RESEARCH ARTICLE



Exotic ants (Hymenoptera, Formicidae) of Ohio

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Abstract

The worldwide transfer of plants and animals outside their native ranges is an ever increasing problem for global biodiversity. Ants are no exception and many species have been transported to new locations often with profound negative impacts on local biota. The current study is based on data gathered since the publication of the "Ants of Ohio" in 2005. Here I expand on our knowledge of Ohio's myrmecofauna by contributing new records, new distributional information and natural history notes. The list presented here contains 10 species with origins in a variety of geographic regions, including South America, Europe, Asia, and Indo-Australia. Two distinct groups of exotics, somewhat dissimilar in their geographic origin, occur in Ohio: a) 3 species of temperate Eurasian origin that have established reproducing outdoor populations; and b) 7 tropical tramp species currently confined to man-made structures. Only *Nylanderia flavipes* (Smith, 1874) is currently seen to be of concern although its effects on local ant communities appear to be restricted largely to already disturbed habitats. A systematic sampling of disturbed areas, urban sites, plant nurseries and conservatories, where new arrivals can be expected, would extend and build upon our current knowledge of Ohio's exotic ant fauna.

Keywords

Formicidae, non-native species, distribution, natural history, eastern US, Ohio

Introduction

People rarely travel alone and the worldwide human-mediated transfer of organisms is well documented. In the current era of enhanced commerce, improved transportation and globalization, more and more species are being transported to areas where they did not occur previously. A large number of plant and animal species have been transferred to new locations either purposefully (for food, medicine, landscaping, or as pets) or unintentionally (in ballast water, via potted plants, top soil, or fire wood) (Vitousek et al. 1997). We refer to such organisms that have completed the first step of the introduction process (i.e., initial "dispersal") as non-native, alien or exotic species. Ants are no exception, and most regions of the world now are known to harbor at least a few non-native species. Of the approximately 14 000 described species of ants, over 200 have established populations outside their known native range and even more species have been detected but not established (Sarnat et al. 2016).

Owing to their small body size, social behavior and often pronounced tolerance to, and association with, human-altered habitats, many non-native ants now are widely distributed across the globe and have become an integral part of their new homes (Holway et al. 2002). Non-native ants are not a new problem but their frequency of occurrence has been increasing due to increased rates of travel and trade, along with modification of natural habitats and urbanization. Islands are especially prone to accumulate exotic species and high proportions of non-native ants are known from a number of island systems. For example, the current myrmecofauna of the state of Hawaii includes at least 57 species (Krushelnycky 2015), none of which is native to the Hawaiian Islands. Similar trends have been noted also for certain continental areas where climatic conditions are appropriate for the establishment of a high number of tropical and subtropical ant species. With over 50 established species of non-native ants, Florida harbors the largest known exotic ant fauna of any continental US state (Deyrup et al. 2016).

Many established non-native species (i.e., species that have completed the second step of the dispersal process; "exotic established species" in Wittenborn and Jeschke 2011) possess invasive attributes and constitute a major part of the global environmental change. Such species have the potential to spread, often considerably, upon establishment and affect native ecosystems with devastating ecological consequences to local communities and ecosystem processes (i.e., invasive species; Mack et al. 2000; Mooney and Hobbs 2000, Pimentel et al. 2005). Next to habitat loss and degradation, invasive species are among the most significant drivers of biodiversity loss (Didham et al. 2007).

The Global Invasive Species Database shows that five ant species currently are listed among the World's 100 worst invasives (ISSG 2015). An emerging problem, at least in regard to ants, is the recent increased interest in keeping various ants species as pets. In Europe, where restrictions generally are lacking, Internet-stores offer living ant colonies, formicaries, and various accessories (Buschinger 2004). These shops advertise and sell ants from nearly all over the world, including some well-known ant invaders (Wild 2011). This unfortunate practice has the potential to increase the number of im-

ported colonies and contribute to the spread of additional species. There is, therefore, a clear need for a better documentation of the current and future distribution of such exotic species if we are to better understand and to be able to mitigate the effects associated with their spread. That said, it is important to stress that not all exotic species are, or are likely to become, invasive or to attain a pest status. Aside from the more practical aspect of documenting the spread and the effects of non-native ants, the discovery and study of these species informs our understanding of general ecological principles.

In the context of this paper, I apply the term "exotic species" to designate any species detected outside the confines of its known native range. As such this definition includes both species with well-established populations in natural or human-altered settings as well as species which have been encountered only infrequently, or in low numbers, and whose current status therefore is uncertain. The focus of this paper, accordingly, is on the species that have concluded the first, fundamental, step in the invasion process, namely the completion of human-aided dispersal.

The first known record of an ant exotic in Ohio is from 1917 when *Monomorium pharaonis* (Linnaeus, 1758) was collected by M.R. Smith in Columbus (unpublished material housed at the Ohio State University Collection; in Wetterer 2010). Two additional species, *Tetramorium caespitum* (Linnaeus, 1758) and *Hypoponera ragusai*, (Emery, 1894) subsequently were reported from south-central Ohio by Wesson and Wesson (1940). *Linepithema humile* (Mayr, 1868) (Arnett 1993) and *Paratrechina longicornis* (Latreille, 1802) (Hedges 1998) were added to the list in the next 60 years, thus raising the number of exotic ant species known from Ohio to five prior to 2000. In 1996 a statewide survey of the ant fauna of Ohio was undertaken by Gary Coovert and Brian Rayburn, which resulted in two additional species (*Pheidole bilimeki* Mayr, 1870 and *Tetramorium atratulum* (Schenck, 1852)) reported for Ohio (Coovert 2005). Thus prior to the onset of the current study a total of seven non-native ant species were known from the state (although *P. longicornis* was not included in the Ohio ant list at that time).

Here I extend the current knowledge of the ant fauna of Ohio and provide a summary of the exotic species known to occur in the state at present. I expand the list with the inclusion of species newly discovered or species not included in Coovert (2005) and provide new distributional and/or ecological data. It is my intent that this paper will serve as a stepping stone and will encourage future explorations of Ohio's myrmecofauna.

Methods

The work for this study began in late 2005, following the publication of Coovert (2005) and is ongoing. The methods I used are not precise and most of my survey work, and that of my colleagues, was qualitative. One exception is the formicine *Nylanderia flavipes* (Smith, 1874), for which quantitative data are available (see Uno et al. 2010, Ivanov et al. 2011). The use of tuna baits, Winkler litter extraction and careful observations allowed for a more rigorous assessment of this species' current status in northern Ohio.

During my work I concentrated on documenting as many species as possible at each survey site primarily through the use of hand collecting. I divided my sampling time between natural and human altered habitats alike as disturbed areas are often prone to the accumulation of ant exotics. A substantial part of my sampling was conducted in human-modified habitats including parks, gardens, yards and other urban landscapes. In addition, various man-made structures such as greenhouses, conservatories, plant nurseries and people's homes also were examined. At each site I inspected the ground and vegetation (including flowers and seed pods) looked under bark, stones, logs and other cover objects. I also broke open stems and branches that have fallen on the ground and inspected them for the presence of ant colonies. On a number of occasions I augmented this sampling scheme by checking lights on buildings or by using black light for the collection of alate reproductives. New materials accumulated in the invertebrate collection at the Cleveland Museum of Natural History (CMNH) since 2005 also were examined. Much material, in the form of specimens and/or photographs, was sent to me by friends and colleagues to whom I am indebted (see Acknowledgements).

