

**ECOLOGICAL EFFECTS OF *SOLENOPSIS PAPUANA* ON INVERTEBRATE
COMMUNITIES IN O'AHU FORESTS**

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By

Cassandra S. Ogura-Yamada

Thesis Committee:

Paul Krushelnycky, Chairperson

William Haines

Helen Spafford

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ABSTRACT

The thief ant, *Solenopsis papuana*, is the most common invasive ant found in upper elevations of mesic forests of O‘ahu, raising concerns about its ecological impacts in these areas. I developed monitoring and control methods to measure and reduce *S. papuana* densities in experimental field plots, and subsequently assessed invertebrate community responses to this ant suppression six months and one year later, using leaf litter and pitfall sampling methods. Responses in overall community composition, species richness, and abundances of taxa were mixed, but altogether, suggest that *S. papuana* has broad but relatively weak effects on current ground-dwelling invertebrate communities, which are dominated by nonnative species. Specific taxa, however, may be more vulnerable. Eradication of this ant from the Wai‘anae Mountains is not feasible, but information from this study may help land managers decide whether controlling this ant in small areas to conserve rare and sensitive invertebrate species might be useful.

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CHAPTER 1

Introduction

Predation and competition by alien species are major threats to global biodiversity (Wilcove et al. 1998, Mack et al. 2000). Invasive ants in particular are recognized as especially damaging among invasive invertebrates, and have been documented to exert a wide range of ecological impacts (Holway et al. 2002, Lach and Hooper-Bui 2010). Through their tending of sap-feeding hemipteran insects, invasive ants may negatively affect plants, as a result of higher levels of herbivory, through a build-up of sooty mold growing on excessive honeydew waste, or through a higher transmission of plant diseases vectored by such insects (Jahn et al. 2003, Lach 2003, Handler et al. 2007). Invasive ants may also affect plants through their aggression towards pollinators. Many studies have documented reductions in floral visitation associated with invasive ant presence (Blancafort and Gomez 2005; Lach 2007, 2008; Krushelnycky 2014; LeVan et al. 2014; Hanna et al. 2015), and some have also measured resulting declines in plant reproduction (Blancafort and Gomez 2005, LeVan et al. 2014, Hanna et al. 2015). In some cases, plant reproductive success may also be reduced when invasive ants displace native seed dispersers (Gomez et al. 2003), and the displacement of invertebrate herbivores may change forest structure (O'Dowd et al. 2003). High densities of invasive ants may even impact vertebrates, such as Wedge-tailed Shearwater chicks in the Hawaiian Islands (Plentovich et al. 2009).

Invasive ants interact most directly with other invertebrates, and can strongly alter invertebrate communities. They have been documented to displace native ants worldwide, including in such widely divergent ecosystems as tropical forests in Gabon (Walker 2006), temperate woodlands and meadows in California and Texas (Porter and Savignano 1990, Human and Gordon 1996), and monsoon forests in Australia (Hoffmann et al. 1999, Hoffmann and Parr 2008). Although less frequently reported, invasive ants have been reported to impact other terrestrial invertebrate groups, such as snails (Uchida et al. 2016), crustaceans (O'Dowd et al. 2003), and a wide range of arthropods (e.g. Porter and Savignano 1990, Human and Gordon 1996, Bolger et al. 2000, Hoffmann and Parr 2008).

Invasive ant impacts may be especially strong on oceanic islands (Holway et al. 2002, Krushelnycky and Gillespie 2010b). As the most isolated landmass on Earth, Hawai'i is thought

to have few or no native ant species, but over 60 non-native ant species are now established (AntWeb 2016). Invasive ants in Hawai‘i negatively impact urban areas (Tenorio and Nishida 1995, Leong and Grace 2008), agriculture (Jahn et al. 2003, Souza et al. 2008), and natural areas (Cole et al. 1992, Gillespie and Reimer 1993, Plentovich et al. 2009). In natural areas, the effects on native invertebrate species are far reaching. Native *Tetragnatha* spiders have been found to be vulnerable to chemical and physical attack from invasive ants, often resulting in spider death (Gillespie and Reimer 1993). Native *Hylaeus* bees do not visit flowers occupied by workers of the big-headed ant, *Pheidole megacephala*, while non-native honeybees do (Lach 2008), and Argentine ants (*Linepithema humile*) have been observed to enter *Hylaeus* bee burrows and flush out adults (Cole et al. 1992). The latter study in Haleakalā National Park found that Argentine ants negatively affect a wide range of invertebrate species belonging to multiple taxonomic and functional groups, but that the most severe impacts occurred at higher elevations where a large proportion of the fauna was endemic and occurred at low population densities (Cole et al. 1992).

However, most of what is known about the ecological effects of invasive ants in Hawai‘i results from studies of a small proportion of invasive ant species, and the impacts of other established ant species remain largely unknown (Reimer 1994, Krushelnycky 2015). This makes it difficult for land managers to prioritize the control of invasive ant species. A notable example is the thief ant, *Solenopsis papuana*, which has been in Hawai‘i for over 50 years (Huddleston and Fluker 1968), and has become one of the most common ants found in the upper elevations of the Wai‘anae Mountain Range of O‘ahu (Ogura-Yamada and Krushelnycky unpub. data). A unique aspect of this ant is its ability to thrive in relatively undisturbed mesic and wet upland forests, raising major concerns about its potential effects on native invertebrates in these habitats (Reimer 1992, 1994; Gillespie and Reimer 1993). A recent study showed that *S. papuana* is capable of significantly reducing reproductive success of rare endemic picture-winged *Drosophila* flies in mesic forests of O‘ahu (Krushelnycky et al. 2017), but its broader impacts on ground-dwelling invertebrate communities has not been investigated. Some thief ants are known to make colonies near other ant or termite colonies and prey on their brood or queens (Holldobler and Wilson 1990, Tschinkel 2006), but other species are free-living subterranean generalist predators (Thompson 1980, 1989; Tschinkel 2006). An outstanding question is what supports the high densities of *S. papuana* in the upper elevations of the Wai‘anae Mountains?

The goal of my thesis was to measure the effects of *S. papuana* on ground-dwelling invertebrate communities in the mesic forests of the Wai‘anae Mountains. Studies of the ecological effects of invasive ants are often conducted as observational surveys, where an invaded area is compared with an adjacent uninvaded area. Because *S. papuana* is now so widespread in the upper elevations of the Wai‘anae Mountains, it is difficult if not impossible to find similar adjacent invaded and uninvaded areas to compare. Instead, I opted for an experimental manipulation study design, in which I would suppress ants in randomly selected field plots, and then compare invertebrate community responses between these plots and paired, untreated control plots over the following year. To accomplish this, I first needed to develop experimental monitoring and control methods for *S. papuana*. I tested the relative attractiveness of four non-toxic food baits that could be used for monitoring relative ant densities, and five toxic ant pesticidal baits that might be used for ant control. I then compared the efficacy of the two most attractive pesticidal baits for controlling *S. papuana* in field plots, using specially designed bait stations to avoid non-target effects. With these monitoring and control methods developed, I set out to determine whether *S. papuana* is currently impacting ground-dwelling invertebrates, particularly native species, as has been demonstrated for other invasive ants in Hawai‘i (Cole et al. 1992; Gillespie and Reimer 1993; Krushelnycky and Gillespie 2008, 2010a, 2010b).

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CHAPTER 2

Testing the attractiveness and efficacy of baits for the monitoring and control of the thief ant, *Solenopsis papuana*

Modified from **Ogura-Yamada, C.S & P.D. Krushelnycky**, Testing the attractiveness and efficacy of baits for the monitoring and control of the thief ant, *Solenopsis papuana*. 2016. Proc. Hawaiian. Entomol. Soc. 48: 95-108 to fulfill partial requirements of Master of Science in Entomology.

Abstract

Solenopsis papuana is one of the few introduced ant species that have widely infiltrated undisturbed mesic and wet forests in Hawai‘i. This may be problematic since many endemic Hawaiian insects are limited to mountain forests, and methods for monitoring and controlling *S. papuana* would be useful. Four non-toxic monitoring baits (corn syrup, SPAM[®], peanut butter, and tuna/corn syrup blend) and five ant pesticide baits (Advion[®] Fire Ant Bait[™], Amdro[®] Ant Block[®], Extinguish[™] Plus, MaxForce[®] Complete Brand Granular Insect Bait, and Siesta[™]) were tested for attractiveness to *S. papuana* in choice tests at Lyon Arboretum and Pahole Natural Area Reserve (NAR) on the island of O‘ahu. Amdro[®] Ant Block[®] and Siesta[™] were also tested for efficacy against *S. papuana* in field plots at Pahole NAR. SPAM[®] and peanut butter were the most attractive monitoring baits at both locations. There were few significant differences in attractiveness among the five ant pesticides, but Amdro[®] Ant Block[®] attracted the highest or second highest number of ants at both sites, while rankings among the other baits were inconsistent. Amdro[®] Ant Block[®] presented in bait stations 2.5 m apart greatly reduced the number of ants at monitoring cards in field plots, by an average of 96% from pre-treatment levels over the course of the 246-day trial. Ant numbers also declined in the Siesta[™] plots (by 77%), but more closely mirrored fluctuations in the untreated control plots. These methods were effective for monitoring and suppressing *S. papuana* populations in localized natural areas in the Wai‘anae Mountain Range.

Introduction

Invasive species are major drivers of species endangerment and extinction (Clavero and Garcia-Berthou 2005), and islands are colonized by a disproportionately high number of invaders (Mooney and Cleland 2001) compared to continental ecosystems. Invasive ants can cause major ecological changes because of their impacts on native ants and arthropods through predation or competition (Porter and Savignano 1990, Human & Gordon 1997, McNatty et al. 2009). Invasive ants also cause economic damages; Pimentel et al. (2005) estimated that the Red Imported Fire Ant (*Solenopsis invicta*) alone costs \$1 billion per year in losses, damages, and control expenses in the Southern United States. Invasive ants on islands can be detrimental to multiple trophic levels of ecosystems (Wetterer 2007; O'Dowd et al. 2003), and Hawai'i is not exempt from the impacts of invasive ants, which have caused conservation (Cole et al. 1992, Gillespie and Reimer 1993, Plentovich et al. 2009), agricultural (Jahn et al. 2003, Souza et al. 2008), and urban problems (Tenorio and Nishida 1995, Leong and Grace 2008). Additional information on the ecology and management of Hawai'i's invasive ant species is desirable, as relatively few have been studied in any detail (Reimer 1994, Krushelnycky 2015).

The thief ant currently known as *Solenopsis papuana* Emery in Hawai'i, was first found in the islands in 1966-67 by Huddleston and Fluker (1968), who reported two new, unidentified *Solenopsis* taxa: a dark, more widespread species "a", and a lighter, slightly smaller species "b." Their species "a" was later identified as *S. papuana* (Reimer 1992), and this name has since been used for this taxon in the Hawaiian ant literature (e.g. Gillespie and Reimer 1993, Reimer 1994, Krushelnycky et al. 2005). However, the name *S. papuana*, originally designated for specimens from Papua New Guinea in 1900 (Wilson and Taylor 1967), has subsequently also been applied to specimens across the Pacific, including Samoa, Fiji, Society Islands, Cook Islands, and Pohnpei (Wilson and Taylor 1967, Morrison 1996, 1997, Clouse 2007). Of these latter specimens examined (P. Krushelnycky unpub. data, AntWeb 2016), all differ substantially from those in Hawai'i and are unlikely to be conspecific with the Hawaiian species. This conclusion is supported by molecular data, which place Hawaiian specimens in a clade of species described from the Indian Ocean (D. Gotzek pers. comm.). A comprehensive taxonomic revision of small *Solenopsis* species is needed to better understand the species limits, geographic ranges and correct identities of many of the taxa in this group. Until this taxonomy is resolved, I continue to

refer to the species in Hawai‘i as *S. papuana* in the interest of consistency with prior literature in Hawai‘i, recognizing that nomenclature is likely to change in the future.

In 1966-67, *S. papuana* was found at one site on O‘ahu and multiple sites across Maui, where it was already observed as a dominant ant species with large nests in some areas (Huddleston and Fluker 1968). Since then it has spread to Kaua‘i, Moloka‘i, Lāna‘i, and Hawai‘i Island (Nishida 2002). It is one of the few ant species that has successfully infiltrated undisturbed mesic and wet upland forests in Hawai‘i (Reimer 1992, 1994), and field observations suggest that it currently exhibits high population densities across a wide range of natural areas (Plentovich 2010, Ogura-Yamada and Krushelnycky unpub. data). Many endemic Hawaiian insects are now limited to montane habitats (Zimmerman 1948), and can be detrimentally impacted by invasive ants (Cole et al. 1992, Gillespie and Reimer 1993, Krushelnycky and Gillespie 2010).

A broader study investigating the potential impact of *S. papuana* on native arthropod species and food webs required the development of experimental monitoring and control methods for this species. In this chapter, I report on these methods, including the relative attractiveness of four non-toxic monitoring baits and five pesticide ant baits, testing a bait station to effectively deliver pesticide baits while minimizing non-target effects, and the efficacy of two of the toxic ant baits against *S. papuana* in field plots. While *S. papuana* is too widespread for eradication to be realistic, the information in this study may be useful for monitoring distribution, relative densities and control in localized areas of high conservation value.

Materials and Methods

Study Sites

Preference tests for monitoring baits and pesticide baits were conducted in two forested sites on O‘ahu that supported high densities of *S. papuana*. The first site was located within University of Hawai‘i’s Harold L. Lyon Arboretum, in lowland, non-native wet forest in Mānoa Valley in the Ko‘olau Mountain range (150 m elevation, 3836 mm annual rainfall (Giambelluca et al. 2013)). The second site was located in mixed native and non-native mesic forest in Pahole Natural Area Reserve (NAR) in the Wai‘anae Mountain Range (480 m elevation, 1375 mm annual rainfall (Giambelluca et al. 2013)). A pesticide bait efficacy test was conducted only at Pahole NAR.

Monitoring bait preference

Four food baits containing varying amounts of sugar, oil and protein were chosen to compare relative attractiveness to *S. papuana*: 1) light corn syrup (Karo[®], ACH Food Companies, Cordova, Tennessee), 2) peanut butter (Jif[®] Creamy, The J.M. Smucker Company[®], Orville, Ohio), 3) canned, processed meat (SPAM[®], Hormel Foods, Austin, Minnesota), and 4) a tuna and corn syrup blend (one 5 oz. (142g) can of tuna (Chicken of the Sea[®] International, San Diego, California) in water, drained, and blended with 100g light corn syrup in a food processor). Each of these baits has been used for attracting a variety of ants in bait preference and monitoring studies: corn syrup (Eow and Lee, 2007), peanut butter (Lee, 2002; Causton et al. 2005; Hara et al. 2014), processed meats (Porter and Tschinkel 1987; Peck et al. 2015), and tuna/corn syrup blends (Keeler 1980, Krushelnycky et al. 2011).

