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Ecological impacts of the little fire ant (*Wasmannia auropunctata*) in Tahiti

Alice Bousseyroux[A], *Caroline Blanvillain*[A], *Timeri Darius*[A], *Casper Vanderwoude*[B] and *David Beaune*[A,C,D]

[A]Société d'Ornithologie de Polynésie – SOP Manu, BP 7023, 98719 Taravao, Tahiti, Polynésie Française.
[B]Hawaii AntLab, Pacific Cooperative Studies Unit, University of Hawai'i, 3190 Maile Way, Honolulu, HI 96822-2279.
[C]Biogéosciences, UMR 6282 CNRS, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France.
[D]Corresponding author. Email: david.beaune@gmail.com

Abstract. The little fire ant (*Wasmannia auropunctata*) is one of the worst invasive exotic species of the world. Its pantropical expansion is explosive; the ant has been present in Tahiti for more than 20 years. This study is the first to be carried out in Tahiti to assess its ecological impacts. The ecological richness of three invaded environments located in or close to the Key Biodiversity Areas (Maruapo, Papehue, Hopuetamai and Orofero Valleys) was compared with that of adjoining uninvaded sites, in a xerophytic site of ferns and a rainforest in the bottom of a valley for invertebrates and finally a canyon and its cliffs for avifauna. At the last site, one bank is infested and the other bank is free of *W. auropunctata*. Invertebrates and birds were examined respectively by pitfall traps and observation points. The effects of *W. auropunctata* were significantly negative at each study site, and species diversity in infested sites was one-third of that in uninfested sites. For arthropods, the phytophages, omnivores, detritivores, predators and other ants were the most affected. Significantly fewer birds also frequented the infested shoreline, particularly endemic birds such as the Tahiti monarch (81% non-infested shoreline observation) and the Society fruit-dove in comparison with the adjacent non-infested shoreline. Moreover, Tahiti monarchs (which are territorial) were established in three territories located at the bottom of the infested zone or close to it in 2016. These birds have now deserted the areas colonised by *W. auropunctata*. Our results suggest that *W. auropunctata* is a serious threat to Tahitian terrestrial biodiversity, and related ecosystem services.

Additional keywords: ecological interaction, Hymenoptera, invasive species, island conservation, Polynesia

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Introduction

The little fire ant (LFA) *Wasmannia auropunctata* (Roger, 1863) (Hymenoptera: Formicidae) is one of the world's worst invasive species (Lowe *et al.* 2000). This social Myrmicinae from South America causes severe impacts in all invaded ecosystems (Wetterer and Porter 2003). Its small size (1.3 mm) and its biology allow the species to be easily transported in organic material or soil. It readily establishes in a new environment and quickly reproduces to become invasive (Vanderwoude *et al.* 2016). The invasive status of this ant species is strongly associated with a shift in its reproductive system from a classical sexual haplo-diploid system to a clonal reproduction system (Foucaud *et al.* 2006). This shift in reproduction is also associated with a shift in its colony structure, with invasive clonal populations being structured in 'supercolonies' (Le Breton *et al.* 2004). The environmental consequences of this species are overwhelmingly negative: indeed, the LFA disrupts ecological balances in its infested areas, altering the functioning of ecosystems, the relationships between living organisms and causing regression or extinction of indigenous species of insects (Spencer 1941; Fabres and Brown 1978; Lubin 1984; Jourdan 1997; Roque-Albelo *et al.* 2000; Le Breton *et al.* 2003; Sutherst *et al.* 2005; Beavan *et al.* 2008; Vonshak *et al.* 2012; Vanderwoude *et al.* 2014; Bousseyroux *et al.* 2018).

The LFA has spread throughout the Pacific region at an alarming rate. It was reported in French Polynesia in 2004 (Bossin and Padovani 2010) but had likely arrived there at least a decade earlier (Depierre, pers. comm.). It was also found in the Galapagos (Clark *et al.* 1982), Hawai'i (Vanderwoude *et al.* 2010), Wallis and Futuna (Gutierrez 1981), New Caledonia (Fabres and Brown 1978), Vanuatu (Rapp 1999), the Solomon Islands (Ikin 1984), Papua New Guinea (Vanderwoude 2008), Guam (Raymundo and Miller 2012) and Yap in the Federated States of Micronesia (CV, pers. obs., 2017).

In French Polynesia, as in many island ecosystems, species diversity is poor with high rates of endemism compared with

