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Changes in an invaded Florida ant (Hymenoptera: Formicidae) community over 25 years

Leo Ohyama^{1,*}, Joshua R. King¹, and Benjamin M. Gochnour²

Abstract

Exotic invasive species are one of the most widespread and common agents of change in ecosystems worldwide. Here, we are focused on community-level changes associated with the appearance and persistence of exotic species in an ecosystem over more than 2 decades. We combined datasets of Florida's ant (Hymenoptera: Formicidae) community from Wekiwa Springs State Park, Florida, USA, spanning 25 yr, which included 3 sampling events in several distinct upland ecosystems. Species accumulation curves, non-parametric species estimators, community similarity indices, and ratios of exotic to native ants were used to assess sampling effort, including patterns of diversity, and changes in community composition. Our data showed that the ant community of Wekiwa Springs has at least 4 exotic species present in all of the ecosystems sampled within the park. These upland ecosystems are accumulating exotics slowly and, with one exception, there is no clear signal that the exotic species are displacing native species. The likely exception is the invasive fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), causing local extinction of the native fire ant *Solenopsis geminata* (Fabricius) (Hymenoptera: Formicidae). Continued long-term monitoring efforts are necessary to understand how these exotics may impact native communities in the future.

Key Words: displacement; fire; fire ants; ecosystem management; invasion; persistence

Resumen

Las especies exóticas invasoras son uno de los agentes comunes más extendidos de cambio en los ecosistemas de todo el mundo. Aquí, nos enfocamos sobre los cambios a nivel comunitario asociados con la aparición y persistencia de especies exóticas en un ecosistema durante más de 2 décadas. Combinamos las series de datos de las comunidades de hormigas de la Florida (Hymenoptera: Formicidae) del Parque Estatal Wekiwa Springs, Florida, EE. UU. que abarcan 25 años e incluyen 3 eventos de muestreo en varios ecosistemas de distintas tierras altas. Se utilizaron curvas de acumulación de especies, estimadores de especies no paramétricas, índices de similitud de la comunidad y proporciones de hormigas exóticas a nativas para evaluar el esfuerzo de muestreo, incluidos los patrones de diversidad y los cambios en la composición de la comunidad. Nuestros datos mostraron que la comunidad de hormigas de Wekiwa Springs tiene al menos 4 especies exóticas presentes en todos los ecosistemas muestreados dentro del parque. Estos ecosistemas de tierras altas están acumulando lentamente especies exóticas y, con una excepción, no hay una señal clara de que las especies exóticas estén desplazando a las especies nativas. La probable excepción es la hormiga de fuego invasiva, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), que causa la extinción local de la hormiga de fuego nativa *Solenopsis geminata* (Fabricius) (Hymenoptera: Formicidae). Los esfuerzos continuos de monitoreo a largo plazo son necesarios para comprender cómo estos organismos exóticos podrían afectar a las comunidades nativas en el futuro.

Palabras Claves: desplazamiento; fuego; las hormigas de fuego; manejo de ecosistemas; invasión; persistencia

Measuring community changes over longer time periods (greater than a few yr or a decade) is challenging. Typically, long-term community change is measured using discrete sampling events of specific taxa that provide only snapshots of a changing "roster" of species. Nevertheless, datasets generated from multiple, discrete sampling points from the same site across many yr provide valuable insights into how invaded communities may change over time. These datasets help inform management decisions as well as conservation planning (Magurran & Dornelas 2010). Evaluating community dynamics in this manner may help to reveal the reshuffling of species rosters and the rate at which they occur. Turnover of species and introductions of new ones signal community changes that may precede significant reduction in biodiversity and change in ecosystem function that sometimes accompany species invasion (Simberloff 2013). Here we describe the changes in an ant community in central Florida over 25 yr, documenting changes in community composition, and the arrival of a number of exotic species.

Florida experiences a high frequency of successful introductions of exotic insect species (Frank & McCoy 1993). The increasing number of these introductions in the state is likely affected by the high number of ports along the Gulf coast and frequent international trade (Jenkins 1996). Many exotic species escape detection for long periods and are identified as exotic only after their populations grow very large and invasive (Crooks & Soule 1999; Deyrup & Cover 2009). Once introduced, the seemingly high rate of success of these insects in Florida is likely due to the unique combination of geographic position, favorable climatic conditions for tropical, subtropical, and temperate species, and a broad diversity of anthropogenic ecosystems available for colonization (Myers & Ewel 1990; Frank & McCoy 1993; Simberloff 1997; Deyrup et al. 2000; King & Porter 2007; King & Tschinkel 2008; Noss 2013). Given their propensity for success in the state, understanding long-term invasion patterns of exotics may provide insight for other hotspots around the world with similar climatic conditions. A primary concern is iden-

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tifying where and when exotic species have appeared in Florida's ecosystems and what impacts have resulted over time as a result of their interactions with native species.

Ants were used as the community of interest for this study. Invasive ants are ranked among the most widespread and troublesome exotic species in the world (Holway et al. 2002; Lowe et al. 2004; Miravete et al. 2014). Numerous studies comparing invaded with uninvaded sites have documented negative impacts (Clark et al. 1982; Porter & Savignano 1990; Human & Gordon 1997; Berman et al. 2013). However, the scope and duration of exotic ant impacts upon native communities are probably better understood through long-term studies (Morrison 2002). For example, native ant communities often are reorganized as a result of being invaded (Porter & Savignano 1990; Sanders et al. 2003; Hoffmann & Parr 2008; Lessard et al. 2009). Such community-scale disruption may decline or disappear entirely several yr after the initial invasions for some species (Morrison 2002; Heller et al. 2008) but persist for others (Hoffmann & Parr 2008). At the scale of communities, the appearance and effects of exotic species may be seen by comparing presence and abundance of native species over time (Reitz & Trumble 2002). Long-term studies of ant communities may provide (1) key information in our understanding of the impacts of exotic ant invasions, especially the role of interactions among native and exotic species, (2) insight into mitigation of those impacts, and (3) detection of recently introduced exotic species.

The ant fauna of Florida is unusual in that it contains the largest percentage of non-native ants in North America with over 50 exotic species across 25 genera. This exotic ant fauna is the largest and most diverse in the region and, by proportion, is likely one of the most invaded mainland regional faunas in the world (Deyrup et al. 2000; King & Porter 2007). Some exotic ant species have been determined to be economically and ecologically significant in Florida for decades (Deyrup et al. 2000). Of these, the red imported fire ant (*Solenopsis invicta* Buren), Argentine ant (*Linepithema humile* [Mayr]), and little fire ant (*Wasmannia auropunctata* [Roger]) (both Hymenoptera: Formicidae) have received the most attention. However, a majority of the other exotic ant species in Florida are understood poorly, and their impacts and changes in distribution over time are largely unknown (Deyrup et al. 2000; King & Porter 2007). In this study we documented the changes in ant communities from a single locality over the course of nearly 25 yr where patterns of invasion, potential impacts of exotic invasive ant species, and patterns of diversity were identified for this relatively extensive time period.

Materials and Methods

STUDY SITE

The study was conducted in Wekiwa Springs State Park, approximately 2,752-ha located in Orange and Seminole counties in central Florida. Elevation ranges from 1.5 to 30.2 masl. For the 2012 survey, we focused our sampling effort within the park to the 3 ecosystems that presently and historically comprise the majority of ground cover: hydric hammock, sandhill, and flatwoods. These ecosystems also represent 3 of the most common and widespread upland ecosystems in central Florida (Myers and Ewel 1990), and share similar species rosters with other north and central Florida sites (Deyrup et al. 2000; King & Porter 2007).

