UNIVERSITY OF CALIFORNIA SAN DIEGO

The recent invasion of southern California by the big-headed ant (*Pheidole megacephala*): implications for future expansion

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Biology

by

Mandy Frazer

Committee in charge:

Professor David Holway, Chair
Professor James Nieh, Co-Chair
Professor Noah Rose

2024

The Thesis of Mandy Frazer is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2024

DEDICATION

I would like to dedicate this thesis to my parents, who despite my many — and most definitely unwanted — invitations extended from the yard into our home, never pressured me to grow out of being a bug kid. I love you.

TABLE OF CONTENTS

Thesis Approval Page……...iii

Dedication……iv

Table of Contents……...v

List of Figures……...vi

List of Supplemental Data Files…….……..vii

Acknowledgments……...viii

Abstract of the Thesis……...….ix

Introduction……1

Methods……..4

Results……8

Discussion……10

Figures……..14

References……19

LIST OF FIGURES

Figure 1: Mapping of observed occurrences of *P. megacephala* (yellow) and *L. humile* (purple) in San Diego (A) and Costa Mesa, California (B). Blue dashed lines show perimeters used for calculation of area estimates in arcGIS.……14

Figure 2: Plot of $\delta^{15}N$ vs $\delta^{13}C$ values for collected *P. megacephala* (yellow) and *L. humile* (purple); (*n* = 18 pairs of 60 homogenized worker ants)……..15

Figure 3: Box plot showing (A) $\delta^{15}N$ values and (B) $\delta^{13}C$ for *L. humile* (purple) and *P. megacephala* (yellow); outliers shown in red. Each box shows the median worker stable isotope value in the center with the interquartile range (IQR) within the box (*n* = 18 pairs of 60 homogenized worker ants)…….……..16

Figure 4: Line chart showing survival curves for *P. megacephala* and *L. humile* under different desiccation conditions (*n* = 10 pairs of 10 worker ants per tube). The solid lines show curves for *L. humile* and the dashed lines show curves for *P. megacephala*, with curves for air treatment shown in red, Drierite shown in green, and water shown in blue…...17

Figure 5: Box plot showing median lethal time (LT50) in hours for collected *L. humile* (purple) and *P. megacephala* (yellow) for air (left) and Drierite (right) treatments; outliers shown in red. Each box shows the median LT50 value in the center with the interquartile range (IQR) within the box (*n* = 10 pairs of 10 worker ants per tube)…….18

LIST OF SUPPLEMENTAL DATA FILES

Frazer_Coordinates&RawData.xlsx

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Professor David Holway, for all of his mentorship and contribution towards this work. Thank you for encouraging me to take this first step into the field of entomology. My appreciation is also owed to Dr. James Nieh and Dr. Noah Rose for serving on my thesis committee.

Thank you to my wonderful family and friends for all of the support and encouragement throughout my master's degree, especially Sam Crolla; I couldn't have done it without you. Special thanks to all of my peers in the Holway Lab who contributed time towards this project and made me feel a sense of community in this program, including Rebecca Stiling, Lizzie Spencer, Christopher Winters, Ellie Fausett, Grace Jurgela, and Jess Mullins.

This thesis, in part, is currently being prepared for submission for publication of the material. Frazer, Mandy; Holway, David A. This thesis is coauthored with Holway, David A. The thesis author was the primary investigator and author of this material.

ABSTRACT OF THE THESIS

The recent invasion of southern California by the big-headed ant (*Pheidole megacephala*): implications for future expansion

by

Mandy Frazer

Master of Science in Biology

University of California San Diego, 2024

Professor David Holway, Chair
Professor James Nieh, Co-Chair

The big-headed ant, *Pheidole megacephala*, is an ecologically destructive invader of tropical and subtropical environments worldwide. In April 2014, an established infestation of *P. megacephala* was discovered in a residential neighborhood in Costa Mesa, Orange County, and a second infestation was found in a residential neighborhood in San Diego, San Diego County, in 2019. Although big-headed ants are regularly detected in commerce in California, the records from Costa Mesa and San Diego represent the first established infestations known from the state. To learn more about the distribution of *P. megacephala* in California and to

assess its potential for further spread, we delineated both known infestations and compared this species to another widespread invader, the Argentine ant (*Linepithema humile*), with respect to desiccation tolerance and resource assimilation ($\delta^{15}N$). Both known *P. megacephala* infestations extend over multiple hectares of suburban development, with the San Diego infestation exceeding 100 ha and the Costa Mesa infestation exceeding 10 ha. Both infestations are spatially continuous and encompassed by established populations of the Argentine ant. The big-headed ant overlapped broadly with the Argentine ant both in terms of desiccation tolerance and $\delta^{15}N$ values. These similarities suggest that the big-headed ant could continue to spread in urban environments in coastal southern California and cause impacts comparable to those resulting from invasion by the Argentine ant.

Introduction

Invasive species profoundly disrupt the ecosystems in which they are introduced and can have far-reaching, cross-ecosystem impacts (Peller & Altermatt 2024). Both biotic and abiotic factors affect introduced species, and these factors often differ between the native and introduced ranges of an invader. Such differences can promote (Zhang et al. 2020, Barral 2019) or limit invasion success (Soti et al. 2020). Invasive ant species are especially pervasive invaders, with five ant species included on the IUCN list of the "100 Worst Invasive Alien Species" (Lowe et al. 2004).

Ant invasions are an increasing cause for concern (Wong et al. 2023, Schwindt et al. 2023). Ant species are often introduced to new areas largely through human commerce (Bertelsmeier et al. 2017), and once established are difficult to eliminate (Zanola et al. 2024, Howse et al. 2023). Invasive ant species have become globally widespread and abundant, perturbing community structure and threatening biodiversity in areas where they are introduced; these effects compromise ecological and agricultural systems worldwide (Aulus-Giacosa et al. 2024, Siddiqui et al. 2021, Holway et al. 2002).

The big-headed ant, *Pheidole megacephala* (Fabricius), is a widely introduced ant species (Wetterer 2011) that disrupts ecosystems in a variety of ways (Kamaru et al. 2024, Gaynor 2024). Recently introduced to California, an established infestation of *P. megacephala* was first discovered in a residential neighborhood in Costa Mesa, Orange County in April 2014 (CDFA 2015). A second infestation was found in a residential neighborhood in San Diego, San Diego County in 2019 (Menke & Holway 2020). Although big-headed ants are regularly detected in commerce in California (CDFA 2015), the infestations in Costa Mesa and San Diego are the first

known cases of establishment in the state. Since the first report a decade ago (CDFA 2015), there have been no follow-up studies to address the potential for *P. megacephala* to spread in California.

