

Long-term impact of exotic ants on the native ants of Madeira

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Abstract. 1. The earliest exotic records for two notorious invasive ants, the big-headed ant (*Pheidole megacephala*) and the Argentine ant (*Linepithema humile*), both come from the Atlantic islands of Madeira, where the two species underwent population explosions in the 1850s and 1890s respectively. Researchers have long assumed that these invaders spread across all of Madeira and exterminated most or all native ants, despite no research actually documenting such impact.

2. Re-examination of first-hand nineteenth century accounts suggest that *P. megacephala* and *L. humile* may never have spread beyond coastal lowland areas, representing < 10% of Madeira's land area. In 2002, native ants dominated most of Madeira; *P. megacephala* and *L. humile* were restricted to $\approx 0.3\%$ and $\approx 6\%$ of Madeira's land area respectively.

3. Of the 10 native ant species known from Madeira, only one (*Temnothorax wollastoni*) was not present in 1999–2002 surveys. Although exotic ants may have exterminated *T. wollastoni*, it seems likely that this species still survives.

4. Thus, even after 150 or more years of residence, *P. megacephala* and *L. humile* have come to occupy only a small part of Madeira, and appear to have had little impact.

5. Most of Madeira may be too cool for *P. megacephala* and perhaps too moist for *L. humile* to dominate. Also, Madeira's vast natural areas may generally lack weedy vegetation that can support high densities of plant-feeding Hemiptera critical for the ecological dominance of invasive ants. Finally, a dominant native ant, *Lasius grandis*, inhabiting $\approx 84\%$ of Madeira, may actively exclude *P. megacephala* and *L. humile*.

Key words. Argentine ant, big-headed ant, biodiversity, biological invasions, exotic species, Formicidae, *Lasius grandis*, *Linepithema humile*, Madeira, *Pheidole megacephala*.

Introduction

Exotic species, spread through human commerce, are threatening native species worldwide. The impact of exotics is considered one of the two major ongoing causes (along with destruction of native habitat) leading to the decline and extinction of species

(Wilson, 1992). Several ant species are known to have major ecological impacts in exotic locales (Hölldobler & Wilson, 1990; Williams, 1994). When these species invade, they commonly experience enormous population explosions and come to dominate widespread areas. Where these species occur at high densities, they negatively impact native species and act as important agricultural pests by enhancing populations of phloem-feeding Hemiptera (Hölldobler & Wilson, 1990).

Two of the most widespread and destructive invasive ants are the big-headed ant (*Pheidole megacephala* (Fabricius)), originally from tropical Africa, and the Argentine ant (*Linepithema*

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humile (Mayr), formerly *Iridomyrmex humilis*), originally from subtropical South America. Where *P. megacephala* occurs in high densities, this species can be remarkably thorough in exterminating native ant species (Wetterer, 2002). For example, Wheeler (1908) surveyed ants on the tiny Caribbean island of Culebrita, and reported that *P. megacephala* 'was nesting under every stone and log, from the shifting sand of the sea-beach to the walls of the light-house on the highest point of the island. The most careful search failed to reveal the presence of any other species ... It is highly probable that *Ph. megacephala* ... had exterminated all the other ants which must have previously inhabited Culebrita.' In areas where it dominates, *L. humile* is also highly destructive to native species. The spread and impact of *L. humile* has received much attention, no doubt because it is a major pest in the USA and Europe (e.g. see Human & Gordon, 1997; Suarez *et al.*, 1998; Holway, 1999; Wetterer *et al.*, 2001).

Early invasions by P. megacephala and L. humile: Hawaii, Bermuda, and Madeira

Although *P. megacephala* is primarily tropical and *L. humile* is primarily subtropical, some areas have been invaded by both species, notably the tropical Pacific islands of Hawaii and the subtropical Atlantic islands of Bermuda. In both locales, *P. megacephala* and *L. humile* appear to have had great long-term impacts on the local biota over extensive areas. *Pheidole megacephala* invaded Hawaii in the nineteenth century, and by 1880 it was dominant through much of the lowlands (Blackburn & Kirby, 1880). *Linepithema humile* was a later arrival, first collected in Hawaii in 1940 (Zimmerman, 1941). Currently, *P. megacephala* is the dominant ant below 1000 m elevation in Hawaii, whereas *L. humile* is largely absent from the Hawaiian lowlands, and instead dominates areas above 1000 m elevation (Skaife, 1955; Cole *et al.*, 1992; Reimer, 1994; Wetterer, 1997, 1998; Wetterer *et al.*, 1998). Numerous authors have documented how *P. megacephala* and *L. humile* have caused drastic reductions in the populations of native invertebrate species in Hawaii (e.g. Zimmerman, 1948; Cole *et al.*, 1992; Reimer, 1994). *Pheidole megacephala* was first recorded in Bermuda in 1889 (Dahl, 1892), and was by far the most dominant ant species there in the early twentieth century (Haskins, 1939). When *L. humile* arrived in Bermuda in the 1940s, this new invader quickly overran much territory, driving back *P. megacephala*. *Pheidole megacephala*, however, persisted, and ever since, these two species have been contesting ever-shifting battlefronts between mutually exclusive territories that together occupy most of the land area of Bermuda (Haskins, 1939; Haskins & Haskins, 1965, 1988; Crowell, 1968; Lieberburg *et al.*, 1975; Wetterer & Wetterer, 2004). In addition to the two dominant ant species, 18 other ant species are known from Bermuda, though currently all are inconspicuous and/or very rare (Wetterer & Wetterer, 2004).

