RESEARCH ARTICLE

Short Title: Fuster et al.— Pollination effectiveness of vertebrates

Pollination effectiveness of specialist and opportunistic nectar feeders influenced by invasive alien ants in the Seychelles

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PREMISE: Opportunistic nectar-feeders may act as effective pollinators; nonetheless, we still lack information on whether these opportunistic species differ in their pollination effectiveness from specialized nectarivorous vertebrates and insects. Many nectar specialists have coevolved with the plants on which they feed; therefore, we would expect higher pollination effectiveness in specialists than in opportunistic feeders. Here, we assessed quantity and quality components of pollination effectiveness in specialist and opportunistic vertebrate nectarivores and insects, focusing on three plants from the Seychelles: *Thespesia populnea*, *Polyscias crassa*, and *Syzygium wrightii*.

METHODS: We determined the quantity component (QNC) of pollination effectiveness with pollinator observations, and the quality component (QLC) by measuring fruit and seed set resulting from single visits by each pollinator. To detect potential negative effects of invasive ants on native plant-pollinator interactions, we classified pollinator visits (quantity component) as disturbed (>6 ants/30 min) vs. undisturbed.

RESULTS: All focal plants were visited by insects, and vertebrate specialist and opportunist nectarivores, yet their pollination effectiveness differed. Flying insects were the most effective pollinators of *T. populnea*. The other two plants were most effectively pollinated by vertebrates; i.e., sunbirds (nectar specialists) in *S. wrightii* and *Phelsuma* geckos (nectar opportunists) in *P. crassa*, despite marked variation in QNC and QLC. Ant presence was associated with lower pollinator visitation rate in *P. crassa* and *S. wrightii*.

CONCLUSIONS: Our study highlights the importance of all pollinator guilds, including opportunist nectarivorous vertebrates as pollinators of island plants, and the vulnerability of such interactions to disruption by nonnative species.

KEY WORDS: Araliaceae; Aride; island ecosystems; Mahé; Malvaceae; mutualistic disruption; Myrtaceae; opportunistic pollination; tropical ecosystems; vertebrate pollination

Pollination is a mutualistic function mainly performed by insects, but also by a variety of vertebrate groups (Ratto et al., 2018). Most vertebrate pollinators specialize in nectar consumption, and belong to different families of birds (e.g., Meliphagidae, Nectariniidae, Trochilidae) and mammals (e.g., bats of the subfamily Glossophaginae) (Schmidt-Lebuhn et al., 2007; Fleming et al., 2009). An increasing number of studies show that vertebrates not specialized in nectar consumption visit flowers opportunistically to obtain nectar or pollen including birds, mammals, and reptiles (Da Silva et al., 2014; Fuster et al., 2019). Opportunistic nectarivory can result in legitimate pollination, sometimes contributing significantly to plant reproduction (Frick et al., 2013; Rodríguez-Rodríguez et al., 2013; Hervías-Parejo and Traveset, 2018; Cozien et al., 2019). Nonetheless, we still lack information on whether these opportunistic species differ in their pollination effectiveness (Schupp et al., 2017) from more specialized nectarivorous species (but see Diller et al., 2019).

Pollination effectiveness (PE, hereafter) is measured as the product of a quantity component (QNC) and a quality component (QLC) (Ne’eman et al., 2010; Schupp et al, 2017). QNC measures the frequency of the interaction, e.g., the frequency of visits to a plant or its flowers (Rocca and Sazima, 2013; Custodio et al., 2017). QLC measures the per capita effect of visits on reproductive performance, i.e., the probability that a pollen grain on a stigma produces a viable seed. It is usually estimated as fruit or seed set (Sahli and Conner, 2007; Rodríguez-Rodríguez et al., 2013), but can also be measured as number of seedlings produced (e.g., Herrera, 2000; Valverde et al., 2019). Estimating QNC and QLC is critical to better understand the contribution of each pollinator species to reproductive performance.

Many nectar or pollen specialists have coevolved with the plants on which they feed (Thompson, 1994; Baker et al., 1998). We would therefore expect higher PE in specialists than in opportunistic feeders. However, there is increasing evidence that opportunistic flower visitors can be more effective pollinators than specialists, either by being more abundant or more efficient with each visit (e.g., Motten et al., 1981; Frick et al., 2013; Rodríguez-Rodríguez et al., 2013). Although the role of nectar-opportunist vertebrates is increasingly recognized (Frick et al., 2013; Cozien et al., 2019; Fuster and Traveset, 2019, 2020), we know little about how quantity and quality components of pollination effectiveness differ between vertebrate feeding guilds and between insects and vertebrates (Hervías-Parejo and Traveset, 2018; Ratto et al., 2018; Jaca et al., 2019a).

Natural variation in PE may be due to fluctuations in pollinator abundance, animal foraging behavior on flowers and in the floral community, pollinator body size, weather, or flowering phenology (e.g., Rafferty and Ives, 2012), all of which may respond differently to anthropogenic effects. Among the most serious current effects are the spread of invasive nonnative species (Sax and Gaines, 2008; Bellard et al., 2017), which can disrupt mutualistic interactions, potentially affecting QNC and QLC, and compromising the fitness of some or all partners (Traveset and Richardson, 2014). Invasive animals can prey on native pollinators or, if they are flower visitors, can compete with and displace native pollinators (Traveset and Richardson, 2006; 2014). Invasive ants, in particular, have a disruptive effect on native insect pollinators (Lach, 2008; LeVan et al., 2014; Sinu et al., 2017) but also on vertebrate pollinators, as has been reported for *Technomyrmex albipes* in Mauritius (Hansen and Müller, 2009; Bissessur et al., 2017). Island ecosystems are particularly vulnerable to invasive species (Bellard et al., 2017), and understanding their effect on native plant-pollinator interactions can help with predicting and mitigating such negative effects.

Insights into PE are not only of ecological relevance but also of conservation concern. For example, prioritizing nectar specialists versus feeding opportunists can have different consequences for sustaining plant diversity and ecosystem functioning depending on which groups provide the best pollination service. Opportunistic nectarivory is more common than previously thought in insular ecosystems (Olesen and Valido, 2003; Fuster et al., 2019); therefore, it is likely that some insular plant species depend on opportunistic pollination. Moreover, island ecosystems harbor high numbers of endemic plants (Kier et al., 2009) that may depend on both specialist and opportunistic vertebrates, as well as insects, for pollination. With vertebrates suffering disproportionately from anthropogenic perturbations (Bellard et al., 2014), plant population viability may be more threatened for those species that depend on vertebrate pollinators.

The aim of our study was to assess the ability of opportunistic vertebrate nectar feeders to perform effective pollination compared to vertebrate specialized nectarivores and insect pollinators. Moreover, we aimed to determine whether disturbance in the form of invasive nonnative ants correlated with PE of different pollinators. Specifically, we compared PE of specialist and opportunistic vertebrate nectarivores and insects. We focused on three plant species from the Seychelles: *Thespesia populnea*, *Polyscias crassa*, and *Syzygium wrightii*, which differ in flower morphology and are visited by vertebrate and insect pollinators. We evaluated the QNC and QLC of pollination effectiveness of all floral visitors in the field, predicting that PE would be higher in specialist nectarivorous vertebrates and insects than in opportunistic vertebrates in undisturbed conditions. To assess the effect of invasive ants on PE and flower visitation frequency, we quantified QNC and PE of pollinators in the presence or absence of invasive nonnative ants that frequently visited flowers of the endemic *P. crassa* and *S. wrightii*, anticipating a negative effect.