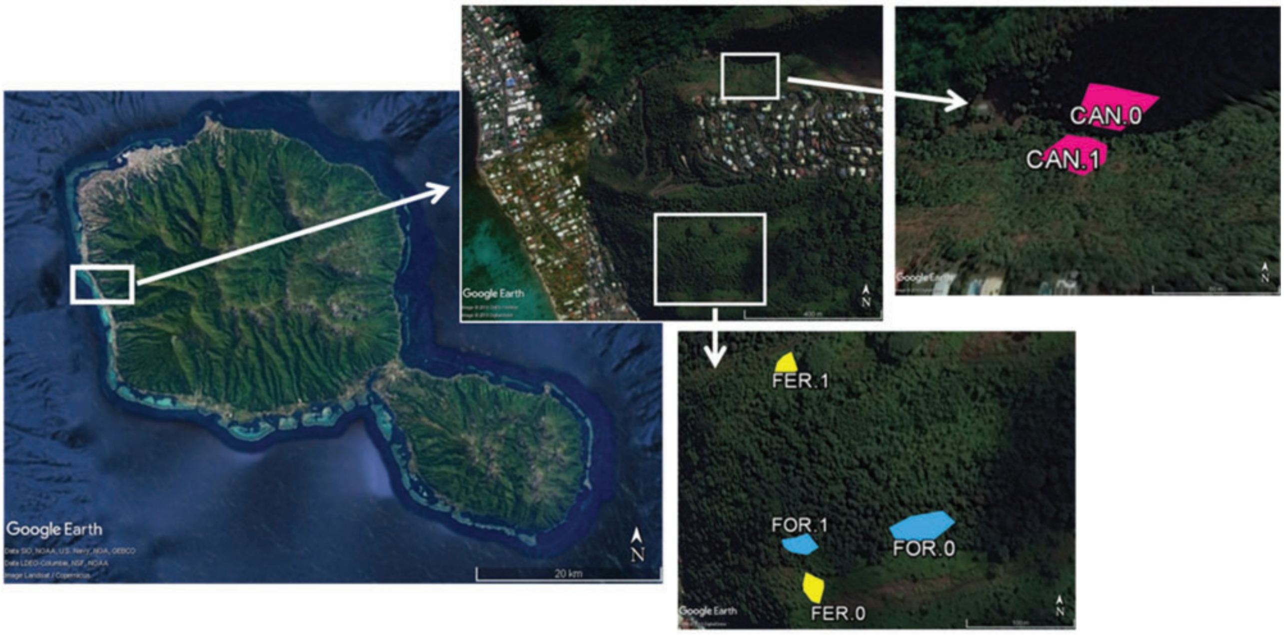

Fig. 1. Map of studied sites in Tahiti with (1) or without (0) the LFA: canyon (CAN) in pink, ferns (FER) in yellow and forest (FOR) in blue.

fauna assemblages on continents (IUCN 2016). This poses challenges for conservation efforts because many native species have restricted distributions and are particularly vulnerable to ecological disturbances. LFA supercolonies were recently discovered in Maruapo and Papehue valleys in Tahiti. These are 'Key Biodiversity Areas' and also 'Important Bird and Biodiversity Areas in Danger' (BirdLife International 2017). These two valleys, as well as that of Tiapa, contain several endemic and endangered species of birds, plants or snails (eg: *Pomarea nigra*, *Partula clara*, *Samoana attenuate*, *Erythrina tahitensis*, *Grewia tahitensis*, etc.) and insects (Ramage 2017). These habitats were partially invaded 10–15 years ago, which offered an opportunity to describe the impacts of the LFA on the avian and invertebrate fauna of these habitats.

Polynesian terrestrial arthropods are divided into four major taxonomic groups: arachnids, crustaceans, myriapods and true insects. Knowledge about certain families and orders in French Polynesia is far from exhaustive (Seguin 2015; Ramage 2017). There are 337 species and subspecies of arachnids: 104 known spider species (including 46 endemic species), 4 species of pseudoscorpions, 2 species of scorpions and 227 species of mites divided into 4 orders (Seguin 2015). Polynesian crustaceans are essentially decapods and terrestrial amphipods. The centipedes, represented by 19 species, of which 4 are endemic, have not been studied since 1930 (Seguin 2015). Insects of French Polynesia have been inventoried but only for the island of Tahiti. True insects and springtails are represented by 2409 species and subspecies. The most important insect order in terms of species richness in French Polynesia is Coleoptera: 770 taxa have been recorded, with an endemism rate of 60%. Three of the 45 families in the area account for more than 60% of the species: Curculionidae (weevils) with 250 species (210 endemic), Carabidae (carabids) with 133 species (112 endemic), and Staphylinidae (staphylins) with 116 species (69 endemic) (Seguin 2015).

The eastern Pacific region has a depauperate ant fauna with most ant species being cosmopolitan tramp species that arrived with human commerce and exploration (Wilson and Taylor 1967*a*, 1967*b*). In total, 51 ant species are known from French Polynesia, including three endemic species (T. Ramage, unpubl. data). In contrast, the western Pacific region is more speciose.

The birds present in the study canyon are endemic, native or introduced. Of the endemic birds, the Tahiti monarch is critically endangered and the object of an intensive recovery program since 1998 (Blanvillain *et al.* 2017).

To date, no studies have examined the ecological impact of this invasive species in French Polynesia. Our goal was to assess the ecological impacts of the LFA on soil invertebrates and birds in the Key Biodiversity Areas of Maruapo, Papehue, Hopuetamai and Orofero valleys in Tahiti. Three representative habitats of those natural ecosystems were studied in areas with and without the LFA: a xerophytic site with ferns, a wet forest, and a canyon with its cliffs.

Materials and methods

Study sites

We studied three habitats infested by the LFA – (1) a xerophytic site with ferns, (2) a wet forest, and (3) a canyon and its cliffs – and compared these with adjacent sites where LFAs were absent. These six studied sites are mapped in Figs 1 and 2. Observation sites within these habitats were selected in order to minimise the impact of other environmental factors. Altitude, pedology, geographical orientation, plants, etc. were similar in the fern site and the forest. For the survey of impacts on birds, the sites selected in Maruapo valley consisted of two steep

