

RESEARCH

Ants of the Florida Keys: Species Accounts, Biogeography, and Conservation (Hymenoptera: Formicidae)

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ABSTRACT. As a tropical archipelago, the Florida Keys provide an ideal environment to examine the historic and short-term processes that structure and influence biological diversity. Through a new survey of the ants of the Florida Keys, we increase our knowledge of the number of species to 94 representing 34 genera and 8 subfamilies. Through detailed collection information, we provide an in depth picture of the distribution of each species across the Keys. On the basis of these data and information on the native and known distributions of each species, we confirm the historical trend toward continued immigration of nonnative species into the Florida Keys and present these findings in the context of the proportion of native to nonnative species. We find a similar number of species introduced from the Old World and Neotropical mainland and discuss the probable immigration of mainland Florida species during the exposure of the Florida Shelf during the last glacial episode and the subsequent isolation of some populations as sea level rose following the last glaciation. Lastly, we discuss the possible threats to these populations due to rapid climate change and other human influences.

Key Words: biodiversity, climate change, biogeography, insect, invasive species

The Florida Keys are a tropical archipelago south and southwest of the Florida peninsula. The Florida Keys are the result of exposed ancient coral reefs and the total land area of these islands is ~356 km². The Keys lie along the Florida Straits, which divide the Atlantic Ocean and the Gulf of Mexico. In addition to being very near mainland Florida, the Keys are also in close proximity to many of the Caribbean Islands (the tip of Key West is only 140 km from Cuba). Because of the geographic location of the Florida Keys, the biota includes species that arrived naturally from nearby mainland Florida, species that arrived naturally from the nearby West Indies, species introduced by humans, and a small number of endemic species and subspecies (Snyder et al. 1990).

The ant fauna reported from the Florida Keys reflects these origins (Deyrup et al. 1988). Although diverse for island standards, the ant fauna is depauperate compared with that of peninsular Florida; this is probably due primarily to the limited number of habitat types found in the Keys and the long dry season during the winter and spring (Deyrup et al. 1988). The native ant fauna may be affected by habitat conversion, pesticide use, current and future climate changes (Ross et al. 2009, Maschinski et al. 2011, Schmidt et al. 2012), and recent introductions of exotic species, especially the red imported fire ant (*Solenopsis invicta* Buren), a species whose abundance in the Keys seems correlated with increasing urbanization (Forys et al. 2002, Forys and Allen 2005). There have been two previously published surveys of the ants of the Florida Keys: Wilson (1964) and Deyrup et al. (1988).

The goals of our study are 1) to provide results of a recent survey of the ants of the Florida Keys, including the Keys where each species has been recorded and changes to ant names used in the lists published by Wilson (1964) and Deyrup et al. (1988); 2) to document changes in the ant fauna since the 1988 publication; 3) to present the most plausible geographic origin for each species and summarize the biogeography of the ants of the Florida Keys; and 4) to consider the possible conservation status of native species that are restricted to the Florida Keys or to the Keys and a small area of tropical peninsular Florida.

Materials and Methods

We surveyed ants of the Florida Keys ants during six expeditions between 2006 and 2013. We used general collecting, baiting, twig snapping, Davis leaf litter sifting, and Tulgren funnel extraction of leaf litter. Voucher specimens for these new collections reported here have been deposited at the Field Museum of Natural History (FMNH), Chicago, IL, Florida State Collection of Arthropods (FSCA), Gainesville, FL, and the Archbold Biological Station Arthropod Collection (ABS), Venus, FL. We also consulted the previous literature on the documented species of the Florida Keys (Wilson 1964, Deyrup et al. 1988) to compile a complete picture of ant diversity. Species listed in these previous studies will be denoted as EOW1964 and DCTU1988 with specimens identified by the authors or as listed in these articles. Collection records are listed alphabetically by the Keys from which each species has been recorded. High-resolution images of all species can be found on Antweb (<http://www.antweb.org/floridakeys.jsp>).

Alphabetical List of Ant Species of the Florida Keys.

Anochetus mayri Emery. New record for Florida Keys. Introduced from Neotropics. Found on Key Largo in the Dagny Johnson Key Largo Hammock Botanical State Park and the Crocodile National Wildlife Refuge in 2010. First mainland Florida collection: 1987; large Palm Beach population reported in 2002 (Deyrup 2002). Dealate queens and workers collected in tropical hammock leaf litter indicate that *An. mayri* is established in the Keys. Collected on Key Largo. Data, and voucher specimens: FMNH and FSCA.

Aphaenogaster flemingi Smith. Native to southeastern North America. Generally in grassy areas, dry or wet (Carter 1962), also known from salt marsh (M.A.D., unpublished data). In Keys found on Big Pine Key in pine rockland. Data: DCTU1988.

Aphaenogaster miamiana Wheeler. Native to southeastern North America, where sometimes confused with *Aphaenogaster carolinensis* Wheeler (Umphrey 1996). In tropical hammocks on Big Pine, Big Torch, Elliot, Key Largo, Middle Torch, and Upper Matecumbe Keys. Data: EOW1964 and DCTU1988.

Brachymyrmex depilis Emery. Listed as *Brachymyrmex* sp. nr. *depilis* in DCTU1988. Native North American species with transcontinental range, assuming that all populations are the same species. In the Florida Keys usually found in rotten wood and leaf litter in shaded habitats, but also in mats of low plants on rocky mangrove flats. Collected on Adams, Big Pine, Big Torch, Elliott, Fat Deer, Grassy, Key Largo, Little Duck, Long, Middle Torch, No Name, Plantation, Totten, and Vaca Keys. Data: DCTU1988 and present study.

Brachymyrmex minutus Forel. New record for Florida Keys. Probably introduced from West Indies (Deyrup et al. 2000), but possibly arrived naturally. Widespread but rarely collected in tropical Florida. Collected in leaf litter near Blue Hole abandoned rock quarry on Big Pine Key, and on Key Largo. Data: present study; voucher specimens: FMNH, ABS.

Brachymyrmex obscurior Forel. Listed as *Brachymyrmex* sp. nr. *obscurior* in DCTU1988. Probably native, arriving naturally from West Indies, but easily transported by humans and possibly introduced (Deyrup et al. 2000). In the Keys in natural open areas such as beaches, and also abundant in roadsides and lawns. Collected on Bahia Honda, Big Pine, Grassy, Key West, Key Largo, Middle Torch, Stock Island, and Vaca Keys. Data: DCTU1988 and present study.

Brachymyrmex patagonicus Mayr. New record for Florida Keys. Introduced into southeastern North America from southern South America, now widespread in Southeast (MacGown et al. 2007). In Keys common in urban and heavily disturbed areas, often seen on pavement or trees. Collected on Bahia Honda, Big Coppitt, Big Pine, Grassy, Key West, Little Duck, Saddlebunch 5, and Vaca Keys. Data: present study; voucher specimens: ABS.

Brachymyrmex sp. Three microgyne queens collected on No Name Key by car netting. Their small size and undistended gaster suggests they might be social parasites (Deyrup et al. 1988). A similar species occurs in mainland Florida (M.A.D., unpublished data). Presumed native. Data: DCTU1988.

Camponotus decipiens Emery. Native to southeastern North America. An arboreal species, in the Keys known only from Key West. Data: DCTU1988.

Camponotus floridanus (Buckley). Listed as *C. abdominalis floridanus* in DCTU1988. Native throughout Florida. In the Keys common in dead wood in hammocks and along the beach. Collected on Bahia Honda, Big Coppitt, Big Pine, Big Torch, Boca Chica, Elliott, Grassy, Indian Key Fill, Key West, Key Largo, Little Duck, Lower Sugarloaf, No Name, Plantation, Ramrod, Saddlebunch 1, Saddlebunch 2, Saddlebunch 5, Shark, Stock Island, Sugarloaf, Upper Matecumbe and Vaca Keys. Data: EOW1964, DCTU1988, and present study.

