

ISSN 1994-4136 (print)

ISSN 1997-3500 (online)

Myrmecological News

Volume 27

August 2018



Schriftleitung / editors

Florian M. STEINER (Editor-in-Chief), Birgit C. SCHLICK-STEINER, Daniel J.C. KRONAUER

Fachredakteure / subject editors

Jens DAUBER, Falko P. DRIJFHOUT, Evan ECONOMO, Heike FELDHAAR, Nicholas J. GOTELLI,
Heikki O. HELANTERÄ, John S. LAPOLLA, Philip J. LESTER,
Timothy A. LINKSVAYER, Alexander S. MIKHEYEV, Ivette PERFECTO, Christian RABELING,
Bernhard RONACHER, Helge SCHLÜNS, Chris R. SMITH, Andrew V. SUAREZ, Herbert ZETTEL

Online Editor / online editor

Patrick KRAPP

Wissenschaftliche Beratung / editorial advisory board

Barry BOLTON, Jacobus J. BOOMSMA, Alfred BUSCHINGER, Daniel CHERIX, Jacques H.C. DELABIE,
Katsuyuki EGUCHI, Xavier ESPADALER, Bert HÖLLDOBLER, Ajay NARENDRA, Zhanna REZNIKOVA,
Michael J. SAMWAYS, Bernhard SEIFERT, Philip S. WARD

Eigentümer, Herausgeber, Verleger / publisher

© 2018 **Österreichische Gesellschaft für Entomofaunistik**

c/o Naturhistorisches Museum Wien, Burgring 7, 1010 Wien, Österreich (*Austria*)



Diversity and distribution of *Solenopsis* (Hymenoptera: Formicidae) thief ants belowground

Leo OHYAMA, Joshua R. KING & David G. JENKINS



Abstract

Subterranean ant communities are vastly understudied relative to aboveground ant communities. The thief ants of the genus *Solenopsis* are a globally abundant and widespread group that is a conspicuous and important part of the belowground ant community. Thief ant ecology, including their distribution and diversity at local scales, has also rarely been documented. In this study, we sampled the subterranean ant community of central Florida, a region with conspicuously high subterranean thief ant abundance. We used a stratified-random sampling protocol and collected soil environmental variables at each sampling plot to model subterranean ant diversity in relation to abiotic conditions in the soil environment. Furthermore, we utilized non-parametric ordination methods and permutation-based analyses of variance to visualize and quantify associations of species based on habitats and soil strata. Our study yielded 15 species from six genera of which five were thief ant species. These five *Solenopsis* species represented 64% of all ant individuals found. We also identified distinct differences in species composition between two habitat types (pine flatwoods and high pine sandhills) and significant associations of soil abiotic conditions with the diversity of the subterranean community. This study finds that thief ants dominate belowground and respond predictably to soil habitat conditions. Biotic effects among ant species may be important given their purported lestopibiotic behaviors.

Key words: Cryptic, fire ants, hypogaecic, lestopibiosis, ant sampling, soil temperature, soil moisture, subterranean.

Myrmecol. News 27: 47-57 (online 29 May 2018)

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 23 February 2018; revision received 4 May 2018; accepted 9 May 2018

Subject Editor: Chris R. Smith

Leo Ohyama (contact author), Joshua R. King & David G. Jenkins, University of Central Florida, Biology Department, 4110 Libra Drive, Orlando, FL 32816, USA. E-mail: leoohyama@knights.ucf.edu

Introduction

Subterranean ants nest and forage almost entirely belowground. They are a group that may represent the final unexplored frontier for global ant biodiversity (WILKIE & al. 2007). In general, these ants are usually small-bodied and cryptic in their morphology, most likely a result of a hypogaecic life history (WONG & GUÉNARD 2017). Despite recent evidence of the diversity represented in subterranean communities as well as their potential impacts on soil ecosystems, little information exists on their basic biology and ecology (WILKIE & al. 2007, SCHMIDT & DIEHL 2008, ANDERSEN & BRAULT 2010, WILKIE & al. 2010, RIBAS & al. 2012, WONG & GUÉNARD 2017). This also extends to what little is known about the ecology and belowground activities of most epigeic ants. Subterranean sampling has not been integral to ant diversity assessments, and its practice has only recently become more widespread (SCHMIDT & SOLAR 2010). Most sampling of subterranean ant communities has only been done in the Neotropics (WONG & GUÉNARD 2017). Thus, subterranean ant distributions and interactions with other soil invertebrates are scarcely known. This dearth of information is because of the difficulties associated with sampling belowground where traps and direct soil sampling are usually the only logistically feasible approaches.

Given this sparse background, an important question is: What are the potential drivers of subterranean ant species distributions at local scales? At broader scales, soils (type, compression, temperature) and elevation have been shown to

affect subterranean ant diversity (LYNCH & al. 1988, WILKIE & al. 2010, BERMAN & ANDERSEN 2012, CANEDO-JÚNIOR 2015). However, substantial variation exists among local sample sites in the above studies. For example, subterranean ant abundances in Ecuador are not predicted by some soil conditions, such as soil pH or mineral content (JACQUEMIN & al. 2012). However, another study in the Brazilian savannah showed significant effects of soil temperature and compression in association with changing subterranean ant species compositions (CANEDO-JÚNIOR 2015). Collectively, these few studies represent most of what is known about environmental factors affecting subterranean ant diversity and distributions (WONG & GUÉNARD 2017). These studies suggest that the relationship between the diversity and distributions of subterranean ants and soil conditions may jointly depend on broad-scale geography and the local composition of the local subterranean ant community.

Subterranean ant communities, especially in the tropics, contain a variety of genera. However, the genus *Solenopsis* is found globally in belowground communities and is among the most abundant group of species in these communities and thus warrants special attention (WILKIE & al. 2007, BERMAN & ANDERSEN 2012, PACHECO & MACKAY 2013). Thief ants in the genus *Solenopsis* are a group of relatively small-bodied, largely subterranean or litter-dwelling species (although there are even some arboreal species) that are abundant in communities from the warm temperate to the

tropical zones (PACHECO & al. 2007, ANDERSEN & BRAULT 2010, HERNÁNDEZ 2010, PACHECO & MACKAY 2013). About 86 described thief ant species occur across the globe as a common and conspicuous group in most ant communities (MACKAY & MACKAY 2002, PACHECO & MACKAY 2013). In Florida, the thief ant species considered to be completely subterranean are *Solenopsis tonsa* THOMPSON, 1989, *Solenopsis pergandei* FOREL, 1901, and quite possibly *Solenopsis tennesseensis* SMITH, M.R., 1951. Some (or perhaps most) thief ant species are purported to be “lestobiotic“, nesting near the nests of host ant colonies, tunneling belowground into their nests, and stealing their brood (HÖLLDOBLER 1973, HÖLLDOBLER & WILSON 1990, TSCHINKEL 2006, DEYRUP 2016). Thief ants are assumed to practice lestobiosis upon a wide range of ant species that are often much larger in size, as this interaction often emphasizes the interaction between small and large-bodied ants (HÖLLDOBLER & WILSON 1990). Although thief ants may also be dietary generalists and even predators of other ants when not stealing brood as they have also been observed actively preying on founding queens (WHEELER 1901, BLUM & al. 1980, THOMPSON 1980, BUREN 1983, LAMMERS 1987, NICHOLS & SITES 1991, VINSON & RAO 2004, DEYRUP 2016). The small body size of thief ants (which includes some of the smallest workers among all ants) may also allow them to move through soil and escape via pathways not accessible to their larger-bodied prey (KASPARI & WEISER 1999). This potential behavior coupled with their high abundance and broad, global distribution suggests that lestobiosis by thief ants, and preying directly on brood and, especially, founding queens (LAMMERS 1987, NICHOLS & SITES 1991, VINSON & RAO 2004), may be an important regulator of both subterranean and aboveground ant communities.