The establishment of *P. megacephala* is relatively recent in southern California, however, the consequences of other invasive ant introductions in the region are well-known (Suarez et al. 1998, Tsutsui & Suarez 2003). The Argentine ant, *Linepithema humile* (Mayr), was first reported in California in 1907 (Newell & Barber 1913), and has since expanded statewide (Richmond et al. 2021). Similar to the big-headed ant, the Argentine ant greatly disrupts native fauna in the wake of its invasion (Loope & Krushelnycky 2007, Lowe et al. 2004, Holway et al. 2002). *Pheidole megacephala* and *L. humile* are both native to subtropical climates (Wetterer 2011, Wild 2007), and *P. megacephala* shares many colony structure traits with the Argentine ant that are believed to contribute to its invasive success (Tsutsui & Suarez 2003). Like the Argentine ant, *P. megacephala* is polygynous (multi-queened) and polydomous, where many spatially separated nests remain socially connected with low levels of intraspecific aggression, and form large supercolonies in their introduced ranges (Hoffman et al. 1999, Giraud et al. 2002). The structure of these supercolonies allows both species to amass large numbers and successfully establish new colonies with propagules as small as one fertile queen and 10 workers (Chang 1985, Hee et al. 2000). Additionally, both species are highly aggressive to other ant species, and in areas where they are both introduced, engage in territory disputes with each other that can last multiple decades (Haskins & Haskins 1965, Wetterer 2017).

The above similarities make the Argentine ant a good comparative species to assess other characteristics of *P. megacephala*. Comparative assays can then benchmark potential invasion limitations of the big-headed ant with factors that are known to affect invasion dynamics of the

Argentine ant. For example, spread of the Argentine ant in seasonally dry environments is limited by soil moisture (Menke et al. 2007). In Bermuda and Hawaii, the spread of *L. humile* is affected by the presence of *P. megacephala*, and vice versa, where the two species strongly compete for resources (Wetterer & Cirranello 2004, Reimer 1994). Like these past invasions, as well as laboratory manipulation observations (Mothapo & Wossler 2014), we expect there to be direct resource competition between the two species now that both are present in coastal southern California. In invaded areas, Argentine ants out compete native ants by aggressive displacement, but cannot successfully establish or spread in areas that are too dry (Menke et al. 2007). Because *P. megacephala* frequently invades disturbed areas where water is supplied from anthropogenic sources (Hoffman & Parr 2007), we expect *P. megacephala* spread to also be limited by water availability. Because most *P. megacephala* workers (minors) are smaller in body size than Argentine ant workers (Fisher & Fisher 2013, Wild 2007), we expect *P. megacephala* to have lower desiccation resistance than *L. humile,* as smaller body size often makes insects more vulnerable to desiccation (Chown & Gaston 1999).

In this study, we assess the potential for *P. megacephala* to become a problematic invader in California by delineating both known infestations and comparing its desiccation resistance and stable isotope values with a second widespread invader, the Argentine ant. First, we used stable isotope analysis to determine the extent to which *P. megacephala* and *L. humile* overlap in food resource assimilation by comparing $\delta^{15}N$ and $\delta^{13}C$ values. Next, we compared desiccation resistance between the two species. Considered together, results from these assays reveal similarities between *P. megacephala* and *L. humile,* and suggest that the big-headed ant has potential to invade and impact urban environments in coastal southern California to a similar degree as the invasion by the Argentine ant.

Methods

Delineation of infestations

We mapped the spatial extent of two *Pheidole megacephala* infestations in southern California: Costa Mesa, Orange County. and San Diego, San Diego County. To delineate infestations at each location, we used visual searches and baits to detect *P. megacephala* and then mapped positive detections as well as detections of other ant species (especially the Argentine ant). Both infestations are in urban locations, and this fact simplified delineation efforts. Delineation efforts proceeded under the assumption that *P. megacephala* expansion is spatially continuous as a result of colony budding (Beardsley et al. 1982) and that this species does not co-occur with the Argentine ant as a result of competitive exclusion (Haskins & Haskins 1965, Reimer 1994). We delineated the San Diego infestation in the fall of 2023 and the Costa Mesa infestation in spring 2024. To determine the approximate size of each infestation, we used the polygon area estimation tool in ArcGIS Pro (ESRI; v3.1.1) and formed polygon vertices at approximate perimeter coordinates of each infestation.

Stable-isotope comparisons

To assess whether or not *P. megacephala* and *L. humile* overlap in stable isotope composition, we used stable isotope analysis to compare $\delta^{15}N$ and $\delta^{13}C$ values. We collected spatially-paired samples of each species as follows. Samples for a given pair were collected near the border of the *P. megacephala* infestations at locations where *L. humile* was present just outside of the border between the two species. Collecting locations thus paired a *P. megacephala* location with an *L. humile* location separated by 50 – 150 m. Pairs of locations were at least 200 m from one another. At each sampling location we collected either 60 *P. megacephala* (minors) or 60 *L. humile* (workers) from existing recruitment trails along publicly accessible streets and

sidewalks. For the San Diego infestation, we collected 18 *P. megacephala* / *L. humile* pairs in December 2023. All ants were collected into 50 mL centrifuge tubes, immediately placed in a cooler with ice packs, and then transferred to a freezer at ≤ 0°C within 2 h after collection. To prepare samples for stable isotope analysis, we followed the protocol described in Tillberg et al. (2006) and removed gasters from all ants. Samples were desiccated in a drying oven (Quincy Lab Model 20 Lab Oven, #20GC) for a minimum of 2 d at 55-60°C. A homogenized mass of 0.8 - 1.2 mg of each sample was packed into a 5 x 9 mm tin capsule and sent to the University of California Davis Stable Isotope Facility for analysis. Samples were analyzed using a Sercon Europa ANCA-GSL elemental analyzer interfaced to a Sercon Europa 20-20 IRMS.

Desiccation tolerance

To assess whether or not *P. megacephala* and *L. humile* exhibit comparable responses to arid conditions, we performed desiccation tolerance assays using methods described in Whyte et al. (2023). Samples were collected in the same manner as described under *Stable-isotope collections* except that we collected 30 workers of the two focal species at each sampling location. The 30 workers were transferred from the collecting tube to shallow plastic transfer containers in order to separate ants from any debris also collected during aspiration. Transfer containers were lined with fluon (polytetrafluoroethylene) (Fuel Cell Earth, #DISP30) to prevent ants from escaping during transfer to assay tubes. We collected 10 *P. megacephala* / *L. humile* pairs in April 2024.

We compared the tolerances of *P. megacephala* and *L. humile* under three different conditions: humid (relative humidity (RH) ≈ 100%), ambient (RH ≈ 55%), and dry (RH ≈ 0%). For each experimental group workers (n = 10) were transferred from the transfer containers by hand to a 15 mL centrifuge tube. In the humid group, each 15 mL centrifuge tube contained 2

mL of water held in place at the tube's tip with a 100% cotton ball that made contact with the water and a 4 mm air gap in between the first cotton ball and the second cotton ball. In the ambient and dry experimental groups, water was replaced by either air (ambient) or desiccant (dry). We used freshly opened Drierite (W. A. Hammond Drierite Company, #23001) as our desiccant. All tubes were prepared 24 h before the start of the assay to allow RH to stabilize before introducing ants to the tubes. At 2 h intervals we assessed ant mortality by gently rolling each tube and tapping the sides; immobile ants were considered dead. We recorded mortality counts of each tube every 2 h for the first 12 h of the assay and then every 4 h until no ants remained alive in the Drierite or ambient air tubes.