Remarkably, the earliest known exotic records for both *P. megacephala* and *L. humile* come from the subtropical Atlantic islands of Madeira, where these two species underwent population explosions in the 1850s and 1890s respectively (Heer, 1852; Schmitz, 1896). Numerous researchers have drawn

parallels between the successive invasions of *P. megacephala* and *L. humile* in Hawaii and Bermuda and events that took place earlier in Madeira. Many of these retellings report how *P. megacephala* and/or *L. humile* impacted the native ants of Madeira. Some even reported that these exotic ants had completely exterminated most or all the native ants of Madeira (e.g. Newell & Barber, 1913; Wheeler, 1922, 1934; Donisthorpe, 1927; Haskins, 1939; Brian, 1956; Skaife, 1961; Larson & Larson, 1965; Haskins & Haskins, 1965, 1988; Simberloff, 1978). For example, Haskins and Haskins (1965) wrote: 'Heer's careful studies (1852, 1856) leave no doubt that by the middle of the nineteenth century *Pheidole megacephala* had supplanted the entire native ant fauna of Madeira. By 1898 it had itself been as completely supplanted by *I. humilis*.' This account, if true, would be remarkable. Published reports concerning the impacts of exotic ants in Madeira, however, misrepresent actual first-hand observations (see Wetterer, 2006a); no previous study has examined the impact of *P. megacephala* and *L. humile* on any native species in Madeira. The present paper evaluates the possible long-term impacts of *P. megacephala* and *L. humile* on the native ants of Madeira.

Nineteenth century records of ants in Madeira

Oswald Heer, a Swiss botanist and paleontologist, visited Madeira from winter 1850 to spring 1851. Heer's (1852) article 'On the house ant of Madeira' (in German, translated into English in 1856) described how *P. megacephala* was 'found on the whole south side of the island of Madeira, up to a height of about 1000 feet above the sea, in incalculable numbers, especially in hot sunny places. In turning over 10 stones in such places, these ants are pretty sure to be living under eight. In the city of Funchal there can scarcely be a house which does not harbour millions of these creatures.' Heer (1852) did not mention any impact of *P. megacephala* on other ants, and mentioned only one other ant species in Madeira, *Formica fusca* L.

In 1894, Ernst Schmitz, a German priest and ornithologist who moved to Madeira in 1878 (da Silva & de Menezes, 1940), sent ant specimens to Auguste Forel, a Swiss psychiatrist and myrmecologist, for identification. Forel (1895) wrote (translated here from German): 'to my surprise Mr Schmitz twice sent me from Madeira the typical *Iridomyrmex humilis* Mayr from the Neotropical fauna, which is already a house and land pest in Madeira.' Schmitz (1896); translated here from Portuguese) published a detailed account of the *L. humile* outbreak in Madeira, writing: 'in Funchal and its outskirts, ants have become, in the past few years, a true plague and public calamity. By the millions they invade everything, fields, gardens, parks, and particularly houses... Outside the city of Funchal and its outskirts, [*L. humile*] already often dominates on the southern coast of Madeira. On the east and north coast of the island it is still uncommon.' Schmitz (1896) wrote that *P. megacephala* had 'fled entirely from Funchal and its suburbs ahead of the South American invader. Only at a distance of one league from Funchal, near the S. Gonalo crossroad, in sandy and rocky land, can it be encountered.' Although Schmitz (1896) did not evaluate the impact of *L. humile* on native ants, he cautioned

that 'It must be feared, as Dr Forel says, that Iridomyrmex will destroy little by little all the other local species and it will not delay also to invade the south of Europe.

Although nineteenth century reports did not examine the impact of exotic ants on native ants in Madeira, nineteenth century ant collections allow us to examine long-term changes in the ant fauna of Madeira. The earliest ant collection on Madeira was made by Thomas V. Wollaston, an English coleopterist who visited Madeira numerous times beginning in 1847. Wollaston's only published reference to Madeiran ants concerned a beetle inhabiting *P. megacephala* nests (Wollaston, 1854). Other authors, however, published records of 12 ant species from Madeira based on specimens that Wollaston collected (Smith, 1858; Saunders, 1903; Donisthorpe, 1940; Bolton, 1977, 1980, 1987; Tables 1 and 2). Smith (1858) also listed unattributed records for two ant species from Madeira (*F. fusca* and *Paratrechina longicornis*). A second major ant

collection in nineteenth century Madeira was made by Schmitz (1896), who wrote: 'I endeavored to document the principal ant species currently existing in the Madeira archipelago and the Selvagens, encouraged by Dr Forel, who in good will offered to classify and describe all the material sent to him.' In total, Forel (1895, 1904) identified 14 ant species among the specimens sent by Schmitz (Tables 1 and 2). The ant collections in Madeira by Wollaston and Schmitz coincided with the outbreaks of *P. megacephala* and *L. humile* respectively. Between these periods, Mayr (1865, 1876) and Emery (1882, 1893) published records of minor ant collections from Madeira, totalling six species (Tables 1 and 2).

The present study attempted to document all ant species ever collected in Madeira, based on published accounts and examination of ant specimens collected by Wollaston and Schmitz. Then, in 2002, ants were collected in Madeira to determine which species are still present and thus evaluate whether Forel's

Table 1. Madeira ant records during the outbreaks of *Pheidole megacephala* (a) and *Linepithema humile* (c), between the outbreaks (b), and after the outbreaks (d–e), and the documented range on Atlantic islands and inferred origin and status of each species.

