

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

James K. Wetterer

Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive, Jupiter, FL 33458.

(e-mail: wetterer@fau.edu)

Abstract

I have compiled a list of 42 "cosmopolitan" ant species, i.e., ants with multiple well-established populations in both the Old World and New World, spread through human commerce. Twenty of the 42 cosmopolitan ant species have established populations in all seven of the world's ant-inhabited biogeographic regions (i.e., all except the Antarctic): Afrotropic, Palearctic, Indomalay, Australasia, Oceania, Nearctic and Neotropic. Of the 42 cosmopolitan ant species, 35 (83%) are Old World natives and seven (17%) are New World natives. Cosmopolitan ant species are most often originally native to the Indomalay bioregion (17 species) and are least often native to the Nearctic bioregion (only one species). Only twelve cosmopolitan ants have become major ecological, agricultural, and/or household pest species: *Anoplolepis gracilipes*, *Linepithema humile*, *Monomorium pharaonis*, *Nylanderia bourbonica*, *Paratrechina longicornis*, *Pheidole megacephala*, *Solenopsis geminata*, *Solenopsis invicta*, *Tapinoma melanocephalum*, *Technomyrmex difficilis*, *Trichomyrmex destructor*, and *Wasmannia auropunctata*. The other 30 species are, at most, minor pests. Documenting the exotic spread of ant species within their own native hemisphere will be more complicated because it is often difficult to evaluate what geographic area constitutes the native range and what area, if any, constitutes the exotic range.

Key words: *ants, exotic species, invasive species.*

Received: 7 February 2015; Revised: 28 May 2015; Online: 2 July 2015.

Introduction

Numerous tramp ant species have been transported around the world, hidden in our plant products, packaging material, building supplies, and heavy machinery such as logging and military equipment. Some of these ant species have had great population explosions in areas they have invaded, causing serious ecological and economic problems. Other species have remained rare and/or inconspicuous and have had no discernable impact.

Forel (1911) compiled a list of ant species, spread by humans, which had achieved or were in the process of achieving broad cosmopolitan distributions in both the Old World and the New World (Table 1). Eight of these species are now global pests: *Anoplolepis gracilipes* (Smith, 1857), *Linepithema humile* (Mayr, 1868), *Monomorium pharaonis* (Linnaeus, 1758), *Paratrechina longicornis* (Latreille, 1802), *Pheidole megacephala* (Fabricius, 1793), *Solenopsis geminata* (Fabricius, 1804), *Tapinoma melanocephalum*

(Fabricius, 1793), and *Trichomyrmex destructor* (Jerdon, 1851). Five others are widespread, but have not developed into major pests, with substantial ecological and/or economic impacts (see below): *Cardiocondyla emeryi* Forel, 1881, *Monomorium floricola* (Jerdon, 1851), *Tetramorium bicarinatum* (Nylander, 1846), *Tetramorium lanuginosum* Mayr, 1870, and *Tetramorium simillimum* (Smith, 1851), though in Forel's time, *Tetramorium "simillimum"* also encompassed a second distinct tramp species, *Tetramorium caldarium* (Roger, 1857). The last two species on Forel's list, *Nylanderia vividula* (Nylander, 1846) and *Odontomachus haematodus* (Linnaeus, 1758), may not be cosmopolitan tramps at all. Instead, in Forel's time these two names, each represented what are now recognized as several species with different regional ranges and whose taxonomic boundaries remain uncertain. After dropping *N. vividula* and *O. haematodus*, and adding *T. caldarium* to Forel's (1911) list, a striking trend

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

emerges: only two of these 14 cosmopolitan species are native to the New World: *L. humile* and *S. geminata* (Table 1).

Over the past century, many additional ant species, not on Forel's list, have achieved cosmopolitan distributions, with broad ranges in both the Old World and New World. In the present study, I evaluate the worldwide distribution of all ant species reported to have established populations outside their native hemisphere.

Methods

I compiled both published and unpublished site records for all ant species that have been reported as having exotic populations. I obtained unpublished site records from museum specimens in the collections of Archbold Biological Station, the Museum of Comparative Zoology, the Smithsonian Institution, and (for Forel's (1911) cosmopolitan species) the British Museum. In addition, I used online databases with collection information on specimens by Antweb (www.antweb.org), and the Global Biodiversity Information Facility (www.gbif.org). I also received unpublished collection information from numerous other researchers.

For analyzing the worldwide distributions of the ants, I categorized each site record as belonging to one of seven terrestrial biogeographic realms (following Olson *et al.*, 2001; Old World = bioregions 1-5; New World = bioregions 6-7): 1) The Afrotropic bioregion (22.1 million km²) includes sub-Saharan Africa, the southern and eastern coasts of the Arabian Peninsula, southern Iran, southwestern Pakistan, Madagascar, western Indian Ocean islands, Cape Verde, and southern mid-Atlantic islands. 2) The Palearctic bioregion (54.1 million km²) includes Europe, northern Africa, Canary Islands, Madeira, northern and central Arabian Peninsula, and Asia north of the Himalayas, and the main islands of Japan. 3) The Indomalay bioregion (7.5 million km²) includes southeastern Pakistan, the Indian subcontinent, Southeast Asia, southern China, Philippines, Taiwan, and Japan's Ryukyu Islands, and Indonesia west of Wallace's line. 4) The Australasia bioregion (7.6 million km²) includes Australia, New Guinea, Indonesia east of

Wallace's Line, Vanuatu, Solomon Islands, New Caledonia, and New Zealand. 5) The Oceania bioregion (1.0 million km²) includes the Pacific islands of Fiji, Micronesia, and Polynesia (except New Zealand). 6) The Nearctic bioregion (22.9 million km²) includes North America south to the Mexico highlands (except southern Florida), Bermuda, and Greenland. 7) The Neotropic bioregion (19.0 million km²) includes South and Central America, south and central Mexican lowlands, Caribbean islands, southern Florida, and the Bahamas.

