RESEARCH ARTICLE

Invasion of yellow crazy ant *Anoplolepis gracilipes* in a Seychelles UNESCO palm forest

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Abstract

The mature palm forest of the Vallée de Mai, a UNESCO World Heritage Site, on the Seychelles island of Praslin, is a unique ecosystem containing many endemic species, including the iconic coco de mer palm *Lodoicea maldivica*. In 2009, the invasive yellow crazy ant *Anoplolepis gracilipes* was recorded for the first time within the palm forest, raising concern about its potential impacts on the endemic fauna. This research aimed to: (1) assess the current distribution and spread of *A. gracilipes* within the palm forest; (2) identify environmental variables that are linked to *A. gracilipes* distribution; and (3) compare endemic species richness and abundance in *A. gracilipes* invaded and uninvaded areas. *Anoplolepis gracilipes* was confined to the north-east of the site and remained almost stationary between April 2010 and December 2012, with isolated outbreaks into the forest. Infested areas had significantly higher temperature and humidity and lower canopy cover. Abundance and species richness of the endemic arboreal fauna were lower in the *A. gracilipes* invaded area. Molluscs were absent from the invaded area. The current restricted distribution of *A. gracilipes* in this ecosystem, combined with lower abundance of endemic fauna in the invaded area, highlight the need for further research to assess control measures and the possible role of biotic resistance to the invasion of the palm forest by *A. gracilipes*.

Keywords

Introduction

Ants are highly successful invaders, particularly on islands (Ingram et al. 2006; Cerdá et al. 2012). Their invasion is of concern to conservationists due to their broad range of impacts (e.g., Holway et al. 2002; O'Dowd et al. 2003; Lach and Hooper-Bui 2010) and the difficulties of eradicating them once established (Silverman and Brightwell 2008; Hoffmann et al. 2011). Impacts of invasive ants can include direct effects such as displaced vertebrate (Feare 1999; Holway et al. 2002 and references therein), non-ant invertebrate (Lubin 1984; Hill et al. 2003; Causton et al. 2006), and ant species (Walker 2006; Hoffmann and Saul 2010; Roura-Pascual et al. 2010), and indirect effects on key ecological functions such as frugivory (Davis et al. 2010), pollination and seed dispersal (Hansen and Müller 2009), and seedling recruitment and litter breakdown in a forest ecosystem (O'Dowd et al. 2003). The yellow crazy ant *Anoplolepis gracilipes* is ranked amongst the top 100 worst global invasive species (Lowe et al. 2000) and is responsible for catastrophic ecological impacts on islands (O'Dowd et al. 1999; O'Dowd et al. 2003).

In the Seychelles, *A. gracilipes* was first recorded in 1962 on the main island of Mahé (Lewis et al. 1976). The species had spread to the neighbouring island of Praslin by 1975 and was eradicated from this island shortly afterwards (Haines and Haines 1978a, b). Since then, despite control measures on Mahé, its range across the Seychelles islands has expanded and, by 2000, the species occurred on nine of the central islands, including Praslin (Hill et al. 2003).

Although the impacts and ecology of *A. gracilipes* have been well documented in degraded habitats in the Seychelles (Haines and Haines 1978a, Hill et al. 2003), little is known about this ant's invasion potential in endemic palm forest ecosystems. Praslin, the second largest granitic island of the archipelago, is home to Seychelles' native mature palm forest. This habitat represents one of the last island palm forest ecosystems in the world and hosts many species that are endemic to Praslin or the Seychelles (Beaver and Chong-Seng 1992; Fleischer-Dogley et al. 2011). The forest is dominated by the iconic coco de mer palm *Lodoicea maldivica*. This palm species, famous for producing the largest seeds in the plant kingdom, has been fundamental in driving the evolution of endemic fauna species, many of which are restricted to *L. maldivica* habitat (Noble et al. 2011). Moreover, the most pristine area of palm forest, the Vallée de Mai, renowned globally for its natural beauty, is a major visitor attraction and brings considerable financial benefit to the Seychelles, and to Praslin in particular. Threats to the ecological integrity of this habitat, including those from invasive species, therefore have potential economic as well as conservation implications.

