Are tiny subterranean ants top predators affecting aboveground ant communities?

Leo Ohyama [iD],[1] Joshua R. King, and David G. Jenkins [iD]

Department of Biology, University of Central Florida, 4110 Libra Drive, Orlando, Florida 32816 USA

Abstract. Ants are a widespread group of ecologically important insects. Therefore, ants that are important predators of other ants are likely to play key roles by changing the abundance and impacts of their prey. Familiar arthropod predators, like army ants, are known for their overwhelming raids on invertebrate prey but are limited to mostly tropical systems. Thief ants (Genus: *Solenopsis* Westwood) are a cosmopolitan group of mostly subterranean ants found in a wide variety of ecosystem types. They are known for their extremely small sizes and their specialized predation where they stealthily tunnel into the nests of other larger ant species to capture and consume only immature ants (larvae and pupae). Predation of ant colonies by other ants, and specialized predatory behaviors of presumed top ant predators (e.g., army ants) are well known. However long-term predation effects, such as across several seasons, are still poorly understood because of a lack of experimental studies. Here we report results of a ~1.5-year press field experiment where thief ants were reduced in natural ant communities. Potential impacts, such as predator-release, were quantified by sampling the co-occurring ant community. Compared to control plots, overall worker abundance and biomass increased where thief ants were reduced, and effects varied among ant species. Results suggest predator release as select aboveground foraging ant species increased in abundance and that thief ants may act as significant predators. Because thief ants are abundant and widespread, similar predatory effects may occur in many ant communities, and our understanding of important predators may need to adjust to include thieving species as well as army ants. Thief ants are very abundant, tiny, specialized to consume immature life stages, equipped with powerful venom, eusocial, and subterranean. This suite of adaptive traits seems unique to eusocial predators compared to animals, where "thieving" predators are usually larger in size compared to their adult-sized prey. Future work quantifying top-down regulation of prey and cascading consumptive and non-consumptive effects will help to understand thief ant predation and potential effects on ecosystem processes.

Key words: adaptive traits; brood raiding; field experiment; population; prey; Solenopsis; specialized predator; thief ants.

Introduction

Species interactions, such as competition and predation, affect community structure by regulating the abundance of individuals in species' populations (Lynch 1979). Predation can be an especially important interaction in communities, as predators can directly (consumptive effects) or indirectly (non-consumptive effects) impact prey population sizes and stabilize communities (Paine 1974, Schmitz et al. 1997, Terborgh 2015). Top predators are high trophic-level consumers free from predation at adult size and that may regulate prey species abundances and affect community structure and ecosystem function (Sergio et al. 2014). Assessing the effects of predation on prey in the natural environment can be difficult, especially in the context of community-level effects. Predator reduction or removal experiments (e.g., Paine 1974) can provide more powerful inference for understanding predation impacts on community structure than indirect assessments of species co-occurrence patterns (e.g., Jenkins 2006, Bell et al. 2010) or biomass consumption estimates after a predation event (e.g., Kaspari et al. 2011). Likewise, simple communities, such as agricultural-based systems, are ideal to measure predatory impacts at the community-level (Rutledge et al. 2004, Costamagna and Landis 2006). However, there is a lack of direct measurement of predation impacts in natural arthropod communities for key arthropod groups such as the ants.

Ants and ant communities play prominent roles in shaping ecosystems at global scales (Hölldobler and Wilson 1990, Lach et al. 2010). Examples of ant impacts include seed dispersal, soil turnover, and various symbioses with other taxa (Levey and Byrne 1993, Nkem

et al. 2000, Styrsky and Eubanks 2007). Understanding how predation structures ant communities and the ecological processes they impact (Folgarait 1998) is therefore important. The majority of research on interactions among ants has focused on competition, symbiosis, or predation of non-ant insects (e.g. termites; Lach et al. 2010). It is probable that predation plays a significant role in the structure and assembly of ant communities at local scales (LaPolla et al. 2002, Powell and Clark 2004). Quantifying top-down regulation over time by eusocial predators that prey primarily upon eusocial prey species would be a step forward in determining whether top eusocial predators are meaningfully different from more familiar, free living top predators.

Perhaps the best-known ant predators are army ants, which are presumed top predators in tropical ecosystems that raid and attack social insect prey in full confrontational assaults (Hölldobler and Wilson 1990, Kaspari et al. 2011, Powell 2011). Few experimental tests have been conducted on army ant effects on ant community structure (Otis et al. 1986, Hirosawa et al. 2000, Berghoff 2003, Berghoff et al. 2003). A notable exception is provided by Terborgh et al. (2001) who used a natural experiment to show that a lack of army ants on islands lead to a release in populations of leaf-cutting ants resulting in changes in plant community structure.

Ant-specific predation is clearly not limited to the army ants as other ant species have been observed practicing ant-specific predation. Some examples can be found in the invasive ant literature, such as the invasive Argentine ant (*Linepithema humile*) that that has been shown to prey upon native harvester ants and their founding queens (Human and Gordon 1997, Zee and Holway 2006) or the red-imported fire ant (*Solenopsis invicta*) that has been observed preying upon harvester ant colonies (Hook and Porter 1990). Here we test the predatory activities of a cosmopolitan group, the thief ants in the genus *Solenopsis*.

Thief ants in the genus *Solenopsis* are predators within ant communities, though their effects have not been estimated. Stable-isotope studies place thief ants in a predatory trophic position although certain species may be herbivores (Fiedler et al. 2007, Tillberg et al. 2007). Thief ants most likely primarily consume brood in an interaction called 'lestobiosis', a subterranean predatory interaction typically involving small-bodied "thief" ant species that nest and forage belowground near the nests of larger-bodied ant colonies so that they can easily tunnel into nearby ant nests and steal their brood (Wheeler 1901, Hölldobler 1973, Hölldobler and Wilson 1990, Deyrup 2016). It is unlikely that complete colony mortality routinely occurs as a result of this interaction and while the consumption of brood or larvae at the individual scale can be considered as predation, at the colony-level it is more analogous to a host-parasite interaction (Hölldobler and Wilson 1990). Given that brood is the life-stage that thief ants typically prey upon, if they prey upon worker brood or sex brood at a high rate, then

their impact should primarily be to limit colony production of worker or reproductive castes. But if the sum total of brood predation is great enough, then thieving can limit colony productivity or lead to colony mortality, much like an effect of army ants.

