Impacts of invasive ants on pollination of native plants are similar in invaded and restored plant communities

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ABSTRACT

Ants are amongst the most successful invaders worldwide and can markedly modify invaded communities through biotic interactions. Invasive ants, for example, can compete with native pollinators for resources, act as legitimate pollinators, or disrupt plant-pollinator mutualistic interactions, thereby affecting native plant reproduction. Ecological restoration aims to mitigate the impact of invasive species and restore ecological communities and ecosystem functioning. Here we investigated the combined effects of two invasive ant species, the yellow crazy ant (*Anoplolepis gracilipes*) and white-footed ant (*Technomyrmex albipes*), on the pollination and reproduction of native plants in the context of a large-scale plant community restoration experiment. We conducted ant exclusion experiments and pollinator observations to obtain data on plant reproduction and pollination of four plant species. The experiments were conducted across eight granitic inselbergs on the island of Mahé, Seychelles, four of which are undergoing restoration since 2011 and four remained as invaded control sites (unrestored). Our findings indicate that native plants on Seychelles' inselbergs relied primarily on flying flower visitors for pollination, considering that the contribution of ants to fruit set was generally small and substantially lower than that of flying pollinators. Moreover, while flying pollinators approached flowering plants irrespective of invasive ant presence, the number of probed flowers per visit was reduced, in both restored and unrestored communities. Therefore, native plant reproduction was negatively affected by the presence of invasive ants and this effect was similar in restored and unrestored plant communities. Our research suggests that invasive ants may contribute to changes in plant communities by deterring legitimate pollinators of native plants, an impact that is unlikely to be alleviated through early stages of ecological restoration.

1. Introduction

The introduction of species to new locations is increasing worldwide as a result of human activity, and with it the number of species that establish self-sustaining populations outside their native ranges (Mack et al., 2000; Seebens et al., 2017). Invasive non-native

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species are one of the main threats to native biodiversity (Bellard et al., 2016; Butchart et al., 2010; McGeoch et al., 2010) and can disrupt the structure and functioning of native ecosystems by displacing native species and establishing novel interactions (Hobbs et al., 2006). Ants are among the most successful and destructive invaders (Lowe et al., 2000) with around 19 invasive ant species recorded globally (GISD, 2023). This number is gradually increasing (e.g. Chifflet et al., 2018; Cordonnier et al., 2020) due to globalisation and international trade (Bertelsmeier, 2021). Some of the characteristics associated with the invasion success of ants are the formation of super-colonies, high reproduction rates, and strong ability to displace native species and establish novel mutualistic and antagonistic interactions (Hobbs et al., 2006; Lach et al., 2010).

Although ants in their native range can be efficient pollinators of native plants (Ashman and King, 2005; Gómez, 2000; Gómez et al., 1996), most studies show that ants in their invasive range disrupt plant-pollinator interactions, and therefore, can negatively affect native plant reproduction in recipient ecosystems (Holway et al., 2002). For instance, ants can act as floral antagonists by directly damaging or consuming reproductive structures such as anthers or pollen without pollinating, thereby reducing plant reproduction success (Beattie et al., 1984; Rostás et al., 2018). Moreover, due to their high abundances, invasive ants can consume carbohydrate-rich resources in large quantities, thus acting as nectar thieves and competing with native pollinators for resources (Holway et al., 2002; Lach, 2005). Some studies have shown a decrease in flower visitation rates by effective pollinators in the presence of invasive ants (Junker et al., 2007; Lach, 2007, 2008; Ness, 2006), thereby reducing pollination.

As most ant invasions occur in relatively degraded ecosystems (King and Tschinkel, 2008), it is not always clear whether the observed vulnerabilities of native plants and their mutualists are amplified by causally unrelated stressors such as a decline in vegetation diversity due to plant invasion, grazing, land use change, etc (Bissessur et al., 2020). One way to mitigate or reverse the impact of degradation of ecosystems is through ecological restoration (Higgs et al., 2018; Palmer et al., 2016). The removal of non-native plant species is a common approach to reduce competition for resources and space between native and non-native plants, and we know now that such a restoration approach can have positive effects on pollinator interactions and plant reproductive performance (Kaiser-Bunbury et al., 2017). As degraded ecosystems often suffer multiple invasions (Russell and Kaiser-Bunbury, 2019), understanding the consequences of the management of one group of non-native species on other species and their interactions can help in multiple ways. Here, we tested these questions in a large-scale restoration experiment and with plant-level exclusion experiments in an invaded island ecosystem.