Anoplolepis gracilipes was identified in the Vallée de Mai for the first time in August 2009 (L. Chong-Seng & P. Matyot, pers. comm.). Here, we present research into the distribution of *A. gracilipes* over the subsequent 2.5 year period in the Vallée de Mai palm forest, and its potential impact on a key group of animals in the ecosystem, the arboreal vertebrate and invertebrate palm specialist species. The overall aim of this research was to determine the distribution and spread of *A. gracilipes* in the Vallée de Mai

over time and improve understanding of its impact on endemic arboreal species in this unique palm forest. Given the extent of *A. gracilipes'* impacts elsewhere, we expected that the fauna associated with *L. maldivica* would be less abundant where *A. gracilipes* was present. We specifically ask: (1) what are the distribution, spread rate, and activity levels of *A. gracilipes* in the palm forest?; (2) Which environmental variables are associated with *A. gracilipes* distribution?; and (3) Are there differences in the number of species and abundance of endemic arboreal fauna between *A. gracilipes* invaded and uninvaded areas of the Vallée de Mai?

Methods

Study site and species

The study was conducted in the Vallée de Mai (19.5 ha; 4°19'S, 55°44'E) which is located in Praslin National Park (342 ha; Fig. 1). The Vallée de Mai was inscribed as a natural UNESCO World Heritage Site in 1983 for its unique and globally important habitat. The vegetation consists of low-intermediate elevation palm forest dominated by *L. maldivica*. A strip of cleared vegetation with trimmed introduced and native trees is maintained around the area as a firebreak. Outside the firebreak, the vegetation is mixed with more native and introduced broadleaf species. There is a network of paths used by visitors throughout the Vallée de Mai which are regularly swept and kept free of leaf litter. The Seychelles has a tropical climate and experiences temperatures of 24–32 °C and average rainfall of *ca.* 200 mm/month.

    Anoplolepis gracilipes originates from either central east Africa or Asia but now has a pan-tropical and subtropical distribution. The species is a generalist and opportunistic consumer, which will predate and scavenge a variety of food sources. Workers make up >80% of the individuals in the nest and exhibit extensive foraging 24 h/day year round in areas where the climate does not hinder ant activity (Haines and Haines 1978a, Abbott 2005; Abbott 2006). The species can reach very high densities (e.g. supercolony densities can reach >2000 ants per m^2, Abbott 2005) and has been documented to spread at an average rate of 125 m/year on Mahé (Haines and Haines 1978a).

Distribution, ant activity and environmental variables

The main fieldwork was conducted over a 12-week period between March and June 2010. Fieldwork included surveys on ants and the arboreal endemic fauna and recordings of environmental variables. In addition, two ant distribution surveys were conducted in April 2012 (end of the wet season) and December 2012 (end of the dry season). To determine the distribution of *A. gracilipes*, a grid of fifty 10×10 m quadrats (~2.5% of the total area) throughout the valley was surveyed. Quadrats were spaced 75×75 m apart and sampled along parallel N-S transects spanning the entire study
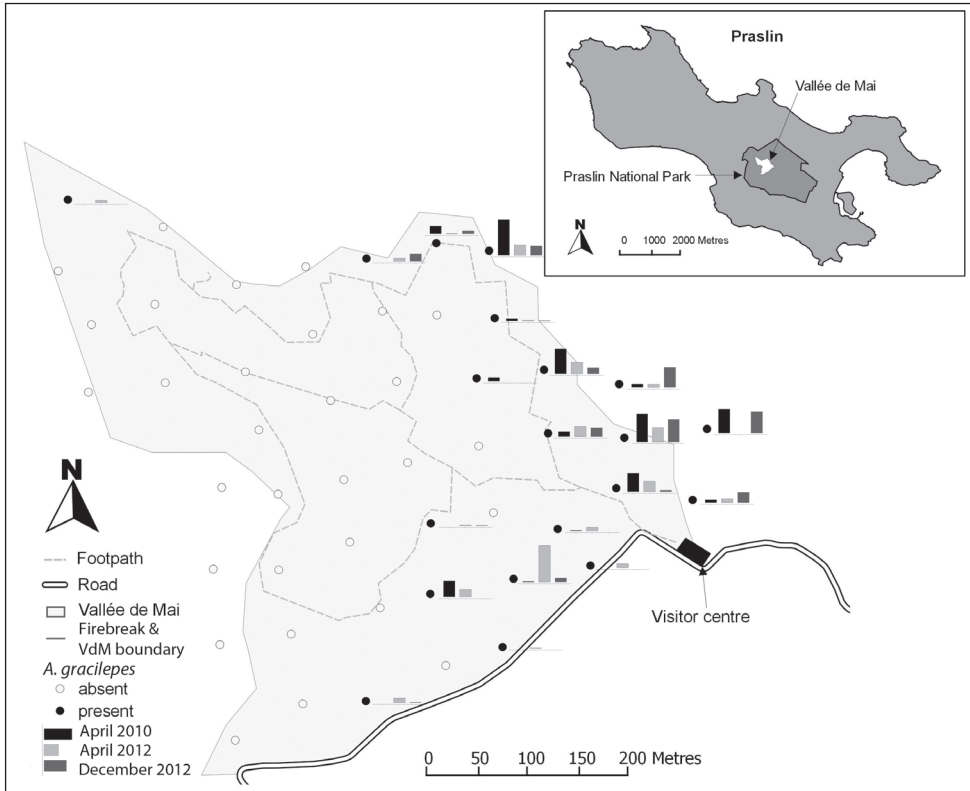
Figure 1. The distribution and abundance of *Anoplolepis gracilipes* in the Vallée de Mai, Seychelles. Circles indicate the sample locations and the presence (closed) or absence (open) of *A. gracilipes* within 10 × 10 m quadrats. In April 2010 and December 2012 *A. gracilipes* were observed at 14 locations, and in April 2012 ants were recorded from 18 locations in the Vallée de Mai. Bars next to full circles show relative *A. gracilipes* activity in April 2010 (black), April 2012 (light grey) and December 2012 (dark grey), and are drawn to the same scale.

