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ORIGINAL PAPER

Extreme host range in an insular bee supports the super-generalist hypothesis with implications for both weed invasion and crop pollination

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Abstract

Super-generalism is a pollinator trait where species obtain floral resources from a very wide range of plant species. Theoretical and empirical studies suggest that on islands with low pollinator diversity, such pollinators should evolve to exploit a very wide range of floral morphologies. Super-generalism has implications not only for securing pollination network stability, but also for the invasibility of potential weeds that require specialist pollinators in their original ranges. Here we expand earlier studies on bees in Fiji to include a wider range of bee-plant interactions for bees that have been recently introduced into Fiji as well as the endemic Fijian halictine bee, *Homalictus fijiensis*. Our data show that the endemic Fijian bee has a much wider range of floral hosts than introduced bees, and this extends to pollen larceny of solanoid plant species that are usually buzz pollinated. Importantly, solanoid plants were not visited by introduced bee species, including the honeybee *Apis mellifera*, which is usually regarded as a super-generalist. Our findings are important because they add critical support to the hypothesis that super-generalism evolves in insular ecosystems with low pollinator diversity and that this may make such ecosystems vulnerable to invasion by exotic weeds. However, insular super-generalists may also have potential to stabilize plant-pollinator networks and may also be effective pollinators for exotic crop species, and this needs to be further explored in agricultural settings.

Keywords Crop pollination · Fiji · *Homalictus* · *Melastoma* · Pollen theft · Poricidal anthers · Weed invasion

Introduction

One factor in the establishment of potentially invasive angiosperm weeds in new regions is the availability of pollen vectors. For potential weeds with specialized pollinators, the co-introduction of suitable pollinators is hypothesized to lead to 'invasion meltdown' where the introduced plant and introduced pollinator mutually enhance each other's spread (Simberloff and Von Holle 1999; Simberloff 2006). As an alternative to the notion of invasion meltdown as a driver of weed proliferation, Olesen et al. (2002) argued that in island ecosystems with very low pollinator diversity, high intraspecific but low interspecific competition would encourage pollinators to evolve into super-generalists, able to exploit a wide variety of plants that might otherwise depend on specialist pollinators.

Homalictus fijiensis (Perkins & Cheesman) (Halictidae) is an endemic bee of the Fijian islands, and previous studies of the pollination systems of Fiji (Crichton et al. 2018;

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Groutsch et al. 2019; Hayes et al. 2019) showed it has a broad floral host range. The range included an introduced weed *Solanum torvum* that requires buzz pollination (Staines et al. 2017), and the utilisation of extra-floral nectaries in a native *Hibiscus* species, suggesting it has evolved to exploit a wide range of food resources (Crichton et al. 2018). Although studies have not explored the efficacy of pollination by *H. fijiensis*, it has been referred to as a super-generalist pollinator due to visitation of all of the 49 angiosperm species documented in previous Fiji pollination network studies (Crichton et al. 2018; Groutsch et al. 2019; Hayes et al. 2019).

Many angiosperm species with poricidal anthers have distinctive flowers with specialised pollen availability, and are referred to as having a 'solanoid' morphology (Faegri 1986). Solanoid plants often do not provide nectar rewards (Vogel 1978), and this is thought to be a strategy that discourages non-capable pollinator visitation (Harder and Barclay 1994; De Luca and Vallejo-Marin 2013). Such anthers have evolved many times in plants as a strategy to prevent excessive pollen loss (Buchmann 1983; Harder and Barclay 1994), restrict access to pollen to capable pollinators (Buchmann and Hurley 1978; De Luca and Vallejo-Marin 2013) and direct pollen delivery by capable pollinators to conspecific plants (Harder and Barclay 1994). To be capable pollinators, bees must be able to sonicate, or 'buzz', anthers at a high enough frequency and amplitude to allow pollen grains to be shaken from the cylindrical structure (Buchmann and Hurley 1978; Vallejo-Marín 2019). For some bees, sonication is an innate behaviour (Morgan et al. 2016), and both small and large bees are capable of floral sonication, although reaching the appropriate vibration amplitudes is harder to achieve for smaller bees (Vallejo-Marín 2019; De Luca et al. 2019). However, some bees (including buzzing and non-buzzing bees) can access and potentially transport pollen for solanoid species without sonication by biting through the anthers to access pollen (see Anderson and Symon 1988; Thorp 2000; Solís-Montero et al. 2015). This behaviour, termed pollen larceny (Inouye 1980), is less efficacious than buzz pollination and negatively impacts plant reproduction, but in some cases successful pollination can occur (Hargreaves et al. 2009). Island ecosystems such as Fiji where native pollinators may be unable to buzz pollinate, yet introduced plants requiring specialized pollination are widespread, raises questions as to how these plants overcame pollinator limitations and whether local pollinators have evolved to exploit these alternative floral resources.