What is actually known about subterranean ant interactions with other ants is largely based on a few descriptions (WHEELER 1901, SCHNEIRLA & al. 1944, DEYRUP 2016). This gap in knowledge is all the more important in regions such as the southeastern US, and especially upland habitats in Florida, where thief ants dominate subterranean ant diversity and abundance (LUBERTAZZI & TSCHINKEL 2003, KING & PORTER 2007, DEYRUP 2016). Furthermore, the subterranean thief ant complex from these localities has been taxonomically well described for many years, meaning that community diversity analyses may be confidently conducted (THOMPSON 1980, 1989, MORENO GONZALEZ 2001).

In the most comprehensive treatment of thief ant ecology to date, THOMPSON (1980) found that thief ant species composition differed between shrubby and grassy habitat types. Otherwise, only unpublished observations inform the ecology of thief ant distributions. Depth to water table or soil moisture content may be the main environmental drivers of thief ant distribution and diversity as long-term soil moisture dynamics may limit the foraging capabilities of these ants (LAMMERS 1987). It is also known that thief ants are sensitive to low humidity when being raised in a laboratory setting but in the wild are incapable of building mounds like the fire ant (*Solenopsis invicta* BUREN, 1972) to escape inundation (THOMPSON 1980, TSCHINKEL 2006). Therefore, well-drained soils in otherwise mesic regions likely maintain conditions ideal for thief ant populations. In Florida, upland habitats such as drier pine flatwoods and especially high pine sandhills (MYERS & EWEL 1990) appear to support robust populations of a number of thief ant species (THOMPSON 1980). Nearby habitats (e.g., more

mesic flatwoods and dry prairies) are more prone to flooding (MYERS & EWEL 1990) and appear to have reduced subterranean ant diversity and abundances (DEYRUP 2016). We therefore conducted this study in upland sandhill and flatwood habitats to determine if there are differences in thief ant communities associated with these common habitat types in this region.

To better understand the factors affecting ant distribution and activity belowground, we sampled belowground foraging ants in the two habitat types (sandhill and flatwoods) using baits and collected associated soil environmental variables to identify relationships between the subterranean ant community and local habitat conditions. Considering that many subterranean ants are known for their small-bodied form and cryptic morphology we specifically targeted small-bodied ants in our sampling. We understand that not all subterranean ants are small-bodied as seen in WONG & GUÉNARD (2017) but based on previous surveys and studies in central Florida and in other parts of the state we have evidence that subterranean ants in our locality were small-bodied (THOMPSON 1980, PRUSAK 1997, LUBERTAZZI & TSCHINKEL 2003, KING & PORTER 2007, KING 2010). Furthermore, our primary focus, the *Solenopsis* thief ants, are all small-bodied (THOMPSON 1989, DEYRUP 2016). However, not all the ants that were baited truly practice a subterranean life history, that is, nesting and foraging entirely belowground but they were still classified as part of the subterranean ant community for the purpose of this study. Therefore, we defined the “subterranean ant community” to be composed of ants with a hypogaecic life history as well as the ants that were found to co-occur with them in our subterranean sampling. These co-occurring species may forage or nest aboveground but may be opportunistically foraging belowground as well. We later differentiate subterranean versus other ant species, based on what is known of their natural history. Nevertheless, even small-bodied aboveground foraging or nesting ants that forage opportunistically belowground likely play a role in the subterranean ant community.

We asked: (1) Do subterranean ant communities (with an emphasis on thief ants) differ in composition and abundance between flatwood and sandhill habitats? (2) Do soil environmental gradients predict the species diversity of this subterranean ant community? (3) Do these gradients also predict the occurrence of thief ant species?

We also compared those data to the only two other subterranean sampling studies conducted in Florida (THOMPSON 1980, LUBERTAZZI & TSCHINKEL 2003). LUBERTAZZI & TSCHINKEL (2003) carried out their subterranean assessment in the longleaf pine forest of the Apalachicola National Forest outside of Tallahassee, Florida. THOMPSON (1980) conducted a sampling survey comprised of two total plots, one in turkey oak woods and the other in an open field outside of Gainesville, Florida. Comparisons to aboveground ant diversity and relative abundance in our study site were also made possible using aboveground pitfall sampling data (from 2012) collected from the same areas as our subterranean sampling.

Materials and methods

Study site: Sampling was conducted during the months of July and August, 2017, at Wekiva Springs State Park (2,750 hectares) situated in Orange County, Florida at 28.7118°N, 81.4628°W. Average annual rainfall in the area is approximately 1350 mm. The general seasonality of the site

Tab. 1: A table showing the top five performing simple linear regression models under AICc (Akaike Information Criterion with correction for small sample sizes) rankings. Predictor variables for each model are shown along with each model's AICc score, the change in AICc for every lower ranked model, AICc weights, and the adjusted- R^2 .

Model	AICc	Δ AICc	Weight (w_i)	Adjusted- R^2
D ~ Habitat * Avg. Change in Daily Soil Temp.	94.4	0.0	0.34	0.60
D ~ Habitat * Avg. Soil Maximum Temp.	96.2	1.8	0.14	0.57
D ~ Habitat + Avg. Soil Moisture * Avg. Soil Temp.	97.2	2.9	0.08	0.58
D ~ Habitat + Avg. Soil Minimum Temp.	97.4	3.0	0.08	0.53
D ~ Habitat + Avg. Soil Moisture	97.6	3.3	0.07	0.53

involves a cycle of wet and dry seasons with the wet season beginning around May and ending in November and the dry season occurring December-April. We distinguished two main habitat types within this park to conduct our survey, high pine sandhills and mesic pine flatwoods.

High pine sandhill is a pyrogenic habitat characterized by well-drained sandy soils, an overstory of longleaf pine (*Pinus palustris*), and a groundcover dominated by wiregrass (*Astrida beyrichiana*) (MYERS & EWEL 1990). The sandhill sites selected for this study were in areas maintained by low intensity fires. High pine sandhill habitats gradually transition downhill to pine flatwoods, which are distinct in vegetation as a result of more poorly-drained soils due to a higher water table and subsequent proneness to flooding (ABRAHAMSON & HARTNETT 1990). Sandhill soils are generally categorized into droughty course sands, sandy clays, or loamy sands; our sites were mostly composed of coarse sand classified as Entisols that are generally low in nutrients (ABRAHAMSON & HARTNETT 1990). Flatwood soils are usually acidic and hold insignificant amounts of extractable nutrients (GHOLZ & FISHER 1982, MYERS & EWEL 1990). Soil moisture of the flatwoods is usually influenced by soil organic matter content as well as a mulching effect from the litter layer (MYERS & EWEL 1990).

Design: A stratified-random sampling design was used in both habitat types, where habitat type boundaries were first identified in the field (based on vegetation) using a handheld GPS. These coordinates were used to generate polygons representative of the two habitat types in ArcMap (ESRI 2017). Coordinates for our sample plots (16 per habitat type) were then randomly generated in ArcMap within the habitat type polygons. A minimum distance of 36 meters between sample plots avoided site overlap. Sample plots were randomly assigned a sampling depth of 10 cm or 20 cm. As a result, eight plots in each of two habitat types were sampled at each of two depths (32 total sample plots) (Fig. 1).

Baits: Baits were made using plastic capped vials 70 mm tall and 30 mm in diameter. A ~ 5 mm diameter hole was made near the bottom edge of the vial and covered with 1 mm screening to exclude larger animals (e.g., fire ants) but permit entry by subterranean ants. This was done to specifically target small-bodied subterranean ants as well as other non-subterranean ants that may forage opportunistically within the subterranean environment. Each bait was loaded with ~ 3 - 4 cm³ of sugar cookie (Pecan Sandies). To deploy the baits a battery-powered 24v drill and a 24-inch auger-bit was used to drill into the soil to a specified depth. The baits were then placed in the holes and covered up with the previously extracted soil. Baits

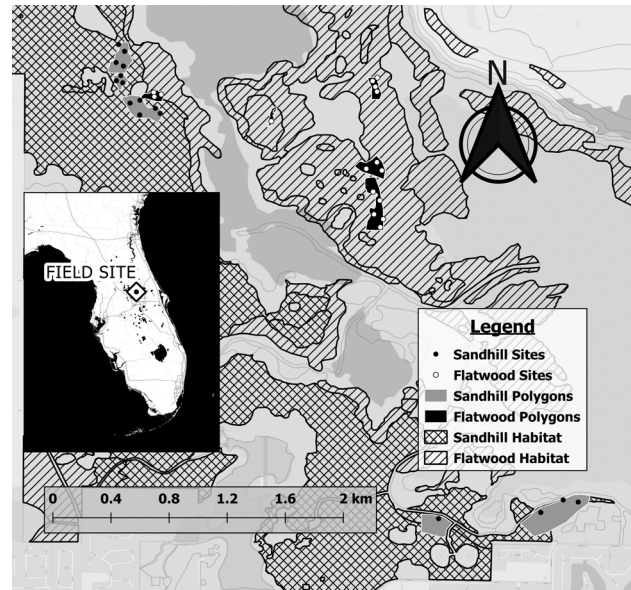


Fig. 1: Map of study site (Wekiva Springs State Park) with sampling sites.

were deployed in the morning and retrieved using a hand trowel ~ 72 hours later. Specimens were kept in sandwich bags and stored in a freezer.

