

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

Francisco Fuster^{1,3}, Christopher Kaiser-Bunbury² and Anna Traveset¹

¹ Global Change Research Group, Institut Mediterrani d'Estudis Avançats (CSIC-UIB),
Miquel Marqués 21, 07190, Esporles, Mallorca, Balearic Islands, Spain.

² Centre for Ecology and Conservation, College of Life and Environmental Sciences,
University of Exeter, Cornwall Campus, Penryn, TR10 9FE, UK.

³ Author for correspondence (e-mail: f.fustbei@gmail.com)

Manuscript received _____; revision accepted _____.

Running title: Pollination effectiveness of vertebrates

ABSTRACT

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 of pollination effectiveness (QNC) 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 non-native species.

Keywords: Araliaceae; Aride island; invasive ants; island ecosystems; Mahé island; Malvaceae; mutualistic disruptions; 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 (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 visit 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 recognised (Frick et al., 2013; Cozien et al., 2019; Fuster and Traveset, 2019a, b), 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 impacts. Among the most serious current impacts is the spread of invasive non-native 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 impact 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 harbour high numbers of endemic plants (Kier et al., 2009) which 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 non-native 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 PE 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 non-native ant that frequently visited flowers of the endemic *P. crassa* and *S. wrightii*, anticipating a negative effect.

MATERIALS AND METHODS

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 (c. 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 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 mid-altitude 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) $\mu\text{l}/\text{flower}$, 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 yellow showy 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 $\mu\text{l}/\text{flower}$, 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 c. 2–3 m in height. Its protandrous flowers sit in terminal inflorescences (Fig. 1c, d), producing a relatively large amount of nectar (13.4 ± 7.26 $\mu\text{l}/\text{flower}$ – standing crop; $N = 9$ 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 volume of nectar with microcapillaries. Nectar sugar concentration was measured with a handheld refractometer.

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 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 – as 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 as 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).

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 behavior. Observation sessions lasted 30 min, totalling 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 5 - 6 censuses per day during 3 - 4 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 ‘Results’ section). In order 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.

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.

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:

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

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

To estimate QNC in *P. crassa*, we only used data from flowers in the female phase.

Pollination effectiveness (PE) was calculated as:

$$PE = QNC \times QLC$$

To test whether disturbance by invasive non-native 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 the invasive yellow crazy ant *Anoplolepis gracilipes*, can interfere with other flower visitors. By contrast, when there were only a few ant individuals observed, such interference was never detected.

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 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 as 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* as 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 dataset with the sample size as in the original dataset 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 GLMs 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.Indscp* package (Jordano and Rodriguez-Sanchez, 2017).

272

273 RESULTS

274 *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*.

281

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 (Table S1 and Fig. S1a, b in Appendix S1 [see Supplementary Data with this article]). Ants of the native *Camponotus grandieri* (Forel, 1886) and the non-native *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* (Table S2). 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) (Table 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 (Table S1, S2). 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 Table 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: $\chi^2 = 34.10$, $df = 3$, $P < 0.001$; Fig. S2a, b). 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) (Fig. S2a, b, Table S1). Most flying insect visits in both male and female flowers were bees, especially *Apis mellifera* (Table S2), which was a frequent visitor only for a short period (c. 7 days). By contrast, vertebrates and the invasive yellow crazy ant visited flowers more evenly over the full period of flower receptivity (c. 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 (Fig. S3a, Table S1). 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 (Fig. S3b).

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; Table S1, Fig. S1c); 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 ($\chi^2 = 1.95$, $df = 2$, $P = 0.376$; Fig. S1d).

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 ($\chi^2 = 1.91$, $df = 3$, $P = 0.590$; Table S1, Fig. S2c, d). Likewise, there were no differences in fruit set in *S. wrightii* among pollinator taxa ($\chi^2 = 0.67$, $df = 3$, $P = 0.880$; Fig. S3c), except for geckos' visits which resulted in no fruits. For this species, ant visits did result in fruit production.

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), whilst 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 insect 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).

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* ($\chi^2 = 9.86$, $df = 1$, $P = 0.002$; 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 ($\chi^2 = 4.16$, $df = 1$, $P = 0.041$, Fig. 3b) across all pollinator taxa (Fig. 2, Table 2). Nevertheless, sunbirds were the most effective pollinators under both disturbed and undisturbed conditions.

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 non-native 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 non-native ants, shown by

378 the decrease of flower visitation rates in presence of ants. In fact, the degree of floral
379 ant infestation of the two threatened island endemics *P. crassa* and *S. wrightii* is likely
380 to have longer-term negative implications for the conservation of both species as their
381 pollination, and consequently seed production, can be compromised (see Rogers et al.,
382 2017).