Baits (approximately 1.5 cm diameter quantity of corn syrup, tuna/corn syrup blend, and peanut butter, or one cube of SPAM[®] approximately 1 x 1 x 0.5 cm) were placed in paper cupcake liners (Bake Fresh White Baking Cups, Rockline Industries[®], Sheboygan, Wisconsin) and presented next to each other at replicate stations, which were approximately 20 m apart, at each site. The cupcake liners prevented liquid baits from spilling, while allowing ants access to the baits both on the upper surface and underneath as the baits soaked through the paper. Ant numbers on each bait were recorded (top and bottom of wrapper summed) every hour for three hours. The preference test was conducted on 18 June 2015, at Lyon Arboretum, using 25 replicate stations, and on 1 August 2015, at Pahole NAR, using 24 replicate stations. Stations

with fewer than 24 ants total across all bait types and hours (i.e., <2 ants/bait/hour on average) were removed from the data set; this left 16 replicate stations at Lyon Arboretum and 19 replicate stations at Pahole NAR. Due to unequal variances among groups, Welch's ANOVA followed by Games-Howell multiple comparison test was used to compare log-transformed numbers of ants among all bait types for each hour at each site. Numbers of ants were subsequently also compared across hours at each site for the two most attractive baits. To compare relative detection rates for the four baits, I compared proportions of stations that attracted any *S. papuana* after one hour at each site, after removing the low ant density stations described above, using a Chi-square contingency table. For the two most attractive baits, I also compared proportions of stations attracting ants at one and two hours at each site, using Fisher's Exact Test.

Pesticide bait preference

Five granular commercial pesticide ant baits were chosen to compare relative attractiveness to *S. papuana*: 1) Advion® Fire Ant Bait (0.045% indoxacarb, EPA# 100-1481, Syngenta Corporation, Greensboro, North Carolina), 2) Amdro® Ant Block® Home Perimeter Ant Bait (0.88% hydramethylnon, EPA# 73342-2, AMBRANDS, Atlanta, Georgia), 3) Extinguish™ Plus (0.365% hydramethylnon and 0.250% S-methoprene, EPA# 2724-496, Wellmark International, Schaumburg, Illinois), 4) MaxForce® Complete Brand Granular Insect Bait (1% hydramethylnon, EPA# 432-1255, Bayer Environmental Science, Research Triangle PK, North Carolina), and 5) Siesta™ (0.063% metaflumizone, EPA# 7969-232, BASF Corporation, Florham Park, New Jersey). These baits were chosen because they target *Solenopsis* fire ants, or because they have been found to be attractive or effective against other species in the subfamily Myrmicinae (Williams et al. 2001, Oi and Oi 2006; Warner et al. 2008, Hara et al. 2014). Advion® Fire Ant Bait, Amdro® Ant Block®, Extinguish™ Plus, and Siesta™ are all based on a similar bait matrix composed of corn grit saturated with soybean oil. MaxForce® Complete is a mixture of two bait matrix types: a corn grit/soybean oil-based granule and a protein-based granule.

Each bait (2.5 ml (0.5 teaspoon)) was placed into paper cupcake wrappers and presented next to each other at replicate stations at both sites, and ant numbers were recorded every hour for three hours as described for the monitoring bait preference test. The pesticide preference test

was conducted on 18 September 2015, at Pahole NAR, using a total of 25 replicate stations, and on 6 November 2015, at Lyon Arboretum, using 25 replicate stations. After excluding stations with fewer than 24 ants total across all bait types and hours, 10 stations at Pahole NAR and 23 stations at Lyon Arboretum remained for analysis. Numbers of ants (log transformed) were compared among bait types at each hour and site as described for the monitoring bait preference test. Since pesticide baits are generally available to ants for longer periods of time, differences in bait attractiveness across the three monitoring hours were not statistically tested.

Pesticide bait efficacy trial

Two baits, Amdro[®] Ant Block[®] and Siesta[™], were chosen to test efficacy of continuous treatment over an eight-month period in field plots at Pahole NAR because both exhibited relatively high attractiveness to *S. papuana* at one or both of the bait preference test sites (see Results). Nine 5 x 5 m plots were established on 3 July 2015, and pre-treatment ant densities were determined in each plot: Ants were counted on the tops and bottoms of 25 monitoring cards (one half of a 7.6 x 12.7 cm index card) baited with a smear of peanut butter. Cards were placed on the ground every 1.25 m in a grid pattern (Fig. 2.1), and collected after 1.5 hours. The nine plots were subsequently randomly assigned to one of three treatments (Amdro[®] Ant Block[®], Siesta[™], or untreated control), with the exception that the two lowest-density plots were assigned to the control treatment to ensure that the pesticide baits were tested in plots with high ant densities. Bait stations were used to apply the baits to limit access to non-target arthropods. Stations were constructed of 3.81 cm (1.5 in) long sections of 3.18 cm (1.25 in) diameter PVC tubing, fitted with PVC endcaps on the upper end. The open bottoms were screened with Amber Lumite Screen (530 μ m mesh size, Lumite Inc., Alto, Georgia) fastened with PVC cement (Oatey[®] Co., Cleveland, Ohio). This design (Fig. 2.2) allowed access to *S. papuana* workers but excluded most other non-target arthropods. Nine bait stations, separated by 2.5 m in a grid pattern (Fig. 2.1), were placed in each plot testing the two pesticide baits. Each station was supplied with 2.5 ml (0.5 teaspoon) of Amdro or Siesta ant baits contained within a disposable polypropylene tea bag (Daiso Industries Co., Hiroshima, Japan). This allowed ants to imbibe pesticide-laden oil from the baits while facilitating their periodic replacement. Stations were staked to the ground using 2.05 mm (12 AWG) diameter galvanized wire to ensure that the

endcaps shielded the bait from rain, and that contact between the screened opening and the ground was maintained.

Baits were first applied on 3 July 2015 after the pre-treatment monitoring, and replaced every four to seven weeks for a total of five times during the experiment, which ended on 5 March 2016 (total 246 days of treatment). On each date that baits were replaced, ant densities in the plots were assessed using the peanut butter card monitoring methods described above. During the first two bait replacement events, the nine bait stations in each plot were also systematically shifted such that each of the 25 monitoring points received a station by the second event in September, 2015. Bait stations were subsequently returned to their original positions (indicated in Fig. 2.1) for the remainder of the trial, except to target occasional localized surges in ant numbers in plots. Since there were only three replicate plots for each treatment, I present only descriptive statistics for trends in ant densities in the plots. To assess whether the bait station spacing interval (2.5 m grid) was effective in the Amdro and Siesta plots, I compared reductions in numbers of ants at the 25 monitoring points in each plot on the first monitoring event, 28 days after bait station placement, according to the distance of the points from the nearest bait station: 0 m (immediately adjacent to bait station), 1.25 m or 1.8 m (Fig. 2.1). Since these monitoring points can be considered independent replicates for this test, a two-factor ANOVA was used to compare reductions in ant numbers for each bait type, including the factors ‘monitoring distance’ ($n = 75$) and ‘plot number’ ($n = 3$) to control for individual plot differences. Statistical analyses were performed using Minitab v. 17.1 (Minitab 2013).

Results

Monitoring bait preference

Among the four foods evaluated as potential monitoring baits, SPAM[®] and peanut butter generally attracted more *S. papuana* than corn syrup and the tuna/corn syrup blend at most of the time intervals at both sites (Fig. 2.3). However, these differences were not always statistically significant (see Fig. 2.3) due to high variation in ant numbers among replicate stations. For SPAM[®] and peanut butter baits, mean recruitment increased over time, but in most cases these increases were not statistically significant. Specifically, numbers of *S. papuana* at peanut butter baits did not differ among hours at either Lyon Arboretum ($F = 0.34$, $p = 0.716$) or Pahole NAR ($F = 2.08$, $p = 0.140$), nor did they differ among hours at SPAM[®] baits at Lyon ($F = 1.34$, $p =$

0.278). However, ant numbers at SPAM[®] baits at Pahole did differ significantly over time ($F = 4.12$, $p = 0.025$), with recruitment at hour 3 being significantly higher than at hour 1 (Games-Howell test, $p = 0.022$). Differences between hours 1 and 2 were marginally significantly different ($p = 0.060$) and differences between hours 2 and 3 were not statistically significant ($p = 0.881$) for SPAM[®] at Pahole.

SPAM[®] and peanut butter also tended to attract *S. papuana* to a higher percentage of baits offered, relative to the other two baits (Fig. 2.4). Again, these differences were not always statistically significant. After one hour, an interval commonly used for ant monitoring and distribution mapping (Blachly and Forschler 1996, Lee et al. 2003, Starr et al. 2008), there was a significant association between percentage of baits found and bait type at Pahole NAR (Chi-square = 10.556, $p = 0.014$), with SPAM[®] and peanut butter baits exhibiting higher than expected occupancy, and corn syrup and tuna/corn syrup blend exhibiting lower than expected occupancy. At Lyon Arboretum, there was no significant association between percentage of baits found and bait type (Chi-square = 5.830, $p = 0.120$). For peanut butter baits, there was no significant difference in occupancy rates between hours 1 and 2 at either Lyon (Fisher's Exact Test, $p = 1$) or Pahole (Fisher's Exact Test, $p = 0.693$). Similarly, there was no significant difference in occupancy rates between hours 1 and 2 at SPAM[®] baits at Lyon (Fisher's Exact Test, $p = 0.172$) or Pahole (Fisher's Exact Test, $p = 0.232$).

Pesticide bait preference

The relative attractiveness of the five pesticide ant baits to *S. papuana* differed somewhat by location, and large variation among replicate stations resulted in little consistent statistically significant separation between the baits (Fig. 2.5). Amdro[®] Ant Block[®] tended to attract the highest or second highest number of *S. papuana* at both sites, but the relative positions of the other baits varied among sites. In particular, Siesta[™] attracted a relatively high number of *S. papuana* at Pahole, but the least number at Lyon.

Pesticide bait efficacy trial

Plots treated with Amdro[®] Ant Block[®] generally had a greater reduction in ant densities than those treated with Siesta[™] (Fig. 2.6). Ant counts in the Amdro[®] Ant Block[®] plots dropped by $90.4 \pm 4.5\%$ from pre-treatment levels by 28 days after bait station placement (mean \pm SE of

the % change in numbers for each of three plots), compared to a $44.8 \pm 10.5\%$ and $3.7 \pm 23.6\%$ reduction over the same period in the Siesta™ and control plots, respectively. Subsequently, numbers of ants in the Siesta™ plots were very similar to those in the control plots, both of which exhibited a strong reduction from October through December of 2015, followed by a resurgence by February of 2016 (Fig. 2.6). In contrast, Amdro® Ant Block® plots exhibited only a very small resurgence in the latter period, and averaged $96.2 \pm 1.1\%$ reduction from pre-treatment levels over the duration of the eight-month experiment (mean \pm SE of % change in numbers for each plot on each date). Ant numbers were reduced on average by $76.8 \pm 7.0\%$ and $42.6 \pm 24.2\%$ from pre-treatment levels over the entire experiment in the Siesta™ and control plots, respectively.

The magnitude of reduction in ant numbers at monitoring stations 28 days after station placement was not significantly related to distance from the nearest bait station for either Amdro® Ant Block® ($F = 1.79$, $p = 0.174$) or Siesta™ ($F = 2.30$, $p = 0.107$). In Siesta™ plots, however, there was a non-significant pattern suggesting potentially weaker reduction at greater distances from bait stations, which was absent in Amdro® Ant Block® plots (Fig. 2.7).

Discussion

These results indicate that both SPAM[®] and peanut butter should be effective baits for monitoring relative densities of *S. papuana* and for mapping its distributions. Temporal trends suggested that exposing baits for more than one hour may increase their effectiveness to some degree, both in terms of higher recruitment and higher bait detection, but these trends were relatively weak and usually statistically non-significant. These benefits may therefore not offset the cost of additional monitoring time. Of the two baits, peanut butter is the more practical choice. It is much less expensive than SPAM[®], requires no preparation and is easy to use in the field, does not spoil after opening, and adheres to monitoring cards or other monitoring substrates. The high attractiveness and ease of use of peanut butter has made it an effective bait for monitoring a variety of other ant species, particularly those in the myrmicine subfamily, such as *Wasmannia auropunctata*, *Monomorium pharaonis*, *Trichomyrmex destructor*, *Pheidole* spp., *Solenopsis geminata*, and others (Lee 2002, Causton et al. 2005, Starr et al. 2008). Placing monitoring baits on substrates that soak through, like the cupcake liners and index cards used in this study, is likely to be important when monitoring *S. papuana*. This species spends most of its time in the soil and leaf litter, and tends to approach baits from underneath: for both SPAM[®] and peanut butter baits, I often observed equal or greater numbers of ants on the bottom of the bait substrate relative to the top.

Relatively weak and/or inconsistent differences were found in attractiveness among the five commercial pesticide baits tested, possibly because they are all based completely or in part on similar corn grit and soybean oil granule matrices. However, each bait may contain additional proprietary ingredients that could influence attractiveness, and some active ingredients may exhibit repellency for certain ant species (Stringer et al. 1964, Reimer and Beardsley 1990, Williams et al. 2001, Montgomery et al. 2015). Of the five baits, Amdro[®] Ant Block[®] and Siesta[™] tended to attract the greatest number of ants at one or both testing sites.

Amdro[®] Ant Block[®] was developed to combat the Red Imported Fire Ant, *S. invicta* (Williams et al. 2001), and has been on the market since 1980. It is a widely-used bait that has been highly effective against *Pheidole megacephala* (Reimer and Beardsley 1990, Hoffmann and O'Connor 2004, Plentovich et al. 2009, Plentovich et al. 2011), *W. auropunctata* in certain situations (Causton et al. 2005), and *S. geminata* to variable degrees (Hoffmann and O'Connor 2004, Plentovich et al. 2009; Plentovich 2011, Hoffmann et al. 2011). Siesta[™], a newer product

registered in 2007, has demonstrated efficacy against *P. megacephala* (Warner et al. 2008), *S. invicta* (Thompson 2008), and *W. auropunctata* (Hara et al. 2011). When the efficacy of these two baits against *S. papuana* were compared in small field plots, Amdro[®] Ant Block[®] yielded greater reductions in ant numbers on average than Siesta[™]. Strong declines in ant numbers in the control plots from approximately October through December, possibly due to seasonality or other weather events that commonly affect ant populations (e.g. Vanderwoude et al. 1997, Rust et al. 2000, Krushelnycky et al. 2004), made it difficult to differentiate between any of the plots during this period. Nevertheless, there were substantial differences in trends among treatment groups in the first month post bait application, as well as in the degree of resurgence in ant numbers in the final two months of the trial (Fig. 2.6). The reason for the lower apparent efficacy of Siesta[™] bait is unknown, but in initial tests with a different bait station design that made entry and exit more difficult, I observed many dead *S. papuana* workers after 24 hours inside stations containing Siesta[™], but many fewer inside stations containing Amdro[®] Ant Block[®]. I therefore suspect that the lower efficacy of Siesta[™] may be related to the speed with which metaflumizone kills *S. papuana*, rather than to issues with bait attractiveness.