area. Quadrats located in water or on large boulders were shifted to the nearest suitable adjacent area. Hereafter, the area of the Vallée de Mai with *A. gracilipes* is referred to as 'invaded' and the area without *A. gracilipes* as 'uninvaded'.

　　We used ant activity counts to quantify *A. gracilipes* abundance. We were not able to apply the more standard pitfall methods to assess *A. gracilipes* abundance because the terrain of the Vallée de Mai consists of thick, multi-level palm leaf litter and boulders; therefore we adapted the method used by Abbott 2005. Using this method limits comparisons with other studies but allows for standardised assessment within the Vallée de Mai. In all three surveys, ant activity was measured by placing a 15×15 cm laminated white sheet on the ground or into the leaf litter with an absorbent cotton pad soaked in 15% sugar solution in the centre. We allowed a 3-min settling period before counting all *A. gracilipes* individuals crossing the sheet within three minutes. The number of individuals that crossed each sheet per minute is referred to as 'ant

activity'. Five ant activity counts were taken per quadrat, one at each corner and one in the centre, and the mean value of each quadrat was used in the analysis. Ant activity was only recorded in fair weather conditions (not during rain or shortly afterwards) between 0800–1600 h when ant activity remained constant (Cuthbert 2010).

At each ant count location we recorded canopy cover, ground surface temperature (recorded to 0.1 °C with a thermometer in the shade on the ground) and relative humidity (humidity meter 'Rapitest', Stanton Hope, Essex). Canopy cover was assessed by counting the number of quarters of a 10×4 cm tube that showed canopy when looking vertically upwards at each ant count location. A quarter was counted only if more than half of that quarter was covered by the canopy. Each counted quarter therefore represents a maximum of 25% canopy cover, i.e., 0 quarters = 0% canopy cover, 2 quarters = 50% canopy cover etc. Records from each ant count location were averaged to produce mean canopy cover, temperature and relative humidity per quadrat.

We also assessed canopy use by *A. gracilipes* via tree trunks for each quadrat in the invaded area by searching trunks for one minute each and recording presence/absence of *A. gracilipes* on five randomly selected adult trees in each invaded quadrat. No other ant activity was recorded on trunks in quadrats in either area.

Impacts on endemic fauna

Preliminary observations suggested that *A. gracilipes* frequently used the palm forest canopy, which is dominated by large *L. maldivica* leaves. Because most of the endemic arboreal fauna of the Vallée de Mai is closely associated with *L. maldivica*, we expected any interference between *A. gracilipes* and endemic arboreal species to occur predominantly on *L. maldivica*. We assessed the effect of *A. gracilipes* presence by surveying eight species of arboreal endemic fauna likely to be directly affected by *A. gracilipes*, which were recorded from all parts of the palm forest prior to the invasion of *A. gracilipes*. The species surveyed were the day geckos *Phelsuma astriata* and *P. sundbergi*, the three species of bronze gecko *Ailuronyx seychellensis*, *A. tachyscopaeus* and *A. trachygaster*; and three arboreal molluscs *Vaginula seychellensis*, *Stylodonta studeriana* and *Pachnodus pralines*. The high density of *L. maldivica* in the Vallée de Mai and almost constant flowering of males provides a reliable food resource for these and other species. Surveys were made on 60 randomly selected trees (20 males, females and juveniles) of *L. maldivica* in each the invaded and uninvaded area. On each tree, a 5-min thorough search of the trunk, all stems, undersides of leaves and fruit/flowers was conducted with binoculars (magnification: 8×42) recording the number of individuals of each of the eight species.