	Madeira records	Atlantic range	Origin/status
Native ants			
<i>Lasius grandis</i> Forel	abcde	_zmc__	M
<i>Plagiolepis schmitzii</i> Forel	a_cde	_zmc__	M
<i>Monomorium carbonarium</i> (Smith)	abcde	_zm__	E
<i>Tapinoma madeirense</i> Forel	a_cde	_m__	M
<i>Monomorium subopacum</i> (Smith)	abcde	_mcva_	M
<i>Hypoponera eduardi</i> (Forel)	a_c_e	_zmcv__	M
<i>Myrmecina graminicola</i> (Latreille)	___e	_m__	P
<i>Temnothorax unifasciatus</i> (Latreille)	a___e	_zm__	M
<i>Pheidole pallidula</i> (Nylander)	___e	_mc__	M
<i>Temnothorax wollastoni</i> (Donisthorpe)	a___	_m__	E
Exotic ants			
<i>Linepithema humile</i> (Mayr)	a_cde	bzmc__h	NT
<i>Tetramorium caldarium</i> Roger	a_c_e	bzmcv_h	PT
<i>Paratrechina longicornis</i> (Latreille)	ab___e	bzmcvah	OT
<i>Cardiocondyla emeryi</i> Forel	___cde	b_mcvah	AT
<i>Pheidole megacephala</i> (Fabricius)	a_c_e	bzmcvah	AT
<i>Hypoponera</i> sp.	___e	_m___h	?
<i>Solenopsis</i> sp. 1	___e	?zm___?	?T
<i>Hypoconera punctatissima</i> (Roger)	ab___e	bzmcv_h	MT
<i>Paratrechina jaegerskioeldi</i> (Mayr)	___e	_mc__	MT
<i>Cardiocondyla mauritanica</i> Forel	___e	_mc_a_	MT
<i>Pyramica membranifera</i> (Emery)	___e	_m_v__	AT
<i>Strumigenys silvestrii</i> Emery	___e	_m__	N
<i>Technomyrmex albipes</i> (Smith)	___e	_m_v__	OT
<i>Solenopsis</i> sp. 2	___e	_m__	?T
<i>Monomorium pharaonis</i> (L)	___e	_mc__	OT
<i>Tetramorium bicarinatum</i> (Nyl.)	a_c__	_zmcv__	AT
<i>Messor structor</i> (Latreille)	___c__	_m__	M
<i>Camponotus</i> sp.	___b__	_m__	?

Species ordered by number of 1989–2002 records (see Table 3) or date last recorded. Madeira records: a = 1847–58 (Wollaston in numerous sources; Heer, 1852; Smith, 1858), b = 1957–1893 (Mayr, 1865, 1876; Emery, 1882, 1893), c = 1894–1904 (Forel, 1895, 1904; Schmitz, 1896, 1897), d = 1935–67 (Stitz, 1940; Wellenius, 1949; Krauss, unpublished), e = 1989–2002 (Espadaler & Báez, 1993; present study). Atlantic range: b = Bermuda, z = Azores, m = Madeira, c = Canary Islands, v = Cape Verde, a = Ascension, h = St Helena. Origin/Status: E = Macaronesian, M = Mediterranean, New = New World, P = Palearctic, A = African, O = Asian, T = tramp species.

Table 2. Erroneous Madeiran ant records from the nineteenth century. Symbols as in Table 1.

<i>Formica fusca</i>	a_	= <i>litres. grandis</i>
<i>Lasius niger</i>	abc	= <i>litres. grandis</i>
<i>Monomorium monomorium</i>	_b_	= <i>M. carbonarium</i>
<i>Monomorium salomonis</i>	_c	= <i>M. subopacum</i>
<i>Plagiolepis pygmaea</i>	a_c	= <i>P. schmitzii</i>
<i>Ponera coarctata</i>	a_	= <i>H. eduardi</i> and <i>H. punctatissima</i>
<i>Tapinoma erraticum</i>	a_c	= <i>T. madeirense</i>
<i>Tetramorium guineense</i>	_c	= <i>T. bicarinatum</i>
<i>Tetramorium simillimum</i>	a_c	= <i>T. caldarium</i>

prediction that *L. humile* would gradually kill off the native ants of Madeira has, in fact, come to pass.

Study site

The subtropical Atlantic archipelago of Madeira, off the coast of North Africa, was originally settled by the Portuguese in the early 1400s, and is now an autonomous region of Portugal. Only the two largest islands, Madeira (737 km²) and Porto Santo (41 km²), are currently inhabited. In addition, there are more than 50 smaller, uninhabited islands (17 km² total), including two island clusters to the south, the Desertas and Selvagens. At 32.6°N, Funchal, Madeira is at approximately the same latitude as Hamilton, Bermuda (32.3°N).

Madeira is part of the Macaronesian biogeographic subregion, which also includes the Azores, Canary Islands, Cape Verde Islands, and part of the north-west African coast. The islands of Macaronesia have acted as a biological conservatory, preserving a large number of species found nowhere else in the world. The absence of many important mainland competitors and predators has allowed the survival of many relicts of the subtropical biota that inhabited the Mediterranean area before the end of the Tertiary Period, two million years ago. Madeira is particularly known for its ancient Laurisilva stands, a broadleaf evergreen forest. In addition, many groups of endemic plants, animals, and fungi have diversified tremendously in Macaronesia (Wollaston, 1854; Enghoff, 1992; Hobohm, 2000). For example, Madeira has 216 species of land snails, twice as many as all of Britain (Cook, 1996).

The island of Madeira is very mountainous, with 90% of its land area above 500 m elevation, and 33% above 1000 m (Sziemer, 1999). Most of Madeira's population lives along the southern coast, below 500 m elevation, leaving much of the rest of the island relatively undisturbed. The easternmost tip of the island of Madeira (Ponta de São Lourenço) is much drier than the rest of the island; the smaller islands of Porto Santo, the Desertas, and the Selvagens are also semiarid. Two-thirds of the island of Madeira, many small islands around Porto Santo, and all of the Desertas and Selvagens are protected as nature reserves. Madeira's Laurisilva forest is now protected as a United Nations World Heritage Site.

Methods

Museum specimens

In 1861, Wollaston sold a collection of his ant specimens from Madeira to the Oxford University Natural History Museum (ONHM). This entire collection, which had remained intact in its original drawer, was examined by XE. All these specimens, collected sometime between 1847 and 1858, were undated and labelled with taxonomic determinations by Smith and Forel.