Voucher specimens of all recorded species are in the invertebrate collections at CMNH and the Virginia Museum of Natural History (VMNH). Nomenclature follows Bolton et al. (2007), except for the *Prenolepis* genus-group and for *Tetramorium* which are based on LaPolla et al. (2010) and Ward et al. (2014), respectively.

All species included here can be identified using the taxonomic keys in Coovert (2005), Ellison et al. (2012), and Sarnat et al. (2015). Additionally, representative high resolution photographs of at least the worker's caste of Ohio's non-native species can be found on AntWeb (www.antweb.org), AntWiki (www.antwiki.org) and on Discover Life (www.discoverlife.org).

Results

As a result of the current work three non-native ant species are newly recorded from the state – *Nylanderia flavipes* (first record in Ivanov and Milligan 2008), *Tapinoma melano-cephalum* (Fabricius, 1793) and *Cardiocondyla obscurior* Wheeler, W.M., 1929 bringing the number of known ant exotics in Ohio to ten. New distributional data are added for most of Ohio's non-natives with the exception of *Paratrechina longicornis, Pheidole bilimeki* and *Hypoponera ragusai* which were not encountered during the survey, and have not been collected in Ohio since their original discovery. *Linepithema humile* (the Argentine ant) is confirmed for Ohio (Arnett 1993 was the first one to mention this ant for the state but didn't provide locality information) and now has established indoor colonies in at least one location in northeastern Ohio. *Paratrechina longicornis*, originally reported in 1998 but not present in Coovert (2005), also is included in the Ohio list. Two of the species (*Tapinoma melanocephalum, Cardiocondyla obscurior*) on this list have not previously been reported from Ohio, and as such represent new state records.

Taxa are arranged alphabetically by subfamily, genus and species. Each species name is followed by the taxon's currently known Ohio distribution, habitat, known

area of origin and brief natural history notes. Precise distributional records of these species for North America and elsewhere can be found in Coovert (2005), Bolton et al. (2007), Klotz et al. (2008), Wetterer (2008, 2009, 2010, 2011), Wetterer et al. (2009), Ellison et al. (2012), Guénard et al. (2012), and Sarnat et al. (2015).

Dolichoderinae

Linepithema humile (Mayr, 1868)

The Argentine ant

Distribution in Ohio. Northern Ohio. Counties: **Cuyahoga** (Cleveland, 27.x.2005 [KI 1176], 15.xi.2005 [KI 1177], and 01.iii.2015 [observed, not coll.], same locality, leg. K. Ivanov, in a greenhouse) and an unspecified Ohio record in Arnett (1993), (Fig. 1).

Where found/Habitat. Indoors, in greenhouses and conservatories.

Origin. The Paraná River drainage basin of South America.

Natural history. The Argentine ant is amongst the world's most successful invasive species and is a nuisance everywhere it occurs. It is established primarily in regions with Mediterranean climate where it has been shown to have profound negative impacts on native biota (Suarez et al. 1998; Touyama et al. 2003). Workers of this genus can be identified by their broadly concave clypeus and the peculiar mandibular dentition arranged in a series of small denticles interspersed with larger single teeth. In the Northeast *L. humile* can be separated from the superficially similar *Tapinoma* by the presence of a well-developed petiolar scale and the vertical orientation of the first gastral segment which does not project over the petiole.

This cosmopolitan species often thrives in disturbed habitats with abundant moisture. Nests are most often in soil, but also under cover objects, refuse piles and more rarely under tree bark. The main dietary component is honeydew from hemipterans, although these ants will also take other sweet substances including household food items, and occasionally will feed on insects (Smith 1965).

Throughout its introduced range Argentine ant colonies are polygynous with pronounced unicoloniality (i.e., the formation of large colonies with multiple nests). A key attribute to the ecological success of this species thus is the absence of intraspecific aggression within the large colony (Tsutsui and Case 2001). These characteristics give argentine ant colonies remarkable capacity to expand, and populations can reach extremely large sizes and cover extensive geographic areas to the detriment of other, less populous, species (Giraud et al. 2002).

Ohio's only confirmed record of this species comes from a greenhouse in Cleveland where I have observed large numbers of ground foragers on paved surfaces, exposed soil, and on tropical plant debris on the ground. In many cases foragers were accumulating around sugar syrup stations, banana, apple and other fruit pieces used for feeding tropical butterflies. Due to logistical limitations, I was not able to conduct

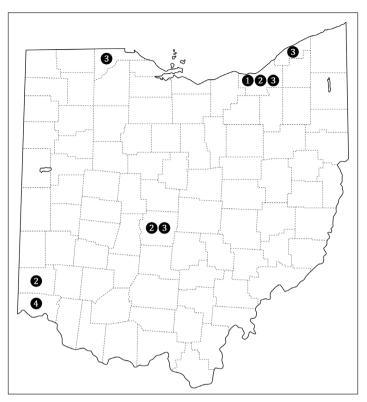


Figure 1. Distribution of L. humile (1), T. melanocephalum (2), N. flavipes (3), and P. longicornis (4) in Ohio.

nest searches at this location. The very high worker densities observed, however, suggest that this species now has well-established indoor colonies at this site. At present, this species can survive in the north only in heated buildings, where occasionally it can be a persistent and troublesome pest.

Tapinoma melanocephalum (Fabricius, 1793)

The ghost ant

Distribution in Ohio. Widespread in Ohio. Counties: **Butler** (material examined: Oxford, Miami University, Belk Greenhouse, 25.ii.2014, leg. S. Mays), **Cuyahoga** (material examined: Cleveland, 07.ii.2008, leg. K. Ivanov, and 04.iii.2008, leg. B. Poynter, same locality, in an animal care zoo facility), and **Franklin** (photographs examined: Columbus 25–29.ii.2008, photos by S. Heideman, in a conservatory), (Fig. 1).

Where found/Habitat. Indoors, abundant in greenhouses, conservatories and zoo buildings.

Origin. Indo-Pacific.



Figure 2. Tapinoma melanocephalum workers from a conservatory in Franklin Co. (Photo: S. Heideman).

Natural history. This widely distributed tramp species is more prevalent in disturbed areas but also has been encountered in natural habitats in its introduced range (Wetterer 2009 and references therein). Unlike many other exotic ants, this species can be distinguished easily by its minute size, peculiar coloration (Fig. 2), and the rapid, erratic movements when disturbed.

Colonies are moderate to large in size, and polygynous, with queens distributed in multiple nests. Additional features characteristic of this ant include unicoloniality, intranidal mating, and colony formation via budding (Bustos and Cherix 1998). Ghost ants are opportunistic nesters, usually in disturbed areas, and frequently relocate their nests (Wetterer 2009). Inside buildings, nests can be found in flowerpots, in small cracks and crevices, beneath baseboards, and in wall spaces (Klotz et al. 2008).

Where it occurs this ant is a major nuisance pest, both indoors and outdoors, that tends mealybugs and scale insects and scavenges for dead insects and food scraps (Smith 1965). The ghost ant is confined to greenhouses and other heated buildings in northerly states, which provide the high temperature and environmental humidity needed for the survival of this tropical species. According to Wetterer (2009), at latitudes greater than 30° this species is largely restricted to living inside buildings.