Analysis

We used a logistic regression model to test the influence of environmental variables on *A. gracilipes* distribution. Dfbeta statistics, similar to Cook's distance in linear models,

is a measure of influence of individual points on logistic regression analysis (Belsley et al. 2005). Two outliers with dfbeta > 1.0 strongly influenced the logit coefficient and were thus removed from our analysis. To examine the effect of environmental variables on *A. gracilipes* activity in the invaded area, we ran a generalised linear model (inverse Gaussian distribution) with *A. gracilipes* activity as response and canopy cover, temperature and humidity as explanatory variables. Full factorial generalised linear models (negative binomial with log-link distribution) and pairwise comparisons were used to determine the effects of area (invaded or uninvaded) and tree type (male, female or juvenile) on species richness and abundance of endemic species. Counts of endemic arboreal species in invaded and uninvaded areas were compared by Chi-square tests. All statistical tests were conducted in SPSS 16.0.

Results

Ant distribution and activity

In 2010, *A. gracilipes* was confined to the north-east part of the Vallée de Mai, occurring in 14 of the 50 (28%) quadrats (Fig. 1). In April 2012, *A. gracilipes* expanded its range to occupy 18 quadrats, including 12 of the 14 previously occupied, with the range expansion being from the firebreak in the east and north-east and from the road along the southern border. This was followed by, a range contraction in December 2012 to 14 previously occupied quadrats (Fig.1). The activity of *A. gracilipes* is lowest in the south-east and highest near the firebreak in the east close to the visitor centre, bordering the Vallée de Mai (Fig. 1). There was no change in mean ant activity (± SE) in the invaded area across surveys (2010: 3.55 ± 0.88 individuals/min^{-1}; April 2012: 2.18 ± 0.58; December 2012: 2.57 ± 0.69; paired Wilcoxon test $p > 0.1$; range: 0.07 – 10.9). Mean *A. gracilipes* activity in invaded quadrats at the edge of the Vallée de Mai (N =6; 4.83 ± 0.94) was higher than those inside the forest (N = 8; 0.87 ± 0.31; Wilcoxon test $p > 0.0036$; Fig. 1) in December 2012, but not in 2010 and April 2012, suggesting a shift in ant abundance towards the firebreak in December 2012.

Ant occurrence and environmental variables

Invaded areas were characterised by higher humidity (invaded vs. uninvaded: 75.8 ± 0.8% vs. 72.9 ± 0.5% mean ± SE), lower canopy cover (2.5 ± 0.2% vs. 3.0 ± 0.1%), and slightly higher temperature (27.6 ± 0.13 °C vs. 27.5 ± 0.083 °C; Table 1), but variation of *A. gracilipes* activity within invaded areas was not related to temperature ($\chi^2_{3,10} = 0.04$, $p = 0.83$), canopy cover ($\chi^2_{3,10} = 1.21$, $p = 0.27$) or humidity ($\chi^2_{3,10} = 0.17$, $p = 0.69$). *Anoplolepis gracilipes* was observed primarily on the ground but was recorded on 35% (54 of 153) of trees in invaded quadrats, most commonly on introduced *Cinnamomum verum* (20%), followed by *L. maldivica* (13%). Overall, the relative abundance of intro-

Table 1. Logistic regression analysis showing the effect of environmental variables on the likelihood of *Anoplolepis gracilipes* presence or absence within quadrats in the Vallée de Mai ($N = 47$) ($R^2 = 0.63$ (Nagelkerke), model $\chi^2 = 26.16$, classifies 94% correctly).

	Coefficient	SE	Wald χ^2	Odds ratio	95% CI for Odds ratio		P
					Lower	Upper	
Temperature	2.68	1.13	5.67	14.6	1.61	132	0.017
Canopy cover	−2.36	0.96	6.05	0.094	0.014	0.619	0.014
Humidity	0.745	7.45	7.45	2.11	1.22	3.60	0.006
Constant	−125	48.4	6.61	0.000			0.010

duced broadleaf trees was more than four times higher in the invaded (native:introduced = 6.75:1) than the uninvaded area (1.57:1). We opportunistically observed *A. gracilipes* tending two species of honeydew-producing hemipterans, the soft scales *Pulvinaria urbicola* (Coccidae) and *Icerya seychellarum* (Margarodidae). Both species are introduced to the Seychelles and were tended on endemic and introduced dicotyledonous trees in and close to the firebreak. We randomly checked several hundred palm leaves during the study period and observed no tended hemipterans on any of the palm species.

