



Infestation by pollination-disrupting alien ants varies temporally and spatially and is worsened by alien plant invasion

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Abstract Plant-pollinator mutualisms may be disrupted by alien ants. Such threats are likely to vary spatio-temporally and with other biological invasions, but these aspects are rarely studied. We examined a threatened island endemic scrambler (*Roussea simplex*, Rousseeaceae) about a decade after its pollination by an endemic reptile was found to be disrupted by an invasive alien ant and we investigated whether progressive invasion by plants has an influence on alien ant distribution. We quantified ant-infestations of the scrambler's flowers and the vertical distribution of alien ants in the habitats through baiting experiment over 2 years and characterised the height of plants within habitat patches that face contrasting levels of alien plant invasion. Two alien and one native ant

species were found visiting the flowers, namely *Technomyrmex albipes*, *Anoplolepis gracilipes* and *Plagiolepis madecassa* respectively. Few flowers (6.1%) had alien ants and ant-infested flowers occurred mostly nearer the ground. Mean alien ant abundance varied annually for *A. gracilipes* but not for *T. albipes* which however is much rarer than a decade previously. Alien ant-occupied baits showed higher probability of occurring predominantly nearer the ground. *Roussea* plants were much shorter where alien plant invasion is high, compared to where habitats are well-preserved. The severity of alien ant-infestation that leads to mutualism-disruption varies spatially and at different time scales. As alien plant invasion progresses, the resulting higher native plants' mortality causes *Roussea* to lose its supporting host plants and collapse closer to the ground where it faces greater infestation of the alien ants that are documented to disrupt its pollination. Incorporating spatio-temporal variation of threats and unravelling possible interactions between sympatric invasive alien species should be important considerations for conservation managers.

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Introduction

Oceanic islands contribute to a disproportionately large share in the current global extinction crisis driven by human activities (Wood et al. 2017). The relative simplicity of insular communities (Simberloff 1974) provides tractable systems to investigate impacts of threats (Kueffer and Kinney 2017) including biological invasions in native ecosystems, which on islands have often reached advanced levels (Caujapé-Castells et al. 2010; Dawson et al. 2017). Highly invaded islands may serve as a window into the future of other insular ecosystems where invasions are still incipient or moderate. Invasive alien species (IAS) pose the second most important global threat to plants and vertebrates (Bellard et al. 2016), delivering deleterious impacts from genetic (e.g. hybridisation) to ecosystem levels (e.g. nitrogen fixation) (Gurevitch and Padilla 2004). Although IAS may, in specific cases, have positive effects as facilitator or ecological substitutes of native species (Foster and Robinson 2007; Natusch et al. 2017), they generally pose direct threats through interspecific ecological interactions like predation, parasitism or competition or more indirect threats such as interference with mutualisms between native species, like seed dissemination or pollination (Traveset and Richardson 2006; Vanbergen et al. 2018).

The disruption of mutualisms by invasive species may come about for example when alien species impacts have driven the mutualist (e.g. seed disseminator or pollinator) either extinct (Traveset and Riera 2005; Potts et al. 2010; Rogers et al. 2017) or ecologically extinct (Sekercioglu 2011), or when the alien species elicits changes in the behaviour of the mutualist leading to impediment of its mutualistic function (Cembrowski et al. 2014; Jaca et al. 2019). In the latter case, the impacts of alien ants on insular plant communities or species have been frequently studied, for example in how they may disrupt seed dispersal mutualisms (Gómez et al. 2003; Davis et al. 2009; but see Blight et al. 2018) or pollination (Cembrowski et al. 2014; LeVan et al. 2014; Hanna et al. 2015; Villamil et al. 2018). This prior body of literature thus sets the stage to enable the much needed longer term studies that are necessary for more fully understanding alien invasion impacts (e.g. Strayer et al. 2006; Dostál et al. 2013), while at the same time facilitating further studies on alien ant invasion impacts, for example

exploring whether concurrent invasion by other alien species, which is a very common situation (Lach et al. 2010; Ness et al. 2013), may interact with the alien ant invasion.

Most studies showing negative impacts of invasive alien ants on plant-pollinator interaction, such as reduced pollinator visits or pollinator deterrence tend to be of short duration extending over a few months or a year (e.g. Barônio and Del-Claro 2018; Villamil et al. 2018). Yet, significant spatio-temporal variations in ant assemblages may occur through time (Manzaneda et al. 2007; Castro et al. 2010). Furthermore, the size of a specific ant colony often varies seasonally and inter-annually (Abbott 2005; Heller and Gordon 2006) and this variation may in turn modulate the severity of the impacts of the ants (Heller et al. 2006). For instance, ant populations can expand or contract depending on rainfall patterns (Heller et al. 2008) and their establishment and colony growth largely depend on food availability (Pinter-Wollman and Brown 2015; Lester and Gruber 2016). Consequently, the impacts of invasive ants on plant-pollinator interactions may vary in time and space, but few studies have explored this situation (Falcão et al. 2016 but see Menke et al. 2018).

Invasive alien ants frequently occur alongside other invasive alien species, including plants (Lach et al. 2010; Stanley et al. 2013). However, there exist relatively few studies dedicated to interactions between alien ants and alien plant species (Helms et al. 2011). Alien ants have been documented to aid alien plants, for example through dispersing seeds (Rowles and O'Dowd 2009). However, the influence of alien plants on alien ants is much less known, although it is plausible that alien plants may affect abundance and/or distribution of alien ants for example through habitat modification or changes in resource levels (Schoeman and Samways 2013). Developing an improved understanding of how concurrent biological invasions may interact between them is important to guide management and the elaboration of more effective conservation measures (Traveset and Richardson 2014).

Mauritius represents an interesting setting to study impacts of IAS on islands and how these impacts vary temporally and with plant invasion extent because the island possesses a mix of little and highly invaded native habitats (Page and D'Argent 1997) - in a much fragmented context (e.g. Hammond et al. 2015), and has been the subject of several studies (e.g. Vaughan

and Wiehe 1937; Cheke 1987; Jones 2008; Florens 2013), which create baseline for more in-depth research. Here, we study *Roussea simplex* Sm. (Rousseaceae), a Mauritius endemic and threatened plant (Walter and Gillett 1998), as a model system to explore spatio-temporal variation of the impacts of the invasive white-footed ant, *Technomyrmex albipes* (F. Smith, 1861) on pollination. About a decade ago, this ant was reported to disrupt the plant's pollinator mutualism (Hansen and Müller 2009a). Preliminary observations since 2014, revealed very few ant-infested flowers compared to the ~ 30% rate reported then (Hansen and Müller 2009a), suggesting that the extent of pollination disruption might have changed. Therefore here, we sought to (1) characterize the seasonal and inter-annual variation of ant visiting flowers and explore its variation between two sites previously studied by Hansen and Müller (2009a), (2) compare the current ant community visiting flowers of *Roussea*, the frequency, abundance and distribution of these ants with what were recorded a decade ago by Hansen and Müller (2009a), and (3) explore whether alien plant invasion, which causes a reduction in height of *Roussea* plants, may affect infestation of floral resources by alien ants. We discuss the implications of the findings in terms of the overall impact on the regeneration of the plant and corresponding conservation recommendations.