When an ant species occurs in both the Old World and the New World, it is almost always clear that one of these ranges is entirely exotic. Within a hemisphere, however, it is often much more difficult to evaluate what geographic area constitutes the native range and what area, in any, constitutes the exotic range. For this reason, when an ant has a fairly continuous distribution in its native hemisphere and I have no evidence to the contrary, I designated the entire continuous distribution as part of the native range, and listed the entire bioregion as native (Tables 1-4).

I defined a cosmopolitan ant as an ant species, with multiple well-established outdoor populations, outside their native hemisphere, spread through human commerce. Although in the tables I included indoor records for species with broad exotic ranges, I did not include species with records outside their native hemisphere known solely from indoors. I also have not included several ant taxa, with reports of spread outside their native hemisphere, whose worldwide status remains unclear due to taxonomic problems analogous to those of *N. vividula* and *O. haematodus* (see Introduction), and may represent multiple species, e.g., *Brachymyrmex cordemoyi* Forel, 1895, *Brachymyrmex obscurior* Forel, 1893, *Camponotus herculeanus* (Linnaeus, 1758), *Lasius alienus* (Foerster, 1850), *Lasius flavus* (Fabricius, 1782), *Lasius niger* (Linnaeus, 1758), *Monomorium monomorium* Bolton, 1987, *Nylanderia vaga* (Forel, 1901), *Ochetellus glaber* (Mayr, 1862), and *Tetramorium caespitum* (Linnaeus, 1758). I have also omitted several species whose extra-hemispheric records are all dubious, e.g., *Pheidole anastasioi cellarum*

Forel, 1908 (= *Pheidole bilimeki* Mayr, 1870) (see Fischer and Fisher, 2013).

Results

My analyses distinguished 60 ant species with outdoor populations established outside their native range hemisphere (Tables 1-4). Of these, 42 species qualified as cosmopolitan, i.e., with multiple well-established outdoors populations outside their native hemisphere (Tables 1-3). Twenty of the 42 cosmopolitan ant species have established populations in all seven of the world's ant-inhabited biogeographic regions (i.e., all except the Antarctic, which ironically has no ants).

I subdivided the 28 cosmopolitan species that were not on Forel's (1911) list into two categories based on a fairly crude evaluation of their degree of geographic spread. Widespread cosmopolitan species (Table 2) have multiple well-established populations in at least five of the world's biogeographic regions: *Cardiocondyla mauritanica* Forel, 1890, *Cardiocondyla minutior* Forel, 1899, *Cardiocondyla obscurior* Wheeler, 1929, *Cardiocondyla wroughtonii* (Forel, 1890), *Hypoponera opaciceps* (Mayr, 1887), *Hypoponera punctatissima* (Roger, 1859), *Nylanderia bourbonica* (Forel, 1886), *Plagiolepis alluaudi* Emery, 1894, *Pseudoponera stigma* (Fabricius, 1804), *Strumigenys emmae* (Emery, 1890), *Strumigenys membranifera* Emery, 1869, *Strumigenys rogeri* Emery, 1890, *Technomyrmex difficilis* Forel, 1892, and *Wasmannia auropunctata* (Roger, 1863).

Incipient cosmopolitan species (Table 3) have multiple well-established populations in fewer than five bioregions: *Brachyponera chinensis* (Emery, 1895), *Cardiocondyla venustula* Wheeler, 1908, *Cerapachys biroi* Forel, 1907, *Hypoponera eduardi* (Forel, 1894), *Hypoponera ragusai* (Emery, 1894), *Leptogenys maxillosa* (Smith, 1858), *Myrmica rubra* (Linnaeus, 1758), *Nylanderia flavipes* (Smith, 1874), *Pheidole teneriffana* Forel, 1893, *Solenopsis invicta* Buren, 1972, *Strumigenys hexamera* (Brown, 1958), *Technomyrmex vitiensis* Mann, 1921, *Tetramorium insolens* (Smith, 1861), and *Tetramorium lucayanum* Wheeler, 1905.

In addition to 42 cosmopolitan ant species, I listed 20 ant species with only minor spread of outdoor populations outside their native hemisphere: *Cardiocondyla tjibodana* Karavaiev, 1935, *Formica lugubris* Zetterstedt, 1838, *Monomorium salomonis* (Linnaeus, 1758), *Monomorium subopacum* (Smith, 1858), *Myrmica specioides* Bondroit, 1918, *Nylanderia steinheili* (Forel, 1893), *Pheidole fervens* Smith, 1858, *Pheidole moerens* Wheeler, 1908, *Pseudomyrmex gracilis* (Fabricius, 1804), *Solenopsis globularia* (Smith, 1858), *Strumigenys silvestrii* Emery, 1906, *Sylophopsis sechellensis* (Emery, 1894), *Tapinoma sessile* (Say, 1836), *Temnothorax longispinosus* (Roger, 1863), *Tetramorium pacificum* Mayr, 1870, *Tetramorium tonganum* Mayr, 1870, *Tetramorium tsushimae* Emery, 1925, and *Vollenhovia emeryi* Wheeler, 1906 (Table 4). Some of these species appear to be spreading quickly, e.g., *T. tsushimae* (Reuther, 2009). Other species are known outside their native hemisphere from only a single outdoor site record: *C. tjibodana* (in Belize; Seifert, 2003), *F. lugubris* (in Quebec, Canada; Finnegan, 1975), *M. subopacum* (in Antigua; Wheeler, 1923), *M. specioides* (in Washington State; Jansen and Radchenko, 2009), *N. steinheili* (in Mauritius; Wheeler, 1922), *P. fervens* (in California; Martinez, 1996), *Tapinoma sessile* (in Hawaii; Buczkowski and Krushelnycky, 2012), *T. longispinosus* (in Spain; Espadaler and Collingwood, 2001), and *T. tonganum* (in Brazil; Fowler *et al.*, 1994). In some cases, these single populations may be (or may have been) only temporary.