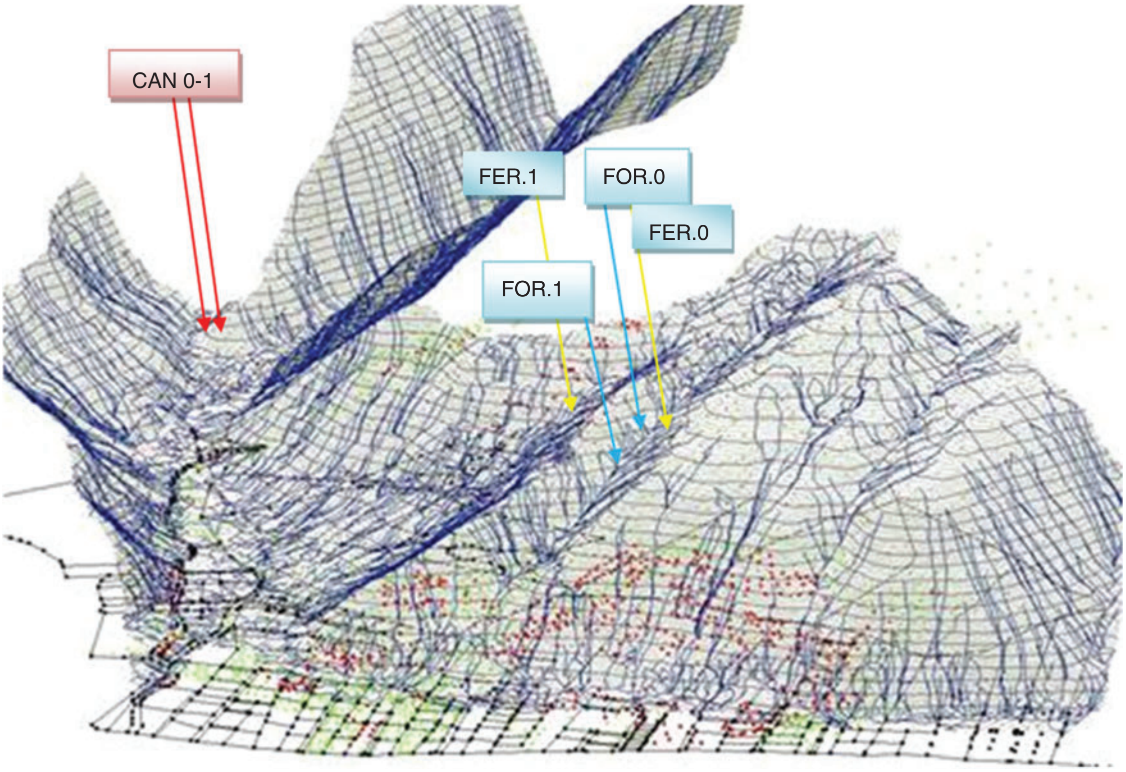

Fig. 2. Three-dimensional plan of the studied sites in Punauuia, Tahiti. Image © G. Peels.

cliffs: one infested by LFAs, the other not. The presence of the LFA was previously determined by ongoing monitoring which began in 2014 (Blanvillain *et al.* 2017) as part of a management program targeting the Tahiti monarch (*Pomarea nigra*).

Fauna sampling

Determination of the LFA distribution

The LFA is readily attracted to lipid and protein food sources and smooth peanut butter is commonly used as an attractant for this species (Williams and Whelan 1992; Vanderwoude *et al.* 2010, 2014). The distribution of the LFA was first determined by surveying sites using small local wooden sticks coated with peanut butter (SKIPPY®, Hormel Foods) which were placed every 10 m along parallel transects spaced 10 m apart. In the cliff, the upper infestation limit was delimited using this method and confirmed from the top by transects 50 m deep every 25 m and the lower infestation limit at its base by using the methodology performed in accessible areas. Several transects (including on the other side of the valley) allowed us to confirm that only one side of the valley was contaminated.

Bait sticks were left in place for 30–120 min before being retrieved. This allowed sufficient time for foraging ants to locate and recruit to the baits without consuming all the bait. At each survey point, trained observers carefully examined ants recruiting to the lure. If doubt existed regarding the identity of ants, samples were collected and examined under a binocular microscope to provide an accurate species determination as several ant species with similar morphological characteristics are known from Tahiti. A key to common invasive ant species in the Pacific (www.piakey.com) was used for identifications.

Invertebrates

Non-lethal smooth plastic pitfall traps, 12 cm high and ~8 cm in diameter, were deployed to sample terrestrial epigeal invertebrates in the study areas. In the forest and in fern areas 30 pitfall traps were installed simultaneously in the areas with and without LFAs. Pitfall traps were positioned every 2 m along 60-m transects. The empty traps were buried with a shovel and pick and their top edges aligned with the surface of the ground. The device remained in place 24 h in dry weather. No lethal substance was used to preserve captured animals, which were released near their place of capture after identification was complete. Only specimens of doubtful taxonomy were removed from the site and identified with a binocular microscope.

Clearly, the non-lethal method has limits: some individuals are likely to escape from the traps and the proportion of each captured species does not necessarily reflect their relative abundance in the environment as the collected animals are those living on the soil surface. Arboreal invertebrates are under-sampled using this method. However, the biases were the same for all experiments and hence the comparison of two sites (of the same habitat) remains relevant. In this study, invertebrates were identified at least to family level and counted. Ants were sorted to species level. A trophic functional group was assigned to each species: predator, phytophage, detritivore, parasite (because parasite species in the latter group often form mutualistic associations with ant species).

Birds

The distribution of birds at the canyon and cliff sites in the Maruapo deep valley were determined by point counts of visual observations and by bird calls. Sampling took place between 0900 and 1100 hours at the same fixed point for three non-consecutive days for a total of 35 count points of 5 min each. Two areas were compared: infested shoreline, river, and non-infested shoreline. All birds within 100 m of the observer were counted. However, the river and its bed constituted a buffer zone separating the two banks. Ants were distributed unevenly in this area, notably on the side of the infested shoreline and in part of the bed (the river was dry during sampling sessions). Data related to the river were therefore not representative and not used in analyses.

Analytical methods

Several metrics were used to compare the abundance and diversity of terrestrial invertebrates between infested and uninfested sites.

At the trap scale

Abundance and average diversity. The mean abundance and diversity of species per trap was compared between site biomes in ferns and forest, and also between these two habitats. A Wilcoxon (non-parametric data) test with statistical software R (R Core Team 2011) was used. For each infested zone, one in ferns and the other one in rainforest, two types of calculations were carried out: first by taking into account LFA presence and then by ignoring their presence. This makes it possible to estimate the influence of this ant on abundance and diversity estimates in infested areas.

At the ecosystem scale

Indices of diversity in areas with and without LFA. The Shannon and Simpson diversity indexes were used (Keylock 2005; Darius *et al.* 2017) to compare infested sites with those where LFAs were absent in ferns and forest. The Shannon index measures the heterogeneity of a population; the higher it is, the greater is the biodiversity. The Simpson index measures the probability that two random individuals belong to the same species; the lower it is, the greater is the biological diversity. Cumulative diversity richness curves were used to estimate the number of species by extrapolation with infinite sampling. The curves are obtained with the 'SPECACCUM' function of the software R (R Core Team 2011) which provides a good estimate of the specific biodiversity of an area and the representativeness of the sampling effort. The extrapolated cumulative diversity richness was estimated by the random resampling method (Palmer 1990) (bootstrap, jackknife of degree 1 and 2, and Chao method – these four estimation methods consider occurrences of rare species and the importance of replication: Chao 1987; Colwell and Coddington 1994) with the SPECPOOL function of R.