Materials and methods

Study sites and study species

Fieldwork was done from January 2016 to October 2017 in Mauritius (1865 km², 828 m a.s.l.), centred on 20° 15' S and 57° 35' E. Main study areas were Pétrin and Bassin Blanc (Supplementary Table 1), the same sites where *T. albipes* was previously reported to disrupt the gecko-plant mutualism (Hansen and Müller 2009a), and Piton Savanne and Le Pouce Mt, the two strongholds of the species (Hansen and Müller 2009b; Bissessur et al. 2017) (Supplementary Table 1), where we gathered additional data on influence of alien plant invasion on alien ants. Pétrin is a 6.2 ha of native habitat fenced and weeded in 1995 where three plants of *Roussea simplex* (hereafter *Roussea*) survive (pers. obs.) in heath and thicket vegetation (Vaughan and Wiehe 1937). Bassin Blanc, in contrast, hosts dense

vegetation predominantly invaded by the strawberry guava *Psidium cattleyanum* Sabine (pers.obs.) (hereafter *Psidium*), where 11 *Roussea* plants are known within an area of about 0.5 ha. *Psidium* is an alien shade tolerant woody plant, which grows in dense stands and up to eight m tall. It is the main alien woody species invading most of the remnants of moist to wet native forests in Mauritius where it comprises over 95% of the alien woody stems that reach at least 1.3 m high, followed by *Ligustrum robustum* (Roxb.) Blume comprising 1.5% of those stems (Florens et al. 2016). Smaller understory alien plants often encountered in those invaded forests include *Clidemia hirta* (L.) D. Don and *Ossaea marginata* (Desr.) Triana.

The high and progressing alien plant invasion is driving an on-going major decline of native trees (Florens et al. 2017). Given the frequent bark shedding habit of *Psidium*, epiphytic roots of *Roussea* which start to grow over its stems are constantly shed with the bark precluding the firm grip that *Roussea* typically develops on native hosts trunks. Consequently, the progressing invasion by *Psidium* (Florens et al. 2016) and the concomitant decline of native woody plants (Florens et al. 2017) result in *Roussea* plants increasingly losing host plants and collapsing closer to the ground. None of the study sites have been controlled specifically for alien ants or for any other insects and all are remote (> 500 m) from agricultural areas where pesticide may be in use. Apart from Pétrin which has been weeded of alien plants since 1995, all three sampled sites are invaded by alien plants.

Roussea is a monotypic Mauritius endemic surviving in nine known wet forests patches (Bissessur et al. 2017). The taxonomy of *Roussea* is still ambiguous. Phylogenetic analyses ascribed the genus to Rousseaceae, which comprises of three other genera (*Abrophyllum*, *Carpodetus* and *Cuttsia*) (Lundberg 2001a, b) while some suggests that *Roussea* belongs to a monotypic family (Koontz et al. 2007). This threatened semi-epiphytic climbing shrub typically grows to 4–6 m tall (Vaughan and Wiehe 1937), tightly supporting itself over woody plants. However, at Pétrin and Bassin Blanc, most plants grow to 1.5–2.0 m high (pers. obs.) but were previously substantially taller having collapsed to the ground as their supporting host plants died and fell to the ground (Supplementary Fig. 1b). Flowering occurs year-round, peaking around September to May (Scott 1997), but peak flowering period might vary spatially

(Supplementary Table 1). Flowers of *Roussea* are protandrous (male: 2–3 days, transitional: 1–2 days, and female: 2–3 days, totalling 5–8 days of lifespan), solitary, bell-shaped and produce up to about 3800 μL of hexose rich nectar during its entire lifespan (Hansen and Müller 2009b). The Mauritius endemic day gecko, *Phelsuma cepediana* (Milbert, 1812) pollinates its flowers (Hansen and Müller 2009b), and more recently, the endemic Mauritius Bulbul (*Hypsipetes olivaceus* Jardine & Selby, 1837) a Vulnerable bird species (BirdLife International 2016) was reported to be a more efficient pollinator (Bissessur et al. 2019). However, this bird is locally extinct at several sites (Hume 2013; BirdLife International 2016) where collectively over 60% of all known *Roussea* occur (Bissessur et al. 2019), resulting in the endemic day-gecko being the most potent pollinator for the majority of *Roussea* individuals.

Technomyrmex albipes, native to Malaysia and Indonesia, is today a widespread ant in the tropics and subtropics and was introduced to Mauritius around 1925 (Williams 1950). In its native range, it survives above 300 m of elevation where annual rainfall exceeds 1500 mm but is ubiquitous in intact and disturbed habitats where it invades (Sharaf et al. 2018). The *Roussea*-gecko mutualism is disrupted by *T. albipes* which nectar robs the flowers and builds ant galleries at the corolla opening and around the fruits and in so doing significantly reduces the gecko's visitation rates to both flowers and fruits, thereby decreasing seed set and dispersal, respectively (Hansen and Müller 2009a).

Natural levels of ant infestation in flowers

Flowers ($n = 1428$) were systematically sampled during the peak flowering period (Supplementary Table 1) on at least two plants at each site to record identity of ants, flower occupancy per ant species (absence or presence of ants), and ant abundance per flower. The phase of each observed flower (male, transitional or female) was also recorded. Presence was defined as 1–5 ants per flower and infestation as over 5 ants per flower to be comparable with categories used by Hansen and Müller (2009a). Observations lasted between about 10 s for a thorough check per flower when no ants were present to about 20 s per flower when ant counts were necessary. To assess whether the height at which the flower occurs

on the plant influences the level of infestation by ants, the vertical distance above ground of each flower observed was measured to the nearest centimetre.

Vertical distribution of alien ants

We investigated any variation of access by ants to different heights above ground within *Roussea* habitat by using a baiting experiment after ascertaining that the alien ants present in the habitat are attracted to the bait. The bait used was a mixture of sugar and 4%-sugared peanut butter in 1:18 ratio by weight. We used 2 m long bamboo sticks each baited using about 4 g of bait at a single, randomly assigned height (which was either 50 cm, 100 cm, 150 cm or 200 cm) until the sample size of 30 sticks was reached for each baited height (120 sticks in total per site and per every 3 months). The baited sticks were randomly placed vertically at least 3–4 m apart throughout each sampled habitat of *Roussea* and at different random locations every 3 months. Baiting at each study site was done on successive days over narrow intervals of temperature (20 ± 25 °C) and similar time (mid-morning). Following 4 h of bait exposure, ant species identity, bait occupancy (frequency of baits with ants) and ant abundance were recorded in situ for each bait by either counting the precise number of ants present (up to 50 ant individuals) or by estimation when more abundant (> 50 ant individuals). The experiment started in January 2016 and it was repeated every three months during two consecutive years.

Plant height and forest invasion level

We investigated the influence of the extent of alien plant invasion (principally *Psidium*) on height of *Roussea*. All but three known *Roussea* individuals occur in invaded native vegetation. We compared the height of randomly selected isolated individual *Roussea* present in well preserved native forests (where they normally scramble over woody native hosts for support (Vaughan and Wiehe 1937)) with height of individuals occurring in native vegetation areas highly invaded by alien plants. For this, we used the categorisation of native Mauritius forest by Page and D'Argent (1997) who defined well preserved native vegetation patches as areas comprising of native cover of at least 70%, in contrast with highly invaded forests which have a native cover of $< 20\%$.

