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Ecology of some lesser-studied introduced ant species in Hawaiian forests

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Abstract Invasive ants can have strong ecological effects on native arthropods, but most information on this topic comes from studies of a handful of ant species. The ecological impacts of the many additional introduced 'tramp' ant species are largely unknown. In mesic upland forests of O'ahu, Hawai'i, ten species of introduced ants were found on four species of understory trees. However, these ants were generally uncommon and occurred at relatively low densities in this habitat type. The most common and abundant ant was *Plagiolepis alluaudi*, which favored the native tree *Pipturus albidus*. Ecological effects of ants on arthropods were found to be modest, with overall arthropod community composition not significantly different between ant-occupied and ant-free trees. Most taxonomic groups were similar in abundance and richness between ant-occupied and ant-free trees, except adventive Coleoptera, adventive Hemiptera, and Lepidoptera were less abundant on ant-occupied trees, and adventive Coleoptera and adventive Hemiptera also had lower richness on ant-occupied trees. Among Lepidoptera, caterpillars of two endemic groups had significantly lower incidences on trees with higher ant abundances, while other caterpillars did not. Arthropod trophic structure was largely unaffected, except that chewing herbivores comprised a smaller fraction of biomass on ant-occupied trees. While overall ecological effects were weak in comparison to prior results involving other ant species in Hawai'i, some of the impacts suggest that higher densities of these introduced ant species could result in similar interactions with arthropods as those of the better-studied invasive ant species.

Keywords Invasive ants · Introduced ants · Tramp ants · Hawai'i · Ecological impacts

Introduction

Invasive ants are recognized to be among the most ecologically damaging groups of invasive organisms. Their strong impacts on native ants are well-documented, and a smaller body of work indicates that they can also have dramatic effects on non-ant arthropods in some situations (e.g., Cole et al. 1992; Porter and Savignano 1990; Human and Gordon 1997; Hoffmann et al. 1999; Bolger et al. 2000). However, the vast majority of information about the ecological effects of invasive ants stems from studies on just five or six species (Holway et al. 2002; Lach and Hooper-Bùi 2010): the Argentine Ant (*Linepithema humile*), the Red Imported Fire Ant (*Solenopsis invicta*), the Tropical Fire Ant (*Solenopsis geminata*), the Big-headed Ant (*Pheidole megacephala*), the Yellow Crazy Ant (*Anoplolepis gracilipes*), and the Little Fire Ant (*Wasmannia auropunctata*). Yet, many other ant species have been introduced beyond their native ranges, often to many locales, and these introduced species are sometimes termed 'tramp ants' (Passera 1994; McGlynn 1999). Much less is known about how the latter group of ants may impact native arthropods.

The ecological effects of introduced tramp ants on native arthropods are rarely studied in part because they often do not spread far beyond human modified or otherwise disturbed habitats (Krushelnycky et al. 2010). This

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attribute has often led to their exclusion from the relatively small group of ants labelled ‘invasive’, which by some definitions are characterized by an ability to penetrate and produce ecological impacts in undisturbed ecosystems distant from their point of introduction, by virtue of their high densities and aggressive behavior (Holway et al. 2002; Lach and Hooper-Bùi 2010). However, most workers also recognize that this distinction between introduced and invasive ant species is not always clear, and that most species exhibit a range of population densities and invasiveness depending on local circumstances (Krushelnycky et al. 2010). Situations in which introduced tramp ants have spread into native habitats therefore offer an opportunity to compare the ecology and potential impacts of these species with those of the small group of better-studied invasive ant species listed above (e.g. Lach et al. 2010).

Nearly 60 species of ants have now been introduced to Hawai‘i (Krushelnycky 2015). The majority of these are most successful in lower elevation habitats (Reimer 1994), which in Hawai‘i are typically highly altered by urbanization, agricultural conversion, or non-native vegetation. Some introduced ant species can be found in more intact mesic upland forests, however, prior observations suggest that ants in general have difficulty attaining high densities in Hawaii’s montane forest ecosystems (Krushelnycky et al. 2005; Buczkowski and Krushelnycky 2012), perhaps because of temperature constraints under closed canopy, or perhaps owing to a shortage of nectar or honeydew that is often associated with high invasive ant densities (Helms and Vinson 2002; O’Dowd et al. 2003; Ness and Bronstein 2004; Tillberg et al. 2007; Wilder et al. 2011). In comparison, more open woodland or shrubland habitats, exposed ridgelines and other canopy gaps, and lower elevation habitats have generally been much more invasible by ants in Hawai‘i. Nevertheless, the occasional occurrence of ants in the interiors of upland forest habitats raises a question about their potential ecological effects in these areas. I took advantage of a situation in which a variety of introduced ant species appeared to be patchily distributed on understory trees in mesic montane forests on O‘ahu, to assess the incidence and possible ecological effects of these ants on native and introduced arthropod communities.