Statistical analysis

All analyses were performed in the statistical programming language R (R Core Team 2022; v.4.2.2). We compared resource assimilation between *P. megacephala* and *L. humile* by analyzing differences in $\delta^{15}N$ or $\delta^{13}C$ between species, and desiccation resistance between *P. megacephala* and *L. humile* by calculating median lethal time (LT50) for each treatment tube (air or Drierite). We used mixed effects models to test two hypotheses: (i) $\delta^{15}N$ and $\delta^{13}C$ values overlapped between species, and (ii) the LT50 for *P. megacephala* would be lower than for *L. humile* in both moderate (air) and severe (Drierite) desiccation conditions. We used three separate mixed effects models to analyze the relationships between $\delta^{15}N$, $\delta^{13}C$, LT50, and species identity using the routine lmer(), R package 'lme4,' with $\delta^{15}N$ or $\delta^{13}C$ and species identity treated as fixed factors for stable isotope comparisons and treatment condition and species identity treated as fixed factors for desiccation analysis. Collection pair was treated as a random factor in all models. ANOVA tests were performed to test the statistical differences between species for each model. We used an alpha level of 0.05 for all statistical tests. Similar to

Whyte et al. (2023), water control tubes had low mortality relative to treatment conditions and were not used to calculate LT50 values. We calculated the LT50 for each treatment tube (n = 10 workers per tube) using the routine dose.p(), R package ‘MASS,’ which calculates the time that half of the ants in each tube were predicted to be dead. Survival curves were generated with smoothed conditional means, using a logistic regression of the alive vs dead worker ants over time.

Results

Delineation of infestations

Figure 1 shows the observed distributions of *P. megacephala* in San Diego and Costa Mesa, California. The area of the San Diego infestation was 102 ha as of November 2023 (Figure 1A), and the area of the Costa Mesa infestation was 14 ha as of May 2024 (Figure 1B). Both infestations were found to be spatially continuous, and encompassed by established populations of *L. humile* (Figure 1).

Stable-isotope comparisons

Figure 2 plots the $\delta^{13}C$ and $\delta^{15}N$ values for *P. megacephala* and *L. humile.* The paired $\delta^{15}N$ values did not differ between species (Figure 3A; linear mixed effects model: $X_1^2 = 0.89$, $P = 0.346$). We found that *P. megacephala* had statistically higher $\delta^{13}C$ values compared to *L. humile* (Figure 3B; linear mixed effects model: $X_1^2 = 5.69$, $P = 0.0171$); this difference, however, was driven by three extreme $\delta^{13}C$ values (Figure 2). Additionally, intraspecific variability of $\delta^{13}C$ values for *P. megacephala* ($s^2 = 6.52$) was found to be greater than intraspecific variability of $\delta^{13}C$ values for *L. humile* ($s^2 = 2.40$) and greater than interspecific variability between the two species ($\sigma^2 = 4.85$).

Desiccation tolerance

Low mortality was observed in the control tubes (water, RH~ 100%) for both species relative to treatment conditions (Figure 4). Mortality was high in both moderate (air, RH~ 55%) and severe (Drierite, RH~ 0%) desiccation treatment conditions for both species (Figure 4). We found the median lethal time (LT50) for *P. megacephala* in moderate and severe desiccation treatment conditions to be 10.8 ± 0.3 h and 3.9 ± 0.2 h, respectively. We found the median lethal

time for *L. humile* in moderate and severe desiccation treatment conditions to be 11.8 ± 0.3 h and 4.8 ± 0.1 h, respectively. Differences in LT50 did not differ between species (Figure 5; linear mixed effects model: $X_1^2 = 1.90$, $P = 0.168$). As expected, treatment condition (air vs Drierite) was a significant predictor of LT50 for both species (Figure 5; linear mixed effects model: $X_1^2 = 47.45$, $P < 0.001$).

Discussion

The big-headed ant, a widespread invader of tropical and subtropical ecosystems (Wetterer 2011), has successfully established in southern California. The population of *Pheidole megacephala* originally discovered in Costa Mesa has persisted over a decade, and the San Diego infestation exceeds 100 ha — an area presumably much larger than the point of introduction. Paired comparisons between *P. megacephala* and *L. humile* reveal that these two species broadly overlap both in measured $\delta^{15}N$ values and desiccation resistance.

Pheidole megacephala was abundant within the mapped infestation boundaries (Fig. 1). Nest density was high in ornamental planters and along the edges of maintained lawns, where water is readily available by irrigation. We considered the limit of *P. megacephala* distribution to be areas where the nearest surrounding *L. humile* could be detected, or where neither *P. megacephala* nor *L. humile* could be detected for ~200 m. Consistent with observations in Bermuda, where both species are introduced and abundant, there were marginal areas adjacent to areas predominantly occupied by *P. megacephala* or *L. humile* found to be "empty" of both species (Haskins & Haskins 1965). Like Haskins and Haskins (1965), we observed that *Brachymyrmex* sp. was common in areas that were empty of *P. megacephala* and *L. humile*. Because both surveyed regions were in urban and residential environments, it is possible that these areas have been treated with insecticides at least one or more times since the localized introduction of either species. Similar to Haskins and Haskins (1965), it seems possible that *Brachymyrmex* might take advantage of the available niche space and establish more quickly than *P. megacephala* or *L. humile*, following the elimination of these two dominant species. This fast recovery could be because *Brachymyrmex* species have winged dispersal, where alates can spread over large distances and successfully establish new colonies (MacGown et al. 2009).

Future experimentation could address if insecticide treatment is the mechanism for this *Brachymyrmex* replacement phenomenon by applying insecticides to transects of both *L. humile* and *P. megacephala* occupied areas at boundary regions and monitoring the ant species that establish after treatment has ceased.

Contrary to our original hypothesis, laboratory manipulations of humidity showed that *P. megacephala* and *L. humile* exhibit similar responses to desiccation stress. This finding may be surprising in light of the smaller body size of *P. megacephala* minors compared to *L. humile* workers (Fisher & Fisher 2013, Wild 2007, Chown & Gaston 1999). In an intraspecific species comparison of the Argentine ant, desiccation resistance increased with body mass (Whyte et al. 2023), however in a community assessment of tropical ants (including *P. megacephala*), surface area to body ratio was not found to be a significant predictor of desiccation resistance (Bujan et al. 2016). To understand how *P. megacephala* minors and *L. humile* workers have similar mortality in desiccation stress, future experimentation could compare how physical and chemical exoskeletal traits that affect water loss (Schilman et al. 2005) might be similar between the two species.