One such case of the spread of an introduced plant with specific pollinator requirements is that of the invasive neotropical weed *Solanum torvum*, where it is unclear how pollination services are provided to enable its spread across Fiji. Despite the presence of an introduced buzz pollinator, *Amegilla pulchra,* it has never been observed on *S. torvum* (Staines et al. 2017; Groutsch et al. 2019; Crichton et al. 2018; Hayes et al. 2019) and therefore cannot be used to explain the species spread across the Fijian archipeligo. *Homalictus fijiensis* however has been observed extracting pollen from *S. torvum* through pollen larceny, where bees were observed extracting pollen from poricidal anthers by biting at their tips with no attempts at locating nectaries (Staines et al. 2017). It is not clear how *H. fijiensis* is able to identify *S. torvum* as suitable for pollen larceny, or whether pollen larceny evolved after the original introduction of this species. Pollen larceny of buzz pollinated plants has been reported from regions outside of Fiji, such as small native *Trigona* bees on *Solanum* flowers in Australia (Anderson and Symon 1988) and *Lasioglossum* and *Augochlorella* bees in Mexico (Solis-Montero et al. 2015), as well as *Apis mellifera* and *Trigona* bees on *Solanum* in Brazil (Vinícius-Silva et al. 2017). Pollen larceny may also be performed by *Trigona* bees in Costa Rica on *Thunbergia grandiflora* (Young 1983) and on multiple Melastomataceae species in Brazil (Renner 1983), but notably pollination efficacy was not investigated in these studies. *Homalictus fijiensis* has been observed on *S. torvum* and another introduced solanoid plant *Dissotus rotundifolia* (Crichton et al. 2018; Hayes et al. 2019), but has not yet been observed exploiting any native solanoid plants. Without prior exposure of *H. fijiensis* to a Fijian native plant with poricidal anthers over evolutionary time, it is difficult to explain the origin of the behaviour of mandibulation to obtain pollen from solanoid plants.

Here, we further explore the breadth of plant species utilized by *H. fijiensis* with additional emphasis on species with solanoid morphologies. We argue that the presence of native Fijian plants with poricidal anthers provided opportunities for generalist bees, in insular regions such as *H. fijiensis,* to evolve abilities to recognize and exploit solanoid floral morphologies. Our findings unambiguously demonstrate the super-generalist status of *H. fijiensis* and provide evidence of the evolution of super-generalists in insular systems, with both positive and negative ecological and economic implications.

Methods

Field observations and species

Staines et al. (2017), Crichton et al. (2018), Groutsch et al. (2019) and Hayes et al. (2019) analysed bee-plant networks covering five bee species and 49 plant species (see *Network Analyses* below) from Viti Levu in Fiji. Here we add additional records and extend the number of plant species to 60 from those in Crichton et al. (2018). Our observations included four additional solanoid plants, leading to a total of seven solanoid species (see Table 1) of which five are nectarless. All plants were identified using Whistler (1995).

Observations were conducted between the 2nd and 21st of April, 2018 from Colo-i-Suva Forest Park, the Laucala Bay campus of the University of the South Pacific (USP), and along roadsides in the Serea and Naqali regions between Colo-i-Suva and Serea, Viti Levu. Field sites were restricted to below 800 m asl as recent studies indicate the existence of multiple *Homalictus* species that can be morphologically difficult to distinguish from *H. fijiensis*, but those species are largely restricted to elevations above 800 m asl (Dorey et al. 2019).

Flowering plants were observed from 1 to 2 m (m) distance with recording commencing 2 min after first approach to the plants to allow insects to resettle after any initial disturbance by the observers. The observational time period of 10 min was started after the resettling time, and observers would then watch for interactions between all bee species and flowers. These interactions were recorded quantitatively. *Homalictus fijiensis* individuals that flew from one flower to another were recorded as a single interaction. Other plants within 3 m of the observation area of the same species were also included in the observation area, and observations were conducted by up to four people at a time. The times of observation were calculated as person-minutes of observation, as detailed in Crichton et al. (2018).

Network analyses

Our 2018 data across all species observed comprised a total of 1460 person-minutes of observation (see Table 1 and below). We combined these data with previous studies conducted by Staines et al. (2017) (670 person-minutes of observation), Crichton et al. (2018) (1260 person-minutes of observation), Groutsch et al. (2019) (825 person-minutes of observation) and Hayes et al. (2019) (540 person-minutes of observation). The combined data set totalled 4755 person-minutes of observations of five bee species and included 60 plant species (Table 1). All observations were transformed into binary data (presence/absence of interactions). Interaction networks were visualized using the *visweb* and *plotweb* commands in *R* ver. 3.3 module Bipartite 2.05 (Dormann et al. 2009).

Network parameters for our binary data were explored using the command *networklevel* in the Vegan module in *R* ver. 3.3. The parameters of interest were (i) C-scores, which quantify levels of aggregation or disaggregation, typically used to explore competition between bees for plants or plants for bees; (ii) connectance, which measures the observed number of interactions compared to the possible number; and (iii) niche overlap for both plants and bees separately. We also examined nestedness of the interaction network using the function *nestednodf* which calculates the NODF parameter which estimates nestedness for both trophic levels as well as the combined levels (Almeida-Neto et al. 2008). We estimated the significance levels for all parameters using the *oecosimu* command in the Vegan module, with 2000 Monte Carlo simulations for null models.

Interactions with *Melastoma denticulatum*

Particular focus was placed on locating and observing plant species with poricidal anthers, in particular the native *M. denticulatum.* A further six solanoid plants were identified with poricidal anthers and all of these were introduced species (Table 1). When *H. fijiensis* was observed interacting with *M. denticulatum* flowers, video evidence was taken using Samsung S4 phone camera to identify potential pollen larceny behaviours.

Specimens of *H. fijiensis* were captured from flowers by sweep nets during observational periods for pollen count analyses. Bees were caught once they had interacted with *M. denticulatum* flowers, and were immediately placed into separate 3 mL pre-filled 98% ethanol vials with as little handling and abrasive contact as possible to prevent loss of pollen or contamination. Samples of *M. denticulatum* pollen were taken by preserving anthers in 3 mL pre-filled 98% ethanol vials.