Materials and methods

Study site and sampling methods

Sampling was conducted in mesic forests in two adjacent management areas, Kahanahāiki Valley and Pahole Natural Area Reserve (NAR), which together encompass several valleys in the northern Wai‘anae Mountains, O‘ahu Island, Hawai‘i. Both areas are comprised of mixed stands of native and alien canopy and understory trees, are located at approximately 500–650 m elevation, and receive approximately 1200–1400 mm of annual rainfall (Giambelluca et al. 2013). Four understory tree species that are common along the central gulches of both areas were selected for arthropod sampling; these included three native trees (*Pipturus albidus*, *Charpentiera tomentosum* and *Pisonia umbellifera*) and one alien tree (*Psidium cattleianum*). I chose eight individuals of each species in each area in a stratified random fashion, such that they spanned the majority of the length of the central gulch in each area, for a total of 64 study trees. During each of six sampling events, I beat each tree five times with a rod while holding a 1 × 1 m beating sheet underneath. All arthropods dislodged were aspirated and stored in ethanol. The six sampling events spanned 3 years, and occurred during the summer of 2009 (5/2/09 and 6/23/09), winter of 2009 (12/14–12/15/2009), summer of 2010 (5/7/10 and 6/23/10), winter of 2010 (12/14–12/15/10), summer of 2011 (5/12/11 and 6/23/11) and summer of 2012 (5/10/12 and 6/26/12).

A total of 384 samples were thus collected, and all arthropods (n = 15,319) were subsequently sorted and identified to various taxonomic levels. Individual Isopoda, Acari, parasitic Hymenoptera, Lepidoptera, Diptera, Psocoptera, and Collembola were counted but not sorted further, with the exception of several endemic groups that were identified to species or morphospecies. For the remainder of taxonomic groups, all individuals were identified to the level of species or morphospecies, with the exception of diverse *Proterhinus* beetles that were lumped by genus and several families that were not further identified (Staphylinidae, Aphididae, Aleyrodidae, Pseudococcidae, Coccidae). Some immature individuals could be definitively identified to species, while others were assigned to species according to the relative proportions of adult individuals in the same genus or family in the sample, if possible. The identities of remaining immatures were retained at higher taxonomic levels. All individuals were then designated as native to Hawaii, adventive (accidentally or purposely introduced), or of unknown provenance based on Nishida (2002) and taxonomic literature. For the purposes of richness estimates, the lowest taxonomic unit available was used for each group. For example, all Psocoptera were treated as a single taxonomic unit, while species designations were used for Araneae.

Biomass estimates were made by measuring the length of up to ten individuals (if available) of taxa identified to species, and using the means in regression relationships of biomass on length reported in Gruner (2003). For taxa that were more variable in size, averages were taken from 30 individuals (for immature Araneae, immature Theridiidae, immature Coleoptera, Diplopoda, Staphylinidae, Aphididae) or 100 individuals (Acari, Collembola, Diptera, parasitic Hymenoptera, Lepidoptera, Psocoptera, Thysanoptera, Isopoda). To analyze trophic structure, I assigned each taxon to its predominant trophic role (carnivore, herbivore, detritivore, omnivore/unknown) based on reports in the literature or expert knowledge. Herbivores where further classified by feeding guilds (chewers, sap feeders, mesophyll feeders, gall formers, seed feeders, pollen feeders, xylophages).

Ant effects

I compared ant incidence rates on the four tree species with a Chi Square contingency table. Samples with more than one to several ants occurred predominantly on two tree species, *P. albidus* and *C. tomentosum* (see "Results" section). Consequently, I assigned all individual trees of these two species that had five or more sampled ants during one or more sampling events as 'ant-occupied trees' (n = 16). These 16 trees had ≥5 ants in a total of 29 samples. I then paired each of these 29 samples with samples from the nearest tree (matched by species, gulch, and date) that had <5 ants during *all* sampling events ('ant-free trees'). For analyses, data from multiple sampling events for the same tree were averaged, to yield a dataset of 16 independent ant-occupied and ant-free tree comparisons. Mean ant abundance (all ant species combined) per sample was 17.0 (median = 10.7) on the ant-occupied trees, compared to 0.5 per sample (median = 0) on the ant-free trees. Ant-free and ant-occupied tree pairs were distributed across the full length of each gulch, such that ant presence or absence was not clumped in any particular area in each gulch, and microhabitat differences associated with ant presence or absence were not apparent.