Discussion

My analyses identified 62 ant species with populations established outside their native range hemisphere. Based on their known world distribution, I classified 42 of these ant species as cosmopolitan, i.e., with multiple well-established outdoor populations outside their native hemisphere (Tables 1-3). Of these 42 cosmopolitan ant species, 35 (83%) are Old World natives and seven (17%) are New World natives. This pattern suggests that Old World species are more likely to be competitively dominant, possibly due to evolving in a more competitive environment. Overall, the highest

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

number of cosmopolitan ant species were originally native to the Indomalay bioregion (17 species; Tables 1-3) and the lowest number were native to the Nearctic bioregion (only one species; Table 2). Of the 20 ant species with only very minor spread of outdoor populations outside their native hemisphere (Table 4), thirteen (65%) are Old World natives and seven (35%) are New World natives.

Comparing the native ranges of Forel's (1911) cosmopolitans with those of the newer cosmopolitans suggests a shift in the main sources of cosmopolitans. For example, only one of Forel's (1911) 14 cosmopolitans (7%) is native to the Palearctic bioregion, despite the Palearctic having the greatest land area. In contrast, eight of the 28 new cosmopolitans (29%) are native to the Palearctic (Tables 1-3).

Of the 42 cosmopolitan ant species, I consider twelve to be major ecological, agricultural, and/or household pest species. Forel's (1911) list of 14 cosmopolitan ant species (Table 1) included eight of these major pest species (see Introduction). In contrast, my list of 28 additional cosmopolitan ant species (Tables 1 and 2) includes only four additional major pest species: *Nylanderia bourbonica* (Forel, 1886), *Solenopsis invicta* Buren, 1972, *Technomyrmex difficilis* Forel, 1892, and *Wasmannia auropunctata* (Roger, 1863). The other 24 new cosmopolitans are at most relatively minor pests. Thus, although the new list of cosmopolitan ants is much longer than that of Forel (1911), few of the additions have developed into major pests.

My classification of what constitutes a major pest, however, is not based on quantitative criteria, but instead is largely subjective, based on my experience with the different species and the papers I have read about their impact. All twelve of these major pest species commonly attain high local densities where they can have measurable ecological and/or economic impacts. There are certainly valid arguments for including other ant species on this list. For example, *T. bicarinatum* can sometimes be a serious agricultural pest and *B. chinensis* and *M. rubra* both have painful stings; all three of these species can attain high densities in some places.

In a related problem of categorization, Sarah Lowe, a staff member of the Invasive

Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN), asked me in 1997 at a scientific meeting in Suva, Fiji, what I thought were the most harmful exotic ants, for inclusion on a list of 100 of the worst invasive species in the world. I was skeptical about the validity of comparing the relative impact of different ant species, much less comparing the impact of invasive ants with that of invasive mammals, fish, trees, etc. Some ants are enormous agricultural pests, others have a great impact on native species, while still others are important household pests. But Lowe assured me that this publication was a "publicity booklet," simply meant to call attention to exotic species and to IUCN's newly created Global Invasive Species Database. She emphasized this was not to be a list of the 100 worst, but instead 100 examples of harmful invasive species. I suggested six ant species based on my experience at the time: *A. gracilipes*, *L. humile*, *P. megacephala*, *S. geminata*, *S. invicta*, and *W. auropunctata*. In the publication, Lowe *et al.* (2000) dropped *S. geminata* because they did not want two species of the same genus. While I would certainly rank *S. geminata* ahead of *A. gracilipes*, Lowe *et al.* (2000) explicitly stated: "Absence from the list does not imply that a species poses a lesser threat." This distinction, however, seems to have been lost in the many dozens of papers that claim species x is one of the 100 worst exotic species, inappropriately citing Lowe *et al.* (2000) as if this paper were an authoritative primary source founded on definitive research, rather than being a collection of illustrative examples selected based on subjective impressions.

Another problem with categorization is exemplified in a paper by McGlynn (1999), which included a list of 147 ant species that have been "recorded outside their native habitat." This paper has been a popular source reference regarding exotic ants, cited in the mistaken belief that it represented a comprehensive list of ant species with established exotic populations. McGlynn's (1999) list, however, included a great many ant species that have no known outdoors populations established in locales beyond their native range, e.g., numerous species that Nishida (1994, 2002) listed as intercepted by quarantine