I have only seen this species at a single animal care facility in the greater Cleveland area where I observed multiple nests in wall spaces and crevices. In addition, numerous foragers were noted near and at reptile feeding stations. In Ohio, this ant is a known conservatory and zoo pest, likely distributed via potted plants or animal feed. Unpublished observations suggest that this ant has been present in the state since at least the early 2000s (B. Poynter and M. Vincent pers. communication).

Formicinae

Nylanderia flavipes (Smith, 1874)

The yellow-footed Nylanderia

Distribution in Ohio. Northern Ohio. Counties: **Cuyahoga** (material examined: Cleveland Heights, 12–14.x.2004 and 22–24.x.2004, leg. H. Clebsch, yellow pan traps in residential area; Cleveland, 19.v.2013 [KI 2319] and 23.iv.2014 [KI 2345], leg. K. Ivanov, in a greenhouse; Cleveland, Case Western Reserve University, main campus, 17.v.2015, leg. A. Perez, pitfall trap, mulch bed adjacent to a concrete path; Shaker Heights, Doan Brook Gorge, multiple records since original discovery in 2005 with last collection event on 06.v.2014 [KI 2346], leg. K. Ivanov, hand collecting, Winkler litter extraction, and baiting in open woodlands; Euclid Creek Reservation, Wildwood Park, 16.ix.2014 [KI 2348], leg. K. Ivanov, open woodland), **Franklin** (Columbus 17.viii.2015, leg. A. Perez, Winkler litter extraction, flower bed adjacent to public library), **Lake** (material examined: Kirtland, multiple records from July and August 2009 and 2010, leg. T. Webster, suburban lawn) and **Lucas** (Uno et al. 2010), (Fig. 1).

Where found/Habitat. This species is abundant in urban and suburban areas including forested green spaces, gardens, yards and vacant lots. It is also found indoors, in conservatories.

Origin. Temperate Asia.

Natural history. This temperate formicine was first reported for Ohio based on material collected at the Doan Brooke Gorge of Shaker Heights in July 2005 (Ivanov and Milligan 2008). Previously unknown material collected via yellow pan traps extends the first known date for Ohio to mid-October 2004 (leg. H. Clebsch). This species has well-established reproducing populations in, at least, northeastern Ohio where I first observed mating leks in July 2005. More recently, colonies containing alate reproductives were collected in May 2014 at the Doan Brook Gorge of Shaker Heights. This species can be relatively easily distinguished by its small size, the presence of paired macrochaetae on the mesosomal dorsum, the indistinct but visible ocelli, and the yellowish color of the antennae, mesosoma and legs.

This is a monogynous species that frequently develops polydomous colonies (Ichinose 1986). While quite common in its native range, this opportunistic species has not been reported as a pest, or as an ecologically dominant species, in its introduced range although data largely are lacking. Observed impacts have been mostly anecdotal and related to the disappearance of the ecologically similar native *Nylanderia faisonensis* (Forel, 1922) along the east coast of the US. New data (Ivanov et al. 2011) seem to contradict earlier views regarding the inconspicuous incorporation of this ant into local ant communities. See Ivanov and Milligan (2008) and Ivanov et al. (2011) for additional ecological data and natural history notes.

In Ohio I have observed and collected this species in a variety of different situations including urban woodlots, residential lawns, flower gardens, on concrete/pavement, as well as inside a greenhouse where I have seen foragers on *Oncidium* flowers. In all outdoor situations nests were in the soil, and were rather small and inconspicuous. Colonies most often were found under small rocks and less frequently under bark and tree limbs on the ground. On few occasions, workers readily came and took tuna in oil placed in open, rather degraded, mesic urban woodlots. *Nylanderia flavipes* maintained high abundance at the baits in the absence of native ants. However, when baits were discovered by native species, *N. flavipes* workers were displaced quickly. Our observations suggest that this species does not engage in aggressive interactions with native ants, and does not recruit to defend food resources.

Paratrechina longicornis (Latreille, 1802)

The longhorn crazy ant

Distribution in Ohio. Southern Ohio. Counties: **Hamilton** (Hedges 1998), (Fig. 1). **Where found/Habitat.** Ohio's single record is from a warehouse in Cincinnati, although this species is undoubtedly more widespread in the state where it should be sought after in heated buildings.

Origin. Southeast Asia or Melanesia.

Natural history. Along with *Monomorium pharaonis* and *Tapinoma melanocephalum*, this is one the most widespread tramp ant species and perhaps the most widespread ant in the world (Wetterer 2008). It is found throughout the Old and the New Worlds where it appears to be a specialist of disturbed and degraded habitats, seemingly absent from undisturbed natural settings. This species can be identified on sight and relatively easily distinguished from other ant species by its erratic movements and the extraordinarily elongated scapes, head, and tibiae.

Longhorn crazy ants are highly adaptable and exhibit pronounced ability to survive even in extremely anthropogenically modified environments including nesting sites with very low humidity (Trager 1984). Nests are usually under cover objects, under dry litter and mulch, in rotten wood, less often in plant cavities, under refuse and debris piles, as well as in wall gaps inside buildings (Smith 1965). Colonies are moderate to large, polygynous, and occupy temporary nests which are highly mobile (Trager 1984). Workers are omnivorous, feeding on live and dead invertebrates, small seeds, fruits, honeydew, and a variety of household food items (Smith 1965).

A contributing factor to the colonizing success of this species is its mode of reproduction with lack of nuptial flights. Wings of queens are removed while still callow. Dealate queens and winged males usually gather around the nest entrance, where mating occurs (Trager 1984). A process known as double cloning allows members of this species to mate with their siblings without exhibiting any of the negative effects associated with inbreeding (Pearcy et al. 2011).

This species is a known household and garden pest across tropical and subtropical areas, where it can also attain a significant agricultural pest status via its symbiotic relationships with sap feeding Hemiptera (Wetterer 2008). It has become established in temperate localities by living in buildings and other man-made structures.

Myrmicinae

Cardiocondyla obscurior Wheeler, W.M., 1929

Distribution in Ohio. Single record from southern Ohio. Counties: **Hamilton** (material examined: Cincinnati, 27-28.vii.2008, leg. R. Gibson and M. Gates, in a conservatory), (Fig. 3).

Where found/Habitat. Indoors, in a conservatory.

Origin. Australasia.

Natural history. This is an Old World genus of small, omnivorous ants that contains several cosmopolitan tramp species (Seifert 2003). Whereas most invasive and pest ants readily make themselves apparent, the presence of these minute ants in a given area often can remain undetected. *Cardiocondyla obscurior* is a species with wellknown dispersal ability that has established populations in many parts of the world (Heinze et al. 2006). Individuals are readily distinguished by their swollen, heartshaped postpetiole and the lack of erect hairs on the body (Fig. 4).

This is a species with arboreal nesting habits and its small colonies (usually <500 individuals) are typically located in nest cavities on low (2–5m) vegetation, or in folded leaves above ground. Similar to many other ants with small colonies, workers of this species do not defend foraging areas or food resources thus colonies can reach very high densities (Heinze et al. 2006). The members of this genus are ecologically subordinate and avoid competition with larger and more aggressive ants. As such they are among the few ants that can coexist with known invasives such as the Argentine ant (Carpintero et al. 2004).