To assess potential effects of ants on non-ant arthropods, I first used multivariate multi-response permutation procedure (MRPP) to compare the assemblages of species on the ant-free versus ant-occupied trees (n = 123 taxa in the dataset, all ant species excluded). I used Sorenson distance measures on taxon abundance data that were log-transformed and relativized by sample totals; this reduces the influence of very abundant species (McCune and Grace 2002). I subsequently compared ordinal-level abundances on ant-free trees with those on the paired ant-occupied trees using a Mann–Whitney test. In the same manner, I also compared abundances of native and adventive subsets for all orders that were identified to the level of species and that included native and adventive species. For Hemiptera, I made additional comparisons for sap-feeding taxa that often or usually produce honeydew (grouping families Aleyrodidae, Aphididae, Cicadellidae, Cixiidae, Delphacidae, Flatidae, Pseudococcidae, Psyllidae, Tingidae, Tropiduchidae) and non-sap-feeding taxa that do not produce honeydew (grouping families Anthocoridae, Derbidae, Lygaeidae, Miridae, Nabidae, Reduviidae, Rhyparochromidae, Saldidae), to assess whether ant presence may be associated with higher densities of honeydew-producing Hemiptera.

I compared species richness on ant-free and ant-occupied trees, with a Mann–Whitney test, for the orders Araneae, Coleoptera, Hemiptera and for all Arthropoda. The remaining orders were not identified to species level or had too few species for meaningful comparison. For this analysis, I generated the same 16 independent comparisons described above for the arthropod abundance analysis. Using the same 16 comparisons, I also compared trophic structure on ant-free and ant-occupied trees: I compared percent composition, with a Mann–Whitney test, of carnivore biomass, herbivore biomass, detritivore biomass, and omnivore/unknown biomass between the two groups, with ants excluded from the biomass calculations. I also compared percent composition of herbivores by the largest feeding guilds: chewers, sap feeders, and all other guilds combined.

Because abundances of Lepidoptera were lower on ant-free trees (see "Results" section), I explored this pattern further using the entire dataset, to see if ant presence was associated with lower incidences of several groups of native Lepidoptera. I compared the incidence rates (presence/absence) of two groups of native Lepidoptera [*Hyposmocoma* spp. caterpillars (Cosmopterigidae), and *Eupithecia orichloris* caterpillars (Geometridae)] in samples that had <5 ants (n = 351) with samples that had ≥5 ants (n = 33), using Fisher's exact test. For a third native Lepidoptera species [*Udara blackburni* caterpillars (Lycaenidae)], I compared incidence rates on *P. albidus* trees only (n = 75 samples with <5 ants, n = 21 samples with ≥5 ants), because the other trees in the study are not used as hosts. Finally, I compared incidence rates of all remaining immature Lepidoptera not belonging to the three groups above; these were not identified beyond order (n = 351 samples with <5 ants, n = 33 samples with ≥5 ants).

The MRPP analysis was conducted in PC-ORD 5.0; all other analyses were conducted in Minitab 17.0.

Results

A total of 714 ants belonging to 10 species were collected in the 384 samples. In order of decreasing total abundance, these were (n): *Plagiolepis alluaudi* (491), *Cardiocondyla obscurior* (81), *Technomyrmex albipes* (71), *Solenopsis papuana* (25), *Nylanderia bourbonica* (16), *Technomyrmex vitiensis* (14), *Ochetellus glaber* (8), *Tapinoma melanocephalum* (6), *Cardiocondyla emeryi* (1) and *Hypoponera punctatissima* (1). Most samples (65.9 %, n = 253) had no ants. Among all ant occurrences, 86.2 % (n = 113) included a single species, 9.9 % (n = 13) included two species, and 3.8 % (n = 5) included three species. Ant occurrences (n = 131) were not evenly distributed across the four tree species ($\chi^2 = 20.334$, $p < 0.001$, Fig. 1a). Occurrences of ≥5 and ≥10 ants per sample were even less common (n = 33 and 15, respectively), and were limited almost completely to *P. albidus* and *C. tomentosum* trees (Fig. 1a). Total ant abundances were also higher on these two trees, especially *P. albidus* (Fig. 1b). Occurrences of ≥5 ants of a given species per sample (n = 30) were dominated by *P. alluaudi*, followed by *T. albipes* and *C. obscurior* (Fig. 2). The three highest sample abundances (30, 97 and 118 ants) were exclusively comprised of *P. alluaudi*. Ant presence on the study trees was usually inconsistent over time. Of the 16 *P. albidus* and *C. tomentosum* trees categorized as ant-occupied, one tree had ants in five of the six samples over the 3 year period, four other trees had ants in three of six samples, and the remaining 11 trees had ants in only one or two of six samples.