<h1>MATERIALS AND METHODS

<h2>Study site and species

The study was conducted on the islands of Aride and Mahé in the Seychelles, Indian Ocean between October 2016 and April 2017, covering the main flowering season of the target plant species. Aride (~71 ha, elevation 153 m), a Strict Nature Reserve, is the northernmost granitic island in the archipelago, covered with native woodland; and Mahé is the largest granitic island of the archipelago (15,730 ha, elevation 905 m). Our target plant species were native *Thespesia populnea* (Malvaceae), characteristic of the native coastal forest on Aride, and the threatened Seychelles endemics *Polyscias crassa* (Araliaceae) and *Syzygium wrightii* (Myrtaceae). On Mahé, we worked on the latter two species on four inselbergs, i.e., large rocky outcrops, which harbor remnants of endemic midaltitude plant communities (Fleischmann et al. 1996); these were Bernica (55°26′51–53″E, 4°40′8–16″ S), Copolia (55°27′23–28″E, 4°40′7–12″S), Salazie (55°26′56”–27′01″E, 4°39′18–20″S), and Trois Frères (55°26′48–53″E, 4°38′10–14″S).

Target species were selected for their different floral morphologies and traits that likely make them attractive to vertebrates (e.g., brightly colored flowers or high nectar production). *Thespesia populnea* (L.) Sol. ex Corrêa is a small evergreen tree (6–10 m height) with bell-shaped pale-yellow hermaphroditic flowers (4–7 cm length; Fig. 1A). Flowers produce small volumes of sugar-rich nectar (average nectar standing crop 2.89 ± 0.39 (SD) μl/flower, 32 ± 3.6% sugar; $N = 3$), resulting in 1.05 ± 0.18 mg sugar/flower. The flowers are receptive for one day. Pollinated flowers develop into dry fruits containing four to five compartments with several seeds inside each. *Syzygium wrightii* (Baker) A. J. Scott is a shrub (2–3 m height) with showy yellow hermaphrodite flowers grouped in suspended inflorescences (Fig. 1B). Flowers produce intermediate volume of nectar with a low sugar concentration (nectar standing crop 10.4 ± 7.15

µl/flower, 5 ± 0.83%; *N* = 11), averaging 0.47 ± 0.29 mg sugar/flower. The flowers produce fleshy drupes, i.e., each fruit contains a single seed. *Polyscias crassa* (Hemsl.) Lowry & G. M. Plunkett is a shrub ~ 2–3 m in height. Its protandrous flowers sit in terminal inflorescences (Fig. 1C, 1D), producing a relatively large amount of nectar (nectar standing crop: 13.4 ± 7.26 µl/flower; *N* = 9 flowers) with a low sugar concentration (5.6 ± 2.65% sugar; *N* = 9 flowers) averaging 0.64 ± 0.35 mg sugar/flower. Nectar measurements were only available on female-phase flowers, but both male-phase and female-phase produce nectar. Each flower bears fleshy fruits with multiple seeds. Nectar standing crop was quantified by collecting and measuring the volume of nectar with microcapillaries. Nectar sugar concentration was measured with a handheld refractometer between 08:00 and 11:00 on a dry day. Nectar was sampled from one fleshy opened flower per plant individual.

<h2>Plant breeding system

Given that no information was available on the breeding system of the three plant species, we conducted a set of breeding experiments to test if our single visit experiments (explained below) were influenced by autonomous selfing, and also assessed the influence of each pollinator on plant reproduction. We recorded fruit and seed set after four pollination treatments: (1) autogamy—flower buds were enclosed prior to anthesis with netted bags to prevent outcrossed pollen transfer; (2) geitonogamy—flower buds were bagged prior to anthesis; once open, flowers were emasculated and hand-pollinated with pollen from a different flower on the same individual and bagged again until fruit collection; (3) xenogamy—the same as the geitonogamy treatment, but flowers were pollinated with outcrossed pollen from flowers of another individual; and (4) control—flowers were tagged and left open to allow access for all pollinators. For the dichogamous *P. crassa,* we did not perform the autogamy treatment because the flowers used for the experiments were all in female phase. For *T. populnea*, we used 39, 27, 30, and 30 flowers for autogamy, geitonogamy, xenogamy, and control treatments, respectively. Likewise, we used 56, 51, 15, and 125 flowers, respectively for *S. wrightii* and 24, 55, and 84 flowers for geitonogamy, xenogamy, and controls, respectively for *P. crassa* (Table 1).

<h2>Pollinator observations

Visitation frequency of pollinators was recorded with timed pollinator observations on all target plants. Observations were carried out between 07:00 and 18:00 hours, in sunny or partly cloudy conditions, using binoculars—from a distance of 5–7 m—to minimize effects on vertebrate pollinators behaviors. Observation sessions lasted 30 min, totaling 80 h for *T. populnea*, 64 (26 in male phase flowers and 38 in female) and 30 hours of observation for *P. crassa* and *S. wrightii*, respectively. We performed five to six censuses per day during three to four days per week for each plant species, depending on the availability of flowering individuals, between October and December for *T. populnea* and between January and March for *P. crassa* and *S. wrightii*. We recorded all visitors to each plant species, as well as the number of observed and visited flowers. Flowers of the target plant species received only legitimate visits, except for some nectar robbing sunbirds in *T. populnea* (see Fig. 1A and the Results section). To assess the role of sunbirds as pollinators compared to other flower visitors, both types of interactions were included for the experiments and data analysis.

<h2>Pollination quality experiment

To assess the quality of visits (QLC), we recorded fruit and seed set for single visits by each pollinator taxon (flying insects, ants, sunbirds [specialist bird], and fodies, skinks, and geckos [the three species considered as generalists]). Bagged flowers were exposed to pollinators shortly after anthesis, the first flower visitor was recorded, and flowers were subsequently emasculated (for *T. populnea* and *S. wrightii*), tagged, and bagged to prevent further visits to the same flower. We treated a total of 59, 191 (female), and 182 flowers of *T. populnea*, *P. crassa*, and *S. wrightii*¸ respectively. Bags were regularly checked for developing fruit, and seeds of *T. populnea* and *P. crassa* (> 1 seed/fruit) were counted once fruit had matured.