Paired comparisons between *P. megacephala* and *L. humile* collected in the San Diego region revealed broad overlap in $\delta^{15}N$ values, suggesting that the two species also overlap in their diets. Similar $\delta^{15}N$ values suggest that *P. megacephala* and *L. humile* have similarly sourced protein intake through predation and scavenging, which is reflective of trophic positioning. We found that *P. megacephala* had statistically higher $\delta^{13}C$ values, but this difference was driven by three extreme points in the data set for *P. megacephala*. Because of the uneven distribution of anthropogenic food sources in mixed urban environments, $\delta^{13}C$ values can be extremely variable, and even small changes in microhabitat can result in significant changes

in $\delta^{13}C$ values for ants, even for ants of the same species (Penick et al. 2015). Our sampling design consisted of paired collections of *L. humile* and *P. megacephala* in which geographical distance between paired points was minimized, rather than pairing by similar microhabitat, and as such it is not entirely clear if the observed difference in $\delta^{13}C$ values is an effect of species preference or simply localized resource availability. To gain more insight into how these trends may be present in our study area, future studies could consider an intraspecific comparison of both *L. humile* and *P. megacephala* to assess the degree to which microhabitat type affects $\delta^{13}C$ values. Additionally, future studies could gauge macronutrient preferences between species and between microhabitat types with baiting experiments to gain more insight into the possible mechanisms for the observed isotopic differences between *L. humile* and *P. megacephala*.

Our results show that the big-headed ant faces similar limitations of invasion as the Argentine ant, which is an established and widespread invader in California. Like the Argentine ant, *P. megacephala* disrupts biodiversity in invaded areas and is particularly destructive to native invertebrate communities (Loope & Krushelnycky 2007, Holway et al. 2002). Both species are highly aggressive and form supercolonies that allow them to grow quickly in population (Tsutsui & Suarez 2003). These similarities may make resource competition and territory feuds with *L. humile* the most influential factor of invasion dynamics of *P. megacephala* in California. However, on its own, presence of the Argentine ant is likely not strong enough as a control measure of *P. megacephala*, as even match-ups between the two species typically favor *P. megacephala* (Mothapo & Wossler 2014), and other tropical ant invaders have successfully become established in urban areas of coastal southern California despite the abundance of *L. humile* (Kabashima et al. 2007, Martinez et al. 2011) Though the infestations in our study are the only two known *P. megacephala* infestations in California to date, it seems plausible that others

exist. Longitudinal studies are needed to determine if *P. megacephala* is spreading within California and to assess the threat that this species poses as a novel invader.

This thesis, in part, is currently being prepared for submission for publication of the material. Frazer, Mandy; Holway, David A. This thesis is coauthored with Holway, David A. The thesis author was the primary investigator and author of this material.

Figures

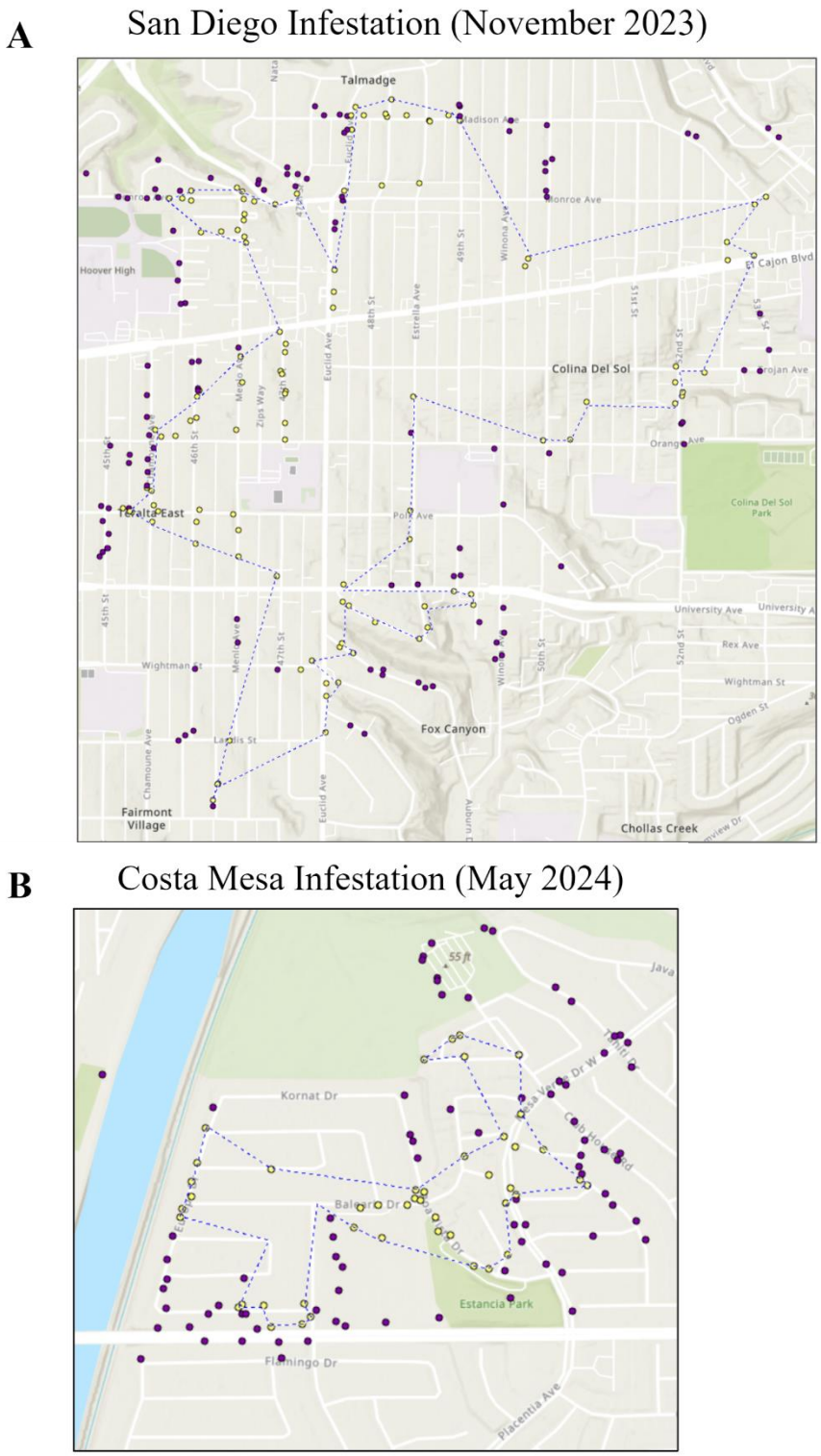


Figure 1: Mapping of observed occurrences of *P. megacephala* (yellow) and *L. humile* (purple) in San Diego (A) and Costa Mesa, California (B). Blue dashed lines show perimeters used for calculation of area estimates in arcGIS.