Multivariate analysis found no significant difference between the overall arthropod assemblages on ant-occupied versus ant-free *P. albidus* and *C. tomentosum* trees [MRPP, $T = -0.510$, A (effect size) = 0.004, $p = 0.232$]. Similarly, ant-occupied trees were not associated with lower or higher abundances of most arthropod groups when compared to paired ant-free trees (Table 1). Exceptions were adventive Coleoptera, adventive Hemiptera, Lepidoptera, and adventive arthropods as a whole, all of which occurred at significantly lower abundances on ant-occupied trees (Table 1). In a follow-up assessment of lepidopteran incidence rates that included all tree species and all samples, native *Hyposmocoma* caterpillars occurred significantly more often in samples with <5 ants (22.5 % incidence) than in samples with ≥5 ants (3.0 % incidence; Fisher's exact test, $p = 0.006$). Native *E. orichloris* caterpillars were marginally significantly more common in samples with <5 ants (10.0 % incidence) than in samples with ≥5 ants (0 % incidence; $p = 0.058$). In contrast, native *U. blackburni* caterpillars did not occur significantly more often in samples with <5 ants (10.7 % incidence) than in samples with ≥5 ants (4.8 % incidence; $p = 0.678$). Similarly, incidence rates of remaining unidentified Lepidoptera caterpillars were not higher in samples with <5 ants (8.5 %) than in sample with ≥5 ants (6.1 %; $p = 1.000$).

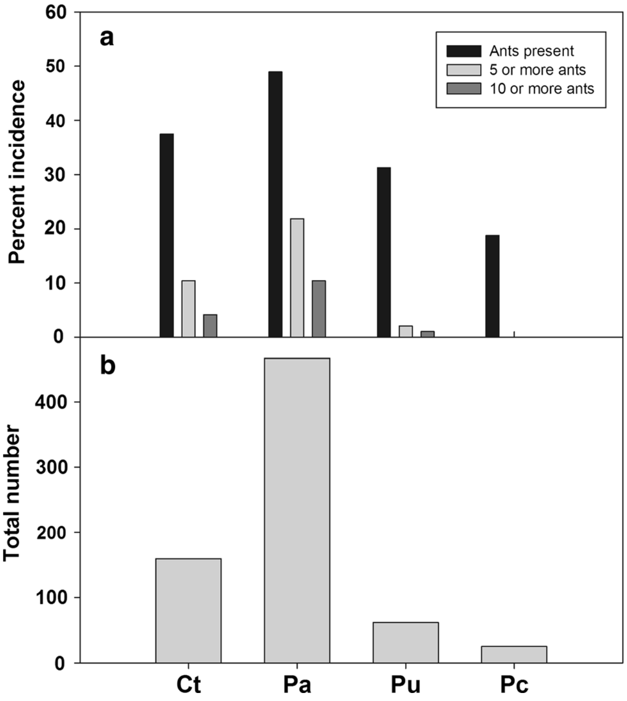

Fig. 1 Percent incidence (**a**) and total numbers (**b**) of ants on the four tree species sampled. Ct: *Charpentiera tomentosum*; Pa: *Pipturus albidus*; Pu: *Pisonia umbellifera*; Pc: *Psidium cattleianum*

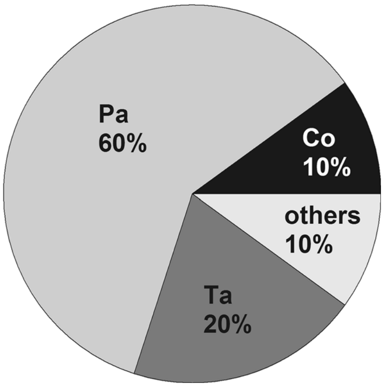

Fig. 2 Ant species representation among sample occurrences with ≥5 ants (n = 30). Pa: *Plagiolepis alluaudi*; Co: *Cardiocondyla obscurior*; Ta: *Technomyrmex albipes*

Patterns in arthropod species richness on ant-free versus ant-occupied trees mirrored those of arthropod abundances. For most groups, there were no significant differences in richness, but richness was significantly lower on ant-occupied trees for adventive Coleoptera, adventive Hemiptera, and adventive Arthropoda overall (Table 2). Trophic structure was not significantly different between ant-free and ant-occupied trees for major trophic groups (Fig. 3). Among herbivores, however, the leaf chewer guild made up a smaller percentage of overall biomass on ant-occupied trees compared to ant-free trees (Mann–Whitney, $p = 0.009$), while sap feeders and other guilds did not differ significantly between ant-occupied and ant-free trees (Fig. 3).

Discussion

Ants were relatively rare on understory trees in these mesic forest montane sites of O'ahu. While ten different species were collected, only about one-third of samples had any ants, and less than 10 % had five or more ants. Ant

Table 1 Mann–Whitney test results comparing abundances of various arthropod groups on ant-free and ant-occupied trees. Comparisons with p values less than 0.05 marked in bold