The hydric hammock ecosystem covers approximately 1,145 ha and occurs on low, flat, and wet sites where limestone may be close to the surface, resulting in seeps or small streams. The sandy soil of the area usually has considerable organic material that, although gener-

ally saturated, is inundated only for short periods following rains. The sandhill ecosystem is characterized by an overstory of longleaf pine (*Pinus palustris* Mill.; Pinaceae) and turkey oak (*Quercus laevis* Walter; Fagaceae) covering approximately 623 ha. Soils are deep, coarse, well-drained, and comprised of yellowish sand. Sandhill soils generally are categorized into droughty coarse sands, sandy clays, or loamy sands; our sites were mostly composed of coarse sand classified as entisols that generally are low in nutrients (Abrahamson & Hartnett 1990). Sandhill ecosystems gradually transition downhill to pine flatwoods that are distinct in vegetation as a result of more poorly drained soils due to a higher water table and are prone to flooding (Abrahamson & Hartnett 1990). The pine flatwoods community consists of an overstory of longleaf pine that covers approximately 1,060 ha. Flatwood soils are usually acidic and hold insignificant amounts of extractable nutrients (Gholz & Fisher 1982; Myers & Ewel 1990). Soil moisture of this ecosystem usually is influenced by organic matter content as well as mulching effect from the litter layers (Myers & Ewel 1990).

SAMPLING

In the 1993 survey, Prusak (1997) sampled the ant communities of the park from Jan to Dec. Ants were sampled every other mo in 6 plots in each of the 3 ecosystems previously mentioned. During this time, pitfall traps were arranged in a 5 × 8 m grid in each plot for a total of 40 traps per plot. Traps were operated for a total of 6 wk (1 wk every other mo). Samples of litter (0.5 m²) were removed from 50 m transects at 10 m intervals at each site every other mo for a total of 90 samples per site, totaling 540 samples. Hand sampling sessions were standardized at 1 h per session per site, and involved actively searching for ant nests and new species based on the collector's field experience, log splitting, and bark flaking. Eighteen hand sampling sessions were conducted in each site over the yr for a total of 108 hand sampling h in the park.

For the 2012 survey, the same ecosystem collection sites were sampled with a third site added for each of the 3 ecosystems. However, the study design was changed from the exhaustive approach used by Prusak (1997) to that of King and Porter (2005) that favored rapid sampling with thorough capture of the ant fauna for comparison with earlier sampling efforts. According to the latter authors, they effectively sampled up to 90% of the known ant fauna elsewhere in Florida from the same ecosystem types we were using. We also sampled 3 roadside sites for comparison with the natural areas. In Aug 2012, one 100 m linear transect was established at each site with pitfall traps placed at 5 m intervals for a total of 20 traps per site with an overall total of 240 traps. Pitfall traps consisted of 85 mm long plastic vials (30 mm internal diam; Thorton Plastics, Salt Lake City, Utah, USA) partially filled with about 15 mL of non-toxic propylene-glycol antifreeze. Traps were buried with the open end flush with the ground surface and operated for 7 d. Traps were installed using a hand-held, battery-powered drill with an auger bit. Litter samples (0.5 m²) also were obtained at 10 m intervals along a parallel transect 10 meters from the original transect for a total of 10 litter samples per site for an overall total of 120 litter samples. Litter samples were removed from the site and immediately placed into 32 cm diameter Berlese funnels under 40-watt light bulbs. Funnels were operated until the samples were dry (about 48 to 72 h). Ants were sorted and identified to species by the authors using the insect collection at the University of Central Florida, Orlando, Florida, USA, as a reference, and Deyrup (2016) (and references therein) as the taxonomic key to species when necessary. Vouchers were deposited in the University of Central Florida insect collection.

In 2018, 10 plots were generated randomly in sandhill ecosystems; some of these plots were in the exact areas as the sampling events from 1993 and 2012. Plot dimensions were about 18 m × 18 m. Pitfall

traps of the same design as the 2012 survey were used for sampling. Four traps were randomly set in each plot and operated for 3 d, totaling 40 pitfall traps at a given sampling event. Plots were sampled every mo with this method from Feb to Aug 2018 (7 mo). Specimens were sorted and identified to species by the authors and vouchers deposited in the Social Insect Laboratory at the University of Central Florida. The 2018 summer season had unusually frequent periods of high intensity rains along with intermittent wk of drought conditions. These abnormalities affected the sampling effort because it influenced the abundance of ant foragers as well as resulted in the frequent flooding of pitfall traps. However, we note that pitfall sampling in the sandhill ecosystem provided a nearly complete sampling of the species present (King & Porter 2007). Therefore, data from the hydric hammock and flatwoods ecosystems were not included in sampling for that yr.

STATISTICAL ANALYSIS

All data used in analyses were based on the worker caste because their presence provides evidence of an established colony (Fisher 1999; Longino et al. 2002). The purpose of the sampling design was to produce a representative, nearly complete, species list for each ecosystem type. The relative abundance of individuals is an important measure when considering species richness (Gotelli & Colwell 2001). However, for ants, foraging worker abundance is not comparable with individuals of other animals. The sociality of ants often may lead to extreme clumping of individuals within samples (particularly litter samples, which may include entire colonies). This fact may skew the relationship when comparing species richness values weighted by abundances (Gotelli & Colwell 2001). To partially remedy this confounding relationship, species occurrence (incidence data) were used in place of individual abundance when evaluating species-based abundance measurements (Fisher & Robertson 2002; Longino et al. 2002). Therefore, data for the 3 ecosystems for 2012 were pooled and converted to a species-sample incidence (presence-absence) matrix (Longino et al. 2002). Also, the 2018 sampling data was converted similarly to incidence-based data.

To determine if sufficient sampling had been undertaken in 2012 and 2018, species accumulation curves were generated for every ecosystem and sampling method. These curves were generated with the sites being added in a random order. Monthly sampling data were pooled to generate the species accumulation curve for 2018. To supplement these curves, species richness estimators also were calculated for the entire park and different sampling methods using first-order and second-order jackknife species richness estimators (jack1 and jack2 hereafter). Both estimators are appropriate for analyzing incidence data (Longino et al. 2002). We also used the suggestion from Longino (2000) of using 80% of the jack1 estimator and comparing it with the observed species richness to assess whether sufficient sampling had been done to capture as much of the species diversity present in these ecosystems. Also, exotic ant to native ant species ratios were calculated as the number of exotic species divided by the number of native species in a given ecosystem of a given yr. Exotic to native ant species ratios also were calculated for the entire park for 1993 and 2012.

Non-metric multidimensional scaling, a non-parametric ordination method, was run on species by site matrices generated from the 2012 and 2018 sampling. Any singletons, species that occurred only once in the sampling, were removed in the matrices prior to running the analyses. We selected Jaccard's similarity index for these analyses regarding presence or absence data. Litter data were separately analyzed from pitfall data given the difference in sampling methods. Subsequent permutation-based analyses of variance (PERMANOVA) were used to test

for significant differences between clusters in the 2012 analyses. The non-metric multidimensional scaling was used to identify patterns in community dissimilarity for the multiple ecosystems sampled in 2012, and to determine if communities differed from each other. Given the repeated-measures design of the 2018 sampling, centroids by each sampling mo were calculated from the non-metric multidimensional scaling analysis and plotted to visualize community changes in sandhill ecosystem over time.