Individuals that were selected for the comparison were also from vegetation of comparable canopy height. Invasion by alien plants have been shown in Mauritius to substantially increase native tree mortality (Florens 2008; Florens et al. 2017) and within a given site, the invasion level is not uniform (Florens et al. 2017), therefore, patches of very degraded forest can be adjacent to those least invaded. In the habitat patches of *Roussea* which were most invaded by alien plants, most native woody plants that usually serve as host trees for *Roussea* were dying or had died, a situation that causes individuals of *Roussea* to lose support and collapse to positions closer to the ground (Supplementary Fig. 2). Given the rarity of *Roussea*, we were able to locate only 39 individuals that fell unambiguously into one or the other category of forest.

Data analysis

We evaluated the proportions of flowers with 1–5 or > 5 ants for the different species, flower phase, years, height and sites. From data exploration, we noted that 92.5% of the flowers had zero alien ant counts (response variable). We thus modelled the presence/absence of alien ants at any given flower to determine whether height at which a flower is located on a plant has any effect on ant occupancy per flower using a series of binomial logistic regression with all explanatory variables and selected the most parsimonious model based on Akaike Information Criterion (AIC). For the baiting experiment, there was an excess of zeros recorded (77.0%) for ant-occupied baits counts across both sites. We pooled the data for presence or absence of the two alien ant species (ant occupancy) at each bait at the end of the 4-h trial as dependent response for the binomial logistic regression with the assumption that the effect of height would not differ between either species. The binomial logistic regression model fits the data to give predicted probabilities of ant presence at any particular bait, we also assessed any interactions between the four explanatory variables. Mean ant abundance per bait with standard error for each site and for each ant species at given years, seasons and heights were computed and compared using Kruskal–Wallis and post hoc Dunn tests with Bonferroni correction for multiple comparisons. Means with standard error for the height of *Roussea* growing in highly invaded versus well preserved native vegetation were

calculated and compared using Mann–Whitney U test. All tests were performed after verifying normality of distribution of data and homogeneity of variances. Statistical analyses were done on R version 3.3.2 (R Core Team 2013).

Results

Natural levels of ant infestation in flowers

Only 87 flowers (6.1%, $n = 1428$, where n is the total number of flowers sampled) harboured alien ants: *Technomyrmex albipes* (1–5 ants: 60 flowers, 4.2%; > 5 ants: nine flowers, 0.6%) and *Anoplolepis gracilipes* F. Smith, 1857 (both 1–5 and > 5 ants: nine flowers, 0.6% each) (Supplementary Fig. 2). The latter is a new record of alien ant species visiting *Roussea* flowers, and it was found at all sites, except for Le Pouce Mt. At the latter site, *Plagiolepis madecassa* Forel, 1892, which is native to Mauritius (Fisher 2005), was recorded instead ($N = 4$, $n = 1428$, where N is the number of flowers with ants, up to 20 individuals/flower). Number of alien ants recorded varied from one to 40 per flower (Mean \pm SD = 4.4 ± 7.4 ants/flower). Although *T. albipes* was more frequently observed in flowers (69 flowers on 1428 flowers sampled; Mean \pm SE = 2.6 ± 0.4 ants/flower), *A. gracilipes* achieved higher mean abundance (18 flowers on 1428 flowers sampled; Mean \pm SE = 11.5 ± 3.0 ants/flower). We even observed flower buds supporting ant-nests and mealy bugs (Pseudococcidae) with up to 25 ants: Bassin Blanc (*A. gracilipes*: two flowers out of 34 flowers sampled) and Pétrin (*T. albipes*: five flowers out of 28 flowers sampled).

Overall, the percentage of alien ant-infested flowers (1–5 and > 5 ants inclusive) was 4.1%, ($N = 27$ flowers; $n = 664$) in 2016 and 6.4% ($N = 45$ flowers; $n = 706$) in 2017. In 2016, the number of female-phase (older) flowers with ants was higher (6.5%, 18 flowers; $n = 279$) than male-phase (younger) ones (2.4%, seven flowers; $n = 297$). This difference was not seen in 2017 (male phase: 7.2%, 32 flowers; $n = 442$ and female phase: 5.0%, 12 flowers; $n = 223$). Only eight transitional flowers were infested during the study (5.4%, $n = 135$). Alien ant-infested flowers (i.e. with > 5 ants) were found on the plants at mean height above ground of 97.0 ± 5.5 cm (range

65–135 cm) ($n = 15$ out of 18 flowers sampled with > 5 ants). The best fitted model showed that the probability of flowers with no alien ants is higher with increasing height ($p < 0.0001$) (Supplementary Table 2).

Vertical distribution of alien ants

Overall results

Ant baiting attracted the same three species that were recorded naturally visiting *Roussea* flowers, the native *P. madecassa* and the alien *T. albipes* and *A. gracilipes*. Given their potential to disrupt pollination mutualism, we focused here on alien species. Of all the 1920 baits used in 2016 and 2017, *T. albipes* and *A. gracilipes* were found on 56 (2.9%) and 391 (20.4%), respectively, with both encountered concomitantly only on 11 baits (0.6%). In all, 622 individuals of *T. albipes* and 44,937 individuals of *A. gracilipes* were counted/estimated on baits. *Anoplolepis gracilipes* dominated at both sites, often in high numbers (mean \pm SE = 116.7 ± 5.3 /bait; range 1–410 ants) compared to *T. albipes* (mean \pm SE = 9.2 ± 1.8 /bait; range 1–55 ants). The best fitted model explaining the presence of alien ants at a specific bait included all four explanatory variables i.e. height, site, month and year (Residual deviance = 1606, df = 1913, AIC = 1638).

Temporal variations

Number of baits occupied by both alien species was lower in 2016 (22.4%, 215 baits, $n = 960$) than in 2017 (24.2%, 232 baits, $n = 960$) for both sites. *Anoplolepis gracilipes* was more frequent in both years (2016: 192 baits, $n = 480$; 2017: 199 baits, $n = 480$) compared to *T. albipes* (2016: 23 baits, $n = 480$; 2017: 33 baits, $n = 480$). According to the logistic regression model, the probability of presence of alien ants at a bait varied between years and months for both sites (Fig. 1 and Supplementary Figs. 3, 4). Concerning mean abundance per bait, *A. gracilipes* was more abundant in Bassin Blanc ($\chi^2 = 5.34$, df = 1, $p = 0.02$) and Pétrin ($\chi^2 = 3.74$, df = 1, $p = 0.05$) in 2017 (Table 1), while no significant inter-annual variation for *T. albipes* was recorded in Bassin Blanc ($\chi^2 = 1.92$, df = 1, $p = 0.17$) and Pétrin ($\chi^2 = 0.08$, df = 1, $p = 0.78$) (Table 1).

Spatial variations

In Bassin Blanc, *A. gracilipes* and *T. albipes* occurred, respectively, on 295 and 19 baits ($n = 960$) and on 96 and 37 baits ($n = 960$) in Pétrin. The logistic regression model showed the probability of presence of alien ants at a bait at both sites dropping as height increased (Fig. 1 and Supplementary Fig. 3). Indeed, for both sites, more baits were occupied at 50–100 cm (*T. albipes*: 75%, 42 baits, $n = 56$; *A. gracilipes*: 71.4%, 279 baits, $n = 391$). More ants were found at 50–100 cm than at 150–200 cm (Supplementary Fig. 3). *Anoplolepis* was most abundant at 50 cm in Bassin Blanc and between 50 and 100 cm in Pétrin for both years. *Technomyrmex* had similar mean abundance in Bassin Blanc (mean \pm SE = 10.0 ± 3.5 /bait) and Pétrin (mean \pm SE = 11.5 ± 3.1 /bait) and occurred primarily between 50 and 100 cm above ground at both sites (Table 1).