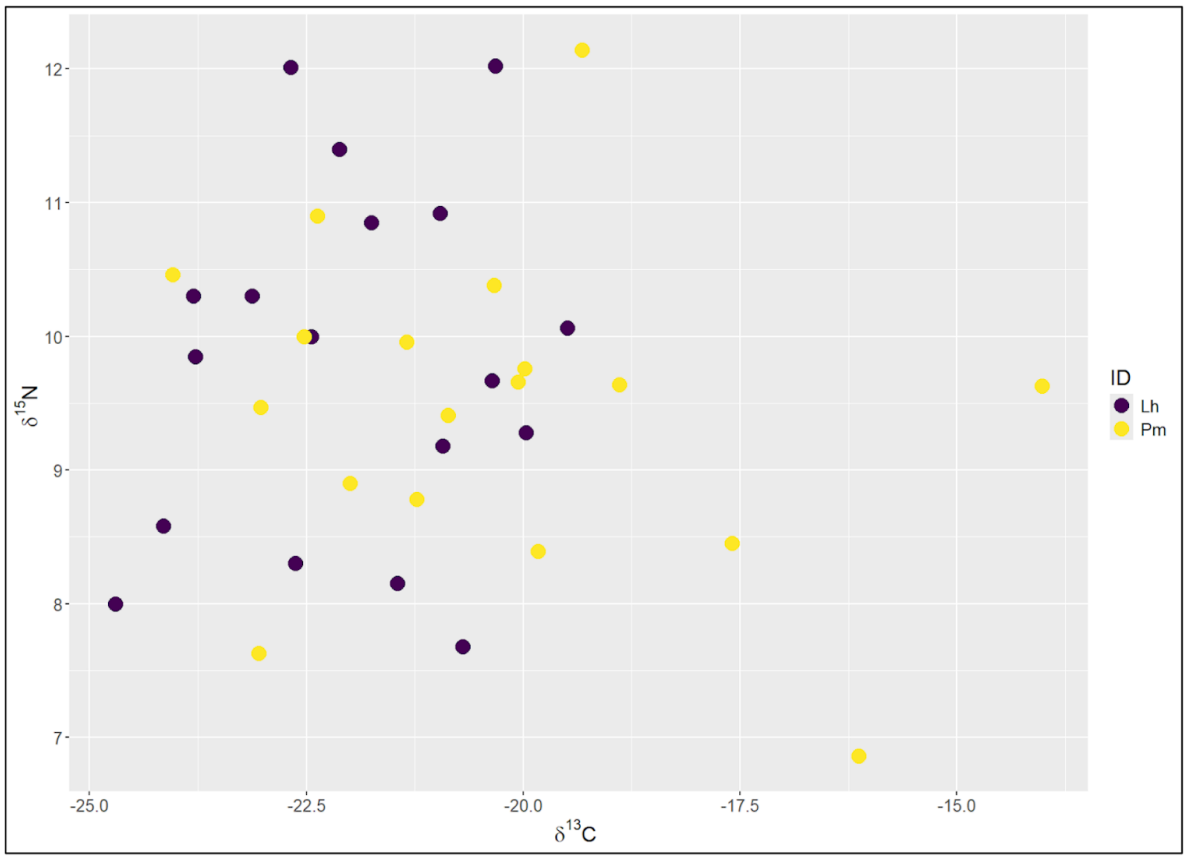
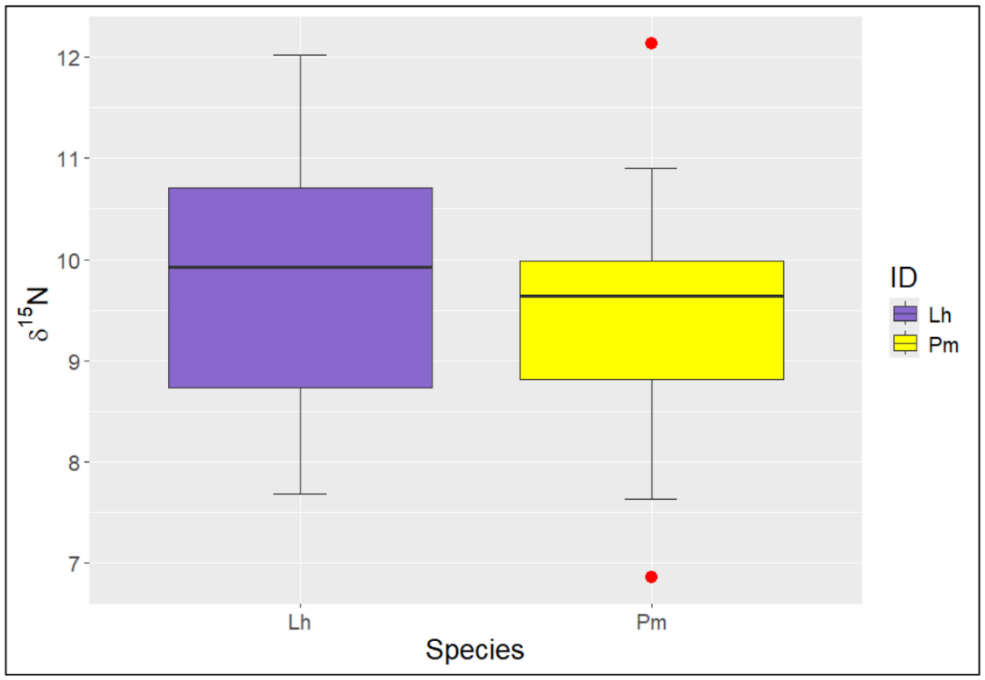


Figure 2: Plot of $\delta^{15}N$ vs $\delta^{13}C$ values for collected *P. megacephala* (yellow) and *L. humile* (purple); (*n* = 18 pairs of 60 homogenized worker ants).