Impacts on endemic arboreal fauna

The endemic arboreal species displayed considerable variation between the invaded and uninvaded areas (Fig. 2). The molluscs *V. seychellensis*, *S. studeriana* and *P. pralines* were less abundant or absent where ants occurred ($\chi^2 = 69$, $p < 0.0001$; $\chi^2 = 9.8$, $p < 0.01$; $\chi^2 = 8.3$, $p < 0.01$, respectively). The white slug *V. seychellensis* was common in the uninvaded area but entirely absent from the invaded area. Of the geckos, only the dwarf bronze gecko *A. tachyscopaeus* was significantly less abundant in the invaded area ($\chi^2 = 7.2$, $p < 0.01$). Abundance of the four species with the greatest differences between invaded and uninvaded areas showed no relationship with humidity or canopy cover (all r < 0.01, $p > 0.05$). Overall, mean species richness (invaded: 0.44 ± 0.08; uninvaded: 1.1 ± 0.10; $\chi^2_{5,114} = 0.25$, $p = 0.002$) and abundance (invaded = 46; uninvaded = 166; $\chi^2_{5,114} = 17.01$, $p < 0.001$) of endemic arboreal species on *L. maldivica* were lower in the invaded compared to uninvaded areas. There was no significant main effect for endemic species richness ($\chi^2_{5,114} = 0.245$, $p = 0.89$) and abundance ($\chi^2_{5,114} = 0.614$, $p = 0.74$) on male, female and juvenile *L. maldivica* within the invaded and uninvaded areas (Fig. 3). Although the abundance of endemic arboreal species on female *L. maldivica* trees was similar in *A. gracilipes* invaded and non-invaded areas ($p = 0.54$), abundance on males and juveniles ($p < 0.001$) in the invaded area was significantly lower (area × tree type interaction effect; $\chi^2_{5,114} = 6.50$, $p = 0.039$; Fig. 3). There was no significant interaction effect between tree type and area in the number of endemic arboreal species ($\chi^2_{5,114} = 2.73$, $p = 0.25$).
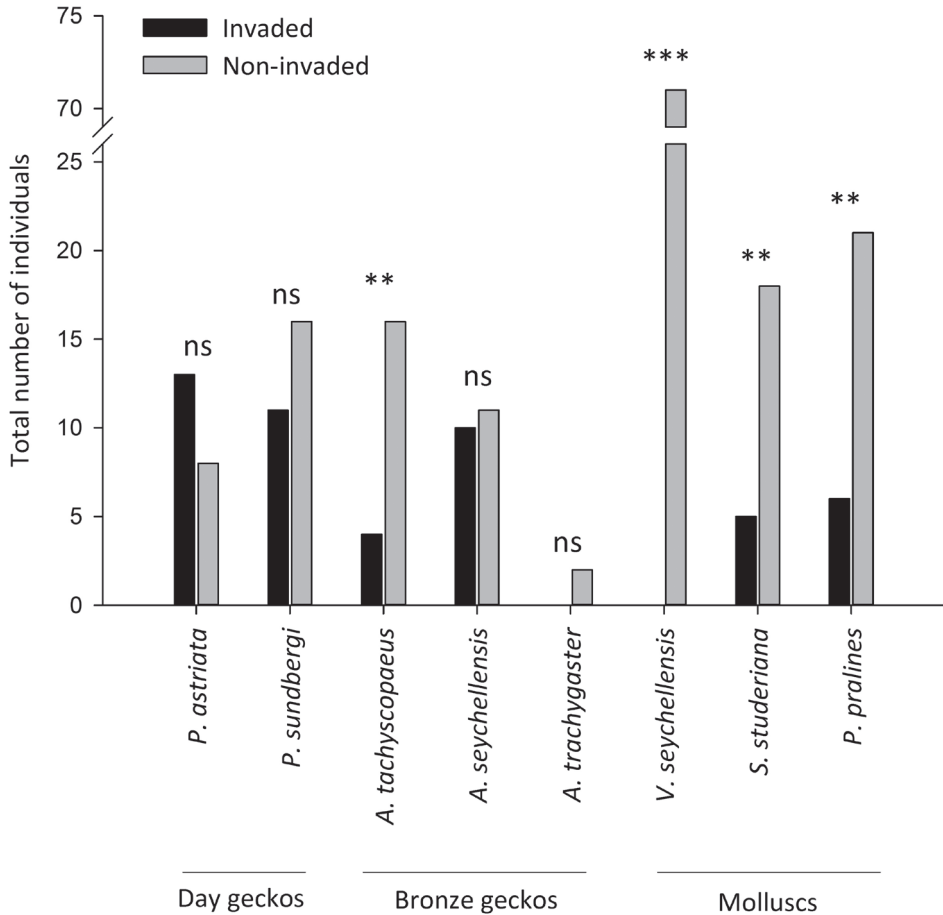
Figure 2. Abundance of eight endemic species in the *A. gracilipes* invaded and uninvaded areas: Number of observed individuals of eight species of endemic arboreal species on *Lodoicea maldivica* palms in the *Anoplolepis gracilipes* invaded (N = 60 trees) and uninvaded areas (N = 60 trees) within the Vallée de Mai. Counts were compared by chi-square test and levels of significance indicate: ns = non-significant, * < 0.05, ** < 0.01, *** < 0.001.