on goods imported into Hawaii, but without any established populations (e.g., *Camponotus exiguoguttatus* Forel, 1886, *Camponotus itoi* Forel, 1912, *Camponotus obscuripes* Mayr, 1879, *Crematogaster lineolata* (Say, 1836), *Formica subpolita* Mayr, 1886, *Lasius interjectus* Mayr, 1866, *Pheidole barbata* Wheeler, 1908, *Pheidole hyatti* Emery, 1895, *Pheidole noda* Smith, 1874, *Pheidole punctatissima* Mayr, 1870, *Carebara affinis* (Jerdon, 1851), *Polyrhachis argentea* Mayr, 1862, *Polyrhachis dives* Smith, 1857, *Polyrhachis femorata* Smith, 1858, *Ponera coarctata* (Latreille, 1802), *Prenolepis imparis* (Say, 1836) and *Prenolepis melanogaster* Emery, 1893). In addition, some species on McGlynn's (1999) list have only exotic indoor populations (e.g., *Camponotus atriceps* (Smith, 1858), *Dolichoderus thoracicus* (Smith, 1860), *Linepithema iniquum* (Mayr, 1870), *Carebara diversus* (Jerdon, 1851) and *Solenopsis texana* Emery, 1895), and a few were based on site error (e.g., *Anoplolepis custodiens* (Smith, 1858), *Dolichoderus quadripunctatus* (Linnaeus, 1771), *Gnamptogenys porcata* (Emery, 1896), *Odontomachus simillimus* Smith, 1858 etc.) (Wetterer 2005, 2014c) or identification error (e.g., *Cardiocondyla nuda* (Mayr, 1866), *N. vividula* (Nylander, 1846), *Pheidole variabilis* Mayr, 1876, *Brachyponera obscurans* (Walker, 1859) etc.) (Seifert 2003). Finally, some species listed actually appear to be native throughout their known range (e.g., *Hypoconeropsis elliptica* (Forel, 1900), *Lasius turcicus* Santschi, 1921) (Taylor, 1987; Seifert, 1992).

A complete list of all ant species that have ever been "recorded outside their native habitat" would be much greater than the 147 listed by McGlynn (1999), especially if the list included species simply intercepted in transit. For example, Suarez *et al.* (2005) listed 232 ant species intercepted by quarantine inspectors in the US. However, Suarez *et al.* (2005) found that only 28 of these "now occur as established nonnative species in the continental United States, and three species can be considered invasive." I believe that distinguishing these different categories is of vital importance.

Future research plans

I have authored or co-authored papers,

reviewing, one species at a time, the known geographic distributions of most cosmopolitan ant species whose taxonomy are well established (Tables 1-3). I am working to review the rest, when the taxonomy can be properly ascertained and specimens with uncertain identities re-examined, often in collaboration with one or more taxonomic experts (e.g., *T. simillimum* with F. Hita-Garcia). My present list of cosmopolitan ant species is almost certainly incomplete. Taxonomic revisions will probably identify additional cosmopolitan ant species, e.g., one or more *Brachymyrmex* species appear to be widespread cosmopolitans. Unfortunately, the taxonomy of *Brachymyrmex* remains very confused.

I am also turning my attention to ant species reported to have exotic populations only within their own native hemisphere. Some of these species have large geographic gaps between their presumed native and exotic populations, e.g., *Gnamptogenys triangularis* (Mayr, 1887) (MacGown and Wetterer, 2012a) and *Pheidole obscurithorax* Naves, 1985 (Naves, 1985), so the limits of the known native and exotic ranges can be discerned. For many species, however, distinguishing where the native range ends and the exotic range begins is difficult, e.g., *Brachyponera sennaarensis* (Mayr, 1862) (Wetterer 2013a) and *Strumigenys margaritae* Forel, 1893 (MacGown and Wetterer, 2013).

In some cases, species that have been reported as exotic are actually native throughout their known range. Wittenborn and Jeschke (2011) wished to compare characteristics of native versus exotic ant species in North America, but appear to have misclassified numerous ant species as exotics, that are actually native to North America, such as *Leptogenys manni* (Wheeler, 1923), a species endemic to Florida (Trager and Johnson, 1988).

For example, Wittenborn and Jeschke (2011) considered *Gnamptogenys hartmani* (Wheeler, 1915), *Labidus coecus* (Latreille, 1802), *Pachycondyla harpax* (Fabricius, 1804), and *Trachymyrmex jamaicensis* (André, 1893) as exotic to North America, but all four have distributions in the southern US that are simply the northern end of continuous native ranges and give no indication that these species are exotic to

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

Table 1. Forel's (1911) fourteen cosmopolitan ant species. x-date = year first found outside native hemisphere. Bioregions: Af = Afrotropic, Pa = Palearctic, In = Indomalay, Au = Australasia, Oc = Oceania, Na = Nearctic, and Nt = Neotropic. Presumed native range in caps and bold and rest shows presumed exotic range

Species name	Worldwide range							x-date	Major exotic reference
<i>Cardiocondyla emeryi</i>	AF	Pa	In	Au	Oc	Na	Nt	1878	Wetterer, 2012d
<i>Pheidole megacephala</i>	AF	Pa	In	Au	Oc	Na	Nt	1858	Wetterer, 2012e
<i>Tetramorium caldarium</i>	AF	Pa	In	Au	Oc	Na	Nt	1908	Wetterer and Hita Garcia, 2015
<i>Tetramorium simillimum</i>	AF	Pa	In	Au	Oc	Na	Nt	1868	Bolton, 1980
<i>Trichomyrmex destructor</i>	Af	PA	In	Au	Oc	Na	Nt	1893	Wetterer, 2009b
<i>Monomorium floricola</i>	Af	Pa	IN	Au	Oc	Na	Nt	1863	Wetterer, 2010a
<i>Monomorium pharaonis</i>	Af	Pa	IN	Au	Oc	Na	Nt	1864	Wetterer, 2010c
<i>Paratrechina longicornis</i>	Af	Pa	IN	Au	Oc	Na	Nt	1859	Wetterer, 2008
<i>Tapinoma melanocephalum</i>	Af	Pa	IN	Au	Oc	Na	Nt	1793	Wetterer, 2009a
<i>Tetramorium lanuginosum</i>	Af	Pa	IN	Au	Oc	Na	Nt	1912	Wetterer, 2010b
<i>Anoplolepis gracilipes</i>	Af	---	IN	Au	Oc	Na	Nt	1859	Wetterer, 2005
<i>Tetramorium bicarinatum</i>	Af	Pa	IN	AU	Oc	Na	Nt	1850	Wetterer, 2009c
<i>Linepithema humile</i>	Af	Pa	In	Au	Oc	Na	NT	1858	Wetterer, <i>et al.</i> , 2009
<i>Solenopsis geminata</i>	Af	Pa	In	Au	Oc	Na	NT	1851	Wetterer, 2011a

Table 2. Fourteen additional widespread cosmopolitan ant species with substantial geographic spread outside their native hemisphere. Symbols and abbreviations as in Table 1.