In Florida, thief ants are a dominant group in belowground ant communities, often comprising over half the total abundance of ants (Lubertazzi and Tschinkel 2003, Ohyama et al. 2018) and species descriptions have had no significant changes for decades (Thompson 1980, 1989, Moreno Gonzalez 2001, Pacheco and MacKay 2013, Deyrup 2016). It is possible that thief ants may compete with co-occurring ants, especially for belowground resources. However, differences in life histories, worker body size and the strata in which they forage suggest otherwise. We experimentally reduced thief ant densities to test whether this group of potential ant predators have impacts on co-occurring ant species, specifically worker abundances. If highly abundant thief ants are actively lestobiotic (as observed) and significantly affect production of workers and/or sexuals of co-occurring aboveground-foraging ant species (as hypothesized here), then release from lestobiosis through multiple generations of brood and workers should quantifiably increase aboveground-foraging ant worker abundances.

MATERIALS AND METHODS

Twenty plots were randomly placed in sandhill ecosystems of Wekiva Springs State Park (2,750 hectares) situated in Orange and Seminole County Florida. A previous study established that this habitat holds a high diversity (species richness) and high abundance of subterranean thief ants relative to the abundance of other co-occurring ants in the belowground strata (Ohyama et al. 2018). High pine sandhill is a pyrogenic habitat characterized by well-drained sandy soils, an overstory of longleaf pine (*Pinus palustris*), and a sparse groundcover dominated by wiregrass (*Astrida beyrichiana*) (Myers and Ewel 1990). The placement of sandhill sites were randomly generated using ArcMap and placed in areas maintained by low intensity prescribed fires. Ten plots were randomly chosen to receive a thief ant reduction treatment while the other 10 plots were left as control plots, receiving no treatments. Plots were 18 m × 18 m. Sixteen point-flags were positioned in these plots in a grid spaced out by 6 m to represent borders and gridlines within plots. Another 16 flags were placed within 1-m of the point flags to represent locations for thief ant reduction and sampling. These locations were randomly moved within a 1-m radius of point flags every sampling and thief ant reduction event to avoid resampling of the same position.

Plastic capped vials (70 mm tall × 30 mm diameter) were loaded with AMDRO™, an ant-specific pesticide. This approach adapted sampling methods used by Ohyama et al. 2018. The main active ingredient in

AMDRO is hydramethylnon (Van der Meer et al. 1982). It has been shown to have minimal effects (limited non-target mortality) on other arthropods, especially when the target species (here thief ants) collect most of the toxic bait (Apperson et al. 1984). In past studies, this pesticide has been used successfully in eradicating invasive ants with few non-target effects (Apperson et al. 1984, Green and O'Dowd 2010, Plentovich et al. 2011). It breaks down rapidly when exposed to light and moisture (Van der Meer et al. 1982). To further reduce the likelihood of non-target impacts, a ~5 mm diameter hole was made at the bottom of the plastic vial and covered with 0.75 mm screening to exclude larger insects and arthropods (e.g., fire ants) but permit entry by thief ants. This approach reduced the likelihood of non-target effects as the vast majority of ants with access to the pesticide baits were thief ants (89% of all belowground ants sampled (285,957 ants) were thief ants). The screening used here had smaller openings than the 1 mm mesh used by Ohyama et al. 2018. As a result, the traps permitted entry by fewer non-thief ant species and in lower numbers. Specifically, small *Pheidole* species (*P. metallescens*, *P. floridana*) still entered vials in relatively small numbers in some plots.

Pesticide-loaded vials were placed belowground to a depth of ~10 cm below the soil surface using a 24-inch auger bit with a 24-volt battery-operated drill. The pesticide-loaded vials remained underground for 2 weeks and the treatment was carried out during the last two weeks of every month starting from February 2018 to June 2019 (except the months of October 2018, December 2018, and January 2019). No baited vials were placed in the control plots during the treatment period but the same amount of disturbance (walking through the plots) occurred. Subterranean sampling of all plots after every pesticide treatment evaluated pesticide effects on thief ant abundance and occurrences, thus there were soil disturbances via drilling and placing vials in all plots. These sampling events took place in the beginning of each month right after the pesticide treatment which lasted for the last two weeks of the month prior. Due to the monthly sampling, all plots experienced similar amounts of anthropogenic disturbance in the form of walking and soil disturbance and thus we chose not to use a sham control (installation of non-baited, empty plastic vials in control plots) during the pesticide-treatment periods. Sampling did not occur in October 2018 because of difficult field conditions. Sampling events used the same vial design as for treatments but were filled with Pecan Sandies™ cookies. Subterranean sampling vials were planted 10 cm belowground and left for 3 d. An initial sampling of plots with subterranean baits and aboveground pitfall traps in February 2018 (prior to the first pesticide treatment) established baseline species richness, species composition, and abundances of both above and belowground ants for all plots.

The known limitation of surface pitfall traps is that certain species or functional groups are more or less susceptible to capture (Bestelmeyer et al. 2000). In particular, leaf litter dwelling and slow-moving surface foraging ants tend to be under-represented in samples. However, in upland ecosystems such as high pine, pitfalls traps perform on par with leaf-litter sampling when assessing species richness and outperforms hand-collecting or baiting methods (King and Porter 2005). Pitfall traps were also noted for being highly effective in capturing aboveground foraging ants (King and Porter 2005). Because the response variable of interest in this study was the abundance of ground foraging ants in sandhill (an open, savanna-like habitat), pitfall trapping is an appropriate method and is expected to provide relatively accurate estimates of these foraging ant abundances. Furthermore, previous sampling done in these habitat types, utilizing a variety of trapping methods for comparison, showed that pitfall traps are representative of the aboveground ant community composition, species richness, and species relative abundance (Prusak 1997, King and Porter 2005, 2007).

Four pitfalls were randomly placed in each plot and operated for 3 d in tandem with the subterranean sampling. Pitfall traps were 85 mm × 30 mm plastic vials partially filled with ~15 ml of non-toxic antifreeze (propylene-glycol). Traps were buried similarly to sampling vials but with the opened end flush with the surface of the ground. All aboveground ants were pooled into one sample to represent the abundance and occurrence per plot rather than per trap. All ants from all pitfalls were identified to species and counted by the authors. Voucher specimens were deposited in the University of Central Florida Collection of Arthropods. Finally, biomass data for the ten most abundant species were calculated by multiplying worker biomass (mg) (King and Porter 2007, King 2010) of a species by the abundance of worker ants caught from pitfall traps.