It appears that colonies of all tramp *Cardiocondyla* species are polygynous and new colonies are formed via budding (Seifert 2003). In at least *Cardiocondyla obscurior*, enhanced propagation rates have been attributed to this species' ability to develop complete and fully functional colonies from very small colony fragments (Heinze et al. 2006). Given the small size of both workers and colonies of this species, such fragments can be easily transported to new localities in small samples of soil or plant material. Unusual among ants, species of this genus have long-lived ergatoid males (in addition to winged males) which usually stay and mate in their natal nests (intranidal mating) resulting in rigorous competition for virgin queens even among closely related males (Seifert 2003).

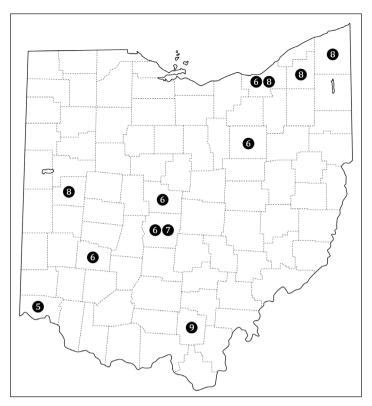


Figure 3. Distribution of *C. obscurior* (5), *M. pharaonis* (6), *P. bilimeki* (7), *T. atratulum* (8), and *H. ragusai* (9) in Ohio.

Due to their small colony size, and the fact that workers forage mostly solitary, members of *Cardiocondyla* are generally not considered pest species (Heinze et al. 2006). This tropical tramp species can survive in Ohio only in heated buildings.

Monomorium pharaonis (Linnaeus, 1758)

The pharaoh ant

Distribution in Ohio. Widespread in Ohio. Counties: **Cuyahoga** (material examined: Cleveland, iii.2007, leg. J.B. Keiper, inside a building, CMNH; also in Headley 1943), **Delaware, Franklin** (M.R. Smith material in the Ohio State University collection; in Wetterer 2010), **Greene** and **Wayne** (see Coovert 2005 and references therein for all listed counties), (Fig. 3).

Where found/Habitat. Indoors, in heated buildings.

Origin. Asia.

Natural history. The pharaoh ant is arguably one of the world's most widespread house-infesting ants and there is a large body of literature on the pest status of this spe-



Figure 4. Lateral view of *Cardiocondyla obscurior* worker (www.antweb.org, specimen CASENT0103429, photo: A. Nobile).

cies. According to Wetterer (2010) this ant is by far the most common species encountered indoors in both North America and in Europe. In tropical and subtropical regions it occurs both indoors and in natural settings, although it is rarely collected outdoors in most parts of the world (Wetterer 2010). Members of the genus *Monomorium* can be identified by their minute size, 12 segmented antennae with a three segmented club, and the dorsally smooth unarmed propodeum. Workers of *Monomorium pharaonis* can be separated from other *Monomorium* species by the densely punctate head and thorax, the yellowish body color, and the often infuscated posterior portion of the gaster.

Like other tramp species *Monomorium pharaonis* possesses features that facilitate its transport and establishment including highly polygynous and extensively polydomous colonies with little intercolony aggression (Passera 1994). A major contributing factor to the invasiveness of this ant is the formation of daughter colonies via fragmentation of the main nest. Newly formed nests remain in contact with the natal nest and may continue to exchange individuals after budding (Buczkowski and Bennett 2009). This results in large polydomous colonies that can quickly monopolize available resources. Inside buildings pharaoh ants breed continuously throughout the year. Mating occurs in the nest and no mating flights have been observed in this species (Passera 1994). In temperate areas nests are located exclusively inside buildings including wall spaces and foundations, under floors, in potted plants, around household items and in furniture. Workers are omnivorous and form pronounced foraging trails. They scavenge for both dead and live insects, as well as household food items, often exhibiting marked fondness for fats and meats (Smith 1965, Collingwood 1979).

In northern temperate regions, this small ant is highly synanthropic and depends on humans for food and shelter (Buczkowski and Bennett 2009). In Ohio, it is known only from people's homes and other heated buildings. In hospitals, this species can be a major nuisance and a serious health threat due to its ability to spread pathogenic bacteria onto sterile equipment and supplies (Beatson 1972).

Pheidole bilimeki Mayr, 1870

Distribution in Ohio. Single record from south-central Ohio. Counties: **Franklin** (Coovert 2005), (Fig. 3).

Where found/Habitat. Indoors. The single Ohio record was discovered in a greenhouse in Franklin Co.

Origin. Neotropics.

Natural history. This is a synanthropic species with pronounced tolerance to disturbed habitats.

Longino and Cox (2009) and Sarnat et al. (2015) provide the most relevant and up to date treatment of this species and its close relatives. This species can be easily confused with members of the *Pheidole punctatissima* clade (*P. anastasii* Emery, 1896; *P. punctatissima* Mayr, 1870) as well as with members of the *Pheidole flavens* complex (Economo et al. 2015; Sarnat et al. 2015). In the southeastern United States, where outdoor colonies of this species can be found, it has often been misidentified as *Pheidole floridana* Emery, 1895. According to Sarnat et al. (2015), the latter often results from the misapplication of the name *P. floridana* to collections of North American *P. bilimeki*. Identification of this species is difficult but the following characteristics may be useful in separating it from other closely related species: antennal scapes relatively short, head margin somewhat flattened posteriorly, anterior half of first gastral tergite foveolate and opaque, body color brown and only occasionally yellow-brown. In addition, it can be separated from the closely related *P. anastasii* by its preference for open, disturbed habitats (see Longino and Cox 2009; Sarnat et al. 2015 for additional information).

According to Longino and Cox (2009), this is an abundant species of open areas regularly found in recently, or frequently, disturbed habitats in its native range. Although it is often associated with anthropogenically altered areas and can be common along roadsides, it is also an abundant house pest. This ant is highly adaptable in its nest site preferences with nests located in dead rotten wood (including fence posts) and under stones. In Costa Rica Longino and Cox (2009) have observed this species in a variety of forested lowland and montane habitats. According to Wilson (2003; as *Pheidole floridana*) this species nests in soil, leaf-litter, and rotten wood in both xeric and mesic woodland habitats with colonies being monogynous and sometimes polydomous. In his account of the biology of *Pheidole bilimeki* (as *Pheidole anastasii*) in Florida Naves (1985) reports that this ant most often nests under the bark at the base, or along the roots, of pines, and only rarely in the soil. The observed colonies

were monogynous and contained 600 workers. Naves (1985) also reports that *P. bilimeki* feeds on seeds, fruits, dead insects, and also preys on small live arthropods.

This species has a history of human-mediated dispersal, which is not surprising given its abundance and synanthropic habitat preferences. In northern regions, both in North America and in Europe, this species occasionally is found in greenhouses, and other heated buildings (Sarnat et al. 2015).

Tetramorium atratulum (Schenck, 1852)

Distribution in Ohio. Records from western and northeastern Ohio. Counties: **Ashtabula** (material examined: North Kingsville Sand Barrens, 20.vii.–11.viii.2007, leg. T. Pucci., Malaise trap, CMNH); **Cuyahoga** (material examined: Cleveland, Cleveland State University, main campus, 10.v.2007 [KI 1730], leg. K. Ivanov), **Geauga** (material examined: Observatory Park, 20.viii.2010, leg. E. Neff, CMNH), and **Shelby** (Coovert 2005 as *Anergates atratulus* (Schenck, 1852)), (Fig. 3).

Where found/Habitat. Along with host *Tetramorium caespitum* (see habitat description below).

Origin. Europe.