Differences in functional community composition with and without LFA. The number of species alone does not necessarily indicate functional ecological changes (e.g. loss of some keystone species such as decomposers, disappearance of predators, etc.). Thus permutation tests (PERMANOVA: Anderson 2006) tested differences in centroid (made from multidimensional projection with species as factors) dispersion of species groups with and without ants in ferns and forest. The PERMUTEST.BETADISPERSER in R was utilised for this purpose.

Birds. In order to establish whether habitat utilisation differs between infested cliff and non-infested cliff into the canyon, the species of each bird heard or seen was determined and each individual was located on either bank. The observed occurrence percentages corresponding to each species at its observation rate on each bank were compared with the theoretical (balanced) percentage of occurrence with the exact binomial test (function BINOM.TEST in R).

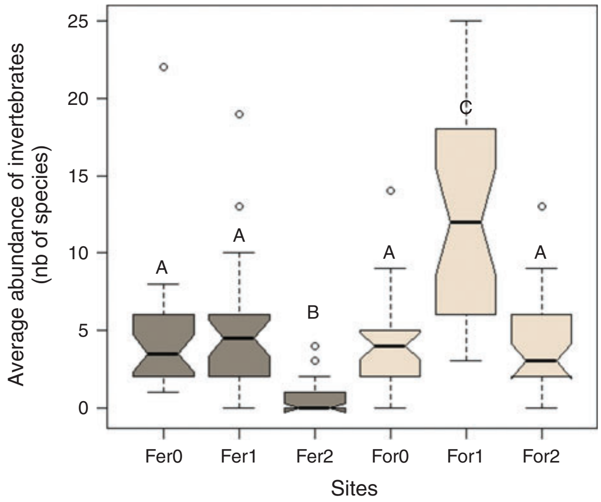

Fig. 3. Average abundance of invertebrates in traps in xerophytic fern (Fer) and rainforest (For) zones with (1 or 2) or without (0) the LFA in Punauuia, Tahiti. The LFA are included in calculations for Fer1 and For1, and are excluded from the calculations for Fer2 and For2. Letters (A, B, C) denote statistically different groups (W test with $P < 0.05$).

Results

Invertebrates

The average abundance of trapped invertebrates is presented in Fig. 3: the Wilcoxon test between sites without LFAs (FER.0 and FOR.0) and sites infested excluding LFAs in calculation (FER.2 and FOR.2) gives $W = 778/P\text{-value} = 9.051e^{-9}$ in ferns and $W = 492.5/P\text{-value} = 0.5302$ for forest areas. In the fern zone, invertebrates were simply replaced by LFAs so the abundance of invertebrates other than LFAs is significantly reduced by the presence of this invasive ant. In the forest area, abundance increased in traps due to the abundance of LFAs, but when this ant was ignored in the calculations, abundance was not significantly reduced. For species diversity (Fig. 4), differences are significant ($W = 775/P\text{-value} = 7.525e^{-9}$ in ferns and $W = 651.5/P\text{-value} = 0.002202$ for forest areas). In fern areas there were, on average, two species per trap in the LFA-free zone compared with only one species in the infested environment. In the forest there were, on average, three species per trap in the LFA-free zone and one of these species was replaced by LFAs in the infested zone.

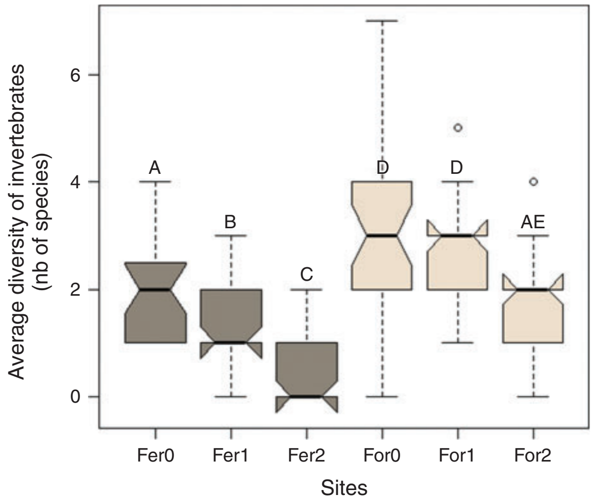

Fig. 4. Average diversity of invertebrates in traps in xerophytic fern (Fer) and rainforest (For) zones with (1 or 2) or without (0) the LFA in Punauuia, Tahiti. The LFA are included in calculations for Fer1 and For1, and are excluded from the calculations for Fer2 and For2. Letters (A, B, C, D, E) denote statistically different groups (W test with $P < 0.05$).

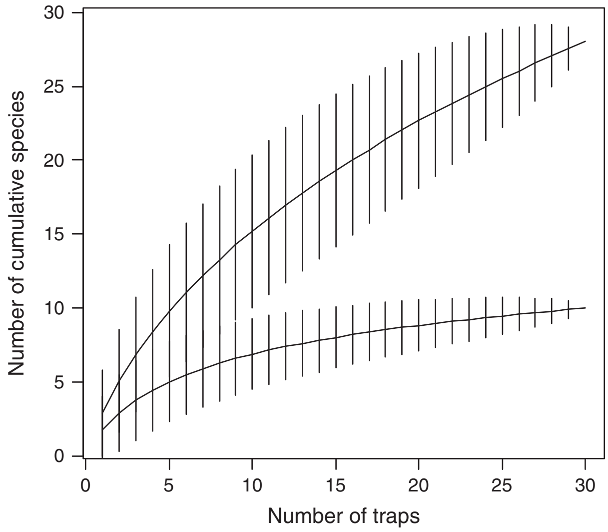

Fig. 5. Cumulative richness curves in rainforest with the LFA (bottom curve) or without (top curve) in Punauuia, Tahiti. LFAs are not included in the calculations.