A δ^{15}N of collected *L. humile* and *P. megacephala*



B δ^{13}C of collected *L. humile* and *P. megacephala*

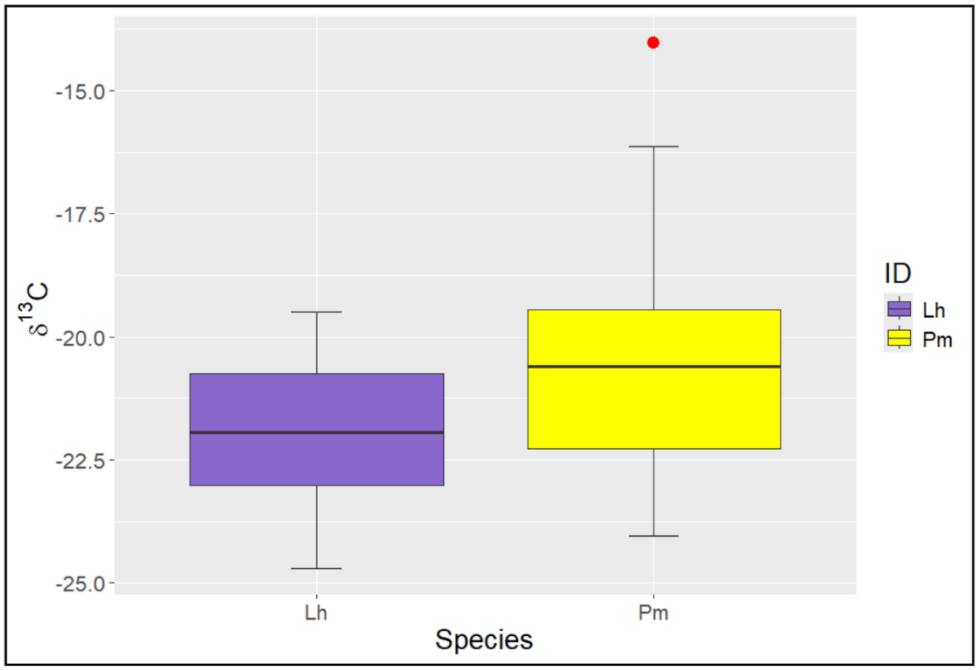


Figure 3: Box plot showing (A) δ^{15}N values and (B) δ^{13}C for *L. humile* (purple) and *P. megacephala* (yellow); outliers shown in red. Each box shows the median worker stable isotope value in the center with the interquartile range (IQR) within the box (n = 18 pairs of 60 homogenized worker ants).

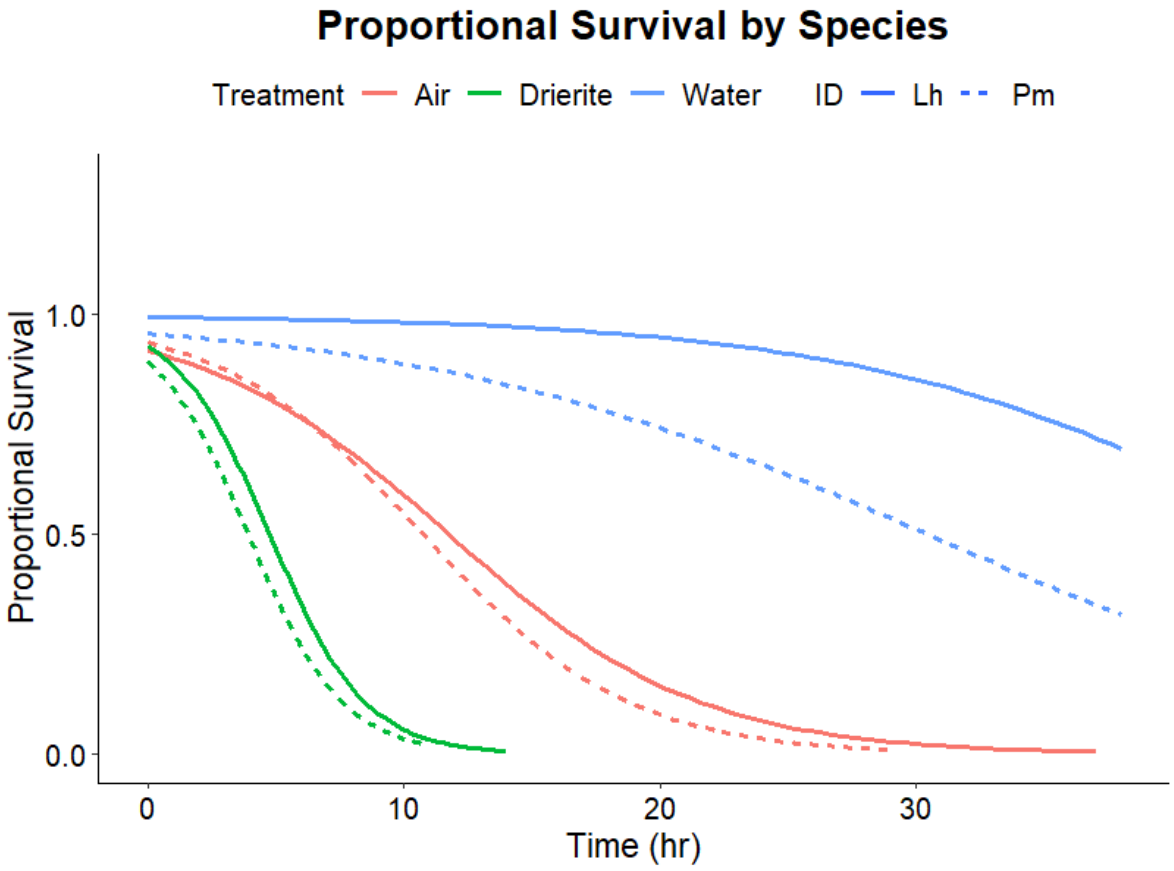


Figure 4: Line chart showing survival curves (logistic regression) for *P. megacephala* and *L. humile* under different desiccation conditions (n = 10 pairs of 10 worker ants per tube). The solid lines show curves for *L. humile* and the dashed lines show curves for *P. megacephala*, with curves for air treatment shown in red, Drierite shown in green, and water shown in blue.