Units of samples differed between the 2012 and 2018 sampling studies. In 2012, 1 trap or litter sample was considered as 1 sampling unit. However, in 2018, due to the design of the survey, 1 plot (made up of 4 pitfall traps) was considered as 1 sample. This was because the pitfall data was pooled for each plot. Due to the discrepancy of sampling units, species accumulation curves were not compared between 2012 and 2018 because sampling units were not comparable. All statistical analyses used R 3.4.1 statistical software (R Development Core Team 2018). All graphics were prepared using the R package 'ggplot2' (Wickham 2009). Species accumulation curves, species richness estimator calculations, and non-metric multidimensional scaling analyses were accomplished using the 'vegan' package (Oksanen 2015).

Results

ANT DIVERSITY

The 1993 survey collected a total of 67 species, 9 of which were exotics (Table 1). The flatwoods sites contained 29 native and 4 exotic species. The sandhill sites contained 33 native and 6 exotic species. Hydric hammock sites contained 36 native and 6 exotic species. The 2012 survey yielded a total of 56 species in all transects and ecosystem types, 14 of which were exotic species (Table 1). A total of 41 species were captured using litter sampling, and 47 species were captured using pitfall trapping. Thirty-two species were captured from both sampling methods, whereas 9 were unique to litter sampling and 15 were unique to pitfall sampling. Fourteen of the 56 species were exotic ants. There were 3 unique exotics to each sampling method. The sandhill ecosystem had a total of 38 species, 21 unique to the pitfalls and 6 unique to the litter sampling. Six of the species from the ecosystem's total species list were exotic, 2 were shared between sampling methods, 1 was unique to the pitfalls, and 3 were unique to the litter sampling. The flatwood ecosystem yielded a total of 32 species, 7 of which were exotics (4 shared between sampling methods). Thirteen species were unique to the pitfalls, whereas 3 were unique to litter sampling. The hydric hammock ecosystem samples yielded a total of 30 species, 9 of which were exotic. Pitfall sampling yielded 8 unique species, and 10 were unique to litter sampling. Roadside sampling yielded a total of 30 species, 9 of which were exotic. Pitfall sampling yielded 13 unique species, and 8 were unique to litter sampling. The 2018 sandhill pitfall sampling yielded a total of 40 species, of which 6 were exotic (Table 1).

SPECIES ACCUMULATION CURVES AND SPECIES ESTIMATORS

Species accumulation curves show the sampling effort for 2012 was sufficient for pitfall and litter sampling in all 4 ecosystem types (Figs. 1, 2). All curves show signs of reaching or nearing asymptotes indicating the lack of collection of new species. The same outcome was shown in the species accumulation curve in 2018 with an increase of 3 new species in the last 20 sampling units (Fig. 3). In 2012, ant species richness in litter samples was within 1 standard error of the estimated species richness, but lower than the actual estimate comparing 80%

Table 1. Species checklist by yr and habitat type. A species list with species authorities from all 3 data sets from the 3 sampling events. The table specifies the yr and the habitat type in which the species was found.

Species	1993			2012				2018
	Hydric hammock	Sandhill	Pine flatwood	Hydric hammock	Sandhill	Pine flatwood	Roadside	Sandhill
<i>Aphaenogaster ashmeadi</i> (Emery, 1895)	—	—	—	—	X	—	—	—
<i>Aphaenogaster carolinensis</i> (Wheeler, 1915)	X	—	—	—	—	—	—	—
<i>Aphaenogaster flemingi</i> (Smith, 1928)	—	—	—	X	—	—	X	—
<i>Aphaenogaster floridana</i> (Smith, 1941)	—	—	—	—	—	—	—	X
<i>Aphaenogaster fulva</i> (Roger, 1863)	X	—	—	—	—	—	—	—
<i>Aphaenogaster lamellidens</i> (Mayr, 1886)	—	X	—	—	X	X	—	—
<i>Aphaenogaster treatae</i> (Forel, 1886)	—	X	X	—	X	X	—	X
<i>Brachymyrmex depilis</i> (Emery, 1893)	X	X	X	X	X	X	—	X
<i>Brachymyrmex obscurior</i> (Forel, 1893)	—	—	X	—	X	—	—	—
<i>Camponotus castaneus</i> (Latreille, 1802)	X	—	X	—	—	X	X	X
<i>Camponotus floridanus</i> (Buckley, 1866)	X	X	X	X	X	X	X	X
<i>Camponotus impressus</i> (Roger, 1863)	X	—	—	—	—	—	—	—
<i>Camponotus nearcticus</i> (Emery, 1893)	—	X	X	—	—	—	—	X
<i>Camponotus socius</i> (Roger, 1863)	—	X	—	—	X	—	—	X
<i>Cardiocondyla emeryi</i> * (Forel, 1881)	—	X	—	—	X	X	X	X
<i>Crematogaster ashmeadi</i> (Mayr, 1886)	X	X	X	—	—	X	—	X
<i>Crematogaster cerasi</i> (Fitch, 1855)	—	X	X	X	X	X	X	—
<i>Crematogaster lineolata</i> (Say, 1836)	—	—	—	—	—	—	X	—
<i>Crematogaster minutissima</i> (Mayr, 1870)	X	—	—	—	—	—	—	—
<i>Crematogaster</i> sp. A.	—	X	X	—	—	—	—	—
<i>Cryptopone gilva</i> (Roger, 1863)	X	—	—	—	—	—	—	—
<i>Cyphomyrmex rimosus</i> * (Spinola, 1851)	X	X	X	X	—	X	X	X
<i>Discothyrea testacea</i> (Roger, 1863)	X	—	—	—	—	—	—	X
<i>Dorymyrmex bossutus</i> (Trager, 1988)	—	X	—	—	X	—	—	X
<i>Dorymyrmex bureni</i> (Trager, 1988)	—	X	X	—	X	X	X	X
<i>Dorymyrmex smithi</i> (Cole, 1936)	—	—	—	—	X	—	—	—
<i>Eurhopalothrix floridana</i> * (Brown & Kempf, 1960)	X	—	—	X	—	—	X	—
<i>Forelius pruinosus</i> (Roger, 1863)	—	X	X	—	X	X	X	X
<i>Formica archboldi</i> (Smith, 1944)	—	—	—	—	X	X	—	X
<i>Formica dolosa</i> (Buren, 1944)	—	—	—	—	X	X	—	—
<i>Formica pallidefulva</i> (Latreille, 1802)	—	X	X	—	—	X	—	X
<i>Hypoconera opaciceps</i> (Mayr, 1887)	X	X	—	—	—	—	X	—
<i>Hypoconera opacior</i> (Forel, 1893)	X	—	—	X	X	—	X	X
<i>Lasius alienus</i> (Foerster, 1850)	X	—	—	—	—	—	—	—
<i>Leptogenys manni</i> (Wheeler, 1923)	X	—	—	—	—	—	—	—
<i>Myrmecina americana</i> (Emery, 1895)	X	—	—	—	—	—	—	—
<i>Neivamyrmex opacithorax</i> (Emery, 1894)	—	X	X	—	—	—	—	—
<i>Nylanderia arenivaga</i> (Wheeler, 1905)	—	X	X	—	X	X	—	X
<i>Nylanderia concinna</i> (Trager, 1984)	X	—	X	—	—	—	—	—
<i>Nylanderia faisonensis</i> (Forel, 1922)	X	—	—	X	—	—	—	—
<i>Nylanderia parvula</i> (Mayr, 1870)	—	—	—	X	—	—	—	—
<i>Nylanderia wojciki</i> (Trager, 1984)	—	X	X	X	X	X	X	X
<i>Ochetellus glaber</i> * (Mayr, 1862)	—	—	X	X	—	X	X	—
<i>Odontomachus brunneus</i> (Patton, 1894)	X	X	—	X	X	X	X	X
<i>Pheidole adrianoi</i> (Naves, 1985)	—	—	—	—	—	—	—	X
<i>Pheidole carrolli</i> (Naves, 1985)	—	—	—	—	—	—	—	X
<i>Pheidole dentata</i> (Mayr, 1886)	X	X	X	X	X	X	X	X
<i>Pheidole dentigula</i> (Smith, 1927)	X	X	X	X	—	X	X	X
<i>Pheidole floridana</i> (Emery, 1895)	X	X	—	X	X	X	X	X
<i>Pheidole metallescens</i> (Emery, 1895)	—	—	—	—	X	—	X	X
<i>Pheidole moerens</i> * (Wheeler, 1908)	X	X	X	X	X	X	X	X
<i>Pheidole morrisii</i> (Forel, 1886)	—	X	X	X	X	X	X	X
<i>Pheidole obscurithorax</i> * (Naves, 1985)	—	—	—	X	X	X	X	—
<i>Pheidole tysoni</i> (Forel, 1901)	—	—	—	—	—	—	—	X
<i>Pogonomyrmex badius</i> (Latreille, 1802)	—	X	—	—	X	—	X	X