<h2>Pollination effectiveness (PE)

We calculated QNC as the product of the plant visitation rate and the proportion of flowers visited in every plant visit, whereas QLC was calculated as the product of fruit set per flower visit and number of seeds produced per fruit:

$$QNC = \frac{number\ of\ visits}{h} \times \frac{proportion\ of\ flowers\ visited}{visit}$$

$$QLC = \frac{fruit}{flower} \times \frac{number\ of\ seeds}{fruit}$$

To estimate QNC in *P. crassa*, we only used data from flowers in the female phase. Pollination effectiveness was calculated as:

$$PE = QNC\ \times QLC$$

To test whether disturbance by invasive nonnative ants is associated with a change in the frequency of flower visits and the effectiveness of each pollinator taxon, we calculated QNC and PE of every flower visitor in the presence and absence of ants in *P. crassa* and *S. wrightii*, in which the invasive yellow crazy ant, *Anoplolepis gracilipes* (Smith, 1857) was frequently observed. We set the threshold to six ant individuals/plant in 30 min censuses to categorize 'presence' vs. 'absence'. The threshold was set based on previous observations, which indicated that a higher abundance of ants, primarily *A. gracilipes,* can interfere with other flower visitors. By contrast, when there were only a few ant individuals observed, such interference was never detected.

<h2>Data analysis

We performed generalized linear mixed models (GLMM) separately for each plant species to test for variation among pollinator taxa in plant visitation rate, proportion of flowers visited, and pollination success (the latter expressed as fruit set and seed set). We used pollinator taxon (flying insects, ants, sunbirds, fodies, skinks, and geckos) or breeding treatment (in another set of GLMMs) as fixed effects, and observation identification (ID, for visitation rate and proportion of flowers visited) nested within plant individual ID as random effects. For *P. crassa* and *S. wrightii*, we also included inselberg ID as a separate random effect because these two species were studied in the four different inselbergs. For the dichogamous *P. crassa*, flower sex and its interaction with pollinator taxon were included as a fixed effect when analyzing visitation rate and proportion of flowers visited. For the visitation rate models, we used a Poisson error distribution and, to control for variation in floral display size, we included the total number of flowers per plant as a covariate. For the proportion of flowers visited (number of flowers visited out of the total number of open flowers) and fruits produced (yes or no, production of fruit per flower), we used models with binomial error distributions. Finally, for seed set (in the case of *T. populnea* and *P. crassa*) we also performed GLMMs using a negative binomial error distribution to deal with overdispersion. We used a Tukey's post hoc test to compare among pollinator taxa or breeding treatments using the *glht* function from the *multcomp* package (Hothorn et al., 2008).

The effect of ant presence on pollinator visitation rate was tested with a second set of GLMMs, using the same structure as the previous models but excluding ants from the 'pollinator taxon' variable, and including the binary effect of ant presence/absence as another predictor. These models were run only for *P. crassa* and *S. wrightii* because ants were rarely seen in *T. populnea* flowers. All models were run with the *glmer* and *glmer.nb* functions from *lme4* package (Bates et al., 2015) in R (version 3.5.1; R Development Core Team 2018).

To estimate PE for each pollinator taxon and plant species, we generated mean PE and SD values based on random resampling simulations from the empirical values of each subcomponent of PE, i.e., visitation rate and proportion of visited flowers (QNC) and fruit and seed set (QLC), following Reynolds and Fenster (2008) and Rodríguez-Rodríguez et al. (2013). The bootstrapping method was necessary because the data that quantify the PE subcomponents were collected with different sampling methods and sample sizes. We used the *sample* function (*base* package) in R (version 3.5.1; R Development Core Team 2018) to run 5000 bootstrapping iterations, sampling each data set with the sample size as in the original data set with replacement (Legendre and Legendre, 1998; Rodríguez-Rodríguez et al., 2013). The simulated mean values for QNC, QLC, and PE were very similar to the empirically calculated values (Table 2), which suggests that the simulated values consistently and accurately reflect the biological patterns in the empirical data. Differences among pollinators in QNC, QLC, and PE for each plant species were tested using generalized linear models (GLM) with a gamma error distribution and including pollinator as fixed effect. Finally, we plotted the different pollinators in the two-dimensional QNC, QLC, and PE landscapes, using the *effectiveness* function from the *effect.lndscp* package (Jordano and Rodriguez-Sanchez, 2017).

<h1>RESULTS

<h2>Breeding system

Fruit and seed set varied significantly among treatments in *T. populnea* ($\chi^2 = 16.43$, $df = 3$, $P < 0.001$), but not in *P. crassa* or *S. wrightii* ($\chi^2 = 4.98$, $df = 2$, $P = 0.083$; and $\chi^2 = 1.79$, $df = 3$, $P = 0.617$; respectively). In *T. populnea*, the autogamy treatment produced fewer fruits and seeds than other treatments (Table 1). Fruit set of open pollinated flowers was low (18%) in *S. wrightii*, intermediate (33%) in *T. populnea*, and relatively high (74%) in *P. crassa*.

<h2>Flower visitors and visitation rate (QNC)

Both insects and vertebrates (birds and lizards) visited flowers of all three plant species, but their frequency differed between species. Flying insects were the most frequent flower visitors in *T. populnea* in *S. wrightii* and in the male phase flowers of *P. crassa*; in the female phase flowers of *P. crassa*, ants were the most frequent visitors. Vertebrates visitation frequency was generally low and varied considerably between plant species and disturbed (by ants) and undisturbed flowers.

In *T. populnea*, flying insects visited flowers more frequently than any of the vertebrates, and they probed on average more flowers than birds and skinks during each visit (Appendices S1, S2). Ants of the native *Camponotus grandieri* (Forel, 1886) and the nonnative *Monomorium pharaonis* (Linnaeus, 1758) occasionally also visited the flowers of this plant; however, the most common insect visitors were bees, especially a megachilid bee in the genus *Chalicodoma* (Appendix S3). Among vertebrates, *T. populnea* flowers on Aride were most frequently visited by Seychelles sunbirds, *Cinnyris dussumieri* (Hartlaub, 1861), followed by Seychelles fodies, *Foudia sechellarum* (Newton, 1865), and Seychelles skinks, *Trachylepis seychellensis* (Duméril & Bibron, 1839) (Appendix S1).

On Mahé, bees and ants, especially the invasive yellow crazy ant, were the most frequent insect visitors of *P. crassa* and *S. wrightii* flowers (Appendices S1, S3). Vertebrate flower visitors of *P. crassa* and *S. wrightii* were Seychelles sunbirds, Seychelles skinks (which had a significantly lower visitation rate than the other vertebrates—see Appendix S1), Seychelles day gecko *Phelsuma astriata* (Tornier, 1901), and Sundberg's day gecko *Phelsuma sundbergi* (Rendahl, 1939). The two geckos behaved similarly on the flowers and were thereafter pooled for the analyses. The Seychelles bulbul (*Hypsipetes crassirostris*) was observed feeding on nectar of *S. wrightii* flowers on two occasions on the same plant individual.