Camponotus impressus (Roger). Native to southeastern North America west to Texas, and the Bahamas. In the Keys found primarily in large red mangroves, known from Big Pine and Key Largo. Data: EOW1964, DCTU1988, and present study.

Camponotus planatus (Roger). The type locality of this species is Cuba, and it was first reported from the Florida Keys in 1910 (Wheeler 1910). We believe, however, that it was introduced from the mainland Neotropics, where it is widespread. Its absence from three major Bahamian islands argues against a Cuban origin (Deyrup 1991, Deyrup et al. 1994). In the Keys nests are in hollow twigs, weed stems, old termite galleries, and occasionally in grass culms. Deyrup et al. (1988) refer to this species as “the dominant ant of Florida’s tropical hammocks.” Collected on Big Pine, Big Torch, Elliott, Grassy, Key West, Key Largo, Little Torch, Long, Middle Torch, No Name, Plantation, Sugarloaf, Stock Island, and Upper Matecumbe Keys. Data: EOW1964, DCTU1988, and present study.

Camponotus tortuganus Emery. *Ca. tortuganus* might be a black and red form of the structurally similar, widespread, neotropical *C. conspicuus inaequalis* Roger, which has a black gaster with pale bands and as we find only the black and red form in the Keys we are only listing *Ca. tortuganus* as present in the Keys. Both *C. conspicuus inaequalis* (listed as *C. inaequalis* in DCTU1988) and *Ca. tortuganus* are reported

in DCTU1988. This species often occurs in man-made enclosed spaces, and could easily be carried around by commerce. Both forms could have been introduced into Florida, but it is also possible that *Ca. tortuganus* is a native population. Common in south Florida, including Keys: Bahia Honda, Big Coppitt, Big Pine, Elliott, Key Largo, Key West, Little Torch, Middle Torch, No Name, Plantation, Saddlebunch 5, Shark, and Sugarloaf Keys. Data: EOW1964, DCTU1988, and present study.

Camponotus (Colobopsis) sp. This tropical coastal species, which also occurs in the Bahamas, may well be a described Cuban species, such as *C. riehlui* (Roger) or *C. baronii* Alayo and Zayas. We lack access to the type specimens of either species, and the descriptions are insufficient to assign a name to the specimens we have collected. Illustrations of *C. baronii* in Alayo and Zayas Montero (1977), and de Zayas (1981) show a strong mesonotal groove in the major; this is also found in Florida specimens. It is also possible that this species is undescribed, although this seems unlikely. This species is undoubtedly the species listed in EOW1964, probably the unidentified mangrove species studied by Simberloff and Wilson (1969) and by Cole (1980; 1983a,b). It is known from the Florida Keys (where it is probably native), the Bahamas and (probably) Cuba. It is found in hollow twigs of red mangrove and sea grape. Collected on No Name Key, Stock Island and Key West, as well as mangrove islets. Data: Z. Prusak (personal communication) and present study; vouchers in FMNH and ABS.

Cardiocondyla emeryi Forel. Introduced from Old World tropics, found throughout Florida. Nests in soil in open grassy areas. Collected on Bahia Honda, Big Pine, Dry Tortugas, Elliott, Key Largo, Key West, Plantation, Sugarloaf, and Upper Matecumbe Keys. Data: EOW1964, DCTU1988, and present study.

Cardiocondyla minutior Forel. Listed as *C. nuda* (Mayr) in DCTU1988. Introduced from Old World tropics, found throughout Florida. Nests in soil in open grassy areas. Collected on Big Pine, Elliott, Key Largo, Key West, Sugarloaf, No Name, Upper Matecumbe, and Vaca Keys. Data: DCTU1988 and present study.

Cardiocondyla venustula (Wheeler). Introduced from Old World tropics, now widespread but not common in Florida. Nests in ground in open areas, including beaches. Collected on Bahia Honda, Dry Tortugas, Upper Matecumbe, and Vaca Keys. Data: DCTU1988, and present study.

Cardiocondyla wroughtonii (Forel). Introduced from Old World tropics, now widespread. Data: Wetterer and O’Hara 2002.

Cephalotes varians (Smith). Listed as *Paracryptocerus (Cyathomyrmex) varians* in EOW1964 and *Zacryptocerus varians* in DCTU1988. Native to southern coastal Florida and the Caribbean. Common in hollow twigs and branches of red mangrove, also in hollow twigs of other tree species, occasional in weed stems. Collected on Bahia Honda, Big Pine, Big Torch, Elliott, Fat Deer, Key Largo, Key West, Little Torch, Long, Lower Sugarloaf, No Name, Ohio, Plantation, Saddlebunch, Stock Island, Sugarloaf, Tea Table, Upper Matecumbe, Vaca, West Summerland, and Windley Keys. Data: EOW1964, DCTU1988 and present study.

Crematogaster ashmeadi Mayr. Native to southeastern North America. Nests in dead tree branches, hollow twigs, and weed stems. Collected on Bahia Honda, Big Pine, Big Torch, Elliott, Fat Deer, Grassy, Key Largo, Key West, Little Torch, Long, Lower Matecumbe, Middle Torch, No Name, Ohio, Plantation, Summerland, and West Summerland Keys. Data: EOW1964, DCTU1988, and present study.

Crematogaster atkinsoni Wheeler. Native to southeastern North America. Nests are almost always in marshes and constructed of carton in small shrubs. Collected on Big Pine, Big Torch, Key West, No Name, Saddlebunch 2, and Torch Keys. Data: DCTU1988 and present study.

Crematogaster minutissima Mayr. Native to southeastern North America. Nests are in rotten wood and deep humus. Collected on Big Pine and Elliott Keys. Data: DCTU1988.

Crematogaster obscurata Emery. Introduced from Central or South America, first discovered in the Keys in 1995; in 2006 still apparently confined to a small area of West Summerland Key (Deyrup 2007) and by 2009 in Key West (present study).

Cyphomyrmex minutus Mayr. A Caribbean species probably native to warmer areas of south Florida. Nests of this fungus-gardening species are in soil, usually under logs and rocks. Collected from Bahia Honda, Big Pine, Big Torch, Boca Chica, Elliott, Grassy, Key West, Key Largo, Long, Little Duck, Middle Torch, No Name, Plantation, Saddlebunch 2, Saddlebunch 5, Stock Island, Sugarloaf, Summerland, Upper Matecumbe, Vaca, and Windley Keys. Data: EOW1964, DCTU1988, and present study.

Discothyrea testacea Roger. Native to the Southeast and lower Midwest of North America. Nests are in humus in wooded areas. Collected on No Name Key, a single specimen. Data: DCTU1988.

Dorymyrmex bureni (Trager). Reported as *Conomyrma pyramica* in EOW1964 and *Conomyrma bureni* in DCTU1988. Native to southeastern North America. Nests in soil in open grassy areas, including lawns, and beaches. The Keys form is conspicuously darker than most mainland populations. Collected on Bahia Honda, Big Pine, Elliott, Grassy, Key Largo, Key West, Long, Middle Torch, Stock Island, Summerland, Vaca, and West Summerland Keys. Data: EOW1964, DCTU1988 and present study.

Eurhopalothrix floridana (Brown and Kempf). This species was originally considered native in Florida, but possibly imported from Mexico (Deyrup et al. 1997), but more recent collecting records suggest that it is a Caribbean species that could be native in Florida. This species is found from the Keys to northern Florida. Collected on Big Pine, Key Largo, Key West, Middle Torch, No Name, and Upper Matecumbe Keys. Data: DCTU1988.

Forelius pruinosus (Roger). Native to the Caribbean and, apparently, most of southern North America. More work is needed on the taxonomy of this species and other North American species of *Forelius*. Nests are in the ground in sandy open areas, beaches, or dry rocky areas. Collected on Boca Chica, Bahia Honda, Big Pine, Elliott, Fat Deer, Grassy, Key Largo, Key West, Little Torch, Long, Lower Matecumbe, No Name, and Saddlebunch 2 Keys. Data: DCTU1988 and present study.