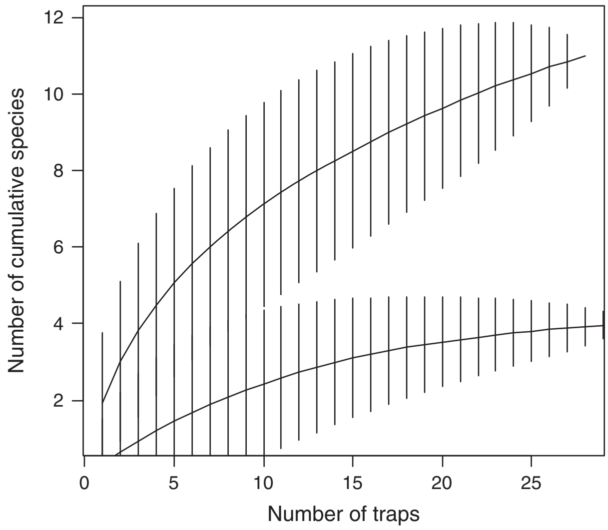

Fig. 6. Cumulative richness curves in fern areas with the LFA (bottom curve) or without (top curve) in Punauuia, Tahiti. LFAs are not included in the calculations.

However, if most species decreased in abundance in the presence of LFAs, the number of individuals of one species increased considerably between LFA-free and infested rainforest sites: e.g. 68 trapped mites in FOR.1 against only 2 individuals in FOR.0. Another species seems not to be impacted by LFAs: an aphid was trapped in ferns with 3 animals in FER.1 and 4 in FER.0.

The Shannon index was lower in LFA areas (0.44 in forest and 0.21 in ferns) compared with areas without LFAs (1.12 in forest and 0.57 in ferns). The Simpson index was also higher in areas without LFAs (0.53 in forest and 0.79 in ferns) compared with infested sites (0.13 in forest and 0.43 in ferns). Both the Shannon and Simpson diversity indices indicated that the presence of LFA reduced species diversity.

Biodiversity sampling in areas with and without LFAs in forest and ferns environments was carried out by analysing some 20 insect traps. Data were used to estimate the total specific diversity (theoretical plateau of the cumulative abundance curves) for each of the studied sites by extrapolation. In both cases local species diversity was substantially greater in sites without LFAs. The species accumulation curves in these environments (Figs 5 and 6) showed that in infested sites the curves appeared to reach an asymptote while no such asymptote was evident for uninfested sites. The sampling effort seems to be representative in infested areas but not in free sites because the asymptote is not reached so more traps would have identified more species.

The total number of species is estimated at a maximum of 49 in a non-infested forest and only 14 in a LFA-invaded forest. In the fern zone this maximum estimate is 15 without LFAs and 5 with LFAs. In both forest and fern environments, and regardless of the estimation formulae used, sites with LFAs had only one-third the species richness of sites without LFAs when the LFA was included in the calculations (Tables 1 and 2).

Functional communities

A PERMANOVA test showed that functional composition for infested sites was significantly different from non-infested ones in forest and fern areas (999 permutations, $F = 4.8$, $P = 0.029$ and $F = 27.0$, $P < 0.001$, respectively). Areas without LFAs contained more functional groups than LFA-infested sites. In both environments other ant communities were greatly affected. Four species commonly found in the uninfested forest were absent in the infested site. Only *Anoplolepis gracilipes* (the yellow crazy ant), which is also an invasive species, was present in sympatry with the LFA. No species except LFAs were

Table 1. Number of identified species and estimated number of species by extrapolation (chao, jackknife of degree 1 and 2 and bootstrap ± standard error) based on 30+28 insect traps in forest areas with (FOR.1) and without (FOR.0) the LFA in Punauuia (Tahiti)

	No. of species	Chao	Jackknife 1	Jackknife 2	Bootstrap
FOR.0, without LFA	28	43.8 ± 11.3	41.5 ± 4.6	49.2	33.9 ± 2.5
FOR.1, with LFA	10	14.4 ± 7.0	12.9 ± 1.7	14.8	11.3 ± 0.9
Factor	2.8	3.0	3.2	3.3	3.0

Table 2. Number of identified species and estimated number of species by extrapolation (chao, jackknife of degree 1 and 2 and bootstrap ± standard error) based on 30+30 insect traps in fern areas with (FER.1) and without (FER.0) the LFA in Punauuia (Tahiti)

	No. of species	Chao	Jackknife 1	Jackknife 2	Bootstrap
FER.0, without LFA	11	13.6 ± 3.4	14.9 ± 1.9	15.9	12.8 ± 1.2
FER.1, with LFA	4	4.5 ± 1.3	5.0 ± 1.0	5	4.5 ± 0.6
Factor	2.8	3.0	3.0	3.2	2.8

Table 3. Functional groups and number of species in forest areas, with and without the LFA (May 2017)

Numbers in parentheses indicate the total number of species belonging to that functional community

	With LFA	Without LFA
Omnivores (5)	1	5
Scavengers (9)	6	7
Carnivorous predators (9)	1	9
Phytophages (3)	0	3
Phloem feeders (2)	1	1
Others (3)	1	2

Table 4. Functional groups and number of species in ferns areas, with and without the LFA (May 2017)

Numbers in parentheses indicate the total number of species belonging to that functional community

	With LFA	Without LFA
Omnivores (3)	0	3
Scavengers (4)	1	4
Carnivorous predators (2)	1	2
Phloem feeders (1)	1	1
Others (1)	1	1

detected in the fern site. In the forest site, predator carnivores and phytophagous insects were also heavily impacted; only one of nine spider species coexisted in the presence of LFAs. In ferns, however, the detritivores were the most affected: no myriapod and only a single collembolan were recorded in the infested areas (Tables 3 and 4).

Birdlife

The avifauna observed in the canyon during the study comprised: (1) endemic birds, such as Tahiti monarch (*Pomarea nigra*), grey-green fruit-dove (*Ptilinopus purpuratus*), Polynesian swiftlet (*Aerodramus leucophaeus*), Tahiti kingfisher (*Todiramphus veneratus*); (2) one native bird, the Pacific swallow (*Hirundo tahitica*); and (3) introduced bird species, such as red-vented bulbul (*Pycnonotus cafer*), swamp harrier (*Circus approximans*), silvereye (*Zosterops lateralis*), zebra dove (*Geopelia striata*) and red junglefowl (*Gallus gallus*). The swiftlet, swallow and harrier were not included in the survey as they capture most of their prey in flight.