Wollaston deposited other ant specimens from Madeira at the British Natural History Museum (BNHM). A Wollaston syn-type of *Temnothorax wollastoni* (Donisthorpe) from the BNHM was examined by XE. Wollaston's other specimens at the BNHM, identified by B. Bolton, were examined by JKW. Wollaston's ant specimens from Madeira at the BNHM were all labelled '1858.' Although Wollaston made his fifth visit to Madeira in 1858, this label may instead indicate that Smith (1858) catalogued Wollaston's specimens in that year.

Schmitz (1896) deposited a set of ant specimens in the Seminary Museum in Funchal, but curators at the Natural History Museum in Bom Sucesso, Madeira, where the Seminary collection now resides, reported that most of the collection, including all ant specimens, had been destroyed in a fire.

Forel deposited ant specimens he received from Schmitz at the Musée d'Histoire Naturelle in Geneva (MHNG). Schmitz's Madeira specimens, representing all species listed by Schmitz (1896, 1897) and Forel (1895, 1904) that were not found occurring in Madeira in 2002, were examined by XE to evaluate possible misidentifications. All these specimens, collected between 1894 and 1904, were undated and labelled with Forel's taxonomic determinations.

The ant collections at the Smithsonian Institute's National Museum of Natural History (SI) in Washington DC, and the Museum of Comparative Zoology (MCZ) at Harvard University were searched for additional ant specimens from Madeira. Ants collected by Arechavaleta *et al.* (2000) were also examined by XE. Specimens from Madeira reported by Mayr (1865, 1876) and Emery (1882, 1893) could not be obtained.

New collections

Between 1989 and 2002, ants were sampled opportunistically by AMFA and several other researchers at the Laboratório Agrícola da Madeira (J. Jesus, J. Andrade, V. Pereira, A. Fernandes, and J.P. de Carvalho), primarily at urban and agricultural sites.

All other new collections were made in 2002. JKW and ALW collected ants through visual search and sifting soil and litter samples in a wide variety of habitats, particularly concentrating on garden, urban, and semiarid areas, where exotic ants could be found. The primary goal was to collect the maximum number of different ant species in the time allotted. Using such direct sampling methods proves much more efficient than site-standardised techniques designed for evaluating relative abundances of species and making detailed comparisons among a limited number of sites (such as the ALL protocol, which requires a minimum of 3 days sampling per site; Agosti & Alonso, 2000; Fisher *et al.*,

2000). Ants were collected by XE and DAP through visual search and vegetation beating, primarily in less disturbed areas and in gardens. Several undergraduates at the University of Madeira in Funchal collected ants from inside their homes.

Classification of sites and species

In the distribution analyses of ants collected by JKW and ALW, all sites that were not currently heavily disturbed by human activity were classified as less disturbed. These sites included not only relatively pristine forest and heath, but also secondary forest, planted pine forest, and grazed seminatural meadow. Under this broad definition, less-disturbed areas of Madeira included almost 90% of Madeira's land area. Sites heavily disturbed by human activity were divided into three categories: urban (built up areas without flower gardens), garden (tended flower gardens), and agriculture (tended crops). Less-disturbed sites, garden sites, and urban sites were subdivided by aridity (semiarid = sites on Madeira's Ponta de São Lourenço, plus Porto Santo, the Desertas, and the Selvagens; non-arid = all others). Non-arid, less-disturbed sites were subdivided by elevation (low: < 500 m; medium: 500–1000 m; high: > 1000 m); all semiarid sites were < 500 m elevation and all disturbed sites were < 700 m elevation. All agricultural sites except one were non-arid. Mixed-use sites were categorised according to the predominant habitat. The amount of Madeira's land area currently fitting each of these categories was estimated using a variety of sources (e.g. Sziemer, 1999; INE, 2001), then the overall occurrence of ants in Madeira was estimated by multiplying the proportion of sites where each species was found in a particular habitat type by the estimated proportion of Madeira's land area matching that habitat type and summing across all habitat types.

The native vs. exotic status of each ant species was evaluated based primarily on its known worldwide distribution. All New World species and all tramp species distributed around the world through human commerce were considered exotic to Madeira. Ant species not widely distributed beyond Macaronesia (the Azores, Madeira, the Canary Islands, and Cape Verde) and the Mediterranean, were classified as native to Madeira (i.e. pre-dating human arrival), with two exceptions described below.

Statistics

To evaluate possible impact of *P. megacephala* and *L. humile* on native and exotic ants in Madeira, mean species counts at collection sites with and without these two exotic species present were compared using two-tailed *t*-tests without assuming equal variance between samples.

Results

Species counts

Combining past and present collections, 28 ant species (10 native; 18 exotic) were recorded from Madeira (Table 1), 27

based on examination of specimens, including 10 new records (one native; nine exotic). One of these species, *Camponotus sylvaticus* (Olivier) (reported by Mayr, 1865), could not be verified with specimens from Madeira, and therefore is listed as *Camponotus* sp. Two species of thief ants, *Solenopsis* spp., were not classified to species because the taxonomy of this group is in disarray. One taxon reported from Madeira, *Plagiolepis schmitzii madeirensis* Emery, was determined by XE to be a junior synonym of another taxon present, *Plagiolepis schmitzii* Forel. *Tapinoma erraticum* var. *madeirense* Forel was raised by XE to a full species, and the European *Tapinoma ambiguum* Emery was determined to be a junior synonym of *Tapinoma madeirense*. A detailed taxonomic analysis of the ants of Madeira will be published elsewhere (Wetterer et al. unpub. ms.).