In the Seychelles, two non-native invasive ant species, the yellow crazy ant (*Anoplolepis gracilipes* (Smith)) and white-footed ant (*Technomyrmex albipes* (Smith, 1861)), are widespread and abundant across the islands, including in native remnant plant communities on inselbergs (i.e. rocky outcrops) on the island of Mahé. Although inselbergs are important refuges for many endemic plant species across the island (proportion of endemism ~63%; Biedinger and Fleischmann (2000)), the communities are severely threatened by plant invasion, particularly by *Cinnamomum verum* (Fleischmann, 1997; Kueffer et al., 2007). In an effort to restore inselberg ecosystems and control the threats posed by plant invasion, all non-native plants were removed from four inselberg sites in 2011/12 with control of re-invading plants thereafter. Most of our understanding of the effects of invasive ants on plant-pollinator interactions is derived from studies on degraded ecosystems (Junker et al., 2010; Lach, 2008, but see Bissessur et al., 2020) and studies that focus on one target plant species. Here, we use inselberg communities, which have undergone ecological restoration six years prior to data collection and compare those with unrestored invaded sites to explore the effects of invasive non-native ants on pollination of native plant species in the Seychelles. We asked the following specific questions: (1) How important are ants as pollinators in inselberg plant communities? (2) What is the effect of invasive ants on plant-pollinator interactions and native plant reproduction (i.e., fruit set) on inselbergs? and (3) Does the observed effect of invasive ants on plant-pollinator interactions and pollination differ between sites that have undergone restoration and invaded control sites? We hypothesise that by changing the foraging behaviour of legitimate insect and gecko pollinators, invasive ants will affect pollination and reduce the reproduction of native plants (Hansen and Müller, 2009; Hargreaves et al., 2009). Further, there is some evidence that non-native flowers are highly attractive to pollinators (Chittka and Schürkens, 2001; Lopezaraiza-Mikel et al., 2007), which could support larger numbers of invasive ants in invaded control sites (Lach et al., 2020). Alternatively, research has shown that native plants in restored communities produce more flowers, thereby providing more resources to flower visitors, including invasive ants (Kaiser-Bunbury et al., 2017; Monty et al., 2013). Therefore, due to a potential shift in ant numbers, we anticipate differences in the impact of invasive ants on pollination with restoration.

2. Methods

2.1. Study system

The study was conducted between March and May 2019 across eight mid-elevation inselbergs (steep-sided granitic rock outcrops) of ca. 1 ha each on Mahé, the largest granitic island of the Seychelles, Indian Ocean (- 4.6953°, 55.4999°, 154 km^2, 900 m a.s.l.). Between 2011 and 2012, all non-native plants were removed from four of the inselbergs to restore plant communities, while the other four sites remained unaltered with both native and non-native species (Kaiser-Bunbury et al., 2015). Hereafter, we refer to sites undergoing restoration as "restored" and sites invaded by non-native plant species as "unrestored". Control sites without invasive ants were not available on the island. Seychelles' climate is tropical, with a mean monthly temperature of 24 °C ± 2 and precipitation 258 mm ± 29 on inselbergs (season 2018–2019; A. Costa unpublished data). Inselberg vegetation is composed of native woody shrubs, palms and small trees and a few dominant non-native plants, such as *Cinnamomum verum*. The average canopy height is 1–2 m and a few trees grow to 4–5 m (see also Kaiser-Bunbury et al., 2011). The pollinator community on the inselbergs includes bees, wasps, four native and two endemic ant species (Hymenoptera); flies (Diptera); beetles (Coleoptera); moths and butterflies (Lepidoptera); and two lizard species (Gekkonidae, Scincidae) (Kaiser-Bunbury et al., 2017). Using this large-scale experimental setup, we quantified the

direct and indirect impact of two highly abundant non-native flower visitors, the white-footed ant *T. albipes* and yellow crazy ant *A. gracilipes* on the reproduction of four native target plant species.