A standard slide mount of *M. denticulatum* pollen was made by crushing anthers with watchmaker forceps and preparing a microscope slide viewed using a Nikon Eclipse 50i compound microscope at ×40 magnification (following methods detailed in Staines et al. 2017). Photographs were taken using a Nikon 5000 SLR camera as references for mature and immature *M. denticulatum* pollen grains. Pollen samples from vials of *H. fijiensis* were obtained by vigorously shaking the vials to suspend pollen and then taking 0.5 mL aliquots to place on a slide and covered with a 2.5 cm × 5.0 cm coverslip. Each pollen grain was then recorded as either *M. denticulatum* or as ‘other pollen’. The slide was observed in sequential zig–zag transects until 100 total pollen grains were observed or until the entire space under the coverslip was observed before a maximum of 100 pollen grains were counted.

Results

Bee-plant network analyses

The binary plant-bee interaction network from our combined 2016–2018 data are shown in Fig. 1. This figure indicates a much wider range of host plants for *H. fijiensis* than for the other bee species, with *Apis mellifera* having the next broadest host range, followed by *Braunsapis puangensis*, and then *Amegilla pulchra* and *Megachile*

Table 1 Plant species observed with bee interactions used for all analyses

Family	Plant species	Authority	Status
Acanthaceae	*Ruellia brittoniana*^{3}	Leonard	Introduced
Apocynaceae	*Allamanda cathartica*^{3}	Linnaeus	Introduced
Apocynaceae*	*Catharanthus roseus*^{3}	(Linnaeus) G. Don	Introduced
Amaryllidaceae	*Crinum asiaticum*^{3}	Linnaeus	Introduced
Asteraceae	*Eclipta alba*^{4}	Linnaeus	Introduced
Asteraceae	*Eclipta prostrata*^{2}	(Linnaeus) Haask	Introduced
Asteraceae	*Elephantopus mollis*^{2,4}	Kunth	Introduced^{B}
Asteraceae	*Sphagneticola trilobata*^{2,4}	(Linnaeus) Pruski	Introduced^{B}
Asteraceae	*Tridax procumbens*^{3}	Linnaeus	Introduced
Boraginaceae	*Cordia subcordata*^{2}	Lamarck	Native^{A}
Combretaceae	*Terminalia capitanea*^{2}	A.C. Smith	Native
Commelinaceae	*Commelina diffusa*^{3}	Burman	Native
Convolvulaceae	*Ipomoea alba*^{3}	Linnaeus	Introduced
Convolvulaceae**	*Ipomoea obscura*	Ker Gawler	Native
Cucurbitaceae	*Momordica charantia*^{3}	Linnaeus	Introduced
Euphorbiaceae**	*Euphorbia heterophylla*	Linnaeus	Introduced
Euphorbiaceae*	*Jatropha integerrima*^{3}	Jacquin	Introduced
Fabaceae*	*Mimosa pudica*^{2,4}	Linnaeus	Introduced^{B}
Fabaceae*	*Senna occidentalis*^{3}	Link	Introduced^{C}
Fabaceae**	*Senna surratensis*	Burman	Introduced^{C}
Goodeniaceae*	*Scaevola taccada*^{2}	(Gaertner) Roxburgh	Native
Lamiaceae*	*Clerodendrum thomsonae*^{3}	J.H Balfour	Introduced
Lamiaceae*	*Hyptis pectinata*^{2,4}	(Linnaeus) Poiteau	Introduced
Lamiaceae	*Leucaena leucocephala*^{3}	(Lamarck) de Wit	Introduced
Lamiaceae	*Plectranthus scutellaroides*^{3}	(Linnaeus) Brown	Introduced
Lamiaceae*	*Vitex trifolia*^{2}	Linnaeus	Native
Lecythidaceae	*Barringtonia asiatica*^{2}	(Linnaeus) Kurz	Native^{A}
Lythraceae	*Cuphea carthagenensis*^{2,4}	(Jacquin) McBride	Introduced
Lythraceae*	*Cuphea hyssopifolia*^{3}	Kunth	Introduced
Malvaceae**	*Hibiscus mutabilus*	Linnaeus	Introduced
Malvaceae	*Hibiscus tiliaceis*^{2}	Linnaeus	Native^{A}
Malvaceae	*Sida rhombifolia*^{2,4}	Linnaeus	Introduced
Malvaceae	*Trichospermum calyculatum*^{2,4}	(Seeman) Burrett	Native
Malvaceae	*Triumfetta rhomboidea*^{2,4}	Jacquin	Introduced
Malvaceae*	*Urena lobata*^{2,3,4}	Linnaeus	Introduced^{B}
Malvaceae**	*Thespesia populnea*	(L.) Sol. ex Correa	Introduced^{A}
Melastomataceae*	*Dissotis rotundifolia*^{2,4}	(Smith) Triana	Introduced^{B,C}
Melastomataceae*	*Melastoma denticulatum*^{2,4}	Labillardie`re	Native^{A,C}
Nyctaginaceae*	*Bougainvillea glabra*^{3}	Choisy	Introduced
Oleaceae**	*Jasminum multiflorum*	Burm. F.	Introduced
Onagraceae*	*Ludwigia octovalvis*^{2,4}	(Jacquin) Raven	Introduced
Orchidaceae	*Arundina bambusifolia*^{2,4}	(D.Don) Hochreutiner	Introduced
Orchidaceae	*Spathoglottis pacifica*^{2,4}	Reichenbach	Native
Oxalidaceae*	*Oxalis barrelieri*^{3}	Linnaeus	Introduced
Phyllanthaceae**	*Breynia disticha*	J.R.Forst. & G.Forst.	Introduced
Polygonaceae	*Antigonon leptopus*^{3}	W. J. Hooker & G. A. Walker-Arnott	Introduced
Polygalaceae	*Polygala paniculata*^{2,4}	Linnaeus	Introduced
Rubiaceae*	*Ixora coccinea* (white var)^{3}	Linnaeus	Native
Rubiaceae	*Ixora coccinea* (red var)^{3}	Linnaeus	Native
Rubiaceae**	*Ixora chinensis*	Linnaeus	Introduced