Discussion

Although *Anoplolepis gracilipes* has occurred across Praslin for at least the last decade and is present in Praslin National Park, there were no reports of the species occurring inside the Vallée de Mai until 2009. Despite its documented ability to rapidly cover large areas in high densities under optimal conditions (Hill et al. 2003; O'Dowd et al. 2003), the current distribution of *A. gracilipes* in the Vallée de Mai appears to be in a dynamic equilibrium and is restricted to the north-east of the reserve, with highest activity levels close to the firebreak and the visitor centre. This confined and relatively stable distribution invokes several possible explanations.
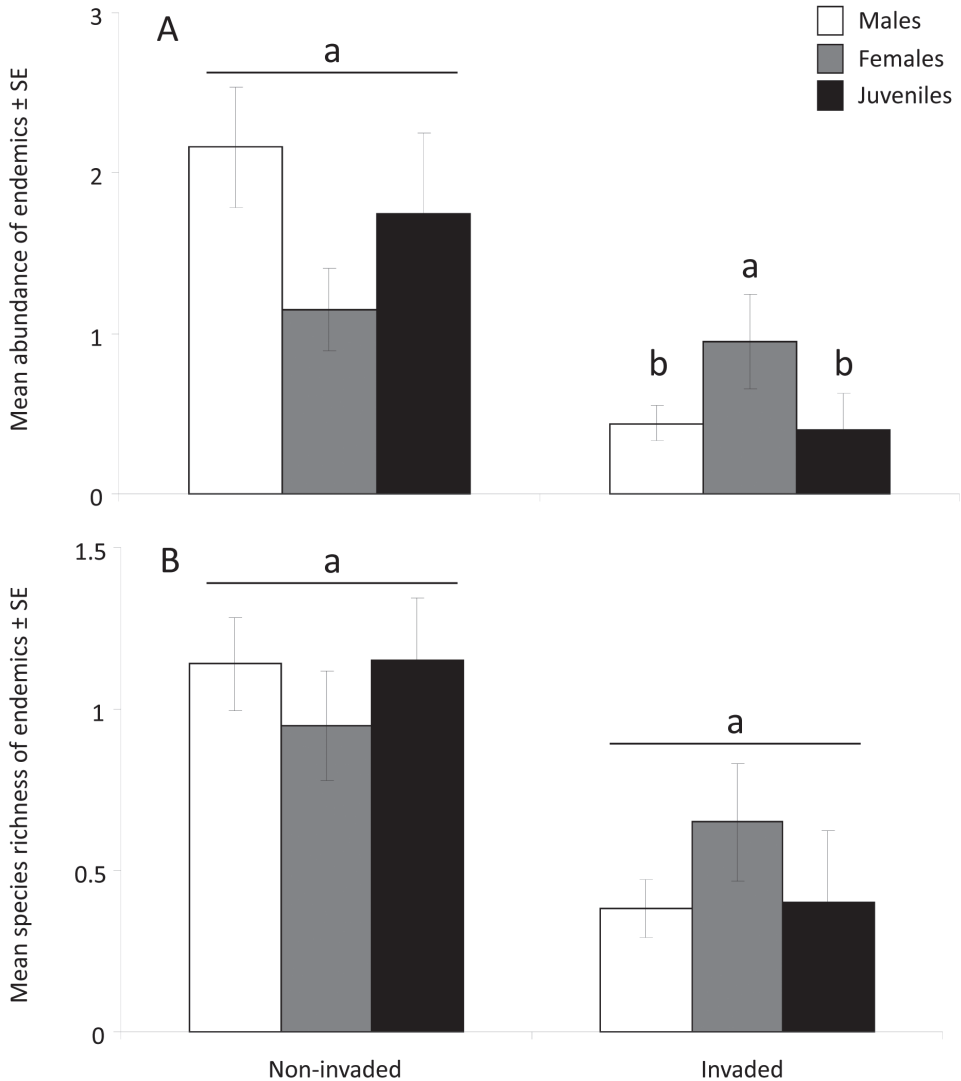
Figure 3. Differences in endemic species abundance and richness between the invaded and uninvaded areas and across tree classes. (**A**) Mean abundance and (**B**) species richness of endemic arboreal species in *A. gracilipes* invaded and uninvaded areas are similar between 20 male, female and juvenile *L. maldivica* palms in the Vallée de Mai. Different small letters indicate significant differences in between-area comparisons (invaded vs. non-invaded) but not within-area comparisons. Full statistics are presented in the text.