2.2. Target species

For this study, we selected four relatively widespread and common native plant species that allowed us to explore between-treatment comparisons as a representative sample of the native inselberg community. These species make up around 21% of total plant individuals and 41% of flowers of the native inselberg community (C. N. Kaiser-Bunbury unpubl. data). Specifically, we monitored *Erythroxylum sechellarum* O. E. Schulz (Erythroxylaceae), *Pyrostria bibracteata* (Baker) Cavaco (Rubiaceae), and the two palm species *Nephrosperma vanhoutteanum* (H.Wendl. ex van-Houtt.) Balf.f. (Arecaceae) and *Roscheria melanochaetes* (H.Wendl.) H. Wendl. ex Balf.f. (Arecaceae). The reproductive systems included dioecy (*Pyrostria*), monoecy with temporally separated male and female flowers (*Roscheria, Nephrosperma*) and protandrous hermaphrodite flowers (*Erythroxylum*) (Fig. 1). Invasive ants have been observed frequently on these plant species, crawling in large quantities over and into the open, simple flowers feeding on nectar, thereby touching the reproductive parts of the flowers.

Anoplolepis gracilipes was accidentally introduced to Mahé around 1962 (Lewis et al., 1976) and is considered today one of the world's worst 100 invasive species (GISD, 2023). This species forms multi-queen 'supercolonies' with a spread rate of 0.1–3 m per day (Green et al., 1999; Haines and Haines, 1978), reaching high densities and making them very difficult to control. *Anoplolepis gracilipes* has several significant ecological consequences, particularly for native fauna (can kill invertebrates and small vertebrates by spraying formic acid) and flora, altering ecosystem dynamics and functions (Lee and Yang, 2022). *Technomyrmex albipes* originates from Malaysia and Indonesia and is now a widespread ant in the Australian, Afrotropical, and Malagasy regions (Bolton, 2007), mainly due to the trade of ornamental plants. The species forages and nests both terrestrially and arboreally and establishes mutualisms with a broad range of honeydew-producing hemipterans (Bolton, 2007). Similarly to *A. gracilipes*, *T. albipes* is hard to control since it can form large colonies of 8000 to 3,000,000 individuals (Tsuji and Yamauchi, 1994).

Fig. 1. Flowers of the four target plant species: a) *Pyrostria bibracteata* (~5 mm diameter), b) *Erythroxylum sechellarum* (~6 mm), c) solitary bee *Lasioglossum mahense* on *Nephrosperma vanhoutteanum* male flower (~9 mm), d) male and e) female of *Roscheria melanochaetes* (~3 mm). Photo credits: (a,c,d,e) A. Costa, (b) C. Kaiser-Bunbury.

2.3. Bagging experiments

To quantify the effects of invasive ants on plant reproduction and determine whether the ants act as legitimate pollinators of our target plant species, we conducted bagging experiments on plant individuals at the budding stage to allow selective access to different groups of flower visitors. Bagging experiments consisted of the following four treatments applied to four separated branches (or inflorescences in palms, hereafter referred to as "branches") on each plant individual: (1) control (CO): access by all flower visitors; (2) ant exclusion (AE): access to flying pollinators and exclusion of ants; (3) ants only (AO): access to ants and exclusion of flying pollinators; and (4) complete exclusion (CE): no access to flowers (Junker et al., 2010). To exclude ants from flowering branches, we manually removed all ants in the branches and applied two 2 cm-wide rings of sticky gel commonly used as a tree insect barrier (Tanglefoot® sticky coating, The Tanglefoot Company, United States) at the base of the branch. To allow access to flowers to ants only and exclude flying pollinators (AO), we covered the branch with a pollination bag, leaving a hole at the base to allow access to small crawling insects only. We covered the branch with a pollination bag completely closed to exclude all flower visitors (CE).

Before setting up the treatments, we counted the number of closed flower buds on each branch. On *E. sechellarum* we removed very small flower buds to standardise the developmental stage of the buds. To ensure sufficiently large and balanced sample sizes per branch we selected branches with a minimum of 10 flower buds. After establishing the treatments, branches were checked weekly for flowers and developing fruits, and the experiment was concluded when there were no flower buds left. We determined pollination success in each bagging treatment as the proportion of buds that set fruit (hereafter referred to as fruit set). To prevent self-pollination in *N. vanhoutteanum* and *R. melanochaetes*, we selected branches with female buds only. Similarly, we only treated female individuals of *P. bibracteata*. Fruit set corresponded closely with seed set because the target plants produce fruits with either one (*E. sechellarum, N. vanhoutteanum, R. melanochaetes*) or maximum two (*P. bibracteata*) seeds. In addition to the two invasive ant species, *A. gracilipes* and *T. albipes*, a total of four ant species (the endemic *Camponotus thomasseti* and *Paraparatrechina illusio*, and the native *Camponotus grandidieri* and *Crematogaster rasoherinae*), are known to visit flowers of the target plants. Their visitation frequency, however, was considerably lower than that of the invasive ants, which were responsible for between 70% and 90% of all ant visits (C. N. Kaiser-Bunbury unpubl. data). To understand the role invasive ants play in pollinating native plants, the results from the exclusion experiment should therefore be interpreted in light of the findings about flying pollinator visitation frequency and ant behaviour.