In *P. crassa*, visitation rate and proportion of flowers visited were generally higher on male than female flowers (rate: $\chi^2 = 18.84$, $df = 4$, $P < 0.001$; proportion: $\chi^2 = 34.10$, $df = 3$, $P < 0.001$; Appendix S4). Male phase flowers of *P. crassa* attracted significantly more flying insects, geckos, and sunbirds than female phase flowers (i.e., higher visitation rate), and those insects and sunbirds that visited male flowers were also more active (i.e., higher proportion of flowers visited) (Appendices S1, S4). Most flying insect visits in both male and female flowers were bees, especially *Apis mellifera* (Appendix S3), which was a frequent visitor only for a short period (~7 days). By contrast, vertebrates and the invasive yellow crazy ant visited flowers more evenly over the full period of flower receptivity (~20 days). Bees primarily foraged on pollen, while other flower visitors fed both on pollen and nectar.

The most frequent flower visitors of *S. wrightii* were ants, followed by sunbirds, and both were significantly more frequent than geckos, skinks, and flying insects (Appendices S1, S5). Although Seychelles skinks showed low visitation rates, the proportion of visited flowers was similar to that of sunbirds, and both species visited more flowers than geckos or flying insects (Appendix S5).

<h2>Pollination quality (QLC)

Pollination quality differed among pollinator taxa only for *T. populnea*. The Seychelles fody and flying insects produced the highest fruit set in this species (0.67, $N = 3$ and 0.47, $N = 30$, respectively; Appendices S1, S2); visits by sunbirds resulted in lower fruit set (0.13, $N = 23$), whereas visits by skinks produced no fruits ($N = 3$). Visits by fodies, sunbirds and insects resulted in similar numbers of seeds per fruit ($\chi^2 = 1.95$, $df = 2$, $P = 0.376$; Appendix S2).

In *P. crassa,* ant visits resulted in no fruits, while all other pollinator taxa contributed similarly to fruit set ($\chi^2 = 7.17$, $df = 3$, $P = 0.067$) and seed set ($\chi^2 = 1.91$, $df = 3$, $P = 0.590$; Appendices S1, S4). Likewise, there were no differences in fruit set in *S. wrightii* among pollinator taxa ($\chi^2 = 0.67$, $df = 3$, $P = 0.880$; Appendix S5), except for geckos' visits, which resulted in no fruits. For this species, ant visits did result in fruit production.

<h2>Pollination effectiveness (PE)

Each plant species had a different most-effective pollinator taxon. Flying insects were the most effective pollinators of *T. populnea*, (Fig. 2; Table 2). The Seychelles sunbird and fody were overall poor pollinators of *T. populnea*, yet for different reasons: sunbirds frequently visited flowers but rarely acted as legitimate pollinators (Fig. 1A), while fodies were highly efficient pollinators on their rare visits to the plant (Fig. 2).

Geckos were the most effective pollinators of *P. crassa*, whereas skinks were the least important (Fig. 2). Skinks, however, were highly efficient pollen vectors in their few visits. Sunbirds and flying insects had similar PE for *P. crassa,* sunbirds were more quantitatively important and insects more qualitatively (Fig. 2, Table 2).

Finally*, S. wrightii* benefitted most from the frequent and efficient visits of sunbirds, resulting in the highest pollination effectiveness for this species (Fig. 2). Geckos and skinks visits were less efficient, resulting in the lowest effectiveness. Flying insects, however, provided an effective pollination service to *S. wrightii* (Table 2).

<h2>Disturbance effect by ants

The presence of ants on flowers, mostly the invasive yellow crazy ant, was associated with lower pollinator visitation rate in *P. crassa* (χ^2= 9.86, *df* = 1, *P* = 0.002; Fig. 3A). Visitation rates of flying insects, however, were not negatively associated with the presence of ants; in fact, ant presence corresponded with higher visitation rates, which made flying insects the most effective pollinators (Fig. 2, Table 2).

In *S. wrightii,* the presence of ants was associated with lower pollinator visitation rates (χ^2 = 4.16, *df* = 1, *P* = 0.041, Fig. 3B) across all pollinator taxa (Fig. 2, Table 2). Nevertheless, sunbirds were the most effective pollinators under both disturbed and undisturbed conditions.

<h1>DISCUSSION

Our study indicates that some Seychelles plant species depend on insects and specialized vertebrate pollinators, but also on opportunistic vertebrate nectar feeders. Our data on *T. populnea* and *S. wrightii* supported the expectation that specialist nectar feeders (flying insects and sunbirds) have higher PE than opportunistic nectar-feeding species (specifically, fodies, skinks, and geckos); by contrast, the generalist geckos were more effective than specialist pollinators on *P. crassa*. Furthermore, we showed that PE of pollinator species varies among plant species, regardless of its feeding behavior. Our study is one of a handful that looks at the effect of nonnative invasive organisms on pollinator effectiveness (e.g., Sinu et al., 2017; Maruyama et al., 2018; Jaca et al., 2019b). Here, pollination effectiveness of vertebrate pollinators appeared to be compromised by the presence of invasive nonnative ants, shown by the decrease of flower visitation rates in presence of ants. In fact, the degree of floral ant infestation of the two threatened island endemics *P. crassa* and *S. wrightii* is likely to have longerterm negative implications for the conservation of both species because their pollination, and consequently seed production, can be compromised (see Rogers et al., 2017).

Coevolution implies specialization among mutualistic partners, and this may be reflected in animal and flower traits (Thompson, 1994; Baker et al., 1998). *Syzygium wrightii* presents a bird-pollination syndrome, with open and bright-yellow flowers with long styles and stigmas and a bell-shaped calyx. This facilitates nectar consumption and pollination by long-billed birds (Vogel, 1954; Faegri and Van der Pijl, 1979; Rebelo et al., 1984) such as sunbirds, which were their most important pollinators. Floral syndromes, however, are not always a good predictor of the pollinator assemblage of a plant species (Ollerton et al., 2009; Rosas-Guerrero, 2014). Multiple selection pressures on floral traits may result in adaptations to multiple effective and ineffective pollinators (Aigner, 2001). For instance, *T. populnea,* pollinated by insects elsewhere in its native range (Woodell, 1979; Gandhi, 2000) and mostly by bees in our study, produces small volumes of highly concentrated nectar that fits with nectar feeding insects (Faegri and Van der Pijl, 1979). However, its large, yellow, bell-shaped flowers also fit a bird-pollination syndrome, but the importance of Seychelles fodies and sunbirds was low. In contrast, geckos were the most important pollinators of the apparently entomophilous *P. crassa*. Possible adaptations of *P. crassa* to pollination by geckos include rigid inflorescences that can support the weight of these animals, and big leaves that they may use as resting places and refuge. Both *P. crassa* and *S. wrightii* produce high amounts of diluted nectar, a common trait in bird-pollinated flowers (Faegri and van der Pijl, 1979; Fleming et al., 2009), which may be useful to other animals with high energy demands, such as reptiles (Brown et al., 1978; Cronk and Ojeda, 2008). Specialist vertebrate pollinators are assumed to shape selection pressures on certain floral traits (e.g., Guimarães et al., 2011, Bartkowska and Johnston, 2012), and our results suggest that opportunistic vertebrates may also contribute to selection, as is also suggested in Hervías-Parejo et al. (2019).