Results aimed to verify the reduction of thief ants were evaluated graphically and statistically. Abundances and occurrences were modeled as a function of treatment type and a covariate of the initial values. Both occurrences and raw abundance were evaluated as ants are eusocial and both are useful estimates of species abundance where raw abundance is reflective of the total number of workers captured and occurrence data is the frequency of occurrence of a species per trap or per plot (Longino 2000, Gotelli et al. 2011). Occurrence data may be preferred for some analyses as it is a more conservative estimate of total abundance as it reduces the variability in worker abundance that results from differences across species and traps from forager behavior, colony size, or seasonal variation (Gotelli et al. 2011). However, consistent trapping through seasons for 1.5 yr should also reflect large changes in colony sizes and/or numbers of colonies in the relatively small sampling area (Andersen 1991, King and Tschinkel 2006, 2013, Schlick-Steiner et al. 2006).

Data were analyzed using a generalized linear mixed-effects model (GLMM) with a negative binomial error

distribution and month as a random intercept term. The covariate of the initial values which accounted for natural variation among plots was scaled to z-scores. The random intercept of months was not nested within years because the experiment did not run to the completion of the second year. Instead months based on year was used as a random effect resulting in 14 levels within the random effect.

The reduction of thief ants was also assessed using heat maps at the plot level for the months of August 2018 to June 2019 (except the months of October 2018, December 2018, and January 2019 when sampling was not done). Heat maps were used because a single belowground bait could at times hold up to ~600 thief ant workers and skew the abundance of thief ants throughout the entire plot.

Potential effects of thief ant reduction on aboveground ants were evaluated with a similar modeling approach. Ten species found in belowground baits were removed from aboveground pitfall analyses (average of two species per plot, per month) to avoid false inferences from species that could have been affected by the pesticide. The species removed were *Nylanderia wojciki*, *Pheidole adrianoi*, *P. floridana*, *P. metallescens*, *P. moerens*, *Solenopsis carolinensis*, *S. invicta*, *S. nickersoni*, *S. tennesseensis*, and *Wasmannia auropunctata*. A GLMM, with a negative binomial error distribution, and a random intercept (months) to account for repeat sampling was used. Pre-treatment sampling data (February 2018) for aboveground ants were included as a covariate in analyses because data were collected prior to pesticide treatment. Finally, the same model structure was applied to aboveground ant biomass for the ten most abundant species but using a gamma distribution (inverse link function).

All models were computed using R statistical programming (Version 3.5.1) and the package lme4 (Bates et al. 2015). All graphics were made using the package 'ggplot2' (Wickham 2009). Pseudo-R^2 values for marginal and conditional effects were calculated using the R package 'MuMIn' and using the tri-gamma function, which is best suited for distributions using logarithmic links (Barton 2019).

Results

Thief ant abundances and occurrences were reduced throughout the duration of 14 sampled months in treated plots, though significant reduction was not observed until May and June 2018 for both abundances and occurrences, respectively (Fig. 1). Differences between pesticide-treated and control plots rapidly increased after initial reductions (Fig. 1). Thief ants strongly dominated belowground samples, whereas aboveground ants included only 2 of the 5 species of thief ants found in belowground samples. Across all plots, thief ants made up 88.5% of the total ant abundance and 67.7% of all ant occurrences in belowground samples. Non-thief ant

species were occasionally caught in our belowground bait traps and included only other small-bodied species of *Pheidole* (*P. adrianoi*, *P. floridana*, *P. metallescens*, and *P. moerens*), *Nylanderia wojciki* (number of workers = 3) and *Wasmannia auropunctata* (number of workers = 84). The latter two species only occurred once and twice respectively across all samples. The total belowground ant count was 285,957 ants, of which 88.5% were *Solenopsis* thief ants. Heat maps of average thief ant abundance generated for both 2018 and 2019 (Fig. 1) indicate that the average thief ant worker abundance at the individual plot scale were lower in thief ant reduced plots than in control plots across most of the 16 sampling points per plot.

Fixed effects from the GLMM showed significant reduction of thief ant occurrence in treated plots relative to control plots ($P < 0.05$, Appendix S1: Table S1). Marginal and conditional Pseudo-R^2 values were 0.25 and 0.30, where marginal values represent the variation explained by the fixed effects and conditional values represent the variation explained by the both fixed and random effects. Fixed effects from the mixed-effects model assessing thief ant abundance showed significant reduction of abundance in treated plots relative to control plots (GLMM: R^2-marginal = 0.15 R^2-conditional = 0.29, $P < 0.05$, Appendix S1: Table S2).

Where thief ants were reduced belowground, aboveground ant worker abundance significantly increased relative to control plots (GLMM: R^2-marginal = 0.09 R^2-conditional = 0.44, $P < 0.05$, Fig. 2C, D, Appendix S1: Table S3). This effect was general, in that experimental reduction of thief ants also significantly increased biomass of the ten most abundant ant species relative to control plots (GLMM: R^2-marginal = 0.05, R^2-conditional = 0.30, $P = 0.008$, Fig. 2A, B, Appendix S1: Table S4). Increases in abundance and biomass were density dependent because the greatest increases occurred where there were naturally greater aboveground ant abundance and biomass.

Certain species were especially sensitive to thief ant reduction. For example, *Dorymyrmex bureni* and *Nylanderia arenivaga*, showed large increases in worker abundance where thief ants were reduced (GLMM: R^2-marginal = 0.12, R^2-conditional = 0.30, $P < 0.05$, Fig. 3A, B; GLMM: R^2-marginal = 0.07, R^2-conditional = 0.23, $P < 0.05$, Fig. 3C, D, Appendix S1: Table S5 and S6). Both species are widespread, common, and abundant members of ant communities in the Southeastern United States (MacGown and Forster 2005, King and Porter 2005, 2007, Deyrup 2016).