2.4. Ant – pollinator observations

To test the effects of invasive ants on pollination, we conducted observations and recorded pollinator visitation frequency to flowers in the presence of invasive ants. At each inselberg, fully flowering individuals from each target species were observed for a total of 33.5 h across all plant species and sites. During each observation unit (30 min) we recorded the number of individuals visiting flowers (i.e. number of visitors), the number of flowers visited by each individual before leaving the plant, and any aggressive behaviour by *A. gracilipes* and *T. albipes* against flying pollinators. Interactions were classified as 'aggressive' if flying pollinators left the flower after contact with an invasive ant or when an invasive ant was approaching during the visit of a pollinator, and as 'non-aggressive' if invasive ants and other flower visitors shared the flower (Junker et al., 2010). We also registered the number of individual ants of both invasive species at the beginning, half time and the end of each observation unit to calculate the mean number of ants present at any one time during the observation unit. For technical reasons, ants were not observed or sampled by species, as both non-native ant species could be found on the same plant individuals and flowers at the same time. Unknown pollinators were collected with an insect net and a pooter, stored in ethanol and identified by comparing specimens to a reference collection (Kaiser-Bunbury et al., 2017) or by an expert taxonomist (Dr Andrew E. Whittington, *FlyEvidence* insect identification service, UK).

2.5. Data analyses

To study the effects of invasive ants on native plant reproduction and determine whether they acted as legitimate pollinators, we compared fruit set (no. of fruits / no. of flower buds) across bagging treatments by fitting a linear mixed model (LMM). We further tested whether ant effects differed with the removal of non-native plants and among plant species. The model included fruit set as a response variable, bagging treatment (CO, AE, AO, CE), restoration treatment (restored, unrestored) and plant species as fixed effects, as well as the interactions between bagging treatment × restoration treatment and bagging treatment × plant species. Fruit set was logit-transformed to meet model assumptions and site and plant individual ID were included as random effects. We performed post-hoc contrast tests for pairwise comparisons of significantly different groups while correcting for multiple comparisons using the Tukey method with the "lsmeans" package (Lenth, 2016).

To evaluate whether invasive ant activity influenced the activity of other flower visitors and whether it differed with restoration, we ran two GLMMs with a negative binomial error distribution (log link) with the number of flower visitors and the number of visited flowers per observation unit as response variables. Both models included the mean number of ant individuals recorded (from both *A. gracilipes* and *T. albipes* combined) and restoration treatment as fixed effects, and site as a random crossed effect.

To test whether the number of invasive ants differed between restoration treatment, we fitted a linear mixed model (LMM) with the $\log (x + 1)$ – transformed mean number of invasive ants per plant individual observed as response variable. We included treatment as fixed effect and site and plant species as random effects.

All analyses were conducted in R 4.1.1 (R Core Team, 2021) and GLMMs were fitted using packages "le4" (Bates et al., 2015) and "glmmTMB" (Brooks et al., 2017). Model design and selection followed the recommendations by Zuur et al. (2009) and Harrison et al. (2018). To deal with overdispersion in the Poisson GLMMs, we used a negative binomial distribution (Hilbe, 2011). Model diagnostics

were performed using a simulation–based approach to calculate scaled (quantile) residuals and test typical model misspecification problems such as overdispersion and zero-inflation using the "DHARMa" package (Hartig, 2020).

3. Results

3.1. Bagging experiments

We bagged a total of 19,148 buds in 472 branches from 118 plant individuals. When considering all plant species together, fruit set differed between the two bagging treatments allowing access to flying pollinators (CO and AE) and those excluding them (AO and CE) (Table 1) at both restored and unrestored communities (Fig. 2, Table S1). On average, fruit set was higher on open pollinated branches (CO) and in branches where ants were excluded but flying pollinators were allowed (AE), compared to branches where only ants had access (AO) and from which all visitors were excluded (CE) (Fig. 2, Table 1 & S1). Fruit set across all bagging treatments was similar at restored and unrestored sites.