Plant height and forest invasion level

Average height of *Roussea* growing in well preserved patches of native vegetation as climbing shrub and supported by standing host trees at Le Pouce Mt and in Piton Savanne were 2.79 ± 0.14 m ($n = 17$; range 2.00–3.92 m) and 3.57 ± 0.46 m ($n = 5$; range 2.40–5.05 m), respectively. In patches of native vegetation that are highly invaded by alien plants and where most native woody plants are dying or dead, and where *Roussea* consequently lost firm host support, mean height of plants was 0.92 ± 0.21 m ($n = 7$; range 0.27–1.85 m) at Le Pouce Mt and 1.22 ± 0.22 m ($n = 10$; range 0.25–2.50 m) at Piton Savanne. *Roussea* plants in well preserved native vegetation patches were significantly taller than those surviving in highly invaded native vegetation areas ($p < 0.001$) (Fig. 2).

Discussion

Ecological implications

Invasive alien ants may disrupt pollination mutualism as illustrated by *Technomyrmex albipes* on the pollination interaction between *Roussea simplex* and *Phelsuma cepedianana* (Hansen and Müller 2009a). Studying the same system about a dozen years later,

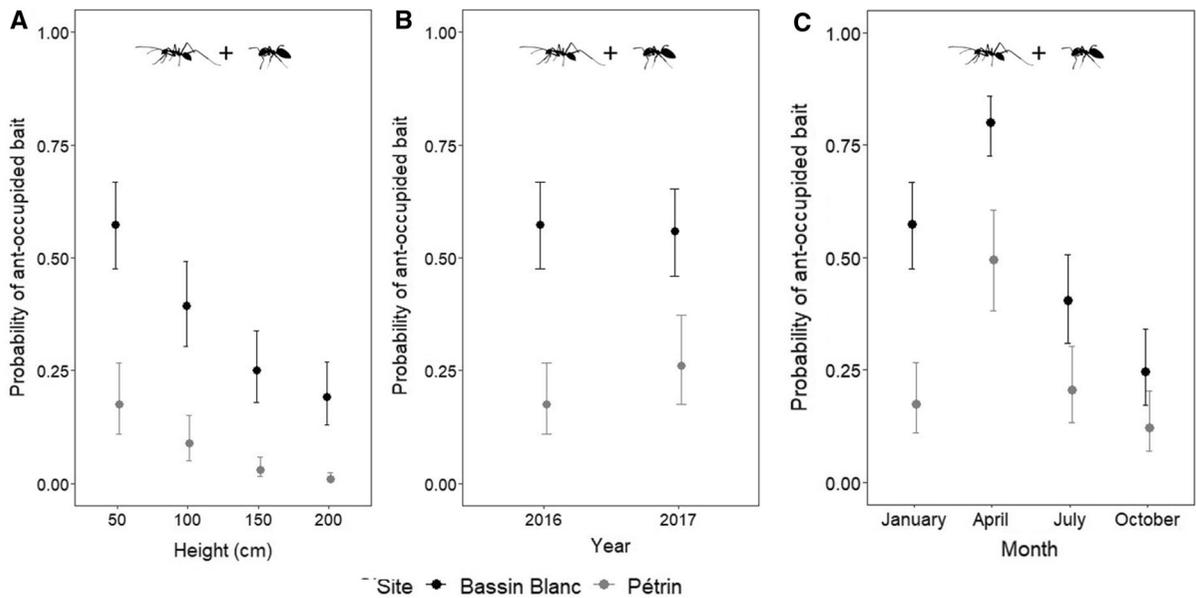


Fig. 1 a Probability of presence of both alien ants' species (*Technomyrmex albipes* and *Anoplolepis gracilipes*) at a bait at each of four different heights, b in 2016 and 2017 and c between

months for Bassin Blanc and Pétrin following the best-fitted binomial logistic regression model

we found two new records of ant species visiting *Roussea* flowers: the native *Plagirolepis madecassa* and the invasive alien *Anoplolepis gracilipes* along with the previously recorded *T. albipes*. Given its native origin, relatively small size (1.25–2.5 mm; Forel 1895) and non-aggressive behaviour, *P. madecassa* is not expected to influence the mutualism compared to the larger and more aggressive aliens, *T. albipes* (2.4–2.9 mm; Sharaf et al. 2018) and *A. gracilipes* (4.0–5.0 mm; Sarnat 2008). These two alien species rarely co-occurred in flowers (~ 0.6%). *Anoplolepis gracilipes* is considered to be among the most invasive species (Lowe et al. 2000) and is particularly aggressive and may actively exclude other ant species and monopolise food resources (Abbott 2005; Drescher et al. 2011). For instance, this alien ant has been reported to exert interference competition with other alien ants causing their displacement (Lach 2005; Lach and Hoffmann 2011) but also hinders other native insect pollinators from foraging on plants (Sinu et al. 2017) and even predate on native caterpillars (Lach et al. 2016).

We found much lower infestation rates by alien ants in 2016–2017 in comparison to a dozen years earlier (Hansen and Müller 2009a). Similar low infestation rates were also observed in Le Pouce Mt in 2012–2015

(pers. obs.), where only 2.4% of flowers were infested with *T. albipes* ($N = 40$, $n = 1698$), suggesting low infestation is more the norm than the exception. Interestingly, female-phase flowers in 2016 were more frequently ant-infested than the invariably younger male-phase flowers, suggesting that detectability of floral resources by ants increases with time over several days. This in turn suggests that disruption of mutualism with geckos may operate more often at pollen deposition than at pollen uptake stage. An alternative explanation for varying infestation rates between male and female phase flowers could be that attractiveness of flowers (for instance resource contents) vary with the phenological phase, but this is unlikely given that the female and male diurnal nectar production differ minimally in terms of volume and concentration (Hansen and Müller 2009b).

More flowers were ant-infested 50–100 cm above ground as compared to 150–200 cm, a result that also reflects the greater abundance of ants closer to the ground as revealed by the baiting experiment. This points to lower lying plants being at greater risks of disruption of pollination by alien ants. However, it is important to emphasize that alien ant floral infestation rates were much lower than a dozen years earlier. In 2004–2005, Hansen and Müller (2009a) showed a

Table 1 Summary of mean (\pm SE) of invasive alien ant abundance (both species) sampled by ant baiting at Bassin Blanc and Pétrin for the two consecutive years at each baited height