In total, 340 birds of eight different species were recorded during the 35 5-min censuses carried out between 7 June and 14 September 2017. Generally, species were detected on both sides of the river but habitat utilisation was clearly different, quantified by the number of times the species were observed or heard on each bank. Significantly fewer birds were recorded in areas infested with the LFA (38.2%, $IC_{95} = 32.60$–44.0%, $P < 0.001$). Individuals observed in the dry river bed, which was a non-infested buffer zone, have been identified but were not included in the calculations nor presented in the results.

The zebra dove was the only species that utilised both infested and uninfested areas equally. The Tahiti monarch, an insectivorous species, was recorded significantly fewer times on the infested shore (18.7%, $IC_{95} = 4.0$–45.6%, $P < 0.001$). Similarly, green pigeons, silvereyes and bulbuls were significantly less abundant on the infested shoreline (Table 5). Kingfishers and chickens were also observed (respectively $n = 3$ and $n = 7$) but these were not included in the analyses due to the low numbers recorded.

Discussion

The observations reported here have not been repeated in other environments and may vary in other ecosystems.

Table 5. Percentage of bird occurrence on sites without the LFA (CAN.0) relative to sites with the LFA (CAN.1)
Results of the exact binomial test relative to sites and 95% confidence intervals are also shown

Species	Diet	% of occurrence in CAN.0 (*n* total in both sites)	Exact binomial test	IC_{95}
Tahiti monarch (*Pomarea nigra*)	Insectivorous	81.3 (16)	$P < 0.001$	54.3–95.9
Revered kingfisher (*Todiramphus veneratus*)	Insectivorous	66.7 (3)	$P = 1$, n.s.	9.4–99.1
Green pigeon (*Ptilinopus purpuratus*)	Frugivorous	77.1 (35)	$P < 0.001$	59.8–89.6
Geopelia (*Geopelia striata*)	Granivorous	52.5 (158)	$P = 0.57$, n.s.	44.4–60.5
Bulbul (*Picnonotus cafer*)	Omnivorous	64.8 (54)	$P < 0.04$	50.6–77.3
Silvereye (*Zosterops lateralis*)	Omnivorous	87.0 (23)	$P < 0.001$	66.4–97.2
Chicken (*Gallus gallus*)	Omnivorous	42.9 (7)	$P = 1$, n.s.	9.9–81.6
All species combined		61.8 (294)	$P < 0.001$	56.0–67.4

Effects of W. auropunctata *on the invertebrate fauna*

In the rainforest habitat

The presence of the LFA caused a decrease in biological richness but not in the abundance of invertebrates in forest habitat. When the site is infested by this invasive ant, only a single mite species appeared to benefit. Several hypotheses potentially explain the increase in mite abundance in invaded sites. These mites may somehow benefit from the presence of the ant and fulfill a role in feeding, protection, colonisation, etc. (Bruneau De Miré 1969; Delabie *et al.* 1994), or the ecological niches occupied by mites and by the LFA may be mutually exclusive. In several countries, it has been observed that homopterans producing honeydew, such as mealy bugs and aphids, are not eliminated by LFAs because the LFAs actively 'farm' these species in order to maximise nutritional benefits derived from sugary exudates (Bruneau De Miré 1969; Delabie *et al.* 1994). Finally, LFAs may have eliminated species that compete with, or prey on, the mite, allowing the mite population to increase.

Myrmecofauna were particularly affected by LFA infestation. Only the yellow crazy ant, which is also an invasive species, could have applied adaptive strategies that enabled it to survive in this competitive environment. But this remains to be demonstrated. It is substantially larger and faster than the LFA. Additionally, it utilises microhabitats in the tree stratum as well as the ground layer and appears to resist better than other insects or reach a competitive equilibrium with the LFA.

The LFA eliminated many phytophagous and predatory invertebrates, including spiders, and negatively affected the abundance and diversity of scavengers. These changes are likely to alter carbon and nutrient cycling in invaded ecosystems, and prey–predator relationships, and also impact on larger fauna unable to adapt to changing environmental conditions.

In the fern habitat

For soil invertebrates in ferns the presence of the LFA resulted in a significant decrease of the abundance and diversity of local precolonial species. There appeared to be approximately three times more species in the LFA-free zone than in the invaded area. No other species of ants were detected at the fern site. Other affected communities included detritivores (Table 4), which could possibly negatively affect nutrient cycling, humus quality, the food chain, etc. (Del Toro *et al.* 2012).

The colonisation by the LFA in this insular context induced a profound modification of functional community structure, both in qualitative and quantitative terms. Almost all species of terrestrial invertebrates appeared to be impacted in all studied habitats. When present, the LFA reduced the local terrestrial invertebrate species richness by a factor of at least three in ferns and forest sites. When species are removed from impacted environments, impacts flow on to larger species and their roles in maintaining an ecological equilibrium cease. In insular environments subjected to rapid changes (especially those with low biological diversity) (Lieberman *et al.* 1994; Doherty *et al.* 2016), ecosystem resilience is low (Loreau *et al.* 2002; Loreau and Mazancourt 2013): when a species is eliminated by an invasive species or by another event such as a disease or a climatic event, the ecological niche it leaves vacant will not necessarily be occupied by a new local species but it may be occupied by an invasive and hypercompetitive species such as the LFA. In this way, this ubiquitous species can rapidly occupy a large number of niches in forest environments such as those studied.

The results demonstrate that the LFA dominated both food and space resources. Rather than forming individual colonies, LFA colonies remained interconnected and acted as a single supercolony (Le Breton *et al.* 2004), occupying a contiguous area, leaving little room for other terrestrial species.