Habitat variables: Soil temperature and soil moisture were recorded at each bait site. Soil temperature was recorded for the entirety of the 72-hour baiting period using data loggers (iButton, Maxim). Each plot had two data loggers installed on both east and west sides at 10 cm below the soil surface to record temperatures every hour during the baiting period. Using those data, we extrapolated average minimum, maximum, and temporal changes in soil temperatures per site. Soil moisture was collected by using a soil moisture sensor at 10 cm depth (Procheck, Decagon Devices). Ten readings were taken from each plot at the time of retrieval and averaged to represent the soil moisture level of the plot.

Sorting: All ants collected from the baits were sorted to species utilizing identification pointers from DEYRUP (2016). Additional reference specimens from J. R. King's personal collection were used to confirm identifications.

Aboveground sampling: Aboveground ant communities were sampled previously in the same area and habitat types of the park as the belowground sampling. In August 2012, three 100 m linear transects were established in each habitat type (a total of six transects), separated by at least 100 meters from one another or forest roads. In each transect,

Tab. 2: Pseudo- R^2 values for most plausible logistic regression model of successfully modeled species collected in the subterranean sampling (eight of 15 possible species). Model predictor variables are also displayed.

Species	Pseudo- R^2 of most plausible model	Model
<i>Solenopsis carolinensis</i>	0.16	Occurrence ~ Avg. Soil Moisture + Avg. Soil Temp.
<i>Solenopsis pergandei</i>	0.59	Occurrence ~ Avg. Soil Moisture * Avg. Minimum Soil Temp.
<i>Solenopsis tennesseensis</i>	0.23	Occurrence ~ Avg. Soil Temp.
<i>Solenopsis tonsa</i>	0.33	Occurrence ~ Avg. Soil Moisture + Avg. Soil Temp.
<i>Brachymyrmex depilis</i>	0.74	Occurrence ~ Avg. Minimum Soil Temp. * Avg. Soil Moisture
<i>Pheidole floridana</i>	0.11	Occurrence ~ Avg. Maximum Soil Temp.
<i>Pheidole metallescens</i>	0.12	Occurrence ~ Avg. Minimum Soil Temp + Avg. Soil Moisture
<i>Pheidole morrisii</i>	0.21	Occurrence ~ Maximum Soil Temp.

sampling was performed using pitfall traps placed at 5-meter intervals for a total of 20 traps per site and 120 traps for the two habitat types. Pitfall traps were 85 mm long plastic vials with 30 mm internal diameter partially filled with ~ 15 ml of non-toxic, propylene-glycol antifreeze. Traps were buried with the opened end flush with the surface of the ground and operated for seven days. Traps were installed using a hand-held, battery-powered drill using an auger bit.

Analyses: Each occurrence of a species in a baited vial was considered an occurrence of one colony of that species based on the spatial distances between baits (KING & PORTER 2007, KING 2010). Potential differences in community composition between habitats and depths were evaluated with nonmetric multi-dimensional scaling (NMDS), which is a nonparametric ordination method. Subsequent permutation-based analyses of variance (PERMANOVAs) were used to test for significant differences between detected clusters. The NMDS utilized beta diversity distances based on the Bray-Curtis index, a measure of dissimilarity that allowed for the separation of sites based on differences in species composition (while also accounting for species abundance as measured by frequency of occurrences). Bray-Curtis distances are also robust to sampling errors and preferred to other beta diversity measures (SCHROEDER & JENKINS 2018). Potential effects of environmental gradients on ant diversity were modeled using both linear mixed-effect models and linear regressions. Species estimators were also calculated using Chao1 estimators (all values listed in Appendix S1, as digital supplementary material to this article, at the journal's web pages) to provide further evidence of the robustness of sampling methods. The response variable for all models was the Jost Diversity index ($D = e^{H'}$; JOST 2006) per site calculated using number of species occurrences per site. Independent variables included depth of the baited vial, soil temperature (averages of maximum, minimum, and daily range), and average soil moisture (Tab. 1). Model assumptions were evaluated based on residual diagnostic plots (Appendix S2). Finally, the occurrence of all species in the baited vials was modeled using logistic regressions, where the occurrence of each ant species was predicted by soil parameters. All regressions were compared and ranked using corrected Akaike Information Criterion weights ($AICc w_i$) from the R package "bbmle" (BOLKER & R DEVELOPMENT CORE TEAM 2017) as they allowed an appropriate comparison for model parsimony compared to evaluating individual R^2 -values (Tab. 1). Logistic regressions were also

evaluated with pseudo- R^2 values calculated by subtracting the null deviance of the model from the residual deviance and dividing the total by the residual deviance (Tab. 2). All soil environmental variables were standardized during analyses and all statistical analyses were conducted using R 3.4.1 statistical software (R DEVELOPMENT CORE TEAM 2017). Mixed-effect models were computed using the R package "lme4" (BATES & al. 2015) and the "vegan" package (OKSANEN & al. 2017) was used to compute NMDS ordinations and PERMANOVAs. All graphics for regressions and ordinations were done using the R package "ggplot2" (WICKHAM 2009).

Results

Ant diversity and abundance: A total of 15 species encompassing six genera were captured and identified from all our belowground baits (full species list in Appendix S3). 98% of the 1152 baited vials deployed were recovered; 23 baited vials were lost during sampling. Species-sampling estimates indicate that all existing species were observed in most samples (Appendix S1). We assessed relative abundances as the occurrence of a species at each baited vial. The most common genus was *Solenopsis* (in 70% of baits), followed by *Pheidole* (21.5%) and *Brachymyrmex* (8.3%). The last three genera, *Forelius*, *Hypoponera*, and *Nylanderia* occurred in one baited vial, each. *Solenopsis* was the most species-rich genus with six species (all thief ants except for the introduced fire ant, *S. invicta*). The 8 most common species were *Solenopsis pergandei* (occurring in 209 baited vials, 27.6% of total), *Solenopsis carolinensis* FOREL, 1901 (98, 12.9%), *Solenopsis nickersoni* THOMPSON, 1982 (93, 12.3%), *Pheidole floridana* EMERY, 1895 (69, 9%), *Brachymyrmex depilis* EMERY, 1893 (63, 8.3%), *Solenopsis tennesseensis* (50, 6.6%), *Solenopsis invicta* (40, 5.3%), and *Pheidole morrisii* FOREL, 1886 (39, 5.2%).

Soil strata composition: Most ant taxa other than *Solenopsis*, *Nylanderia wojciki* (TRAGER, 1984), and *Pheidole dentata* MAYR, 1886 were less frequently sampled at the greater depth (20 cm). *Nylanderia wojciki* and *Pheidole dentata* were relatively rare and were only detected at 20 cm (Appendix S3). Among the *Solenopsis* species, *S. carolinensis* occurrence decreased 42% from 10 cm to 20 cm soil depth and *S. nickersoni* occurrence decreased (25%), but *S. pergandei* occurrence increased (78%), *S. tennesseensis* occurrence had no change, and *S. tonsa* occurrence increased (145%). The most frequently captured species at both depths

was *S. pergandei*. Based on an NMDS analysis and a subsequent PERMANOVA, depth did not significantly affect species compositions (PERMANOVA, $P > 0.05$).