383 Coevolution implies specialization among mutualistic partners, and this may be
384 reflected in animal and flower traits (Thompson, 1994; Baker et al., 1998). *Syzygium*
385 *wrightii* presents a bird-pollination syndrome, with open and bright yellow flowers
386 with long styles and stigmas and a bell-shaped calyx. This facilitates nectar
387 consumption and pollination by long-billed birds (Vogel, 1954; Faegri and Van der Pijl,
388 1979; Rebelo et al., 1984) such as sunbirds, which were their most important
389 pollinators. Floral syndromes, however, are not always a good predictor of the
390 pollinator assemblage of a plant species (Ollerton et al., 2009; Rosas-Guerrero, 2014).
391 Multiple selection pressures on floral traits may result in adaptations to multiple
392 effective and ineffective pollinators (Aigner, 2001). For instance, *T. populnea*,
393 pollinated by insects elsewhere in its native range (Woodell, 1979; Gandhi, 2000) and
394 mostly by bees in our study, produces small volumes of highly concentrated nectar
395 that fits with nectar feeding insects (Faegri and Van der Pijl, 1979). However, its large,
396 yellow, bell-shaped flowers also fit a bird-pollination syndrome, but the importance of
397 Seychelles fodies and sunbirds was low. In contrast, geckos were the most important
398 pollinators of the apparently entomophilous *P. crassa*. Possible adaptations of *P.*
399 *crassa* to pollination by geckos include rigid inflorescences that can support the weight
400 of these animals, and big leaves that they may use as resting places and refuge. Both *P.*
401 *crassa* and *S. wrightii* produce high amounts of diluted nectar, a common trait in bird-

402 pollinated flowers (Faegri and van der Pijl, 1979; Fleming et al., 2009), which may be
403 useful to other animals with high energy demands, such as reptiles (Brown et al., 1978;
404 Cronk and Ojeda, 2008). Specialist vertebrate pollinators are assumed to shape
405 selection pressures on certain floral traits (e.g. Guimarães et al., 2011, Bartkowska and
406 Johnston, 2012), and our results suggest that also opportunistic vertebrates may
407 contribute to selection, as also is suggested in Hervías-Parejo et al. (2019).

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

417 The analysis of PE and their components reveals the effect of pollinator visits
418 on plant reproductive success (Schupp et al., 2017). For pollinators to be considered
419 highly effective, they must either be frequent visitors (Rodríguez-Rodríguez and Valido,
420 2011; Cavallero et al., 2018) or be very efficient pollen vectors (Pellmyr and Thompson,
421 1996; Castro et al., 2013), and these components can differ within a pollinator species
422 when visiting different plant species. In *T. populnea*, fodies and sunbirds had similar
423 PEs, and so did flying insects and sunbirds in *P. crassa* in the absence of ants; yet, the
424 quantitative and qualitative component of PE varied considerably in both plant
425 species. Similarly, in the same plant communities, geckos were negligible pollinators of

426 *S. wrightii* compared to sunbirds or flying insects, but were the most important
427 pollinators for *P. crassa*. Specialist nectar-feeders such as sunbirds have evolved
428 mechanisms to become nectar robbers for some plant species (*T. populnea*) and
429 legitimate pollinators for others (*S. wrightii*), which appears to be a relatively common
430 behavior of specialist nectarivores (Irwin et al., 2010). Thus, neither specialist nor
431 opportunistic nectar-feeders consistently act as effective or ineffective pollinators.

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

444 Despite some overlap in the pollinator community among our focal plant
445 species, PE indicated a low functional redundancy, as there was only one highly
446 effective pollinator taxon for each plant species: insects in *T. populnea*, geckos in *P.*
447 *crassa*, and sunbirds in *S. wrightii*. This low functional redundancy and high mutual
448 dependency appears typical for depauperate insular pollinator communities (Kaiser-
449 Bunbury et al., 2010; Traveset et al., 2015). On *P. crassa*, presence of ants was

450 associated with reduced visitation rates of vertebrates but not flying insects. Indeed,
451 visitation rates and PE of flying insects in the presence of ants was high, which may be
452 explained by ants deterring vertebrate pollinators and thereby causing a competitive
453 release of flying insects. This suggests that, at least in this plant species, a reduction in
454 vertebrate pollinators may be compensated by flying insects, suggesting higher
455 functional redundancy in the presence of ants compared to the non-disturbed
456 situation. However, it must be also noted that a higher frequency of insect visits does
457 not necessarily translates into higher pollination success; in our case, bees (the main
458 flying insects) were frequent visitors during a very short period (c. 7 days), which sheds
459 doubt on their role as reliable pollinator.