An asterisk (*) following a species name indicates an exotic species.

An "X" indicates presence; a dash "—" indicates absence.

Table 1. (Continued) Species checklist by yr and habitat type. A species list with species authorities from all 3 data sets from the 3 sampling events. The table specifies the yr and the habitat type in which the species was found.

Species	1993			2012				2018
	Hydric hammock	Sandhill	Pine flatwood	Hydric hammock	Sandhill	Pine flatwood	Roadside	Sandhill
<i>Prenolepis imparis</i> (Say, 1836)	—	—	—	—	—	—	—	X
<i>Proceratium silaceum</i> (Roger, 1863)	X	—	—	—	—	—	—	—
<i>Pseudomyrmex ejectus</i> (Smith, 1858)	X	—	—	—	—	—	—	—
<i>Pseudomyrmex gracilis</i> * (Fabricius, 1804)	X	X	—	—	X	—	—	—
<i>Pseudoponera stigma</i> * (Fabricius, 1804)	—	—	—	—	—	—	—	X
<i>Solenopsis abdita</i> (Thompson, 1989)	X	X	X	—	—	—	—	—
<i>Solenopsis carolinensis</i> (Forel, 1901)	X	X	X	X	X	X	X	X
<i>Solenopsis geminata</i> (Fabricius, 1804)	X	—	X	—	—	—	—	—
<i>Solenopsis globularia</i> (Smith, 1858)	—	—	—	—	X	X	—	—
<i>Solenopsis invicta</i> * (Buren, 1972)	—	—	X	X	X	X	X	X
<i>Solenopsis nickersoni</i> (Thompson, 1982)	X	X	X	X	X	X	X	X
<i>Solenopsis pergandei</i> (Forel, 1901)	—	—	—	—	—	—	—	X
<i>Solenopsis picta</i> (Emery, 1895)	X	—	—	—	X	—	—	—
<i>Solenopsis tennesseensis</i> (Smith, 1951)	—	—	—	X	X	X	—	X
<i>Stigmatomma pallipes</i> (Haldeman, 1844)	X	—	—	X	—	—	—	—
<i>Strumigenys angulata</i> (Smith, 1931)	—	X	—	—	—	—	—	—
<i>Strumigenys eggerti</i> * (Emery, 1890)	X	—	—	X	X	—	X	X
<i>Strumigenys emmae</i> * (Emery, 1890)	—	—	—	X	—	—	—	—
<i>Strumigenys laevinasis</i> (Smith, 1931)	X	—	—	—	—	—	—	—
<i>Strumigenys louisianae</i> (Roger, 1863)	X	X	—	X	—	—	—	—
<i>Strumigenys margaritae</i> * (Forel, 1893)	—	—	—	—	—	X	—	—
<i>Strumigenys membranifera</i> * (Emery, 1869)	X	X	—	—	—	X	—	—
<i>Strumigenys ornata</i> (Mayr, 1887)	X	X	—	—	—	—	—	—
<i>Strumigenys pilinasis</i> (Forel, 1901)	X	—	—	—	—	—	—	—
<i>Strumigenys pulchella</i> (Emery, 1895)	X	—	—	—	—	—	—	—
<i>Strumigenys rogeri</i> * (Emery, 1890)	X	X	—	X	—	—	—	—
<i>Strumigenys talpa</i> (Weber, 1934)	—	X	X	—	—	—	—	—
<i>Temnothorax pergandei</i> (Emery, 1895)	—	X	X	—	X	X	X	—
<i>Temnothorax texanus</i> (Wheeler, 1903)	—	X	X	—	X	X	—	—
<i>Tetramorium simillimum</i> * (Smith, 1851)	—	—	—	X	—	—	X	—
<i>Trachymyrmex septentrionalis</i> (McCook, 1881)	—	X	X	—	X	—	X	X
<i>Xenomyrmex floridanus</i> (Emery, 1895)	X	—	—	—	—	—	—	—

An asterisk (*) following a species name indicates an exotic species.

An "X" indicates presence; a dash "—" indicates absence.

of the jack1 estimator (Table 2). Pitfall sampling during 2012 and 2018 also exceeded 80% of their respective jack1 estimates. Overall, these comparisons further suggest that sampling captured a majority of the species present in the park.

EXOTIC TO NATIVE RATIOS

The percentage of exotic species at the park level increased from 1993 to 2012. Exotic to native ant ratios showed overall modest increases in the park but evidence of leveling-off in one of the ecosystems occurred in the sandhill ecosystem. The ratio within this ecosystem that accounted for a high proportion of species diversity and richness showed a slight decline in the percentage of exotic species over the course of the 3 sample yr (Table 3). However, the rest of the ecosystems between 1993 and 2012 showed increases in exotic to native ant species ratios. Flatwood exotic to native ant species ratios increased from 0.14 to 0.22 and almost doubled in the hydric hammock ecosystem (0.17 to 0.30; Table 3).

CHANGES FROM 1993 TO 2012

In 2012, 17 native species appeared in new ecosystems in the park along with 8 exotic species. Most notable was *S. invicta*, having

increased its presence from the flatwoods to all 3 ecosystem types as well as roadside sites. The exotic big-headed ant, *Pheidole obscurithorax* Naves (Hymenoptera: Formicidae), was newly present in the park and was found in all 3 ecosystems as well as on the roadside. Another widespread exotic of note was *Pheidole moerens* Wheeler (Hymenoptera: Formicidae). *Pheidole moerens* was present in all 3 ecosystems in 1993 and 2012 as well as the roadside in 2012. Similarly, in 2012, the small-bodied native *Pheidole floridana* Emery and *Pheidole metallescens* Emery (both Hymenoptera: Formicidae), had appeared in flatwoods and sandhills, respectively.