Hypoponera inexorata (Wheeler). Native to southern North America, into Central America. Found in leaf litter tropical hammocks in the Keys. Collected on Bahia Honda, Big Pine, Big Torch, Key Largo, No Name, Sugarloaf, and West Summerland Keys. Data: DCTU1988 and present study.

Hypoponera opaciceps (Mayr). Probably native to the Western Hemisphere (Wilson and Taylor 1967), this species occurs in moist disturbed habitats, including accumulations of beach wrack from southern North America through South America, also found in the Old World Tropics. Since this species is well adapted to beaches, it could easily have moved around the Gulf of Mexico and from island to island in the Caribbean. Collected on Big Pine, Dry Tortugas, Grassy, Key Largo, Long, No Name, Stock Island, Vaca, and West Summerland Keys. Data: DCTU1988 and present study.

Hypoponera opacior (Forel). This species occurs through southern North America, Central and South America, and the Caribbean, assuming that this is not a species complex. There is no reason to believe that it is introduced anywhere in this range. Nests in soil, leaf litter, and rotten wood in mesic and xeric forests. Collected on Bahia Honda, Big Pine, Elliott, Grassy, Key Largo, Little Duck, Middle Torch, No Name, Plantation, Sugarloaf, Totten, Upper Matecumbe, and Vaca Keys. Data: DCTU1988 and present study.

Hypoponera punctatissima (Roger). A pantropical species introduced from the Old World. Usually found in moist habitats in accumulations of organic matter. Collected on Big Pine, Key Largo, Key West, Saddlebunch 2, and Stock Island Keys. Data: DCTU1988 and present study.

Monomorium destructor (Jerdon). Introduced from the Old World. It is not common in Florida and Deyrup et al. (1988) speculated that it

may be on the decline in the Keys, except Key West where it was commonly found around buildings. Although we did not sample extensively in lawns and around buildings in Key West, we did not collect this species during this resurvey. Collected on Key Largo, Key West, and Plantation Keys. Data: EOW1964 and DCTU1988.

Monomorium ebeninum Forel. This West Indian species was considered a poorly established exotic (Deyrup et al. 1988), but has persisted to the present, at least on Big Pine Key. If it is a recently established species, it is likely to become common in dry, open habitats similar to those it occupies in the Bahamas. Queens of this species have a relatively large gaster, and do not appear well adapted for long flights over open sea from the Bahamas to the Keys. Collected on Big Pine and Upper Matecumbe Keys. Data: DCTU1988 and present study.

Monomorium floricola (Jerdon). An Old World introduced species found in disturbed habitats nesting in dead twigs. Collected on Bahia Honda, Big Pine, Big Torch, Dry Tortugas, Elliot, Grassy, Indian Key Fill, Key Largo, Key West, Little Duck, Middle Torch, No Name, Plantation, Stock Island, and Sugarloaf Keys. Data: EOW1964, DCTU1988, and present study.

Monomorium pharaonis (L.). An Old World introduced species found in and around buildings in urban areas throughout Florida. Collected on Big Pine, Elliott, and Plantation Keys. Data: EOW1964 and DCTU1988.

Myrmecina americana Emery. A widespread native North American species, often found in wooded habitats. Collected in hammocks on Big Pine, Big Torch, Elliott, Middle Torch, No Name, Plantation, and Sugarloaf Keys. Data: DCTU1988 and present study.

Neivamyrmex opacithorax (Emery). A native army ant widely distributed across southern North America. In the Keys, specimens have been collected on Bahia Honda, Big Pine, Cudjoe, Key West, and Middle Torch Keys. Data: DCTU1988.

Nylanderia bourbonica (Forel). Listed as *Paratrechina bourbonica* in EOW1964 and DCTU1988. Introduced from the Old World tropics, usually found in disturbed habitats and around buildings, also in naturally disturbed areas such as beach and mangrove swamps. Collected on Big Pine, Boca Chica, Dry Tortugas, Elliott, Fat Deer, Grassy, Key Largo, Key West, Little Duck, Little Torch, Middle Torch, No Name, Saddlebunch 5, Shark, Sugarloaf, Upper Matecumbe, and West Summerland Keys. Data: EOW1964, DCTU1988, and present study.

Nylanderia concinna (Trager). Listed as *Paratrechina concinna* in DCTU1988. Native to southeastern North America, usually found in rotten wood or near swamps or marshes. Collected in a rotten palm stump in a rocky brackish swamp on Key Largo, also collected on Little Torch Key. Data: DCTU1988 and present study.

Nylanderia pubens (Forel). New record for the Florida Keys. Introduced from the West Indies, presently not common in Florida Keys. Collected by sifting litter on Key Largo, No Name and Vaca Keys. It is possible that some or all collections are a similar introduced species, *Nylanderia fulva* (Mayr). The species are most easily distinguished by examination of male genitalia (Gotzek et al. 2012); no males were found during our survey. Data: present study; voucher specimens have been deposited at FMNH and FSCA.

Nylanderia steinheili (Forel). Listed as *Paratrechina guatemalensis* in DCTU1988. Introduced from Central America (Trager 1984), spreading rapidly through disturbed and natural habitats in south Florida. Collected on Bahia Honda, Big Pine, Dry Tortugas, Key Largo, No Name, Plantation, Sugarloaf, Stock Island, Vaca, and Windley Keys. Data: DCTU1988 and present study.

Nylanderia wojciki (Trager). Listed as *Paratrechina wojciki* in DCTU1988. Native to southeastern North America. Usually found in upland forests. Specimens have been collected on Big Pine, Elliott, and No Name Keys. Data: DCTU1988 and present study.

Odontomachus brunneus (Patton). Native to southeastern North America. Nests under stones and in rotten wood in moist wooded habitats. Not commonly collected in Florida Keys; on Key Largo and No Name Key. Data: DCTU1988.

Odontomachus ruginodis Smith. Neotropical, probably introduced (Deyrup et al. 2000), expanding its range into central Florida. Nests in soil and under stones, and can be common in coastal areas. Collected on Bahia Honda, Big Pine, Big Torch, Boca Chica, Elliott, Fat Deer, Grassy, Key Largo, Key West, Little Torch, Lower Matecumbe, Middle Torch, No Name, Plantation, Saddlebunch 1, Saddlebunch 2, Saddlebunch 5, Sugarloaf, Stock Island, Upper Matecumbe, Vaca, and Windley Keys. Data: EOW1964, DCTU1988, and present study.

Paratrechina longicornis (Latreille). Introduced from Old World tropics. Nests under rotten logs, under stones and in the ground. Very common in Florida Keys. Collected on Bahia Honda, Big Coppitt, Big Pine, Dry Tortugas, Elliott, Grassy, Indian Key Fill, Key Largo, Key West, Little Duck, Little Torch, Long, Middle Torch, No Name, Plantation, Saddlebunch 2, Stock Island, Sugarloaf, Upper Matecumbe, and Windley Keys. Data: EOW1964, DCTU1988, and present study.

Pheidole dentata Mayr. Native to southeastern North America. Nests in soil and rotten wood. Collected on Bahia Honda, Big Pine, Dry Tortugas, Elliott, Key Largo, Little Torch, Middle Torch, No Name, Saddlebunch 2, Shark, Stock Island, and Sugarloaf Keys. Data: DCTU1988 and present study.

Pheidole dentigula Smith. Native to southeastern North America. Nests in mesic sites in moist leaf litter and rotten wood. Collected on Grassy, Key Largo, Middle Torch, and No Name Keys. Data: DCTU1988 and present study.

Pheidole flavens Roger. Not listed in DCTU1988, but in Deyrup (1991). Probably introduced from the Neotropics (Wilson 2003). Collected on Big Pine, Key Largo, Key West, No Name, Plantation, and Vaca Keys. Data: present study; voucher specimens have been deposited at FMNH, FSCA, and ABS.