460 Despite the potential impact of ants on flower visitors, there is evidence that
461 ants can also act as pollinators (García et al., 2012; de Vega and Gómez, 2014), as our
462 data showed in *S. wrightii*. Thus, whether ants act as mutualists or antagonists seem to
463 be context-dependent and should be considered individually. For instance,
464 *Technomyrmex albipes*, an invasive ant species in many areas (including the
465 Seychelles), has caused several problems on native fauna and flora displacing other
466 animals and disrupting mutualistic interactions (e.g. Lach, 2008; Hansen and Müller,
467 2009). The same ant species has been reported, however, as an effective pollinator for
468 a conspecific *Syzygium* species, *S. occidentale*, in India (Kuriakose et al., 2018).

469 Our findings, albeit relatively strong and biologically convincing, should be
470 interpreted carefully because of high stochasticity, low pollinator visitation rate, and a
471 relatively small and unbalanced sample size for some interactions and treatments (see
472 Table 2 and Table S1). In addition, the coarse taxonomic resolution of insect visitors
473 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.

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 non-native species. Hence, controlling or eradicating invasive species in vulnerable island ecosystems is a priority management intervention to avoid mutualistic disruptions.

ACKNOWLEDGEMENTS

We thank the Island Conservation Society, especially Pierre-André Adam, and Aride Nature Reserve staff including Uzice Samedi, Licia Calabrese and Melinda Curran, which granted permission and provided administrative and field support to work on Aride Island. Further, we thank the Seychelles National Park Authority, especially James Mougat, for providing permission and support to work in Morne Seychellois National Park on Mahé. We are particularly grateful to Andrew Whittington for insect identifications and Nancy Bunbury for editing and critical review of earlier drafts. Two anonymous reviewers made constructive comments to a previous version. This work was part of projects CGL2013-44386-P and CGL2017-88122-P awarded to AT. FF was funded by a PhD fellowship (BES-2014-068207), both financed by the Spanish

498 Government. CNK-B was supported by funding from the German Research Foundation
499 (DFG; KA 3349/2-1 and KA 3349/3-1).

500

501 **AUTHOR CONTRIBUTIONS**

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

505

506 **DATA AVAILABILITY**

507 The datasets generated for this study are available on request to the
508 corresponding author.

509

510 **SUPPORTING INFORMATION**

511 Additional Supporting Information may be found online in the supporting
512 information section at the end of the article, Appendix S1 (containing Table S1, S2,
513 Figure S1, S2, S3).

514

515 **REFERENCES**

- 516 Aigner, P. A. 2001. Optimality modeling and fitness trade-offs: when should plants
517 become pollinator specialists? *Oikos* 95(1): 177–184.
- 518 Aslan, C. E., E. S. Zavaleta, B. Tershy, and D. Croll. 2013. Mutualism disruption
519 threatens global plant biodiversity: a systematic review. *PLoS ONE* 8(6): e66993.

520 Baker, H. G., I. Baker, and S. A. Hodges. 1998. Sugar composition of nectars and fruits
521 consumed by birds and bats in the tropics and subtropics. *Biotropica* 30: 559–
522 586.

523 Bartkowska, M., and M. O. Johnston. 2012. Pollinators cause stronger selection than
524 herbivores on floral traits in *Lobelia cardinalis* (Lobeliaceae). *New Phytologist*
525 193(4): 1039–1048.

526 Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects
527 models using lme4. *Journal of Statistical Software* 67(1): 1–48.

528 Bellard, C., C. Leclerc, B. Leroy, M. Bakkenes, S. Veloz, W. Thuiller, and F. Courchamp.
529 2014. Vulnerability of biodiversity hotspots to global change. *Global Ecology*
530 *and Biogeography* 23(12): 1376–1386.

531 Bellard, C., J. F. Rysman, B. Leroy, C. Claud, and G. M. Mace. 2017. A global picture of
532 biological invasion threat on islands. *Nature Ecology and Evolution* 1: 1862–
533 1869.

534 Bissessur, P., C. Baider, and F. B. V., Florens. 2017. Rapid population decline of an
535 endemic oceanic island plant despite resilience to extensive habitat destruction
536 and occurrence within protected areas. *Plant Ecology & Diversity* 10(4): 293–
537 302.