Firstly, the occurrence of *A. gracilipes* in the Vallée de Mai may be due to localised introduction and disturbance close to the palm forest. Repeated introductions and anthropogenic disruption of ecosystems both increase the likelihood of successful species invasions (Lockwood et al. 2005; Roura-Pascual et al. 2011; Bacon et al. 2014). The current distribution of *A. gracilipes* in the Vallée de Mai includes the visitor centre and entrance

area and it is possible that the recent construction of this centre (2007–2009) facilitated *A. gracilipes* establishment and invasion into the palm forest, through both the transport of *A. gracilipes* with construction materials and anthropogenic disturbance at the forest edge. The highest *A. gracilipes* activity and a continuous increase in activity throughout the study period close to the visitor centre suggest that the disturbance has generated favourable conditions, such as high carbohydrate supply, good abiotic conditions and potentially lower biotic resistance, for the establishment and spread of *A. gracilipes*. Similar findings were reported by Drescher et al. (2007) in Borneo where ant densities were highest in anthropogenically disturbed sites. This raises questions about reasons for the unfavourable conditions for colony establishment and growth in non-degraded forest inside the reserve.

Secondly, the lack of population growth in the Vallée de Mai may be due to a shortage of liquid sugary substances, which is an important energy source for workers, especially during invasions (Savage et al. 2011; Shik and Silverman 2013). To secure large quantities of carbohydrates, *A. gracilipes* establishes a mutualism with hemipterans, which provide a reliable source of honeydew as food (Delabie 2001; Abbott and Green 2007; Blüthgen and Feldhaar 2010). In the Vallée de Mai, hemipterans, such as introduced *Pulvinaria urbicola* and *Dysmicoccus* sp., which are invasive elsewhere in Seychelles (Gaigher et al. 2011), were rarely observed on palms (CKB, pers. obs.). This may explain why *A. gracilipes* made substantially lower use of trees in the Vallée de Mai (35%), compared to the numbers observed by O'Dowd et al. (1999) who recorded 98.5% of trees being utilised by *A. gracilipes* on Christmas Island. Similarly, Haines and Haines (1978b) reported 59–100% of trunks occupied by *A. gracilipes* at four sites on Mahé, Seychelles. The lack of hemipterans on palms may restrict the spread of *A. gracilipes* to the boundaries of the mixed forest where broadleaved vegetation and associated hemipterans are abundant (Haines and Haines 1978a). Of the trees that are used in the Vallée de Mai by *A. gracilipes*, 20% were the introduced broadleaf *C. verum*, which is disproportionately high compared to its relative abundance (2.9%; SIF, unpubl. data), suggesting an active preference for *C. verum* in the palm forest.