Fruit set of the bagging experiment differed between plant species (Fig. 3; Table S2). Fruit set on branches without ants (AE) was higher than on those with ants (AO) and similar than in open branches (CO) for all target plant species. Moreover, in the two palm species, *N. vanhoutteanum* and *R. melanochaetes*, branches accessed by ants only (AO) resulted in higher fruit set than branches where all insects were excluded (CE).

3.2. Ant – pollinator observations

During 67 observation sessions we observed 18 insect taxa, including the invasive ants *A. gracilipes* and *T. albipes,* and one day gecko individual (*Phelsuma astriata*) visiting flowers. We recorded a total of 1,437 visits (number of individual flower visitors) during which pollinators probed 3,596 flowers, i.e. a pollinator probed several flowers on the same plant during one visit. The most common flower visitors were *T. albipes* with 553 (38%) visits, and the species that probed most flowers was the native solitary bee *Lasioglossum mahense* (Halictidae; 27% of all probed flowers). The mean number of invasive ants per plant individual observed was similar at restored and unrestored sites (mean $\pm$ SE: restored = 3.49 $\pm$ 0.09, unrestored = 2.98 $\pm$ 0.09; z = - 0.06, p = 0.22).

The number of visits to flowering plants was not affected by the number of invasive ants present on the plant (z = 0.02, p = 0.821; Fig. 4a). With an increase in the presence of ants on flowers, however, pollinators changed their foraging behaviour and reduced the number of consecutively probed flowers (z = −0.03, p = 0.033; Fig. 4b). These observed patterns were similar at restored and unrestored sites (restored: z = −0.07, p = 0.763; unrestored: z = −0.06, p = 0.623). Overall, we recorded a total of 29 interactions between the two invasive ant species and other flower visitors, 59% of which were classified as aggressive, 24% as non-aggressive, and for 17% no specific behaviour could be observed (Table S3).

4. Discussion

Our findings suggest that ants contributed to the pollination of native plants on Seychelles' inselbergs, but their contribution to fruit set was generally small and considerably lower than that of flying pollinators. More importantly, we show that invasive ants appear to change the foraging behaviour of flying pollinators, resulting in fewer probed flowers per pollinator visit. This behavioural change may negatively impact on native pollination and plant reproduction.

Our exclusion experiment provided evidence that pollination across all plant species was primarily provided by flying pollinators. Nevertheless, ant visitation increased fruit set compared to fully bagged flowers in two plant species, which suggests that ants play a role in the pollination of some Seychelles natives. The visitation experiment does not discriminate between the two invasive ant species and other, native and non-native ant species that also occur in the inselberg communities. A previous study identified a total of four additional ant species visiting flowers of our target plant species, five of which are native or endemic to the Seychelles (C. N. Kaiser-Bunbury, unpubl. data). Two of these species were generalised and regular flower visitors across the inselberg plant community (*Camponotus grandidieri* and *Crematogaster rasoherinae* performed each about 20% of the total visits by all ants). These observations and results taken together suggest that endemic plants may have coevolved with ants as pollinators and therefore benefit from ant-flower visitation, albeit in a much smaller degree than from flying pollinators.

Our visitation data showed that the presence of ants is not deterring pollinators from approaching plants and visiting one flower,

Table 1
Results of the LMM fitted to test changes in fruit set with bagging treatment (CO: control, AE: ant exclusion, AO: ants only, CE: complete exclusion), restoration treatment (restored, unrestored) and plant species (*Erythroxylum sechellarum, Pyrostria bibracteata, Nephrosperma vanhoutteanum* and *Roscheria melanochaetes*). Statistically significant results (P < 0.05) are marked in bold.