538 Brown, J. H., W. A. Calder, and A. Kodric-Brown. 1978. Correlates and consequences of
539 body size in nectar-feeding birds. *American Zoology* 18(4): 687–700.

540 Castro, S., J. Loureiro, V. Ferrero, P. Silveira, and L. Navarro. 2013. So many visitors and
 541 so few pollinators: variation in insect frequency and effectiveness governs the
 542 reproductive success of an endemic milkwort. *Plant Ecology* 214: 1233–1245.

543 Cavallero, L., C. L. Morales, A. Montero-Castaño, J. H. Gowda, and M. A. Aizen. 2018.
 544 Scale-dependent effects of conspecific flower availability on pollination
 545 quantity and quality in an invasive shrub. *Oecologia* 188: 501–513.

546 Cerdà, X., E. Angulo, S. Caut, and F. Courchamp. 2012. Ant community structure on a
 547 small Pacific island: only one native species living with the invaders. *Biological*
 548 *Invasions* 14: 323–339.

549 Cozien, R. J., T. van der Niet, S. D. Johnson, and S-L. Steenhuisen. 2019. Saurian
 550 surprise: lizards pollinate South Africa's enigmatic hidden flower. *Ecology*
 551 100(6): e02670.

552 Cronk, Q., and I. Ojeda. 2008. Bird-pollinated flowers in an evolutionary and molecular
 553 context. *Journal of Experimental Botany* 59(4): 715–727.

554 Custodio, T., P. Comtois, and A. C. Araujo. 2017. Reproductive biology and pollination
 555 ecology of *Triplaris gardneriana* (Polygonaceae): a case of ambophily in the
 556 Brazilian Chaco. *Plant Biology* 19: 504–514.

557 Da Silva, L.P., J. A. Ramos, J. Olesen, A. Traveset, and R. Heleno. 2014. Flower visitation
 558 by birds in Europe. *Oikos* 123(11): 1377–1383.

559 De Vega, C., and J. M., Gómez. 2014. Polinización por hormigas: conceptos, evidencias
 560 y futuras direcciones. *Ecosistemas* 23(3): 48–57.

Con formato: Español

561 Diller, C., M., Castañeda-Zárate, S. D., Johnson. 2019. Generalist birds outperform
562 specialist sunbirds as pollinators of an African *Aloe*. *Biology Letters* 15(7) (in
563 press). doi: 10.1098/rsbl.2019.0349

564 Faegri, K., and L., Van der Pijl. 1979. The principles of pollination ecology. Pergamon
565 Press, Oxford.

566 Fleischmann, K., S., Porembski, N., Biedinger, and W., Barthlott. 1996. Inselbergs in the
567 sea: vegetation of granite outcrops on the islands of Mahé, Praslin and
568 Silhouette (Seychelles). *Bulletin of the Geobotanical Institute ETH* 62: 61–74.

569 Fleming, T. H., C., Geiselman, and W. J., Kress. 2009. The evolution of bat pollination: a
570 phylogenetic perspective. *Annals of Botany* 104: 1017–1043.

571 Frick, W. F., R. D., Price, P. A., Heady III, and K. M., Kay. Insectivorous bat pollinates
572 columnar cactus more effectively per visit than specialized nectar bat. *The*
573 *American Naturalist* 181(1): 137–144.

574 Fuster, F., C., Kaiser-Bunbury, J. M., Olesen, and A., Traveset. 2019. Global patterns of
575 the double mutualism phenomenon. *Ecography* 42(4): 826–835.

576 Fuster, F., and A., Traveset. 2019a. Evidence for a double mutualistic interaction
577 between a lizard and a Mediterranean gymnosperm, *Ephedra fragilis*. *AoB*
578 *Plants* 11: plz001. doi: 10.1093/aobpla/plz001

579 Fuster, F., and A., Traveset. 2019b. Importance of intraspecific variation in the
580 pollination and seed dispersal functions of a double mutualist animal species.
581 *Oikos* (in press). doi: 10.1111/oik.06659

582 Gandhi, T. 2000. Birds and plant regenerations. Ravi Dayal. New Delhi.

583 García, M. B., X., Espadalaer, and J. M., Olesen. 2012. Extreme reproduction and
584 survival of a true cliffhanger: the endangered plant *Borderea chouardii*
585 (Dioscoreaceae). *PLoS ONE* 7(9): e44657.

586 Guimarães, P. R., P., Jordano, and J. N., Thompson. 2011. Evolution and co- evolution
587 in mutualistic networks. *Ecology Letters* 14: 877–885.