Table 1 (continued)

Family	Plant species	Authority	Status
Rubiaceae	*Morinda citrifolia*[2]	Linnaeus	Native[A]
Rubiaceae	*Mussaenda raiateensis*[2]	J.W. Moore	Native
Rubiaceae**	*Pentas lanceolata*	Forssk	Introduced
Rubiaceae	*Spermacoce assurgens*[2,4]	Ruiz & Pavon	Introduced
Rutaceae*	*Euodia hortensis*[2]	Forster & Forster	Native
Solanaceae**	*Capsicum frutescens*	Linnaeus	Introduced[C]
Solanaceae**	*Physalis angulata*	Linnaeus	Introduced[C]
Solanaceae*	*Solanum torvum*[1,2,3,4]	Swartz	Introduced[B,C]
Verbenaceae	*Duranta erecta*[3]	Linnaeus	
Verbenaceae**	*Lantana camara*	Linnaeus	Introduced
Verbenaceae	*Stachytarpheta urticaefolia*[2,3,4]	Sims	Introduced[B]

*plants with additional observation time added by this study, **observed plants unique to this study, [1]plants observed by Staines et al. (2017), [2]plants observed by Crichton et al. (2019), [3]plants observed by Groustch et al. (2019), [4]plants observed by Hayes et al. (2019), [A]indicates the possible Aboriginal introduction of native species, [B]denotes species classified as invasive by IUCN, and [C]indicates 'solanoid' plants

species. Of the seven plant species with poricidal anthers, only one, *Senna surattensis*, was visited by a bee species (*Apis mellifera*) in addition to *H. fijiensis*.

Of the plants observed to be receiving visits from only a single bee species, 14 of these were visited by *H. fijiensis*, one was visited by *Amegilla pulchra*, and three were visited by *B. puangensis* (Fig. 1). Four of these 'single-pollinator' plants were native to Fiji and only one of these was not visited by *H. fijiensis*. Of the four plant species receiving visits from all bee species, only one, *Vitex trifolia*, was a native Fijian species.

For the five bee and 60 plant species in our study we observed 132 species-pair interactions out of a theoretically maximum of 300. Our Monte Carlo simulations show that this value is significantly higher ($P < 0.001$) than expected from a null model. Our value is also higher than any of the 29 plant-pollinator network studies reviewed by Olesen and Jordano (2002), and which ranged across very diverse continental and island habitats. Our connectance value reflects that three of the four introduced bee species in Fiji are generalists and the endemic *H. fijiensis* is a super-generalist, as is evident from Fig. 1. The estimated number of compartments in our *networklevel* analyses was 1.0, suggesting that we do not have well-defined clusters of interacting species, which is also evident in the interaction network in Fig. 1. Niche overlap for plants was 0.59 and for bees was 0.37 for plants; both were statistically different from random interaction models ($P < 0.001$, for both cases) and indicate moderate niche overlaps.

The C-score for plants was 0.17 ($P < 0.001$) and for bees was 0.30 ($P < 0.001$). The relatively lower C-score value for plants suggests they may be competing for bee pollinators less than bees compete for floral resources, though the C-score value for bees is still low, suggesting little competition among the species. However, it is likely that the C-score value for bees partially reflects the situation where all but two plant species with poricidal anthers only received visits from *H. fijiensis*; this situation may not reflect competition between bees for plant species and instead reflect differential abilities of bees to access solanoid flowers, with *H. fijiensis* being the only species to commonly exploit such flowers in Fiji. However, exclusive visits by *H. fijiensis* to some plant species extends beyond just the solanoid plant species (Fig. 1).

Lastly, we examined nestedness in the combined data set, and this is visualized in Fig. 2 which indicates differences in the breadth of host plants for each bee species. Host breadth for each species was 16 plants for *Amegilla* (1 unique), 25 for *Braunsapis* (3 unique), three plants for *Megachile*, 35 plants for *Apis* (1 unique) and 53 for *Homalictus* (14 unique). The NODF values for plants, bees and the combined matrix were similar (7.10, 8.61 and 7.10, respectively, each with $P < 0.001$) substantiating the apparent nestedness in Fig. 2.

Bee interactions with *Melastoma denticulatum*

The observations were conducted at several roadside locations along the Suva-Monasavu road in the Serea district at elevations of ~ 20–30 m asl. A total of 240 person-minutes of observations were conducted in 2018 across nine observational events of *M. denticulatum*. A total of 13 interactions between *H. fjiiensis* and *M. denticulatum* were observed and 19 bee specimens (with 6 specimens caught outside the observation time) were acquired for pollen analysis (see below). Observations of these long interactions between *H. fijiensis* and *M. denticulatum* not only showed the bees concentrated their physical contact to the anthers, but also crawling over the petals and stigma while mandibulating the