| Response variable	Random effects	Predictors	Mean Square	df	F value	P value
Fruit set (logit transformed)	site, plant individual ID N_{obs}= 472; N_{site}= 8; $N_{plantID}$ = 118	Bagging treatment	119.70	3	120.90	**< 0.001**
		Restoration treatment	0.24	1	0.24	0.636
		Plant species	20.01	3	20.21	**< 0.001**
		Bagging treatment × Restoration treatment	3.66	3	3.69	**0.012**
		Bagging treatment × Plant species	3.21	9	3.24	**< 0.001**
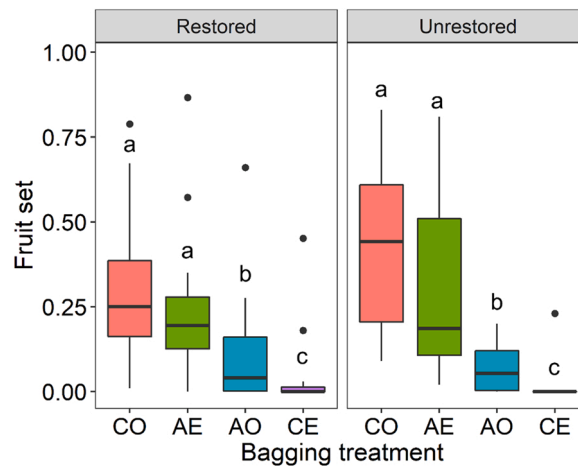
Fig. 2. Boxplots depicting differences in fruit set across bagging treatments for all target plant species at sites undergoing restoration (left panel) and sites with non-native plants (right panel). Boxes indicate the 25th to 75th percentiles, the middle line is the median, and the maximum length of the whiskers is 1.5 times the interquartile range. CO: control, AE: ant exclusion, AO: ants only, CE: complete exclusion. Different lowercase letters represent significant (p < 0.05) differences between predicted means.
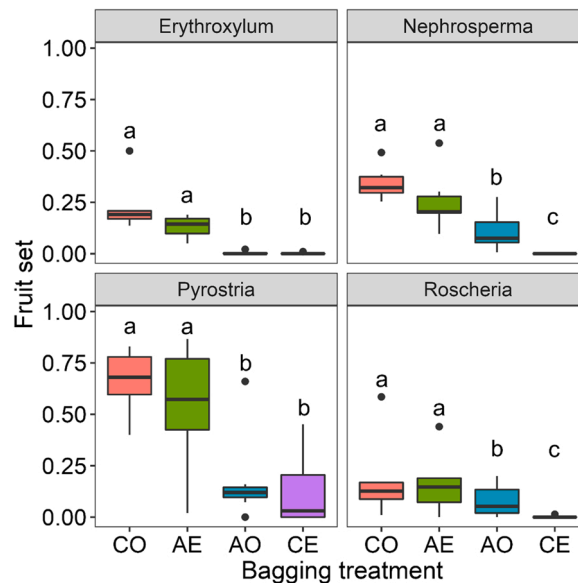

Fig. 3. Boxplots depicting differences in fruit set across bagging treatments for each target plant species individually. Boxes indicate the 25th to 75th percentiles, the middle line is the median, and the maximum length of the whiskers is 1.5 times the interquartile range. CO: control, AE: ant exclusion, AO: ants only, CE: complete exclusion. Different lowercase letters represent significant (p < 0.05) differences between predicted means.

which means that the number of visits is unaffected by ants. In the absence of ants, flying pollinators will continue their foraging bout and probe neighbouring flowers. Ants appear to disrupt such foraging bouts as the numbers of probed flowers declines in the presence of invasive ants. This change in foraging behaviour may be triggered by aggressive behaviour of the ants directed at flying pollinators (Junker et al., 2007) or possibly through indirect interactions such as resource competition (Lach, 2005). Similar changes in behaviour of pollinators triggered by ants have been reported in Mauritius, where *T. albipes* prevented the blue-tailed day-gecko *Phelsuma cepediana*, one of the three vertebrate pollinators so far known of the endangered endemic plant *Roussea simplex* (Rousseaceae), from accessing the flowers (Hansen and Müller, 2009). Furthermore, in South Africa floral arthropods were displaced by the non-native Argentine ant *Linepithema humile* (Lach, 2007). In our study, aggressive behaviour against other flower visitors was common (59% of all interactions with other flower visitors), which suggests that this was a frequent cause for legitimate, flying pollinators to change their foraging behaviour. In the remaining 41%, no adverse behaviour was recorded, which means that other, more inconspicuous or indirect effects may have caused the observed change in foraging of flying pollinators. One possible mechanism is the marking of flowers with chemical signals, which can deter pollinators from visiting flowers and exploiting floral resources (Tsuji et al., 2004).
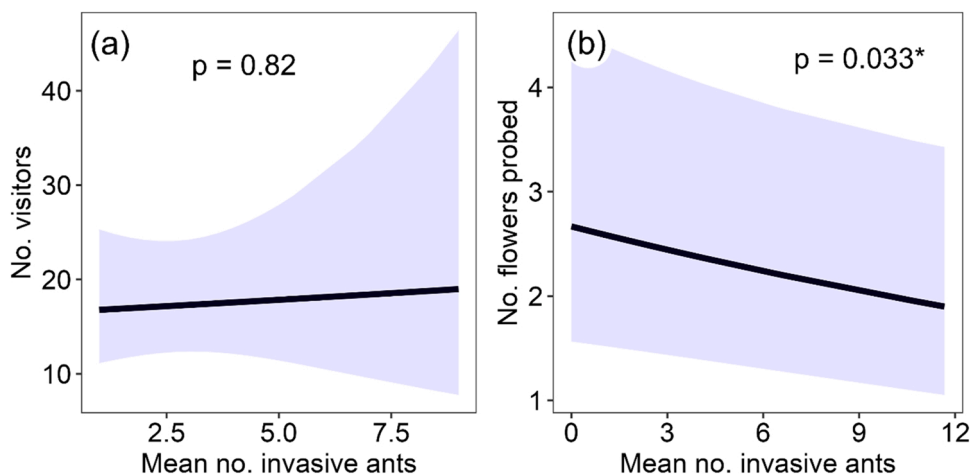
Fig. 4. Effects of mean number of invasive ant individuals (*T. albipes* and *A. gracilipes* combined) on (a) the number of flower visitor individuals and (b) the number of flowers probed per observation unit of 30 min. Lines represent model predictions and shaded areas 95% CI. (*) $p < 0.05$. Mean number of invasive ants per plant individual observed and response variables were similar at restored and unrestored sites.