Based on examinations of museum specimens by XE, published records of seven ant species from nineteenth century Madeira were determined to be misidentifications (Table 2). Two additional species records, *Formica fusca* and *Monomorium monomorium* Bolton, were probably also misidentifications. Heer's (1852) and Smith's (1858) Madeiran records of *F. fusca* were almost certainly *Lasius grandis* Forel, by far the most common ant now on Madeira. Wheeler (1927) noted that an early record of *F. fusca* from the Canary Islands was probably *Lasius niger* (L), and he omitted *F. fusca* from his list of known Madeiran ants. Mayr (1865) reported *Monomorium minutum* Mayr (now *Monomorium monomorium*) from Madeira, but this was probably a misidentification of the very common *Monomorium carbonarium* (F. Smith), which at the time was considered a subspecies of *M. minutum*.

In total, 17 ant species (eight native; nine exotic) were collected in Madeira before 1904, and 24 ant species (nine native; 15 exotic) were collected between 1995 and 2002. These included a previously unreported *L. humile* specimen in the BNHM collected by Wollaston in Madeira between 1847 and 1858. In 2002, 22 ant species were collected in Madeira and specimens for two other species collected in 1995 (by AMFA) and 1999 (by M. Arechavaleta) were examined. Four ant species (one native; three exotic) collected before 1904 were not collected in 2002; 11 species (two native; nine exotic) collected between 1995 and 2002 were not collected before 1904.

Although there is necessarily some uncertainty in evaluating native vs. exotic status, the classifications of most ant species in Madeira, including all common species, appear to be robust. Tentative natives include only *Myrmecina graminicola* and *Pheidole pallidula*, the former known from Europe, the latter from the Mediterranean. Doubts arise primarily because these species were first found in Madeira only recently (1989 and 1999 respectively). Tentative exotics include three species not known to be tramp species: *Camponotus* sp., *Hypoponera* sp., and *Messor structor* (Latreille). Mayr (1865) reported *Camponotus sylvaticus* collected in Madeira by the Novara Expedition, which spent 9 days in Funchal in November 1857 (Mayr, 1865). *Camponotus sylvaticus* is a soil-nesting European species that seems unlikely to occur in Madeira. This record was probably a different species of exotic *Camponotus* that temporarily infested an imported wood product (see Wetterer & Wetterer, 2004). *Hypoponera* sp. was classified as exotic because it is also known from St Helena in the South Atlantic and

it may be synonymous with a *Hypoconera* known from Japan (XE unpublished data). Schmitz (1896) found *Messor structor* only in an urban flower garden in Funchal and considered this conspicuous Mediterranean species to be an exotic in Madeira.

Ant records in 1989–2002 collections

Because different collectors made new ant collections using different methods, in different habitats, and for different purposes, data from each collector were analysed separately.

Between 1989 and 2002, 12 ant species (four native; eight exotic) were recorded by AMFA and researchers from the Laboratório Agrícola da Madeira, primarily from urban and agricultural sites (Table 3). Despite this collection coming almost exclusively from highly disturbed environments, with a probable bias toward conspicuous and pest species, the three most commonly recorded species were all native. The most common exotic ant collected, *L. humile*, was a distant fourth. It was the subjective impression of AMFA that *L. humile* was less common in 2002 than it was 10 years earlier.

Arechavaleta *et al.* (2000) listed *Monomorium salomonis* (L) (identified by XE) collected in 1999 on two arid islands in the

far south of Madeira, Selvagem Pequena and Selvagem Grande. A re-examination of these specimens by XE indicated that these specimens actually were *M. subopacum*. Arechavaleta *et al.* (2000) accidentally omitted a record of *Pheidole pallidula* (Nylander) from Selvagem Grande in 1999.

Twenty ant species (seven native; 13 exotic) were collected by JKW and ALW at 94 sites on Madeira and 19 sites on Porto Santo (Tables 3 and 4). *Lasius grandis* was the most common species collected; *Tetramorium caldarium* Roger was the most common exotic ant collected. These records are analysed more thoroughly below.

Five ant species (all native) were collected by DAP and two undergraduates at the University of Madeira (Élvio Nunes and Iola Martins) in 196 standardised vegetation-beating samples from relatively natural habitat. Every sample had only one ant species present. *Lasius grandis* was by far the most common ant collected, making up over 90% of the samples (Table 3).

Seventeen ant species (eight native; nine exotic) were collected by XE at 23 sites on Madeira, primarily in relatively natural areas, but also in a few urban gardens. The four most commonly recorded species were all native; *Tetramorium caldarium* and *Paratrechina longicornis* (Latreille) were the most common exotics.

Table 3. Ant species collected Madeira in 1989–2002.

	D1	D2	D3	D4	D5	D6	D7
Samples	195	2	113	196	24	4	10
% native species	77	100	60	100	75	46	85
Native ants (no. of records)							
<i>Lasius grandis</i>	78	–	61	177	14	–	4
<i>Plagiolepis schmitzi</i>	32	–	46	3	12	2	3
<i>Monomorium carbonarium</i>	32	–	35	–	9	2	3
<i>Tapinoma madeirense</i>	6	–	13	12	10	–	–
<i>Monomorium subopacum</i>	–	2	20	–	2	2	1
<i>Hypoconera eduardi</i>	–	–	16	–	4	–	–
<i>Myrmecina graminicola</i>	–	–	9	2	4	–	–
<i>Temnothorax unifasciatus</i>	–	–	–	2	1	–	–
+ <i>Pheidole pallidula</i>	–	1	–	–	–	–	–
Exotic ants (no. of records)							
<i>Linepithema humile</i>	18	–	28	–	3	3	1
<i>Tetramorium caldarium</i>	4	–	40	–	6	2	–
<i>Paratrechina longicornis</i>	9	–	21	–	5	1	–
<i>Cardiocondyla emeryi</i>	1	–	20	–	1	1	–
<i>Pheidole megacephala</i>	8	–	7	–	1	–	–
<i>Hypoconera</i> sp.	–	–	14	–	1	–	–
+ <i>Solenopsis</i> sp. 1	–	–	9	–	–	–	–
<i>Hypoconera punctatissima</i>	–	–	6	–	–	–	–
+ <i>Paratrechina jaegerskioeldi</i>	1	–	3	–	1	–	–
+ <i>Cardiocondyla mauritanica</i>	–	–	3	–	1	–	–
+ <i>Pyramica membranifera</i>	–	–	2	–	–	–	–
+ <i>Strumigenys silvestrii</i>	1	–	1	–	–	–	–
+ <i>Technomyrmex albipes</i>	–	–	1	–	–	–	1
+ <i>Solenopsis</i> sp. 2	–	–	–	–	1	–	–
+ <i>Monomorium pharaonis</i>	1	–	–	–	–	–	–