| Height (cm) | Mean abundance of alien ants sampled \pm SE | | | | | | | |
|----------------------------|---|------------------|-----------------|------------------|---------------|------------------|---------------|-------------------|
| | 50 | | 100 | | 150 | | 200 | |
| | <i>Tech.</i> | <i>Anop.</i> | <i>Tech.</i> | <i>Anop.</i> | <i>Tech.</i> | <i>Anop.</i> | <i>Tech.</i> | <i>Anop.</i> |
| <i>Bassin Blanc (2016)</i> | | | | | | | | |
| January | 7.5 \pm 2.5 | 200.3 \pm 26.6 | 0 | 131.3 \pm 22.4 | 0 | 203.1 \pm 21.5 | 5.0 \pm 0.0 | 191.9 \pm 26.8 |
| April | 0 | 102.0 \pm 15.6 | 0 | 69.7 \pm 13.8 | 0 | 63.3 \pm 15.8 | 3.0 \pm 1.0 | 65.3 \pm 22.8 |
| July | 0 | 2.0 \pm 0.0 | 0 | 8.0 \pm 4.0 | 0 | 0 | 0 | 0 |
| October | 0 | 120.4 \pm 56.7 | 0 | 112.5 \pm 49.1 | 0 | 160.8 \pm 12.1 | 1.0 \pm 0.0 | 120.5 \pm 119.5 |
| <i>Bassin Blanc (2017)</i> | | | | | | | | |
| January | 0 | 287.2 \pm 29.6 | 4.0 \pm 0.0 | 308.1 \pm 22.7 | 0 | 153.7 \pm 93.9 | 1.0 \pm 0.0 | 213.8 \pm 148.8 |
| April | 28.5 \pm 26.5 | 160.3 \pm 20.1 | 28.0 \pm 17.0 | 115.8 \pm 20.6 | 1.0 \pm 0.0 | 34.6 \pm 13.8 | 2.3 \pm 1.3 | 53.3 \pm 15.8 |
| July | 7.3 \pm 6.3 | 231.9 \pm 18.6 | 0 | 165.5 \pm 31.6 | 0 | 123.3 \pm 33.0 | 0 | 96.6 \pm 27.9 |
| October | 0 | 178.5 \pm 20.3 | 0 | 146.7 \pm 23.3 | 0 | 0 | 0 | 1.0 \pm 0.0 |
| <i>Pétrin (2016)</i> | | | | | | | | |
| January | 15.7 \pm 12.2 | 36.9 \pm 11.3 | 0 | 79.1 \pm 23.9 | 1.0 \pm 0.0 | 45.3 \pm 42.3 | 2.0 \pm 0.0 | 0 |
| April | 19.1 \pm 7.8 | 38.8 \pm 37.1 | 5.3 \pm 3.1 | 101.3 \pm 57.9 | 1.0 \pm 0.0 | 0 | 0 | 0 |
| July | 0 | 3.7 \pm 1.5 | 0 | 0 | 0 | 0 | 0 | 0 |
| October | 1.0 \pm 0.0 | 1.0 \pm 0.0 | 0 | 5.5 \pm 4.5 | 1.0 \pm 0.0 | 1.0 \pm 0.0 | 1.0 \pm 0.0 | 0 |
| <i>Pétrin (2017)</i> | | | | | | | | |
| January | 0 | 48.0 \pm 47.0 | 0 | 0 | 0 | 0 | 0 | 0 |
| April | 20.4 \pm 6.5 | 54.8 \pm 18.8 | 13.3 \pm 9.3 | 40.8 \pm 19.9 | 0 | 48.8 \pm 42.1 | 0 | 6.8 \pm 5.8 |
| July | 1.8 \pm 0.8 | 81.1 \pm 22.4 | 4.7 \pm 3.7 | 88.6 \pm 35.6 | 1.0 \pm 0.0 | 0 | 0 | 0 |
| October | 3.0 \pm 0.0 | 91.3 \pm 71.3 | 5.0 \pm 0.0 | 72.5 \pm 37.5 | 0 | 21.3 \pm 16.3 | 0 | 0 |

Anop. and *Tech.* stand for *Anoplolepis gracilipes* and *Technomyrmex albipes*, respectively

mean seed set reduction of 82.7% per fruit originating from an ant-infested flower which is proportional to an overall seed set reduction at population level of \sim 19.5% once the infestation rates of flowers by *T. albipes* on a plant (\sim 32%) and infestation rate of plants in a population (\sim 74%) are accounted for ($82.7 \times 0.32 \times 0.74$). In contrast, assuming all other things equal, our results, 12 years later, would predict a corresponding seed set reduction at population level of only \sim 0.3%. This stems mainly from the much lower floral infestation rate during 2016–2017 (*T. albipes*: 0.6%) compared to \sim 32% in 2004–2005 (Hansen and Müller 2009a). Consequently, the impacts of *T. albipes* on seed set reduction of *Roussea* appear now to be minute and negligible. If the newly recorded alien ant, *A. gracilipes*, has comparable impacts as *T. albipes*, the overall population level drop

in seed set caused by both alien ant species would still remain negligible (\sim 0.6%).

Experimental baiting confirmed that alien ant abundance on baits and bait occupancy vary seasonally, between sites and with height of *Roussea* plants. *Technomyrmex* showed a similar occupancy pattern for both years; while *A. gracilipes* was more abundant in 2017, suggesting that it may also dominate floral resources within the study areas. Alien ant abundance can collapse or substantially decline over time (like we found for *T. albipes*) due to pathogens or parasites or variations in food availability (Lester and Gruber 2016); their low abundance consequently reduces their competitive ability for resource acquisition and, expectedly, would also modulate their impact on plant-gecko pollination mutualism. High alien ant-infestations periods are known to attract more research attention than lower ant-infestation periods (Lester

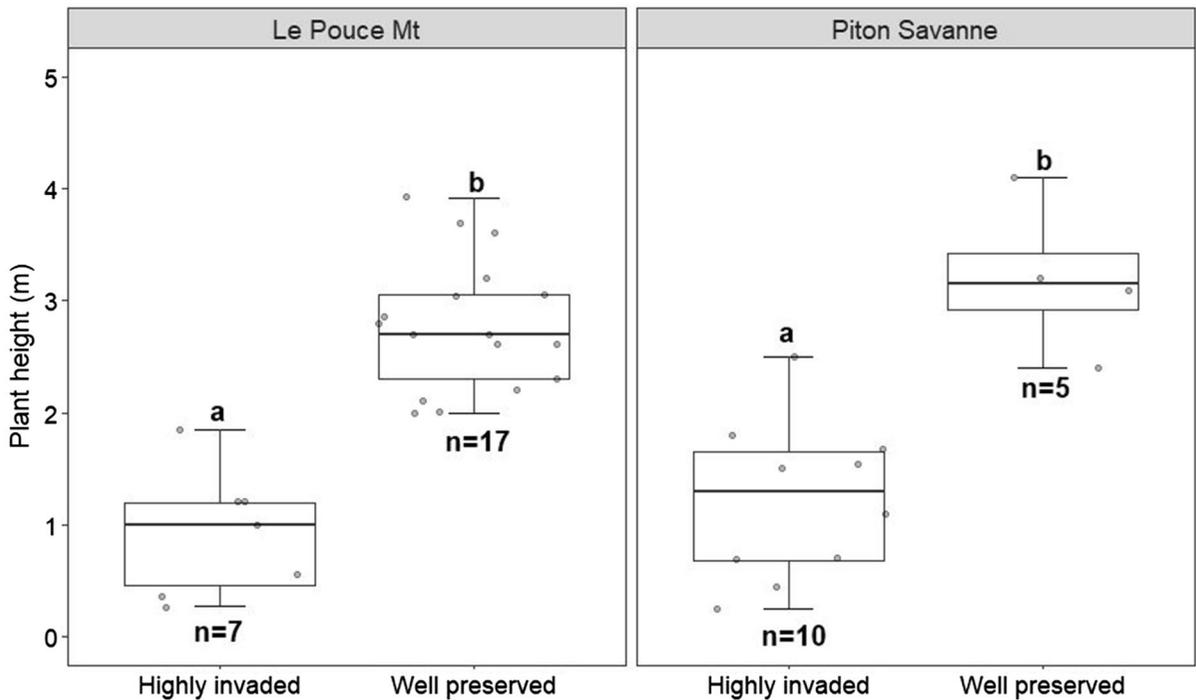


Fig. 2 Height (m) of *Roussea simplex* at Le Pouce Mt and Piton Savanne when growing in habitats that are highly invaded by alien plants as compared to in habitats that are only lightly invaded by alien plants ('Well preserved'). Letters "a" and "b"