A preliminary trial suggested that broadcast application of Amdro[®] Ant Block[®] was very effective at controlling *S. papuana*, and broadcasting Amdro[®] Ant Block[®] could in fact yield faster and perhaps greater control than that obtained with bait stations. However, broadcasted bait granules formulated with hydramethylnon have been found to impact some non-ant arthropod groups, like cockroaches and crickets, in some situations (Plentovich et al. 2010, Plentovich et al. 2011). In this case, the goal was to suppress numbers *S. papuana* while not directly influencing populations of other arthropods, both native and or non-native. If minimizing impacts on non-target arthropods is of overriding importance, bait stations can be an effective, if more expensive and laborious, solution. This bait station design and spacing interval provided good control for *S. papuana* when using Amdro[®] Ant Block[®]. The strong reduction in *S. papuana* numbers at monitoring stations suggested that this species was able to easily access the bait. The interior of the stations remained fairly dry provided that the stations were not dislodged by heavy rain or animals, bait replacement was relatively easy, and very few ants or other arthropods were observed trapped inside them. It is possible that a greater spacing interval may remain effective with Amdro[®] Ant Block[®] bait, although observations around the peripheries of

treated plots suggest that *S. papuana* forages relatively short distances and may not effectively retrieve baits located more than several meters away from the nest.

While the attractiveness of Amdro[®] Ant Block[®] was not overwhelmingly stronger than the other baits tested, it was consistently attractive to *S. papuana*, and has other characteristics that make it a good option for controlling *S. papuana* in natural areas. It is widely available, relatively inexpensive, and has the broadest label language regarding allowable uses, including in forested areas. The US EPA (1998) considers hydramethylnon, the active ingredient in Amdro[®] Ant Block[®], to be unlikely to contaminate ground water, of low risk to birds, and to have minimal effects on terrestrial non-target organisms when used for insect control. Hydramethylnon degrades quickly when exposed to light (Vander Meer et al. 1982), so presenting the bait in stations can not only reduce non-target exposure, but also prolong the potency of the active ingredient and protect the granules from adverse weather (Taniguchi et al. 2003). Although not practical over larger areas, I believe the methods discussed in this paper can be an effective tool for land managers to help monitor and control *S. papuana* populations at small scales in sensitive natural areas.

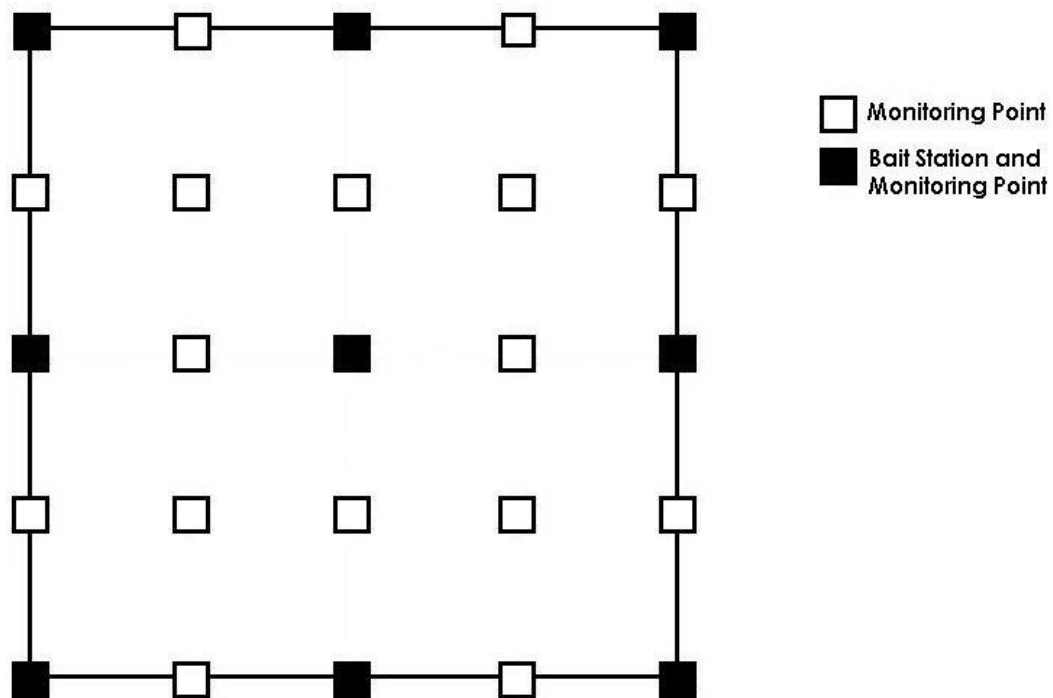


Figure 2.1. Layout of 5 x 5 m pesticide bait efficacy plots. Each plot contained nine bait stations and 25 monitoring points, whose positions were as indicated except on occasions when bait stations were shifted (see text). Monitoring points were either 0 m, 1.25 m, or 1.8 m from bait stations.



Figure 2.2. Amdro bait station design. Stations were constructed of PVC piping with removable endcap tops and glued screened bottoms, and staked to the ground. This facilitated easy bait replacement and allowed for ants to access the baits.

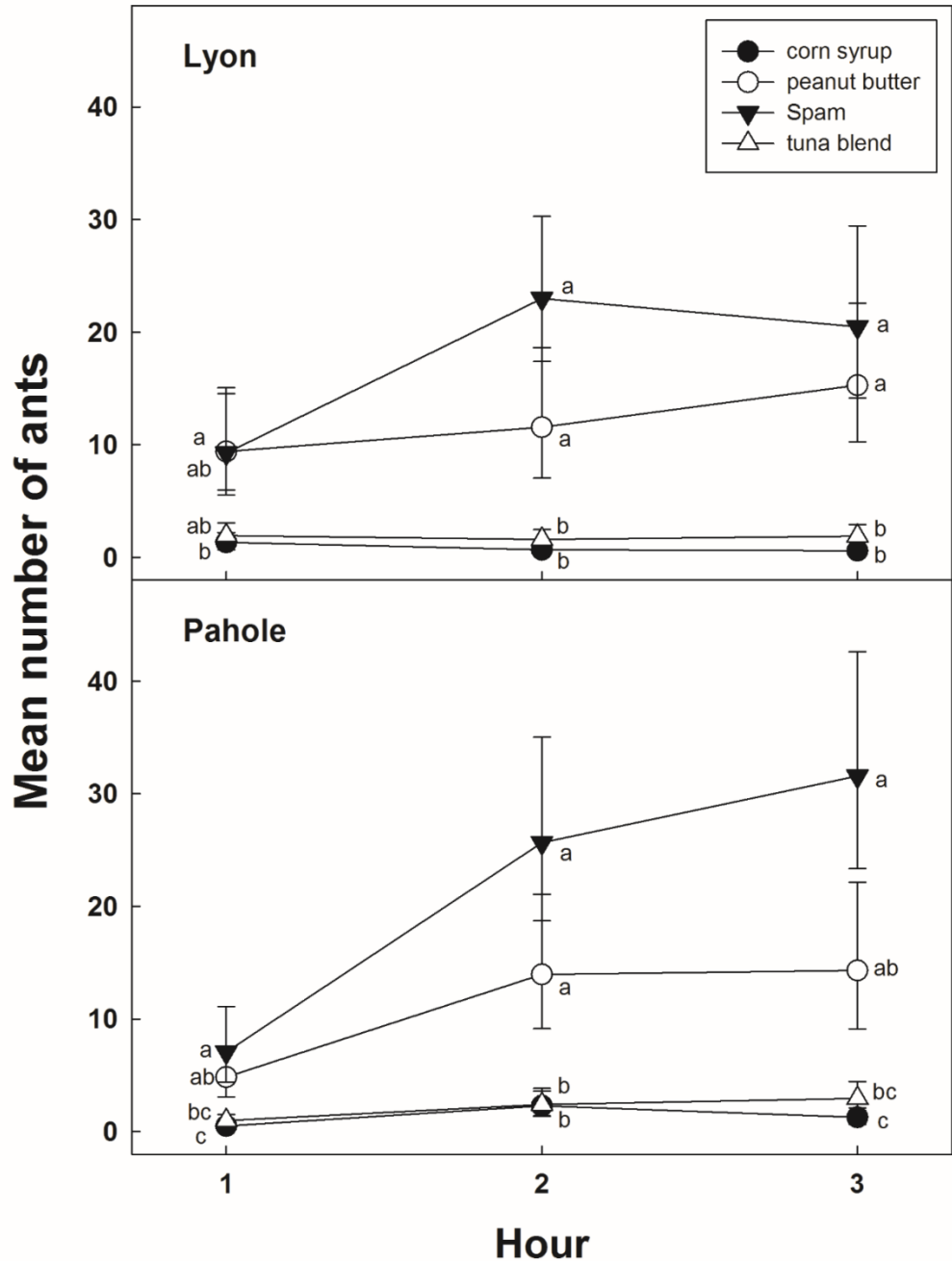


Figure 2.3. Mean number (\pm SE) of *S. papuana* attracted to food baits at Lyon (top) and Pahole (bottom) over the course of three hours. Means sharing the same letters within each hour at each site are not significantly different (Welch's ANOVA and Games-Howell posthoc test on log-transformed counts, $\alpha=0.05$; depicted means and SEs are back-transformed).

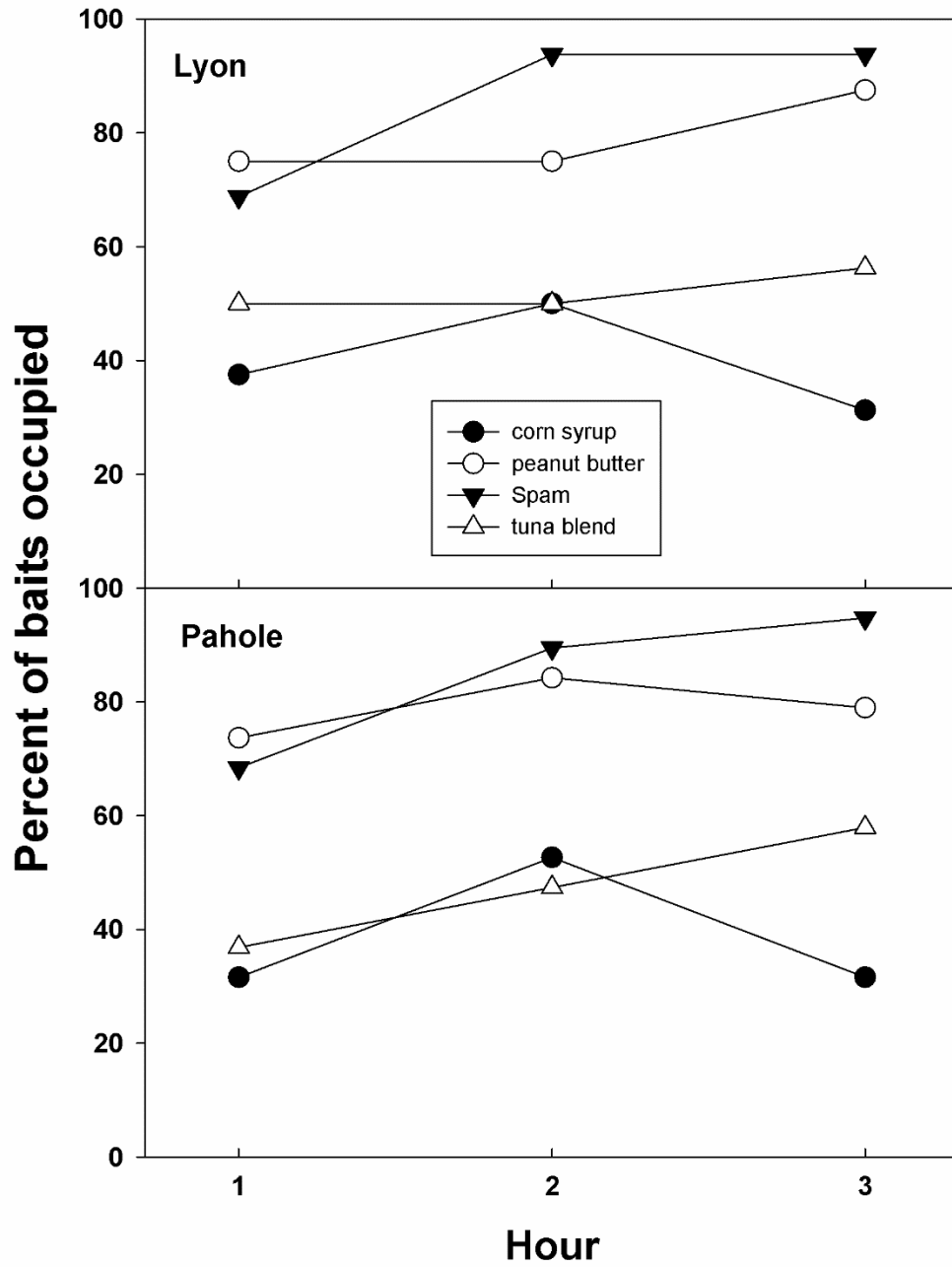


Figure 2.4. Percent of baits occupied by *S. papuana* at Lyon (top) and Pahole (bottom) over the course of three hours.

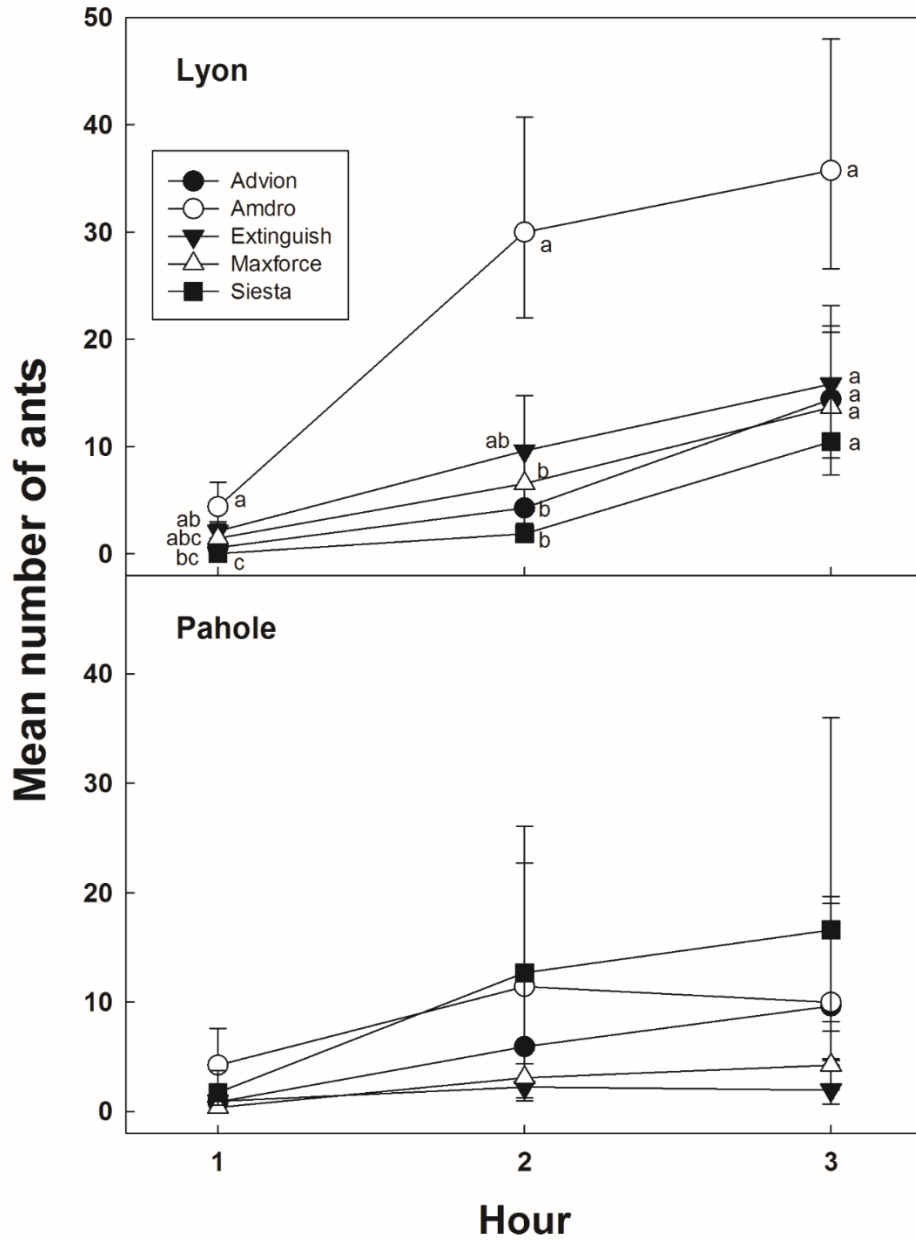


Figure 2.5. Mean number (\pm SE) of *S. papuana* attracted to pesticide baits at Lyon (top) and Pahole (bottom) over the course of three hours. Means sharing the same letters within each hour are not significantly different (Welch's ANOVA and Games-Howell posthoc test on log-transformed counts, $\alpha=0.05$; depicted means and SEs are back-transformed). None of the means were significantly different at any hour at Pahole.