Taxonomic group	Ant-free median	Ant-occupied median	p
Diplopoda	0.00	0.00	0.655
Isopoda	0.00	0.00	0.455
Acari	0.75	1.00	0.455
Araneae (all)	2.25	2.00	0.806
Nat[a] Araneae	0.75	1.00	0.969
Adv[b] Araneae	0.43	1.00	0.162
Blattodea	0.00	0.00	0.279
Coleoptera (all)	2.43	2.00	0.280
Nat Coleoptera	1.00	1.00	0.519
Adv Coleoptera	1.50	0.33	**0.037**
Collembola	3.90	10.80	0.079
Diptera	0.00	0.00	0.615
Hemiptera (all)	8.67	9.67	0.534
Nat Hemiptera	8.00	9.50	0.385
Adv Hemiptera	1.00	0.00	**0.011**
Sap[c] Hemiptera	3.17	3.90	0.462
Non-sap[d] Hemiptera	3.50	1.10	0.177
Hymenoptera (non-ants)	0.17	0.00	0.370
Lepidoptera	0.37	0.00	**0.021**
Orthoptera	0.00	0.00	0.081
Psocoptera	1.00	2.00	0.137
Thysanoptera	0.00	0.75	0.118
Arthropoda[e]	29.37	43.00	0.122
Nat Arthropoda	12.10	12.50	0.497
Adv Arthropoda	3.90	2.00	**0.033**

[a] Native species

[b] Adventive species

[c] Sap-feeding Hemiptera that often or usually produce honeydew

[d] Non-sap-feeding Hemiptera that do not produce honeydew

[e] Totals of all arthropods excluding ants

presence on individual trees appeared to be unpredictable and in most cases was ephemeral. Because the sampling was conducted over a period of 3 years, these results may be somewhat indicative of general patterns in ant incidence and densities in these habitat types. It should be noted, however, that subsequent to the end of this study, the Yellow Crazy Ant (*A. gracilipes*) became established within one portion of the study site characterized by larger canopy gaps, and other such exceptions may occur. Furthermore, *S. papuana*, which was uncommon in arboreal samples in this study, can reach much higher densities on the floor of closed canopy mesic and wet forests (Gillespie and Reimer 1993; Reimer 1994), including at this site (C. Ogura-Yamada and P. Krushelnycky unpubl. data). Finally, warmer and drier conditions, which are predicted for the Wai‘anae Mountains (Elison Timm et al. 2015), could make these forests more accessible to ants in the future.

When ants did occur on trees in this system, both total abundances and incidence rates were dominated by *P. alluaudi*. Ants, including *P. alluaudi*, preferred *C. tomentosum* and especially *P. albidus* trees over the other tree species sampled. Both of these trees produce inconspicuous flowers that appear to produce little or no nectar, and lack extra-floral nectaries (Keeler 1985), so ants may be attracted to these two trees because they both support species of endemic sap-feeding delphacid planthoppers, while the other two trees do not. Other ant species (*L. humile* and *P. megacephala*) have been observed to collect the honeydew cast off by native planthoppers onto their host plants in Hawai‘i, and to show little or no aggression towards these insects despite not actively tending them (Krushelnycky 2007). *Plagiolepis alluaudi* is also commonly associated with honeydew-producing Hemiptera (Wetterer 2014). A similar dynamic may therefore exist in the present study system, although if so it did not result in

Table 2 Mann–Whitney test results comparing species richness of various arthropod groups on ant-free and ant-occupied trees. Comparisons with p values less than 0.05 marked in bold

Taxonomic group	Ant-free median	Ant-occupied median	p
Araneae (all)	1.58	1.53	0.970
Nat[a] Araneae	0.65	1.00	1.000
Adv[b] Araneae	0.35	1.00	0.174
Coleoptera (all)	2.00	2.00	0.195
Nat Coleoptera	1.00	1.00	0.463
Adv Coleoptera	1.17	0.33	**0.042**
Hemiptera (all)	2.50	2.00	0.243
Nat Hemiptera	2.00	2.00	0.894
Adv Hemiptera	0.83	0.00	**0.010**
Arthropoda[c]	10.10	9.30	0.485
Nat Arthropoda	4.00	3.67	0.650
Adv Arthropoda	3.17	1.80	**0.034**

[a] Native species

[b] Adventive species

[c] Totals of all arthropods excluding ants

higher abundances of sap-feeding Hemiptera on ant-occupied individuals of the two preferred tree species, or in higher percent composition of sap-feeding herbivore biomass on ant-occupied trees.

In fact, there was generally only relatively modest evidence for ecological effects on arthropod communities by the ants in this system, at least in comparison to some of the more dramatic impacts reported for other ants in other Hawaiian ecosystems (Cole et al. 1992; Gillespie and Reimer 1993; Krushelnycky and Gillespie 2008, 2010) and elsewhere (Holway et al. 2002; Lach and Hooper-Bùi 2010). Non-ant species assemblages, taken as a whole, were not significantly different between ant-free and ant-occupied individuals of *P. albidus* and *C. tomentosum* trees, and in most cases ordinal-level arthropod abundances and species richness also did not appear to be strongly affected by ant presence. Trophic structure was also similar between ant-free and ant-occupied trees, with the exception that leaf-chewing herbivores comprised a smaller percentage of overall biomass on ant-occupied trees, which could result in a net benefit for these trees. An increase in plant fitness caused by the suppression of non-honeydew-producing herbivores is a possible outcome in situations where ants are attracted to honeydew-producing hemipterans (Styrsky and Eubanks 2007), although Lach and Hooper-Bùi (2010) concluded that it may be rare outside of agricultural settings involving *S. invicta*.