588 Hansen, D. M., and C. B., Müller. 2009. Invasive ants disrupt gecko pollination and seed
589 dispersal of the endangered plant *Roussea simplex* in Mauritius. *Biotropica*
590 41(2): 202–208.

591 Herrera, C. M. 2000. Flower-to-seedling consequences of different pollination regimes
592 in an insect-pollinated shrub. *Ecology* 81(1): 15-29.

593 Hervías-Parejo, S., and A., Traveset. 2018. Pollination effectiveness of opportunistic
594 Galápagos birds compared to that of insects: From fruit set to seedling
595 emergence. *American Journal of Botany* 105(7): 1142–1153.

596 Hervías-Parejo, S., R., Heleno, M., Nogales, J. M., Olesen, and A., Traveset. 2019.
597 Divergence in floral trait preferences between nonflower-specialized birds and
598 insects on the Galápagos. *American Journal of Botany* 106(4): 540–546.

599 Holway, D. A., L., Lach, A. V., Suarez, N. D., Tsutsui, and T. J., Case. 2002. The causes
600 and consequences of ant invasions. *Annual Review of Ecology and Systematics*
601 33: 181–233.

602 Hothorn, T., F., Bretz, and P., Westfall. 2008. Simultaneous inference in general
603 parametric models. *Biometrical Journal* 50(3): 346–363.

604 Irwin, R. E., J. L., Bronstein, J.S., Manson, and L., Richardson. 2010. Nectar robbing:
 605 ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution,*
 606 *and Systematics* 41: 271–292.

607 Jaca, J., M., Nogales, and A., Traveset. 2019a. Reproductive success of the Canarian
 608 *Echium simplex* (Boraginaceae) mediated by vertebrates and insects. *Plant*
 609 *Biology* 21(2): 216–226.

610 Jaca, J., N., Rodríguez, M., Nogales, and A., Traveset. 2019b. Impact of alien rats and
 611 honeybees on the reproductive success of an ornithophilous endemic plant in
 612 Canarian thermosclerophyllous woodland relicts. *Biological invasions* 21(10):
 613 3203–3219.

614 Jordano, P., and F., Rodríguez-Sánchez. 2017. pedroj/effectiveness_pckg: R package:
 615 effect.Indscp v.0.2 (Version v.0.2). *Zenodo*. doi: 10.5281/zenodo.376763

616 Kaiser-Bunbury, C. N., A., Traveset, and D. M., Hansen. 2010. Conservation and
 617 restoration of plant-animal mutualisms on oceanic islands. *Perspectives in Plant*
 618 *Ecology, Evolution and Systematics* 12: 131–143.

619 Kaiser-Bunbury, C. N., H., Cuthbert, R., Fox, D., Birch, and N., Bunbury. 2014. Invasion
 620 of yellow crazy ant *Anoplolepis gracilipes* in Seychelles UNESCO palm forest.
 621 *NeoBiota* 22: 43–57.

622 Kier, G., H., Kreft, T. M., Lee, W., Jetz, P. L., Ibisch, C., Nowicki, J., Mutke, and W.,
 623 Barthlott. A global assessment of endemism and species richness across island
 624 and mainland regions. *Proceedings of the National Academy of Sciences of the*
 625 *United States of America* 106(23): 9322–9327.

626 Kuriakose, G., P. A., Sinu, and K. R. Shivanna. 2018. Ant pollination of *Syzygium*
627 *occidentale*, an endemic tree species of tropical rain forest of the Western
628 Ghats, India. *Arthropod-Plant Interactions* 12: 647–655.

629 Lach, L. 2008. Argentine ants displace floral arthropods in a biodiversity hotspot.
630 *Diversity and Distributions* 14(2): 281–290.

631 Legendre, P., and L. Legendre. 1998. Numerical ecology. Amsterdam: Elsevier Science.

632 LeVan, K. E., K. L., James Hung, K. R., McCann, J. T., Ludka, and D. A., Holway. 2014.
633 Floral visitation by the Argentine ant reduces pollinator visitation and seed set
634 in the coast barrel cactus, *Ferocactus viridescens*. *Oecologia* 174: 163–171.

635 Lewis, T., J. M., Cherrett, I., Haines, J. B., Haines, and P. L., Mathias. 1976. The crazy ant
636 (*Anoplolepis longipes* (Jerd.) (Hymenoptera, Formicidae)) in Seychelles, and its
637 chemical control. *Bulletin of Entomological Research* 66: 97–111.