Discussion

Results here suggest that thief ants prey on immature life stages in belowground nests of other ants (Wheeler 1901, Hölldobler and Wilson 1990, Deyrup 2016) at a scale that affects natural populations of other ants most by likely limiting worker production. Our data are
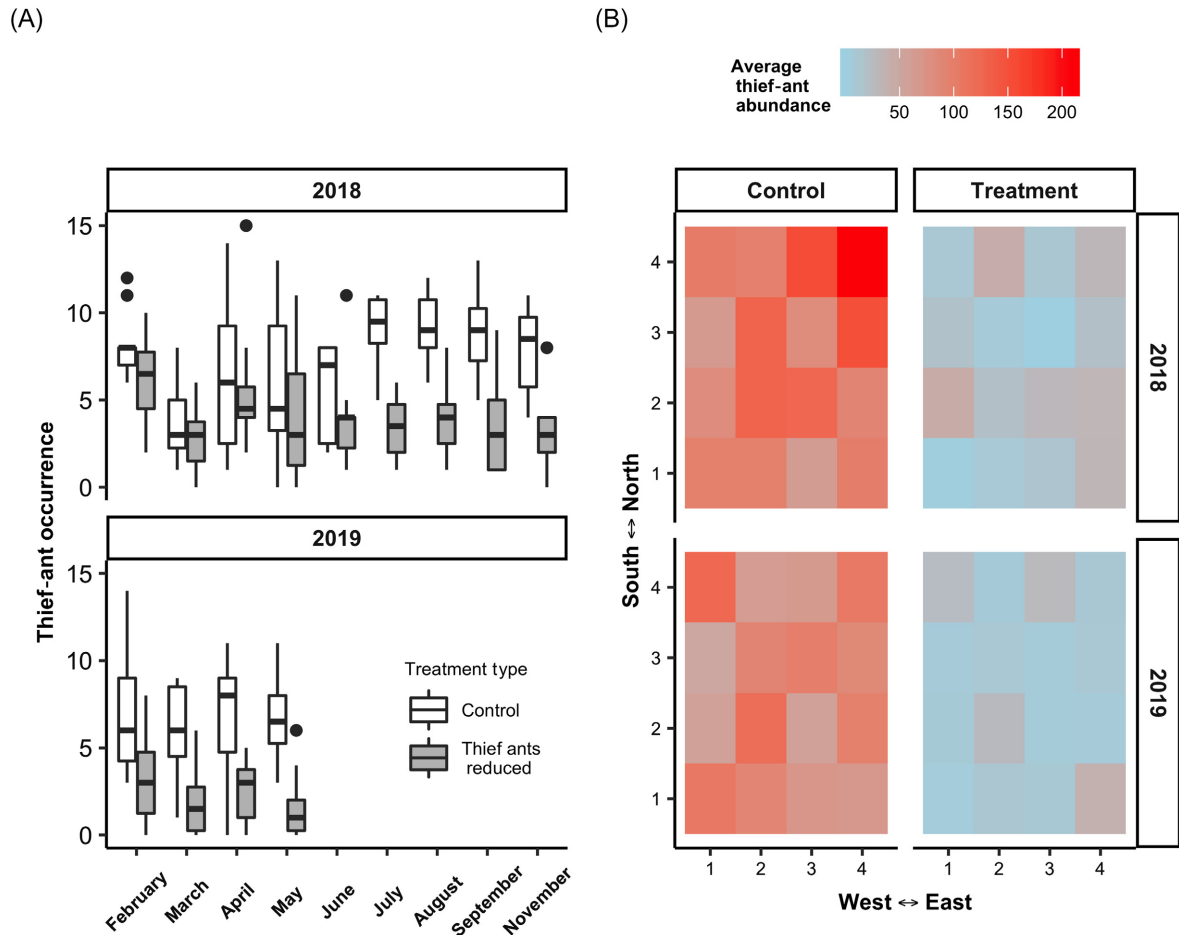
(A)

(B)

FIG. 1.   Thief ant worker occurrences in control and treatment plots (*n* = 20). (A) Boxplots of thief ant worker abundance from all sampled months of 2018 and 2019 color-coded by treatment levels. (B) Heatmaps showing average thief ant worker abundance across months for each year at each sampling point within a plot. Higher shades of red indicate higher levels of average thief ant worker abundance.

consistent with release from a predator with widespread impacts. We note that worker abundances from pitfalls cannot be used to distinguish between impacts on colony sizes or the recruitment of new colonies. However, a brood predator that has impacts through limiting worker production on a large scale, as shown in this system, is likely impacting colony fitness, as the size and activity of the worker population is what determines caloric intake, calorie storage, and successful defense of nest and territory (Tschinkel 2006). Predation is the presumed mechanism driving these results given the sustained increase of aboveground ant abundance over time and the known natural history of thief ants. However, effects of indirect competition cannot be completely discounted.

These interactions are occurring belowground and thus largely underappreciated, but the unusual nature and apparent effects of this interaction are noteworthy. Thief ants dominate at belowground food resources and rarely if ever appear at aboveground food resources in

this region (King and Porter 2005), suggesting that thief ants and species foraging aboveground are not competing for the same food resources. There is also no evidence that any of the common aboveground ant species are competing with thief ants for nest sites as all of these species nest within open, sandy soils, with no apparent space limitation (Prusak 1997). Thus, thief ants are likely affecting colony output via brood predation across multiple colonies given the distribution of predators and prey in plots, but the measures of impact used in this study limit our ability to make any further inferences.