Despite an absence of large compositional differences in arthropod communities associated with ant presence, abundances and species richness of several groups were lower on ant-occupied trees. Inspection of species-level patterns suggests that the lower abundances of adventive beetles on ant-occupied trees resulted mainly from lower numbers of several species of coccinellid beetles, which as a group typically prey on sap-feeding Hemiptera, and consequently are commonly attacked by guard ants (Bartlett 1961; Bach 1991; González-Hernández et al. 1999). Among adventive Hemiptera, lower numbers among a wider range of species, including members of Cicadellidae,

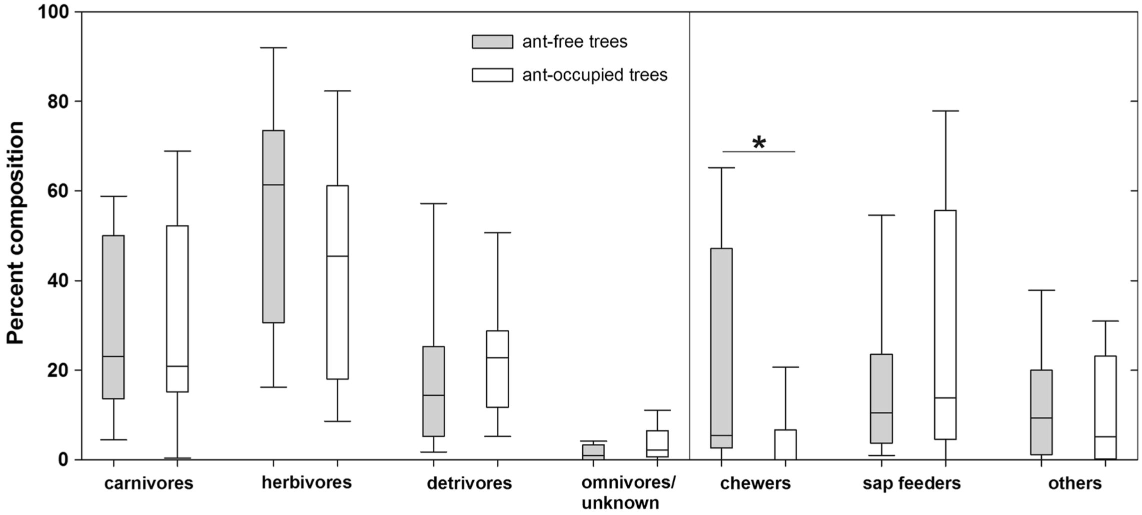

Fig. 3 Trophic structure on ant-free and ant-occupied *P. albidus* and *C. tomentosum* trees, in percent composition of total biomass (excluding ants). *Left panel* shows major trophic groups, *right panel* shows composition of main herbivore feeding guilds: leaf chewers, sap feeders, and all other guilds combined. Only leaf chewers were significantly different between ant-free and ant-occupied trees ($p = 0.009$). *Box plots* show median and 25th and 75th percentiles, *whiskers* show 5th and 95th percentiles

Miridae and Tingidae, appear to have contributed to the lower overall abundances on ant-occupied trees.

Most Lepidoptera captured were caterpillars, and as a group also occurred at lower abundances on ant-occupied trees. When considering the entire dataset, incidence rates of caterpillars of two endemic groups were significantly higher in samples with less than five ants than in samples with five or more ants. One of these groups (*Hyposmocoma* spp.), is a hyper-diverse radiation of case-making species that can occur in relatively high densities and in a wide range of habitat types (Haines et al. 2014). These characteristics suggest that this group may be somewhat resistant to certain types of invasive species pressures, but in this system they appeared to be very sensitive to ant presence (22.5 % incidence in samples with <5 ants vs. 3 % in samples with ≥5 ants). Caterpillars of another endemic species, *E. orichloris*, belong to a group of ambush predators, a behavior that may be unique among Lepidoptera worldwide (Montgomery 1982). These caterpillars were absent from samples with five or more ants, compared to an incidence rate of 10 % in samples with <5 ants, a difference that was marginally statistically significant. In contrast, caterpillars of the endemic lycaenid butterfly *U. blackburni* were not significantly less common in samples with higher ant densities. Unlike many lycaenid species, *U. blackburni* caterpillars do not have specialized organs for secreting nutritional exudates for ants, and are not known to be tended by ants. However, a variety of other adaptations for appeasing and tolerating ants are possessed by nearly all lycaenids, even if they don't form mutualistic associations with them (Pierce et al. 2002), and this may explain the apparent lower sensitivity to ants by *U. blackburni*. All remaining unidentified caterpillars had similar incidence rates in samples with <5 and ≥5 ants. It is unknown what proportion of these caterpillars may have been native to Hawai‘i.