638 Maruyama, P. K., C. E. P., Nunes, J., Vizentin-Bugoni, S., Gustafsson, and L. P. C.,
639 Morellato. 2018. Are native bees and *Apis mellifera* equally efficient pollinators
640 of the rupestrian grassland daisy *Aspilia jolyana* (Asteraceae)? *Acta Botanica*
641 *Brasilica* 32(3): 386–391.

642 Motten, A. F., D. R., Campbell, D. E., Alexander, H. L., Miller. 1981. Pollination
643 effectiveness of specialist and generalist visitors to a North Carolina population
644 of *Claytonia virginica*. *Ecology* 62(5): 1278–1287.

645 Nebot, A., D., Cogoni, G., Fenu, and G., Bacchetta. 2020. Breeding system and
646 inbreeding depression in a translocated population of the endangered plant

Con formato: Español

647 *Dianthus morisianus* (Caryophyllaceae). *Flora: Morphology, Distribution,*
648 *Functional Ecology of Plants* 262: 151488.

649 Ne'eman, G., A., Jürgens, L., Newstrom-Lloyd, S. G., Potts, and A., Dafni. 2010. A
650 framework for comparing pollinator performance effectiveness and efficiency.
651 *Biological Review* 85: 435–451.

652 Olesen, J. M., and A., Valido. 2003. Lizards as pollinators and seed dispersers: an island
653 phenomenon. *Trends in Ecology and Evolution* 18(4): 177–181.

654 Ollerton, J., R., Alarcón, N.M., Waser, M.V., Price, S., Watts, L., Cranmer, A., Hingston,
655 et al. 2009. A global test of the pollination syndrome hypothesis. *Annals of*
656 *Botany* 103(9): 1471–1480.

657 Pellmyr, O., and J. N., Thompson. 1996. Sources of variation in pollinator contribution
658 within a guild: the effects of plant and pollinator factors. *Oecologia* 107: 595–
659 604.

660 Plentovich, S., T., Russell, and C. C., Fejeran. 2018. Yellow crazy ants (*Anoplolepis*
661 *gracilipes*) reduce numbers and impede development of a burrow-nesting
662 seabird. *Biological Invasions* 20: 77–86.

663 Rafferty, N. E., and A. R., Ives. 2012. Pollinator effectiveness varies with experimental
664 shifts in flowering time. *Ecology* 93(4): 803-814.

665 Ratto, F., B. I., Simmons, R., Spake, V., Zamora-Gutierrez, M. A., MacDonald, J. C.,
666 Merriman, C. J., Tremlett, et al. 2018. Global importance of vertebrate
667 pollinators for plant reproductive success: a meta-analysis. *Frontiers in Ecology*
668 *and the Environment* 16(2): 82–90.

669 Rebelo, A. G., W. R., Siegfried, and E. G. H., Oliver. 1985. Pollination syndromes of *Erica*
 670 species in the south-western Cape. *South African Journal of Botany* 51: 270–
 671 280.

672 Reynolds, R. J., and C. B., Fenster. 2008. Point and interval estimation of pollinator
 673 importance: a study using pollination data of *Silene caroliniana*. *Oecologia*
 674 156(2): 325–332.

675 Rocca, M., and M., Sazima. 2013. Quantity versus quality: identifying the most
 676 effective pollinators of the hummingbird-pollinated *Vriesea rodigasiana*
 677 (Bromeliaceae). *Plant Systematics and Evolution* 299: 97–105.

678 Rodríguez-Rodríguez, M. C., and A., Valido. 2011. Consequences of plant-pollinator and
 679 floral-herbivore interactions on the reproductive success of the Canary Islands
 680 endemic *Canarina canariensis* (Campanulaceae). *American Journal of Botany*
 681 98(9): 1465–1474.

682 Rodríguez-Rodríguez, M. C., P., Jordano, and A., Valido. 2013. Quantity and quality
 683 components of effectiveness in insular pollinator assemblages. *Oecologia*
 684 173(1): 179–190.

685 Rogers, H. S., E. R., Buhle, J., HilleRisLambers, E. C., Fricke, R. H., Miller, and J. J.,
 686 Tewksbury. 2017. Effects of an invasive predator cascade to plants via
 687 mutualism disruption. *Nature Communications* 8: 14557.

688 Rosas-Guerrero, V., R., Aguilar, S., Martén-Rodríguez, L., Ashworth, M., Lopezaraiza-
 689 Mikel, J. M., Bastida, and M., Quesada. 2014. A quantitative review of
 690 pollination syndromes: do floral traits predict effective pollinators? *Ecology*
 691 *Letters* 17: 388–400.