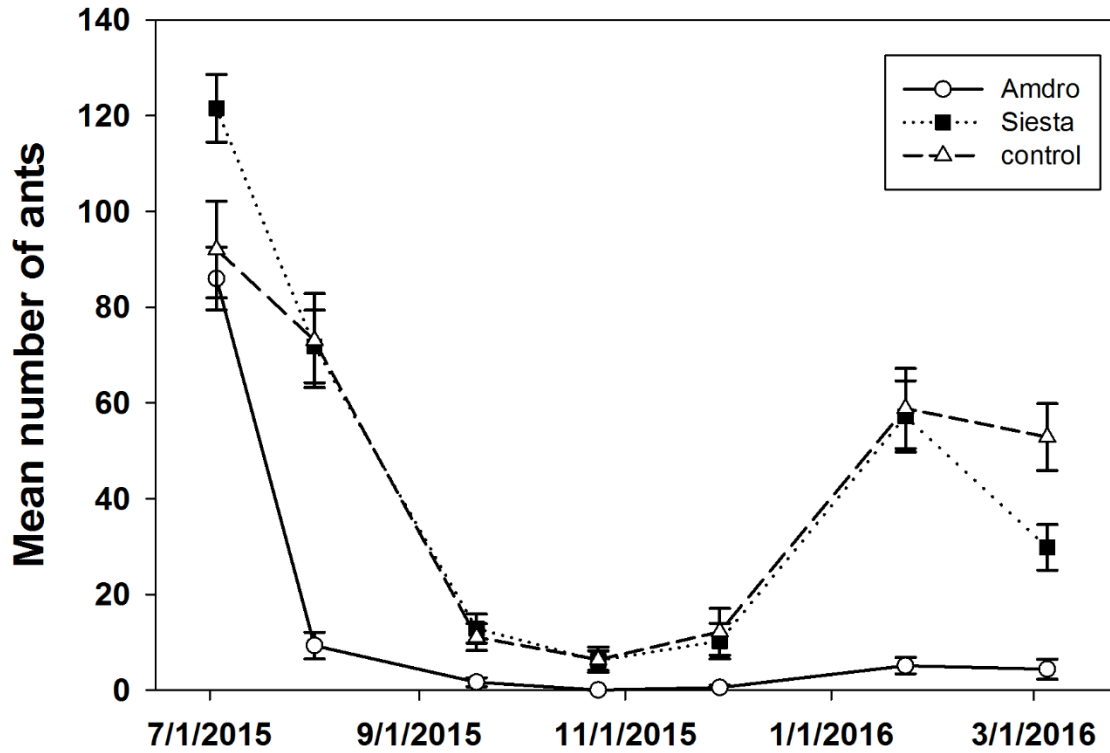


Figure 2.6. Mean (\pm SE) number of *S. papuana* in field plots treated with Amdro[®] Ant Block[®] and Siesta[™] baits, in comparison to untreated control plots. Bait stations were installed in the Amdro[®] Ant Block[®] and Siesta[™] plots on the first monitoring date (3 July 2015) immediately after monitoring, and baits were replaced on each subsequent monitoring event except the final date (5 March 2016).

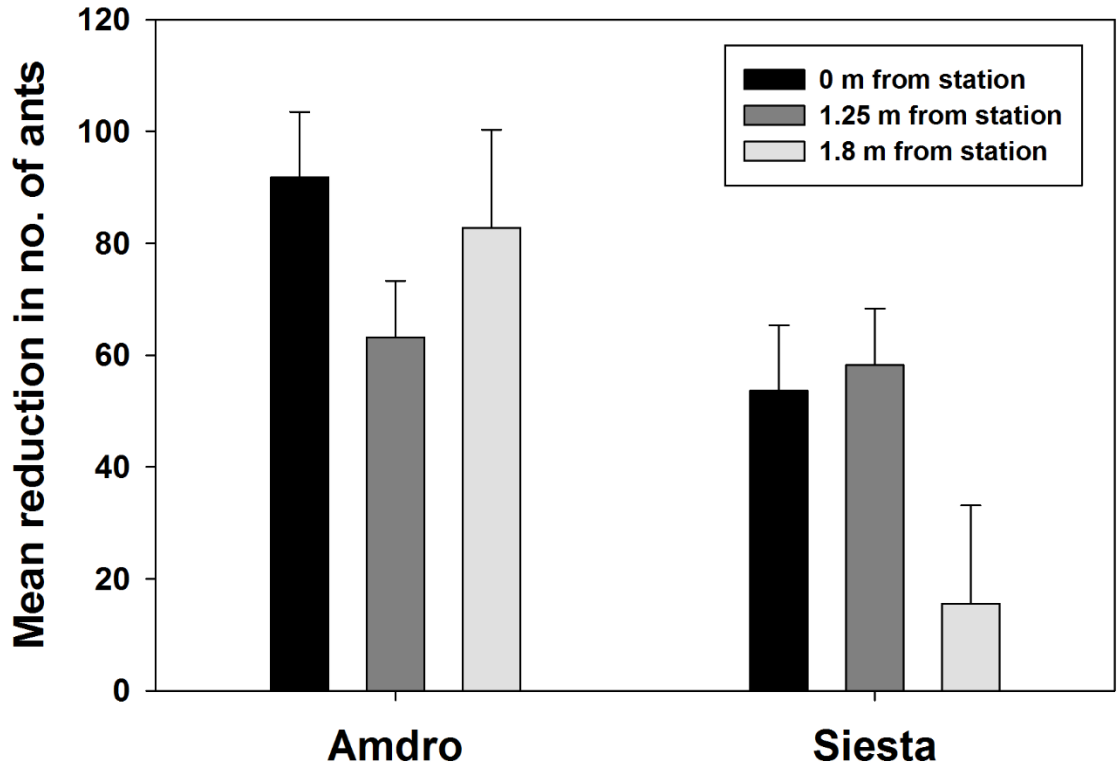


Figure 2.7. Mean (\pm SE) reduction in numbers of *S. papuana* 28 days after bait station placement in the field plots, categorized by distance of monitoring points from pesticide bait stations. There was no significant difference (based on ANOVA, $\alpha=0.05$) in degree of reduction among distances for either ant bait.

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CHAPTER 3

The effects of the invasive thief ant, *Solenopsis papuana*, on ground-dwelling invertebrates in the Wai‘anae Mountains of O‘ahu.

Abstract

Impacts of invasive predators are often hypothesized to negatively affect native invertebrates, but have not been measured for most invaders. I attempted to quantify the effects of *Solenopsis papuana*, an invasive thief ant, on invertebrate communities in Hawai‘i via an experimental manipulation study. I established six pairs of plots in the Wai‘anae Mountains of O‘ahu, in which Amdro[®] ant bait was used to reduce ant densities in half of the plots, and the responses of invertebrates were measured six months and one year later. Leaf litter and pitfall sampling revealed that ground-dwelling invertebrate communities were highly invaded, with native species comprising 24% of the taxa but only ~1-2% of the individuals captured. Relatively few taxonomic groups significantly increased in abundance following suppression of *S. papuana*, and responses were generally inconsistent between the two sampling periods. However, significant increases in species richness in ant-suppressed plots were more common, particularly in pitfall samples. Most of the significant changes involved introduced species, though native Hemiptera and Orthoptera appeared to benefit from the suppression of *S. papuana*. Although statistically significant responses were relatively uncommon and/or inconsistent, nearly all taxonomic groups exhibited non-significant increases in abundance and species richness in response to ant suppression. Moreover, there were no significant decreases in either abundance or species richness for any taxonomic group. This suggests that in their current highly invaded states, mesic forest ground-dwelling invertebrate communities are broadly but relatively weakly altered by *S. papuana* presence. However, this conclusion may be tempered by the difficulty of accurately measuring the vulnerability of rare species, many of which may now be absent from these communities.

Introduction

Predation and competition by alien species, along with habitat degradation and loss of native host plants, are major threats to terrestrial invertebrates (Wilcove et al. 1998, Mitchell et al. 2005). Invasive ants in particular are recognized as especially damaging to invertebrate abundance and diversity (Holway et al. 2002, Lach and Hooper-Bui 2010). Invasive ants have been most commonly documented to displace native ants worldwide, including in tropical forests in Gabon (Walker 2006), in temperate woodlands and meadows in California and Texas (Porter and Savignano 1990, Human and Gordon 1996), and in monsoon forests in Australia (Hoffmann et al. 1999, Hoffmann and Parr 2008), to name just a few cases. Although less frequently reported, impacts from invasive ants on other terrestrial invertebrate groups have also been detected, including snails (Uchida et al. 2016), crustaceans (O'Dowd et al. 2003), and a wide range of arthropods (e.g. Porter and Savignano 1990, Human and Gordon 1996, Bolger et al. 2000, Hoffmann and Parr 2008).

The Hawaiian Islands are thought to have had few or no native ants (Zimmerman 1970, Wilson 1996), but the >60 non-native ant species now established (AntWeb 2017) have long been reported to exert strong impacts on the rest of the native invertebrate fauna (Perkins 1913, Howarth 1985, Krushelnycky et al. 2005). For example, Gillespie and Reimer (1993) found that native *Tetragnatha* spiders were vulnerable to chemical and physical attack from invasive ants. Cole et al. (1992) determined that many invertebrate species, belonging to a wide range of taxonomic and functional groups, were negatively affected by the presence of the Argentine ant, *Linepithema humile*, at Haleakalā National Park. These impacts were most severe at higher elevations where a large percentage of the fauna was endemic and present at low population densities. Cole et al. (1992) also observed Argentine ants entering an endemic *Hylaeus* bee burrow and flushing out an adult, and found no ground-nesting *Hylaeus* larvae in ant-infested areas. The effects of invasive ants in Hawai'i are not restricted to the ground. Lach (2008) found that *Hylaeus* bees would not visit flowers occupied by workers of the big-headed ant, *Pheidole megacephala*, but that non-native honeybees would. At the community level, non-native arthropods increase relative to native arthropods in both the proportion of species and individuals occurring after ant invasion (Krushelnycky and Gillespie 2008, 2010a). Krushelnycky and Gillespie (2008) reported that richness of endemic species was reduced by 32-54% in some invaded areas. However, endemic species may in some cases benefit directly or indirectly from

ant invasions, such as the psocid *Ptycta distinguenda* that appeared to benefit from severely reduced number of introduced spiders in areas invaded by ants (Krushelnycky and Gillespie 2010a).

Most of what is known about the impacts of invasive ants on invertebrates in Hawai‘i comes from studies on just a handful of ant species, and information on the effects of other ant species is largely lacking (Reimer 1994, Krushelnycky 2015). A prime example concerns the thief ant, *Solenopsis papuana*. This ant was first discovered in Hawai‘i in 1966-67, at which time it occurred at one known site on O‘ahu and had already infested multiple areas of Maui (Huddleston and Fluker 1968). Today, it has also been recorded on Kaua‘i, Moloka‘i, Lāna‘i, and Hawai‘i island (Nishida 2002). On O‘ahu, it is now one of the most abundant invasive ant species in the upper elevations of the Wai‘anae Mountains and Ko‘olau Mountains (Ogura-Yamada and Krushelnycky, unpub data). This small and slow-moving ant is easily overlooked, but recruits heavily to attractive food items, revealing its high densities in the soil and leaf litter layers (see Chapter 1, Figure 1.3). Its ability to thrive in relatively undisturbed mesic and wet upland forests separates it from most other ants in Hawai‘i, and raises major concerns about its potential effects on native invertebrates in these habitats (Reimer 1992, 1994, Gillespie and Reimer 1993). While little is known about *S. papuana* and its biology, some thief ants (*Solenopsis* species formerly placed in the subgenus *Diplorhoptum*) are known to live close to colonies of other ant or termite species and prey on their brood or queens (Holldobler and Wilson 1990, Tschinkel 2006), but other species have been found to be free-living subterranean generalist predators (Thompson 1980, 1989, Tschinkel 2006).

Although *S. papuana* can often be found in leaf litter and is relatively uncommon in trees, they have been inferred to potentially exert some pressure on invertebrates in vegetation distant from the ground (Krushelnycky 2015). It was recently demonstrated that *S. papuana* significantly reduces reproductive success of rare endemic picture-winged *Drosophila* flies in mesic forests of O‘ahu (Krushelnycky et al. 2017), but ecological impacts on the wider invertebrate community are unknown. The goal of the present study was to determine the effects *S. papuana* on ground-dwelling invertebrates in the Wai‘anae Mountains of O‘ahu. To do this, I employed an experimental manipulation study in which paired plots were established in areas infested by *S. papuana*, and ants were subsequently suppressed in half of the plots. I concurrently measured changes in invertebrate communities over the course of one year to see if this

treatment results in the recovery of invertebrate abundance or diversity, particularly among native species, as would be predicted from the known impacts of other invasive ants on native invertebrates in other natural areas of Hawai'i (Cole et al. 1992, Gillespie and Reimer 1993, Krushelnycky and Gillespie 2008, 2010b).

Materials and Methods

Study Sites

The study was conducted at four locations in the northern and southern portions of the Wai‘anae Mountain Range that supported high densities of *S. papuana*, as determined by prior distribution mapping (Ogura-Yamada and Krushelnycky, unpub. data). The study sites were: Kahanahāiki (665 m elevation, 1384 mm mean annual rainfall), Pahole Natural Area Reserve (NAR) (475 m elevation, 1339 mm mean annual rainfall), Pu‘u Hāpapa (813 elevation, 1186 mm mean annual rainfall), and ‘Ēkahanui (634 m elevation, 1210 mm mean annual rainfall). All sites were situated in mesic montane forest supporting a mixture of native and alien vegetation. Reported estimates of mean annual rainfall were obtained from the Rainfall Atlas of Hawai‘i (Giambelluca et al. 2013).