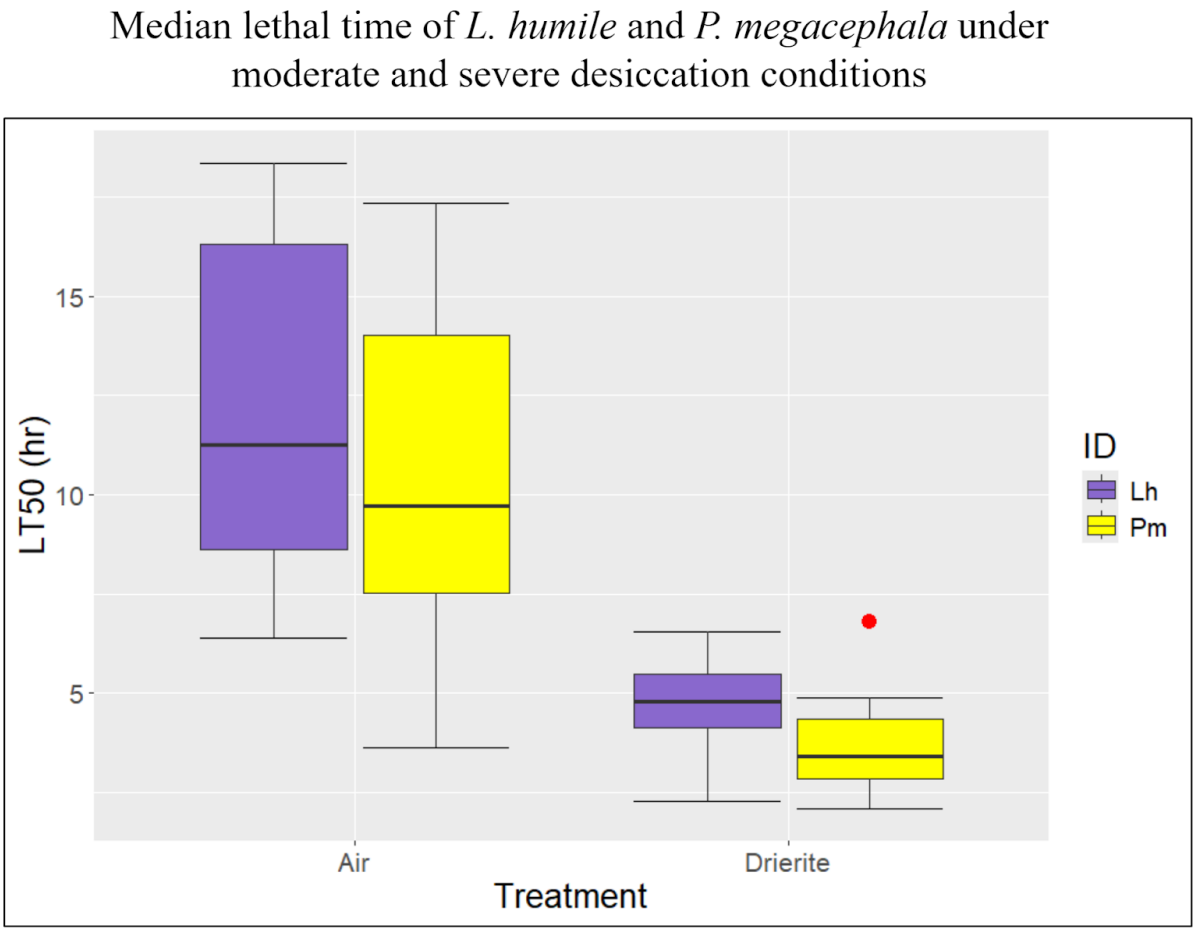


Figure 5: Box plot showing median lethal time (LT50) in hours for collected *L. humile* (purple) and *P. megacephala* (yellow) for air (left) and Drierite (right) treatments; outliers shown in red. Each box shows the median LT50 value in the center with the interquartile range (IQR) within the box (n = 10 pairs of 10 worker ants per tube).

REFERENCES

Aulus-Giacosa, L., Ollier, S., & Bertelsmeier, C. (2024). Non-native ants are breaking down biogeographic boundaries and homogenizing community assemblages. *Nature Communications,* 15, 2266. https://doi.org/10.1038/s41467-024-46359-9

Barral, A. (2019). Invasive species like it hot. *Nature Plants,* 5, 645 https://doi.org/10.1038/s41477-019-0483-z

Beardsley, J., Su, T. H., Mcewen, F. L., & Gerling, D. (1982). Field investigations on the interrelationships of the big-headed ant, the gray pineapple mealybug, and pineapple mealybug wilt disease in Hawaii. *Proceedings of the Hawaiian Entomological Society,* 24(1), 51-67.

Bertelsmeier, C., Ollier, S., Liebhold, A., & Keller, L. (2017). Recent human history governs global ant invasion dynamics. *Nature Ecology & Evolution,* 1, 0184. https://doi.org/10.1038/s41559-017-0184

Bujan, J., Yanoviak, S. P., & Kaspari, M. (2016). Desiccation resistance in tropical insects: causes and mechanisms underlying variability in a Panama ant community. *Ecology & Evolution,* 6(17), 6282-91. https://doi.org/10.1002/ece3.2355

California Department of Food and Agriculture. (2015). California Pest Rating for Pheidole megacephala (Bigheaded Ant) Hymenoptera: Formicidae Pest Rating: A. Retrieved from: https://blogs.cdfa.ca.gov/Section3162/?p=566

Chang, V. C. S. (1985). Colony revival and notes on rearing and life history of the big-headed ant Pheidole megacephala. *Proceedings of the Hawaiian Entomological Society,* 25, 53–58.

Chown, S. L., & Gaston, K. J. (1999). Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biological Reviews*, 74, 87-120. https://doi.org/10.1111/j.1469-185X.1999.tb00182.x

Fischer, G., & Fisher, B. L. (2013). A revision of Pheidole Westwood (Hymenoptera: Formicidae) in the islands of the Southwest Indian Ocean and designation of a neotype for the invasive Pheidole megacephala. *Zootaxa*, 3683, 301–356. https://doi.org/10.11646/zootaxa.3683.4.1

Gaynor, K. M. (2024). A big-headed problem drives an ecological chain reaction. *Science,* 383, 370-371. https://doi.org/10.1126/science.adn3484

Giraud, T., Pedersen, J. S., & Keller, L. (2002). Evolution of supercolonies: The Argentine ants of southern Europe. *Biological Sciences,* 99(9), 6075-6079. https://doi.org/10.1073/pnas.092694199

Haskins, C. P., & Haskins, E. F. (1965). Pheidole Megacephala and Iridomyrmex Humilis in Bermuda-Equilibrium or Slow Replacement? *Ecology,* 46(5), 736-740. https://www.jstor.org/stable/1935016

Hee, J. J., Holway, D. A., Suarez, A. V., & Case, T. J. (2000). Role of propagule size in the success of incipient colonies of the invasive Argentine ant. *Conservation Biology,* 14, 559–563.

Hoffmann, B. D., & Parr, C. L. (2008). An invasion revisited: the African big-headed ant (Pheidole megacephala) in northern Australia. *Biological Invasions,* 10, 1171–1181. https://doi.org/10.1007/s10530-007-9194-x

Hoffmann, B. D., Andersen, A. N., & Hill, G. J.(1999). Impact of an introduced ant on native rain forest invertebrates: Pheidole megacephala in monsoonal Australia. *Oecologia,* 120(4), 595-604. https://doi.org/10.1007/PL00008824

Holway, D. A., Lach, L., Suarez, A., Tsutsui, N., & Case, T. J. (2002). The causes and consequences of ant invasions. *Annual Review of Ecology & Systematics,* 33, 181-233. https://doi.org/10.1146/annurev.ecolsys.33.010802.150444

Howse, M.W. F., Haywood, J., & Lester, P. J. (2023). Sociality reduces the probability of eradication success of arthropod pests. *Insectes Sociaux,* 70, 285–294. https://doi.org/10.1007/s00040-023-00921-8

Kabashima, J. N., Greenberg, L., Rust, M. K., & Paine, T. D. (2007). Aggressive Interactions Between Solenopsis invicta and Linepithema humile (Hymenoptera: Formicidae) Under Laboratory Conditions. *Journal of Economic Entomology,* 100(1), 148–154. https://doi.org/10.1093/jee/100.1.148

Kamaru D. N., Palmer T. M., Riginos C., Ford A. T., Belnap J., Chira R. M., Githaiga J. M., Gituku B. C., Hays B. R., Kavwele C. M., Kibungei A. K., Lamb C. T., Maiyo N. J., Milligan P. D., Mutisya S., Ng'weno C. C., Ogutu M., Pietrek A. G., Wildt B. T., & Goheen J. R. (2024). Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. *Science,* 383, 433-438. https://doi.org/10.1126/science.adg1464

Loope, L. L., & Krushelnycky, P. D. (2007). Current and Potential Ant Impacts in the Pacific Region. *Proceedings of the Hawaiian Entomological Society,* 39, 69–73.