+ = species not previously reported from Madeira. D1 = 1989–2002; AMFA *et al.*; disturbed sites, D2 = 1999; Arechavaleta; natural sites, D3 = 2002; JKW and ALW; primarily disturbed sites, D4 = 2002; DAP; natural sites, D5 = 2002; XE; mostly natural sites, D6 = 2002; XE and DAP; arid sites, D7 = 2002; University of Madeira students; inside houses.

Seven ant species (three native; four exotic) were collected by XE and DAP at four arid sites on Porto Santo. *Linepithema humile* was the most commonly collected species.

Undergraduates at the University of Madeira collected six ant species (four native, two exotic) from their homes in and around Funchal. The three most commonly collected species were natives. Two exotics, *L. humile* and *Technomyrmex albipes* (F. Smith), were collected only once each. Because *T. albipes* had no previous records from Madeira, the student's apartment was visited by JKW and ALW where *T. albipes* was also collected outdoors in nearby flower gardens.

Ant species distributions in 2002

Subdividing samples collected by JKW and ALW, average total species count was fairly consistent across all habitat types except gardens, averaging 2.1–2.8 species per site. Species composition, however, showed striking differences among the different habitat types (Table 4). Non-arid less-disturbed site samples (LN, MN, HN in Table 4) had virtually only native ant species (92–100% of species records), semiarid less-disturbed sites (DN) had 64% native species records, and urban and agri-

cultural sites (U, DU, A) had about half native species records (40–54%). Flower garden sites (G, DG) had higher total species counts (4.4–4.7 species per site), about twice that of other sites; fewer than half the site records (43–45%) were for native species. *Pheidole megacephala* was found in a very limited area: 15 records in Funchal and one record 5 km west of Funchal. *Linepithema humile* was widespread in highly disturbed low-land habitats, but essentially absent from less-disturbed habitats, except in semiarid areas.

Comparing species counts at the 85 sites without *L. humile* and the 28 sites with *L. humile*, mean number of native species was significantly higher at the former (2.0 ± 1.1 vs. 1.2 ± 1.3 ; $t_2 = 3.09$, d.f. = 40.9, $P = 0.004$), mean number of other exotic species was not significantly different (1.0 ± 1.5 vs. 1.4 ± 1.7 ; $t_2 = -1.04$, d.f. = 41.2, $P = 0.30$), mean number of all other species was not significantly different (3.0 ± 1.9 vs. 2.6 ± 2.7 ; $t_2 = 0.84$, d.f. = 36.0, $P = 0.40$).

Comparing species counts at the 106 sites without *P. megacephala* and the seven sites with *P. megacephala*, mean number of native species was significantly higher at the former (1.9 ± 1.2 vs. 0.6 ± 1.1 ; $t_2 = 3.02$, d.f. = 6.9, $P = 0.02$), mean number of other exotic species was not significantly different (1.3 ± 1.6 vs. 1.9 ± 1.6 ; $t_2 = -0.98$, d.f. = 6.9, $P = 0.36$), mean number of

Table 4. Ants in different habitats (survey by JKW & ALW in 2002; D3 in Table 3).

	Less-disturbed sites					Heavily disturbed sites				
	LN	MN	HN	DN	G	U	DG	DU	A	Overall
% land area (est.)	3	47	33	7	0.1	2	0.1	0.3	8	100
No. of sites surveyed	5	8	17	16	27	20	5	10	5	113
Mean no. of species per site	2.4	2.5	2.2	2.3	5.0	2.8	4.4	2.5	2.6	2.4
% native species	92	100	97	64	43	46	45	40	54	91
Native ants (% of sites)										
<i>Lasius grandis</i>	100	100	88	6	59	50	–	30	40	84
<i>Plagiolepis schmitzii</i>	40	50	29	38	55	35	80	10	20	39
<i>Monomorium carbonarium</i>	40	38	12	19	34	40	60	30	20	27
<i>Tapinoma madeirense</i>	–	13	65	–	3	–	–	–	–	27
<i>Monomorium subopacum</i>	–	–	–	69	3	–	60	30	40	8.2
<i>Hypoconera eduardi</i>	40	25	12	6	24	5	–	–	20	19
<i>Myrmecina graminicola</i>	–	25	–	6	21	–	–	–	–	12
Exotic ants (% of sites)										
<i>Linepithema humile</i>	20	–	–	25	31	35	20	40	40	6.4
<i>Tetramorium caldarium</i>	–	–	–	38	55	50	60	40	20	5.5
<i>Paratrechina longicornis</i>	–	–	–	–	24	40	40	30	20	2.6
<i>Cardiocondyla emeryi</i>	–	–	6	–	34	10	60	20	40	5.5
<i>Pheidole megacephala</i>	–	–	–	–	14	15	–	–	–	0.3
<i>Hypoconera</i> sp.	–	–	–	19	28	–	40	10	–	1.4
<i>Solenopsis</i> sp. 1	–	–	–	–	28	–	20	–	–	0.0
<i>Hypoconera punctatissima</i>	–	–	–	–	21	–	–	–	–	0.0
<i>Paratrechina jaegerskioeldi</i>	–	–	–	–	10	–	–	–	–	0.0
<i>Cardiocondyla mauritanica</i>	–	–	–	–	7	–	–	10	–	0.0
<i>Pyramica membranifera</i>	–	–	–	–	7	–	–	–	–	0.0
<i>Strumigenys silvestrii</i>	–	–	–	–	3	–	–	–	–	0.0
<i>Technomyrmex albipes</i>	–	–	–	–	3	–	–	–	–	0.0