Flower visitors differ in their behavior on flowers, which can affect reproductive performance. Geckos and skinks walking on the inflorescences contact more flowers on the same individual plant in the same visit compared to sunbirds or flying insects; this increases the likelihood of geitonogamy. *Thespesia populnea* or *S. wrightii*, which may experience high rates of geitonogamy, did not show any negative effect on fruit or seed set. Indeed, PE values in the self-compatible *S. wrightii*, may be elevated through pollinator-mediated self-pollination. Quantifying this effect and assessing the potential consequences of inbreeding depression, however, would require further experiments (Nebot et al., 2020).

The analysis of PE and their components reveals the effect of pollinator visits on plant reproductive success (Schupp et al., 2017). For pollinators to be considered highly effective, they must either be frequent visitors (Rodríguez-Rodríguez and Valido, 2011; Cavallero et al., 2018) or be very efficient pollen vectors (Pellmyr and Thompson, 1996; Castro et al., 2013), and these components can differ within a pollinator species when visiting different plant species. In *T. populnea*, fodies and sunbirds had similar PEs, and so did flying insects and sunbirds in *P. crassa* in the absence of ants; yet, the quantitative and qualitative component of PE varied considerably in both plant species. Similarly, in the same plant communities, geckos were negligible pollinators of *S. wrightii* compared to sunbirds or flying insects, but were the most important pollinators for *P. crassa*. Specialist nectar feeders such as sunbirds have evolved mechanisms to become nectar robbers for some plant species (*T. populnea*) and legitimate pollinators for others (*S. wrightii*), which appears to be a relatively common behavior of specialist nectarivores (Irwin et al., 2010). Thus, neither specialist nor opportunistic nectar feeders consistently act as effective or ineffective pollinators.

Insular ecosystems, in particular, are fragile and sensitive to disturbances by nonnative invasive species (Traveset and Richardson, 2006; Aslan et al., 2013; Bellard et al., 2017), including the effect caused by invasive ants (Cerdà et al., 2012; Kaiser-Bunbury et al., 2014). In our study, the most common ant flower visitor was the yellow crazy ant—invasive to large parts of Asia and the Pacific region (Wetterer, 2005), and was first introduced to Seychelles in 1962 (Lewis et al., 1976). Ants prey on or displace vertebrates and invertebrates (Holway et al., 2002; Plentovich et al., 2018), and can indirectly affect native plant reproductive performance by displacing native pollinators (e.g., Hansen and Müller, 2009; LeVan et al., 2014; Sinu et al., 2017). Our findings support earlier observations about the negative influence of invasive ants on the visitation rate of other flower visitors, especially vertebrates, resulting in lower pollination effectiveness.

Despite some overlap in the pollinator community among our focal plant species, PE indicated a low functional redundancy, because there was only one highly effective pollinator taxon for each plant species: insects in *T. populnea*, geckos in *P. crassa,* and sunbirds in *S. wrightii*. This low functional redundancy and high mutual dependency appears typical for depauperate insular pollinator communities (Kaiser-Bunbury et al., 2010; Traveset et al., 2015). On *P. crassa*, the presence of ants was associated with reduced visitation rates of vertebrates but not flying insects. Indeed, visitation rates and PE of flying insects in the presence of ants was high, which may be explained by ants deterring vertebrate pollinators and thereby causing a competitive release of flying insects. This suggests that, at least in this plant species, a reduction in vertebrate pollinators may be compensated by flying insects, suggesting higher functional redundancy in the presence of ants compared to the nondisturbed situation. However, it must be also noted that a higher frequency of insect visits does not necessarily translates into higher pollination success; in our case, bees (the main flying insects) were frequent visitors during a very short period (~7 days), which sheds doubt on their role as reliable pollinator.

Despite the potential effect of ants on flower visitors, there is evidence that ants can also act as pollinators (García et al., 2012; de Vega and Gómez, 2014), as our data showed in *S. wrightii*. Thus, whether ants act as mutualists or antagonists seems to be context dependent and should be considered individually. For instance, *Technomyrmex albipes*, an invasive ant species in many areas (including the Seychelles), has caused several problems on native fauna and flora displacing other animals and disrupting mutualistic interactions (e.g., Lach, 2008; Hansen and Müller, 2009). The same ant species has been reported, however, as an effective pollinator for a conspecific *Syzygium* species, *S. occidentale,* in India (Kuriakose et al., 2018).

Our findings, albeit relatively strong and biologically convincing, should be interpreted carefully because of high stochasticity, low pollinator visitation rate, and a relatively small and unbalanced sample size for some interactions and treatments (see Table 2 and Appendix S1). In addition, the coarse taxonomic resolution of insect visitors might underestimate the importance of some taxa for the pollination of the target plant species, suggesting that functional redundancy might be higher than described here.

<h1>CONCLUSIONS

We show that opportunist nectarivorous vertebrates, specialist vertebrates, and insects vary in importance as pollinators with plant species and ant presence. Moreover, our findings highlight the importance of considering both components (QNC and QLC) of PE to better understand their pollination function and assess to what extent different pollinators are functionally equivalent for the plants. Moreover, our findings emphasize the vulnerability of plant-pollinator interactions to invasive nonnative species. Hence, controlling or eradicating invasive species in vulnerable island ecosystems is a priority management intervention to avoid mutualistic disruptions.

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<h1>AUTHOR CONTRIBUTIONS

F. F., C. N. K.-B., and A. T. designed the research. F. F. conducted the fieldwork, analyzed data, and led the writing, with significant contributions from the other authors.

<h1>DATA AVAILABILITY

The data sets generated for this study are available on FigShare: https://doi.org/10.6084/m9.figshare.12029580.v2 (Fuster et al., 2020).

<h1>SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

Appendix S1. Subcomponents values of QNC and QLC from original data sets.

Appendix S2. QNC and QLC subcomponents plots of *Thespesia populnea*.

Appendix S3. Insect flower visitors of *Thespesia populnea*, *Polyscias crassa* and *Syzygium wrightii*.

Appendix S4. QNC and QLC subcomponents plots of *Polyscias crassa*.

Appendix S5. QNC and QLC subcomponents plots of *Syzygium wrightii.*

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TABLE 1. Mean and standard deviation (SD) of the subcomponents of the fruit set (fruit/flower) and seed set (number of seeds/fruit) from the breeding system experiments. Different letters indicate significant differences (Tukey's post hoc tests, $P < 0.05$) among treatments within plant species. *Syzygium wrightii* fruits always contained one seed. Npl, Nflw, and Nfrt indicate number of plants, flowers, and fruits, respectively.