692 Sahli, H. F., and J. K., Conner. 2007. Visitation, effectiveness, and efficiency of 15
693 genera of visitors to wild raddish, *Raphnus raphanistrum* (Brassicaceae).
694 *American Journal of Botany* 94(2): 203–209.

695 Sax D. F., and S. D., Gaines. 2008. Species invasions and extinction: the future of native
696 biodiversity on islands. *Proceedings of the National Academy of Sciences of the*
697 *United States of America* 105: 11490–11497.

698 Schmidt-Lebuhn, A. N., M., Kessler, and I., Hensen. 2007. Hummingbirds as drivers of
699 plant speciation? *Trends in Plant Science* 12 (8): 329–331.

700 Schupp, E. W., P., Jordano, and J. M., Gómez. 2017. A general framework for
701 effectiveness concepts in mutualisms. *Ecology Letters* 20: 577–590.

702 Sinu, P. A., V. C., Sibisha, M. V. N., Reshmi, K. S., Reshmi, T. V., Jasna, K., Aswathi, and P.
703 P., Megha. 2017. Invasive ant (*Anoplolepis gracilipes*) disrupts pollination in
704 pumpkin. *Biological Invasions* 19: 2599–2607.

705 Thompson, J. N. 1994. The Coevolutionary Process. University of Chicago Press,
706 Chicago.

707 Traveset, A., and D. M., Richardson. 2006. Biological invasions as disruptors of plant
708 reproductive mutualisms. *Trends in Ecology and Evolution* 21(4): 208–216.

709 Traveset, A., and D. M., Richardson. 2014. Mutualistic interactions and biological
710 invasions. *Annual Review of Ecology, Evolution, and Systematics* 45: 89–113.

711 Traveset, A., C., Tur, K., Trøjelsgaard, R., Heleno, R., Castro-Urgal, and J. M., Olesen.
712 2015. Global patterns of mainland and insular pollinator network. *Global*
713 *Ecology and Biogeography* 25(7): 880–890.

714 Valverde, J., F., Perfectti, and J. M., Gómez. 2019. Pollination effectiveness in a
715 generalist plant: adding the genetic component. *New Phytologist* 223(1): 354–
716 365.

717 Vogel, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung dargestellt
718 anhand der Flora Südafrikas. *Botanische Studien* 1: 1-338

719 Wetterer, J. K. 2005. Worldwide distribution and potential spread of the long-legged
720 ant, *Anoplolepis gracilipes* (Hymenoptera: Formicidae). *Sociobiology* 45: 1–21.

721 Woodell, S. R. J. 1979. The role of unespecialized pollinators in the reproductive
722 success of Aldabra plants. *Philosophical Transactions of the Royal Society of*
723 *London. Series B* 286(11): 99–108.

724

725

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 \pm SD	Npl	Nfrt	Mean \pm SD
<i>Thespesia populnea</i>	Control	10	30	0.33 \pm 0.48 ^a	7	10	8.90 \pm 4.15 ^a
	Autogamy	12	39	0.08 \pm 0.27 ^b	2	3	1.00 \pm 1.00 ^b
	Geitonogamy	7	27	0.48 \pm 0.51 ^a	4	13	7.77 \pm 3.83 ^a
	Xenogamy	9	30	0.50 \pm 0.51 ^a	6	15	7.00 \pm 2.04 ^a
<i>Polyscias crassa</i> (female phase)	Control	6	84	0.74 \pm 0.44 ^a	5	62	13.23 \pm 2.28 ^a
	Geitonogamy	1	24	0.96 \pm 0.20 ^a	1	23	12.87 \pm 1.35 ^a
	Xenogamy	3	55	0.95 \pm 0.23 ^a	3	52	12.60 \pm 1.14 ^a
<i>Syzygium wrightii</i>	Control	6	125	0.18 \pm 0.38 ^a	-	-	-
	Autogamy	5	56	0.05 \pm 0.23 ^a	-	-	-
	Geitonogamy	4	51	0.10 \pm 0.30 ^a	-	-	-
	Xenogamy	1	15	0.13 \pm 0.35 ^a	-	-	-

740 TABLE 2. Mean and standard deviation (SD) of visitation rate, proportion of flowers visited, fruit set and seed set from original datasets considering the presence and absence of ants. Values of the quantity (QNC) of
 741 quality components (QLC) of pollination effectiveness (PE) were obtained from the mean values of original datasets; mean and SD values from resampled datasets (N = 5000) are also given. Values of QNC, QLC and
 742 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 for the
 743 same pollinator taxon and plant species. Note that QLC values are the same in presence and absence of ants. Note also that values of *Thespesia populnea* are only provided once, as the effect of presence
 744 was not tested.
 745