Sites were classified as less disturbed (N) or heavily disturbed (G = garden, U = urban, A = agriculture). Sites were subdivided by aridity (D = semiarid; all others = non-arid). Non-arid natural sites were subdivided by elevation (L: < 500 m, M: 500–1000 m, H: > 1000 m). See text for more details.

all other species was not significantly different (3.2 ± 2.1 vs. 2.4 ± 2.5 ; $t_2 = 0.75$, d.f. = 6.6, $P = 0.48$).

A detailed analysis of each ant species in Madeira, including its ecology and distribution with respect to elevation, precipitation, and disturbance will be published elsewhere (Wetterer *et al.* unpublished data).

Discussion

The native and exotic ant fauna

Combining past and present collections, a total of 28 ant species with reliable records were documented from Madeira; 10 species appear to be native to Madeira and 18 exotic. In contrast, the more temperate Macaronesian archipelago of the Azores has only 14 known ant species (Wetterer *et al.*, 2004), 12 of which have also been collected in Madeira (five native and seven exotic; Table 1). Bermuda, in the Western Atlantic at the same latitude as Madeira, and Saint Helena, in the tropical South Atlantic, both share the same six (or possibly seven) ant species with Madeira, all common tramp species (Table 1; Wetterer & Wetterer, 2004; small thief ants, *Solenopsis* spp., found in Bermuda and Saint Helena may be the same as *Solenopsis* sp. 1).

Distribution and long-term impact of P. megacephala and L. humile

Heer (1852) and Schmitz (1896) described great nineteenth century plagues of *P. megacephala* and *L. humile* in Funchal and the south coast of Madeira, with *L. humile* also reaching the east and north coasts. Schmitz (1896) believed that *L. humile* had been introduced to Madeira 'in recent years.' It was therefore surprising to discover a previously unreported *L. humile* specimen collected in Madeira before 1858 that pre-dates all other known specimens of *L. humile*, including the type specimens from Argentina collected in 1866 (Mayr, 1868). This raises the question as to why *L. humile* apparently remained uncommon in Madeira from 1858 until about 1890, and then underwent a population explosion. Large populations of *L. humile* invariably depend heavily on honeydew produced by phloem-feeding Hemiptera, such as aphids, mealybugs, and scale insects. The population explosion of *L. humile* in Madeira therefore may have been triggered by the arrival in Madeira of a new species of mutualist scale insect or a new crop variety that made a better host for a mutualist scale insect already present in Madeira (see Wilson, 2005).

The great outbreaks of *P. megacephala* and *L. humile*, however, apparently did not extend beyond the lowlands, which make up just a small fraction of Madeira's land area. Assuming Heer's (1852) account was accurate, and the great plague of *P. megacephala* occupied the entire south side of Madeira below 1000 feet (308 m) elevation, this would represent less than 5% of the island's land area. Schmitz (1896) also mentioned *L. humile* only in coastal areas of Madeira, suggesting he did not observe them in the interior. Including the east and north coasts

of Madeira and much of Porto Santo, *L. humile* may have spread to as much as 10% of Madeira. Thus, even at their peak population densities, *P. megacephala* and *L. humile* may have impacted native ant species on only a small portion of Madeira. In addition, the population explosions of *P. megacephala* and *L. humile* may have been fairly short-lived. For example, the ant specimens reported by Mayr (1865, 1876) and Emery (1882, 1893) included neither *P. megacephala* nor *L. humile*, suggesting that *P. megacephala* populations crashed long before the *L. humile* outbreak of the 1890s.

In 2002, native ants dominated most of Madeira, despite a higher number of exotic ant species. Exotic ants were completely absent from $\approx 85\%$ of Madeira. Exotic ants were very rare in less-disturbed non-arid areas (found at 3% of sites representing $\approx 83\%$ of Madeira's land area). In contrast, exotic ants were very common in highly disturbed lowland areas (urban, garden, and agricultural sites; found at 87% of sites representing $\approx 10\%$ of land area), and fairly common in less-disturbed semiarid areas (found at 56% of sites representing $\approx 7\%$ of land area). Surprisingly, in 2002, most house ants collected were Madeira natives. Overall, *P. megacephala* and *L. humile* were restricted to about 0.3% and 6% of Madeira's land area respectively. Although it is possible that *P. megacephala*, *L. humile*, and other exotic ants spread to much of Madeira and that the native ant fauna has subsequently rebounded to reclaim most of Madeira, no evidence was found to support this.

At sites with *P. megacephala* or *L. humile* present, significantly fewer native ant species were present than at sites without these species present. Nonetheless, the long-term impact of *P. megacephala* and *L. humile* on the native ant fauna of Madeira appears to have been very limited. No evidence was found that *P. megacephala* and *L. humile* caused any widespread extinction of native ants on Madeira. Of the 10 total native ant species ever recorded in Madeira, the only one not found between 1999 and 2002 was *Temnothorax wollastoni*, a Madeiran endemic that Donisthorpe (1940) described from specimens collected by Wollaston. It is possible that *T. wollastoni* lived only in parts of Madeira that were overrun by *P. megacephala* and *L. humile* and was driven extinct by these exotics. Further, it is possible that other native ant species were exterminated before they could be collected. Because, however, it appears that exotic ants never invaded most of Madeira, it seems likely that *T. wollastoni* and possibly additional endemic ant species have survived and will be found in the future.