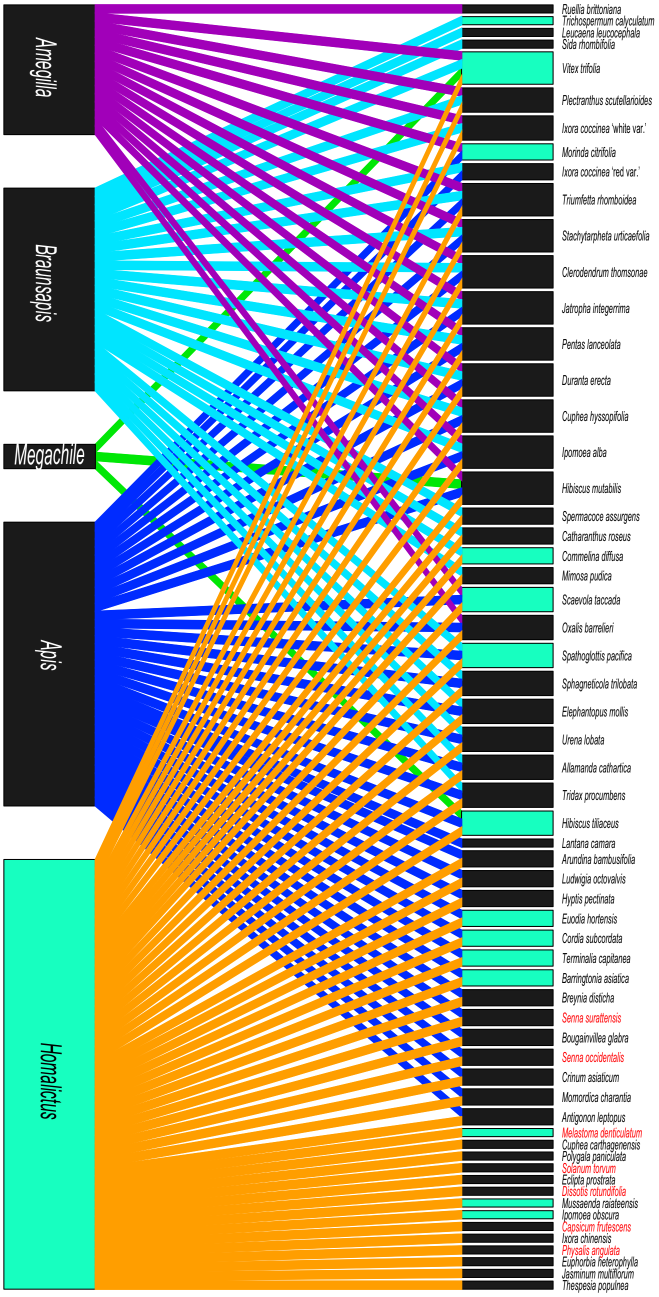

Fig. 1 Network diagram of the bee-plant interactions observed in Fiji. Native species are indicated by green boxes, introduced species by black boxes, and plants with poricidal anthers are in red text. The network diagram contains bee-plant interactions as indicated in Table 1. *Homalictus fijiensis* was seen to be the sole visitor of all but two solanoid plant species

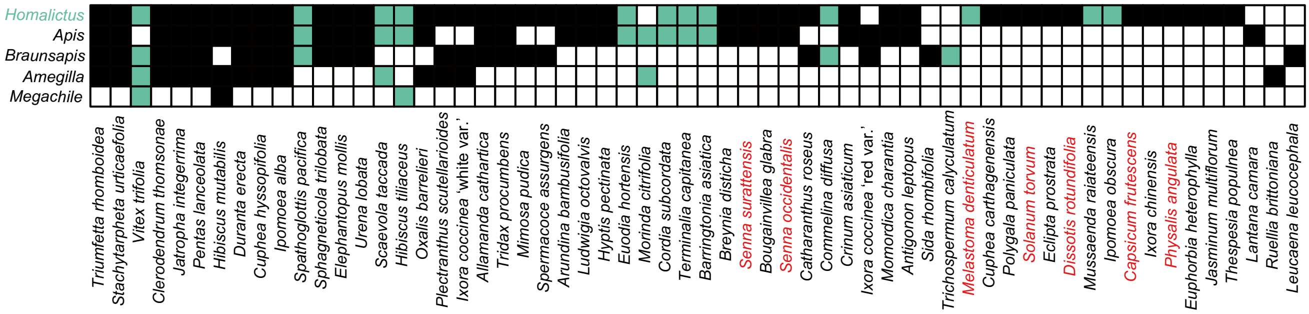

Fig. 2 Nestedness of the bee-plant network of the listed observed species in Table 1. Observation of an interaction between the bee species and plant is indicated by black squares, green squares and green text indicate interactions between Fijian native *Homalictus fijiensis* and native plant species, and solanoid plants with poricidal anthers are in red text

