations in wetland ecosystems (Meza-Lopez and Siemann 2015).

Importantly, our results show broader floral host ranges for both *Ap. mellifera* and *H. fijiensis* when *Sp. trilobata* is absent. This suggests that *Sp. trilobata* could reduce pollination services to other plants whilst benefitting introduced bees, but in the process receive few benefits itself. Our analyses also suggest that reduced connectance in regions where *Sp. trilobata* is present may also increase extinction proneness.

Conclusion

Our findings support the hypothesis that island native super-generalist pollinators can provide pollination services to a wide variety of introduced plants, some of which can have specialised pollinator needs. At the same time, we find that a major pan-tropical weed, *Sp. trilobata*, provides disproportionately higher floral resources for introduced bee species, compared to the native bee species. The combination of a native super-generalist pollinator and an exotic Parlourmaid plant that supports exotic pollinators suggests an alarming vulnerability of tropical island ecosystems to ecological disruption. Whilst *H. fijiensis* may be resilient to the effects of introduced bees due to its floral host breadth, it is possible that this may change as exotic bee populations increase.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. Environ Model Softw 26:173–178

Ash J (1992) Vegetation ecology of Fiji: past, present, and future perspectives. Pac Sci 46:111–127

Beekman M, Ratnieks F (2000) Long-range foraging by the honey-bee, *Apis mellifera* L. Funct Ecol 14:490–496. https://doi.org/10.1046/j.1365-2435.2000.00443.x

Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. BMC Ecol 6:1–12. https://doi.org/10.1186/1472-6785-6-9

Chao A, Chazdon RL, Colwell RK, Shen T-J (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol Lett 8:148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x

Colwell R (2013) EstimateS: Statistical estimation of richness and shared species from samples. Version 9

Crichton A, Francis N, Doherty S, Tuiwawa M, Hayes S, Stevens MI, Schwarz MP (2018) Low endemic bee diversity and very wide host range in lowland Fiji: support for the pollinator super-generalist hypothesis in island biogeography. Pac Conserv Biol. https://doi.org/10.1071/pc18037

D'Antonio C, Dudley T (1993) Alien species: the insidious invasion of ecosystems by plants and animals from around the world has become a major environmental problem. Pac Discov 1993(summer):9–11

da Silva CRB, Groom SVC, Stevens MI, Schwarz MP (2016) Current status of the introduced allodapine bee *Braunsapis puangensis* (Hymenoptera: Apidae) in Fiji. Aust Entomol 55:43–48. https://doi.org/10.1111/aen.12149

Davies OK, Groom SV, Ngo HT, Stevens MI, Schwarz MP (2013) Diversity and Origins of Fijian Leaf-Cutter Bees (Megachilidae). Pac Sci 67:561–570. https://doi.org/10.2984/67.4.7

Dormann CF, Gruber B, Fruend J (2008) Introducing the bipartite package: analysing ecological networks. R News 9:8–11. ISSN 1609-3631

Gillespie RG, Roderick GK (2002) Arthropods on Islands: colonization, speciation, and conservation. Annu Rev Entomol 47:595–632. https://doi.org/10.1146/annurev.ento.47.091201.145244

Gillespie R, Brewer M, Roderick G (2017) Ancient biogeography of generalist predators on remote oceanic islands. J Biogeogr 44:1098–1109. https://doi.org/10.1111/jbi.12967

Groom SV, Stevens MI, Schwarz MP (2013) Diversification of Fijian halictine bees: insights into a recent island radiation. Mol Phylogenet Evol 68:582–594. https://doi.org/10.1016/j.ympev.2013.04.015

Groom SVC, Stevens MI, Schwarz MP (2014) Parallel responses of bees to Pleistocene climate change in three isolated archipelagos of the southwestern Pacific. Proc R Soc Lond B Biol Sci 281:20133293. https://doi.org/10.1098/rspb.2013.3293

Groom SV, Tuiwawa MV, Stevens MI, Schwarz MP (2015) Recent introduction of an allodapine bee into Fiji: a new model system for understanding biological invasions by pollinators. Insect Sci 22:532–540. https://doi.org/10.1111/1744-7917.12136

Groutsch JK, Miller NC, Tuiwawa M, Hayes SE, Stevens MI, Schwarz MP (2018) Not all exotic pollinator introductions are bad: an introduced buzz-pollinating bee *Amegilla pulchra* (Hymenoptera: Apidae) in Fiji indicates little potential for enhancing the spread of weeds. Aust Entomol. https://doi.org/10.1111/aen.12346

Heaney LR (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Glob Ecol Biogeogr 9:59–74. https://doi.org/10.1046/j.1365-2699.2000.00163.x

Heaney LR, Patterson BD (1986) Island biogeography of mammals. Academic, London

Kier G et al (2009) A global assessment of endemism and species richness across island and mainland regions. Proc Natl Acad Sci 106:9322–9327. https://doi.org/10.1073/pnas.0810306106