Effects of W. auropunctata *on the avifauna*

Significantly fewer birds frequented the infested shoreline, particularly endemic birds such as the Tahiti monarch (81% non-infested shoreline observation) and the Tahiti fruit-dove (77%), in comparison with the adjacent non-infested shoreline. We acknowledge that these results may be influenced by differences in habitat, aspect and topography. Habitat preference could also have been partially driven by the aspect of the cliff faces (north for the non-infested areas and south in the infested areas) and diverging ecological factors such as temperature or sunlight, inducing subtle changes in habitat quality and/or bird behaviour rather than a behaviour induced by LFA presence. Moreover, some birds may have escaped detection during sampling by a lack of motion and bird call due to diverging ecological factors such as temperature or sunlight.

However, the fact that all three Tahiti monarch territories located at the bottom of the infested zone in 2016 were deserted by early 2018 strongly suggests that the LFA played an active role in the difference observed between valley ridges, for the Tahiti monarch and probably also for the other species. For other birdlife, except the granivorous zebra dove, the non-invaded shoreline was utilised more (number of individuals and number of species), suggesting that birds may avoid LFA-invaded areas. Furthermore, a change in the food chain and food availability in invaded areas is likely to reduce foraging success in insectivorous birds such as the Tahiti monarch. In the study area, birds were able to choose one site over another. A decline in habitat quality could have led to the final abandonment of the last Tahiti monarch–occupied territory in the study areas during the study period. However, LFA impacts on birds may be different when this choice is not available. Surprisingly, the only species that appeared to be more tolerant of the new invader is a seed-eating species foraging on the ground, where it is more susceptible to LFA impacts, including competition for seeds. The endemic Society fruit-dove was significantly affected by the invasive ant. This result is surprising because the LFA appears to prefer lipids and proteins over carbohydrates, so is less likely to alter availability of fruit within its foraging areas. Here, the increase of mite or other honeydew insects may reduce fruit production, as observed in Tahiti gardens (Bousseyroux *et al.* 2018). Its susceptibility to insect sting may also differ and the results may be a consequence of birds trying to avoid being stung or to protect young chicks from stings and predation (C. Blanvillain, pers. obs.)

Clearly, the presence of the LFA caused large and measurable changes to the biological diversity, abundance and community ecology of the invaded sites. As this species continues to spread throughout the Pacific region, these impacts may well manifest themselves in other jurisdictions. Preventing this continuing spread should therefore be a priority for other Pacific nations if these impacts are to be avoided.

Conflicts of interest

The authors declare no conflict of interest.

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References

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **62**, 245–253. doi:10.1111/J.1541-0420.2005.00440.X

Beavan, A., McWilliam, J., van Strydonck, E., Rumboll, N., and Beynon, J. (2008). Impact of the invasive little red fire ant *Wasmannia auropunctata* on the herpetofauna of the West African rainforest. James Rennie Bequest, University of Edinburgh.

BirdLife International (2017). Important bird and biodiversity areas in danger. Available at: http://datazone.birdlife.org/site/ibasindanger [accessed 12 June 2018].

Blanvillain, C., Peels, G., and Bousseyroux, A. (2017). Plan opérationnel pour l'éradication de méga-colonies de petite fourmi de feu y compris celle située dans une falaise dans le cadre de la sauvegarde du monarque de Tahiti, oiseau endémique en danger critique d'extinction (Polynésie française). SOP Manu, Taravao, Tahiti.

Bossin, H., and Padovani, E. (2010). Audit des actions menees depuis 2006 en matiere de lutte contre la petite fourmi de feu *Wasmannia auropunctata* sur l'ile de Tahiti. Technical Report, Institut Louis Malarde, 2010:1–27. Available at: http://www.littlefireants.com/Audit%20des%20actions%20menees%20depuis%202006.pdf [accessed 19 October 2018].

Bousseyroux, A., Blanvillain, C., and Beaune, D. (2018). La petite fourmi de feu (*Wasmannia auropunctata*): impacts écologiques en zone infestée dans le monde et risques en Polynésie. Société des etudes océanniennes. In press.

Bruneau De Miré, P. (1969). Une fourmi utilisée au Cameroun dans la lutte contre les mirides du cacaoyer: *Wasmannia auropunctata* Roger. *Cafe, Cacao, The (Paris)* **13**, 209–212.

Chao, A. (1987). Estimating the population size for capture–recapture data with unequal catchability. *Biometrics* **43**, 783–791. doi:10.2307/2531532

Clark, D. B., Guayasamin, C., Pazamino, O., Donoso, C., and Paez de Villacis, Y. (1982). The tramp ant *Wasmannia auropunctata*: autoecology and effect on ant diversity and distribution on Santa Cruz Island, Galapagos. *Biotropica* **14**, 196–207. doi:10.2307/2388026

Colwell, R. K., and Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **345**, 101–118. doi:10.1098/RSTB.1994.0091

Darius, T., A. Bousseyroux, and D. Beaune. (2017). Impacts écologiques de la petite fourmi de feu (*Wasmannia auropunctata*) sur les invertébrés de Tahiti. Technical Report, SOP Manu, Taravao.

Del Toro, I., Ribbons, R. R., and Pelini, S. L. (2012). The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News* **17**, 133–146.

Delabie, J., A. Da Encarnaçao, and I. Cazorla. (1994). Relations between the little fire ant, *Wasmannia auropunctata*, and its associated mealybug, *Planococcus citri* in Brazilian cocoa farms. In 'Exotic Ants: Biology, Impact, and Control of Introduced Species'. (Ed. D. F. Williams.) pp. 91–103. (Westview Press: Boulder, CO.)

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., and Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 11261–11265. doi:10.1073/PNAS.1602480113

Fabres, G., and Brown, W., Jr. (1978). The recent introduction of the pest ant *Wasmannia auropunctata* into New Caledonia. *Journal of the Australian Entomological Society* **17**, 139–142. doi:10.1111/J.1440-6055.1978.TB02220.X

Foucaud, J., Jourdan, H., Le Breton, J., Loiseau, A., Konghouleux, D., and Estoup, A. (2006). Rare sexual reproduction events in the clonal reproduction system of introduced populations of the little fire ant. *Evolution* **60**, 1646–1657. doi:10.1111/J.0014-3820.2006.TB00509.X

Gutierrez, G. J. (1981). Updating of data on economic entomology on Wallis and Futuna. Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM, Noumea, New Caledonia.