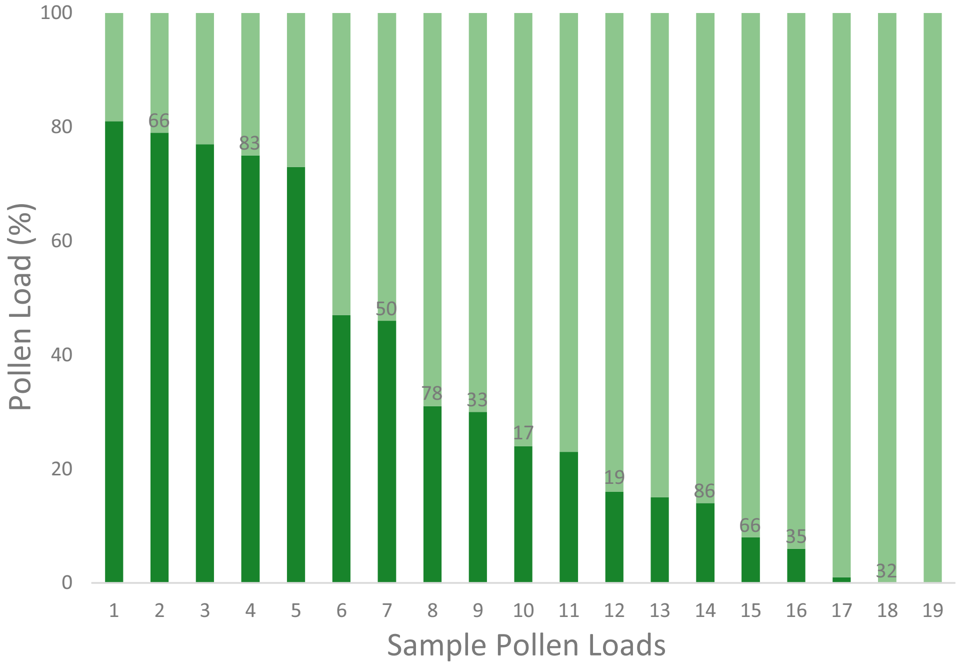

Fig. 3 Graph of the percentage of *Melastoma denticulatum* pollen grains found in ethanol washings of *Homalictus fijiensis* captured after interacting with *M. denticulatum* flowers. Unless otherwise indicated by numbers within bars, sample size was 100 pollen grains

Fig. 4 **a** *Homalictus fijiensis* performing pollen larceny by chewing on the anthers of the *Melastoma denticulatum* flower; **b** microscope image of *M. denticulatum* pollen taken under ×40 magnification; (i) a mature pollen grain of lighter colour; (ii) an immature pollen grain of darker colour. See video in electronic supplementary material

anthers before leaving (see video in electronic supplementary material). The behaviour of *H. fijiensis* also showed no signs of attempts to locate nectaries, nor behaviours consistent with sonication.

Homalictus fijiensis was the only bee observed to approach or make contact with *M. denticulatum* flowers, despite a large number of *Apis mellifera* and *B. puangensis* present in the immediate areas (< 2 m distance from *M. denticulatum* plants) where they primarily foraged on *Breynia disticha*, *Pentas lanceolata* and *Clerodendrum thomsoniae* in the vicinity of the observation areas. *Amegilla pulchra* was never observed on or near *M. denticulatum* flowers.

The 19 *H. fijiensis* specimens collected after interacting with *M. denticulatum* flowers were used to examine the prevalence of *M. denticulatum* pollen grains on bees. This prevalence ranged up to 81%, and *M. denticulatum* pollen was present on all bees except for one (Fig. 3), but for eleven specimens fewer than 100 pollen grains could be counted on the pollen slide preparations. This may not be surprising because bees were collected after their first observed interaction with *M. denticulatum* flowers, and those bees may have only just started foraging shortly before collection. Both mature and immature *M. denticulatum* pollen grains were found during microscope examination (see Fig. 4), suggesting that some pollen was retrieved before maturation, consistent with pollen larceny (Solís-Montero et al. 2015; Staines et al. 2017; De Luca et al. 2019).

Discussion

Our data indicate five clear results. Regarding super-generalism: (i) *H. fijiensis* has a substantially broader host range than the introduced bee species, including *Apis mellifera*, a species that is widely regarded as a super-generalist; (ii) interaction networks display significant nestedness for both bees and plants; (iii) the parameter estimating disaggregation, C-score, was significantly different from the null model for plants and bees, suggesting either competitive exclusion or host/bee specialization; and regarding pollen larceny: (iv) *H. fijiensis* also visits six other solanoid plant species (five of which are nectarless) and only one of those species was observed to be visited by another bee species (*Apis mellifera*); and (v) *H. fijiensis* extracts pollen from the poricidal anthers of the native Fijian solanoid plant *M. denticulatum* by biting at anthers. The implications for these findings are discussed below.

The super-generalism of *H. fijiensis* suggested by Crichton et al. (2018), and extended by our new data and covering multiple solanoid plants, is interesting. *Apis mellifera* is regarded as a super-generalist, but its host range in Fiji is narrower than *H. fijiensis*. Importantly, most plants in our interaction network are not native to Fiji. *Apis mellifera* evolved in Eurasian continental regions (Ruttner 1988) that have much greater plant diversities than Fiji, so the greater level of super-generalism in *H. fijiensis*, compared to *Apis mellifera*, cannot be explained by exposure to a larger number of host plant species over evolutionary time. Instead, it seems likely that *H. fijiensis* has evolved its host breadth in a situation where intra-specific competition was high and floral morphologies were diverse.

We observed *H. fijiensis* visiting a total of seven plant species with poricidal anthers (five of which are nectarless), but only *M. denticulatum* is native to Fiji. Of these seven plants, only one was visited by a bee (*Apis mellifera*) other than *H. fijiensis*, suggesting a strong ability for bees introduced to Fiji to recognize and avoid floral morphologies that do not provide nectar or high pollen rewards. This was particularly evident from our observations of *M. denticulatum* plants where non-native bee species were highly abundant in the immediate vicinity but never approached *M. denticulatum* flowers, despite their showy appearance. It is therefore likely that bees unable to exploit solanoid plants have evolved or efficiently adapted behaviour to avoid those plants.