The 1993 study collected 9 species of dacetine ant species, 3 of which were exotic. Dacetines are small, specialized hunters of litter arthropods. The 2012 study collected 6 dacetines, 5 of which were exotic. Only 4 of the species, *Strumigenys eggerti* Emery, *Strumigenys membranifera* Emery, *Strumigenys louisianae* Roger, *Strumigenys rogeri* Emery (all Hymenoptera: Formicidae) were collected in both studies and 3 were exotic (*S. louisianae* native). The 2 new exotic dacetines to the park, *Strumigenys emmae* Emery and *Strumigenys margaritae* Forel (both Hymenoptera: Formicidae), moved into hydric hammock and flatwood ecosystems, respectively, while the recurring exotic, *S. eggerti*, moved into the sandhill ecosystem

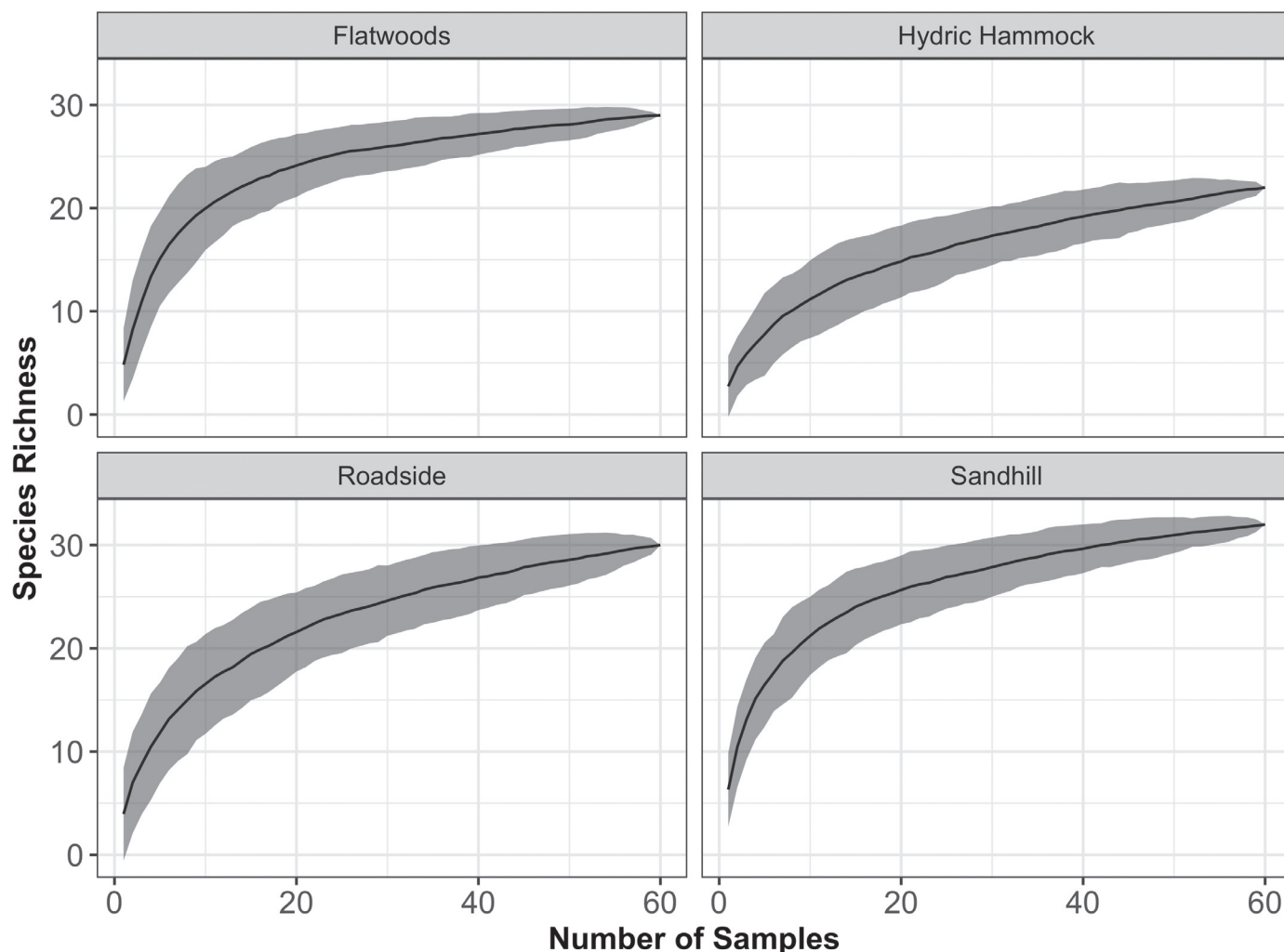


Fig. 1. Species accumulation curves for 2012 pitfall sampling with each facet representing a distinct habitat. Curves were generated with incidence data and sites were added randomly to generate these curves. Shaded areas represent the 95% confidence intervals.

during 2012. The exotic dacetine originating from Africa, *S. rogeri*, has exclusively remained in the hydric hammock ecosystem since the initial study 20 yr ago.

In 2012, a native Florida upland pine and scrub endemic ant species that is a new record for the site, *Formica archboldi* Smith (Hymenoptera: Formicidae), was collected in sandhill and flatwoods ecosystems. The presence of this species may indicate an expansion of its range from the recent past. Another member of the *Formica* genus, *Formica dolosa* Buren (Hymenoptera: Formicidae), is a new record for the site and also was collected in sandhill and flatwoods ecosystems in 2012. In the same yr, a native species with a very high density in hydric hammock and a preference for more humid environments, *Odontomachus brunneus* (Patton) (Hymenoptera: Formicidae), was captured in the flatwoods and sandhill ecosystems, where it was not found previously.

CHANGES FROM 2012 TO 2018

Comparisons between the 2018 sampling and the previous samplings are made with caution due to the limitations of a single sampling method (pitfall traps) and ecosystem sampled. Only 1 of the exotic species found in 2018, *Pseudoponera stigma* Fabricius (Hymenoptera: Formicidae), was new. *Pseudoponera stigma*, a species originally from Asia, is the only species of the genera known to have established in

Florida. We observed a major range shift for the native species, *Pheidole tysoni* Forel (Hymenoptera: Formicidae). This ant is found in northern Florida where Deyrup (2016) had reported its occurrence, but its presence in our samples was evidence that this species has a broader range that includes central Florida. Unexpectedly, we did not collect *P. obscurithorax* from the 2018 pitfalls. Based on the 2012 data, the species had established itself in all ecosystem types across the park including sandhill. However, the extensive 7 mo sampling effort in some of the same sites as the 2012 sampling yielded no evidence of its presence.

COMMUNITY SIMILARITY AND DISSIMILARITY

The non-metric multidimensional scaling analysis of the 2012 data show distinct communities affiliated with different ecosystems in the park for litter and pitfall sampling. There was significant clustering based on these ecosystems and a permutation-based analysis of variance verified the separation of the centroids of these clusters ($P < 0.05$) for both analyses. The pitfall non-metric multidimensional scaling ($k = 3$; stress = 0.15) show the flatwood ant community is most distinct from the other communities (Fig. 4). The roadside and sandhill ecosystem appear to be similar in structure, but this overlap is lost when viewing the third non-metric multidimensional scaling axis (supplementary