Liu H, Pemberton RW (2009) Solitary invasive orchid bee outperforms co-occurring native bees to promote fruit set of an invasive *Solanum*. Oecologia 159:515–525. https://doi.org/10.1007/s00442-008-1232-6

Lomolino MV (2000) A call for a new paradigm of island biogeography. Glob Ecol Biogeogr 9:1–6. https://doi.org/10.1046/j.1365-2699.2000.00185.x

Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmott J (2007) The impact of an alien plant on a native plant–pollinator network: an experimental approach. Ecol Lett 10:539–550. https://doi.org/10.1111/j.1461-0248.2007.01055.x

Losos JB, Ricklefs RE (2009) The theory of island biogeography revisited. Princeton University Press, Princeton

MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution 17:373–387. https://doi.org/10.1111/j.1558-5646.1963.tb03295.x

Meza-Lopez M, Siemann E (2015) Experimental test of the invasional meltdown hypothesis: an exotic herbivore facilitates an exotic plant, but the plant does not reciprocally facilitate the herbivore. Freshw Biol 60:1475–1482. https://doi.org/10.1111/fwb.12582

Michener CD (1979) Biogeography of the bees. Ann Missouri Bot Garden. https://doi.org/10.2307/2398833

Nielsen A, Bascompte J (2007) Ecological networks, nestedness and sampling effort. J Ecol 95:1134–1141. https://doi.org/10.1111/j.1365-2745.2007.01271.x

Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Simpson G, Solymos P, Henry M, Stevens H, Wagner H (2016) Vegan: community ecology package. R Package version 2.3-5. https://CRAN.R-project.org/package=vegan

Olesen JM, Eskildsen LI, Venkatasamy S (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Divers Distrib 8:181–192. https://doi.org/10.1046/j.1472-4642.2002.00148.x

Padrón B, Traveset A, Biedenweg T, Díaz D, Nogales M, Olesen JM (2009) Impact of alien plant invaders on pollination networks in two archipelagos. PLoS ONE 4:e6275. https://doi.org/10.1371/journal.pone.0006275

Parham JW (1958) Weeds of Fiji. Colony of Fiji at the Government Press, Suva

Ploquin EF, Herrera JM, Obeso JR (2013) Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. Oecologia 173:1649–1660. https://doi.org/10.1007/s00442-013-2731-7

Prasad A, Hodge S (2013) Factors influencing the foraging activity of the allodapine bee *Braunsapis puangensis* on creeping daisy (*Sphagneticola trilobata*) in Fiji. J Hymenopt Res 35:59–69. https://doi.org/10.3897/jhr.35.6006

Qi S-S et al (2014) Light limitation and litter of an invasive clonal plant, *Wedelia trilobata*, inhibit its seedling recruitment. Ann Bot 114:425–433. https://doi.org/10.1093/aob/mcu075

Rebola C (2015) Nesting biology of the Fijian *Lasioglossum* (*Homalictus*) indicates an extension of the 'Australian Enigma'. Honours thesis, School of Biology, Flinders University, Adelaide

Shay K, Drake DR, Taylor AD, Sahli HF, Euaparadorn M, Akamine M, Imamura J, Powless D, Aldrich P (2016) Threatened pollination systems in native flora of the Ogasawara (Bonin) Islands. Pac Sci 70(4):409–429. https://doi.org/10.2984/70.4.2

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Spengler A, Hartmann P, Buchori D, Schulze CH (2011) How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia. J Biogeogr 38:247–258. https://doi.org/10.1111/j.1365-2699.2010.02395.x

Staines M, Vo C, Puiu N, Hayes S, Tuiwawa M, Stevens MI, Schwarz MP (2017) Pollen larceny of the tropical weed *Solanum torvum* by a Fijian endemic halictine bee with implications for the spread of plants with specialized pollinator requirements. J Trop Ecol 33:183–187. https://doi.org/10.1017/S0266467417000098

Sugiura S (2010) Species interactions–area relationships: biological invasions and network structure in relation to island area. Proc R Soc Lond B Biol Sci 277:1807–1815. https://doi.org/10.1098/rspb.2009.2086

Thaman R (1999) *Wedelia trilobata*: daisy invader of the Pacific Islands. IAS technical report 99

Thaman R (2012) Trees of life: a guide to the trees and shrubs of the University of the South Pacific. University of the South Pacific Press, Adelaide

Traveset A et al (2013) Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. Proc R Soc Lond B Biol Sci 280:20123040. https://doi.org/10.1098/rspb.2012.3040

Warren BH et al (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecol Lett 18:200–217. https://doi.org/10.1111/ele.12398

Whistler WA (1995) Wayside plants of the islands: a guide to the lowland flora of the Pacific Islands including Hawai'i, Samoa, Tonga, Tahiti, Fiji, Guam and Belau. Isle Botanica, Honolulu

Williams NM, Cariveau D, Winfree R, Kremen C (2011) Bees in disturbed habitats use, but do not prefer, alien plants. Basic Appl Ecol 12:332–341. https://doi.org/10.1016/j.baae.2010.11.008