Staines et al. (2017) showed that *H. fijiensis* exhibits pollen larceny for the introduced solanoid weed *S. torvum*, and when doing so may effect pollination as pollen was present on the bodies of *H. fijiensis* and contact is made with both the anthers and stigma. The same was observed in our study of *M. denticulatum*. Visits to this plant never involved attempts to locate nectaries suggesting that these bees have evolved the ability to recognize plants with poricidal anthers, which was a puzzle because *S. torvum* was only introduced to Fiji in the 1800s. There is only one potentially indigenous *Solanum* species, *Solanum viride* (Smith 1991), however, it is unclear if this species existed there prior to the arrival of the Lapita or the Polynesians. All other species of *Solanum* are considered to be of known introduced origin to the islands. Pollen larceny has not been recorded for any halictine bees that we are aware of, but was also recorded from a further five introduced plants in the present study. *Melastoma denticulatum* is native to the Indo-Papuan, Fijian and some other South West Pacific (SWP) regions (Meyer 2001) and has a broadly similar floral appearance to *S. torvum* (see Fig. 2 in Staines et al. 2017), so it is possible that *Homalictus* evolved an ability to recognize this kind of floral morphology before these introduced solanoid plants arrived in Fiji. In particular, a lack of floral specialisation and broad host range of *H. fijiensis* would have likely assisted in the exploitation of the familiar morphology of the invasive *S. torvum* (Padyšáková et al. 2013).

Interestingly, several native *Homalictus* species have been recorded on flowers of *M. denticulatum* in New Caledonia (Pauly et al. 2015) and *Capsicum annuum* from Papua New Guinea (Ibalim et al. 2020), while two other halictines, *Lasioglossum* sp. and *Nomia* sp. (with six other bee species) have been recorded from *M. affine* from tropical Australia but pollen larceny was not observed for these halictines (Gross 1993). The Fijian *Homalictus* species comprise a separate clade to both New Caledonian and Papua New Guinean species (Groom et al. 2014; Ibalim et al. 2020), suggesting either that the ability to utilize plants with poricidal anthers has evolved multiple times or that it evolved prior to the crown age of the Fijian clade, which is at least 400,000 ya (Groom et al. 2014).

It is puzzling that *H. fijiensis* is able to exploit so many solanoid plants in Fiji when reports of similar behaviour for non-buzz pollinators are very rare for other regions (but see Gross 1993 for other bee species). We suggest two possible factors: (i) Fiji does not have any native buzz-pollinating insects (Groom et al. 2014; Staines et al. 2017; Dorey et al. 2019), so plants with poricidal anthers that have colonized this archipelago would have comprised a pollen resource that was unavailable to other invertebrate pollinators; and (ii) prior to human settlement, approximately 3000 ya (Clark and Anderson 1999) Fiji largely comprised dense tropical forests that are unsuitable for ground-nesting bees (Ash 1987, 1992), so competition to exploit local floral resources in non-forested areas could have been intense. Because Fijian native bee diversity is extremely low in lowland habitats, with only one species prevalent below 800 m asl (Michener 1979; Dorey et al. 2019), intra-specific competition to exploit all available resources could have been high, selecting for super-generalism rather than species-specific niches.

Future research

Our finding that *H. fijiensis* commonly visits solanoid plants raises the issue if this bee may be able to pollinate solanaceous species, as has been suggested with *S. torvum* (Staines et al. 2017). To confirm pollination and determine the efficacy of pollen larceny, however, further research is required (see Gross 2005; Solís-Montero et al. 2015). If *H. fijiensis* is found to successfully effect pollination, the combination of pollen larceny behaviour and wide host range will pose a greater invasion threat from introduced solanaceous weeds because pollination services may be provided without invader complexes, previously thought to be required (Simberloff and Von Holle 1999; Simberloff 2006). However, this behaviour of *H. fijiensis* also has the potential to improve solanaceous crop pollination services in tropical countries. The only solanaceous crop plant in our study was *C. frutescens*, but visits to *S. torvum* suggests that this bee may also exploit other cultivated solanceous crops, such as tomatoes, eggplants, capsicums and chillies. The use of native bees to pollinate crop plants is being investigated world-wide to secure the agricultural industry in the face of declining insect populations (Sánchez-Bayo and Wyckhuys 2019) and native carpenter bees have been investigated as an alternative to bumble bees in Australia (Hogendoorn et al. 2000). In Brazil, native bee alternatives for pollinating crop plants have been successful, where 10 of 13 native bee species studied could pollinate *Lycopersicon esculentum* (Bartelli and Nogueira-Ferreira 2014). It was also suggested that even in the presence of typical crop pollinating species there are greater benefits in utilising many pollinating species to avoid reliance and overexploitation of a single species but a crucial factor in the successful use of native species for agricultural crop pollination was to understand commercial management of each species (Bartelli and Nogueira-Ferreira 2014).

The ability of *H. fijiensis* to exploit a very wide variety of introduced weeds with varying floral morphologies may extend to introduced crop species that benefit from pollination services. However, in this sense, super-generalism in insular bees may be a two-edged sword, encouraging the spread of weedy species but could possibly provide additional or alternative pollinators for agricultural crop pollination. More research is needed regarding population management and sustainability for a super-generalist such as *H. fijiensis* to ensure effectiveness in supporting crop pollination.

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References

Almeida-Neto M, Guimaraes P, Guimaraes PR Jr, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239

Anderson GJ, Symon D (1988) Insect foragers on *Solanum* flowers in Australia. Ann Missouri Bot 75:842–852

Ash J (1987) Stunted cloud-forest in Taveuni, Fiji. Pacific Sci 41:191–199

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

Bartelli BF, Nogueira-Ferreira FH (2014) Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. Econ Bot 107:987–994

Buchmann SL (1983) Buzz pollination in angiosperms. In: Little RJ, Jones CE (eds) Handbook of experimental pollination biology. Scientific and Academic Editions, New York, pp 73–113

Buchmann SL, Hurley JP (1978) A biophysical model for buzz pollination in angiosperms. J Theor Biol 72:639–657

Clark GR, Anderson A (1999) The age of Lapita settlement in Fiji. Atchaeol Oceania 34:31–39