Plant species	**Treatment**	**Fruit set**			**Seed set**		
		Npl	**Nflw**	**Mean ± SD**	**Npl**	**Nfrt**	**Mean ± SD**
Thespesia populnea	Control	10	30	0.33 ± 0.48^{a}	7	10	8.90 ± 4.12^{a}
	Autogamy	12	39	0.08 ± 0.27^{b}	2	3	1.00 ± 1.00^{b}
	Geitonogamy	7	27	0.48 ± 0.51^{a}	4	13	7.77 ± 3.47^{a}
	Xenogamy	9	30	0.50 ± 0.51^{a}	6	15	7.00 ± 2.04^{a}
Polyscias crassa (female phase)	Control	6	84	0.74 ± 0.44^{a}	5	62	13.23 ± 2.26^{a}
	Geitonogamy	1	24	0.96 ± 0.20^{a}	1	23	12.87 ± 1.25^{a}
	Xenogamy	3	55	0.95 ± 0.23^{a}	3	52	12.60 ± 1.14^{a}
Syzygium wrightii	Control	6	125	0.18 ± 0.38^{a}	-	-	-
	Autogamy	5	56	0.05 ± 0.23^{a}	-	-	-
	Geitonogamy	4	51	0.10 ± 0.30^{a}	-	-	-
	Xenogamy	1	15	0.13 ± 0.35^{a}	-	-	-

TABLE 2. Mean and standard deviation (SD) of visitation rate, proportion of flowers visited, fruit set, and seed set from original data sets considering the presence and absence of ants. Values of the quantity (QNC) and quality components (QLC) of pollination effectiveness (PE) were obtained from the mean values of original data sets; mean and SD values from resampled data sets (N = 5000) are also given. Values of QNC, QLC, and PE are multiplied per 100 to improve readability. Different letters indicate significant differences (Tukey's post hoc tests, $P < 0.05$) among pollinator taxa (fly insects, sunbird [*Cinnyris dussumieri*], fody [*Foudia sechellarum*], skink [*Trachylepis sechellensis*], and geckos [*Phelsuma* sp.]) within plant species. Asterisks indicate significant differences (Tukey's post hoc tests, $P < 0.05$) between presence and absence of ants within the same pollinator taxon and plant species. Note that QLC values are the same in the presence and absence of ants. Note also that values of *Thespesia populnea* are only provided once, because the effect of presence of ants was not tested.

			QNC						**QLC**						**PE**	
s ct	**Plant species**	**Pollinator**	**Visitation rate**		**Proportion of flowers visited**		**QNC**	**QNC resampled**	**Fruit set**		**Seed set**		**QLC**	**QLC resampled**	**PE**	**PE resamp**
			Nplants/ Nobservations	**Mean ± SD**	**Nvisits**	**Mean ± SD**		**Mean ± SD**	**Nplants/ Nflowers**	**Mean ± SD**	**Nplants/ Nfruits**	**Mean ± SD**		**Mean ± SD**		**Mean ± SD**
hout	*Thespesia populnea*	Flying insects	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Cinnyris dussumieri	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Foudia sechellarum	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Trachylepis sechellensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polyscias crassa (male phase)	Flying insects	6/39	14.41 ± 26.66^{a}	125	0.41 ± 0.29^{ab}	-	-	-	-	-	-	-	-	-	-
	Cinnyris dussumieri	6/39	1.74 ± 2.68^{b}	34	0.48 ± 0.22^{b}	-	-	-	-	-	-	-	-	-	-
	Trachylepis sechellensis	6/39	0.67 ± 1.40^{c}	13	0.66 ± 0.33^{a}	-	-	-	-	-	-	-	-	-	-
	Phelsuma sp.	6/39	1.69 ± 2.18^{b}	32	0.52 ± 0.27^{ab}	-	-	-	-	-	-	-	-	-	-
Polyscias crassa (female phase)	Flying insects	8/48	0.88 ± 2.29^{ab}	21	0.20 ± 0.14^{a}	17.6	17.27 ± 7.05^{a}	2/12	0.50 ± 0.52^{a}	1/6	11.83 ± 1.47^{a}	591.50	588.74 ± 173.28^{a}	104.10	101.76 52.88^{a}
	Cinnyris dussumieri	8/48	1.29 ± 1.87^{a}	31	0.26 ± 0.17^{a}	33.54	33.18 ± 7.97^{b}	4/53	0.23 ± 0.42^{a}	3/12	12.92 ± 1.83^{a}	297.16	293.39 ± 75.19^{b}	99.67	97.21 ± 35.13^{b}
	Trachylepis sechellensis	8/48	0.42 ± 1.09^{b}	10	0.24 ± 0.30^{b}	10.08	9.91 ± 5.54^{c}	3/58	0.48 ± 0.50^{a}	2/28	13.64 ± 2.09^{a}	654.72	657.65 ± 89.45^{c}	66.00	65.22 ± 38.04^{c}

		Phelsuma sp.	8/48	1.25 ± 2.46^{a}	24	0.39 ± 0.32^{b}	48.75	49.03 ± 15.91^{d}	4/51	0.55 ± 0.50^{a}	3/28	13.18 ± 1.85^{a}	724.9	722.45 ± 93.97^{d}	353.39	354.34 125.23^{c}
	Syzygium wrightii	Flying insects	10/51	0.71 ± 2.71^{a}	18	0.26 ± 0.23^{a}	18.46	18.67 ± 10.84^{a}	2/7	0.29 ± 0.49^{a}	1/2	-	29	28.20 ± 16.88^{a}	5.35	5.20 ± 4.81^{a}
		Cinnyris dussumieri	10/51	2.39 ± 3.18^{b}	61	0.45 ± 0.28^{b}	107.55	106.70 ± 21.23^{b}	4/63	0.14 ± 0.35^{a}	2/9	-	14	14.37 ± 4.47^{b}	15.06	15.34 ± 5.75^{b}
		Trachylepis sechellensis	10/51	0.47 ± 1.17^{ac}	12	0.40 ± 0.32^{b}	18.8	18.69 ± 7.89^{a}	2/39	0.03 ± 0.16^{a}	1/1	-	3	2.58 ± 2.52^{c}	0.56	0.48 ± 0.54^{c}
		Phelsuma sp.	10/51	0.24 ± 0.65^{c}	6	0.30 ± 0.17^{ab}	7.2	7.15 ± 3.15^{c}	1/26	0 .00 ± 0.00	-	-	0	0.00 ± 0.00^{d}	0	0.00 ± 0.00^{d}
n	*Thespesia populnea*	Flying insects	9/85	6.87 ± 9.49^{a}	142	0.93 ± 0.18^{a}	638.91	638.56 ± 95.14^{a}	9/30	0.47 ± 0.50^{a}	6/14	7.71 ± 4.36^{a}	362.37	360.82 ± 88.35^{a}	2315.22	2305.71 669.03^{a}
		Cinnyris dussumieri	16/115	0.70 ± 1.24^{b}	41	0.74 ± 0.29^{b}	51.8	51.49 ± 9.12^{b}	7/23	0.13 ± 0.34^{b}	2/3	4.67 ± 2.52^{a}	60.71	60.89 ± 36.85^{b}	31.45	31.35 ± 19.96^{b}
		Foudia sechellarum	16/115	0.10 ± 0.52^{c}	6	0.67 ± 0.32^{b}	5.2	6.95 ± 3.51^{c}	1/3	0.67 ± 0.58^{a}	1/2	7.00 ± 0.00^{a}	469	469.75 ± 190.69^{c}	24.39	32.61 ± 22.09^{c}
		Trachylepis sechellensis	16/115	0.02 ± 0.19^{d}	1	1.00 ± -^{ab}	2	1.72 ± 1.72^{d}	3/3	0.00 ± 0.00	-	-	0	0.00 ± 0.00^{d}	0.00	0.00 ± 0.00^{d}