Natural history. This workerless inquiline social parasite is rarely observed and collected in both its native and introduced ranges, presumably because of its parasitic lifestyle or simply because it is indeed rare. This species' known distribution includes Europe and North America broadly following that of its host *Tetramorium caespitum*. In North America it is mostly found in the eastern part of the continent (Dash and Sanchez 2009). The pupoid wingless males are found only inside the host nests while the queens can be easily recognized by their small size and the unique, conspicuous median longitudinal depression on the dorsal surface of the gaster (Fisher and Cover 2007).

Colonies consist of males and females that live with their hosts on which they rely for work and food. Unlike many other obligate social parasites, queens of this species are adopted by queen-less host colonies (Buschinger 2009). As such every parasitized colony has a limited lifespan determined by the lifespan of the youngest host members present. See Wheeler (1908) and Francoeur and Pilon (2011) for excellent natural history notes and images.

My only encounter with this species in Ohio was in downtown Cleveland in early May 2007 when my attention was attracted by a single dealate queen which was swiftly running on the soil surface exploring exposed entrances to what later turned out to be *Tetramorium* cf. *caespitum* colonies. I was unable to observe any interactions between the two species in the short period of time before I collected the specimen. The location where this observation occurred is urban and heavily dominated by impervious surfaces, including pavement and mowed grass, interspersed with a multitude of non-native flowering plants and few scattered crab apples (*Malus* sp.), serviceberries (*Amelanchier* sp.), and tulip trees (*Liriodendron tulipifera* L.).

Tetramorium cf. *caespitum* (Linnaeus, 1758), (*Tetramorium* sp. E of Schlick-Steiner et al. 2006)

The pavement ant

Distribution in Ohio. Statewide in Ohio. Counties: Listed for 74 of Ohio's 88 counties in Coovert (2005); **Geauga** (material examined: multiple records from well-separated localities within the county [KI 1206, 1219, 1261, 1281, 1322, 1351, 1356, 1375, 1411, 1427, 1454, 1509, 1601, 1986], leg. K. Ivanov)

Where found/Habitat. Along roadsides, in cracks in driveways, pavement and roads, under rocks and logs in open woodlands and wood edges, in grassy fields and many disturbed areas. Also in gardens, lawns and inside residences.

Origin. Europe.

Natural history. A temperate species commonly found in urban habitats and adjacent natural settings in Ohio. *Tetramorium* cf. *caespitum* has been continuously documented in the state since its first discovery and undoubtedly occurs in all of Ohio's counties. In North America this species has been reported as an agricultural pest, and shown to expand into natural habitats where it displaces native ants (Steiner et al. 2008 and references therein). Despite its wide ranging distribution it is relatively unstudied especially in its native habitats. This is a dark brown to black ant that can be identified by its 12 segmented antennae, the lateral portion of the clypeus which is raised into a sharp ridge anterior to the antennal insertion, the presence of abundant unbranched hairs on the mesosomal dorsum, and the regular longitudinal rugulation on the head behind the eyes. The East Asian *Tetramorium tshushimae* Emery, 1925 (known from Missouri and Illinois; Steiner et al. 2006) is smaller and typically has light colored individuals in addition to dark ones.

Pavement ant colonies are large to very large and usually monogynous. Nests are initiated by a single reproductive queen that carries out reproduction for the lifespan of the colony. In North America nuptial flights most commonly occur in mid-summer and generally one sex predominates in the reproductives produced by a particular colony (Bruder and Gupta 1972). In spring, large-scale battles between workers from unrelated colonies commonly can be observed when pavement ants are developing their territories (Ellison et al. 2012). This is an omnivorous species whose diet includes live and dead animal matter, seeds, plant exudates, occasional honeydew gathering, and kitchen food items (Smith 1965). Although common in outdoor situations this species is also an abundant indoor pest in parts of eastern North America (Klotz et al. 2008).

I have observed this species in every Ohio County in which I have had the opportunity to collect material. This is undoubtedly one of the most common ants I have encountered in the state although it is largely restricted to human-modified environments where workers are nearly ubiquitous on paved surfaces, near and inside buildings and in open grass situations (including mowed lawns). I have rarely encountered this ant in natural, relatively undisturbed, settings in Ohio. Nearly all colonies I have seen were located in open situations usually under some type of cover object, most commonly large rocks, or at the bases of grasses. Notable exceptions include two rather large colonies from northeastern Ohio, the first of which [KI 1375] was found in a naturalized open grass field at Eldon Russel Park in Geauga County and comprised a large, de-vegetated, soil mound akin to those of young *Formica exsectoides* Forel, 1886 colonies. The second colony [KI 2332] was found inside a very large rotten stump in the park manager's service area of Acacia Reservation in Cuyahoga County.

Ponerinae

Hypoponera ragusai (Emery, 1894)

Distribution in Ohio. Southern Ohio. Counties: **Jackson** (Wesson and Wesson 1940, as *Ponera oblongiceps* Smith, M.R., 1939), (Fig. 3).

Where found/Habitat. The following quote from Wesson and Wesson (1940) summarizes all the information we have for the single record of this species in Ohio - "A few workers of this species were found under a stone in partial shade, on moist but well drained soil, in Jackson."

Origin. Old World, with assumed African origin. The current confirmed distribution includes Europe, Africa and India (Bolton and Fisher 2011).

Natural history. The genus *Hypoponera* includes small cryptic ants with global distribution, although the highest diversity of the group occurs in the tropics. *Hypoponera ragusai* is a species with known tramping ability widespread in most parts of the world (Bolton and Fisher 2011). This species can be easily separated from most other North American *Hypoponera* by its smooth and shiny mesopleuron which lack punctures; and from the closely related *Hypoponera punctatissima* (Roger, 1859) by its smaller body size, and the lower and relatively longer petiolar node.

The success of this ant as a tramp species is attributed to the presence of unusual ergatoid males which remain in their natal nest where they mate with virgin queens (Taylor 1967). These ants are predators of small soil arthropods with nests usually located in soil, leaf-litter or rotting wood (Fisher and Cover 2007). This species was also found nesting under rocks and guano deposits inside caves in the Iberian Peninsula (Tinaut 2001). Workers of this relatively nondescript small ant are rarely collected due to their subterranean habits.

This species often has been refferred to as *Hypoponera gleadowi* (Emery, 1895) in the literature (including Coovert 2005), and often has been misidentified as the closely related *Hypoponera punctatissima* (Bolton and Fisher 2011). It is likely that this species shares natural history with *H. punctatissima*, which is often found in association with disturbed habitats, in addition to buildings in colder climates. Generally neither *Hypoponera ragusai*, or any of its synonyms, have been reported as nuisance species in their introduced ranges.

Discussion

Biological invasions by plants and animals are an ever increasing problem for global biodiversity and ants are no exception. Many ant species have been transported to new locations with often profound negative impacts on local biota (e.g., *Linepithema humile, Solenopsis invicta* Buren, 1972). The collection of precise distributional records is the first, fundamental, step in establishing the extent of the current spread of these species. Such data are critical if we are to better understand the factors that govern the spread and establishment of these exotics and their potential to disturb native ecosystems.