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2004). 100 of the World's Worst Invasive Alien Species: A selection from the Global Invasive Species Database. https://doi.org/10.1163/9789004278110_019

Macgown, J. A., Hill, J. G., & Deyrup, M. (2009). Brachymyrmex patagonicus (Hymenoptera: Formicidae), an emerging pest species in the southeastern United States. *Florida Entomologist,* 90, 457-464. https://doi.org/10.1653/0015-4040(2007)90[457:BPHFAE]2.0.CO;2

Martinez, M. J., Wrenn, W. J., Tilzer, A., & Cummings, R. F. (2011). New records for the exotic ants Brachymyrmex patagonicus Mayr and Pheidole moerens Wheeler (Hymenoptera: Formicidae) in California. *The Pan-Pacific Entomologist,* 87(1), 47-50. https://doi.org/10.3956/2011-03

Menke, S. B., Fisher, R. N., Jetz, W., & Holway, D. A. (2007). Biotic and abiotic controls of Argentine ant invasion. *Ecology,* 88(12), 3164–3173. https://doi.org/10.1890/07-0122.1

Menke, S.B., & Holway, D.A. (2020). Historical resurvey indicates no decline in Argentine ant site occupancy in coastal southern California. *Biological Invasions,* 22, 1669-1679. https://doi.org/10.1007/s10530-020-02211-x

Mothapo, N. P., & Wossler, T. C. (2014). Resource competition assays between the African big-headed ant, Pheidole megacephala (Fabricius) and the invasive Argentine ant, Linepithema humile (Mayr): mechanisms of inter-specific displacement. *Ecological Entomology,* 39, 501-510. https://doi.org/10.1111/een.12126

Newell, W., & Barber, T. C.. (1913). The Argentine Ant. U. S. Department of Agriculture, *Bureau of Entomology Bulletin,* 122. Washington, Government Printing Office

Peller, T., & Altermatt, F. (2024). Invasive species drive cross-ecosystem effects worldwide. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-024-02380-1

Penick, C. A., Savage, A. M., & Dunn, R. R. (2015). Stable isotopes reveal links between human food inputs and urban ant diets. *Proceedings of the Royal Society B: Biological Sciences,* 282(1806), 20142608. https://doi.org/10.1098/rspb.2014.2608

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reimer, N. J. (1994). Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. Exotic ants: biology, impact, and control of introduced species. *Westview Press,* 11-22.

Richmond, J. Q., Matsuda, T., Brehme, C. S., Perkins, E. E., & Fisher, R. N. (2021). Predictability of Invasive Argentine Ant Distribution Across Mediterranean Ecoregions of Southern California. *Western North American Naturalist,* 81(2), 243-256. https://doi.org/10.3398/064.081.0208

Schilman, P. E., Lighton, J. R., & Holway, D. A. (2005). Respiratory and cuticular water loss in insects with continuous gas exchange: comparison across five ant species. *Journal of Insect Physiology,* 51(12), 1295-305. https://doi.org/10.1016/j.jinsphys.2005.07.008

Schwindt, E., August, T.A., Vanderhoeven, S., McGeoch, M.A., Bacher, S., Galil, B.S., Genovesi, P., Hulme, P.E., Ikeda, T., Lezner, B., Nuñez, M.A., Ordonez, A., Pauchard, A., Rahlao, S.J., Renard Truong, T., Roy, H.E., Sankaran, K.V., Seebens, H., Sheppard, A.W., Stoett, P., Vandvik, V., Wilson, J.R., & Meyerson, L.A. (2023). Overwhelming evidence galvanizes a global consensus on the need for action against Invasive Alien Species. *Biological Invasions,* 26, 621–626. https://doi.org/10.1007/s10530-023-03209-x

Soti, P.G., Purcell, M., & Jayachandran, K. (2020). Soil biotic and abiotic conditions negate invasive species performance in native habitat. *Ecological Processes,* 9, 18. https://doi.org/10.1186/s13717-020-00220-1

Suarez, A.V., Bolger, D.T. & Case, T.J. (1998). Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology,* 79, 2041-2056. https://doi.org/10.1890/0012-9658

Tillberg, C. V., McCarthy, D. P., Dolezal, A. G., & Suarez, A. V. (2006). Measuring the trophic ecology of ants using stable isotopes. *Insectes sociaux,* 53, 65-69.

Tsutsui, N.D. & Suarez, A.V. (2003), The Colony Structure and Population Biology of Invasive Ants. *Conservation Biology,* 17, 48-58. https://doi.org/10.1046/j.1523-1739.2003.02018.x

Wetterer, J. (2012). Worldwide spread of the African big-headed ant, Pheidole megacephala (Hymenoptera: Formicidae). *Myrmecological News,* 17, 51-62.

Wetterer, J. (2017). Invasive ants of Bermuda revisited. *Journal of Hymenoptera Research,* 54. https://doi.org/10.3897/jhr.54.11444

Wetterer, J., & Cirranello, A. (2004). Ants (Hymenoptera: Formicidae) of Bermuda. *Florida Entomologist,* 87, 212-221.

Whyte, B. A., Sandidge, R., Buellesbach, J., Cash, E. I., Scheckel, K. J., Gibson, J. D., & Tsutsui, N. D. (2023). The role of body size and cuticular hydrocarbons in the desiccation resistance of invasive Argentine ants (Linepithema humile). *Journal of Experimental Biology,* 226, 16. https://doi.org/10.1242/jeb.245578

Wild, A. (2007). Taxonomic revision of the ant genus Linepithema (Hymenoptera: Formicidae). *University of California Publications in Entomology,* 126, 1-151.

Wong, M. K. L., Economo, E. P., & Guénard, B. (2023). The global spread and invasion capacities of alien ants, *Current Biology,* 33 (3), 566-571. https://doi.org/10.1016/j.cub.2022.12.020.

Zanola, D., Czaczkes, T.J. & Josens, R. (2024). Ants evade harmful food by active abandonment. *Communications Biology*, 7, 84. https://doi.org/10.1038/s42003-023-05729-7

Zhang, Z., Liu, Y., Brunel, C., & van Kleunen, M. (2020). Soil-microorganism-mediated invasional meltdown in plants. *Nature Ecology & Evolution,* 4, 1612–1621. https://doi.org/10.1038/s41559-020-01311-0