Habitat-based community structure: *Brachymyrmex* (one occurrence in high pine sandhills, 62 occurrences in pine flatwoods), was more prevalent in the flatwoods than in sandhill habitats. *Forelius* (1, 0), *Hypoponera* (1, 0), and *Nylanderia* (1, 0) were present in flatwoods but absent in the sandhills. *Pheidole* (125, 38) and *Solenopsis* (359, 169) were more common in the sandhills. Within *Solenopsis*, *S. nickersoni* was found more commonly in flatwoods than in sandhill habitats. However, all other thief ant species (*S. carolinensis*, *S. pergandei*, *S. tennesseensis*, *S. tonsa*) were more prevalent in the sandhills.

The NMDS analysis (Fig. 2, Fig. 3) showed a distinct separation between communities of the two habitat types along with the separation of species that was congruent with our raw data. A subsequent PERMANOVA verified significant separation of centroids in this analysis ($P < 0.05$). All thief ant and *Pheidole* species, except for *Solenopsis nickersoni*, *P. dentata*, and *P. morrisii*, were clustered tightly within the sandhill cluster. Positions for *S. tonsa* and *Pheidole adrianoi* NAVES, 1985 in the NMDS were furthest away from the flatwood cluster. The species within and around the flatwood cluster had a higher degree of spread, most likely due to several species (*Forelius pruinosis* (ROGER, 1863), *Hypoponera opacior* FOREL, 1893, *N. wojciki*, and *P. dentata*) having been collected only once. *Brachymyrmex depilis*' position in the NMDS mirrors *S. tonsa* and is one of the few frequently collected species in the flatwoods. Finally, the fire ant, *S. invicta*, is positioned more along the upper edge of the flatwood cluster and towards the center between both habitat clusters. To further validate these results, we removed singletons from the species by site matrix (four total species / columns removed) and ran the NMDS at the same dimensions ($k = 2$) with the same number of starting iterations (1000) and found no differences in patterns. The stress value remained the same at ~ 0.127 .

Modeling species diversity: Although not all species caught at our baits are truly subterranean ants, for the purposes of this study, we included species captured in below-ground samples as part of the subterranean community as these species were clearly actively foraging belowground. Subterranean ant diversity was most effectively explained in regression models as an interaction between habitat types and average daily soil temperature range ($AICc w_i = 0.34$, Tab. 1). This model represented a majority of variance in ant diversity ($P = 0.02$, $R^2 = 0.60$). Residuals met assumptions of the model. The simple linear regression model outperformed the random-intercept model, and conditional pseudo R -squared values indicated that random intercepts explained very little variation and both models indicated approximately the same effect sizes. A second linear model also included an interaction between habitat type and average soil maximum temperature ($AICc w_i = 0.14$). However, the model using average daily temperature ranges accounted for more variation and was more plausible. In all our initial models we added soil depth as a covariate but the differences between the top-ranked models with and without the covariate was negligible as effect sizes and adjusted- R^2 values barely differed.

Predicting species occurrences: Logistic regression models of thief ant species occurrence per site using soil environment variables significantly predicted four of five

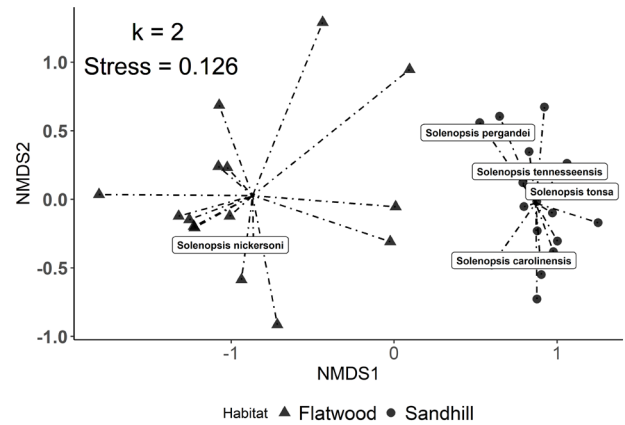


Fig. 2: Nonmetric multi-dimensional analysis of the species by site matrix from the subterranean sampling. Triangles represent pine flatwood sites and circles represent high pine sandhill sites. Lines connect the sites to each habitat's respective centroid in multivariate space. Labels for thief ant species represent the position of species within this space. The analysis had acceptable stress values of 0.126 at two dimensions ($k = 2$).

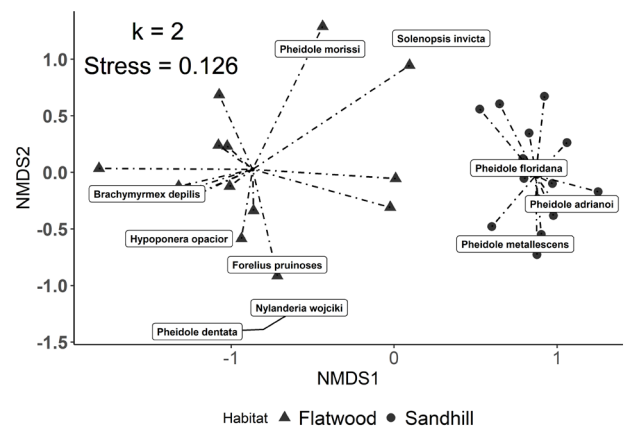


Fig. 3: A replicate nonmetric multi-dimensional analysis visual of Figure 2. Labels differ here to show the position of non-thief ant species. Flatwood species labels have a higher degree of spread due to extreme low occurrences of some species (e.g., *Pheidole dentata*, *Nylanderia wojciki*).

thief ant species and helped in further understanding the NMDS result (full models listed in Appendix S4); only *Solenopsis nickersoni* occurrence was not predicted. *Solenopsis pergandei*'s most plausible model was a function of the interaction between average soil moisture and average minimum soil temperature ($P = 0.02$, Pseudo- $R^2 = 0.59$, Tab. 2). *Solenopsis tonsa*'s most plausible model was a function of the additive effects of average soil moisture and temperature ($P = 0.02$, 0.01 respectively, Pseudo- $R^2 = 0.33$). *Solenopsis carolinensis*' most plausible model was also a function of the same predictors ($P = 0.04$, $P = 0.04$, Pseudo- $R^2 = 0.16$). Finally, *S. tennesseensis*' most plausible model was a function of average soil temperature ($P = 0.01$, Pseudo- $R^2 = 0.23$).

Other co-occurring ant species found in our samples were also modeled by logistic regression, though not all species had sufficient occurrences to model (Tab. 5, models

Tab. 3: Simple linear model coefficients and their 95% confidence intervals for the top five most plausible models in predicting diversity based on AICc (Akaike Information Criterion corrected for small sample sizes) rankings. Coefficients represent changes in the Jost diversity index relative to different soil abiotic variables. Bolded coefficients were significant at $P < 0.05$. All coefficients are based on the flatwood habitat as being the reference level in the model and all quantitative predictor variables were standardized.

Independent Variables	D ~ Habitat + Avg. Soil Moisture * Avg. Soil Temp.	D ~ Habitat * Avg. Soil Maximum Temp.	D ~ Habitat * Avg. Change in Daily Soil Temp.	D ~ Habitat + Avg. Soil Moisture	D ~ Habitat + Avg. Soil Minimum Temp.
Intercept	2.25±0.66	2.82±0.53	2.73±0.49	2.59±0.51	2.69±0.50
Sandhill	2.55±1.03	2.15±0.73	2.27±0.69	2.25±0.74	2.05±0.71
Avg. Change in Daily Soil Temp.	-	-	-0.23±0.48	-	-
Avg. Soil Maximum Temp.	-	-0.39±0.59	-	-	-
Soil Minimum Temp.	-	-	-	-	-0.20±0.36
Avg. Soil Moisture	0.31±0.48	-	-	0.19±0.37	-
Avg. Soil Temp.	-0.08±0.53	-	-	-	-
Sandhill:Avg. Change in Daily Soil Temp.	-	-	0.87±0.70	-	-
Sandhill:Avg. Soil Maximum Temp.	-	0.85±0.76	-	-	-
Avg. Soil Moisture: Avg. Soil Temp.	-0.53±0.43	-	-	-	-

listed in Appendix S5). AICc model selection on the logistic regressions for *Pheidole adrianoi* and *Solenopsis invicta* showed the null model being ranked the best indicating the lack of any statistical signal in their species-respective models. *Brachymyrmex depilis*' most plausible model was a function of the interaction between average soil moisture and average minimum soil temperature ($P = 0.04$, Pseudo- $R^2 = 0.74$). *Pheidole floridana*'s most plausible model was a function of average maximum soil temperature ($P = 0.05$, Pseudo- $R^2 = 0.11$). *Pheidole metallescens*' EMERY, 1895 most plausible model was a function of the additive effects of average soil moisture and average minimum soil temperature ($P = 0.07, 0.09$, Pseudo- $R^2 = 0.12$). It is important to note that the next plausible model for *P. metallescens* was the null model, and the two models were only different by a $\Delta AICc$ of 0.2 with similar AICc weights (Appendix S5). Therefore, we did not evaluate *P. metallescens* occurrences. *Pheidole morrisii*'s most plausible model was a function of average minimum soil temperature ($P = 0.02$, pseudo- $R^2 = 0.21$).