Ikin, R. (1984). Cocoa tree-ant. *Quart. Newsl. FAO Asia Pac. Plant Protect. Comm* **27**, 8.

IUCN (2016). Profil d'écosystèmes de la Polynésie Française – Région Pacifique. Union européenne Régions Ultra-périphériques et Pays et Territoires d'Outre-mer; BEST, Technical Report Commission

Européenne. Available at: http://ec.europa.eu/environment/nature/biodiversity/best/pdf/best-profil_d-ecosysteme_polynesie_francaise_2016.pdf [accessed 19 October 2018].

Jourdan, H. (1997). Threats on Pacific islands: the spread of the tramp ant *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Pacific Conservation Biology* **3**, 61–64. doi:10.1071/PC970061

Keylock, C. (2005). Simpson diversity and the Shannon–Wiener index as special cases of a generalized entropy. *Oikos* **109**, 203–207. doi:10.1111/J.0030-1299.2005.13735.X

Le Breton, J., Chazeau, J., and Jourdan, H. (2003). Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology* **28**, 204–209. doi:10.1046/J.1442-9993.2003.01266.X

Le Breton, J., Delabie, J. C. H., Chazeau, J., and Jourdan, H. (2004). Experimental evidence of large-scale unicoloniality in the tramp ant *Wasmannia auropunctata* (Roger). *Journal of Insect Behavior* **17**, 263–271. doi:10.1023/B:JOIR.0000028575.28700.71

Lieberman, A., Kuehler, C., Varney, A., and Everett, W. (1994). Island conservation: a biological imperative. *Zoonooz* **67**, 18–21.

Loreau, M., and Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* **16**, 106–115. doi:10.1111/ELE.12073

Loreau, M., Naeem, S., and Inchausti, P. (2002). 'Biodiversity and Ecosystem Functioning: Synthesis and Perspectives.' (Oxford University Press: Oxford.)

Lowe, S., Browne, M., Boudjelas, S., and De Poorter, M. (2000). 100 of the World's worst invasive alien species. A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). First published as a special lift-out in *Aliens* **12**.

Lubin, Y. D. (1984). Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant, *Wasmannia auropunctata. Biological Journal of the Linnean Society. Linnean Society of London* **21**, 229–242. doi:10.1111/J.1095-8312.1984.TB02064.X

Palmer, M. W. (1990). The estimation of species richness by extrapolation. *Ecology* **71**, 1195–1198. doi:10.2307/1937387

R Core Team (2011). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramage, T. (2017). Checklist of the terrestrial and freshwater arthropods of French Polynesia (Chelicerata; Myriapoda; Crustacea; Hexapoda). *Zoosystema* **39**, 213–225. doi:10.5252/Z2017N2A3

Rapp, G. (1999). Introduction of the fire ant *Wasmannia auropunctata* into Vanuatu. *Ag Alert* **18**, 1.

Raymundo, M. L., and Miller, R. H. (2012). Little fire ant, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae), established at several locations on Guam. *Proceedings of the Hawaiian Entomological Society* **44**, 85–87.

Roque-Albelo, L., Causton, C., and Mieles, A. (2000). The ants of Machena Island, twelve years after the introduction of the little fire ant *Wasmannia auropunctata*. *Noticias De Galapagos* **61**, 17–20.

Seguin, F. (2015). L'état de l'environnement en Polynésie française 2007/2014. Technical Report DIREN, Papeete. Available at: http://creocean.fr/sites/default/files/Diren-etat-environnement-integral.pdf [accessed 19 October 2018].

Spencer, H. (1941). The small fire ant *Wasmannia* in citrus groves – a preliminary report. *The Florida Entomologist* **24**, 6–14. doi:10.2307/3492285

Sutherst, R. W., Maywald, G. F., and Skarratt, D. B. (2005). A climate model for the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): implications for invasion of new regions, particularly Oceania. *Environmental Entomology* **34**, 317–335. doi:10.1603/0046-225X-34.2.317

Vanderwoude, C. (2008). Operational plan for management of *Wasmannia auropunctata* (little fire ant) in East Sepik Province, Papua New Guinea. VCL, New Zealand.

Vanderwoude, C., Onuma, K., and Reimer, N. (2010). Eradicating *Wasmannia auropunctata* (Hymenoptera: Formicidae) from Maui, Hawaii: the use of combination treatments to control an arboreal invasive ant. *Proceedings of the Hawaiian Entomological Society* **42**, 23–31.

Vanderwoude, C., Haynes, D., Richards, E., Quinquis, B., Moverley, D., and Skelton, P. (2014). Managing the impacts of the little fire ant (*Wasmannia auropunctata*) in French Polynesia. Secretariat of the Pacific Regional Environmental Programme, Apia, Samoa.

Vanderwoude, C., Montgomery, M. P., Forester, H., Hensley, E., and Adachi, M. K. (2016). The history of little fire ant *Wasmannia auropunctata* Roger in the Hawaiian islands: spread, control, and local eradication. *Proceedings of the Hawaiian Entomological Society* **48**, 39–50.

Vonshak, M., Dayan, T., and Hefetz, A. (2012). Interspecific displacement mechanisms by the invasive little fire ant *Wasmannia auropunctata*. *Biological Invasions* **14**, 851–861. doi:10.1007/S10530-011-0122-8

Wetterer, J. K., and Porter, S. D. (2003). The little fire ant, *Wasmannia auropunctata*: distribution, impact, and control. *Sociobiology* **42**, 1–42.

Williams, D. F., and Whelan, P. M. (1992). Bait attraction of the introduced ant *Wasmannia auropunctata* (Hymeoptera: Formicidae) in the Galapagos Islands. *Journal of Entomological Science* **27**, 29–34. doi:10.18474/0749-8004-27.1.29

Wilson, E. O., and Taylor, R. W. (1967*a*). The ants of Polynesia. *Pacific Insects Monograph* **14**, 1–109.

Wilson, E. O., and Taylor, R. W. (1967*b*). An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. *Evolution* **21**, 1–10. doi:10.1111/J.1558-5646.1967.TB00125.X