Study Design

Six pairs of plots were established across the four study sites. The Pahole and Pu‘u Hāpapa sites each had one pair of plots, while the Kahanahāiki and ‘Ēkahanui sites each had two pairs of plots. Plots were 20 x 20 m, except for one pair of plots at ‘Ēkahanui that was 10 x 10 m in size because of topographic constraints. One plot in each pair was randomly assigned to either an ant suppression treatment (treatment) or an unmanipulated control (control).

Ant suppression was achieved using bait stations containing Amdro[®] Ant Block[®] Home Perimeter Ant Bait (0.88% hydramethylnon, EPA# 73342-2, AMBRANDS, Atlanta, Georgia; hereafter referred to as Amdro[®]). Bait stations were used to minimize impacts of the treatment on non-target invertebrates, while effectively reducing numbers of *S. papuana*. The station design, described in Chapter 1, allowed access to *S. papuana* workers but excluded most other invertebrates. A total of 81 bait stations were spaced 2.5 m apart in a grid pattern in each plot (Fig. 3.1), beginning in mid-April to early May of 2015, and Amdro[®] bait inside the stations was replaced every 4-8 weeks, for a total of eight times over the course of the one-year study (Fig. 3.2). During each of the first three bait replacement events, stations were systematically shifted 1.25 m, such that each point on a 1.25 m-spaced grid in the plot received a station once. Subsequently, stations were returned to their original positions (as indicated on Fig. 3.1) where they remained for the rest of the study period, except when they were occasionally moved to target increases in ant numbers detected within the plot.

Ant densities were monitored in the plots using peanut butter-baited monitoring cards. A smear of peanut butter was placed on each of 44 cards (one-half of a 7.6 x 12.7 cm index card) spaced systematically throughout the plots (16 cards were used in the two smaller plots) (Fig. 3.1) for 90 minutes, after which ants on the top and bottom of the cards were counted and summed. Ants were monitored at the beginning of the experiment (pre-treatment), and every 4-8 weeks subsequently on the same dates that Amdro[®] was replaced in the bait stations (Fig. 3.2).

Ground-dwelling invertebrates were sampled in each plot using pitfall traps and leaf litter extraction. Both sample types were collected at five fixed points within the central portion of the plots (Fig. 3.1) on three occasions: immediately before, six months after, and one year after ant suppression was initiated. Litter samples were obtained by collecting approximately 3-4 L of leaf litter from an area extending 1 m around the sampling point, removing 2 L of this litter in the lab, and placing the resultant sample in a Berlese funnel for approximately 72 hours. Pitfall traps consisted of 10 oz. plastic cups (#TP10D, Solo[®] Cup Company, Lake Forest, Illinois) buried flush with the ground, partially filled with a 50% propylene glycol and 50% water solution, and shaded with a square plastic cover. Pitfalls were opened for seven days during each sampling event.

Invertebrate Identification

Invertebrate samples were sorted to the following taxonomic levels. Snails were not identified beyond the class Gastropoda. Arthropods were sorted to class or subclass (in the case of Acari, Chilopoda and Diplopoda) or order (remaining groups), then individuals in Araneae, Blattodea, Chilopoda, Coleoptera, Dermaptera, Diplopoda, and Hemiptera were identified to species or morphospecies, using taxonomic keys and by comparing with University of Hawai'i Insect Museum and other reference specimens from the Wai'anae Mountain Range. If immature individuals in these latter groups could not be identified to species or morphospecies, they were sorted to the lowest taxonomic level possible; subsequently, immatures identified to at least genus or family were allocated to species in proportion to the number of adults of species of the same taxonomic group occurring in the sample. All individuals were then classified as native, introduced, or of unknown origin based on Nishida (2002) and other taxonomic literature.

Data Analysis

Differences in ant densities between treatment and control plots for each plot pair were assessed for each monitoring date using a Median test on ant abundances found on peanut butter monitoring cards (n=44 for each plot pair, except 'Ēkahanui B for which n=16). To test for differences in overall invertebrate community composition among treatment and control plots during each sampling event, I used Blocked Multi-response Permutation Procedure (MRBP) analysis on taxon-by-plot matrices for both pitfall trap and litter extraction samples. MRBP is a variation of MRPP (Multi-response Permutation Procedure) that uses blocked sample data; in my case the blocking factor was the plot pair. It is a non-parametric permutation method that tests the differences among groups of sample units based on within-group similarities (Peck 2016), and calculates a test statistic (T), an effect size (A) that measures the chance-corrected within-group agreement, and a p-value that indicates the probability of obtaining the test statistic by chance. The effect size A is 0 when the heterogeneity within groups is the same as expected by chance, equals 1 when all items are identical within groups, and is <0 when there is less agreement within groups than expected by chance (McCune and Grace 2002). A becomes larger as between-group differences increase, and is commonly below 0.1 in community ecology (McCune and Grace 2002). An A -value equal to or greater than 0.4 is considered a large effect (Peck 2016). For this analysis, samples for each collecting method were pooled by plot (n=12), and abundances of taxa in the plots were log transformed and relativized by the largest value in the plot. Log transformation reduces the influence of highly abundant taxa in the samples, and relativization by plot totals places more emphasis on differences in species' relative abundances among samples rather than on absolute differences in species or total community abundances among samples (Peck 2016). Two missing pitfall samples were represented in the pooled data sets with dummy samples created by averaging the remaining four pitfall samples in the plots. All invertebrates in the samples were included at the lowest taxonomic level available, as described in the Invertebrate Identification section above. For example, Acari were grouped at the subclass level, Diptera were grouped at the order level, and Coleoptera were included at the species/morphospecies level. *Solenopsis papuana* individuals were excluded from the samples for these analyses. Euclidean distance was used as the metric of similarity among plots.

For all MRBP comparisons that indicated statistically significant differences in invertebrate community composition between treatment and control plots, I subsequently conducted a Blocked Indicator Species Analysis (BISA) on the taxon-by-plot matrices to assess

which taxa contributed most strongly to these differences. BISA creates an indicator value (IV) by combining the relative abundance and relative frequency of each taxon within plots of each treatment group, and calculates a p-value that measures the probability of obtaining the indicator value using a Monte Carlo method (Peck 2016). BISA therefore highlights taxa that were unusually abundant or prevalent, or both, within plots of a given treatment group. Matrices for BISA used untransformed and unrelativized abundance data, because each taxon is analyzed separately. MRBP and BISA analyses were performed in PC-ORD 7.02 (McCune and Mefford 2011).

To assess whether invertebrates in major taxonomic groups changed in abundance in the treatment plots relative to the control plots after ant suppression, I calculated abundance changes from the pre-treatment sampling event to the six-month and one year post-treatment sampling events, for both pitfall and leaf litter samples. Invertebrates were grouped at the class or order level, and groups that were sorted and identified to the species/morphospecies level were further subdivided according to native or introduced provenance. Up to three abundance change calculations were therefore possible for each group: native individuals, introduced individuals, and total individuals (which included native, introduced and unknown provenance individuals). I also calculated changes in abundance among all Arthropoda combined, as well as all native and all introduced Arthropoda combined. For Hymenoptera, *S. papuana* individuals were excluded, but other ants (Formicidae) were analyzed as a separate category to assess whether suppression of *S. papuana* led to changes in abundances of other ants. Changes for each time period (six-month, one-year) and each sample type (pitfall, litter) were then analyzed with linear mixed models, in which abundance change was the response, treatment was included as a fixed explanatory effect, and plot nested within treatment was included as a random effect to accommodate the subsampling within each plot. Separate models were constructed for each taxonomic grouping described above, except for a minority of cases in which the distribution of the data did not meet assumptions for parametric linear models; the latter groups were not analyzed.

I calculated and analyzed changes in species richness in an analogous fashion to that described for changes in abundance, for the following taxonomic groups that were sorted and identified to species/morphospecies: Araneae, Chilopoda, Diplopoda, Blattodea, Coleoptera, Dermaptera and Hemiptera. I also calculated changes in richness among all arthropods; for this

calculation I included each class or order that was not sorted to lower levels as a single taxon. Changes in abundance and species richness were analyzed using JMP Pro 13 (SAS 1989-2007). Because statistical power was relatively low for these analyses ($n = 12$ plots), I considered p-values between 0.05 and 0.1 to be marginally significant, and p-values below 0.05 to be significant. I did not adjust α for the many comparisons conducted, but I discuss results in relation to the number of statistically significant results expected by chance, based on the number of analyses run.

To characterize specific taxa that had the most consistent responses to the ant suppression treatment, I identified all taxa that either consistently increased or consistently decreased in relative abundance over both time intervals and for both sampling methods. Relative abundance changes were calculated as the mean abundance change averaged over all samples in all treatment plots in a given time interval and sample type, minus the corresponding mean abundance change averaged over all samples in all control plots. For these taxa, I also calculated the percent abundance change as a measure of effect size, by dividing the relative abundance changes in the treatment plots by their corresponding pre-ant suppression mean abundance values and converting to a percentage.

Results

A total of 89,212 individual invertebrates were collected during this experiment, which were classified into 169 taxa. Of these taxa, 24% were native, 51% were introduced, and 25% were of unknown origin. Sixteen percent of the taxa were found exclusively in pitfalls, and 29% were found exclusively in litter. The majority of the individuals (59,668, 67%) were caught in litter samples. In the litter samples, 20% of individuals (12,185) belonged to introduced species, 1% (735) belonged to native species, and 78% (46,748) belonged to species of unknown origin. The majority of the unknown individuals were made up of Acari (20,340 or 44%) and Isopoda (15,520 or 33%). Of the 29,544 individuals caught in pitfall traps, 67% (19,865) were introduced species, 2% (526) were native, and 31% (9,153) were of unknown origin. A majority of the introduced individuals were the amphipod, *Talitroides topitotum* (13,016 or 66%), while the majority of the unknown individuals were made up of Isopoda (4,357 or 48%) and Collembola (2,656 or 29%).

Ant densities

Ant densities in treatment and control plots were not significantly different prior to ant suppression at four of the six study sites, according to Median test results (Figure 2). However, ant densities were initially significantly higher in the treatment plot at Kahanahāiki A site ($\chi^2 = 9.83$, $p = 0.002$), and were initially significantly higher in the control plot at 'Ēkahanui A ($\chi^2 = 6.47$, $p = 0.011$) (Figure 2). After ant suppression was initiated, median tests indicated that ant densities were significantly different between treatment and control plots from the first or second monitoring event onwards at five of the six study sites (Figure 2). At Kahanahāiki A site, however, ant densities did not significantly differ between treatment and control plots on eight of the nine post-treatment ant monitoring dates. Kahanahāiki A site did not have very many ants in either plot type throughout most of the experiment.

Invertebrate community composition

The MRBP analyses showed that invertebrate community composition was not significantly different between the treatment and control plots prior to ant suppression ($A = 0.0053$, $p = 0.3509$ for litter samples; $A = 0.0016$, $p = 0.4732$ for pitfall samples; Table 3.1). After ant suppression was initiated, invertebrate communities were also not significantly

different between treatment and control plots, with the exception of communities sampled with pitfall traps at one-year post treatment ($A = 0.0280$, $p = 0.0483$; Table 3.1). In litter samples, the effect size (A) did not increase over time, suggesting that litter communities in treatment and control plots were not diverging from one another. In contrast, in pitfall samples, A values became increasingly larger over time, indicating greater between-group separation, until treatment and control groups were significantly different one year after ant suppression was initiated. However, a BISA analysis of the 91 taxa occurring in the one-year post-treatment pitfall samples only identified one individual taxon (Collembola) that was marginally significantly more prevalent or abundant (or both) in treatment plots than in control plots ($IV = 64.2$, $p = 0.0672$; Table 3.2). It is important to note that among 91 total comparisons, 4-5 significant results (at $\alpha = 0.05$) or 9-10 marginally significant results (at $\alpha = 0.1$) can be expected purely by chance. However, it is also notable that eight of the nine taxa with the highest indicator values were more commonly present or abundant in treatment plots than in control plots (although not significantly so, Table 3.2), with only one taxon showing the reverse pattern. This suggests that the significant overall community composition divergence between treatment and control plots as measured with pitfall sampling at one-year post-suppression (MRBP analysis above) was caused by relatively weak differences among a wide range of taxa, rather than by strong differences among a few taxa.

Changes in invertebrate abundance and species richness

In the following summaries, statements of relative increases in abundance or species richness in treatment plots following ant suppression include larger positive changes as well as smaller negative changes, when compared to control plots. For both leaf litter and pitfall samples, there were few abundance changes that were significantly different between treatment and control plots (Tables 3 and 4). In litter samples, significant or marginally significant abundance increases in treatment plots, relative to control plots, occurred among total Coleoptera ($F=4.82$, $p=0.0528$), introduced and total Hemiptera ($F=3.60$, $p=0.0871$ and $F=5.65$, $p=0.0388$), and all introduced Arthropoda combined ($F=4.60$, $p=0.0577$) at six months post-suppression, and among all introduced Arthropoda combined ($F=4.84$, $p=0.0525$) at one-year post-suppression (Table 3.3). In pitfall samples, significant or marginally significant abundance increases in treatment plots, relative to control plots, occurred among introduced Araneae ($F=7.69$, $p=0.0196$)

and native Hemiptera ($F=4.13$, $p=0.0694$) at six months post-suppression, and among native Orthoptera ($F=3.60$, $p=0.0865$) at one-year post-suppression (Table 3.4). The two significant abundance changes, and five marginally significant abundance changes, listed above are fewer than would be expected purely by chance: among the 117 total comparisons made for leaf litter and pitfall sampling abundance changes (Tables 3.3 and 3.4), one can expect 5-6 significant changes (at $\alpha = 0.05$) and 11-12 marginally significant changes (at $\alpha = 0.1$) by chance. However, it is notable that there were no significant or marginally significant decreases in abundance in the treatment plots relative to the control plots for either sample type and for both time periods post ant-suppression. In addition, 102 of the 117 (87%) total comparisons measured increases of some magnitude in the treatment plots relative to control plots post ant-suppression, although again most of these increases were not statistically significant.

There was only one species richness change post ant-suppression that was significantly different between treatment and control plots for leaf litter samples (Table 3.5), and this was for Blattodea at six months post-suppression ($F=6.43$, $p=0.0296$). All species of Blattodea are introduced. For pitfall samples, significant or marginally significant increases in species richness in treatment plots, relative to control plots, at six months post-suppression occurred for introduced and total Araneae ($F=6.90$, $p=0.0251$ and $F=3.91$, $p=0.0764$), total Diplopoda ($F=5.85$, $p=0.0359$), Blattodea ($F=4.74$, $p=0.0544$), introduced and total Coleoptera ($F=5.96$, $p=0.0347$ and $F=4.11$, $p=0.07$), native Hemiptera ($F=4.13$, $p=0.0694$), and all introduced and total Arthropoda ($F=9.45$, $p=0.0117$ and $F=7.08$, $p=0.0239$) (Table 3.6). At one-year post suppression, significant or marginally significant increases in richness in treatment plot pitfall samples was observed for total Diplopoda ($F=3.95$, $p=0.0748$), introduced and total Coleoptera ($F=7.51$, $p=0.0207$ and $F=14.77$, $p=0.0031$), and all introduced and all Arthropoda ($F=11.54$, $p=0.0067$ and $F=12.84$, $p=0.0049$) (Table 3.6). The 10 listed significant species richness changes, and five marginally significant species richness changes, are more than expected by chance: among the 62 total comparisons made for leaf litter and pitfall sampling species richness changes (Table 3.5 and 3.6), one can expect 3-4 significant ($\alpha = 0.05$) changes and 6-7 marginally significant ($\alpha = 0.1$) changes. There were no significant or marginally significant decreases in species richness in treatment plots relative to control plots after ant suppression (Table 3.5 and 3.6). Furthermore, 46 of the 62 (74%) total comparisons measured increases of

some magnitude in the treatment plots relative to the control plots, although most were not statistically significant.