Species name	Worldwide range							x-date	Major exotic reference
<i>Strumigenys membranifera</i>	AF	Pa	In	Au	Oc	Na	Nt	1890	Wetterer, 2011b
<i>Strumigenys rogeri</i>	AF	Pa	In	Au	Oc	Na	Nt	1862	Wetterer, 2012a
<i>Plagiolepis alluaudi</i>	AF	Pa	In	Au	Oc	Na	Nt	1928	Wetterer, 2014a
<i>Technomyrmex difficilis</i>	AF	----	In	Au	Oc	Na	Nt	1986	Wetterer, 2013b
<i>Hypoponera punctatissima</i>	AF	PA	In	Au	Oc	Na	Nt	1892	Bolton and Fisher, 2011
<i>Cardiocondyla mauritanica</i>	Af	PA	In	Au	----	Na	Nt	1967	Wetterer, 2012f
<i>Nylanderia bourbonica</i>	Af	Pa	IN	Au	Oc	Na	Nt	1924	Deyrup <i>et al.</i> , 2000
<i>Cardiocondyla minutior</i>	Af	----	IN	Au	Oc	Na	Nt	1924	Wetterer, 2014b
<i>Cardiocondyla wroughtonii</i>	Af	Pa	IN	Au	Oc	Na	Nt	1939	Seifert, 2003
<i>Cardiocondyla obscurior</i>	Af	Pa	IN	----	Oc	Na	Nt	1982	Seifert, 2003
<i>Strumigenys emmae</i>	Af	----	In	AU	Oc	----	Nt	1890	Wetterer, 2012c
<i>Hypoconera opaciceps</i>	----	Pa	In	Au	Oc	NA	Nt	1892	Wilson and Taylor, 1967
<i>Pseudoponera stigma</i>	----	----	In	Au	Oc	Na	NT	1858	Wetterer, 2012b
<i>Wasmannia auropunctata</i>	Af	Pa	----	Au	Oc	Na	NT	1893	Wetterer, 2013d

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

Table 3. Fourteen incipient cosmopolitan ant species with several well-established outdoor populations outside their native hemisphere. Symbols and abbreviations as in Table 1.

Species name	Worldwide range							x-date	Major exotic reference
<i>Cardiocondyla venustula</i>	AF	----	In	----	Oc	Na	Nt	1906	Seifert, 2003
<i>Leptogenys maxillosa</i>	AF	Pa	In	----	----	----	Nt	1861	Roger, 1861
<i>Pheidole teneriffana</i>	AF	PA	In	----	----	Na	Nt	1930	Wetterer, 2011e
<i>Monomorium salomonis</i>	Af	PA	----	----	----	----	Nt	1913	Wheeler and Mann, 1914
<i>Myrmica rubra</i>	----	PA	----	----	----	Na	----	1900	Wetterer and Radchenko, 2011
<i>Hypoponera eduardi</i>	Af	PA	----	Au	Oc	----	Nt	1914	Bolton and Fisher, 2011
<i>Nylanderia flavipes</i>	----	PA	IN	----	----	Na	----	1939	Wetterer, 2011c
<i>Brachyponera chinensis</i>	----	PA	IN	Au	----	Na	----	1932	Nelder <i>et al.</i> , 2006
<i>Tetramorium tsushimae</i>	----	PA	IN	----	----	Na	----	1988	Reuther, 2009
<i>Hypoponera ragusai</i>	Af	Pa	IN	Au	Oc	----	Nt	1939	Bolton and Fisher, 2011
<i>Cerapachys biroi</i>	Af	----	IN	----	Oc	----	Nt	1930	Wetterer <i>et al.</i> , 2012
<i>Technomyrmex vitiensis</i>	Af	Pa	IN	AU	OC	Na	Nt	1987	Bolton, 2007
<i>Solenopsis invicta</i>	----	----	In	Au	----	Na	NT	2001	Wetterer, 2013c
<i>Solenopsis globularia</i>	Af	----	----	----	Oc	----	NT	1958	Wetterer <i>et al.</i> , 2007

Table 4. Twenty ant species with a small number of outdoor populations outside their native hemisphere. Symbols and abbreviations as in Table 1.