Ants effect	Plant species	Pollinator	QNC				QLC								PE	
			Visitation rate		Proportion of flowers visited		QNC	QNC resampled	Fruit set		Seed set		QLC	QLC resampled	PE	PE
			Nplants/ Nobservations	Mean ± SD	Nvisits	Mean ± SD		Mean ± SD	Nplants/ Nflowers	Mean ± SD	Nplants/ Nfruits	Mean ± SD		Mean ± SD		
Without ants	<i>Thespesia populnea</i>	Flying insects	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Cinnyris dussumieri</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Foudia sechellarum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Trachylepis sechellensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Polyscias crassa</i> (male phase)	Flying insects	6/39	14.41 ± 26.66 ^a	125	0.41 ± 0.29 ^{ab}	-	-	-	-	-	-	-	-	-	-
		<i>Cinnyris dussumieri</i>	6/39	1.74 ± 2.68 ^b	34	0.48 ± 0.22 ^b	-	-	-	-	-	-	-	-	-	-
		<i>Trachylepis sechellensis</i>	6/39	0.67 ± 1.40 ^c	13	0.66 ± 0.33 ^a	-	-	-	-	-	-	-	-	-	-
		<i>Phelsuma</i> sp.	6/39	1.69 ± 2.18 ^b	32	0.52 ± 0.27 ^{ab}	-	-	-	-	-	-	-	-	-	-
	<i>Polyscias crassa</i> (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	101.50
		<i>Cinnyris dussumieri</i>	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	97.50
		<i>Trachylepis sechellensis</i>	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	65.00
		<i>Phelsuma</i> 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	354.00

	<i>Syzygium wrightii</i>	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
		<i>Cinnyris dussumieri</i>	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
		<i>Trachylepis sechellensis</i>	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
		<i>Phelsuma sp.</i>	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
With ants	<i>Thespesia populnea</i>	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
		<i>Cinnyris dussumieri</i>	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
		<i>Foudia sechellarum</i>	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
		<i>Trachylepis sechellensis</i>	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
	<i>Polyscias crassa</i> (male phase)	Flying insects	3/13	0.15 ± 0.56 ^{a*}	1	0.04 ± - ^{a*}	-	-	-	-	-	-	-	-	-	-
		<i>Cinnyris dussumieri</i>	3/13	1.69 ± 3.99 ^b	11	0.34 ± 0.18 ^b	-	-	-	-	-	-	-	-	-	-
		<i>Trachylepis sechellensis</i>	3/13	0.00 ± 0.00 ^{ab}	-	-	-	-	-	-	-	-	-	-	-	-
		<i>Phelsuma sp.</i>	3/13	2.62 ± 2.36 ^b	18	0.36 ± 0.30 ^c	-	-	-	-	-	-	-	-	-	-
	<i>Polyscias crassa</i> (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*}
		<i>Cinnyris dussumieri</i>	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*}
		<i>Trachylepis sechellensis</i>	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*}
		<i>Phelsuma sp.</i>	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*}
	<i>Syzygium wrightii</i>	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*}
		<i>Cinnyris dussumieri</i>	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*}
		<i>Trachylepis sechellensis</i>	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*}
		<i>Phelsuma sp.</i>	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

748 FIGURE 1. (a) Flowers of *Thespesia populnea* visited by the Seychelles sunbird (*Cinnyris*
749 *dussumieri*) which inserts the head inside the flower in some visits, consequently contacting
750 reproductive parts, whilst in other visits, it makes poor contact. (b) *Syzygium wrightii* flowers
751 visited by the Seychelles skink (*Trachylepis seychellensis*) which sometimes has difficulties to
752 reach the pendulous flowers to insert the head inside. (c) *Polyscias crassa* flowers in male
753 phase visited by *Phelsuma sundbergi* gecko which walks over the exposed stamens, sweeping
754 pollen on its head and body as it moves from flower to flower. (d) Flowers of *P. crassa* in
755 female phase visited by the invasive yellow crazy ant (*Anoplolepis gracilipes*) which frequently
756 visits the flowers to feed on the nectar (d). Photo credits: F. Fuster.

757

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

764

765 FIGURE 3. Visitation rate (mean \pm SE) for *Polyscias crassa* (a) and *Syzygium wrightii* (b) with
766 and without ants. Different letters indicate significant differences (Tukey's post hoc tests, $P <$
767 0.05).