In general, the majority of the world's known established non-native ants come from tropical and subtropical areas and the spread of temperate ant exotics is rather limited (Sarnat et al. 2016). The exotic ant fauna of virtually all northern US states and Canadian provinces is depauperate and relatively few non-native species occur in this region, especially those capable of living outdoors. Patterns observed in Ohio are consistent with this general trend as the state's climate and weather conditions offer little opportunity for the establishment of exotic ants. The rather poor representation of non-native ants in more northern latitudes likely is a result of the fact that ants as a group have their greatest diversity in tropical and subtropical areas. As a result, the pool of species which can be transferred and become established in temperate regions is much smaller as compared to that of tropical and subtropical areas. In addition, ecological reasons such as more aggressive competition from native species of similar ecological function, and reduced variability in nesting ecology in temperate conditions may be as important in determining the establishment of exotic ant species in higher latitudes.

As a result of the current work three ant exotics are added to the state's species list (but see *Paratrechina longicornis* comments above) thus increasing the number of known ant taxa in Ohio to 135 (Ivanov 2016). At present, the exotic ant fauna of Ohio comprises 10 species from 9 genera, and 4 of the 7 subfamilies known to occur in the state (Table 1). Ohio's exotic ant fauna contains 4 of the 19 ant species currently listed on the Global Invasive Species Database (*Linepithema. humile*, *Paratrechina longicornis*, *Monomorium pharaonis*, and *Tapinoma melanocephalum*; ISSG 2016). The presence of major nuisance pests and notorious invaders in the state leaves no doubt regarding their economic impact on the pest control industry and the general public. However, most of Ohio's non-native species probably have little ecological impact (but see *Nylanderia flavipes* comments below) due to their current confinement to man-made structures.

Two rather distinct groups of ant exotics with somewhat dissimilar geographic origin occur in Ohio. The first group comprises species of temperate Eurasian origin (*Nylanderia flavipes, Tetramorium* cf. *caespitum*, and *Tetramorium atratulum*) that have established outdoor populations in the state. The first two of these species were found to be common inhabitants of street medians in New York City by Pećarević et al. (2010). The ecology of *T. caespitum* has received relatively little attention, despite its wide-ranging distribution outside of its native range. This is likely due to its propensity

Species	First record (year, source)	Last record (year, source)	# localities	Where found
Dolichoderinae				
Linepithema humile (Mayr)	1993, Arnett	2015, this study	1	Indoors only
Tapinoma melanocephalum (Fabricius)	2008, this study	2014, this study	2–5	Indoors only
Formicinae				
Nylanderia flavipes (Smith)	2004, this study	2015, this study	6–9	Outdoors, occasionally indoors
Paratrechina longicornis (Latreille)	1998, Hedges	1998, Hedges	1	Indoors only
Myrmicinae				
Cardiocondyla obscurior Wheeler	2008, this study	2008, this study	1	Indoors only
Monomorium pharaonis (Linnaeus)	1917, OSU collection	2007, this study	6–9	Indoors only
<i>Pheidole bilimeki</i> Mayr	2005, Coovert	2005, Coovert	1	Indoors only
Tetramorium atratulum (Schenck)	2005, Coovert	2010, this study	2–5	Outdoors
Tetramorium cf. caespitum (Linnaeus)	1940, Wesson and Wesson	2015, this study	>10	Outdoors/ indoors
Ponerinae				
Hypoponera ragusai (Emery)	1940, Wesson and Wesson	1940, Wesson and Wesson	1	Unspecified, likely indoors

Table 1. List of Ohio's exotic ant species.

to nest in highly disturbed and human-modified environments. The second group includes seven tropical tramp species currently confined to man-made structures (Table 1). Not surprisingly the majority of these records in the state come from the major metropolitan areas of Cleveland, Columbus, and Cincinnati (Figs 1 and 3). With the exception of *Tapinoma melanocephalum* and *Monomorium pharaonis*, the remaining five of these species are restricted in their distribution in the state and are known only from a single locality or a single collecting event.

Published accounts suggest that only a handful of temperate species have established outdoor populations in northeastern US. These include: *Brachyponera chinensis* (Emery, 1895), *Formica paralugubris* Seifert, 1996, *Lasius* cf. *niger* (Linnaeus, 1758), *Nylanderia flavipes, Myrmica rubra* (Linnaeus, 1758), *M. scabrinodis* Nylander, 1846, *Tetramorium atratulum, Tetramorium* cf. *caespitum, Tetramorium tsushimae*, and *Vollenhovia emeryi* Wheeler, W.M., 1906 (Deyrup et al. 2000; Ellison et al. 2012; J. Trager pers. communication). The populations of some of these species (*B. chinensis, M. rubra, T. tsushimae*) are expanding and it will not be surprising if any or all of them are found in Ohio in future surveys (Steiner et al. 2006; Wetterer and Radchenko 2011, MacGown 2016). In addition, the tropical invasive red imported fire ant (*Solenopsis invicta*) has been increasing its range northward along the coastal plain of the eastern US and has recently been found as far north as northern Virginia and Maryland (Wetterer 2013). Given predictions for future climate change it is possible that this species will be found farther north in the not so distant future (IPCC 2007).

Tropical and subtropical exotic ants are more widespread and a larger number of species have been reported from more northerly states. However, given physiological restrictions all of these species currently are confined to indoor situations, being unable to survive the cold, harsh winter conditions. Although I do expect that the number of these species in Ohio will increase, it is difficult to predict which of these warmer climate species will turn up in the state. However, given the astonishing amount of personal and commercial transport in the US, it is relatively easy to foresee that we have not yet seen the last members of these exotics in Ohio. It is most likely that the first individuals to arrive in Ohio will be members of some of the most abundant and widespread among the synanthropic species (i.e., Technomyrmex difficilis Forel, 1892, Brachymyrmex patagonicus Mayr, 1868), Nylanderia bourbonica (Forel, 1886), Cardiocondyla emervi Forel, 1881, Monomorium floricola (Jerdon, 1851), M. destructor (Jerdon, 1851), Pheidole anastasii, P. megacephala (Fabricius, 1793), P. moerens Wheeler, W.M., 1908, Tetramorium bicarinatum (Nylander, 1846), Wasmannia auropunctata (Roger, 1863)). Future survey efforts should focus on plant nurseries, botanical gardens, zoo facilities and other heated buildings to document the arrival and establishment of these species.

In eastern US, there is a clear pattern of increasing number of both native and non-native ant species from north to south, with the peak in the number of ant exotics reached in the southeastern US. In total, only 10 of Ohio's ant species are non-native with even a smaller number of these established in the state at present (including indoor and outdoor populations). These records are comparable with the number of ant exotics known from other northerly states, such as Illinois (8 species; Trager and Rericha 2016), Michigan (2; Wheeler et al. 1994), Pennsylvania (5; Butler and Coulter 2016), and New England (14, Ellison et al. 2012). In comparison at least 67 ant exotics are known from the southeastern US (MacGown 2016), with 52 species occurring in the state of Florida alone (approximately 25% of the local fauna; Deyrup et al. 2016).

Ants often are inconspicuous immigrants, and may remain unnoticed until many years after their arrival in an area. This is most likely the case with the recent finding of *Nylanderia flavipes* in Ohio. This species has been present in the eastern US since at least the 1930s when it was first discovered in Philadelphia, PA (Trager 1984). Around the time of its first discovery in Ohio, colonies of this Asian formicine already were well established, abundant and reproducing. Quantitative data from baiting and leaf-litter extraction suggest that this ant is one of the most abundant ant species in the disturbed urban and suburban green spaces where it occurs. Colonies can reach extremely high densities and worker numbers accounted for over 85% of total ant abundance at a site in northeastern Ohio (Ivanov et al. 2011; Ivanov unpubl.). At present, I am unable to confirm if this ant is expanding its range in Ohio or if it has been present in all localities and has remained undetected due to lack of sampling effort in the areas where it occurs. Nonetheless I advocate that efforts should be made to monitor the spread and potential impact of this species in Ohio and elsewhere.