Species name	Worldwide range							x-date	Major exotic reference
<i>Tetramorium lucayanum</i>	AF	Pa	---	---	---	---	Nt	1904	Wetterer, 2011d
<i>Monomorium subopacum</i>	Af	PA	In	---	---	---	Nt	1920	Wheeler, 1923
<i>Formica lugubris</i>	---	PA	---	---	---	---	Nt	1973	Finnegan, 1975
<i>Myrmica specioides</i>	---	PA	---	---	---	Na	---	<2007	Jansen and Radchenko, 2009
<i>Myrmica scabrinodis</i>	---	PA	---	---	---	Na	---	2009	Clark <i>et al.</i> , 2011
<i>Vollenhovia emeryi</i>	---	PA	IN	---	---	Na	---	1986	Wetterer <i>et al.</i> , 2015
<i>Strumigenys hexamera</i>	---	PA	IN	---	---	Na	---	1987	MacGown and Wetterer, 2012b
<i>Cardiocondyla tjobodana</i>	---	PA	IN	AU	---	---	Nt	1997	Seifert, 2003
<i>Pheidole fervens</i>	---	PA	IN	AU	OC	Na	---	1995	Martinez, 1996
<i>Tetramorium pacificum</i>	Af	---	IN	AU	OC	Na	---	1950	Creighton, 1950
<i>Tetramorium tonganum</i>	---	Pa	IN	AU	OC	---	Nt	<1994	Fowler <i>et al.</i> , 1994
<i>Sylophopsis sechellensis</i>	Af	---	IN	AU	Oc	---	Nt	2003	Wetterer, in prep.
<i>Tetramorium insolens</i>	Af	Pa	IN	AU	OC	Na	---	1979	Bolton, 1979
<i>Temnothorax longispinosus</i>	---	Pa	---	---	---	NA	---	1923	Espadaler and Collingwood, 2001
<i>Tapinoma sessile</i>	---	---	---	---	Oc	NA	---	2009	Buczowski and Krushelnycky, 2012
<i>Pseudomyrmex gracilis</i>	---	Pa	---	---	Oc	NA	NT	1912	Wetterer, 2010d
<i>Strumigenys silvestrii</i>	---	Pa	In	---	---	Na	NT	2001	MacGown <i>et al.</i> , 2013
<i>Nylanderia steinheili</i>	Af	---	---	---	---	---	NT	1908	Wheeler, 1922
<i>Pheidole moerens</i>	---	---	---	---	Oc	Na	NT	2000	Wilson, 2003
<i>Cyphomyrmex minutus</i>	Af	---	---	---	---	---	NT	2011	B. Fisher (pers. comm.)

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

North America (Wetterer 2014c, Wetterer and Snelling 2015).

I eventually plan to make a comprehensive analysis of all ant species with well-established exotic populations, including those that have not spread beyond their native hemisphere. This, however, will take much additional effort in compiling and evaluating specimen records.

More than 100 years ago, Forel (1911) compiled a list of cosmopolitan ants, calling attention to this important group of invasive species, spread around the world by human commerce. Forel (1911) identified most of what remain the dominant tramp ant species today. I hope that my present compilation will prove to be a useful extension of Forel's (1911) prescient work.

Acknowledgements

I thank M. Wetterer and reviewers J. Fellowes and M. Terayama for comments on this manuscript; S.P. Cover (MCZ) and T. Schultz (SI) for help with their respective ant collections; D.P. Wojcik and S.D. Porter for compiling their valuable FORMIS bibliography; R. Pasos and W. Howerton of the FAU library for processing so many interlibrary loans; Florida Atlantic University and the National Science Foundation (DES-0515648) for financial support.

References

- Bolton, B. 1979. The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Malagasy region and in the New World. Bulletin of the British Museum (Natural History) Entomology 38: 129-181.
- Bolton, B. 1980. The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Ethiopian zoogeographical region. Bulletin of the British Museum (Natural History) Entomology 40: 193-384.
- Bolton, B. 2007. Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. Contributions of the American Entomological Institute 35: 1-149.
- Bolton, B. and Fisher, B.L. 2011. Taxonomy of Afrotropical and West Palaearctic ants of the ponerine genus *Hypoponera* Santschi (Hymenoptera: Formicidae). Zootaxa 2843: 1-118.
- Buczowski, G. and Krushelnycky, P. 2012. The odorous house ant, *Tapinoma sessile* (Hymenoptera: Formicidae), as a new temperate-origin invader. Myrmecological News 16: 61-66.
- Clark, A.T., Rykken, J.J. and Farrell, B.D. 2011. The effects of biogeography on ant diversity and activity on the Boston Harbor Islands, Massachusetts, U.S.A. PLoS ONE 6(11): e28045.
- Creighton, W.S. 1950. The ants of North America. Bulletin of the Museum Comparative Zoology 104: 1-585.
- Deyrup, M., Davis, L. and Cover, S. 2000. Exotic ants in Florida. Transactions of the American Entomological Society 126: 293-326.
- Espadaler, X. and Collingwood, C. 2001. Transferred ants in the Iberian Peninsula (Hymenoptera, Formicidae). Nouvelle Revue d'Entomologie 17: 257-263.
- Finnegan, R.J. 1975. Introduction of a predacious red wood ant, *Formica lugubris* (Hymenoptera: Formicidae), from Italy to eastern Canada. Canadian Entomologist 107: 1271-1274.
- Fischer, G. and Fisher, B.L. 2013. A revision of *Pheidole* Westwood (Hymenoptera: Formicidae) in the islands of the Southwest Indian Ocean and designation of a neotype for the invasive *Pheidole megacephala*. Zootaxa 3683 (4): 301-356.
- Forel, A. 1911. Aperçu sur la distribution géographique et la phylogénie des fourmis. Mémoires 1er Congrès International d'Entomologie 2: 81-100.
- Fowler, H.G., Schlindwein, M.N. and Medeiros M.A. 1994. Exotic ants and community simplification in Brazil: a review of the impact of exotic ants on native ant assemblages. In: D. F. Williams, (ed.). Exotic ants: biology, impact, and control of introduced species. Boulder, Colorado: Westview Press. 151-162pp.