denote significant differences between the two categories following Mann–Whitney U Test ($p < 0.001$) and n is the number of plants sampled per category

and Gruber 2016). It is thus plausible that Hansen and Müller (2009a) reported on a situation when *Technomyrmex* infestation was unusually high because apart from a brief period, we have not observed comparable degrees of *Technomyrmex* infestation of *Roussea* flowers as reported by these authors, since we started more focussed attention on the plant in 2011. At lower abundances, alien ants would exert less direct exploitative competition. Indeed, Hansen and Müller (2009a) observed geckos waiting when there were only three patrolling ants on a flower and entering the flower only upon the ants' departure, while regular activity of ants entering and leaving a flower (implying up to 5–30 ants) deterred geckos altogether, reducing pollination. This contrasts with the Mauritius Bulbul (*Hypsipetes olivaceus*), whose behaviour remains unaltered in presence of ants, contributing towards making it a better pollinator (Bissessur et al. 2019).

Roussea plants supported naturally on native tree hosts were about three times taller than those on collapsed host trees in habitats highly invaded by alien plants. As alien ant infestation correlated negatively

with height, plants bearing flowers at higher levels above ground are expected to be least infested, and indeed this trend was discernible among naturally infested flowers. The overall habitats of each population of *Roussea* are variously invaded by alien plants (Supplementary Fig. 1) which can reach extreme densities in Mauritius wet native vegetation (Florens et al. 2016). Alien plants are likely to favour ant infestation by providing additional arboreal access routes to the flowers. However, in the longer term, alien plants increase alien ant infestation rate by inducing a decline in tree density (Florens et al. 2017) through increased mortality of native plants (Florens 2008), reduced fruit production (Monty et al. 2013) and regeneration (Baider and Florens 2011). For a scrambler like *Roussea*, this represents loss of host plants on which to take support. Consequently, increased alien plant invasion leads to *Roussea* progressively collapsing closer to the ground, hence increasing floral infestation rates by alien ants and the severity of mutualism disruption that they deliver.

Conservation implications

Our findings revealed how the density of pollination-disrupting alien ants varies markedly through time and space and how the composition of the alien ant-community that uses floral resources may shift through time. Conservation managers should integrate such variation through time and space when planning conservation management of threatened plants. Here, we showed that alien plant invasion facilitates infestation of alien ants which has been previously shown to disrupt pollination mutualism (Hansen and Müller 2009a) of a rapidly declining threatened island plant (Bissessur et al. 2017). Consequently, alien ants per se would be less impactful and likely of negligible influence, if habitats are protected from alien plants in the first place. Addressing alien plant driven habitat degradation would therefore not only reduce direct deleterious influences of alien plants but also reduce alien ant infestations. However, weed control should be gradual to minimise disturbance, because the latter may enhance alien ant establishment (Fisher 2005). Our study thus stresses the need for conservation managers to adopt a longer temporal view, and addressing the deeper source threat (here, alien plant invasion) instead of the proximal one cascading from it (here, infestation by alien-ant known to disrupt pollination mutualism).

Given the variability in alien ant occupancy, abundance and their consequential often minor negative impacts on the plant-gecko mutualism, conservation management would be more impactful if geared towards more important threats. For instance, alien rats (*Rattus rattus*) and macaques (*Macaca fascicularis*) damage flower buds, flowers, fruits and branches through nectar robbing and florivory (Bissessur et al. 2019). Destruction of flower buds and flowers can reach 75%, leaving few exposed to potential infestation by alien ants. Consequently, although florivory by rats and macaques would act to minimise the detrimental effect of alien ants, it would above all directly and majorly disrupt the pollination mutualism reducing seed set by a far greater extent than even the maximum known alien ant impacts.

In conclusion, our findings highlighted how infestation by an invasive alien ant known to disrupt pollination mutualism in a relatively well studied model threatened endemic island plant species, may change through time. Managers would therefore

devise more impactful conservation strategies for endangered plants facing threats from invasive alien species when they incorporate the longer view that would reveal such variation. We also showed that the severity of infestation of flowers by pollination-disrupting alien ants is linked through cascading effect to another simultaneously acting threat, namely invasive alien plants which, in high density, increase mortality of host trees over which *Roussea* takes support, causing *Roussea* plants to collapse to positions closer to the ground where infestation by pollination-disrupting alien ants is higher. Thus, conservation measures should focus more on active and gradual control of invasive alien plants and of alien vertebrates, especially black rats and macaques (Bissessur et al. 2019) in the native habitat remnants of *Roussea*. This would directly benefit plant regeneration through reduced shoot competition as well as enhance the plant-pollinator mutualisms through greater availability of flowers for pollinators to forage on. These measures would also indirectly benefit endemic bird populations by improving the foraging quality of their habitats and reduce predation pressure from alien mammals, which should in turn loop back to reinforce the mutualism with *Roussea*. It appears judicious for conservation managers to first hierarchize the various threats besetting a species to allow addressing the most impactful ones first, while paying attention to fluctuations in the threat's severity through time. Finally, for more impactful conservation management, it is also recommended that conservation managers pay attention to any ultimate and more basal threats that may cascade into other more proximal ones so that they may address ultimate threats in priority over proximal ones.

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Compliance with ethical standards

Conflict of interest No potential conflict of interest was reported by the authors.