Pheidole floridana Emery. Native to southern North America. Prefers dry partially shaded habitats, nests are usually in soil. Collected on Big Pine, Big Torch, Boca Chica, Elliott, Fat Deer, Grassy, Key Largo, Key West, Middle Torch, No Name, Plantation, Saddlebunch 2, Stock Island, Sugarloaf, and Vaca Keys. Data: EOW1964, DCTU1988, and present study.

Pheidole megacephala (F.). Introduced from Old World tropics. Nests in soil, under objects on the ground, and in dead wood in highly disturbed areas and around buildings. Collected on Big Pine, Dry Tortugas, Key Largo, Key West and Vaca Key. Data: DCTU1988 and present study.

Pheidole moerens (Wheeler). Introduced from the Neotropics. Common in disturbed habitats and mesic woodlands in moist areas. Collected on Bahia Honda, Big Pine, Grassy, Key Largo, Key West, Little Duck, Little Torch, Lower Sugarloaf, No Name, Plantation, Stock Island, Upper Matecumbe, Vaca, and Windley Keys. Data: DCTU1988 and present study.

Platythyrea punctata (Smith). Probably introduced from Neotropics, where it is widespread. Nests are usually in dead wood in forested areas. Collected on Big Pine, Key Largo, Middle Torch, No Name, Stock Island, Sugarloaf, and Vaca Keys. Data: EOW1964, DCTU1988, and present study.

Pogonomyrmex badius (Latreille). Native to southeastern North America; possibly not established in the Florida Keys as there appears to be little suitable habitat. A single alate queen collected on Saddlebunch 5. Data: DCTU1988.

Pseudomyrmex cubaensis (Forel). A West Indian species that probably spread naturally to the Keys. Nests in hollow twigs and plant stalks. Collected on Big Pine, Dry Tortugas, Elliott, Key Largo, Key West, Lower Matecumbe, No Name, and Saddlebunch 5 Keys. Data: DCTU1988, Wetterer and O'Hara (2002), and present study.

Pseudomyrmex ejectus (Smith). Native to southern North America, extending south into Central America. Nests in hollow twigs and plant stalks. Collected on Elliott, Key Largo, and Key West. Data: DCTU1988 and present study.

Pseudomyrmex elongatus (Mayr). Probably introduced; occurs in mainland Neotropics and north to Texas, but not north Florida or The

Bahamas. Might have spread around Gulf of Mexico during a warm climatic episode, but more likely introduced. Nests in hollow twigs and plant stalks. Collected on Bahia Honda, Big Pine, Big Torch, Boca Chica, Dry Tortugas, Elliot, Grassy, Key Largo, Key West, Little Duck, Little Torch, Long, Lower Sugarloaf, No Name, Plantation, Saddlebunch 5, Sugarloaf, Tea Table, Vaca, Upper Matecumbe, and West Summerland Keys. Data: EOW1964, DCTU1988, and present study.

Pseudomyrmex gracilis (Santschi). Listed as *Pseudomyrmex mexicana* in DCTU1988. Native to mainland Neotropics, now common throughout the southern two-thirds of Florida, sporadic farther north in Florida. Nests in hollow twigs and large plant stalks, natural and disturbed habitats. Collected on Big Pine, Big Torch, Elliot, Key Largo, Key West, Little Duck, Little Torch, Lower Matecumbe, Lower Sugarloaf, No Name, Tea Table, and Upper Matecumbe Keys. Data: DCTU1988 and present study.

Pseudomyrmex pallidus (Smith). Native to southern North America from New Jersey, through Texas down into Central America. Found primarily in plant stalks and infrequently in hollow twigs. Collected on Bahia Honda, Big Pine, Cudjoe, Elliott, Grassy, Key Largo, Key West, Lower Matecumbe, Middle Torch, No Name, Plantation, and Saddlebunch 5 Keys. Data: EOW1964, DCTU1988, and present study.

Pseudomyrmex seminole Ward. A native species extending north around the Gulf of Mexico. Nests in plant stalks, especially culms of grasses and sawgrass. Collected on Bahia Honda, Key Largo, and Key West. Data: DCTU1988 and present study.

Pseudomyrmex simplex (Smith). Native to the West Indies and probably Florida (subfossil specimens from Hispaniola: Ward 1992). Nests in hollow twigs. Collected on Big Pine, Big Torch, Elliot, Grassy, Key Largo, Lower Sugarloaf, No Name, Plantation, and Sugarloaf Keys. Data: DCTU1988 and present study.

Pseudoponera stigma (F.). Listed as *Pachycondyla stigma* in DCTU1988, taxonomy updated by Schmidt and Shattuck (2014). Pantropical, origin uncertain, probably introduced (Deyrup et al. 2000). In dead wood, often with termites. Collected, once, on Elliott Key. Data: DCTU1988.

Solenopsis abdita Thompson. Listed as *Solenopsis* sp. in DCTU1988. Native to southeastern North America. Nests in soil and in leaf litter. Collected on Bahia Honda, Big Pine, Boca Chica, Elliott, Key Grassy, Key Largo, Key West, Little Duck, Lower Matecumbe, Middle Torch, No Name, Plantation, Stock Island, Sugarloaf, and Vaca Keys. Data: present study; voucher specimens have been deposited at FMNH and FSCA.

Solenopsis carolinensis Forel. New record for Florida Keys. Native to eastern North America. Collected by sifting litter on Key Largo. Nests in rotten wood, in dead twigs on the ground, and in leaf litter. Data: present study; voucher specimens have been deposited at FMNH and FSCA.

Solenopsis corticalis Forel. A West Indian species (Thompson 1989). Like other Caribbean mangrove ants, this species is probably native in southern Florida. Nests in hollow twigs and plant stems. Collected on Bahia Honda, Big Pine, Big Torch, Key Largo, Key West, Little Torch, Long, No Name, and Sugarloaf Keys. Data: DCTU1988 and present study.

Solenopsis geminata (F.). Native to southern North America (Trager 1991). Nests in sandy soil in open areas, including beaches. Collected on Bahia Honda, Big Pine, Big Torch, Dry Tortugas, Elliott, Key Largo, Key West, Little Duck, Long, Middle Torch, No Name, Plantation, Shark, Stock Island, Sugarloaf, and Upper Matecumbe Keys. Data: EOW1964, DCTU1988, and present study.

Solenopsis globularia littoralis Creighton. Native to southern North America. Nests in open sandy areas and in tussocks in salt marshes. Collected on Big Pine, Dry Tortugas, Elliott, Geiger, Grassy, Key Largo, Key West, Ohio, Plantation, and Saddlebunch 2 Keys. Data: EOW1964, DCTU1988, Wetterer and O'Hara (2002), and present study.

Solenopsis invicta Buren. Introduced from South America. This invasive species is not as dominant in the Keys as in other parts of the southeastern states. Nests are usually in sandy soil in disturbed areas and along roads. Collections of this species have been made on Bahia Honda, Big Pine, Big Torch Key, Boca Chica, Cudjoe, Elliot, Grassy, Key Largo, Key West, Little Duck, Lower Sugarloaf, No Name, Ramrod, Saddlebunch 5, Stock Island, and Summerland Keys. Data: DCTU1988, Forsys et al. (2002), and present study.

Solenopsis pergandei Forel. New record for Florida Keys. Native to southeastern North America. A single ground nest found on Big Pine Key. Data: present study; voucher specimens have been deposited at FMNH and FSCA.

Solenopsis picta Emery. Native to southern North America. Nests in twigs, holes in the bark of live pine trees, and plant stems. Collected on Bahia Honda, Elliot, Key Largo, Key West, Lower Matecumbe, Plantation, and Upper Matecumbe Keys. Data: EOW1964, DCTU1988 and present study.

Solenopsis tennesseensis Smith. Native to southeastern North America. Listed as *S. longiceps* M.R. Smith in EOW1964. Nests in wooded areas in soil and leaf litter. Collected on Bahia Honda, Big Pine, Boca Chica, Elliot, Grassy, Key Largo, Little Torch, Long, No Name, Plantation, and Stock Island Keys. Data: EOW1964, DCTU1988 and present study.