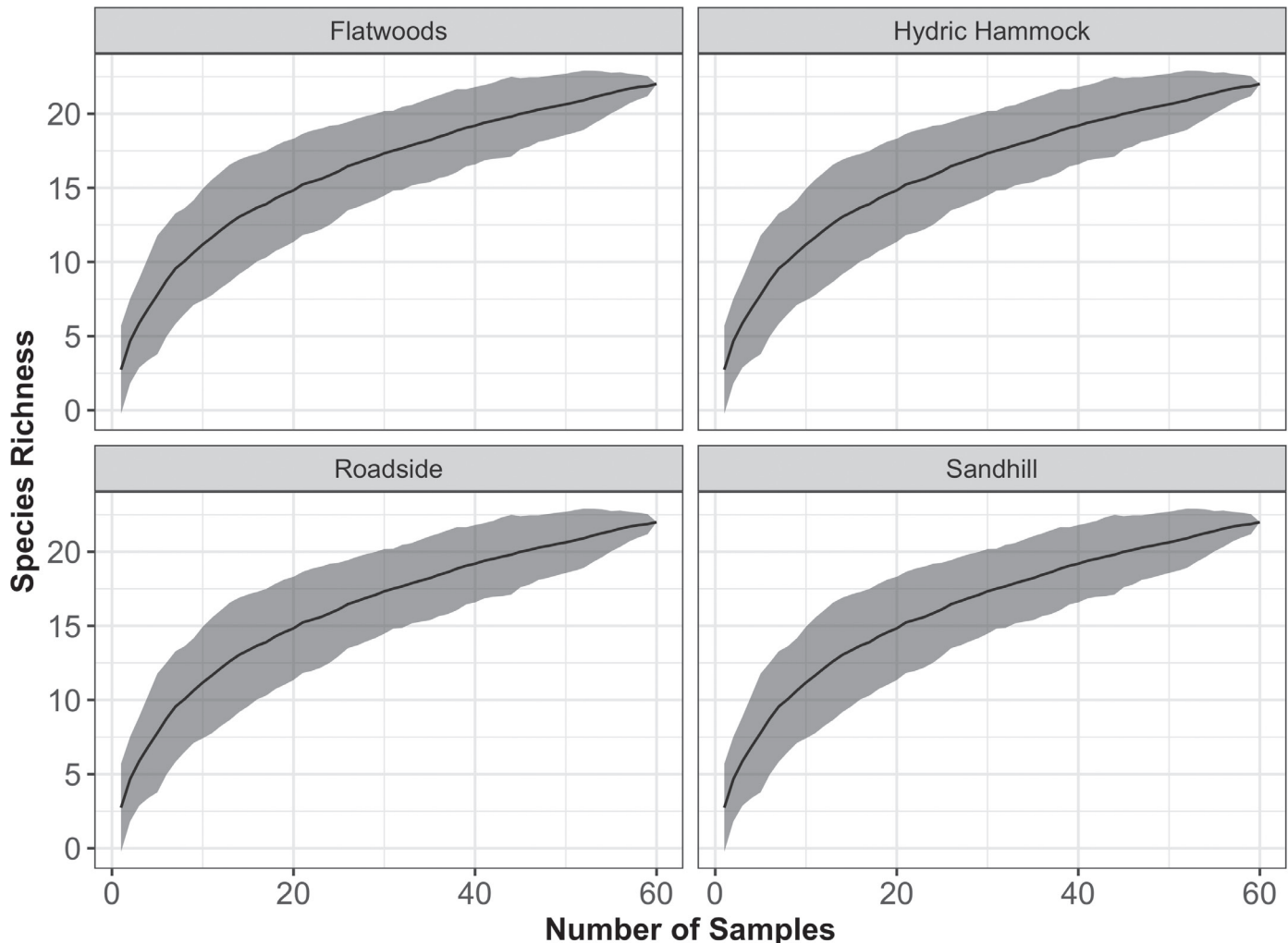


Fig. 2. Species accumulation curves for 2012 litter sampling with each facet representing a distinct habitat. Curves were generated with incidence data and sites were added randomly to generate these curves. Shaded areas represent the 95% confidence intervals.

material). The 2012 litter non-metric multidimensional scaling ($k = 3$; stress = 0.09) show similar distinct community structures, but the flatwood community is not as dissimilar from the rest of the habitats compared with that observed in the pitfall analysis (Fig. 5). However, when viewing the analysis from 3 dimensions (supplementary material) and calculating centroid distance in 3 dimensions, the flatwood community remains the most distinct by distances between habitat centroids, especially from the roadside community. The closest similarity between communities was between roadside and sandhill. The non-metric multidimensional scaling analysis from 2018 ($k = 2$; stress = 0.19) and the subsequent plotting of monthly centroids show community structure shifts through time. The largest shifts in structure came from the transition of Mar to Apr 2018 and Jun to Jul 2018 (Fig. 6).

Discussion

Our data indicates a complex dynamism in the ant communities in Florida's upland ecosystems. Although exotic to native ant species ratios show an overall trend of increasing exotics, there are limitations to inferences that can be made beyond that of the sandhill habitat. The exotic to native ant species ratios for this ecosystem over the 3 sample yr do not vary but show a slight decreasing trend through time suggest-

ing that exotic species are not necessarily increasing relative to native species. This pattern suggests that sandhill habitats may be in a period of stability and not accruing additional exotic species.

In contrast, more mesic habitats (such as pine flatwoods), and especially hydric hammock habitats, had higher exotic to native ant species ratios in 2012 compared with 1993. There was a nearly 2-fold increase in exotic to native ant species ratios in hydric hammock habitat between 1993 and 2012 (from 0.17 to 0.30, respectively). This increase occurred despite not capturing any dacetina ant species (many of which are exotic) in 2012, a group that made up many of the exotics in this habitat in 1993. This is congruent with a study conducted by King and Porter (2007) where the highest percentage of exotic ants based on several upland habitat types was from hydric hammock habitat.

The increasing number of exotic ants in these 2 habitats over the past 2 decades is worth noting. Mesic habitats like hydric hammock may experience higher degrees of natural disturbances, such as inundation events or infrequent high intensity fires, than sandhill (Abrahamson & Hartnett 1990). Such disturbances may facilitate the introduction of exotics. Unfortunately, the ecological mechanisms that influence exotic to native ant species ratios cannot be parsed out in the context of this study due to the absence of land-use or prescribed fire data. Another factor that may be the root of higher proportions of exotics in hydric hammocks is the naturally low number of species associated with this

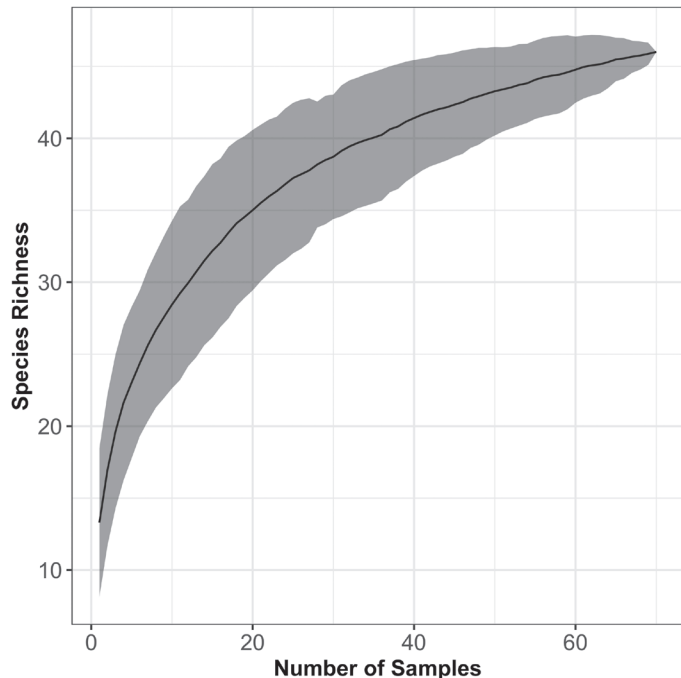


Fig. 3. Species accumulation curves for 2018 pitfall sampling done in sandhill habitat. Monthly sampling data was pooled into a single dataset. The curve was generated with incidence data and sites were added randomly to generate the curve. Shaded areas represent the 95% confidence intervals.

ecosystem. Sampling points from 1993 and 2012 showed that these habitats ranked lowest in terms of species richness. In addition, roadside habitats were found to be species poor in 2012. Furthermore, King and Porter (2007) found similar results in hydric hammock habitat and anthropogenically disturbed habitats.