It is notable that certain groups of native arthropods previously found to be especially vulnerable to invasive ants, such as spiders and beetles (Cole et al. 1992; Gillespie and Reimer 1993; Krushelnycky and Gillespie 2010), showed no evidence of lower abundances or diversity when co-occurring with ants in this study. The reasons for this discrepancy are unclear, however, the modest signs of ecological impact found here, particularly among native species, may simply be a consequence of the relatively low densities of ants that occurred in this system, rather than an indication of behavioral differences with other invasive ant species. For instance, the sensitivity of some native Lepidoptera to even relatively low densities of ants in this study matches reports of lepidopteran vulnerability to other invasive ant species, such as *L. humile* (Cole et al. 1992; Abril et al. 2007; Rowles and O'Dowd 2009; Estany-Tigerstrom et al. 2010; Krushelnycky and Gillespie 2010), *S. invicta* (Eubanks 2001; Vogt et al. 2001), *S. geminata* (Way et al. 1998), *A. gracilipes* (Holway et al. 2002) and *P. megacephala* (Bach 1991). Such similarities could support the hypothesis that tramp ant species may not differ substantially from some of the better-studied invasive ants in the nature of their interactions with other arthropods, and that the ecological impacts of many introduced ant species may largely be a function of their density.

In this view, conditions that promote higher densities of ant species that are not usually considered to be severely damaging could thus lead to ecological effects that are of greater concern. The most common and abundant species in this study, *P. alluaudi*, has been recorded from 46 geographic areas, including many of the world's tropical and subtropical islands (Wetterer 2014). While ecological information on this species is sparse, most reports describe it as a pest in urban and greenhouse settings (Wetterer 2014). However, in certain situations it has been reported to defend baits or avoid territorial displacement when encountering other highly invasive and dominant ant species like *P. megacephala* and *W. auropunctata* (Burwell et al. 2012; Le Breton 2003 cited in Wetterer 2014). Similarly, the second most common species in this study, *T. albipes*, is a well-known urban pest (Bolton 2007), but has also been found to exert strong ecological effects in some natural areas (Gaume et al. 2005; Hansen and Müller 2009; Lach et al. 2010). The results of this study provide some additional evidence that the distinction between introduced tramp ants and invasive ants is not rigid and is likely subject to some degree of context dependency.

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References

Abril S, Oliveras J, Gómez C (2007) Foraging activity and dietary spectrum of the Argentine ant (Hymenoptera: Formicidae) in invaded and natural areas of the northwest Iberian Peninsula. Environ Entomol 36:1166–1173

Bach CE (1991) Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). Oecologia 87:233–239

Bartlett BR (1961) The influence of ants upon parasites, predators, and scale insects. Ann Entomol Soc Am 54:543–551

Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ (2000) Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecol Appl 10:1230–1248

Bolton B (2007) Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker cast. Contrib Am Entomol Inst 35:1–150

Buczkowski G, Krushelnycky P (2012) The odorous house ant, *Tapinoma sessile* (Hymenoptera: Formicidae), as a new temperate-origin invader. Myrmecol News 16:61–66

Burwell CJ, Nakamura A, McDougall A, Nelder VJ (2012) Invasive African big-headed ants, *Pheidole megacephala*, on coral cays of the southern Great Barrier Reef: distribution and impacts on other ants. J Insect Conserv 16:777–789

Cole FR, Medeiros AC, Loope LL, Zuehlke WW (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology 73:1313–1322

Elison Timm O, Giambelluca TW, Diaz HF (2015) Statistical downscaling of rainfall changes in Hawai‘i based on the CMIP5 global model projections. J Geophys Res Atmos 120:92–112

Estany-Tigerstrom D, Maria Bas J, Pons P (2010) Does Argentine ant invasion affect prey availability for foliage-gleaning birds? Biol Invasions 12:827–839

Eubanks MD (2001) Estimates of the direct and indirect effects of Red Imported Fire ants on biological control in field crops. Biol Control 21:35–43

Gaume L, Zacharias M, Grosbois V, Borges RM (2005) The fitness consequences of bearing domatia and having the right ant partner: experiments with protective and non-protective ants in a semi-myrmecophyte. Oecologia 145:76–86

Giambelluca TW, Chen Q, Frazier AG, Price JP, Chen YL, Chu PS, Eischeid JK, Delparte DM (2013) Online rainfall atlas of Hawai‘i. Bull Am Meteor Soc 94:313–316. doi:10.1175/BAMS-D-11-00228.1

Gillespie RG, Reimer NJ (1993) The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). Pac Sci 47:21–33

González-Hernández H, Johnson MW, Reimer NJ (1999) Impact of *Pheidole megacephala* (F.) (Hymenoptera: Formicidae) on the biological control of *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae). Biol Control 15:145–152