References

- Abbott KL (2005) Supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes*, on an oceanic island: forager activity patterns, density and biomass. *Insectes Soc* 52:266–273. <https://doi.org/10.1007/s00040-005-0800-6>
- Baider C, Florens FBV (2011) Control of invasive alien weeds averts imminent plant extinction. *Biol Invasions* 13:2641–2646. <https://doi.org/10.1007/s10530-011-9980-3>
- Barônio GJ, Del-Claro K (2018) Increase in ant density promotes dual effects on bee behaviour and plant reproductive performance. *Arthropod-Plant Interact* 12:201–213. <https://doi.org/10.1007/s11829-017-9573-x>
- Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. *Biol Lett* 12:20150623. <https://doi.org/10.1098/rsbl.2015.0623>
- BirdLife International (2016) *Hypsipetes olivaceus*. In: IUCN red list of threatened species 2016. e.T22713239A94366667. <https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22713239A94366667.en>. Accessed 25 Jan 2020
- Bissessor P, Baider C, Florens FBV (2017) Rapid population decline of an endemic oceanic island plant despite resilience to extensive habitat destruction and occurrence within protected areas. *Plant Ecol Divers* 10:293–302. <https://doi.org/10.1080/17550874.2017.1402382>
- Bissessor P, Bunsy Y, Baider C, Florens FBV (2019) Non-intrusive systematic study reveals mutualistic interactions between threatened island endemic species and points to more impactful conservation. *J Nat Conserv* 49:108–117. <https://doi.org/10.1016/j.jnc.2019.04.002>
- Blight O, Orgeas J, Le Menn A et al (2018) Interaction between a threatened endemic plant (*Anchusa crispera*) and the invasive Argentine ant (*Linepithema humile*). *Arthropod-Plant Interact* 12:725–731. <https://doi.org/10.1007/s11829-018-9619-8>
- Castro S, Ferrero V, Loureiro J et al (2010) Dispersal mechanisms of the narrow endemic *Polygala vayredae*: dispersal syndromes and spatio-temporal variations in ant dispersal assemblages. *Plant Ecol* 207:359–372. <https://doi.org/10.1007/s11258-009-9679-z>
- Caujapé-Castells J, Tye A, Crawford DJ et al (2010) Conservation of oceanic island floras: present and future global challenges. *Perspect Plant Ecol Evol Syst* 12:107–129. <https://doi.org/10.1016/j.ppees.2009.10.001>
- Cembrowski AR, Tan MG, Thomson JD, Frederickson ME (2014) Ants and ant scent reduce bumblebee pollination of artificial flowers. *Am Nat* 183:133–139. <https://doi.org/10.1086/674101>
- Cheke AS (1987) The ecology of the smaller land-birds of Mauritius. In: Diamond AW (ed) *Studies of Mascarene island birds*. Cambridge University Press, Cambridge, pp 151–207
- Davis NE, O’Dowd DJ, Mac Nally R, Green PT (2009) Invasive ants disrupt frugivory by endemic island birds. *Biol Lett* 6:85–88. <https://doi.org/10.1038/s41559-017-0186>
- Dawson W, Moser D, van Kleunen M et al (2017) Global hot-spots and correlates of alien species richness across taxonomic groups. *Nat Ecol Evol* 1:0186. <https://doi.org/10.1038/s41559-017-0186>
- Dostál P, Müllerová J, Pyšek P et al (2013) The impact of an invasive plant changes over time. *Ecol Lett* 16:1277–1284. <https://doi.org/10.1111/ele.12166>
- Drescher J, Feldhaar H, Blüthgen N (2011) Interspecific aggression and resource monopolization of the invasive ant *Anoplolepis gracilipes* in Malaysian Borneo. *Biotropica* 43:93–99. <https://doi.org/10.1111/j.1744-7429.2010.00662.x>
- Falcão JC, Dáttilo W, Rico-Gray V (2016) Sampling effort differences can lead to biased conclusions on the architecture of ant–plant interaction networks. *Ecol Complex* 25:44–52. <https://doi.org/10.1016/j.ecocom.2016.01.001>
- Fisher B (2005) A new species of *Discothyrea* Roger from Mauritius and a new species of *Proceratium* Roger from Madagascar (Hymenoptera: Formicidae). *Proc Calif Acad Sci* 56:657–667
- Florens FBV (2008) *Ecologie des forêts tropicales de l’Île Maurice et impact des espèces introduites envahissantes*. PhD thesis, Université de la Réunion
- Florens FBV (2013) *Conservation in Mauritius and Rodrigues: challenges and achievements from two ecologically devastated oceanic islands*. In: Sodhi NS, Gibson L, Raven -PH (eds) *Conservation biology: voices from the tropics*. Wiley, West Sussex, pp 40–50
- Florens FBV, Baider C, Martin GM et al (2016) Invasive alien plants progress to dominate protected and best-preserved wet forests of an oceanic island. *J Nat Conserv* 34:93–100. <https://doi.org/10.1016/j.jnc.2016.09.006>
- Florens FBV, Baider C, Seegoolam NB et al (2017) Long-term declines of native trees in an oceanic island’s tropical forests invaded by alien plants. *Appl Veg Sci* 20:94–105. <https://doi.org/10.1111/avsc.12273>
- Forel A (1895) Nouvelles fourmis de l’Imerina orientale (Moramanga etc.). *Ann Société Entomol Belg* 39:243–251
- Foster JT, Robinson SK (2007) Introduced birds and the fate of Hawaiian rainforests. *Conserv Biol* 21:1248–1257. <https://doi.org/10.1111/j.1523-1739.2007.00781.x>
- Gómez C, Pons P, Bas JM (2003) Effects of the Argentine ant *Linepithema humile* on seed dispersal and seedling emergence of *Rhamnus alaternus*. *Ecography* 26:532–538. <https://doi.org/10.1034/j.1600-0587.2003.03484.x>
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Hammond DS, Gond V, Baider C et al (2015) Threats to environmentally sensitive areas from peri-urban expansion in Mauritius. *Environ Conserv* 42:256–267. <https://doi.org/10.1017/S0376892914000411>
- Hanna C, Naughton I, Boser C et al (2015) Floral visitation by the Argentine ant reduces bee visitation and plant seed set. *Ecology* 96:222–230. <https://doi.org/10.1890/14-0542.1>