Overall, subterranean ant diversity was dominated by *Solenopsis* species and different in composition between high pine sandhills and pine flatwoods. Those patterns appeared to be related to soil temperature and moisture, which consistently predicted belowground ant diversity and species' occurrences in the two different habitat types.

Discussion

Differences among habitats: Distinct multivariate differences between sandhill and flatwood sites are consistent with the expectation that ant communities differ between habitat types at local scales (BERMAN & ANDERSEN 2012, CROSS & al. 2016) (Fig. 2 & 3). Distinct species compositions existed between habitats, but sandhill sites were more similar to one another than flatwood sites, indicating the greater

homogeneity in soil habitat conditions in the sandhills. This suggests that heterogeneous soil habitat conditions affecting thief ants in flatwoods may result in more variation in the species present in any given area. This clustering also indicates the presence of a potential ecological driver (soil temperature and moisture conditions by regressions) for dissimilar species rosters found in both habitats. Such drivers may be environmental filters resulting in different survivorship or competitive abilities among species, ultimately resulting in different species found in pine flatwoods and high pine sandhills. Results here describe patterns in species composition; elucidating actual drivers of these patterns will require experiments and careful observation of species' natural histories.

The known natural history of most of these species agrees with their positions within the NMDS. Of the sandhill thief ant species, only *Solenopsis tonsa*, one of the few truly subterranean species, is expected to occur strictly in sandhill (DEYRUP 2016). *Solenopsis pergandei*, another true subterranean species can be found in other soils but tends to be most common in open sandy areas such as sandhills. *Solenopsis tennesseensis*, a suspected subterranean but also litter-dwelling thief ant, is a supposed habitat generalist but in this case, was closely associated with the sandhill sites. Other species that were tightly clustered to the sandhills were *Pheidole metallescens*, *P. adrianoi*, and *P. floridana*. *Pheidole metallescens* is considered a predominantly upland species that is usually found in high pine sandhills and usually co-occurs with *P. adrianoi*. *Pheidole floridana* is associated with drier habitats, like the sandhills, and is less likely to be found in moist forested areas (DEYRUP 2016). Flatwood species other than *S. nickersoni* included *B. depilis* and *P. morrisii*. *Brachymyrmex depilis*, predominantly sampled in the flatwoods, is considered a generally

Tab. 4: Logistic regression model coefficients and their 95% confidence intervals for the most plausible model for every successfully modeled thief ant species. Coefficients represent the log odds of the occurrence of the ant species relative to different soil abiotic conditions. Bolded coefficients were significant at $P < 0.05$. All predictor variables were standardized for the models.

Independent variables	<i>Solenopsis carolinensis</i> coefficients	<i>Solenopsis pergandei</i> coefficients	<i>Solenopsis tennesseensis</i> coefficients	<i>Solenopsis tonsa</i> coefficients
Intercept	0.02±0.79	2.76±2.49	0.37±0.84	-0.57±0.94
Avg. Minimum Soil Temp.	-	-2.40±2.20	-	-
Avg. Soil Moisture	-1.04±0.99	-3.61±3.06	-	-1.85±1.37
Avg. Soil Temp.	-1.04±1.01	-	-1.42±1.07	-1.71±1.50
Avg. Soil Moisture: Avg. Minimum Soil Temp.	-	2.36±2.02	-	-

Tab. 5: Logistic regression model coefficients and their 95% confidence intervals for the most plausible model for every successfully modeled non-thief ant species. Coefficients represent the log odds of the occurrence of the ant species relative to different soil abiotic conditions. Bolded coefficients were significant at $P < 0.05$. All predictor variables were standardized for the models.

Independent variables	<i>Brachymyrmex depilis</i> coefficients	<i>Pheidole floridana</i> coefficients	<i>Pheidole metallescens</i> coefficients	<i>Pheidole morrisii</i> coefficients
Intercept	-3.26±0.91	-0.27±0.75	-0.77±0.82	-0.75±0.89
Avg. Maximum Soil Temp.	-	-0.86±0.85	-	-1.48±1.26
Avg. Minimum Soil Temp.	4.49 ±1.06	-	-0.83±0.97	-
Avg. Soil Moisture	5.56±1.08	-	-1.01±1.07	-
Avg. Soil Temp.	-	-	-	-
Avg. Soil Moisture: Avg. Minimum Soil Temp.	-3.70±1.02	-	-	-

subterranean species like subterranean thief ants except they are usually found in a wider variety of habitat types across North America (DEYRUP 2016). However, its general absence in the sandhills may be indicative of it preferring mesic conditions or being out-competed by the thief ants or species of small-bodied *Pheidole*. The fire ant, *S. invicta*, is a known invasive and weedy species, capable of surviving in inundation-prone habitats (TSCHINKEL 2006). Its position in the NMDS analysis indicates its prevalence in both habitats (Figs. 2 & 3) which would be logical considering its ability to establish in a variety of conditions, especially if there are forest roads or other disturbances nearby.

Environmental gradients with diversity and species occurrence: Local scale ant diversity is often weakly correlated with abiotic conditions and is usually more strongly associated with local vegetation (CROSS & al. 2016). However for subterranean communities, gradients of abiotic conditions such as soil moisture and temperature may heavily influence their distribution at local scales (THOMPSON 1980, LUBERTAZZI & TSCHINKEL 2003, WILKIE & al. 2010). Teasing apart how local scale abiotic conditions affect diversity can be useful in discerning drivers of diversity. Here we found that diversity was predicted by an interaction between habitat types and average daily soil temperature range, where subterranean ant diversity increased with average daily temperature range in sandhill habitats but decreased slightly in the flatwoods (Fig. 4, Tab. 3). Flatwood sites also experienced higher variation in average daily soil temperature range than sandhill sites. This result may indicate a more dynamic environment in the flatwoods, where soil temperature can be influenced by flooding events due to poorly drained soils. Flooding

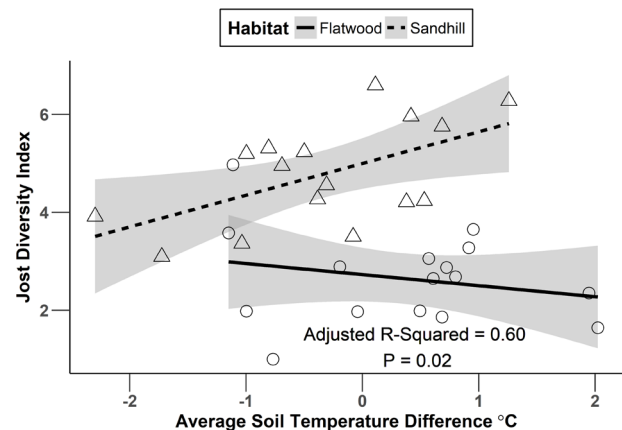


Fig. 4: Most plausible simple linear regression model for subterranean diversity. Y-axis represents the Jost diversity index; X-axis represents average daily soil temperature range (standardized) of the 3-day baiting period. Triangles represent high pine sandhill sites and circles represent pine flatwoods sites. Grey shading represents the 95% confidence intervals of the model. The dashed line represents the interaction of sandhill habitat with soil temperature range while the solid line represents the interaction of flatwood habitats with soil temperature range ($P = 0.02$). Adjusted- $R^2 = 0.60$.