Polyscias crassa (male phase)	Flying insects	3/13	0.15 ± 0.56^{a*}	1	0.04 ± -^{a*}	-	-	-	-	-	-	-	-	-	-
	Cinnyris dussumieri	3/13	1.69 ± 3.99^{b}	11	0.34 ± 0.18^{b}	-	-	-	-	-	-	-	-	-	-
	Trachylepis sechellensis	3/13	0.00 ± 0.00^{ab}	-	-	-	-	-	-	-	-	-	-	-	-
	Phelsuma sp.	3/13	2.62 ± 2.36^{b}	18	0.36 ± 0.30^{c}	-	-	-	-	-	-	-	-	-	-
Polyscias crassa (female phase)	Flying insects	4/28	5.57 ± 18.84^{a}	78	0.26 ± 0.07^{a}	144.82	145.72 ± 91.38^{a*}	2/12	0.50 ± 0.52^{a}	1/6	11.83 ± 1.47^{a}	591.50	588.74 ± 173.28^{a}	856.61	856.28 622.44^{a}
	Cinnyris dussumieri	4/28	0.21 ± 0.83^{b*}	3	0.25 ± 0.17^{a}	5.25	5.33 ± 4.26^{b*}	4/53	0.23 ± 0.42^{a}	3/12	12.92 ± 1.83^{a}	297.16	293.39 ± 75.19^{b}	15.60	15.62 ± 13.58^{b*}
	Trachylepis sechellensis	4/28	0.00 ± 0.00^{abc}	-	-	0	0.00 ± 0.00^{c*}	3/58	0.48 ± 0.50^{a}	2/28	13.64 ± 2.09^{a}	654.72	657.65 ± 89.45^{c}	0	0.00 ± 0.00^{c*}
	Phelsuma sp.	4/28	0.86 ± 1.67^{c}	12	0.36 ± 0.25^{a}	30.96	31.12 ± 12.82^{d*}	4/51	0.55 ± 0.50^{a}	3/28	13.18 ± 1.85^{a}	724.9	722.45 ± 93.97^{d}	224.43	224.65 98.79^{d*}
Syzygium wrightii	Flying insects	6/10	0.00 ± 0.00^{a}	-	-	0	0.00 ± 0.00^{a*}	2/7	0.29 ± 0.49^{a}	1/2	-	29	28.20 ± 16.88^{a}	0	0.00 ± 0.00^{a*}

Cinnyris dussumieri	6/10	1.20 ± 2.53^{a}	6	0.50 ± 0.34^{a*}	60	60.57 ± 42.39^{b*}	4/63	0.14 ± 0.35^{a}	2/9	-	14	14.37 ± 4.47^{b}	8.4	8.70 ± 6.83^{b*}
Trachylepis sechellensis	6/10	0.00 ± 0.00^{a}	-	-	0	0.00 ± 0.00^{a*}	2/39	0.03 ± 0.16^{a}	1/1	-	3	2.58 ± 2.52^{c}	0	0.00 ± 0.00^{a*}
Phelsuma sp.	6/10	0.20 ± 0.63^{a}	1	0.03 ± -^{a}	0.6	0.62 ± 0.60^{c*}	1/26	0 .00 ± 0.00	-	-	0	0.00 ± 0.00^{d}	0	0.00 ± 0.00^{a}

FIGURE 1. (A) Flowers of *Thespesia populnea* visited by the Seychelles sunbird (*Cinnyris dussumieri*), which inserts the head inside the flower in some visits, consequently contacting reproductive parts, while in other visits, it makes poor contact. (B) *Syzygium wrightii* flowers visited by the Seychelles skink (*Trachylepis seychellensis*), which sometimes has difficulties to reach the pendulous flowers to insert the head inside. (C) *Polyscias crassa* flowers in male phase visited by geckos (*Phelsuma sundbergi*), which walks over the exposed stamens, sweeping pollen on its head and body as it moves from flower to flower. (D) Flowers of *Polyscias crassa* in female phase visited by the invasive yellow crazy ant (*Anoplolepis gracilipes*), which frequently visits the flowers to feed on the nectar (D). Photo credits: F. Fuster.

FIGURE 2. Quantity component (QNC), quality component (QLC) and pollination effectiveness (PE) landscapes of different flower visitors for *Thespesia populnea*, *Polyscias crassa*, and *Syzygium wrightii*. Red and black dots and symbols refer to values with and without ants present, respectively. Values of proportion of flowers visited and fruit set are given as percentages, visitation rate in visits/h, and seed set in number of seeds/fruit. Mean and SD values are provided in Table 2.

FIGURE 3. Visitation rate (mean ± SE) for *Polyscias crassa* (A) and *Syzygium wrightii* (B) with and without ants. Different letters indicate significant differences (Tukey’s post hoc tests, $P < 0.05$).

Fig. 1

Fig. 2.