- Jansen, G. and Radchenko, A. 2009. *Myrmica specioides* Bondroit: a new invasive ant species in the USA?. *Biological Invasions* 11: 253-256.
- Lowe, S., Browne, M., Boudjelas, S. and De Poorter, M. 2000. 100 of the world's worst invasive species. A selection from the Global Invasive Species Database. *Aliens* 12: 1-12.
- MacGown, J.A. and Wetterer, J.K. 2012a. Geographic spread of *Gnamptogenys triangularis* (Hymenoptera: Formicidae: Ectotamminae). *Psyche* 2012 (571430): 1-4.
- MacGown, J.A. and Wetterer, J.K. 2012b. Geographic spread of *Pyramica hexamera* (Hymenoptera: Formicidae: Dacetini) in the southeastern USA. *Terrestrial Arthropod Reviews* 5: 3-14.
- MacGown, J.A. and Wetterer, J.K. 2013. Distribution and biological notes of *Strumigenys margaritae* (Hymenoptera: Formicidae: Dacetini). *Terrestrial Arthropod Reviews* 6: 247-255.
- MacGown, J.A., Wetterer, J.K. and Hill, J.G. 2013. Geographic spread of *Strumigenys silvestrii* (Hymenoptera: Formicidae: Dacetini). *Terrestrial Arthropod Reviews* 5: 213-222.
- Martinez, M.J. 1996. The first North American record of the ant *Pheidole fervens*. *Pan-Pacific Entomologist* 72: 171-172.
- McGlynn, T.P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* 26: 535-548.
- Naves, M.A. 1985. A monograph of the genus *Pheidole* in Florida, USA (Hymenoptera: Formicidae). *Insecta Mundi* 1: 53-90.
- Nelder, M.P., Paysen, E.S., Zungoli, P.A. and Benson, E.P. 2006. Emergence of the introduced ant *Pachycondyla chinensis* (Formicidae: Ponerinae) as a public health threat in the southeastern United States. *Journal of Medical Entomology* 43: 1094-1098.
- Nishida, G.M. 1994. Hawaiian terrestrial arthropod checklist. 2nd edition. Bishop Museum Technical Report 4: 1-287.
- Nishida, G.M. 2002. Hawaiian terrestrial arthropod checklist. 4th edition. Bishop Museum Technical Report 22: 1-313.
- Olson, D.M., Dinerstein, E., Wikramanayake, E., Burgess, N., Powell, G., Underwood, E.C., D'Amico, J., Itoua, I., Strand, H., Morrison, J., Loucks, C., Allnutt, T., Ricketts, T.H., Kura, Y., Wettengel, W. and Kassem, K. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51: 933-938.
- Reuther, K.D. 2009. Early invasion dynamics of the Japanese pavement ant, *Tetramorium tsushimae*, in the Saint Louis, Missouri metropolitan area. PhD dissertation, Saint Louis, Missouri: Saint Louis University. 135 pp.
- Roger, J. 1861. Die *Ponera*-artigen Ameisen (Schluss). *Berliner Entomologische Zeitschrift* 5: 1-54.
- Seifert, B. 1992. A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 66 (5): 1-166.
- Seifert, B. 2003. The ant genus *Cardiocondyla* (Insecta: Hymenoptera: Formicidae) a taxonomic revision of the *C. elegans*, *C. bulgarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi* and *C. minutior* species groups. *Annalen des Naturhistorischen Museums in Wien* 104 (B): 203-338.
- Suarez, A.V., Holway, D.A. and Ward, P.S. 2005. The role of opportunity in the unintentional introduction of nonnative ants. *Proceedings of the National Academy of Sciences of the United States of America* 102: 17032-17035.
- Taylor, R.W. 1987. A checklist of the ants of Australia, New Caledonia and New Zealand (Hymenoptera: Formicidae). *CSIRO Division of Entomology Report* 41: 1-92
- Trager, J.C. and Johnson, C. 1988. The ant genus *Leptogenys* (Hymenoptera: Formicidae, Ponerinae) in the United States. *In: J.C. Trager, (ed.) Advances in myrmecology*. Leiden: E. J. Brill. 29-34pp.
- Wetterer, J.K. 2005. Worldwide distribution and potential spread of the long-legged ant, *Anoplolepis gracilipes*. *Sociobiology* 45: 77-97.

Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae)