Several native species were found in hydric hammock habitat in 1993 but were not observed in 2012 within the same habitat. Such species included *Aphaenogaster carolinensis* Wheeler, *Aphaenogaster fulva* Roger, *Camponotus impressus* (Roger), *Crematogaster minutissima* Mayr, *Crematogaster lineolata* (Say), *Cryptopone gilva* (Roger), and *Lasius alienus* (Foerster) (all Hymenoptera: Formicidae). This group includes a species that is arboreal (*C. impressus*) and thus not readily captured using ground-sampling methods like pitfalls and litter sampling. The remainder of these species are likely uncommon and thus may still be present but were not sampled in 2012. The Dacetini group from the 1993 survey was largely absent from the 2012 survey as well. This may be a result of a standardized sampling approach conducted in 2012 which differed from the approach used in 1993, and included hand sampling that may be more effective at capturing some species. The new found presence of *P. stigma* in 2018 suggests that this species likely is expanding its range beyond the Florida Keys to central Florida.

Table 3. Exotic to native ant species ratios for habitat types that were sampled, and for the entire park from 1993 to 2012. Species data from different sampling methods were pooled to calculate exotic to native ant species ratios. Blanks represent unsampled habitats across all sampling points.

Habitat	1993	2012	2018
Flatwoods	0.14	0.22	—
Hydric hammock	0.17	0.30	—
Roadside	—	0.30	—
Sandhill	0.18	0.16	0.15
Whole park	0.16	0.25	—

Other evidence of community changes can be seen in certain species that are intermittent in their appearance within the community, such as *P. obscurithorax*, *Camponotus nearcticus* Emery (Hymenoptera: Formicidae) (another arboreal species), and other species that were present in 1 but not other yr. It's important to note that the presence of intermittent species in our datasets may be due to the rarity of the species or sampling deficiency (i.e., species were present but remained unsampled). For example, *Neivamyrmex opacithorax* Emery (Hymenoptera: Formicidae), a member of the New World army ants, was found in pitfalls in sandhill and flatwood habitats in 1993 but never appeared in subsequent sampling events. This species along with others from the same genus spend a portion of their lives in a hypogaeic environment, but when on the move may migrate or raid other ants aboveground. The absence of the species in 2012 and 2018 is not enough evidence to definitively determine local extinction. The same can be said of other rare ground-dwelling species like *A. carolinensis* or *C. gilva* because many species may require greater sampling effort to be captured. The 1993 and 2018 sampling efforts spanned multiple months from dry to wet seasons. In both surveys a native species, *Discothyrea testacea* Roger (Hymenoptera: Formicidae), was found but was absent in 2012. The initial finding in 1993 was located in the hydric hammock; however, in 2018 it was in sandhill only, supporting what little natural history is known about this species. It resides in mesic and xeric environments and is a relatively uncommon species (Deyrup 2016).

Our data does suggest a local extinction event with the native fire ant, *S. geminata*. It was found in hydric hammock and pine flatwoods in 1993; however, subsequent sampling points show no evidence of this species. *Solenopsis geminata* is not a rare species, is readily sampled using pitfalls when present, and is known to be prevalent in sandhills due to its well-drained soils. In the past, *S. geminata* was common and widespread prior to the introduction of *S. invicta* throughout Florida (Deyrup 2016). Previous studies have demonstrated that *S. invicta* can reduce the abundance and even cause local extinctions of *S. geminata* (Porter et al. 1988; Morrison 2002; Deyrup 2016). The complete absence of *S. geminata* from sampling points in 2012 and 2018 (Table 1) suggests that likely there was a local extinction event of this native fire ant in the park that resulted from the invasion and population growth of red imported fire ants from the 1970s through the present (Tschinkel 2006).

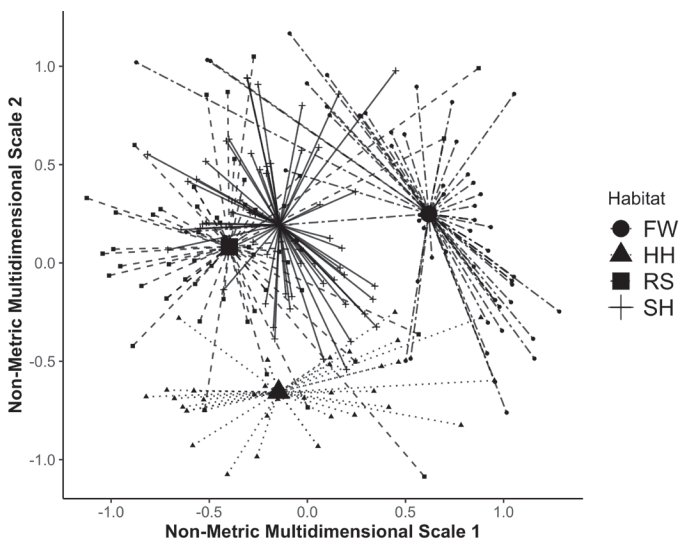


Fig. 4. Non-metric multidimensional scaling of 2012 pitfall data ($k = 3$; stress = 0.15). Shapes represent clusters in multi-dimensional space based on habitat type (FW = Flatwoods, HH = Hydric hammock, RS = Roadside, SH = Sandhill). Larger points represent centroids of these clusters.

Table 2. Habitat and yr, sampling method, species richness, Jackknife 1 estimates, Jackknife 1 standard error (SE), 80% of Jackknife 1 estimates, and Jackknife 2 estimates conducted in 2012 and 2018. All habitats were pooled for 2012 calculations.

Habitat and yr	Sampling method	Species richness	Jackknife 1 estimate	Jackknife 1 SE	80% of Jackknife 1 estimator	Jackknife 2 estimate
Whole park 2012	Litter sampling	41	53.89	3.58	43.12	60.82
Whole park 2012	Pitfall sampling	47	52.98	2.44	42.38	53.99
Sandhill 2018	Pitfall sampling	40	47.89	3.12	38.31	50.87

The widespread presence of *P. obscurithorax* in 2012 was unexpected, as was its absence in the sandhill habitat in 2018. King and Tschinkel (2007) speculated that this species is experiencing a similar range expansion in North America as *S. invicta*. Specifically, *P. obscurithorax* is most likely being spread by human transport with isolated occurrences as far west as Texas, where it readily inhabits natural areas and disturbed sites without discrimination, unlike *S. invicta* (King & Tschinkel 2007). This ant’s potential to displace other species is suggested from the 2012 sampling with the occupation of hydric hammock sites by *Pheidole morrisii* Forel (Hymenoptera: Formicidae), a species known to inhabit sandhills and open-canopy habitats, suggesting pressure from *P. obscurithorax*. However, the intermittent presence of this latter species in natural areas, such as sandhills, suggests that local patterns of invasion may include occasional local extinction events. Its absence in 2018, despite a high sampling effort, is indicative that it still may be in the initial stages of establishment within the sandhill habitat or may ultimately fail to establish at all in this ecosystem.

The 2012 roadside sampling indicated that of the 14 exotic species collected in the current study, 8 were found in this habitat. It is important to note that many exotic ant species thrive in this habitat type throughout Florida, and roadsides often are found in close proximity to natural areas throughout the state (King & Tschinkel 2007). Certain

native species of ants known as ‘disturbance specialists’ such as *Dorymyrmex bureni* (Trager) (Hymenoptera: Formicidae) also were found frequently and often in high numbers along roadside sites. Exotic species that may first appear in disturbed roadside areas before moving into the natural communities adjacent to them include *S. invicta*, *S. eggersi*, *P. moerens*, and more recently *P. obscurithorax*. In our study we noted that fire breaks (loose sand roads maintained in natural areas) were being inhabited by several exotic species, most notably *S. invicta*. It is likely that fire breaks may be similar to paved roadside sites that may act as a pathway for exotic species to move into natural areas. Fire breaks are potentially more troublesome given their prevalence in more remote natural areas.