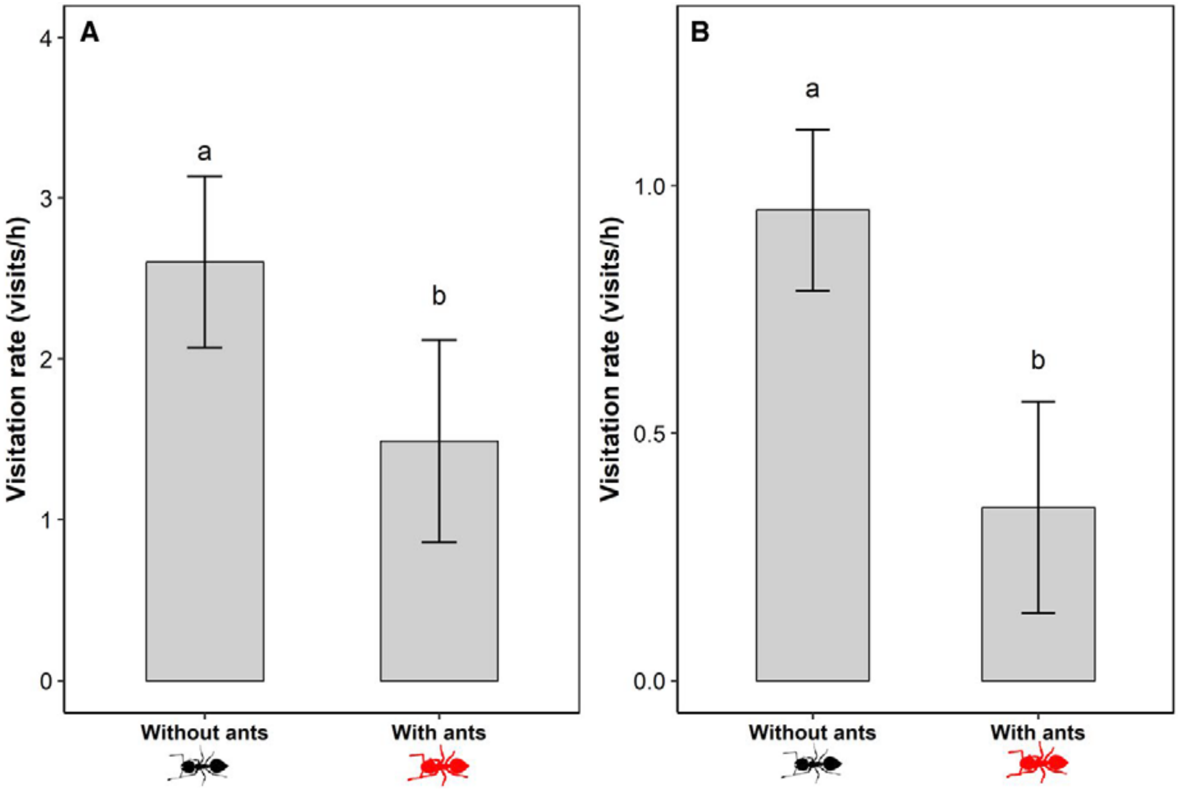
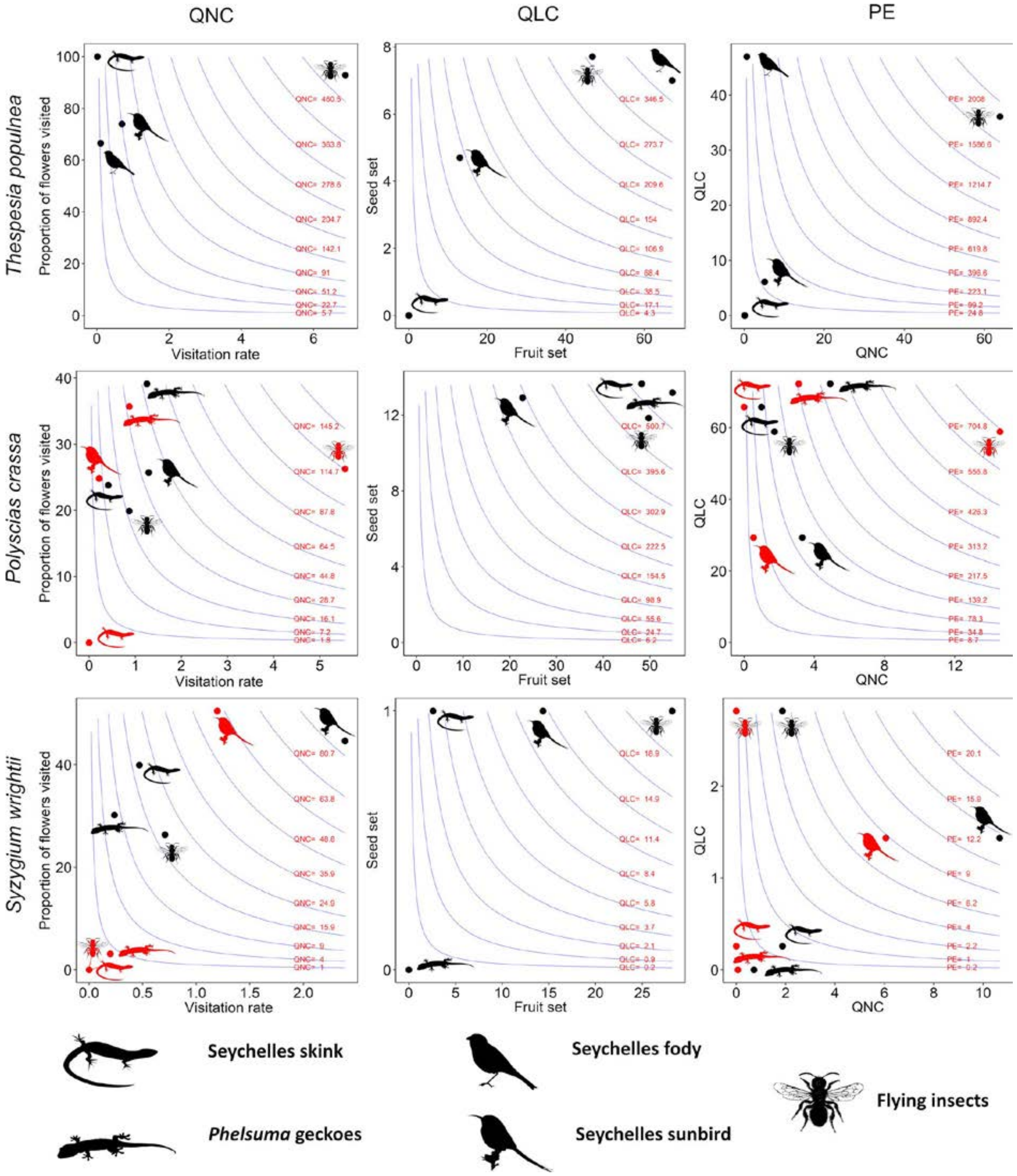

A
Visitation rate (visits/h)
0
1
2
3
4
a
b
Without ants
With ants
B
Visitation rate (visits/h)
0.0
0.5
1.0
a
b
Without ants
With ants

Fig. 3


QNC
QLC
PE
Thespesia populnea
Polyscias crassa
Syzygium wrightii
Proportion of flowers visited
Visitation rate
Seed set
Fruit set
QLC
QNC
QNC= 450.5
QNC= 353.8
QNC= 278.6
QNC= 204.7
QNC= 142.1
QNC= 91
QNC= 51.2
QNC= 22.7
QNC= 5.7
QLC= 346.5
QLC= 273.7
QLC= 209.6
QLC= 154
QLC= 106.9
QLC= 68.4
QLC= 38.5
QLC= 17.1
QLC= 4.3
PE= 2008
PE= 1586.6
PE= 1214.7
PE= 892.4
PE= 619.8
PE= 396.6
PE= 223.1
PE= 99.2
PE= 24.8
QNC= 145.2
QNC= 114.7
QNC= 87.8
QNC= 64.5
QNC= 44.8
QNC= 28.7
QNC= 16.1
QNC= 7.2
QNC= 1.8
QLC= 500.7
QLC= 395.6
QLC= 302.9
QLC= 222.5
QLC= 154.5
QLC= 98.9
QLC= 55.6
QLC= 24.7
QLC= 6.2
PE= 704.8
PE= 556.8
PE= 426.3
PE= 313.2
PE= 217.5
PE= 139.2
PE= 78.3
PE= 34.8
PE= 8.7
QNC= 80.7
QNC= 63.8
QNC= 48.8
QNC= 35.9
QNC= 24.9
QNC= 15.9
QNC= 9
QNC= 4
QNC= 1
QLC= 18.9
QLC= 14.9
QLC= 11.4
QLC= 8.4
QLC= 5.8
QLC= 3.7
QLC= 2.1
QLC= 0.9
QLC= 0.2
PE= 20.1
PE= 15.9
PE= 12.2
PE= 9
PE= 6.2
PE= 4
PE= 2.2
PE= 1
PE= 0.2
Seychelles skink
Phelsuma geckoes
Seychelles fody
Seychelles sunbird
Flying insects