Stigmatomma pallipes (Haldeman). Listed as *Amblyopone pallipes* in DCTU1988. Native to most of North America. In the Florida Keys only known from males collected in Malaise traps on Big Pine, Sugarloaf, and Cudjoe Keys. Data: DCTU1988.

Strumigenys dietrichi Smith. Listed as *Smithistruma dietrichi* in DCTU1988. Native to eastern North America, west to eastern Texas. Nests in rotten wood and deep leaf litter in wooded areas. Collected on Bahia Honda, Big Pine, Grassy, Middle Torch, and No Name Keys. Data: DCTU1988 and present study.

Strumigenys eggersi Emery. Probably introduced from mainland Neotropics. Nests are usually in shaded or partially shaded leaf litter. Collected on Bahia Honda, Big Pine, Key Largo, Key West, Little Torch, Little Duck, Long, Plantation, Stock Island, Sugarloaf, Upper Matecumbe, Vaca, and Windley Keys. Data: DCTU1988 and present study.

Strumigenys emmae (Emery). Listed as *Quadristruma emmae* in DCTU1988. Introduced, probably from Australasian area (Bolton 2000). Nests in leaf litter and rotten logs. Collected on Bahia Honda, Big Pine, Big Torch, Boca Chica, Elliot, Grassy, Key Largo, Key West, Long, Lower Matecumbe, No Name, Plantation, Stock Island, Sugarloaf, and Vaca Keys. Data: DCTU1988 and present study.

Strumigenys gundlachi (Roger). Introduced from mainland Neotropics. Nests in leaf litter in shaded areas. Collected on Big Pine, Big Torch, Elliot, Grassy, Key Largo, Long, No Name, Sugarloaf, Upper Matecumbe, and Vaca Keys. Data: EOW1964, DCTU1988, and present study.

Strumigenys louisianae Roger. Native to southern North America, Central and South America. Nests in leaf litter in shaded areas. Collected on Big Pine, Big Torch, Key Largo, No Name, and Plantation Keys. Data: DCTU1988.

Strumigenys membranifera Emery. New record for Florida Keys. Introduced from Old World Tropics. Nests in leaf litter. Collected on Big Pine, Key West, and Little Duck Keys. Data: present study; voucher specimens at ABS.

Strumigenys silvestrii Emery. Introduced from mainland Neotropics. Nests in leaf litter. Collected on Bahia Honda, Big Pine, Key Largo, Little Duck, No Name, Plantation, Vaca, and West Summerland Keys. Data: DCTU1988 and present study.

Tapinoma litorale Wheeler. Native to West Indies and Florida. Nests in hollow twigs and vines. Collected on Big Pine, Big Torch, Bush, Elliot, Fat Deer, Key Largo, Key West, Little Torch, Long, Lower Sugarloaf, Middle Torch, No Name, Plantation, Tea Table, Vaca, and Windley Keys. Data: EOW1964, DCTU1988, and present study.

Tapinoma melanocephalum (F.). Introduced from Old World tropics. Nests under bark, at the base of palm leaves, and similar cavities in disturbed habitats. Collected on Big Pine, Dry Tortugas, Elliot, Grassy, Key Largo, Key West, Little Duck, Little Torch, Long, Plantation, Saddlebunch 2, Stock Island, Upper Matecumbe, and Vaca Keys. Data: DCTU1988 and present study.

Tapinoma sessile (Say). Listed as *Tapinoma* sp. in DCTU 1988. Native to North America. In marshy areas and mangrove flats. Collected on Grassy, Sugarloaf, and Vaca Keys. Data: DCTU1988 and present study.

Technomyrmex difficilis Forel. New record for Florida Keys. Introduced from Old World Tropics. Nests in hollow twigs above ground. Collected on Key West, Long, No Name, and Upper Matecumbe Keys. Data: present study; voucher specimens have been deposited at FMNH and FSCA.

Temnothorax allardycei (Mann). Listed as *Leptothorax allardycei* in DCTU1988. West Indian, probably native in the Florida Keys. Nests in dead twigs and vines in dense tropical hammock. Collected on Big Pine, Big Torch, Elliot, Key Largo, Little Torch, Middle Torch, and Sugarloaf Keys. Data: DCTU1988 and present study.

Temnothorax pergandei (Emery). Listed as *Leptothorax* sp. nr. *pergandei* in DCTU1988. Native to North America. Nests in salt marsh and sparse woodlands. Collected on Big Pine, Key Largo, and Little Torch Keys. Data: DCTU1988 and present study.

Temnothorax torrei (Aguayo). Listed as *Leptothorax torrei* in DCTU1988. A West Indian species, probably native to Florida. A ground nesting species, collected on Big Pine, Fat Deer, Key Largo, Key West, Little Torch, Middle Torch, and No Name Keys. Data: DCTU1988 and present study.

Tetramorium bicarinatum (Nylander). Introduced from the Old World tropics. Listed as *Tetramorium guineense* in EOW1964. Apparently not common in the Florida Keys. Collected on Bahia Honda and Key Largo. Data: EOW1964 and DCTU1988.

Tetramorium caldarium (Roger). Introduced from the Old World tropics. Nests in open disturbed areas. Collected on Big Pine, Dry Tortugas, Key Largo, Key West, Stock Island, Upper Matecumbe, and West Summerland Keys. Data: DCTU1988 and present study.

Tetramorium lanuginosum Mayr. New record for the Florida Keys. Introduced from Old World Tropics. Two nests of this species were found under stones on Plantation Key. Data: present study; voucher specimens have been deposited at FMNH and FSCA.

Tetramorium simillimum (Smith). Introduced from Old World Tropics. Usually found in disturbed open habitats. Collected on Bahia Honda, Big Pine, Elliot, Key Largo, Key West, Long, No Name, Upper Matecumbe, and Vaca Keys. Data: EOW1964, DCTU1988, and present study.

Trachymyrmex jamaicensis (André). Listed as *Trachymyrmex* sp. nr. *jamaicensis* in DCTU1988. Native to Florida and West Indies. This is a fungus-growing species that constructs conspicuous thatch turrets and usually occurs in moist, shaded, tropical hammock. Collected on Bahia Honda, Big Pine, Elliot, Grassy, Indian, Key Largo, Long, and Shark Keys. Data: DCTU1988 and present study.

Trachymyrmex septentrionalis (McCook). Native to southeastern North America. A fungus-growing species nesting in dry, open, sandy areas. Collected from several colonies on Long Key. Data: DCTU1988.

Wasmannia auropunctata (Roger). Introduced from mainland Neotropics. Appears to be spreading in the Florida Keys. Collected on Bahia Honda, Big Pine, Key Largo, Key West, Little Torch, Long, Middle Torch, Plantation, Sugarloaf, Upper Matecumbe, and Windley Keys. Data: DCTU1988 and present study.

Xenomyrmex floridanus Emery. Native to the West Indies and Florida. Nests in hollow twigs; may be common in mangroves. Collected on Big Pine, Elliot, Grassy, Key Largo, Key West, Long, Lower Sugarloaf, No Name, Ohio, Plantation, Ramrod, and Tea Table Keys. Data: EOW1964, DCTU1988, and present study.

Listed in Error in Previous Species Lists for the Florida Keys.

Cyphomyrmex rimosus (Spinola). Listed in Deyrup (1991), based on misidentification; see Snelling and Longino (1992) for identification of species in the *Cy. rimosus* group.

Discussion

Changes in the Fauna and in the List of Species. The current list of ants of the Florida Keys includes 94 species, 11 more than in the DCTU1988 list. These species represent 34 genera and eight subfamilies of ants.

One species, *Cy. rimosus*, was based on a single misidentified specimen in Deyrup (1991) and has been removed from the list. *Ca. tortuganus* and *Camponotus inaequalis* are suspected of being forms of one species, and are provisionally combined in this list.

Three native species, *So. carolinensis*, *So. pergandei*, and “*Camponotus* sp.” are added to the list; the latter species appears in EOW1964 and is not an addition to the fauna.