Twenty-one of the 166 taxa identified (13%) exhibited relative abundance changes that were consistent in direction across both sampling types and at both post-ant suppression monitoring intervals (Table 3.7). Nineteen of these taxa (90%) consistently increased in relative abundance in response to ant suppression, while the remaining two taxa (10%) consistently decreased in abundance in response to ant suppression. One of the latter, the ant *Solenopsis* HI01, is similar in size to *S. papuana* and most likely declined in abundance because it also fed on the Amdro bait. Over half of the taxa that responded consistently to ant suppression are introduced to Hawai‘i, and only 19% of the taxa are known to be native. Many of the changes in relative abundance were quite large when calculated as a percentage change from pre-treatment levels (Table 3.7), suggesting large effect sizes in some cases. However, these percentages should be viewed with some caution, because percentage changes are prone to inflation when the pre-treatment reference values are small. Furthermore, the probabilities of obtaining the measured changes by chance for these individual taxa are unknown.

Discussion

Reducing *Solenopsis papuana* densities and measuring the response in the ground-dwelling invertebrate community showed that this ant is capable of causing significant changes in overall invertebrate community composition, as well as in abundances and species richness of a variety of taxonomic groups. However, these response patterns were not overwhelmingly strong, and while certain individual taxa showed consistent trends in their responses to ant suppression (Table 3.7), responses for larger taxonomic groups were generally not very consistent over the two time periods or between the two sampling methods (Tables 3.3-3.6). The number of statistically significant changes in invertebrate abundance or species richness was often similar to or fewer than expected by chance, although the study design had relatively low statistical power to detect such changes. Nevertheless, it is important to note that all of the significant changes indicated increases in invertebrate abundance or richness in response to ant suppression, with no significant decreases in response to ant suppression. Similarly, 83% of all (including non-significant) abundance or richness changes, across the spectrum of taxonomic groups sampled, indicated relative increases in the ant-suppressed plots. These patterns suggest that most of the measured changes were unlikely to have simply resulted from random sampling error. Instead, they suggest that the effects of *S. papuana* on current invertebrate communities at these sites are relatively broad but also relatively weak.

Within this overall characterization, several more specific patterns were apparent. First, introduced species responded more often than native species to suppression of *S. papuana*. Among native taxa, only Hemiptera and Orthoptera appeared to increase in abundance (Table 3.4). In comparison, introduced Araneae, Hemiptera, and introduced arthropods as a whole increased in abundance (Table 3.3 and 3.4), and introduced Araneae, Diplopoda, Blattodea, Coleoptera, and introduced arthropods as a whole increased in species richness (Table 3.5 and 3.6). A similar study examining ant effects on arboreal arthropod communities in the northern Wai'anae Mountains also found that introduced taxa appeared to benefit more than native taxa from ant absence (Krushelnycky 2015). These results seem to contrast with the more typical findings that native Hawaiian arthropods are highly vulnerable to invasive ants, often more so than introduced species (Cole et al. 1992, Gillespie and Reimer 1993, Liebherr and Krushelnycky 2007, Krushelnycky and Gillespie 2010b). However, this difference may be attributed in part to the high proportion of non-native arthropods occurring in mesic forests in the

Wai‘anae Mountains, as well as to the low taxonomic resolution in the present study and the Krushelnycky (2015) study. Among the soil- and leaf litter-dwelling invertebrates that I was able to identify, very few were native, which may explain the relatively weak response among this portion of the community. At the same time, a large fraction of individuals were not identified below class or order either because of time constraints or because they were immature or belonged to difficult taxonomic groups (e.g. Acari, Collembola, Thysanoptera). These individuals could therefore not be classified as native or introduced, and this may have obscured patterns of more widespread vulnerability among native species. Specific endemic taxa were nevertheless identified as likely vulnerable to ants in my study, such as *Laupala* crickets and the flightless mirid bug, *Nesidiorchestes hawaiiensis*. Vulnerability of *Laupala* crickets to ants has been previously suggested (LaPolla et al. 2000).

Secondly, species richness of invertebrate taxonomic groups responded to ant suppression more strongly than did invertebrate abundances. Only approximately 7% of all groups tested increased significantly or marginally significantly in abundance, whereas about 26% of groups increased in richness. The majority of the species richness increases occurred in pitfall samples (15 compared to 1 in litter samples), with the highest number of significant changes occurring after one year (Tables 3.5 and 3.6). Consistent with these results, overall invertebrate community composition differences between treatment and control plots were significant only in pitfall samples collected one year after ant suppression (Table 3.1). Among arboreal arthropod communities in similar mesic forests, Krushelnycky (2015) also found species richness to be more commonly affected than arthropod abundance by ant presence. Both studies may therefore suggest that assessing abundance changes at higher levels like class or order might obscure finer patterns occurring at the species level. Although my BISA analysis on one-year post-suppression pitfall samples failed to identify any individual species that demonstrated a statistically significant individual response to the treatment, more informal inspection of patterns within the entire data set identified 17 species that exhibited consistent directional responses to the ant suppression (Table 3.7). In addition to the native species mentioned above, two other invasive ant species (*Nylanderia bourbonica* and *Technomyrmex albipes*) present at the study sites consistently increased in abundance after *S. papuana* densities were reduced.

Several additional factors related to the design of this study may have contributed to the absence of a stronger or more consistent response among invertebrates to the suppression of *S.*

papuana. As mentioned above, statistical power to detect responses was relatively low, with only 12 total plots. However, establishing and maintaining even this number of independent replicate plots was laborious and logistically difficult; obtaining greater statistical power with this study design would be challenging. A longer study duration may also have allowed a stronger community response. The decrease in similarity of the community compositions of pitfall samples over time suggests that this may be the case, although most other measures did not generally support a conclusion of strengthening responses from six months to one year after ant suppression was initiated. Another factor concerns sampling methods: additional sampling techniques may have also detected effects on species that are not well sampled with pitfall traps or leaf litter extraction. Finally, while initial scouting suggested that all of the study sites should support moderate to high densities of *S. papuana*, densities of ants were not very high in several of the treatment plots during part or most of the study period (Fig. 3.2). This would naturally weaken my ability to measure the ant's effects.

An additional important limitation, however, may have to do with the experimental manipulation design itself, at least as employed in this setting. Impacts of invasive ants on arthropods have commonly been assessed using observational studies, in which arthropod communities are compared between invaded sites and similar uninvaded sites nearby (Porter & Savignano 1990, Cole et al. 1992, Holway 1998, Hoffmann et al. 1999, Hoffmann & Parr 2008; Krushelnycky & Gillespie 2008). This approach has the advantage of comparing patterns between relatively large contiguous blocks of invaded and uninvaded habitats, using ostensibly intact and diverse uninvaded communities as the baseline. Its disadvantage, however, is that the ant distribution may be correlated with habitat differences that independently influence the arthropod communities in invaded and uninvaded sites, and this may partially confound any measured differences that are attributed to ant presence. Experimental manipulations are typically regarded as superior to observational studies in terms of inferential power and statistical rigor, but they also have practical drawbacks in ecological studies of this type (Krushelnycky and Gillespie 2010a). In my case, detecting a negative effect of *S. papuana* on invertebrate taxa relied on these taxa increasing in abundance or incidence in the treatment plots. Yet, for species that may already be rare or absent in the wider area, owing to their vulnerability to *S. papuana* or other non-native species, the likelihood of colonizing the treatment plots and increasing in density sufficient to be detected may be quite low. A larger plot size may increase this likelihood

to some degree, but larger plots were not feasible in the terrain under study, and because *S. papuana* is already so widespread, it is unclear how much this would help. Rare species are much more vulnerable to invasive ants than are more abundant species, and they also make up the majority of arthropod diversity (Krushelnycky and Gillespie 2010b). To the extent that *S. papuana* may have already eliminated or strongly suppressed rare species within the wider regions around the study sites, the experimental manipulation design would likely underestimate its negative effects on such species.

The foregoing points are illustrated by a related study in which eggs of the endemic picture-winged fly, *Drosophila crucigera*, were added to plots in which *S. papuana* was suppressed (Krushelnycky et al. 2017). Emergence rates of adult flies were 2.4 times higher in these plots than in untreated control plots, indicating a strong negative effect of *S. papuana* on fly reproductive success, and presumably on population levels. This vulnerability was not detected in the present study, in which only two *D. crucigera* flies were captured. Similar experimental introductions of other rare species into treated and control plots might reveal impacts on additional species, but this approach has limitations for characterizing community-level effects.

In conclusion, the results show that *S. papuana* negatively affects both native and introduced ground-dwelling invertebrates, but does not appear to play a major role in altering invertebrate community compositions in their current states at the study sites. Although the study suggests that impacts are greater for introduced species, this is likely a consequence of the high abundance and diversity of non-native species in contemporary communities. Rare native invertebrates may also be impacted, but this is now difficult to demonstrate with generalized sampling methods. While it is not feasible to completely eradicate *S. papuana* from the Wai‘anae Mountains, the results from this study may help land managers decide if controlling this ant in small areas may help conserve other invertebrate species.

Table 3.1. Results from MRBP analyses comparing overall invertebrate community compositions between treatment and control plots in three sampling events: before, six months after, and one year after ant suppression was initiated. *A* is the effect size, which measures within-group similarity (and therefore estimates between-group separation), and *p* is the probability of obtaining the observed within-group similarity by chance. Bold and italicized numbers indicate significant ($p < 0.05$) statistical results.

Event	Litter		Pitfall	
	<i>A</i>	<i>p</i>	<i>A</i>	<i>p</i>
Before	0.0053	0.3509	0.0016	0.4732
Six months after	-0.0015	0.5681	0.0029	0.3847
One year after	-0.0176	0.9705	0.0280	<i>0.0483</i>

Table 3.2. Taxa with the 9 highest (top 10%) indicator values in the BISA analysis conducted on the one-year post-suppression pitfall samples (n = 91 taxa analyzed). Shown are the indicator values (IV, range 0 to 100), which measure the degree to which a taxon occurred more frequently or at higher abundance, or both, in either the treatment or control group plots; the treatment group favored; and the probability (p) of exhibiting the measured degree of distributional asymmetry between groups by chance. Italicized numbers indicate marginally significant ($p < 0.1$) statistical results.

Order	Taxon	IV	Group favored	p
Amphipoda	<i>Talitroides topitotum</i>	58.4	Treatment	0.1296
Araneae	Linyphiidae sp. 4	61.7	Treatment	0.2541
Coleoptera	<i>Cryptomorpha desjardinsii</i>	61.1	Treatment	0.1240
Coleoptera	All Staphylinidae species	62.4	Treatment	0.2248
Coleoptera	<i>Sericoderus ?pubipennis</i>	66.7	Control	0.2410
Coleoptera	Immatures, all species	62.5	Treatment	0.2180
Collembola	All Collembola species	64.2	Treatment	<i>0.0672</i>
Hemiptera	<i>Rhytidoporus indentatus</i>	64.4	Treatment	0.1548
Polydesmida	Pyrgodesmidae sp.	67.3	Treatment	0.1290

Table 3.3. Mean (\pm SE) invertebrate abundance changes in litter samples in treatment and control plots post ant suppression. Marginally significant ($p < 0.1$) increases in treatment plots relative to control plots italicized; significant ($p < 0.05$) increases in treatment plots relative to control plots italicized and bolded. There were no marginally significant or significant decreases in treatment plots relative to control plots. All comparisons made using linear mixed models

	Litter Abundance Changes, 6 mo.			Litter Abundance Changes, 1 yr.		
	Control	Treatment	p	Control	Treatment	p
Gastropoda	0.3 \pm 0.32	0.6 \pm 0.32	0.5222	-0.1 \pm 0.22	0.1 \pm 0.22	0.5785
Amphipoda	55.70 \pm 13.09	75.37 \pm 13.09	0.3132	2.20 \pm 5.00	7.3 \pm 5.00	0.4864
Isopoda	58.53 \pm 38.66	99.13 \pm 38.66	0.4749	9.67 \pm 18.75	11.4 \pm 18.75	0.9492
Chilopoda	0.30 \pm 0.42	0.73 \pm 0.42	0.4842	0.5 \pm 0.17	0.1 \pm 0.17	0.1258
Diplopoda	9.03 \pm 2.98	11.37 \pm 2.98	0.5923	4.27 \pm 2.73	4.83 \pm 2.73	0.8863
Acari	119.83 \pm 107.05	266.57 \pm 107.05	0.3553	79.7 \pm 33.51	67.0 \pm 33.51	0.7942
Araneae						
native	-0.67 \pm 0.6	-0.27 \pm 0.6	0.6471	-0.5 \pm 0.68	-0.47 \pm 0.68	0.9731
introduced				2.37 \pm 1.68	2.63 \pm 1.68	0.9101
total	8.03 \pm 3.5	10.1 \pm 3.5	0.6892	1.97 \pm 2.08	4.27 \pm 2.08	0.4523
Blattodea	0.1 \pm 0.34	0.77 \pm 0.34	0.1945	0.03 \pm 0.4	0.64 \pm 0.4	0.3115
Coleoptera						
native	0.7 \pm 0.45	1.3 \pm 0.45	0.3674	0.7 \pm 0.46	0.97 \pm 0.46	0.6918
introduced	1.97 \pm 1.58	3.27 \pm 1.58	0.5733	1.03 \pm 1.74	1.63 \pm 1.74	0.8119
total	2.0 \pm 1.7	7.2 \pm 1.7	0.0528	7.0 \pm 6.12	13.37 \pm 6.12	0.4786
Collembola	27.93 \pm 20.52	45.7 \pm 20.52	0.5540	20.27 \pm 11.82	27.67 \pm 11.82	0.6675
Diptera	6.43 \pm 4.79	12.13 \pm 4.79	0.4202	6.67 \pm 4.46	1.7 \pm 4.46	0.4495
Dermaptera						
introduced	0.9 \pm 0.48	0.93 \pm 0.48	0.9614	1.0 \pm 0.3	0.27 \pm 0.3	0.1150
total	0.77 \pm 0.46	0.9 \pm 0.46	0.8410	0.87 \pm 0.25	0.23 \pm 0.25	0.1042

Table 3.3. (Continued) Mean (\pm SE) invertebrate abundance changes in litter samples in treatment and control plots post ant suppression. Marginally significant ($p < 0.1$) increases in treatment plots relative to control plots italicized; significant ($p < 0.05$) increases in treatment plots relative to control plots italicized and bolded. There were no marginally significant or significant decreases in treatment plots relative to control plots. All comparisons made using linear mixed models.