Possible factors limiting the distribution and impact of P. megacephala and L. humile

Even after about 150 years of residence and population explosions, *P. megacephala* and *L. humile* have failed to achieve widespread distribution and ecological dominance in Madeira, a result much different than what has been documented in Hawaii and Bermuda (see Introduction). A number of factors may have contributed to this failure, including climate, vegetation, and competitors. The extensive highlands of Madeira may be too cool for the primarily tropical *P. megacephala*, and most of Madeira may be too moist for *L. humile* to dominate. In contrast,

Bermuda, at the same latitude as Madeira, lacks highlands. Interestingly, at high elevations on the Big Island of Hawaii, *L. humile* dominates on the semiarid western slope of Mauna Kea, but does not penetrate less-disturbed parts of the more humid Kilauea Caldera region (Wetterer, 1998; Wetterer *et al.*, 1998). In addition, most of Madeira's vast protected areas may lack sufficient weedy vegetation to support high densities of plant-feeding Hemiptera critical for the ecological dominance of invasive ants. In fact, the scarcity of appropriate weedy vegetation outside highly disturbed areas may be an important factor limiting the spread of invasive ants in areas with relatively undisturbed native vegetation worldwide.

The presence of dominant native ants, notably *Lasius grandis*, which occupies an estimated 84% of Madeira's area, may also play a role in limiting the spread of *P. megacephala* and *L. humile*. In natural areas of Madeira, *L. grandis* was by far the most common ant beaten from vegetation, where they were probably tending Hemiptera; presumably *L. grandis* excludes other ant species from exploiting this resource. Both *P. megacephala* and *L. humile* have also invaded the Azores, where they are currently uncommon and restricted only to highly disturbed areas (Wetterer *et al.*, 2004). As in Madeira, the most commonly collected ant in the Azores also is *L. grandis* (Wetterer *et al.*, 2004). In contrast, Hawaii apparently never had any native ants and Bermuda currently has no dominant native ant species (Wetterer & Wetterer, 2004). In Bermuda, it is possible that a previously dominant *Lasius* species was driven extinct by *P. megacephala*; the first ant identified to species from Bermuda, collected in 1873, was classified as *Formica nigra* (= *Lasius niger*) by Kirby (1884). Unfortunately, Wetterer (2006b) was unable to find any ant specimens from nineteenth century Bermuda, nor any *Lasius* specimens from Bermuda to confirm this record.

Catastrophic vs. minimal impact of exotic ants

Observations of great ecological impacts of *P. megacephala* and/or *L. humile*, particularly in Hawaii and Bermuda, combined with misreading and misrepresentation of first-hand accounts from Madeira, led many researchers to the pessimistic belief that *P. megacephala* and *L. humile* had similar great impacts in Madeira (see Wetterer, 2006a). The present study, however, indicates that invasions and population explosions of two of the world's most destructive invasive ants do not inevitably lead to long-term ecological dominance and widespread negative impacts on other species. Some other recent studies also offer similar cause for optimism concerning the long-term impacts of destructive exotic ants. After initial population explosions, exotic ants commonly show significant declines in population density (e.g. see Deyrup *et al.*, 2000; Wilson, 2005). As a result, the long-term ecological impact of exotic ant species may not always be as severe as anticipated based on short-term studies conducted at times of peak population densities (Morrison, 2002; Morrison & Porter, 2003). As long as vulnerable species have invader-free refuges during the peak population densities of invasive ants, recovery is possible after the invaders' populations decline. For example, Torres and Snelling (1997) resurveyed ants on Culebrita, where

P. megacephala had previously exterminated all other ant species (Wheeler, 1908). They found 16 ant species present in 1982, probably colonising Culebrita from nearby islands after *P. megacephala* populations receded.

Still, in the absence of invader-free refuges, invasive ants certainly may drive many native species to extinction. For example, in 2003, JKW (unpublished data) surveyed ants on Monte Gordo, the highest mountain of the Atlantic island of São Nicolau, Cape Verde, and found only *P. megacephala* at all sites sampled except for sites within 100 m of the mountain's peak. Here, where *P. megacephala* had not yet spread, a small pocket of other ant species survived, including an endemic species known only from this mountain, *Monomorium boltoni* Espadaler & Agosti. If *P. megacephala* continues its spread up the mountain, it seems unlikely that *M. boltoni* will survive once *P. megacephala* overruns what may be its last refuge.

Although Forel's dire prediction that *L. humile* would kill off the native ants of Madeira has not come to pass, another of his predictions was quickly realised. Concerning *L. humile*, Schmitz (1897) reported 'I had occasion to establish its presence in Lisbon in September 1896. This fulfilled the prediction of Dr. Forel in 1895; that this South American ant, after having invaded Madeira, would quickly make its appearance on the European continent.' In fact, after the records of *L. humile* in Madeira starting before 1858, the next earliest exotic records all come from mainland Portugal (1890–96: Schmitz, 1897; Martins, 1907; Coutinho, 1929) suggesting that *L. humile* may have spread from South America to southern Europe (and perhaps to other parts of the world) via Madeira and then Portugal (see Wetterer & Wetterer, 2006).

Pheidole megacephala and *L. humile* began their worldwide spread in the nineteenth century and have already spread through much of their potential range (JKW, unpublished analysis). Several other highly destructive ants, however, have thus far come to occupy only a small portion of their potential ranges, most notably the little fire ant (*Wasmannia auropunctata* (Roger)) and the red imported fire ant (*Solenopsis invicta* (Buren)) (Wetterer & Porter, 2003; Morrison *et al.*, 2004). More research is needed to analyse not only where various invasive species may be able to become established based on climatic requirements, but also their potential long-term impact, which may be catastrophic (e.g. in Hawaii and Bermuda) or may be minimal (e.g. in the Azores and Madeira).

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