Nine introduced species are added to the list. Several of these were first reported from Florida relatively recently and probably invaded the Keys in the last few decades. In the following list of apparent recent arrivals, the date of the first mainland Florida record is in parentheses, derived from Deyrup et al. (2000), names updated to reflect current nomenclature: *An. mayri* (1987), *Br. patagonicus* (1988), *Br. minutus* (1984), *Cr. obscurata* (1995), and *Tec. difficilis* (1986). The four remaining previously uncollected introduced species have a longer record of residence in Florida: *Ny. pubens* (1953), *Ph. flavens* (1951), *St. membranifera* (1943), and *Tet. lanuginosum* (1933).

Several long-established introduced species in the DCTU1988 list were not found in our survey; dates in parentheses from Deyrup et al. (2000): *M. destructor* (1933), *Mo. pharaonis* (1908), *Ps. stigma* (1887), and *Tet. bicarinatum* (1895).

Eight native species known from the Keys were not collected in our survey: *Ap. flemingi*, *Ap. miamiana*, *Brachymyrmex* sp. (the possibly parasitic species), *Ca. decipiens*, *Cr. minutissima*, *D. testacea*, *Ne. opacithorax*, and *Od. brunneus*. Some of these species are best collected with light traps or flight traps, which we did not use. Others have only been collected once and are rare or difficult to sample. Species that should have been found, given our methods and sampling effort, are *Ap. miamiana*, *Cr. minutissima*, and *Od. brunneus*.

Several species of ants that we did not find are listed from unspecified sites in the lower Keys (Forys and Allen 2005). We do not include these because there appear to be some problems with identifications; the voucher specimens are missing or mislaid.

In addition to providing a new survey of the ants of the Keys system, we wished to document the occurrence of species on individual keys to indicate the distribution of ant species. This resulted in 199 new records of ants for specific Keys.

In summary, we found only two additional native ant species in the Florida Keys, but nine additional introduced species. It is clear that the Keys are gradually accumulating more species of introduced ants. This increase in introduced species is compelling, as some of these species are now common and would not have been overlooked if they had been present in high density during these previous sampling regimes. The failure to find 12 previously reported species suggests that there may be some long-term changes in the ant fauna, with some native and introduced species becoming rare or disappearing, while other introduced species are becoming commoner or are invading for the first time. The Florida Keys may be undergoing a modified and accelerated form of the taxon cycle proposed by Wilson (1961) for the Melanesian ant fauna, with waves of newly arrived species displacing or reducing populations of certain native species and previously introduced species.

Origins of the Ant Fauna of the Florida Keys. The ants of the Florida Keys may be divided into groups that reflect probable time and mode of arrival. A group of 41 species that are widespread in southeastern North America may have moved into the Keys as long ago as 16,000 yr before present (ybp), and are considered native in our list of species above. A group of 12 species that appear to be native to Cuba

and the Bahamas may have also colonized the Keys in Pre-Columbian times, probably in the last 6,000 yr. A group of 18 Neotropical species were probably imported by humans in Post-Columbian times. A group of 19 species from the Old World tropics and subtropics were clearly imported by humans in Post-Columbian times. A series of four species cannot be assigned to any of these groups without further data. The factors determining the arrival of the first four groups of ants are discussed below.

The area occupied by the present Florida Keys was submerged during the Sangamon Interglacial, about 125,000 ybp, when sea levels were about 6–8-m higher than at present (Randazzo and Halley 1997, Lodge 2010). Much of the present coralline rock and other limestone deposits that make up the present Keys were laid down during this submergence (Hoffmeister and Multer 1968, Robbin 1984, Lidz and Shinn 1991). In an evolutionary sense, therefore, the native ants of the Keys are a recently constituted fauna, without ancient lineages that evolved in the Keys themselves. As subsequent cooling relocated water into ice sheets, sea level dropped to about 120 m below the present level about 16,000 ybp, exposing not only the present Keys, but also the entire Florida Shelf, extending far out to the west and to the edge of the Florida Straits on the eastern and southern boundaries of the Keys (Fairbridge 1974, Robbin 1984, Randazzo and Halley 1997, Lodge 2010). During this low stand of the sea ants could have moved relatively freely from the region of present mainland peninsular Florida south down a “Keys Peninsula” at least 150 km in width. Pine cones and bits of pinewood from this time have been found in sediments about 60 km west of Key West in 12 m of water indicating the width of the southern end of the Keys Peninsula (Ross et al. 2009).

Even at the low stand of the sea around 16,000 ybp, the Florida Straits prevented overland exchange for West Indian ants and those of North America. Moreover, the climate of Florida during the last glaciations was probably not suitable for tropical ants, but cooler and drier than now (Lodge 2010). West Indian plants, many of which have fruits whose seeds are transported by birds allowing them to cross the Florida Straits, did not begin to colonize the Florida Keys until about 6,000 ybp (Lodge 2010), after the climate became warmer and the sea had risen to near its present level (Robbin 1984).

In our consideration of whether a species is native or introduced in the Keys, we have made the assumption that ant species that are widespread in southeastern North America could have made their way to the Keys unassisted, either overland when sea level was lower, or by areal dispersal of queens later. It is always possible, however, that some native mainland species were brought to the Keys through commerce, especially through the nursery trade. There is no convenient way to discover how long a particular species of North American ant has been established in the Keys, although genetic tests might reveal populations of ants that have been isolated in the Keys since the islands were connected to the mainland. We have not observed any obvious morphological indicators comparable to those found in some isolated Keys populations of plants and vertebrates (Snyder et al. 1990), or invertebrates, such as flightless Keys endemic species of *Belocephalus* katydidids (Tettigoniidae) (Walker 1994).

Tropical species of ants could have strayed to the Keys as alate, mated queens from Cuba or the Bahamas at any time after climate and habitats became suitable. Such colonization has always been obstructed by the Florida Straits on the eastern and southern margins of the Keys, separating the Keys from the Bahamas and Cuba by distances of about 100–200 km. Some ants that are widely distributed and common in coastal habitats of the Bahamas have not attained the Keys. These include *Crematogaster steinheili* Forel, *Camponotus ramulorum* Wheeler, and the beach-inhabiting *Dorymyrmex antillana* Snelling. There are 12 species that we believe could have colonized the Keys without human assistance. Seven of the 12 are coastal species often found in mangrove twigs. These mangrove species might have arrived either as alate queens or in floating trees after a storm. The former mode seems likely, as mangrove ants are adapted for dispersal over open

water to colonize isolated mangrove islets (Simberloff and Wilson 1970).

We have listed 17 species that we consider were probably introduced from the mainland Neotropics. There is documentation of the arrival of six of these into mainland Florida. The remaining 11 are widespread Neotropical species, 10 of which also occur in the Bahamas (Deyrup et al. 1994). We do not consider it likely that these species arrived from the West Indies in Pre-Columbian times because there is ample evidence that the ant fauna of the Greater Antilles and the derived fauna of the Bahamas evolved in isolation (Wilson 1988). It is highly unlikely, although not impossible, that members of this isolated fauna went on to conquer the hyperdiverse mainland Neotropics once they were imported to the mainland. It is much more likely that these species originated in the mainland Neotropics and prospered after being imported into the West Indies and the Florida Keys.

In the Florida Keys, there are 19 species of ants imported from the Old World tropics or subtropics. Most of these species have been widely dispersed through the warm parts of the world, usually before any investigation of their regions of origin. Fifteen of these species were already established in Florida at the time of the earliest surveys of Florida ants (Smith 1930, 1933; Wheeler 1932). The Old World provenance of these species, however, does not seem to be in doubt; it is based on their taxonomic affinities. The significance of this large number of species brought from continents thousands of miles away is that it emphasizes the ease with which ants may be inadvertently transported. There were centuries of unregulated commerce between Florida and every part of the globe following the European discovery of Florida. This commerce included plants in tubs of soil (Deyrup et al. 2000) and was codified in an 1838 Act of Congress intended to “encourage the introduction and promote the cultivation of tropical plants in the United States” (Gifford 1972). Many of the 37 species of ants that we consider introduced into the Keys have probably arrived not once, but multiple times. Every load of landscape plants rumbling down Route 1 from Homestead probably repetitively introduces exotic ants.