Past studies and observations have suggested thief ants are important components of ant communities due to their diversity and lestobiotic behaviors (Thompson 1980, Pacheco and MacKay 2013). This study provides experimental evidence that these ants significantly impact ant communities. This result and conclusion is congruent with and builds upon previous studies that suggest that thief ants may be important predators of
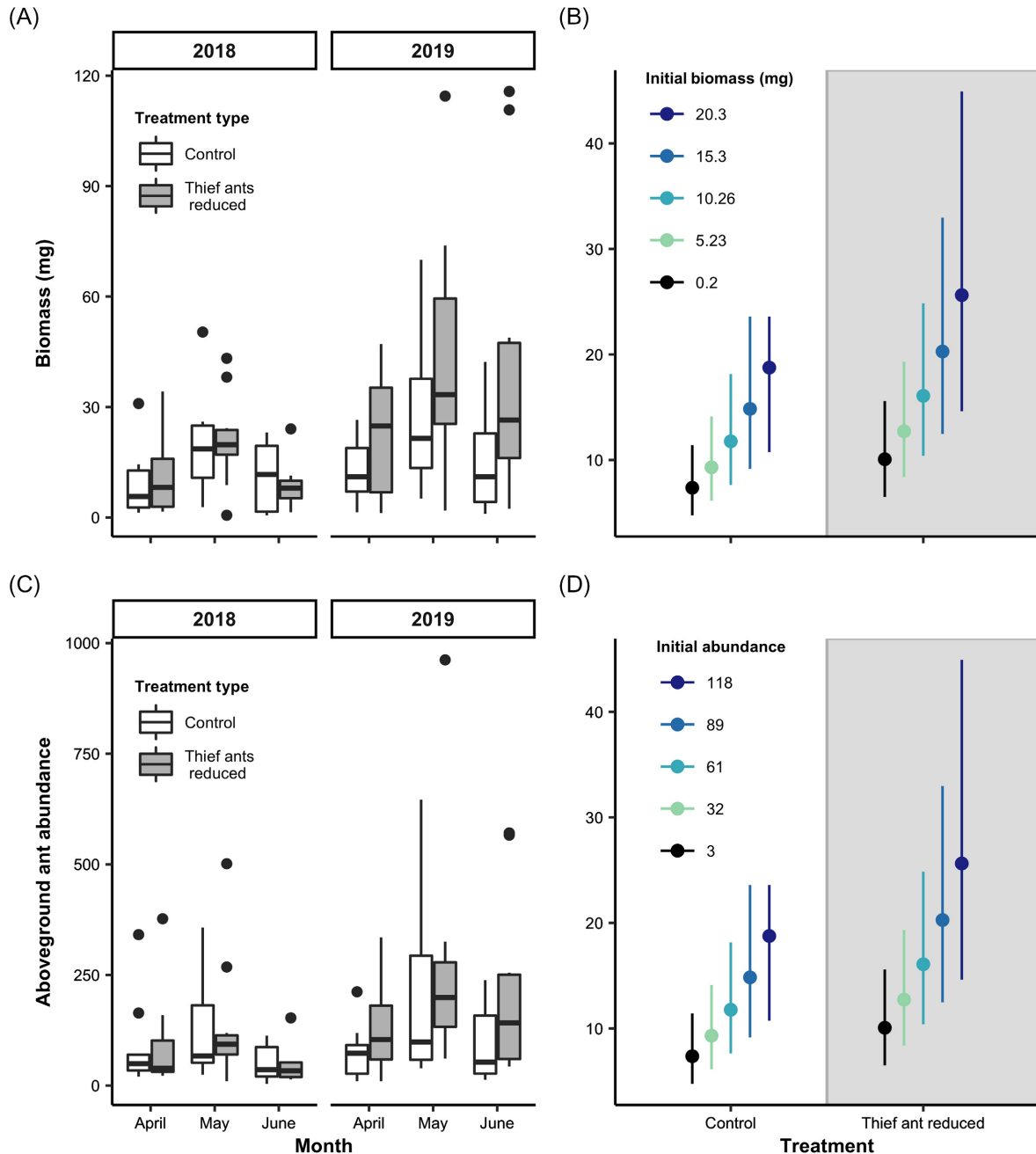
FIG. 2. Boxplots and fitted values of the fixed-effects from generalized linear mixed-effect models (GLMM) for aboveground worker ant biomass (using estimates of worker biomass from King 2010) and aboveground ant abundance ($n = 20$). For full data in boxplots see Appendix S1: Figs S3 and S4. Aboveground ant biomass is comprised of worker biomass for the top ten most abundantly sampled species. (A) Boxplots of biomass from the months of April, May, and June of two separate years color-coded by treatment levels. (B) Predicted values from the fixed effects of the GLMM for aboveground ant biomass based on the covariate of initial biomass and treatment type. Five values representing five equidistant intervals spanning the entirety of the covariate were used for the points at both treatment levels. Error bars represent 95% confidence intervals. (C) Boxplots of aboveground ant abundance from the months of April, May, and June of two separate years color-coded by treatment levels. (D) Predicted values from the fixed effects of the GLMM predicting aboveground ant abundance based on a covariate of initial aboveground ant abundance and treatment type.