- Wetterer, J.K. 2008. Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). *Myrmecological News* 11: 137-149.
- Wetterer, J.K. 2009a. Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae). *Myrmecological News* 12: 23-33.
- Wetterer, J.K. 2009b. Worldwide spread of the destroyer ant, *Monomorium destructor* (Hymenoptera: Formicidae). *Myrmecological News* 12: 97-108.
- Wetterer, J.K. 2009c. Worldwide spread of the penny ant, *Tetramorium bicarinatum* (Hymenoptera: Formicidae). *Sociobiology* 54: 811-830.
- Wetterer, J.K. 2010a. Worldwide spread of the flower ant, *Monomorium floricola* (Hymenoptera: Formicidae). *Myrmecological News* 13: 19-27.
- Wetterer, J.K. 2010b. Worldwide spread of the wooly ant, *Tetramorium lanuginosum* (Hymenoptera: Formicidae). *Myrmecological News* 13: 81-88.
- Wetterer, J.K. 2010c. Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae). *Myrmecological News* 13: 115-129.
- Wetterer, J.K. 2010d. Worldwide spread of the graceful twig ant, *Pseudomyrmex gracilis* (Hymenoptera: Formicidae). *Florida Entomologist* 93: 535-540.
- Wetterer, J.K. 2011a. Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). *Myrmecological News* 14: 21-35.
- Wetterer, J.K. 2011b. Worldwide spread of the membraniferous dacetine ant, *Strumigenys membranifera* (Hymenoptera: Formicidae). *Myrmecological News* 14: 129-135.
- Wetterer, J.K. 2011c. Worldwide spread of the yellow-footed ant, *Nylanderia flavipes* (Hymenoptera: Formicidae). *Florida Entomologist* 94: 582-587.
- Wetterer, J.K. 2011d. Worldwide spread of *Tetramorium lucayanum* (Hymenoptera: Formicidae). *Florida Entomologist* 94: 827-831.
- Wetterer, J.K. 2011e. Worldwide spread of *Pheidole teneriffana* (Hymenoptera: Formicidae). *Florida Entomologist* 94: 843-847.
- Wetterer, J.K. 2012a. Worldwide spread of Roger's dacetine ant, *Strumigenys rogeri* (Hymenoptera: Formicidae). *Myrmecological News* 16: 1-6.
- Wetterer, J.K. 2012b. Worldwide spread of the stigma ant, *Pachycondyla stigma* (Hymenoptera: Formicidae). *Myrmecological News* 16: 39-44.
- Wetterer, J.K. 2012c. Worldwide spread of Emma's dacetine ant, *Strumigenys emmae* (Hymenoptera: Formicidae). *Myrmecological News* 16: 69-74.
- Wetterer, J.K. 2012d. Worldwide spread of Emery's sneaking ant, *Cardiocondyla emeryi* (Hymenoptera: Formicidae). *Myrmecological News* 17: 13-20.
- Wetterer, J.K. 2012e. Worldwide spread of the African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Myrmecological News* 17: 51-62.
- Wetterer, J.K. 2012f. Worldwide spread of the Moorish sneaking ant, *Cardiocondyla mauritanica* (Hymenoptera: Formicidae). *Sociobiology* 59: 985-997.
- Wetterer, J.K. 2013a. Geographic spread of the samsun or sword ant, *Pachycondyla (Brachyponera) sennaarensis* (Hymenoptera: Formicidae). *Myrmecological News* 18: 13-18.
- Wetterer, J.K. 2013b. Worldwide spread of the difficult white-footed ant, *Technomyrmex difficilis* (Hymenoptera: Formicidae). *Myrmecological News* 18: 93-97.
- Wetterer, J.K. 2013c. Exotic spread of *Solenopsis invicta* (Hymenoptera: Formicidae) beyond North America. *Sociobiology* 60: 53-63.
- Wetterer, J.K. 2013d. Worldwide spread of the little fire ant, *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Terrestrial Arthropod Reviews* 6: 173-184.
- Wetterer, J.K. 2014a. Worldwide spread of Alluaud's little yellow ant, *Plagiolepis alluaudi* (Hymenoptera: Formicidae). *Myrmecological News* 19: 53-59.
- Wetterer, J.K. 2014b. Worldwide spread of the lesser sneaking ant, *Cardiocondyla minutior* (Hymenoptera: Formicidae). *Florida Entomologist* 97: 567-574.

- Wetterer, J.K. 2014c. Geographic distribution of *Gnamptogenys hartmani* (Hymenoptera: Formicidae), an "agro-predator" that attacks fungus-growing ants. *Terrestrial Arthropod Reviews* 7: 147-157.
- Wetterer, J.K. 2015. Geographic distribution of *Trachymyrmex jamaicensis* (Hymenoptera, Formicidae). *Florida Entomologist*, in press.
- Wetterer, J.K. and Radchenko, A. 2011. Worldwide spread of the ruby ant, *Myrmica rubra* (Hymenoptera: Formicidae). *Myrmecological News* 14: 87-96.
- Wetterer, J.K. and Hita Garcia, F. 2015. Worldwide spread of the hothouse ant, *Tetramorium caldarium* (Hymenoptera: Formicidae). *Myrmecological News* 21: 93-99.
- Wetterer, J.K. and Snelling, G.C. 2015. Geographic distribution of *Labidus coecus* (Hymenoptera, Formicidae), a subterranean army ant. *Journal of Hymenoptera Research* 44: 31-38.
- Wetterer, J.K., Espadaler, X., Ashmole, P., Cutler, C. and Endeman, J. 2007. Ants (Hymenoptera: Formicidae) of the South Atlantic islands of Ascension Island, St Helena, and Tristan da Cunha. *Myrmecological News* 10: 29-37.
- Wetterer, J.K., Wild, A.L., Suarez, A.V., Roura-Pascual, N. and Espadaler, X. 2009. Worldwide spread of the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *Myrmecological News* 12: 187-194.
- Wetterer, J.K., Kronauer, D.J.C. and Borowiec, M.L. 2012. Worldwide spread of *Cerapachys biroi* (Hymenoptera: Formicidae: Cerapachyinae). *Myrmecological News* 17: 1-4.
- Wetterer, J.K., Guénard, B. and Booher, D.B. 2015. Geographic spread of *Vollenhovia emeryi* (Hymenoptera: Formicidae). *Asian Myrmecology* 7: 1-8.
- Wheeler, W.M. 1922. Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. IX. A synonymic list of the ants of the Malagasy region. *Bulletin of the American Museum of Natural History* 45: 1005-1055.
- Wheeler, W.M. 1923. Report on the ants collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. *Studies in Natural History, Iowa University* 10 (3): 3-9.
- Wheeler, W.M. and Mann, W.M. 1914. The ants of Haiti. *Bulletin of the American Museum of Natural History* 33: 1-61.
- Wilson, E.O. and Taylor, R.W. 1967. Ants of Polynesia. *Pacific Insects Monograph* 14: 1-109.
- Wilson, E.O. 2003. *Pheidole* on the New World: A dominant, hyperdiverse ant genus. Cambridge, Massachusetts: Harvard University Press. 794 pp.
- Wittenborn, D. and Jeschke, J.M. 2011. Characteristics of exotic ants in North America. *NeoBiota* 10: 47-64 (Appendix 1).