Conservation Implications of This Survey

Potential Effects of Newly Discovered Introduced Species. The discovery of nine additional introduced ant species is not good news from a conservation perspective (Holway et al. 2002), but the ecological effects of introduced species can vary widely (Deyrup et al. 2000). Several of these nine species have no record of population outbreaks in south Florida, where they remain minor elements of the fauna, even in disturbed sites. These apparently relatively innocuous species are *An. mayri*, *Br. minutus*, *Ph. flavens*, *St. membranifera* and *Tet. lanuginosum*. There is no reason to suspect that any of these species will behave differently in the Florida Keys than in other parts of South Florida.

Three newly discovered introduced species have undergone population outbreaks in mainland Florida: *Br. patagonicus*, *Tec. difficilis* and *Ny. pubens*, (or possibly *N. fulva*). Like many other invasive ant species, these are strongly dependent on honeydew producing sap-sucking insects, and exudates from extrafloral nectaries (Oliver et al. 2008). The potential effects include both disrupting the activities of native ants and other insects associated with nectar and honeydew, and promoting population outbreaks of sap-sucking insects, including nonnative species (Oliver et al. 2008). *Br. patagonicus*, which has achieved pest status in the northern part of its range (MacGown et al. 2007), might be able to displace the supposedly native species *Br. obscurior*, except on dry and sandy sites. *Tec. difficilis* is also a pest species, especially around buildings (Warner et al. 2005) and might displace native ants associated with dead wood, palm leaf bases and hollow twigs in coastal strand habitat. *Ny. pubens* became abundant at one site in south Florida, but if the Keys specimens are actually *N. fulva*, there might be population explosions in the Keys as there have been elsewhere (Gotzek et al. 2012).

Crematogaster obscurata has no record of outbreaks in North America, but it has become abundant in two sites. It is known to occur

in mangroves (Deyrup 2007) and might disrupt the native mangrove fauna, including native ants.

Conservation Status of Native Ants in the Florida Keys. Native ants normally live in tightly structured associations of species. In the Florida Keys, these associations are probably degraded if not threatened by the introduction of 37 exotic species of ants (~40% of the ant fauna), as well as other changes to habitats as the Keys become more heavily developed by humans. The only natural community that has been extensively studied is that of mangroves (Simberloff and Wilson 1969, 1970; Cole 1983a,b). This system has been invaded by *Ca. planatus*, *Cr. obscurata*, *Mo. floricola*, *Ps. gracilis*, and *Ps. elongatus*. Nonetheless, we found mangroves retained all the ant species of earlier surveys, demonstrating at least temporary resilience of this community. Leaf litter ant communities, in contrast, were heavily polluted with introduced ants at the time of the DCTU1988 survey. The current survey emphasizes the disproportionate number of leaf-litter inhabiting introduced ants: eight of the nine introduced species reported for the first time occur often or always in leaf litter. Two habitats in the Florida Keys have not been extensively surveyed: salt marshes and rocky mangrove flats.

Among plants, vertebrates, and butterflies, there are numerous West Indian species whose North American populations are confined to the Florida Keys, or the Florida Keys and small nearby areas of the Mainland (Snyder et al. 1990). Several Keys ants show this biogeographic pattern: *Camponotus (Colobopsis)* sp. (mangrove species), *Ce. varians*, *So. corticalis*, *Tem. allardycei*, *Tem. torrei*, and *Tr. jamaicensis*. If conditions for isolated West Indian populations of other groups of organisms continue to deteriorate, West Indian ants will probably be affected as well.

Among the ants that probably immigrated to the Florida Keys via that broad land bridge of the last Ice Age, some may have been isolated long enough to have become genetically distinct as in the case of many plants and vertebrates (Snyder et al. 1990), although populations of some southeastern species may have been supplemented by movements of horticultural plants from the Mainland. Ant species, however, that seem rare in mainland South Florida or that seem confined to natural habitats are less likely to have been imported or to have moved into the Keys independently in recent times. The army ant *Ne. opacithorax* is almost certainly an Ice Age relict species, as the wingless queens are unable to cross water barriers, and its huge, active colonies are unlikely to be transported by commerce. Some southeastern species may have adapted to Florida Keys habitats that are not generally suitable for their mainland relatives. Examples are *H. inexorata* and *Tem. pergandei*, which generally occur in sandy uplands in peninsular Florida, and *My. americana*, which seems to tolerate seasonal drought in the lower Keys and require moister leaf litter on the Mainland. The most probable southeastern species for long-term isolation on the Keys are listed below; the numbers in parentheses refer to the number of Keys where each has been found: *Ap. flemingi* (1), *D. testacea* (1), *H. inexorata* (7), *My. americana* (5), *Ne. opacithorax* (3), *Ny. concinna* (2), *N. wojciki* (3), *Od. brunneus* (2), *So. pergandei* (1), *St. pallipes* (3), *St. dietrichi* (5), *Ta. sessile* (3), *Tem. pergandei* (1), and *Tr. septentrionalis* (1). Most of these are known from the Middle and Lower Keys. Only six were found in our survey. Genetic studies of possible relict populations of Keys ants would contribute to a general understanding of the biogeography of the Florida Keys.

Both long-isolated populations of southeastern ants and isolated populations of West Indian ants could be diminished or extirpated by climate changes that increase the likelihood of salt water intrusion into terrestrial habitats, a problem that is already affecting plants of the pine-land habitat of the Lower Keys (Ross et al. 2009). An increase in strong storms that damage vegetation or send storm surges inland could also affect isolated populations of ants on the Keys. In addition, habitat destruction and any increase in use of pesticides for mosquito control could also affect native ants. These factors coupled with land conversion and the introduction of large numbers of exotic species on the

Florida Keys suggests that all native species on the Florida Keys are likely under immediate and long-term threats.