events in these areas as well as shallow water tables may strongly constrain habitat space for these ants (LAMMERS 1987, LUBERTAZZI & TSCHINKEL 2003, TSCHINKEL & al. 2012). Another possible explanation is that some ant species may

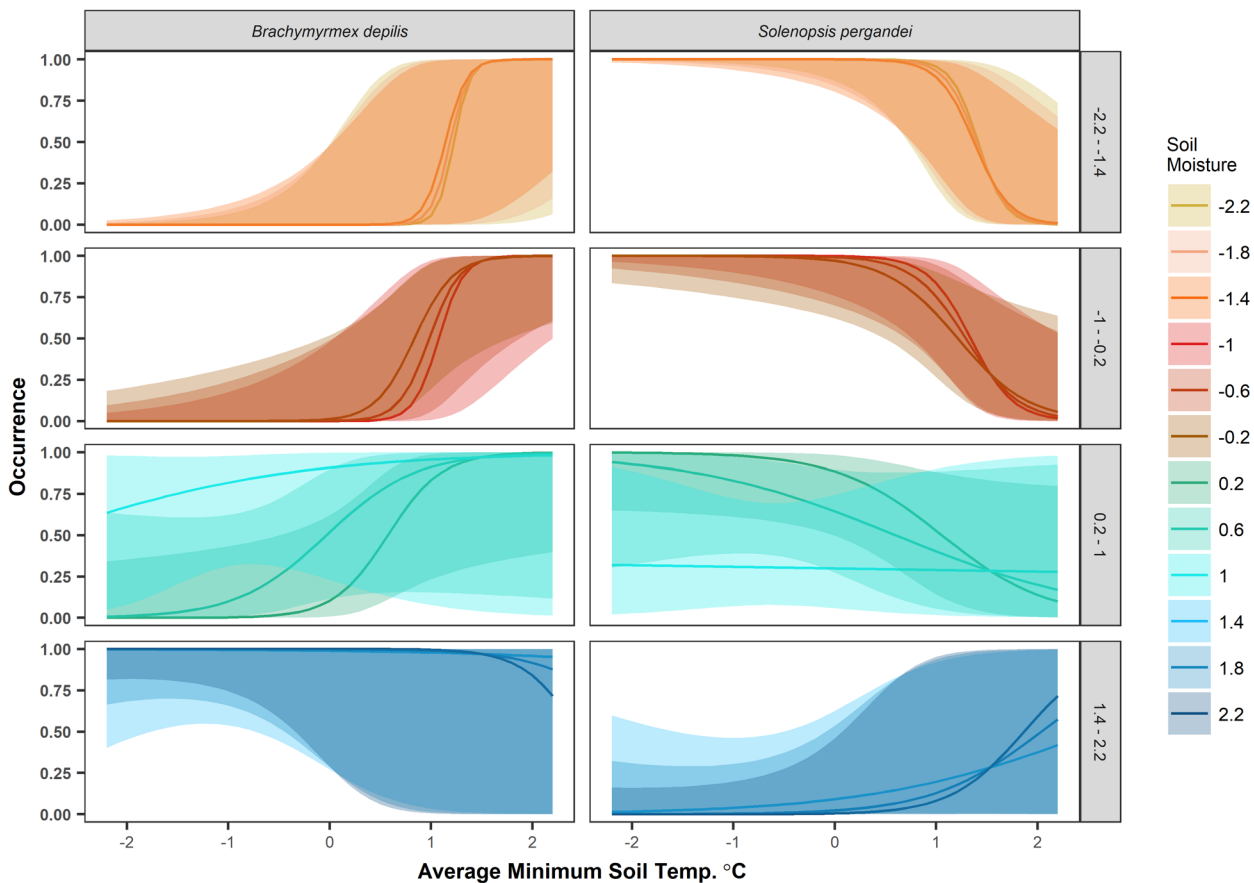


Fig. 5: Logistic regression models of *Brachymyrmex depilis* (left) and *Solenopsis pergandei* (right). Y-axis represents occurrence; X-axis represents average minimum soil temperature (standardized). The interaction between average minimum soil temperature and average soil moisture (standardized) is represented through 4 facets (labels on right). Each facet shows the model at three different average soil moisture levels and average soil moisture increases from the top to the bottom facet. Colors differ for each average soil moisture level and colored shading represents the 95% confidence intervals of the model at various levels of moisture. Pseudo- R^2 values for *B. depilis* and *S. pergandei* models were 0.74 and 0.59 and P-values for each model's interaction were 0.04 and 0.02, respectively.

not be able to tolerate the wide temperature differences and therefore prefer the lower soil temperature variation. It was surprising to find no significant effects on diversity from soil moisture as it could be a better proxy for indicating periodic flooding. However, the relatively brief study did not collect moisture data throughout a wet-dry season cycle, so the full variation of soil moisture that may affect colony distributions was not fully evaluated.

Depths to water tables and inundation dynamics may not drive species composition and diversity differences between the two habitat types. Logistic regressions showed that environmental soil gradients serve a significant role in the occurrence of thief ants and co-occurring ants found in our sampling. For example, in low soil moisture, cooler minimum soil temperature increases the chance of *Solenopsis pergandei* occurrence but in high moisture soils, lower minimum soil temperature decreases the chances of occurrence. This suggests that *S. pergandei* might be sensitive to the synergistic effects of both soil moisture and temperature.

The logistic regression for *Solenopsis carolinensis* showed significant negative effects on the chances of its occurrence as soil temperature and moisture increased. The same significant effect on the same parameters were also

observed for *S. tonsa*. Finally, *S. tennesseensis* occurrence was negatively affected by increasing soil temperature. Across these four thief ant species there is thus a trend of decreasing occurrence as soil moisture or temperature increases (Tab. 4). These four species were also all positioned tightly within the same sandhill cluster from the NMDS analysis suggesting, again, soil abiotic conditions as a potential driver for that thief ant clustering. This is congruent with previous assumptions found from THOMPSON (1980) that highly moist and inundation-prone areas may not be suitable for the persistence of these species as well as a study from Texas (LAMMERS 1987) where it was suggested that subterranean foraging by thief ants may be limited by soil moisture.

When considering the occurrence of other non-thief ant species in flatwoods within the context of the NMDS analysis, only *B. depilis* occurrence was modeled successfully in the flatwoods. A sandhill species, *Solenopsis pergandei*, was modeled with the same predictors but responded in opposite directions (Fig. 5, Tabs. 4, 5). These contrasting patterns suggest environmental filtering as potential mechanism explaining their occurrence in disparate habitats. *Brachymyrmex depilis* could be more sensitive to xeric conditions as indicated by lower occurrences at lower