Gruner DS (2003) Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. Pac Sci 57:325–336

Haines WP, Schmitz P, Rubinoff D (2014) Ancient diversification of *Hyposmocoma* moths in Hawai‘i. Nat Commun. doi:10.1038/ncomms4502

Hansen DM, Müller CB (2009) Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. Biotropica 41:202–208

Helms KR, Vinson SB (2002) Widespread association of the invasive ant *Solenopsis invicta* with an invasive mealybug. Ecology 83:2425–2438

Hoffmann BD, Andersen AN, Hill GJE (1999) Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. Oecologia 120:595–604

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. Annu Rev Ecol Evol Syst 33:181–233

Human KG, Gordon DM (1997) Effects of Argentine ants on invertebrate biodiversity in northern California. Conserv Biol 11:1242–1248

Keeler KH (1985) Extrafloral nectaries on plants in communities without ants: Hawai‘i. Oikos 44:407–414

Krushelnycky PD (2007) The effects of invasive ants on arthropod species and communities in the Hawaiian Islands. Dissertation, University of California, Berkeley

Krushelnycky PD (2015) AntWeb: Hawai‘i ants. http://www.antweb.org/page.do?name=hawaii. Accessed 28 June 2015

Krushelnycky PD, Gillespie RG (2008) Compositional and functional stability of arthropod communities in the face of ant invasions. Ecol Appl 18:1547–1562

Krushelnycky PD, Gillespie RG (2010) Correlates of vulnerability among arthropod species threatened by invasive ants. Biodivers Conserv 19:1971–1988

Krushelnycky PD, Loope LL, Reimer NJ (2005) The ecology, policy, and management of ants in Hawai‘i. Proc Hawaii Entomol Soc 37:1–25

Krushelnycky PD, Holway DA, LeBrun EG (2010) Invasion processes and causes of success. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University Press, Oxford, pp 245–260

Lach L, Hooper-Bùi LM (2010) Consequences of ant invasions. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University Press, Oxford, pp 261–286

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

Le Breton J (2003) Étude des interactions entre la fourmi *Wasmannia auropunctata* et la myrmécofaune. Comparison d’une situation en zone d’introduction: la Nouvelle-Calédonie et d’une situation en zone d’origine: la Guyane Française. Thesis, Université de Toulouse III

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

McGlynn TP (1999) The worldwide transfer of ants: geographic distribution and ecological invasions. J Biogeogr 26:535–548

Montgomery SL (1982) Biogeography of the moth genus *Eupithecia* in Oceania and the evolution of ambush predation in Hawaiian caterpillars (Lepidoptera: Geometridae). Entomol Gen 8:27–34

Ness JH, Bronstein JL (2004) The effects of invasive ants on prospective ant mutualists. Biol Invasions 6:445–461

Nishida GM (2002) Hawaiian terrestrial arthropod checklist, 4th edn. Bishop Museum Press, Honolulu

O’Dowd DJ, Green PT, Lake PS (2003) Invasional ‘meltdown’ on an oceanic island. Ecol Lett 6:812–817

Passera L (1994) Characteristics of tramp species. In: Williams DF (ed) Exotic ants: biology, impact and control of introduced species. Westview Press, Boulder, pp 23–43

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant associations in the Lyceanidae (Lepidoptera). Annu Rev Entomol 47:733–771

Porter SD, Savignano DA (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71:2095–2106

Reimer NJ (1994) Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: Williams DF (ed) Exotic ants: biology, impact and control of introduced species. Westview Press, Boulder, pp 11–22

Rowles AD, O’Dowd DJ (2009) Impacts of the invasive Argentine ant on native ants and other invertebrates in coastal scrub in south-eastern Australia. Aust Ecol 34:239–248

Styrsky JD, Eubanks MD (2007) Ecological consequences of interactions between ants and honeydew-producing insects. Proc R Soc B 274:151–164

Tillberg CV, Holway DA, LeBrun EG, Suarez AV (2007) Trophic ecology of invasive Argentine ants in their native and introduced ranges. Proc Natl Acad Sci USA 104:20856–20861

Vogt JT, Grantham RA, Smith WA, Arnold DC (2001) Prey of the Red Imported Fire Ant (Hymenoptera: Formicidae) in Oklahoma peanuts. Environ Entomol 30:123–128

Way MJ, Islam Z, Heong KL, Joshi RC (1998) Ants in tropical irrigated rice: distribution and abundance, especially of

Solenopsis geminata (Hymenoptera: Formicidae). Bull Entomol Res 88:467–476

Wetterer JK (2014) Worldwide spread of Alluaud's little yellow ant, *Plagiolepis alluaudi* (Hymenoptera: Formicidae). Myrmecol News 19:53–59

Wilder SM, Holway DA, Suarez AV, LeBrun EG, Eubanks MD (2011) Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasions. Proc Natl Acad Sci USA 108:20639–20644