Despite nearly ten years of surveying, I have sampled a rather small portion of the potential habitats in the state and thus many "exotic-ant-friendly" areas remain unexplored. This work is not complete and there is still much to do. A more extensive systematic sampling of disturbed areas, urban and suburban sites, plant nurseries and conservatories would be worthwhile and undoubtedly reveal the presence of yet undiscovered species in Ohio.

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References

- Arnett RH (1993) American insects. A handbook of the insects of America north of Mexico. Sandhill Crane Press, Gainsville, 1–1024.
- Beatson SH (1972) Pharaoh ants as pathogen vectors in hospitals. Lancet 1: 425–427. doi: 10.1016/S0140-6736(72)90869-0
- Bolton B, Fisher B (2011) Taxonomy of Afrotropical and West Palaearctic ants of the ponerine genus *Hypoponera* Santschi (Hymenoptera: Formicidae). Zootaxa 2843: 1–118.
- Bolton B, Alpert G, Ward PS, Naskrecki P (2007) Bolton's catalogue of ants of the world: 1758–2005. Harvard University Press, Cambridge, MA, CD-ROM.
- Bruder KW, Gupta AP (1972) Biology of the pavement ant, *Tetramorium caespitum* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 65: 358–367. doi: 10.1093/aesa/65.2.358
- Buczkowski G, Bennett G (2009) Colony budding and its effects on food allocation in the highly polygynous ant, *Monomorium pharaonis*. Ethology 115: 1091–1099.
- Buschinger A (2004) International pet ant trade, increasing risk and danger in Europe (Hymenoptera, Formicidae). Aliens 19: 24–26.
- Buschinger A (2009) Social parasitism among ants: a review (Hymenoptera: Formicidae). Myrmecological News 12: 219–235.
- Bustos X, Cherix D (1998) Contribution à la biologie de *Tapinoma melanocephalum* (Fabricius) (Hymenoptera, Formicidae). Actes des Colloques Insectes Sociaux 11: 95–101.
- Butler WB, Coulter B (2016) AntWeb: Ants of Pennsylvania. http://www.antweb.org/page. do?name=pennsylvania [retrieved on 31 March 2016]

- Carpintero S, Reyes-López J, Arias de Reyna L (2004) Impact of human dwellings on the distribution of the exotic Argentine ant: a case study in the Doñana National Park, Spain. Biological Conservation 115: 279–289. doi: 10.1016/S0006-3207(03)00147-2
- Collingwood CA (1979) The Formicidae (Hymenoptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 8: 1–174.
- Coovert GA (2005) The ants of Ohio (Hymenoptera: Formicidae). Bulletin of the Ohio Biological Survey 15: 1–202.
- Dash ST, Sanchez L (2009) New distribution record for the social parasitic ant Anergates atratulus (Schenck, 1852) (Hymenoptera: Formicidae): An IUCN Red-Listed Species. Western North American Naturalist 69: 140–141. doi: 10.3398/064.069.0109
- Deyrup P, Davis L, Cover S (2000) Exotic Ants in Florida. Transactions of the American Entomological Society 126: 293–326.
- Deyrup P, Prusak Z, Davis L (2016) AntWeb: Ants of Florida. http://www.antweb.org/page. do?name=florida [retrieved on 31 March 2016]
- Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology and Evolution 22: 489–496. doi: 10.1016/j.tree.2007.07.001
- Economo EP, Klimov P, Sarnat EM, Gúenard B, Weiser MD, Lecroq B, Knowles LL (2015) Global phylogenetic structure of the hyperdiverse ant genus *Pheidole* reveals repeated evolution of macroecological patterns. Proceedings of the Royal Society of London B 282: 1–10.
- Ellison AM, Gotelli NJ, Farnsworth EJ, Alpert GD (2012) A field guide to the ants of New England. Yale University Press, 1–256.
- Fisher BL, Cover SP (2007) Ants of North America: a guide to genera. University of California Press, Berkeley, 1–216.
- Francoeur A, Pilon C (2011) Découverte au Québec de la fourmi parasite *Anergates atratulus* (Formicdae, Hymenoptera). Le Naturaliste Canadien 135: 30–33.
- Giraud T, Pedersen JS, Keller L (2002) Evolution of supercolonies: the Argentine ants of southern Europe. Proceedings of the National Academy of Sciences 99: 6075–6079. doi: 10.1073/pnas.092694199
- Gúenard B, Maccaffrey KA, Lucky A, Dunn RB (2012) Ants of North Carolina: an updated list (Hymenoptera: Formicidae). Zootaxa 3552: 1–36.
- Headley AE (1943) The Ants of Ashtabula County, Ohio (Hymenoptera, Formicidae). The Ohio Journal of Science 43: 22–31.
- Hedges SA (1998) Field guide for the management of structure-infesting ants. 2nd ed. GIE Incorporated, Cleveland, 1–304.
- Heinze J, Cremer S, Eckl N, Schrempf A (2006) Stealthy invaders: the biology of *Cardiocondyla* tramp ants. Insectes Sociaux 53: 1–7. doi: 10.1007/s00040-005-0847-4
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. Annual Review of Ecology, Evolution, and Systematics 33: 181–233. doi: 10.1146/annurev.ecolsys.33.010802.150444
- Ichinose K (1986) Occurrence of polydomy in a monogynous ant, *Paratrechina flavipes* (Hymenoptera, Formicidae). Konty 54: 208–217.