	Litter Abundance Changes, 6 mo.			Litter Abundance Changes, 1 yr.		
	Control	Treatment	p	Control	Treatment	p
Hemiptera						
native	-1.93 \pm 0.85	-1.43 \pm 0.85	0.6876	0.6 \pm 0.96	1.03 \pm 0.96	0.7570
introduced	<i>-1.5 \pm 0.91</i>	<i>0.93 \pm 0.91</i>	<i>0.0871</i>	<i>-2.77 \pm 7.23</i>	<i>12.8 \pm 7.23</i>	<i>0.1591</i>
total	<i>-3.53 \pm 0.88</i>	<i>-0.57 \pm 0.88</i>	<i>0.0388</i>	<i>0.1 \pm 2.70</i>	<i>5.93 \pm 2.70</i>	<i>0.1581</i>
Hymenoptera						
Formicidae	-1.03 \pm 5.98	2.43 \pm 5.98	0.6904			
total	-1.0 \pm 5.94	2.43 \pm 5.94	0.6916	<i>-2.63 \pm 7.25</i>	<i>12.77 \pm 7.25</i>	<i>0.1639</i>
Lepidoptera						
native	0.57 \pm 0.22	0.57 \pm 0.22	1.0	0.13 \pm 0.15	0.3 \pm 0.15	0.4442
total	0.27 \pm 0.83	0.97 \pm 0.83	0.5621	2.6 \pm 1.05	3.9 \pm 1.05	0.4007
Orthoptera						
native	-0.07 \pm 0.12	0.03 \pm 0.12	0.5737	0.07 \pm 0.15	0.1 \pm 0.15	0.8766
total	-0.07 \pm 0.12	0.07 \pm 0.12	0.4608	0.07 \pm 0.15	0.1 \pm 0.15	0.8766
Psocoptera	-0.3 \pm 1.17	-2.47 \pm 1.17	0.2188	2.0 \pm 1.9	-0.9 \pm 1.9	0.3037
Thysanoptera	-4.67 \pm 4.02	-0.93 \pm 4.02	0.5264	6.17 \pm 5.33	6.43 \pm 5.33	0.9725
Arthropoda						
native	-1.53 \pm 1.42	0.17 \pm 1.42	0.4166	0.87 \pm 0.77	1.9 \pm 0.77	0.3669
introduced	<i>70.0 \pm 10.86</i>	<i>102.93 \pm 10.86</i>	<i>0.0577</i>	<i>8.07 \pm 8.69</i>	<i>35.1 \pm 8.69</i>	<i>0.0525</i>
total	279.67 \pm 160.06	530.13 \pm 160.06	0.2944	141.33 \pm 58.44	166.9 \pm 58.44	0.7634

Table 3.4. Mean (\pm SE) invertebrate abundance changes in pitfall samples in treatment and control plots post ant suppression. Marginally significant ($p < 0.1$) increases in treatment plots relative to control plots italicized; significant ($p < 0.05$) increases in treatment plots relative to control plots italicized and bolded. There were no marginally significant or significant decreases in treatment plots relative to control plots. All comparisons made using linear mixed models.

	Pitfall Abundance Changes, 6 mo.			Pitfall Abundance Changes, 1 yr.		
	Control	Treatment	p	Control	Treatment	p
Gastropoda	0.10 \pm 0.34	0.23 \pm 0.33	0.7861	0.41 \pm 0.47	0.4 \pm 0.46	1.0
Amphipoda	-89.28 \pm 56.02	-77.2 \pm 54.89	0.8309	-78.35 \pm 45.53	-65.17 \pm 44.61	0.8125
Isopoda				-5.69 \pm 8.98	11.57 \pm 8.80	0.2221
Chilopoda	0.0 \pm 0.11	-0.03 \pm 0.11	0.8392	-0.03 \pm 0.16	-0.03 \pm 0.16	1.0
Diplopoda	-5.31 \pm 1.12	-3.7 \pm 1.10	0.3574	-2.59 \pm 1.78	1.37 \pm 1.75	0.1792
Acari	-5.38 \pm 3.91	-1.93 \pm 3.83	0.5570	-2.86 \pm 3.68	-0.13 \pm 3.61	0.6423
Araneae						
native	0.03 \pm 0.2	-0.07 \pm 0.2	0.7711	-0.14 \pm 0.28	0.1 \pm 0.27	0.5357
introduced	<i>-0.48 \pm 0.31</i>	<i>0.67 \pm 0.3</i>	<i>0.0196</i>	0.66 \pm 0.37	0.8 \pm 0.36	0.8150
total	-2.03 \pm 1.2	-0.63 \pm 1.17	0.4100	-0.83 \pm 1.40	-0.23 \pm 1.37	0.7724
Blattodea	-0.41 \pm 0.53	0.5 \pm 0.52	0.2336	-0.38 \pm 0.24	-0.2 \pm 0.24	0.5840
Coleoptera						
introduced	-25.14 \pm 12.08	-14.4 \pm 11.84	0.5542	-17.21 \pm 12.52	5.53 \pm 12.27	0.2379
total	-25.52 \pm 12.50	-15.17 \pm 12.45	0.5813	-15.72 \pm 15.08	9.83 \pm 14.78	0.2664
Collembola	-4.62 \pm 5.75	-3.63 \pm 5.63	0.9115	-0.10 \pm 3.85	9.6 \pm 3.77	0.1175
Dermaptera						
native	-1.59 \pm 0.89	-1.07 \pm 0.87	0.5672	-1.10 \pm 0.86	-0.4 \pm 0.83	0.4641
introduced	-1.62 \pm 0.88	-1.4 \pm 0.87	0.8082	0.10 \pm 1.11	0.3 \pm 1.08	0.8915
total	-3.21 \pm 1.37	-2.47 \pm 1.34	0.5988	-1.0 \pm 1.52	-0.1 \pm 1.49	0.6065
Diptera	-0.17 \pm 0.73	-0.57 \pm 0.72	0.7040			

Table 3.4. (Continued) Mean (\pm SE) invertebrate abundance changes in pitfall samples in treatment and control plots post ant suppression. Marginally significant ($p < 0.1$) increases in treatment plots relative to control plots italicized; significant ($p < 0.05$) increases in treatment plots relative to control plots italicized and bolded. There were no marginally significant or significant decreases in treatment plots relative to control plots. All comparisons made using linear mixed models.

	Pitfall Abundance Changes, 6 mo.			Pitfall Abundance Changes, 1 yr.		
	Control	Treatment	p	Control	Treatment	p
Hemiptera						
<i>native</i>	<i>-0.07 \pm 0.08</i>	<i>0.17 \pm 0.08</i>	<i>0.0694</i>	-0.03 \pm 0.15	0.2 \pm 0.14	0.2667
<i>introduced</i>				<i>-5.55 \pm 7.97</i>	10.9 \pm 7.80	0.1777
<i>total</i>				<i>-5.62 \pm 7.95</i>	10.9 \pm 7.79	0.1744
Hymenoptera						
Formicidae	-1.45 \pm 0.91	-0.97 \pm 0.89	0.6309	-0.97 \pm 0.94	-0.73 \pm 0.93	0.7499
<i>total</i>	<i>-1.45 \pm 0.89</i>	<i>-0.77 \pm 0.88</i>	<i>0.5185</i>	<i>-0.86 \pm 0.90</i>	<i>-0.4 \pm 0.89</i>	<i>0.6142</i>
Lepidoptera						
<i>native</i>	0.76 \pm 0.40	0.6 \pm 0.39	0.8401	-0.03 \pm 0.15	0.13 \pm 0.15	0.3825
<i>total</i>	0.41 \pm 0.46	0.9 \pm 0.45	0.4153	0.10 \pm 0.34	0.7 \pm 0.33	0.2192
Orthoptera						
<i>native</i>	-0.45 \pm 0.56	0.7 \pm 0.55	0.1794	<i>-0.45 \pm 0.28</i>	<i>0.3 \pm 0.27</i>	<i>0.0865</i>
<i>total</i>	<i>-0.45 \pm 0.7</i>	<i>0.93 \pm 0.68</i>	<i>0.1905</i>			
Psocoptera	-0.07 \pm 0.08	0.03 \pm 0.08	0.4145	-0.03 \pm 0.11	0.17 \pm 0.11	0.2257
Thysanoptera	-0.03 \pm 0.09	0.03 \pm 0.08	0.6865	-0.10 \pm 0.11	0.13 \pm 0.11	0.1637
Arthropoda						
<i>native</i>	-2.31 \pm 1.7	-1.53 \pm 1.66	0.6706	-2.52 \pm 0.56	-1.57 \pm 1.53	0.6009
<i>introduced</i>	-129.79 \pm 52.60	-97.17 \pm 51.54	0.6222	-104.59 \pm 46.41	-47.5 \pm 45.47	0.3909
<i>total</i>	-170.34 \pm 63.42	-106.1 \pm 62.14	0.4494	-118.03 \pm 50.29	-22.97 \pm 49.27	0.2076

Table 3.5. Mean (\pm SE) invertebrate richness changes in litter samples in treatment and control plots post ant suppression. Marginally significant ($p < 0.1$) increases in treatment plots relative to control plots italicized; significant ($p < 0.05$) increases in treatment plots relative to control plots italicized and bolded. There were no marginally significant or significant decreases in treatment plots relative to control plots. All comparisons made using linear mixed models.

	Litter Species Richness Changes, 6 mo.			Litter Species Richness Changes, 1 yr.		
	Control	Treatment	p	Control	Treatment	p
Chilopoda	0.2 \pm 0.14	0.23 \pm 0.14	0.8684	0.4 \pm 0.13	0.07 \pm 0.13	0.1114
Diplopoda				0.33 \pm 0.25	0.5 \pm 0.25	0.6493
Araneae						
native	-0.07 \pm 0.14	0.07 \pm 0.14	0.5245	-0.13 \pm 0.19	-0.03 \pm 0.19	0.7125
introduced	0.57 \pm 0.2	0.7 \pm 0.2	0.6484	0.43 \pm 0.27	0.27 \pm 0.24	0.6374
total	0.93 \pm 0.39	1.17 \pm 0.39	0.6786	0.6 \pm 0.38	0.43 \pm 0.38	0.7608
Blattodea	<i>-0.07 \pm 0.06</i>	<i>0.13 \pm 0.06</i>	<i>0.0296</i>	0.03 \pm 0.07	0.1 \pm 0.07	0.5413
Coleoptera						
native	0.33 \pm 0.15	0.47 \pm 0.15	0.5490	0.47 \pm 0.23	0.3 \pm 0.23	0.6269
introduced	0.93 \pm 0.21	0.93 \pm 0.21	1.0000	0.7 \pm 0.17	0.67 \pm 0.17	0.8943
total	1.37 \pm 0.33	2.07 \pm 0.33	0.1701	0.13 \pm 0.42	0.15 \pm 0.42	0.6996
Dermaptera	0.5 \pm 0.2	0.13 \pm 0.2	0.2269	0.4 \pm 0.13	0.17 \pm 0.13	0.2456
Hemiptera						
native	-0.23 \pm 0.11	-0.13 \pm 0.11	0.5350	0.13 \pm 0.09	0.0 \pm 0.09	0.3035
introduced	0.1 \pm 0.23	0.4 \pm 0.23	0.3842			
total	-0.23 \pm 0.56	0.2 \pm 0.26	0.2601	0.13 \pm 0.22	0.13 \pm 0.22	1.000
Arthropoda						
native	0.3 \pm 0.25	0.67 \pm 0.25	0.3219	0.57 \pm 0.32	0.5 \pm 0.32	0.8853
introduced	3.27 \pm 0.75	4.0 \pm 0.75	0.5045	2.63 \pm 0.91	2.43 \pm 0.91	0.8799
total	4.53 \pm 1.09	6.3 \pm 1.09	0.2788	4.73 \pm 1.50	5.0 \pm 1.50	0.9028

Table 3.6. Mean (\pm SE) invertebrate richness changes in pitfall samples in treatment and control plots post ant suppression. Marginally significant ($p < 0.1$) increases in treatment plots relative to control plots italicized; significant ($p < 0.05$) increases in treatment plots relative to control plots italicized and bolded. There were no marginally significant or significant decreases in treatment plots relative to control plots. All comparisons made using linear mixed models.

	Pitfall Species Richness Changes, 6 mo.			Pitfall Species Richness Changes, 1 yr.		
	Control	Treatment	p	Control	Treatment	p
Chilopoda	-0.03 \pm 0.1	-0.03 \pm 0.1	1.0	-0.07 \pm 0.12	-0.1 \pm 0.12	0.8468
Diplopoda	<i>-0.76 \pm 0.14</i>	<i>-0.3 \pm 0.01</i>	<i>0.0359</i>	<i>-0.38 \pm 0.21</i>	<i>0.23 \pm 0.21</i>	<i>0.0748</i>
Araneae						
native	-0.10 \pm 0.12	0.07 \pm 0.12	0.3116	-0.14 \pm 0.14	0.07 \pm 0.14	0.3052
introduced	<i>-0.41 \pm 0.23</i>	<i>0.4 \pm 0.22</i>	<i>0.0251</i>	0.07 \pm 0.17	0.47 \pm 0.17	0.1279
total	<i>-0.79 \pm 0.43</i>	<i>0.33 \pm 0.42</i>	<i>0.0764</i>	-0.10 \pm 0.39	0.5 \pm 0.38	0.2996
Blattodea	<i>-0.28 \pm 0.15</i>	<i>0.17 \pm 0.15</i>	<i>0.0544</i>	-0.14 \pm 0.08	0.0 \pm 0.08	0.1936
Coleoptera						
native	-0.34 \pm 0.13	-0.2 \pm 0.13	0.4232	-0.14 \pm 0.14	-0.2 \pm 0.14	0.7691
introduced	<i>-1.24 \pm 0.31</i>	<i>-0.2 \pm 0.31</i>	<i>0.0347</i>	<i>-0.38 \pm 0.24</i>	<i>0.53 \pm 0.24</i>	<i>0.0207</i>
total	<i>-1.21 \pm 0.38</i>	<i>-0.17 \pm 0.37</i>	<i>0.0700</i>	<i>-0.10 \pm 0.18</i>	<i>0.87 \pm 0.18</i>	<i>0.0031</i>
Dermaptera	-0.76 \pm 0.15	-0.57 \pm 0.15	0.8811	-0.21 \pm 0.11	-0.23 \pm 0.11	0.9165
Hemiptera						
native	<i>-0.07 \pm 0.08</i>	<i>0.17 \pm 0.08</i>	<i>0.0694</i>	-0.03 \pm 0.11	0.13 \pm 0.11	0.2943
introduced	-0.38 \pm 0.28	-0.3 \pm 0.28	0.8219	-0.07 \pm 0.20	0.21 \pm 0.2	0.2549
total	-0.55 \pm 0.35	-0.17 \pm 0.34	0.4428	<i>-0.21 \pm 0.24</i>	<i>0.47 \pm 0.23</i>	<i>0.0651</i>
Arthropoda						
native	-0.79 \pm 0.43	0.13 \pm 0.42	0.1380	-0.72 \pm 0.41	-0.1 \pm 0.4	0.2722
introduced	<i>-3.9 \pm 0.75</i>	<i>-0.8 \pm 0.73</i>	<i>0.0117</i>	<i>-1.17 \pm 0.51</i>	<i>1.2 \pm 0.5</i>	<i>0.0067</i>
total	<i>-5.28 \pm 1.41</i>	<i>-0.2 \pm 1.38</i>	<i>0.0239</i>	<i>-1.41 \pm 0.76</i>	<i>2.33 \pm 0.74</i>	<i>0.0049</i>

Table 3.7. Relative average abundance changes in treatment plots relative to control plots for 21 taxa that exhibited consistent directional responses to ant suppression for both time intervals and both sampling methods. Only two taxa, which are italicized, decreased in relative abundance in treatment plots after ant suppression. Also shown in parentheses is the percent change in abundance in treatment plots relative to pre-treatment values, a measure of effect size. “NA” indicates that the taxon was not captured in pre-treatment samples.