Community dissimilarity analyses between habitats and through time suggest that ant communities do differ from each other. In our study, the significant differences between habitats is congruent with previous studies showing that ant communities (including those that are subterranean) differ at the local level relative to factors such as soil type mentioned earlier (Berman & Andersen 2012; Cross et al. 2016; Ohyama et al. 2018). The large dissimilarity between habitats, such as pine flatwoods and a more anthropogenically impacted roadside habitat, indicate that anthropogenically altered habitats have a distinct, exotic species-dominated community structure. The patterns of shifting

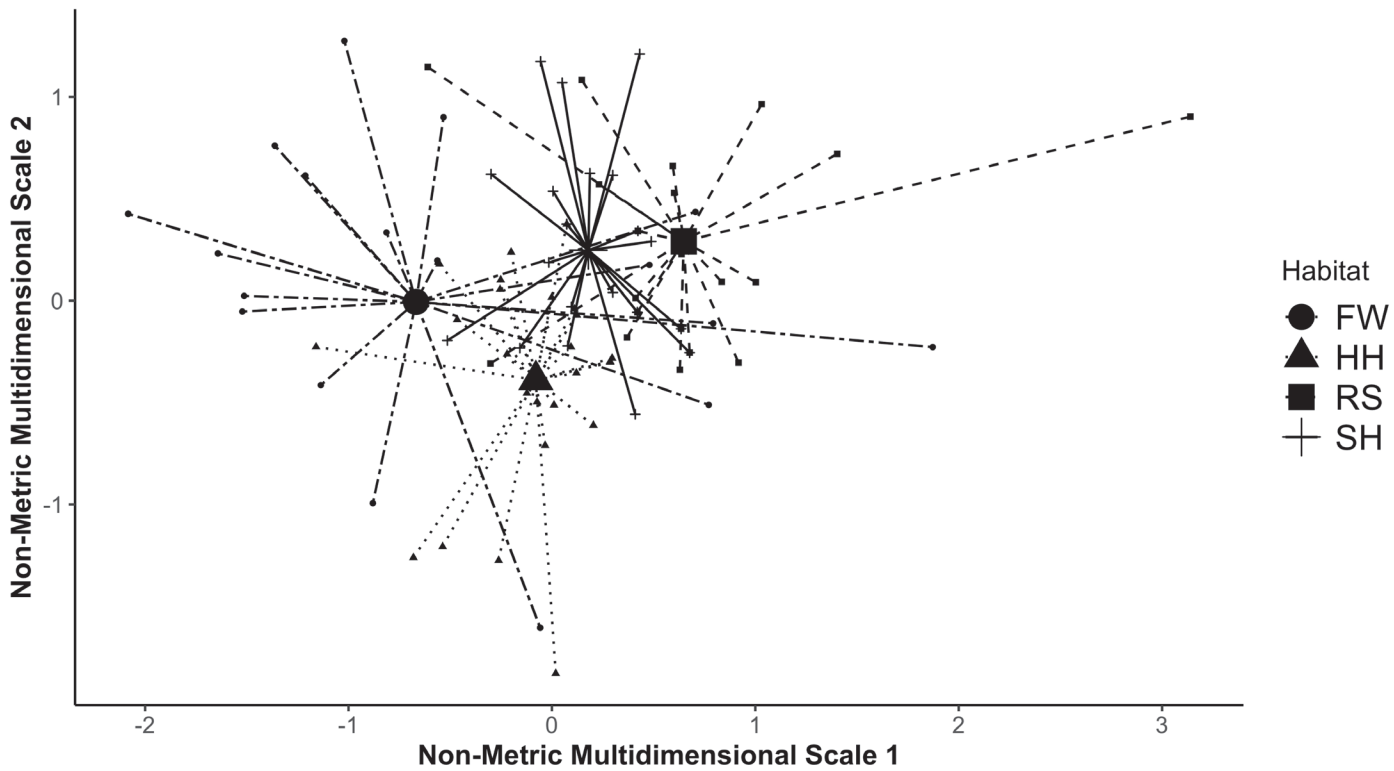


Fig. 5. Non-metric multidimensional scaling of 2012 litter data ($k = 3$; stress = 0.09). Shapes represent clusters in multi-dimensional space based on habitat type (FW = Flatwoods, HH = Hydric hammock, RS = Roadside, SH = Sandhill). Larger points represent centroids of these clusters.

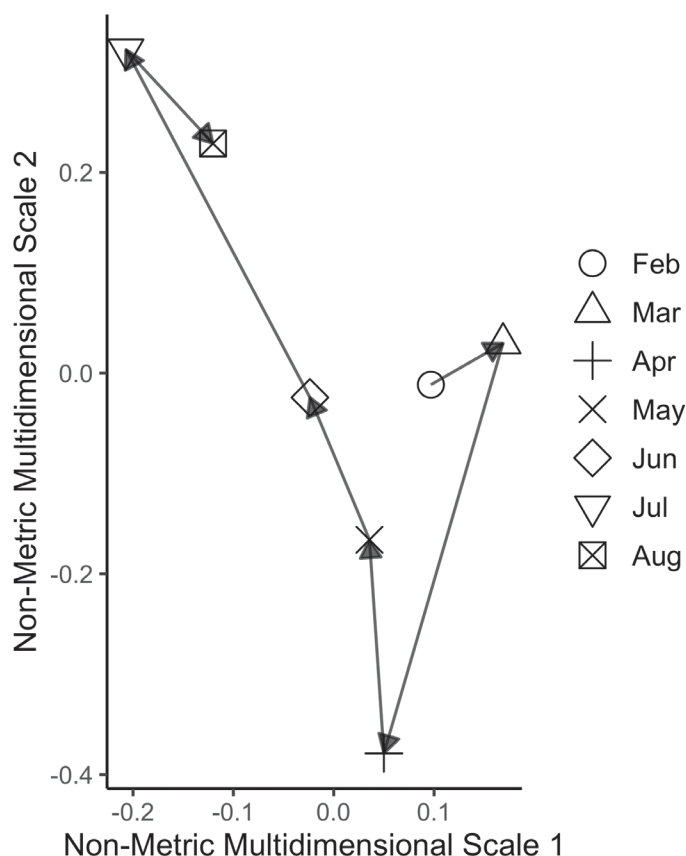


Fig. 6. Centroids of clusters based on mo of the 2018 monthly pitfall sampling done in sandhill habitat. Centroids were calculated from a non-metric multidimensional scaling analysis run on the pooled sampling data from 2018 ($k = 2$; stress = 0.19). Vectors connect each centroid in the directionality of mo-based time. Longer vectors represent larger changes in community structure between sampling events. Each mo is distinguished between centroids based on shape.

occurrence records of a number of exotic and native ant species is not surprising given sampling limitations, the snapshot nature of the study, and the changing community roster present in regions like the peninsula of Florida that is so frequently invaded. It has been suggested that Florida may experience waves of exotic ants. For example, prior to 1940 many of Florida's exotic ants originated from the Old World tropics; however, the majority of the exotics found post 1940 originate from the New World tropics (Deyrup et al. 2000). Reasons why Florida may be experiencing this wave of exotic ants most likely reside with anthropogenic activities such as shipping patterns, changing economy, and land use change. The exotic plant-trade and the increased interconnectedness in the state pose as 'highway' for exotic ants, and the pattern of exotic species accumulation we note in this site is likely ongoing in natural areas throughout Florida (Deyrup et al. 2000).

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