- IPCC (2007) Fourth Assessment Report: Climate Change 2007. https://www.ipcc.ch/publications_and_data/ar4/wg1/en/spmsspm-projections-of.html [retrieved on 21 April 2016]
- ISSG (2015) Global Invasive Species Database: 100 of the World's Worst Invasive Alien species. http://www.issg.org/database/species/search.asp?st=100ss [retrieved on November 16 2015]
- ISSG (2016) Global Invasive Species Database: Formicidae. http://www.issg.org/database/ species/search.asp?sts=tssandst=tssandfr=1andx=23andy=13andli=5andtn=formicidae [retrieved on 1 April 2016]
- Ivanov K (2016) AntWeb: Ants of Ohio. http://www.antweb.org/page.do?name=ohio [retrieved on 21 April 2016]
- Ivanov K, Milligan J (2008) Paratrechina flavipes (Smith) (Hymenoptera: Formicidae), a new exotic ant for Ohio. Proceedings of the Entomological Society of Washington 110: 439–444. doi: 10.4289/07-046.1
- Ivanov K, Lockhart OM, Keiper J, Walton BM (2011) Status of the exotic ant Nylanderia flavipes (Hymenoptera: Formicidae) in northeastern Ohio. Biological Invasions 13: 1945–1950. doi: 10.1007/s10530-011-0021-z
- Klotz JH, Hansen L, Pospischil R, Rust M (2008) Urban ants of North America and Europe: identification, biology, and management. Cornell University Press, Ithaca, 1–196.
- Krushelnycky P (2015) AntWeb: Ants of Hawaii. http://www.antweb.org/page.do?name=hawaii [retrieved on 11 November 2015]
- LaPolla JS, Brady SG, Shattuck SO (2010) Phylogeny and taxonomy of the *Prenolepis* genusgroup of ants (Hymenoptera: Formicidae). Systematic Entomology 35: 118–131. doi: 10.1111/j.1365-3113.2009.00492.x
- Longino JT, Cox DJ (2009) *Pheidole bilimeki* reconsidered (Hymenoptera: Formicidae). Zootaxa 1985: 34–42.
- MacGown JA (2016) Exotic ants of the southeastern US. http://mississippientomologicalmuseum.org.msstate.edu/Researchtaxapages/Formicidaepages/faunal.lists/SE.exotics.htm#. Vv64TeIrLct [retrieved on 01 April 2016]
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences and control. Ecological Applications 10: 689–710. doi: 10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2
- Mooney HA, Hobbs RJ (2000) Invasive species in a changing world. Island Press, Washington, 1–457.
- Naves AA (1985) A monograph of the genus *Pheidole* in Florida, USA (Hymenoptera: Formicidae). Insecta Mundi 1: 53–90.
- Passera L (1994) Characteristics of tramp species. In: Williams DF (Ed.) Exotic ants: biology, impact, and control of introduced species. Westview Press, Boulder, 23–24.
- Pearcy M, Goodisman MAD, Keller L (2011) Sib mating without inbreeding in the longhorn crazy ant. Proceedings of the Royal Society B 278: 2677–2681. doi: 10.1098/ rspb.2010.2562
- Pećarević M, Danoff-Burg J, Dunn RR (2010) Biodiversity on Broadway enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. PLoS ONE 5: 1–8. doi: 10.1371/journal.pone.0013222

- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273–288. doi: 10.1016/j.ecolecon.2004.10.002
- Sarnat EM, Fischer G, Gúenard B, Economo EP (2015) Introduced *Pheidole* of the world: taxonomy, biology and distribution. ZooKeys 543: 1–109. doi: 10.3897/zookeys.543.6050
- Sarnat EM, Suarez A, Fisher B (2016) AntWeb: Ants of Introduced. http://www.antweb.org/ page.do?name=introduced [retrieved on 31 March 2016]
- Schlick-Steiner BC, Steiner FM, Moder K, Seifert B, Sanetra M, Dyreson E, Stauffer C, Christian E (2006) A multidisciplinary approach reveals cryptic diversity in Western Palearctic *Tetramorium* ants (Hymenoptera: Formicidae). Molecular Phylogenetics and Evolution 40: 259–273. doi: 10.1016/j.ympev.2006.03.005
- Seifert B (2003) The ant genus Cardiocondyla (Insecta: Hymenoptera: Formicidae) a taxonomic revision of the C. elegans, C. bulgarica, C. batesi, C. nuda, C. shuckardi, C. stambulofii, C. wroughtonii, C. emeryi, and C. munitior species groups. Annalen des Naturhistorischen Museums in Wien. Serie B. Botonik und Zoologie 104: 203–338.
- Smith MR (1965) House-infesting ants of the eastern United States; their recognition, biology, and economic importance. USDA Technical Bulletin 1326: 1–105.
- Steiner FM, Schlick-Steiner BC, Trager JC, Moder K, Sanetra M, Christian E, Stauffler C (2006) *Tetramorium tsushimae*, a new invasive ant in North America. Biological Invasions 8: 117–123. doi: 10.1007/s10530-004-1249-7
- Steiner FM, Schlick-Steiner BC, VanDerWal J, Reuther KD, Christian E, Stauffer C, Crozier RH (2008) Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. Diversity and Distributions 14: 538–545. doi: 10.1111/j.1472-4642.2008.00472.x
- Suarez AV, Bolger DT, Case TJ (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79: 2041–2056. doi: 10.1890/0012-9658(1998)079[2041:EOFAIO]2.0.CO;2
- Taylor RW (1967) A monographic revision of the ant genus *Ponera* Latreille (Hymenoptera: Formicidae). Pacific Insects Monographs 13: 1–112.
- Tinaut A (2001) Hypoponera ragusai (Emery, 1895) A cevrnicolous ant new for the Iberian Peninsula (Hymenoptera, Formicidae). Graellsia 57: 3–8. doi: 10.3989/graellsia.2001. v57.i1.290
- Touyama Y, Ogata K, Sugiyama T (2003) The Argentine ant, *Linepithema humile*, in Japan: Assessment of impact on species diversity of ant communities in urban environments. Entomological Science 6: 57–62. doi: 10.1046/j.1343-8786.2003.00008.x
- Trager JC (1984) A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the continental United States. Sociobiology 9: 51–162.
- Trager JC, Rericha L (2016) AntWeb: Ants of Illinois. http://www.antweb.org/page. do?name=illinois [retrieved on 1 April 2016]
- Tsutsui ND, Case TJ (2001) Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. Evolution 55: 976–985. doi: 10.1554/0014-3820(2001)055[0976:PGACSO]2.0.CO;2

- Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in urban green spaces. Urban Ecosystems 13: 425–441. doi: 10.1007/s11252-010-0136-5
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. Science 277: 494–499. doi: 10.1126/science.277.5325.494
- Ward PS, Brady SG, Fisher BL, Schultz TR (2014) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Systematic Entomology 40: 61–81. doi: 10.1111/syen.12090
- Wesson LG, Wesson RG (1940) A collection of ants from southcentral Ohio. The American Midland Naturalist 24: 89–103. doi: 10.2307/2421055
- Wetterer JK (2008) Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). Myrmecological News 11: 137–149.
- Wetterer JK (2009) Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hyme-noptera: Formicidae). Myrmecological News: 12: 23–33.
- Wetterer JK (2010) Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae). Myrmecological News 13: 115–129.
- Wetterer JK (2011) Worldwide spread of the yellow-footed ant, *Nylanderia flavipes* (Hymenoptera: Formicidae). Florida Entomologist 94: 582–587. doi: 10.1653/024.094.0323
- Wetterer JK (2013) Exotic spread of *Solenopsis invicta* Buren (Hymenoptera: Formicidae) beyond North America. Sociobiology 60: 50–55. doi: 10.13102/sociobiology.v60i1.50-55
- Wetterer JK, Radchenko AG (2011) Worldwide spread of the ruby ant, *Myrmica rubra* (Hymenoptera: Formicidae). Myrmecological News 14: 87–96.
- Wetterer JK, Wild AL, Suarez AV, Roura-Pascual N, Espadaler X (2009) Worldwide spread of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). Myrmecological News 12: 187–194.
- Wheeler GC, Wheeler JN, Kannowski PB (1994) Checklist of the ants of Michigan (Hymenoptera: Formicidae). The Great Lakes Entomologist 26: 297–310.
- Wheeler WM (1908) Comparative ethology of the European and North American ants. Journal f
 ür Psychologie und Neurologie 13: 404–435.
- Wild A (2011) "World of Ants" store sells extreme pest insects. http://www.myrmecos. net/2011/11/19/world-of-ants-store-sells-extreme-pest-insects/ [retrieved on 21 April 2016]
- Wilson EO (2003) *Pheidole* of the New World: A dominant, hyperdiverse ant genus. Harvard University Press, Cambridge, 1–794.
- Wittenborn D, Jeschke J (2011) Characteristics of exotic ants in North America. ZooKeys 10: 47–64.