queens of red-imported fire ants (*Solenopsis invicta*) (Nichols and Sites 1991, Vinson and Rao 2004). Quantifying and describing predation effects on the most likely prey (here, the abundant, common species *D. bureni* and *N. arenivega*) and measuring direct impacts on colony fitness are a logical next step after this study.
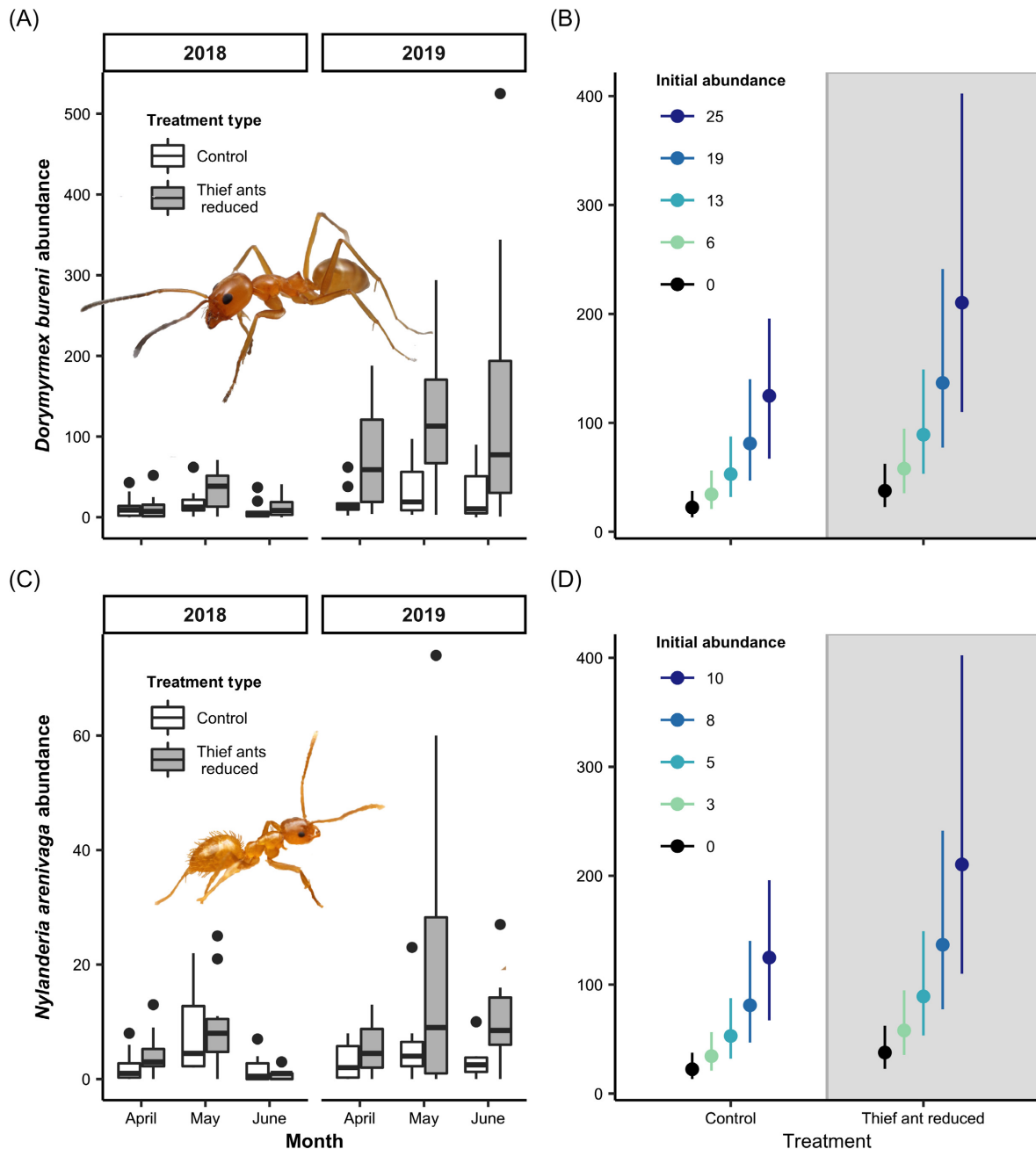
FIG. 3. Boxplots and fitted values of the fixed-effects from generalized linear mixed-effect models (GLMM) for *Dorymyrmex bureni* abundance and *Nylanderia arenivaga* abundance (*n* = 20). For full data in boxplots see Appendix S1: Figs S5 and S6. (A) Boxplots of *D. bureni* abundance from the months of April, May, and June of two separate years color-coded by treatment levels. (B) Predicted values from the fixed effects of the GLMM for *D. bureni* abundance based on the covariate of initial *D. bureni* abundance and treatment type. Five values representing five equidistant intervals spanning the entirety of the covariate were used for the points at both treatment levels. Error bars represent 95% confidence intervals. (C) Boxplots of *N. arenivaga* abundance from the months of April, May, and June of two separate years color-coded by treatment levels. (D) Predicted values from the fixed effects of the GLMM predicting *N. arenivaga* abundance based on a covariate of initial *N. arenivaga* abundance and treatment type. Ant images © Alex Wild, used by permission.

Although a small number of ant species other than thief ants were potentially impacted by treatments, that effect was minimal relative to the impact on thief ants.

Furthermore, thief ants make up 70% of the below-ground ant fauna (occurrence-based abundances) in the same sandhill habitat studied here (Ohyama et al. 2018).

Therefore, pesticide treatments had the greatest impact on the most abundant ants in the belowground environment; thief ants. Nevertheless, we excluded non-thief ant species found in both below and aboveground sampling from our aboveground pitfall trap analyses. Two species of *Pheidole* (*P. floridana* and *P. metallescens*) did show decreased abundance in pesticide-treated plots during the last three months of the experiment. However, the decreases co-occurred with the highest increases seen in aboveground ant abundance (Appendix S1: Figs S1 and S2). These decreases could be due to pesticide exposure, an increase in abundance of other competing ant species, or both.

The experimental demonstration here of predatory release in natural conditions over an extended period of time adds to our understanding of predator-prey relationships in ant communities. In combination with the known natural history of this group (Wheeler 1901, Hölldobler and Wilson 1990, Deyrup 2016), our results demonstrate that thief ants potentially act as an important predator in ant communities despite not showing the typical body size relationships between predator and prey (Cohen et al. 1993) seen in other communities. Some eusocial predators that collectively prey on larger organisms may not adhere to typical size relationships seen between predators and prey because they have evolved alternate prey capture strategies that do not depend on being larger than prey. Collective behavioral strategies are often used for a variety of interactions where "winners" are determined by employing larger numbers rather than larger bodies. For example, honey bees successfully defend their colonies from larger predatory wasps via heat-balling (Ken et al. 2005) and colonies that employ larger numbers of small workers often outcompete colonies that employ fewer, larger workers (Morrison 2000). We suggest that similar eusocial principles also apply to evolved predatory strategies.

Thief ants use aerosolized alkaloid-based venom against brood defenders to aid in capturing larvae (Blum et al. 1980), comparable to adaptive defensive use of venom by harvester ants to defend food (seed) resources within their nests from mammalian seed predators (Schmidt and Blum 1978). These alkaloid-rich venoms repel ants that are orders-of-magnitude larger in size than thief ants (Blum et al. 1980). Thief ant venom chemistry may have evolved under selective pressures where repellent venoms coupled with small body size are advantageous for in-nest predation of ant brood. Exploring venom evolution in eusocial predators like thief ants should improve our understanding of the evolution of venom 'weaponry' when prey species are other ants.

Different effects of thief ants on different prey ant species may be due to nest architecture or in-nest behaviors (e.g., frequency of brood visits, brood care, or protection). Brood predation may act as a selective pressure that shapes nest architecture, where nests that are diffuse and connected by long tunnel networks are more vulnerable to brood predation by thief ants. Such architecture is seen in *Dorymyrmex bureni* nests which are comprised of single, small, flat chambers spread out and vertically connected by a long single tunnel system (Tschinkel 2003, 2015). The same diffuse design is also seen in *Nylanderia arenivaga*, a species known for multiple queens and high abundances (Lapolla et al. 2011, Deyrup 2016). While diffuse distribution of chambers may be more vulnerable to the specific predation of thief ants, it may also positively affect overall survivorship of colony resources and brood by spreading risk from other belowground threats via multiple small targets compared to architectural designs that utilize one major chamber. The relationship between ant nest architecture, in-nest brood care behaviors, and the ability of potential subterranean predators, like thief ants, to access brood piles has not been considered as part of the selective forces shaping ant nest architecture (Tschinkel 2003). Given the abundance and apparent importance of thief ants, belowground predators may be a selective force shaping ant nest architecture or possible nest absconding behavior.