- Hansen DM, Müller CB (2009a) Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. *Biotropica* 41:202–208. <https://doi.org/10.1111/j.1744-7429.2008.00473.x>
- Hansen DM, Müller CB (2009b) Reproductive ecology of the endangered enigmatic Mauritian endemic *Roussea simplex* (Rousseaceae). *Int J Plant Sci* 170:42–52. <https://doi.org/10.1086/593050>
- Heller NE, Gordon DM (2006) Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). *Ecol Entomol* 31:499–510. <https://doi.org/10.1111/j.1365-2311.2006.00806.x>
- Heller NE, Sanders NJ, Gordon DM (2006) Linking temporal and spatial scales in the study of an Argentine ant invasion. *Biol Invasions* 8:501–507. <https://doi.org/10.1007/s10530-005-6411-3>
- Heller NE, Sanders NJ, Shors JW, Gordon DM (2008) Rainfall facilitates the spread, and time alters the impact, of the invasive Argentine ant. *Oecologia* 155:385–395. <https://doi.org/10.1007/s00442-007-0911-z>
- Helms KR, Hayden CP, Vinson SB (2011) Plant-based food resources, trophic interactions among alien species, and the abundance of an invasive ant. *Biol Invasions* 13:67–79. <https://doi.org/10.1007/s10530-010-9790-z>
- Hume JP (2013) A synopsis of the pre-human avifauna of the Mascarene Islands. In: Proceedings of the 8th international meeting of the society of avian paleontology and evolution. Naturhistorisches Museum, Wien, pp 195–237
- Jaca J, Rodríguez N, Nogales M, Traveset A (2019) Impact of alien rats and honeybees on the reproductive success of an ornithophilous endemic plant in Canary thermosclerophyllous woodland relicts. *Biol Invasions* 21:3203–3219. <https://doi.org/10.1007/s10530-019-02040-7>
- Jones CG (2008) Practical conservation on Mauritius and Rodrigues: steps towards the restoration of devastated ecosystems. In: Cheke AS, Hume JP (eds) Lost land of the Dodo. Christopher Helm, London, pp 226–259
- Koontz JA, Lundberg J, Soltis DE (2007) Rousseaceae. In: Kubitzki AK (ed) The families and genera of vascular plants: Eudicots. Springer, Berlin, pp 611–613
- Kueffer C, Kinney K (2017) What is the importance of islands to environmental conservation? *Environ Conserv* 44:311–322. <https://doi.org/10.1017/S0376892917000479>
- Lach L (2005) Interference and exploitation competition of three nectar-thieving invasive ant species. *Insectes Soc* 52:257–262. <https://doi.org/10.1007/s00040-005-0807-z>
- Lach L, Hoffmann BD (2011) Are invasive ants better plant-defense mutualists? A comparison of foliage patrolling and herbivory in sites with invasive yellow crazy ants and native weaver ants. *Oikos* 120:9–16. <https://doi.org/10.1111/j.1600-0706.2010.18803.x>
- Lach L, Tillberg CV, Suarez AV (2010) Contrasting effects of an invasive ant on a native and an invasive plant. *Biol Invasions* 12:3123–3133. <https://doi.org/10.1007/s10530-010-9703-1>
- Lach L, Volp TM, Greenwood TA, Rose A (2016) High invasive ant activity drives predation of a native butterfly larva. *Biotropica* 48:146–149. <https://doi.org/10.1111/btp.12284>
- Lester PJ, Gruber MA (2016) Booms, busts and population collapses in invasive ants. *Biol Invasions* 18:3091–3101. <https://doi.org/10.1007/s10530-016-1214-2>
- LeVan KE, Hung K-LJ, McCann KR et al (2014) Floral visitation by the Argentine ant reduces pollinator visitation and seed set in the coast barrel cactus, *Ferocactus viridescens*. *Oecologia* 174:163–171. <https://doi.org/10.1007/s00442-013-2739-z>
- Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group Auckland, New Zealand
- Lundberg J (2001a) The asteralean affinity of the Mauritian *Roussea* (Rousseaceae). *Bot J Linn Soc* 137:267–276. <https://doi.org/10.1111/j.1095-8339.2001.tb01122.x>
- Lundberg J (2001b) Phylogenetic studies in the Euasterids II: with particular reference to Asterales and Escalloniaceae. PhD thesis, Acta Universitatis Upsaliensis
- Manzaneda AJ, Rey PJ, Boulay R (2007) Geographic and temporal variation in the ant–seed dispersal assemblage of the perennial herb *Helleborus foetidus* L. (Ranunculaceae). *Biol J Linn Soc* 92:135–150. <https://doi.org/10.1111/j.1095-8312.2007.00831.x>
- Menke SB, Ward PS, Holway DA (2018) Long-term record of Argentine ant invasions reveals enduring ecological impacts. *Ecology* 99:1194–1202. <https://doi.org/10.1002/ecy.2200>
- Monty MLF, Florens FBV, Baider C (2013) Invasive alien plants elicit reduced production of flowers and fruits in various native forest species on the tropical island of Mauritius (Mascarenes, Indian Ocean). *Trop Conserv Sci* 6:35–49. <https://doi.org/10.1177/194008291300600107>
- Natusch DJ, Mayer M, Lyons JA, Shine R (2017) Interspecific interactions between feral pigs and native birds reveal both positive and negative effects. *Austral Ecol* 42:479–485. <https://doi.org/10.1111/aec.12465>
- Ness JH, Morales MA, Kenison E et al (2013) Reciprocally beneficial interactions between introduced plants and ants are induced by the presence of a third introduced species. *Oikos* 122:695–704. <https://doi.org/10.1111/j.1600-0706.2012.20212.x>
- Page W, D'Argent GA (1997) A vegetation survey of Mauritius to identify priority rainforest areas for conservation management. Mauritian Wildlife Foundation, Port Louis
- Pinter-Wollman N, Brown MJ (2015) Variation in nest relocation of harvester ants is affected by population density and food abundance. *Behav Ecol* 26:1569–1576. <https://doi.org/10.1093/beheco/arv108>
- Potts SG, Biesmeijer JC, Kremen C et al (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25:345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Rogers HS, Buhle ER, HilleRisLambers J et al (2017) Effects of an invasive predator cascade to plants via mutualism disruption. *Nat Commun* 8:14557. <https://doi.org/10.1038/ncomms14557>
- Rowles AD, O'Dowd DJ (2009) New mutualism for old: indirect disruption and direct facilitation of seed dispersal

- following Argentine ant invasion. *Oecologia* 158:709–716. <https://doi.org/10.1007/s00442-008-1171-2>
- Sarnat, E (2008) PIAkey: identification guide to ants of the Pacific islands, Edition 2.0, Lucid v. 3.4. USDA/APHIS/PPQ Center for Plant Health Science and Technology, University of California, Davis. <http://www.lucidcentral.org/keys/v3/PIAkey/index.html>. Accessed 31 Dec 2018
- Schoeman CS, Samways MJ (2013) Temporal shifts in interactions between alien trees and the alien Argentine ant on native ants. *J Insect Conserv* 17:911–919. <https://doi.org/10.1007/s10841-013-9572-x>
- Scott AJ (1997) 85. Bréxiacées. In: Bosser J, Cadet TH, Guého J, Marais W (eds) Flore des Mascareignes La Réunion, Maurice, Rodrigues. MSIRI/ORSTOM/KEW, Government Printer, Mauritius
- Sekercioglu CH (2011) Functional extinctions of bird pollinators cause plant declines. *Science* 331:1019–1020. <https://doi.org/10.1126/science.1202389>
- Sharaf MR, Al Dhafer HM, Aldawood AS (2018) Review of the ant genus *Technomyrmex* Mayr, 1872 in the Arabian Peninsula (Hymenoptera, Formicidae). *ZooKeys* 780:35–59. <https://doi.org/10.3897/zookeys.780.26272>
- Simberloff DS (1974) Equilibrium theory of island biogeography and ecology. *Annu Rev Ecol Syst* 5:161–182. <https://doi.org/10.1146/annurev.es.05.110174.001113>
- Sinu PA, Sibisha VC, Reshmi MN et al (2017) Invasive ant (*Anoplolepis gracilipes*) disrupts pollination in pumpkin. *Biol Invasions* 19:2599–2607. <https://doi.org/10.1007/s10530-017-1470-9>
- Stanley MC, Nathan HW, Phillips LK et al (2013) Invasive interactions: can Argentine ants indirectly increase the reproductive output of a weed? *Arthropod-Plant Interact* 7:59–67. <https://doi.org/10.1007/s11829-012-9215-2>
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends Ecol Evol* 21:645–651. <https://doi.org/10.1016/j.tree.2006.07.007>
- Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol Evol* 21:208–216. <https://doi.org/10.1016/j.tree.2006.01.006>
- Traveset A, Richardson DM (2014) Mutualistic interactions and biological invasions. *Annu Rev Ecol Evol Syst* 45:89–113. <https://doi.org/10.1146/annurev-ecolsys-120213-091857>
- Traveset A, Riera N (2005) Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conserv Biol* 19:421–431. <https://doi.org/10.1111/j.1523-1739.2005.00019.x>
- Vanbergen AJ, Espíndola A, Aizen MA (2018) Risks to pollinators and pollination from invasive alien species. *Nat Ecol Evol* 2:16–25. <https://doi.org/10.1038/s41559-017-0412-3>
- Vaughan RE, Wiehe PO (1937) Studies on the vegetation of Mauritius: I. A preliminary survey of the plant communities. *J Ecol* 25:289–343. <https://doi.org/10.2307/2256197>
- Villamil N, Boege K, Stone GN (2018) Ant-pollinator conflict results in pollinator deterrence but no nectar trade-offs. *Front Plant Sci* 9:1093. <https://doi.org/10.3389/fpls.2018.01093>
- Walter KS, Gillett HJ (1998) 1997 red list of threatened plants. The World Conservation Union, Gland
- Williams JR (1950) The introduction of *Physonota alutacea* Boheman (Col., Cassid.) into Mauritius. *Bull Entomol Res* 40:479–480. <https://doi.org/10.1017/S0007485300024391>
- Wood JR, Alcover JA, Blackburn TM et al (2017) Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environ Conserv* 44:348–358. <https://doi.org/10.1017/S037689291700039X>

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