Crichton A, Francis N, Doherty S, Tuiwawa M, 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 25:135–142

De Luca PA, Vallejo-Marin M (2013) What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. Curr Opin Plant Biol 16:429–435

De Luca PA, Buchmann S, Galen C, Mason AC, Vallejo-Marín M (2019) Does body size predict the buzz-pollination frequencies used by bees? Ecol Evol 9:4875–4887

Dorey JB, Schwarz MP, Stevens MI (2019) Review of the bee genus *Homalictus* Cockerell (Hymenoptera: Halictidae) from Fiji with description of nine new species. Zootaxa 4674:1–46

Dormann CF, Fründ J, Blüthgen N, Bruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. Open J Ecol 2:7–24

Faegri K (1986) The solanoid flower. Trans Bot Soc Edinburgh 45:51–59

Groom SV, Ngo HT, Rehan SM, Skelton P, Stevens MI, Schwarz MP (2014) Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems. Biol Invasions 16:2293–2302

Gross CL (1993) The breeding system and pollinators of *Melastoma affine* (Melastomataceae); a pioneer shrub in tropical Australia. Biotropica 25:468–474

Gross CL (2005) Pollination efficiency and pollinator effectiveness. In: Kevan PG, Husband BC, Dafni A (eds) Practical pollination biology. Enviroquest Ltd., Cambridge, ON, pp 354–363

Groutsch JK, Miller NC, Tuiwawa M, Hayes S, Stevens MI, Schwarz MP (2019) 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. Austral Entomol 58:533–539

Harder DL, Barclay MRR (1994) The functional significance of poricidal anthers and buzz pollination: Controlled pollen removal from *Dodecatheon*. Funct Ecol 8:509–517

Hargreaves AL, Harder LD, Johnson SD (2009) Consumptive emasculation: the ecological and evolutionary consequences of pollen theft. Biol Rev 84:259–276

Hayes S, Tuiwawa M, Stevens MI, Schwarz MP (2019) A recipe for weed disaster in islands: a super-generalist native pollinator aided by a 'Parlourmaid' plant welcome new arrivals in Fiji. Biol Invasions 21:1643–1655

Hogendoorn K, Steen Z, Schwarz M (2000) Native Australian carpenter bees as a potential alternative to introducing bumble bees for tomato pollination in greenhouses. J Apid Res 39:67–74

Ibalim S, Groom SVC, Dorey JB, Velasco-Castrillon A, Schwarz MP, Stevens MI (2020) Origin and dispersal of *Homalictus* (Apoidea: Halictidae) across New Guinea, the South West Pacific and Australia. Trans R Soc SA 144:1–14

Inouye DW (1980) The terminology of pollen larceny. Ecology 61:1251–1253

Meyer K (2001) Revision of the southeast Asian genus *Melastoma* (Melastomataceae). Blumea 46:351–398

Michener CD (1979) The genus *Homalictus* in Fiji (Hymenoptera: Halictidae) [Includes *Homalictus achrostus*, *Homalictus hadrander*, new taxa]. Pac Insects 21:227–234

Morgan T, Whitehorn P, Lye GC, Vallejo-Marin M (2016) Floral sonication is an innate behaviour in bumblebees that can be fine-tuned with experience in manipulating flowers. J Insect Behav 29:233–241

Olesen JM, Jordano P (2002) Geographic patterns in plant-pollinator mutualistic networks. Ecology 83:2416–2424

Olesen JM, Eskildsen LI, Venkatasamy S (2002) Invasion of pollination network on oceanic islands: importance of invader complexes and endemic super generalists. Divers Distrib 8:181–192

Padyšáková E, Bartoš M, Tropek R, Janeček S (2013) Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristate* (Acanthaceae). PLoS ONE 8:e59299

Pauly A, Donovan B, Munzinger J (2015) Les abeilles du genre *Homalictus* Cockerell, 1919 en Nouvelle-Calédonie (Hymenoptera: Apoidea: Halictidae). Belg J Entomol 34:1–30

Renner S (1983) The widespread occurrence of anther destruction by *Trigona* bees in Melastomataceae. Biotropica 15:251–256

Ruttner F (1988) Evolution. In: Ruttner F (ed) Biogeography and taxonomy of honeybees. Springer, Berlin, pp 20–36

Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: a review of its drivers. Biol Conserv 232:8–27

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

Simberloff D (2006) Risk assessments, blacklists, and white lists for introduced species: are predictions good enough to be useful? Agric Econ Res Rev 35:1–10

Smith AC (1991) Flora Vitiensis Nova, a New Flora of Fiji. Volume 5. SB Printers, Inc, Honolulu, Hawai'i

Solís-Montero L, Vergara CH, Vallejo-Marín M (2015) High incidence of pollen theft in natural populations of a buzz-pollinated plant. Arthropod-Plant Interactions 9:599–611

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

Thorp R (2000) The collection of pollen by bees. Plant Syst Evol 222:211–223

Vallejo-Marín M (2019) Buzz pollination: studying bee vibrations on flowers. New Phytol 224:1068–1074

Vinícius-Silva R, Parma D, Tosetes RB, Arruda VM, Werneck M (2017) Importance of bees in pollination of *Solanum lycopersicum* L. (Solanaceae) in open-field of the Southeast Minas Gerais State, Brazil. Hoehnea 44:349–360

Vogel S (1978) Evolutionary shifts from reward to deception in pollen flowers. In: Richards A (ed) The pollination of flowers by insects. Academic Press, Massachusetts, pp 89–96

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

Young AM (1983) Nectar and pollen robbing of *Thunbergia grandiflora* by *Trigona* bees in Costa Rica. Biotropica 15:78–80