	Relative change 6 months		Relative change 1 year	
	Litter	Pitfall	Litter	Pitfall
Introduced Taxa				
Amphipoda				
<i>Talitroides topitotum</i>	98.3 (265%)	66.5 (11%)	25.5 (69%)	85 (14%)
Araneae				
<i>Camelina elegans</i>	0.2 (200%)	0.5 (100%)	0.2 (200%)	0.7 (133%)
<i>Dysdera crocata</i>	1.0 (120%)	1.2 (233%)	0.8 (100%)	0.8 (167%)
<i>Ostearius melanopygius</i>	1.5 (NA)	0.17 (200%)	0.2 (NA)	0.5 (600%)
Blattodea				
<i>Blatella lituricollis</i>	0.5 (150%)	3.5 (420%)	3.12 (950%)	1.8 (220%)
Coleoptera				
<i>Coccytropes advena</i>	4.8 (118%)	0.5 (120%)	2.2 (53%)	1 (240%)
<i>Stelidota geminata</i>	6.3 (143%)	33.8 (76%)	6.7 (151%)	84.5 (190%)
Hemiptera				
<i>Rhytidoporus indentatus</i>	5.2 (NA)	26.8 (105%)	0.2 (NA)	27.8 (108%)
Hymenoptera				
<i>Nylanderia bourbonica</i>	0.2 (200%)	1.8 (220%)	0.2 (200%)	1.3 (160%)
<i>Solenopsis</i> HI01	-4.8 (-5800%)	-2.3 (-122%)	-1.7 (-2000%)	-3.8 (-200%)
<i>Technomyrmex albipes</i>	5.8 (64%)	3.5 (145%)	22.7 (247%)	3.3 (138%)
Diplopoda				
Pyrgodesmidae sp.	10.7 (154%)	6.2 (34%)	0.5 (7%)	16.5 (91%)
<i>Glyphiulus granulatus</i>	0.3 (NA)	1.5 (225%)	0.3 (NA)	1.3 (200%)
Native Taxa				
Coleoptera				
<i>Sericoderus ?pubipennis</i>	-0.2 (-200%)	-4.3 (-65%)	-0.2 (-200%)	-5.3 (-80%)
Dermaptera				
<i>Euborellia eteronoma</i>	0.5 (120%)	2.8 (38%)	0.5 (120%)	4 (53%)
Hemiptera				
<i>Nesidiorchestes hawaiiensis</i>	2.5 (20%)	0.5 (600%)	2.5 (20%)	0.2 (200%)
Orthoptera				
<i>Laupala</i> spp.	0.5 (86%)	5.7 (151%)	0.2 (29%)	3.7 (98%)
Unknown Provenance Taxa				
Coleoptera immatures	15.8 (238%)	3.8 (2300%)	26.3 (395%)	20 (12100%)
Isopoda	203 (72%)	138 (96%)	8.7 (3%)	95 (66%)
Lepidoptera immatures	3.3 (44%)	2.7 (152%)	5.7 (76%)	1.8 (105%)
Thysanoptera	18.7 (85%)	0.5 (150%)	1.3 (6%)	1.2 (350%)

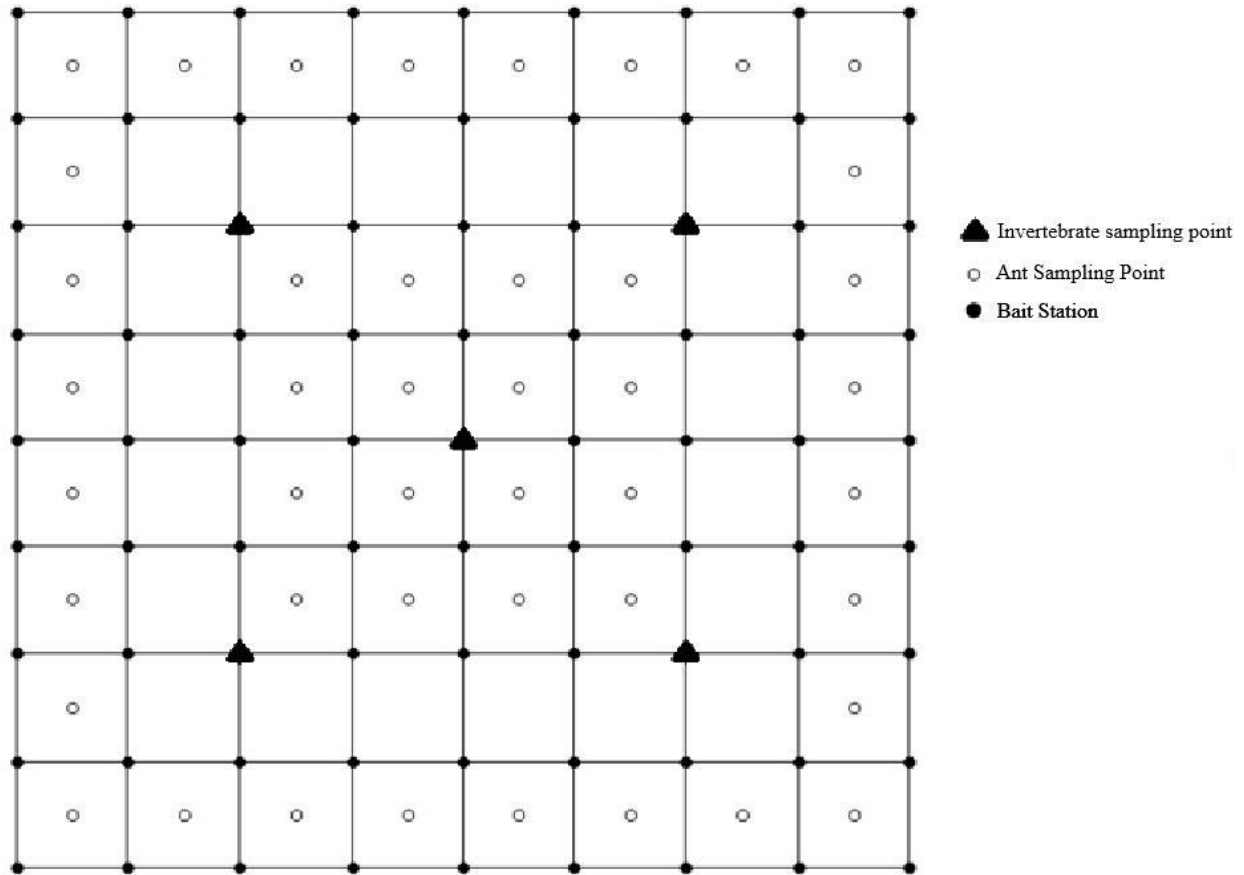


Figure 3.1. Layout of a 20 x 20 m plot assigned to the ant suppression treatment. Each square is 2.5 x 2.5 m. Black circles represent bait station locations (n = 81), white circles represent ant monitoring locations (n = 44), and black triangles indicate where litter and pitfall samples were collected (n = 5) before, six months after, and one year after ant suppression. Control plots had the same layout, except they lacked bait stations. The two 10 x 10 m plots had the same layout, but did not extend past the triangles.

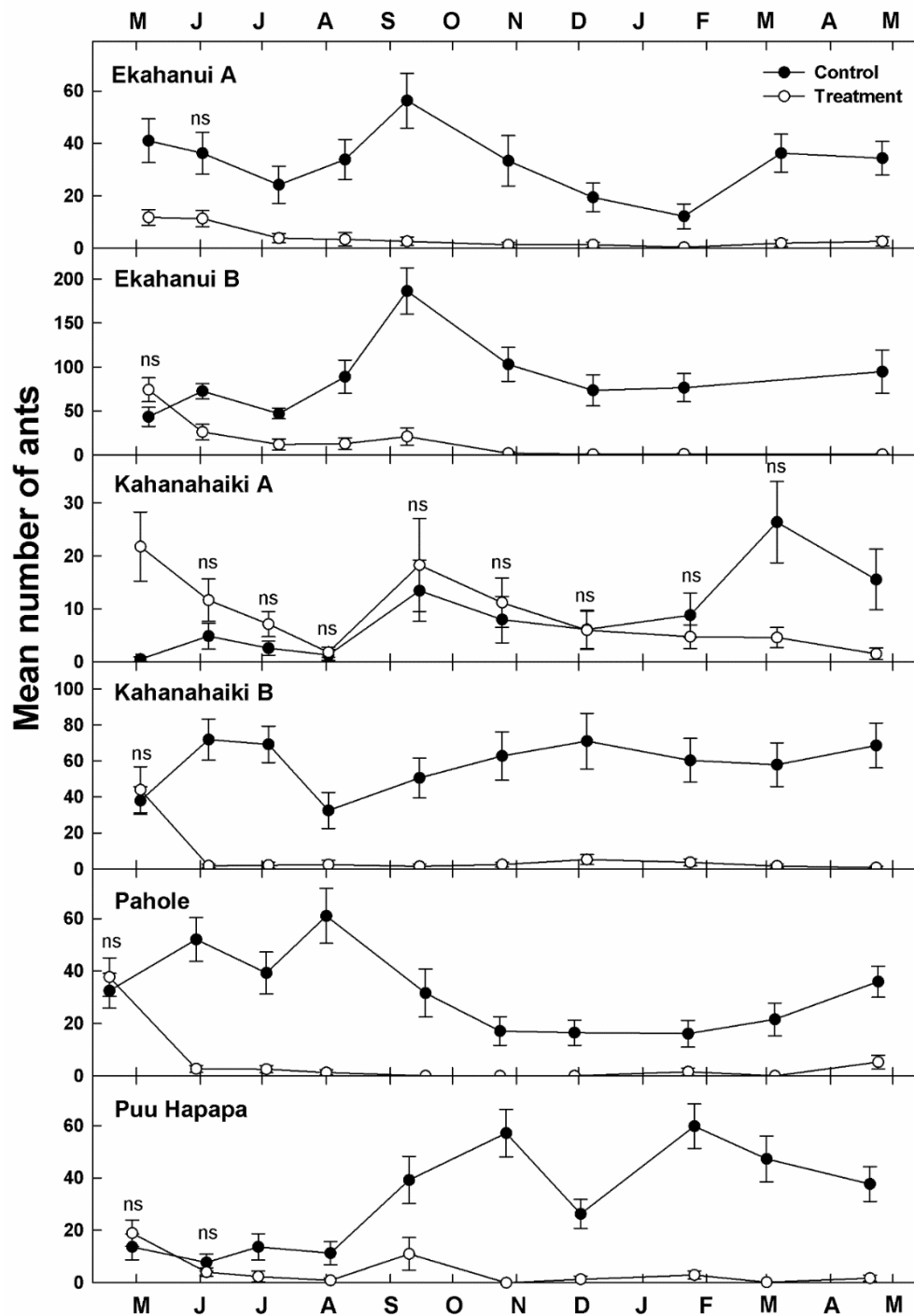


Figure 3.2. Mean number of ants (\pm SE) at peanut butter bait cards in paired treatment and control plots at the six study sites over the course of the one year experiment, from late April/early May of 2015 to late April of 2016. The first monitoring date at each site was the pre-treatment ant count. Ant numbers were significantly different ($p < 0.05$) between treatment and control plots at each site on all dates except those marked as not significant (“ns”). Amdro[®] was replaced in bait stations on each monitoring date shown, except for ‘Ēkahanui B, where bait was replaced in March of 2016 but ant monitoring was not conducted due to rain.

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CHAPTER 4

Conclusion

The thief ant, *Solenopsis papuana*, is a widespread ant in the upper elevations of the Wai‘anae Mountains that thrives in relatively undisturbed wet and mesic forest areas, raising concerns about its ecological impacts in these areas. This pair of studies aimed to develop monitoring and control methods as well as to measure the effects of *S. papuana* on ground-dwelling invertebrate communities. Choice tests conducted at Lyon Arboretum and Pahole Natural Area Reserve (NAR) showed that both peanut butter and SPAM potted meat were reliable baits for recruiting large numbers of ants quickly and consistently, and can be used for monitoring relative ant densities in the field. Peanut butter was chosen over SPAM in subsequent ant monitoring, owing to its superior ease of use and cost effectiveness. Choice tests conducted at the same two sites found that Amdro[®] and Siesta[™] pesticidal ant baits are attractive to *S. papuana* at one or both locations. When deployed within bait stations, Amdro[®] was more effective than Siesta[™] at reducing *S. papuana* densities in field plots at Pahole NAR. Results from this first set of experiments were then used for the second part of the study, to assess the effects of *S. papuana* on ground-dwelling invertebrates.

Results from the experimental suppression of *S. papuana* in field plots located in mixed native and alien mesic forests at ‘Ēkahanui, Kahanahāiki, Pahole NAR, and Pu‘u Hāpapa suggest that the control methods summarized above were generally successful, and that *S. papuana* has a relatively weak, yet broad effect on ground-dwelling invertebrate communities in the Wai‘anae Mountain Range. Of the 169 taxa sampled and classified, 24% were native to Hawai‘i, 51% were introduced (non-native), and 25% were of unknown origin. Furthermore, of the 89,212 individual invertebrates captured, only 1.4% belonged to taxa known to be native. These numbers indicate that the contemporary ground-dwelling communities in these forests are highly invaded by non-native invertebrates. This circumstance likely explains, at least in part, the detection of stronger positive responses to ant suppression among introduced species than among native species. Statistically significant positive responses were more common for changes in species richness than for changes in abundances of higher taxonomic groups. The latter may suggest that assessing abundance changes at higher levels like class or order might obscure patterns occurring at species level. Even so, specific endemic taxa, including *Laupala* crickets and the flightless mirid bug, *Nesidiorchestes hawaiiensis*, were identified as likely vulnerable to *S. papuana*.

Because *S. papuana* is widely distributed across the Wai‘anae Mountains and other areas, it is not feasible at this point to attempt eradication of this ant. Although this study suggests greater impacts from this ant on introduced species, rare native species are also likely affected, but harder to measure with generalized sampling methods such as those employed here. Land managers may find it useful to control *S. papuana* in small sensitive habitats to help recover vulnerable native species, as was demonstrated in a related study that detected a substantial negative effect of *S. papuana* on the reproductive success of rare picture-winged *Drosophila* flies. Additional research using a similar approach, in which rare native species are experimentally added to field plots, may be worthwhile for investigating the vulnerability of other groups, such as native Hemiptera and Orthoptera, to this ant. Such research may provide land managers with a more complete picture of the conservation benefits of controlling this ant in small target areas, using the methods developed here.