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References Cited

- Alayo, P. D., and L. Zayas Montero. 1977. Estudios sobre los Himenopteros de Cuba. 7. Dos nuevas especies para la fauna myrmecologica Cubana. *Poeyana* 174: 1–5.
- Bolton, B. 2000. The ant tribe Dacetini. Part 2. *Mem. Am. Entomol. Inst.* 65: 492–1028.
- Carter, W. G. 1962. Ant distribution in North Carolina. *J. Elisha Mitchell Sci. Soc.* 78: 150–204.
- Cole, B. J. 1980. Repertoire convergence in two mangrove ant, *Zacryptocerus varians* and *Camponotus (Colobopsis)* sp. *Insectes Sociaux* 27: 265–275.
- Cole, B. J. 1983a. Assembly of mangrove ant communities: patterns of geographical distribution. *J. Anim. Ecol.* 52: 339–347.
- Cole, B. J. 1983b. Assembly of mangrove ant communities: colonization abilities. *J. Anim. Ecol.* 52: 349–355.
- de Zayas, F. 1981. Entomofauna Cubana. Seccion Oligoneoptera. Ordenes Hymenoptera y Strepsiptera, 111 pp. Toma VIII. Editorial Cientifica-Technica, Havana, Cuba.
- Deyrup, M. 1991. Exotic ants of the Florida Keys (Hymenoptera: Formicidae), pp. 15–22. *In* W. Hardy Eshbaugh (eds.), *Proceedings of the 4th Symposium on the Natural History of the Bahamas*. Field Station, San Salvador, Bahamas.
- Deyrup, M. 2002. The exotic ant *Anochetus mayri* in Florida (Hymenoptera: Formicidae). *Fla. Entomol.* 85: 658–659.
- Deyrup, M. 2007. An acrobat ant, *Crematogaster obscurata* (Hymenoptera: Formicidae), poses an unusual conservation question in the Florida Keys. *Fla. Entomol.* 90: 753–754.
- Deyrup, M. A., N. Carlin, J. Trager, and G. Umphrey. 1988. A review of the ants of the Florida Keys. *Fla. Entomol.* 71: 163–176.
- Deyrup, M., L. Davis, and S. Buckner. 1994. Composition of the ant fauna of three Bahamian Islands, pp. 23–32. *In* Lee B. Kass (eds.), *Proceedings of the 5th Symposium on the Natural History of the Bahamas*. Field Station, San Salvador, Bahamas.
- Deyrup, M., C. Johnson, and L. Davis. 1997. Notes on the ant *Eurhopalothrix floridana*, with a description of the male (Hymenoptera: Formicidae). *Entomol. News* 108: 183–189.
- Deyrup, M., L. Davis, and S. Cover. 2000. Exotic ants in Florida. *Trans. Am. Entomol. Soc.* 126: 293–326.
- Fairbridge, R. W. 1974. The Holocene sea level record in south Florida, pp. 223–231. *In* P. J. Gleason (ed.), *Environments of South Florida present and past*. I. Miami Geological Society, Coral Gables, FL.
- Forys, E. A., and C. R. Allen. 2005. The impacts of sprawl on biodiversity: the ant fauna of the lower Florida Keys. *Ecol. Soc.* 10: 25.
- Forys, E. A., C. R. Allen, and D. P. Wojcik. 2002. Influence of the proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys. *Biol. Conserv.* 108: 27–33.
- Gifford, J. C. 1972. *On preserving tropical Florida*, 222 pp. University of Miami Press, Coral Gables, FL.
- Gotzek, D., S. G. Brady, R. J. Kallal, and J. S. Lapolla. 2012. The importance of using multiple approaches for identifying emerging invasive species: the case of the raspberry crazy ant in the United States. *PLoS One* 7, e45314: 1–10.
- Hoffmeister, J. E., and H. G. Multer. 1968. Geology and origin of the Florida Keys. *Bull. Geol. Soc. Am.* 79: 1487–1502.
- Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33: 181–233.
- Lidz, B. H. and E. A. Shinn. 1991. Paleoshorelines, reefs and a rising sea: South Florida, USA. *J. Coastal Res.* 7: 203–229.
- Lodge, T. E. 2010. *The everglades handbook: understanding the ecosystem*, 392 pp. CRC Press, Boca Raton, FL.
- MacGown, J. A., J. V. Hill, and M. Deyrup. 2007. *Brachymyrmex patagonicus* (Hymenoptera: Formicidae), an emerging pest species in the southeastern United States. *Fla. Entomol.* 90: 457–464.
- Maschinski, J., M. S. Ross, H. Liu, J. O'Brien, E. J. Von Wettbert, and K. E. Haskins. 2011. Sinking ships: conservation options for endemic taxa threatened by sea level rise. *Clim. Chang.* 107: 147–167.
- Oliver, T. H., T. Pettitt, S. R. Leather, and J. M. Cook. 2008. Numerical abundance of invasive ants and monopolization of exudates-producing resources—a chicken and egg situation. *Insect Conserv. Divers.* 1: 208–214.
- Randazzo, A. F., and R. B. Halley. 1997. Geology of the Florida Keys, pp. 251–259. *In* A. F. Randazzo and D. S. Jones (eds.), *The geology of Florida*. University Press of Florida, Gainesville, FL.
- Robbin, D. M. 1984. A new Holocene sea level curve for the upper Florida Keys and Florida Reef Tract, pp. 427–458. *In* P. J. Gleason (ed.), *Environments of South Florida, present and past*. II. Miami Geological Society, Coral Gables, FL.
- Ross, M. S., J. O. O'Brien, R. G. Ford, K. Zhang, and A. Morkill. 2009. Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems. *Front. Ecol. Environ.* 7: 471–478.
- Schmidt, C. A., and S. O. Shattuck. 2014. The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of Ponerine ecology and behavior. *Zootaxa* 3817: 1–242.
- Schmidt, J. A., R. McCleery, J. R. Seavey, S. E. Cameron Devitt, and P. M. Schmidt. 2012. Impacts of half century of sea-level rise and development on an endangered mammal. *Global Chang. Biol.* 18: 3536–3542.
- Simberloff, D., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50: 278–269.
- Simberloff, D., and E. O. Wilson. 1970. Experimental zoogeography of islands: a two-year record of colonization. *Ecology* 51: 934–937.
- Smith, M. R. 1930. A list of Florida ants. *Fla. Entomol.* 14: 1–6.
- Smith, M. R. 1933. Additional species of Florida ants, with remarks. *Fla. Entomol.* 17: 21–26.
- Snelling, R. R., and J. J. Longino. 1992. Revisionary notes on the fungus-growing ants of the genus *Cyphomyrmex rimosus* group (Hymenoptera: Formicidae: Attini), pp. 480–494. *In* D. Quintero and A. Aiello (eds.), *Insects of Panama and Mesoamerica: selected studies*. Oxford University Press, Oxford, England.
- Snyder, J. R., A. Herndon, and W. B. Robertson, Jr. 1990. South Florida rockland, pp. 230–277. *In* R. L. Myers and J. J. Ewel (eds.), *Ecosystems of Florida*. University of Central Florida Press, Orlando, FL.
- Thompson, C. R. 1989. The thief ants, *Solenopsis molesta* group of Florida (Hymenoptera: Formicidae). *Fla. Entomol.* 72: 268–283.
- Trager, J. C. 1984. A revision of the genus *Paratrechina* (Hymenoptera: Formicidae) of the Continental United States. *Sociobiology* 9: 49–162.
- Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). *J. New York Entomol. Soc.* 99: 141–198.
- Umphrey, G. J. 1996. Morphometric discrimination among sibling species in the *fulva-rudis-texana* complex of the ant genus *Aphaenogaster* (Hymenoptera: Formicidae). *Can. J. Zool.* 74: 528–559.
- Walker, T. J. 1994. Order Orthoptera, family Tettigoniidae, pp. 332–335. *In* M. Deyrup and R. Franz (eds.), *Rare and endangered biota of Florida*, vol. IV. Invertebrates. University Press of Florida, Gainesville, FL.
- Ward, P. S. 1992. Ants of the genus *Pseudomyrmex* (Hymenoptera: Formicidae) from Dominican amber, with a synopsis of the extant Antillean species. *Psyche* 99: 55–85.
- Warner, J., R. H. Scheffrahn, and B. Cabrera. 2005. White-footed, *Technomyrmex albipes* (Fr. Smith). (Insecta: Hymenoptera: Formicidae: Dolichochochodidae). University of Florida IFAS Extension Doc. EENY-273. (<http://edis.ifas.ufl.edu/pdf/IN/IN55100.pdf>).
- Wetterer, J. K., and B. C. O'Hara. 2002. Ants (Hymenoptera: Formicidae) of the Dry Tortugas, the outermost Florida keys. *Fla. Entomol.* 85: 303–307.
- Wheeler, W. M. 1910. The North American ants of the genus *Camponotus* Mayr. *Ann. New York Acad. Sci.* 20: 295–354.
- Wheeler, W. M. 1932. A list of the ants of Florida with descriptions of new forms. *J. New York Entomol. Soc.* 40: 1–17.
- Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95: 169–193.
- Wilson, E. O. 1964. The ants of the Florida Keys. *Breviora* 210: 1–14.
- Wilson, E. O. 1988. The biogeography of West Indian ants (Hymenoptera: Formicidae), pp. 214–230. *In* J. K. Liebherr (ed.), *Zoogeography of Caribbean insects*. Cornell University Press, Ithaca, NY.
- Wilson, E. O. 2003. *Pheidole* in the New World. A dominant, hyperdiverse ant genus, 794 pp. Harvard University Press, Cambridge, MA.
- Wilson, E. O., and R. W. Taylor. 1967. The ants of Polynesia (Hymenoptera: Formicidae). *Pac. Insects Monogr.* 14: 1–109.

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