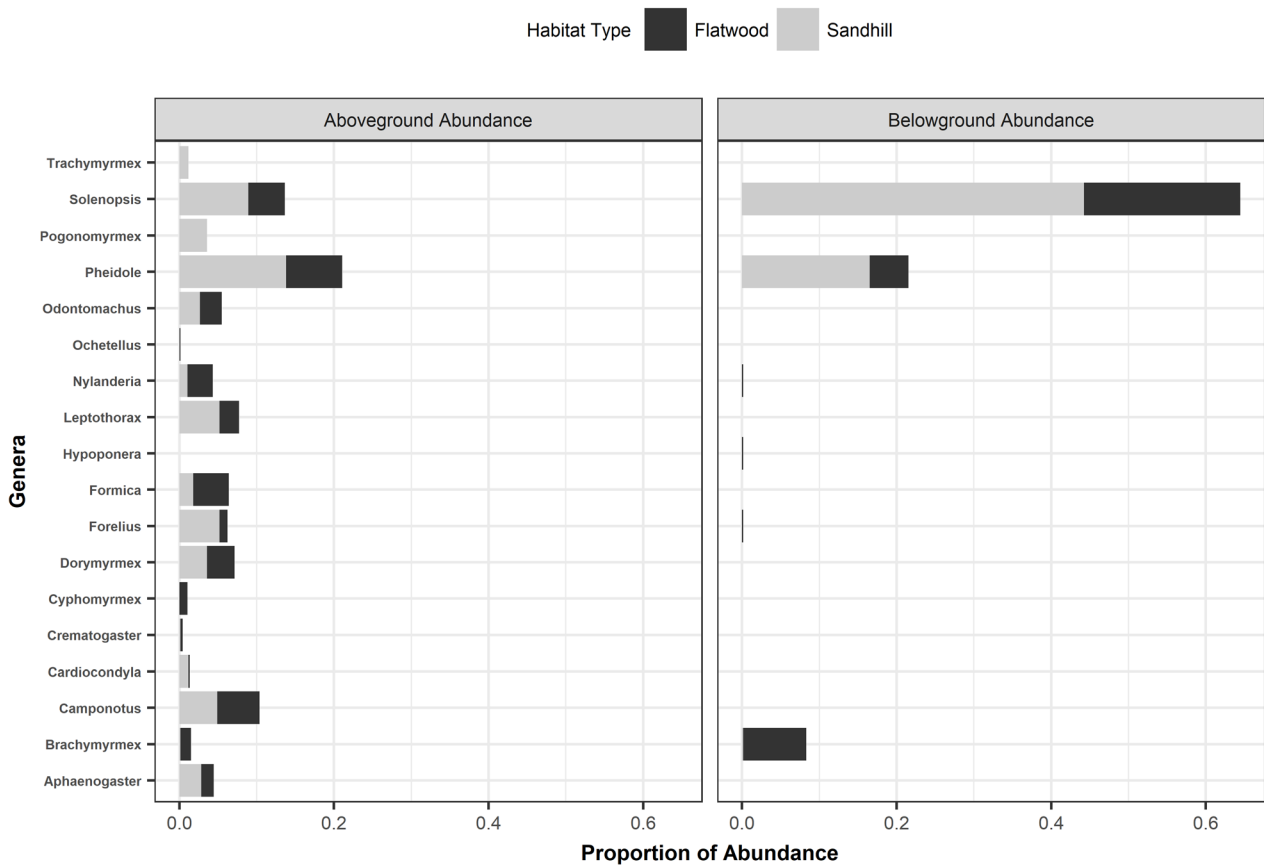


Fig. 6: Abundance of aboveground and belowground sampling. Y-axis represents ant taxa at the genus level. X-axis represents the proportion of total abundance per sampling type. Dark sections of the bars represent abundance found in pine flatwood areas and lighter sections represent abundance found in high pine sandhill areas. Note: *Solenopsis invicta* has been removed from the datasets represented in the figure.

levels of soil moisture while *S. pergandei* tends to show the opposite trend. These results support previous suggestions that Florida's subterranean thief ants may occur more frequently in well-drained soils (e.g., high pine sandhill ecosystems) (THOMPSON 1980, LAMMERS 1987). A wider range of environmental conditions in other habitats and locations should also be considered to verify the patterns observed here, in sandy soils.

Although our models show evidence indicative of environmental filtering in certain subterranean species, patterns of occurrence of thief ants may also be affected by the occurrence and distributions of potential prey in the context of the purported lestoproictic interactions that thief ants have with other ants, especially larger-bodied ant species. To further understand the role that species interactions may play in shaping subterranean ant distributions, there is a need for detailed information on, for example, the local distribution of thief ant colonies in relation to other colonies. Unfortunately, no such data exists but we can cautiously infer patterns of co-occurrence from aboveground pitfall data.

A comparison of studies: This study showed the dominance of thief ants among small-bodied ants in the subterranean environment of central Florida's sandy soils. Furthermore, our community analyses indicate significantly distinct subterranean ant communities between flatwood and sandhill habitat types. Moreover, the diversity of these communities can be predicted using soil abiotic conditions.

Subterranean thief ant diversity patterns remain largely enigmatic in most regions of the world, so the results of this study are the first quantitative assessments of the diversity and distribution of an abundant group of subterranean ants and the abiotic predictors of that diversity.

This study complements two other subterranean sampling studies in Florida (Tallahassee and Gainesville) and is one of few studies globally to assess abiotic predictors of subterranean ant diversity patterns (THOMPSON 1980, LUBERTAZZI & TSCHINKEL 2003). Ants in the *Solenopsis* genus dominate the subterranean thief ant communities in both north and central Florida. 15 total species were found in belowground samples here while 20 species were captured in north Florida (LUBERTAZZI & TSCHINKEL 2003). *Solenopsis pergandei*, was the most dominant species in our study, but not in north Florida. THOMPSON (1980) described *S. pergandei* as an "occasional dominant" species in north-central Florida (Gainesville). The dominant thief ant in both the Tallahassee and Gainesville studies was *S. carolinensis*. This indicates a transition between *S. pergandei* and *S. carolinensis* as dominant thief ants between central and north Florida. Other species occurrences, including *Pheidole dentata*, *P. floridana*, *P. metallescens*, and *Brachymyrmex depilis* were found in studies of THOMPSON (1980), LUBERTAZZI & TSCHINKEL (2013), and results here. Our study provides further evidence of the widespread, high abundances of thief ants in this region. It is also clear

that the subterranean ant communities of semi-tropical and temperate Florida are not as diverse as subterranean communities in the Neotropics (THOMPSON 1980, LUBERTAZZI & TSCHINKEL 2003, WILKIE & al. 2007) where as many as 47 species were recorded at local scales.

Sampling methods differed between 2012 aboveground sampling (pitfall traps) and belowground baits in this study; comparisons are made with caution. Aboveground samples collected more species (37 species in 18 genera), and abundances were more evenly distributed than in our belowground sampling. Aboveground, the genus *Pheidole* is most abundant followed closely by *Solenopsis* and *Camponotus*. *Solenopsis pergandei* and *S. tonsa*, two truly subterranean species, were not recorded in any of the aboveground traps. However, belowground, *Solenopsis* remains dominant by quite a large margin (Fig. 6). Aboveground species richness remains relatively the same with 32 species in the flatwoods and 35 in the sandhill. The aboveground ant community seems to have a higher abundance of individuals across the genera present in sandhill habitat when compared to flatwoods habitat. However, several genera show the opposite trend, including *Formica* and *Nylanderia*. Considering the temporal difference in the pitfall data and the subterranean data we suggest that it is possible that sandhill habitats may serve as areas of higher abundance of larger-bodied ants that can serve as potential prey for thief ants.

Lestobiosis and subterranean ant communities: This study affirms the general dominance of thief ants in Florida upland soils (THOMPSON 1980, LUBERTAZZI & TSCHINKEL 2003). If thief ants are truly lestobiotic, then their widespread abundance, now shown by three studies in Florida (including this one), suggests potential for substantial effects on co-occurring ants, including direct and indirect effects via brood raiding and generalist predation (THOMPSON 1980, BUREN 1983, LAMMERS 1987, NICHOLS & SITES 1991, YAMAGUCHI & HASEGAWA 1996, VINSON & RAO 2004). Further sampling is needed to evaluate subterranean ant communities among various ecosystems, and the environmental conditions that may potentially predict the diversity and distributions of these lesser-known ant communities.

Acknowledgments

Sampling was made possible under Florida Department of Environmental Protection permit no. 06201713. We thank Alice Bard and her team at Wekiva Springs State Park for accommodating this study. Special thanks go to Adam Benzrihem who helped with field work. Thanks also go to Juan D. Bogotá and Federico L. Borghesi who helped with statistical analyses.

References

ABRAHAMSON, W.G. & HARTNETT, D.C. 1990: Pine flatwoods and dry prairies. In: MYERS, R.L. & EWEL, J.J. (Eds.): *Ecosystems of Florida*. – University Press of Florida, Gainesville, FL, pp. 103-149.

ANDERSEN, A.N. & BRAULT, A. 2010: Exploring a new biodiversity frontier: subterranean ants in northern Australia. – *Biodiversity and Conservation* 19: 2741-2750.

BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. 2015: Fitting linear mixed-effects models using lme4. – *Journal of Statistical Software* 67: 1-48.

BERMAN, M. & ANDERSEN, A.N. 2012: New Caledonia has a depauperate subterranean ant fauna, despite spectacular radiations above ground. – *Biodiversity and Conservation* 21: 2489-2497.