Predation belowground is an understudied aspect of ant and general arthropod ecology. Interactions between organisms that occur below our feet can play critical roles in ecosystem services and overall community structure (Wardle 1999). For example, interactions between belowground microbial communities have important impacts on aboveground plant community structure (Reynolds et al. 2003). Here we have shown that belowground predators can have important impacts on aboveground ant abundance. By limiting worker production, these widespread ants appear to exert a large effect on the entire ant community. Results here suggest the need for further studies to unravel the precise interactions that determine these community level impacts.

Literature Cited

Andersen, A. N. 1991. Sampling communities of ground-foraging ants: Pitfall catches compared with quadrat counts in an Australian tropical savanna. Australian Journal of Ecology 16:273–279.

Apperson, C. S., R. B. Leidy, and E. E. Powell. 1984. Effects of AMDRO on the red imported fire ant (Hymenoptera: Formicidae) and some not target ant species and persistence of AMDRO on a pasture habitat in North Carolina. Journal of Economic Entomology 77:1012–1018.

Barton, K.2019. MuMIn: multi-model inference. R package version 1.43.6. http://CRAN.R-project.org/package=MuMIn

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bell, J. R., R. A. King, D. A. Bohan, and W. O. C. Symondson. 2010. Spatial co-occurrence networks predict the feeding histories of polyphagous arthropod predators at field scales. Ecography 33:64–72.

Berghoff, S. M. 2003. Army ants: An evolutionary bestseller? Current Biology 13:676–677.

Berghoff, S. M., U. Maschwitz, K. E. Linsenmair, S. M. Berghoff, U. Maschwitz, and K. E. Linsenmair. 2003. Influence of the hypogaeic army ant Dorylus (Dichthadia) laevigatus on tropical arthropod communities. Oecologia 135:149–157.

Bestelmeyer, B. T., D. Agosti, L. E. Alonso, R. F. Brandao, W. L. Brown, J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ant: an overview, description, and evaluation. Pages 122–144 in D. Agosti, J. Majer, E. Alonso, and T. R. Schultz, editors. Ants: Standard methods for measuring and monitoring. Smithsonian Institution Press, Washington, D.C., USA.

Blum, M. S., B. Hölldobler, H. Fales, and T. Jaouni. 1980. Alkaloidal venom mace: Offensive use by a thief ant. Naturwissenschaften 67:144–145.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldana. 1993. Body size of animal predators and animal prey in food webs. Journal of Animal Ecology 62:67–78.

Costamagna, A. C., and D. A. Landis. 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. Ecological Applications 16:1619–1628.

Deyrup, M. 2016. Ants of Florida: identification and natural history. CRC Press, Boca Raton, Florida, USA.

Fiedler, K., F. Kuhlmann, B. C. Schlick-Steiner, F. M. Steiner, and G. Gebauer. 2007. Stable N-isotope signatures of central European ants – Assessing positions in a trophic gradient. Insectes Sociaux 54:393–402.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodiversity and Conservation 7:1221–1244.

Gotelli, N. J., A. M. Ellison, R. R. Dunn, and N. J. Sanders. 2011. Counting ants (Hymenoptera : Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecological News 15:13–19.

Green, P. T., and D. J. O'Dowd. 2010. Management of invasive invertebrate: Lessons from the management of an invasive ant. Pages 153–172 in Management of invasive species. A handbook of techniques. Oxford University Press, Oxford.

Hirosawa, H., S. Higashi, and M. Mohamed. 2000. Food habits of Aenictus army ants and their effects on the ant community in a rain forest of Borneo. Insectes Sociaux 47:42–49.

Hölldobler, B. 1973. Chemische Strategie beim Nahrungserwerb der Diebsameise (Solenopsis fugax Latr.) und der Pharaoameise (Monomorium pharaonis L.). Oecologia 11:371–380.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, Massachusetts, USA.

Hook, A. W., and S. D. Porter. 1990. Destruction of harvester ant colonies by invading fire ants in south-central Texas (Hymenoptera: Formicidae). The Southwestern Naturalist 35:477–488.

Human, K. G., and D. M. Gordon. 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. Conservation Biology 11:1242–1248.

Jenkins, D. G. 2006. In search of quorum effects in metacommunity structure: Species co-occurrence analyses. Ecology 87:1523–1531.

Kaspari, M., S. Powell, J. Lattke, and S. O'Donnell. 2011. Predation and patchiness in the tropical litter: Do swarm-raiding army ants skim the cream or drain the bottle? Journal of Animal Ecology 80:818–823.

Ken, T., H. R. Hepburn, S. E. Radloff, Y. Yusheng, L. Yiqiu, Z. Danyin, and P. Neumann. 2005. Heat-balling wasps by honeybees. Naturwissenschaften 92:492–495.

King, J. R. 2010. Size-abundance relationships in Florida ant communities reveal how ants break the energetic equivalence rule. Ecological Entomology 35:287–298.

King, J. R., and S. D. Porter. 2005. Evaluation of sampling methods and species richness estimators for ants in upland ecosystems in Florida. Environmental Entomology 34:1566–1578.

King, J. R., and S. D. Porter. 2007. Body size, colony size, abundance, and ecological impact of exotic ants in Florida's upland ecosystems. Evolutionary Ecology Research 9:757–774.

King, J. R., and W. R. Tschinkel. 2006. Experimental evidence that the introduced fire ant, Solenopsis invicta, does not competitively suppress co-occurring ants in a disturbed habitat. Journal of Animal Ecology 75:1370–1378.

King, J. R., and W. R. Tschinkel. 2013. Fire ants are not drivers of biodiversity change: A response to Stuble et al. (2013). Ecological Entomology 38:543–545.

Lach, L., C. Parr, and K. Abbott. 2010. Ant ecology. Oxford University Press, Oxford.

Lapolla, J. S., S. G. Brady, and S. O. Shattuck. 2011. Monograph of Nylanderia (Hymenoptera: Formicidae) of the World: An introduction to the systematics and biology of the genus. Zootaxa 3110:1-9.