Thirdly, biotic resistance may also explain the observed stable population of *A. gracilipes* in the Vallée de Mai. There is little and ambiguous information on the role of native ant species in conferring biotic resistance to the invasion of exotic ant species. Both Way (1953) and Hoffmann and Saul (2010) concluded that habitat suitability, and not the presence of native ants, is the strongest predictor of invasive *A. gracilipes* distribution. The invasion of other ants, such as the Argentine ant *L. humile* in Portugal, however, was prevented by dominant native ants in cork oak plantations and pasture habitat (Way et al. 1997). Whether native ant species have the potential to limit *A. gracilipes* invasion in the Vallée de Mai palm forest is unknown, but the effect of native ants may be largest at early stages of invasion when population size of *A. gracilipes* is still relatively small (Menke et al. 2007). According to biotic resistance theory (Elton 1958), native communities should have higher biotic resistance and therefore be less susceptible to invasion than degraded habitat where native ant species numbers have been reduced. At least 10 native ant species occur in the Vallée de Mai. While this is a relatively low number of species compared to ant communities on mainlands it is among the best

habitat types for ants on Praslin (B. Fisher, pers. comm.). This richness in native ants may not confer biotic resistance, but it suggests that the habitat is suitable for a variety of ant species, which are likely to compete for resources with the generalist *A. gracilipes*.

A final explanation for the apparent dynamic equilibrium of the *A. gracilipes* population concerns abiotic conditions. Hoffmann and Saul (2010) showed that habitat suitability is the primary determinant of *A. gracilipes* incursions, and climatic variables, especially temperature and humidity, are important factors determining ant distribution (Torres 1984; Porter 1988; Hölldobler and Wilson 1990; Krushelnycky et al. 2005). In the Vallée de Mai, higher humidity and temperature and lower canopy cover were correlated with *A. gracilipes* presence. The interior of the palm forest is characterised by dense canopy cover and lower temperatures. Cold and wet conditions have been shown to affect foraging activity of other invasive ant species such as the Argentine ant in Hawaii (Krushelnycky et al 2005). Nevertheless, the total differences in temperature and humidity between invaded and uninvaded areas in our research are so small (e.g., ground temperature difference was only 0.07 °C) that they are unlikely to affect the behaviour of the invasive *A. gracilipes* (Chong and Lee 2009).

We observed marked variation between the presence of *A. gracilipes* and several arboreal species. The number and abundance of endemic arboreal species was lower on *L. maldivica* in invaded areas, and the effect was particularly strong for molluscs, which were abundant throughout the palm forest prior to the arrival of *A. gracilipes* (NB, pers. obs.). To our knowledge this is the first record of *A. gracilipes* invasion coinciding with the disappearance of native molluscs, although cause and effect could not be confirmed. Further spread of *A. gracilipes* through the palm forest could threaten the viability of these species and the relationship between molluscs and palms in this forest. The absence of the slug *V. seychellensis*, a *L. maldivica* specialist, from the invaded area is particularly concerning. Effects of *A. gracilipes* on native species were also recorded on Mahé, where fewer terrestrial reptiles occurred in *A. gracilipes* invaded areas (Haines and Haines 1978a). It is not known whether *A. gracilipes* actively prey upon or aggressively exclude endemic arboreal species in the Vallée de Mai. Our observations suggest that *A. gracilipes* excludes endemic arboreal species from male *L. maldivica* trees, which provide a rich pollen food source for many arboreal species including geckos and molluscs. *Anoplolepis gracilipes* may, however, be attracted to male trees not due to direct pollen resources but to the dead and decaying small invertebrates which accumulate at the base of the catkins (Cuthbert 2010; C. Kaiser-Bunbury pers. obs.).

Conclusion

Island endemics are typically at higher risk of extinction (Gaston 1998) and invasive species can accelerate this process (Wanless et al. 2007; Medina et al. 2011). Attempts to reverse these processes, by controlling the spread and impact of invasive species have been undertaken worldwide (Veitch et al. 2011). Once an invasive species is established it is often difficult to eliminate or prevent further spread (Lewis et al. 1976; Krushelnycky et

al. 2004). In the case of *A. gracilipes* in the Vallée de Mai, further research into control or exclusion options, impacts and potential biotic resistance to ant invasion are required in addition to continued monitoring of distribution and abundance. Chemical control poses a considerable risk to non-target species, such as endemic ants. We therefore advise promoting and researching resistance of the palm forest by, for example, creating and maintaining conditions which restrict *A. gracilipes* populations, such as the removal of introduced broadleaf trees which host high numbers of introduced hemipterans, and targeted control of ant nests in the most disturbed habitats. Removal of introduced trees, however, must be carried out with great care to limit canopy gaps and soil disturbance which favour *A. gracilipes* and other invasive plant and animal species. Future research should experimentally assess and quantify parameters that ensure the resistance of the unique Vallée de Mai palm forest and its co-evolved plant and animal species.

Acknowledgements

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