BLUM, M.S., HÖLLDOBLER, B., FALES, H. & JAOUNI, T. 1980: Alkaloidal venom mace: offensive use by a thief ant. – *Naturwissenschaften* 67: 144-145.

BOLKER, B. & R DEVELOPMENT CORE TEAM 2017: *bbmle: tools for general maximum likelihood estimation*. R package version 1.0.20, <<https://CRAN.R-project.org/package=bbmle>>, retrieved on 12 November 2017.

BUREN, W.F. 1983: Artificial faunal replacement for imported fire ant control. – *Florida Entomologist* 66: 93-100.

CANEDO-JÚNIOR, E. 2015: Can anthropic fires affect epigeaic and hypogaeic Cerrado ant communities in the same way? – *International Journal of Tropical Biology* 64: 95-104.

CROSS, A.T., MYERS, C., MITCHELL, C.N.A., CROSS, S.L., JACKSON, C., WAINA, R., MUCINA, L., DIXON, K.W. & ANDERSEN, A.N. 2016: Ant biodiversity and its environmental predictors in the North Kimberley region of Australia's seasonal tropics. – *Biodiversity and Conservation* 25: 1727-1759.

DEYRUP, M. 2016: *Ants of Florida: identification and natural history*. – CRC Press, Boca Raton, FL, 423 pp.

ESRI 2017: *ArcGIS. Release 10*. – Environmental Systems Research Institute, Redlands, CA.

GHOLZ, H.L. & FISHER, R.F. 1982: Organic matter production and distribution in slash pine (*Pinus elliottii*) plantations. – *Ecology* 63: 1827-1839.

HERNÁNDEZ, V. 2010: Checklist, biological notes and distribution of ants (Hymenoptera: Formicidae) from Barranca de Metztitlán Biosphere Reserve, Hidalgo, Mexico. – *Sociobiology* 56: 397-434.

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

HÖLLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – Harvard University Press, Cambridge, MA, 732 pp.

JACQUEMIN, J., MARAUN, M., ROISIN, Y. & LEPONCE, M. 2012: Differential response of ants to nutrient addition in a tropical brown food web. – *Soil Biology and Biochemistry* 46: 10-17.

JOST, L. 2006: Entropy and diversity. – *Oikos* 113: 363-375.

KASPARI, M. & WEISER, M.D. 1999: The size-grain hypothesis and interspecific scaling in ants. – *Functional Ecology* 13: 530-538.

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. & PORTER, S.D. 2007: Body size, colony size, abundance, and ecological impact of exotic ants in Florida's upland ecosystems. – *Evolutionary Ecology Research* 9: 757-774.

LAMMERS, J.M. 1987: Mortality factors associated with the founding queens of *Solenopsis invicta* BUREN, the red imported fire ant: a study of the native ant community in central Texas. – PhD thesis, Texas A&M University, 203 pp.

LUBERTAZZI, D. & TSCHINKEL, W.R. 2003: Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. – *Journal of Insect Science* 3: art. 21.

LYNCH, J.F., JOHNSON, A.K. & BALINSKY, E.C. 1988: Spatial and temporal variation in the abundance and diversity of ants (Hymenoptera: Formicidae) in the soil and litter layers of a Maryland forest. – *The American Midland Naturalist* 119: 31-44.

MACKAY, W. & MACKAY, E. 2002: *The ants of New Mexico (Hymenoptera: Formicidae)*. – The Edwin Mellen Press, Lewiston, New York, NY, 402 pp.

MORENO GONZALEZ, I. 2001: Systematics of the thief ants of North America (Hymenoptera: Formicidae: *Solenopsis*). – Master's thesis, University of Texas at El Paso, TX, 114 pp.

MYERS, R.L. & EWEL, J.J. 1990: *Ecosystems of Florida*. – University Press of Florida, Gainesville, FL, 765 pp.

- NICHOLS, B. & SITES, R. 1991: Ant predators of founder queens of *Solenopsis invicta* (Hymenoptera: Formicidae) in central Texas. – *Environmental Entomology* 20: 1024-1029.
- OKSANEN, J., BLANCGET, F.G., FRIENDLY, M., KINDT, R., LEGENDER, P., MCGLINN, D., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H., SZOECZ, E. & WAGNER, H. 2017: vegan: Community Ecology Package. R Package version 2.4-4. – <<https://CRAN.R-project.org/package=vegan>>, retrieved on 5 November 2017.
- PACHECO, J., HERRERA, H.W. & MACKAY, W. 2007: A new species of thief ant of the genus *Solenopsis* from the Galapagos Islands (Hymenoptera: Formicidae). – *Sociobiology* 50: 1075-1086.
- PACHECO, J. & MACKAY, W. 2013: The systematics and biology of the new world thief ants of the genus *Solenopsis* (Hymenoptera: Formicidae). – Edwin Mellen Press, Lewiston, NY, 501 pp.
- PRUSAK, Z.A. 1997: Ant fauna in three plant communities within Wekiwa Springs State Park, Florida: assessment of diversity and comparison of collecting methods. – Master's Thesis, University of Central Florida, FL, 154 pp.
- R DEVELOPMENT CORE TEAM 2017: R: A language and environment for statistical computing. – R Foundation Statistical Computing, Vienna, Austria, <<http://www.R-project.org/>>, retrieved on 30 July 2017.
- RIBAS, C.R., SCHMIDT, F.A., SOLAR, R.R.C., CAMPOS, R.B.F., VALENTIM, C.L. & SCHROEDER, J.H. 2012: Ants as indicators of the success of rehabilitation efforts in deposits of gold mining tailings. – *Restoration Ecology* 20: 712-720.
- SCHMIDT, F.A. & DIEHL, E. 2008: What is the effect of soil use on ant communities? – *Neotropical Entomology* 37: 381-388.
- SCHMIDT, F.A. & SOLAR, R.R.C. 2010: Hypogaecic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. – *Insectes Sociaux* 57: 261-266.
- SCHNEIRLA, T.C., SMITH, M.R. & STATION, A.B. 1944: Behavior and ecological notes on some ants from south-central Florida. – *American Museum Novitates* 1261: 1-5.
- SCHROEDER, P.J. & JENKINS, D.G. 2018: How robust are popular beta diversity indices to sampling error? – *Ecosphere* 9: art. e02100.
- THOMPSON, C.R. 1980: *Solenopsis (Diplorhoptrum)* (Hymenoptera: Formicidae) of Florida. – PhD thesis, University of Florida, 115 pp.
- THOMPSON, C.R. 1989: The thief ants, *Solenopsis molesta* group of Florida (Hymenoptera: Formicidae). – *Florida Entomologist* 72: 268-283.
- TSCHINKEL, W.R. 2006: The fire ants. – The Belknap Press of Harvard University Press, Cambridge, MA and London, UK, 706 pp.
- TSCHINKEL, W.R., MURDOCK, T., KING, J.R. & KWAPICH, C. 2012: Ant distribution in relation to ground water in north Florida pine flatwoods. – *Journal of Insect Science* 12: art. 114.
- VINSON, S.B. & RAO, A. 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.
- WHEELER, W.M. 1901: The compound 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: ggplots2: elegant graphics for data analysis. Springer-Verlag, New York, NY, 266 pp.
- WILKIE, K.T.R., MERTL, A.L. & TRANIELLO, J.F.A. 2007: Biodiversity below ground: probing the subterranean ant fauna of Amazonia. – *Naturwissenschaften* 94: 725-731.
- WILKIE, K.T.R., MERTL, A.L. & TRANIELLO, J.F.A. 2010: Species diversity and distribution patterns of the ants of Amazonian Ecuador. – *Public Library of Science One* 5: art. e13146.
- WONG, M.K.L. & GUÉNARD, B. 2017: Subterranean ants: summary and perspectives on field sampling methods, with notes on diversity and ecology (Hymenoptera: Formicidae). – *Myrmecological News* 25: 1-16.
- YAMAGUCHI, T. & HASEGAWA, M. 1996: An experiment on ant predation in soil using a new bait trap method. – *Ecological Research* 11: 11-16.