Considering that invasive ants are very common on flowering plants on inselbergs, it is possible that flying pollinators are prevented from foraging optimally on inselberg plants, which may have negative consequences for pollinator populations and pollination quality (Vanbergen et al., 2018; Vázquez et al., 2005). While invasive ants may contribute – or possibly compensate for the reduced pollination by flying pollinators – to pollination of inselberg plants, it is more likely that co-evolved native ants deliver this service to the plants. To date, comparatively few studies (~40) have documented cases of ant pollination (De Vega and Gómez, 2014), many of which are relatively specialised and, thus, highly co-evolved. Our findings support the general notion that where ants are flower visitors in relatively generalised communities, they tend to contribute little towards pollination and plant reproductive performance (Beattie, 2006; Rico-Gray and Oliveira, 2007; Rostás and Tautz, 2011). Among the reasons for this general observation are the potential of ants to reduce pollen viability of pollen transported on their bodies by producing antibiotic metapleural gland secretions (Beattie et al., 1984) and the low rate of pollen transfer between plants due to short inter-plant distance movements (Domingos-Melo et al., 2017; Faegri and Pijl, 2013).

Our results showed that the frequency of flower visits and fruit set in the presence of invasive ants did not vary with restoration status, which indicates that the impact of invasive ants on pollinator foraging behaviour and plant reproductive performance was not affected by the removal of non-native plants in inselberg plant communities. Previously, it was shown that pollination resilience and function are reduced in unrestored inselberg communities dominated by non-native plants (Kaiser-Bunbury et al., 2017). Moreover, our findings indicate that the removal of non-native plants per se had little effect on invasive ant abundance and their interactions with flying pollinators. This suggests that neither the attractiveness of non-native flowers at unrestored sites nor the increased production of native flowers at restored sites significantly increased invasive ant abundance.

While our research focussed only on four common plant species, the observed variation in the dependency of fruit set among species and restoration treatment suggest that some native species of the inselberg plant community may be more reliant on co-evolved ant pollination or experience more prominent impacts on fruit set as a result of invasive ants' presence. Nevertheless, we can conclude that the high abundance and aggressive behaviour of the yellow crazy ant (*A. gracilipes*) and white-footed ant (*T. albipes*) appear to affect the foraging behaviour of flying pollinators, with potentially longer-term consequences for native plant reproduction on Seychelles inselbergs. The impact of the ants on plant reproductive performance and flying pollinators was similar between restored and unrestored communities, suggesting that this impact is unlikely to be reverted at the early stages of ecological restoration practices focused on non-native plant species removal.

CRediT authorship contribution statement

AC, CNKB, RH conceived the ideas and designed methodology; AC, EFF lead the data collection; EH, YD helped with data collection; AC, EFF analysed the data; AC, CNKB, led the writing of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02413.

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