LaPolla, J. S., U. G. Mueller, M. Seid, and S. P. Cover. 2002. Predation by the army ant Neivamyrmex rugulosus on the fungus-growing ant Trachymyrmex arizonensis. Insectes Sociaux 49:251–256.

Levey, D. J., and M. M. Byrne. 1993. Complex Ant-plant interactions: Rain-forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74:1802–1812.

Longino, J. T. 2000. What to do with data. Pages 186–203 in D. Agosti, J. Majer, E. Alonso, and T. R. Schultz, editors. Ants: Standard methods for measuring and monitoring. Smithsonian Institution Press, Washington, D.C., USA.

Lubertazzi, D., and W. R. Tschinkel. 2003. Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. Journal of Insect Science 3:1-17.

Lynch, M. 1979. Predation, competition, and zooplankton community structure: An experimental study. Limnology and Oceanography 24:253–272.

MacGown, J. A., and J. A. Forster. 2005. A preliminary list of the ants (Hymenoptera: Formicidae) of Alabama, U.S.A. Entomological News 116:61–74.

Moreno Gonzalez, I.2001. Systematics of the thief ants of North America (Hymenoptera: Formicidae: Solenopsis). Thesis. University of Texas at El Paso, Texas, USA.

Morrison, L. W. 2000. Mechanisms of interspecific competition among an invasive and two native fire ants. Oikos 90:238–252.

Myers, R. L., and J. J. Ewel.1990. Ecosystems of Florida. University Press of Florida, Gainesville, Florida, USA.

Nichols, B., and R. Sites. 1991. Ant predators of founder queens of Solenopsis invicta (Hymenoptera: Formicidae) in central Texas. Environmental Entomology 20:1024–1029.

Nkem, J. N., L. A. Lobry de Bruyn, C. D. Grant, and N. R. Hulugalle. 2000. The impact of ant bioturbation and foraging activities on surrounding soil properties. Pedobiologia 44:609–621.

Ohyama, L., J. R. King, and D. G. Jenkins. 2018. Diversity and distribution of Solenopsis (Hymenoptera: Formicidae) thief ants below ground. Myrmecological News 27:47–67.

Otis, G. W., E. C. Santana, D. L. Crawford, and M. Lou Higgins. 1986. The effect of foraging army ants on leaf-litter arthropods. Biotropica 18:56–61.

Pacheco, J., and W. MacKay.2013. The systematics and biology of the new world thief ants of the genus Solenopsis (Hymenoptera: Formicidae). Edwin Mellen Press, Lewiston, New York, USA.

Paine, R. T. 1974. Intertidal community structure – Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

Plentovich, S., J. Eijzenga, H. Eijzenga, and D. Smith. 2011. Indirect effects of ant eradication efforts on offshore islets in the Hawaiian Archipelago. Biological Invasions 13:545–557.

Powell, S. 2011. How much do army ants eat? On the prey intake of a Neotropical top-predator. Insectes Sociaux 58:317–324.

Powell, S., and E. Clark. 2004. Combat between large derived societies: A subterranean army ant established as a predator of mature leaf-cutting ant colonies. Insectes Sociaux 51:342–351.

Prusak, Z. A. 1997. Ant fauna in three plant communities within Wekiwa Springs State Park, Florida: assessment of diversity and comparion of collecting methods. Thesis. University of Central Florida, Orlando, Florida, USA.

Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84:2281–2291.

Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. Annals of the Entomological Society of America 97:240–248.

Schlick-Steiner, B. C., F. M. Steiner, K. Moder, A. Bruckner, K. Fiedler, and E. Christian. 2006. Assessing ant assemblages: Pitfall trapping versus nest counting (Hymenoptera, Formicidae). Insectes Sociaux 53:274–281.

Schmidt, J. O., and M. S. Blum. 1978. A harvester ant venom: chemistry and pharmacology. Science 200:1064–1066.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. Ecology 78:1388–1399.

Sergio, F. et al 2014. Towards a cohesive, holistic view of top predation: A definition, synthesis and perspective. Oikos 123:1234–1243.

Styrsky, J. D., and M. D. Eubanks. 2007. Ecological consequences of interactions between ants and honeydew-producing insects. Proceedings of the Royal Society B: Biological Sciences 274:151–164.

Terborgh, J. et al 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Terborgh, J. W. 2015. Toward a trophic theory of species diversity. Proceedings of the National Academy of Sciences USA 112:11415–11422.

Thompson, C. 1989. The thief ants, Solenopsis molesta group of Florida (Hymenoptera: Formicidae). Florida Entomologist 72:268–283.

Thompson, C. R.1980. Solenopsis Diplorhoptrum (Hymenoptera: Formicidae) of Florida. PhD dissertation. University of Florida, Gainesville, Florida, USA.

Tillberg, C. V., D. A. Holway, E. G. Lebrun, and A. V. Suarez. 2007. Trophic ecology of invasive Argentine ants in their native and introduced ranges. Proceedings of the National Academy of Sciences USA 104:20856–20861.

Tschinkel, W. R. 2003. Subterranean ant nests: Trace fossils past and future? Palaeogeography, Palaeoclimatology, Palaeoecology 192:321–333.

Tschinkel, W. R. 2006. The fire ants. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA and London, UK.

Tschinkel, W. R. 2015. The architecture of subterranean ant nests: beauty and mystery underfoot. Journal of Bioeconomics 17:271–291.

Van der Meer, R. K., D. F. Williams, and L. S. Lofgren. 1982. Degradation of the toxicant AC-217, 300 in 'AMDRO' imported fire ant bait under field conditions. Journal of Agriculture Food Chemistry 30:1045–1048.

Vinson, S. B., and A. Rao. 2004. Inability of incipient Solenopsis invicta (Hymenoptera: Formicidae) colonies to establish in a plot with a high density of Solenopsis (Diplorhoptrum) colonies. Environmental Entomology 33:1626–1631.

Wardle, D. A. 1999. How soil food webs make plants grow. Trends in Ecology and Evolution 14:418–420.

Wheeler, W. M. 1901. The compund and mixed nests of American ants. Part II. The known cases of social symbiosis among American ants. The American Naturalist 35:513–539.

Wickham, H. 2009. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York, New York, USA.

Zee, J., and D. Holway. 2006. Nest raiding by the invasive Argentine ant on colonies of the harvester ant, Pogonomyrmex subnitidus. Insectes Sociaux 53:161–167.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3084/suppinfo