

Native and Exotic Ants of the Azores (Hymenoptera: Formicidae)

by

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ABSTRACT

The Azores, a North Atlantic archipelago, has 14 known ant species. Although some earlier researchers have regarded all ants in the Azores to be exotic, we believe several are native (i.e., predating human arrival). Five ant species found in relatively undisturbed environments and not widely distributed beyond the Azores, neighboring Madeira, and the Mediterranean, we judge to be native to the Azores: *Hypoponera eduardi*, *Lasius grandis*, *Leptothorax unifasciatus*, *Monomorium carbonarium*, and *Plagiolepis schmitzii*. In addition, *Tetramorium caespitum*, though widely distributed, shows variation within the Azores that suggests it is native. Six ant species found only in highly disturbed environments in the Azores and distributed around the world through human commerce, we considered exotic: *Hypoponera punctatissima*, *Linepithema humile*, *Paratrechina longicornis*, *Pheidole megacephala*, *Tetramorium bicarinatum*, and *Tetramorium caldarium*. In addition, *Solenopsis (Diplorhoptrum)* sp. of unknown taxonomic status, and *Aphaenogaster senilis*, which is not widely distributed, were restricted to disturbed sites and appear to be exotic.

Five of the six native ant species (all except *P. schmitzii*), but only two of the eight exotic species (*A. senilis* and *L. humile*) are common and widespread in the Azores. The Argentine ant, *L. humile*, is the only exotic ant species that appears to have some impact on native species, but it was abundant only in scattered urban and agricultural areas. Three ant species that are important tropical pests, *P. longicornis*, *P. megacephala*, and *T. bicarinatum*, all have their highest latitude populations in the Azores, probably a reflection of the relatively mild climate due to the warming influence of the Gulf Stream.

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Relatively natural areas in the Azores have low ant species richness, but usually all the ants present are native. Urban sites often have higher ant species richness due to the presence of both native and exotic species. Thus, the total ant species richness is not a useful indicator of habitat integrity. The presence of exotic ant species, however, is an excellent indicator of disturbance.

Twelve of the 14 recorded ant species (all except *A. senilis* and *T. caespitum*) in the Azores also occur in Madeira. The Azores have far fewer ant species than Madeira (27 species), no doubt related to the Azores' younger age, higher latitude, and greater distance from continental source populations.

Keywords: ants, Azores, exotic species, *Linepithema humile*, Macaronesia, native species

INTRODUCTION

The Azores are a north Atlantic archipelago (36.9 - 39.7°N), ~1500 km west of Portugal. The Azores consist of nine islands: São Miguel (769 km²), Pico (461 km²), Terceira (416 km²), São Jorge (261 km²), Faial (182 km²), Flores (153 km²), Santa Maria (103 km²), Graciosa (70 km²), and Corvo (20 km²). In addition, there are several smaller islets, including the Ilhéus das Formigas ("Islets of the Ants"), which are the easternmost and first-discovered part of the Azores. The Azores make up the most northern part of Macaronesia, a biogeographic subregion that also includes the archipelagos of Madeira, the Canary Islands, and Cape Verde, as well as part of the northwestern coast of Africa.

The Portuguese settled the Azores in the 15th century, and these islands quickly became an important center for commerce, particularly between Europe and the New World. With humans came many animal and plant invaders, including new competitors, predators, and parasites. Among these invaders are several ant species, well known for killing native invertebrates around the world: *Pheidole megacephala* (Fabricius) (the big-headed ant), *Linepithema humile* (Mayr) (the Argentine ant), and *Paratrechina longicornis* (Latreille) (the crazy ant).

We combined published, unpublished, and new ant records from the Azores, including all nine islands and two small uninhabited islets (Ilhéu da Vila next to São Miguel and Ilhéu Vila do Porto next to Santa Maria). Ironically, no ant collecting has been reported from the Ilhéus das Formigas. In addition, based on the distribution and ecology of each species within and outside of the Azores, we attempted to evaluate which species are native and which are exotic to the Azores.

PUBLISHED ANT RECORDS

Yarrow (1967) summarized published ant records from the Azores (Emery 1893, 1908; Wheeler 1908, 1927; Santschi 1933; Donisthorpe 1936; Wellenius 1949; Carthy 1955; records from André 1896 were overlooked -see results) and added new records of specimens collected in 1957. Yarrow (1967) concluded that the known Azores records represented a total of 12 ant species: *Aphaenogaster senilis* Mayr, *Hypoponera eduardi* (Forel), *Hypoponera punctatissima* (Roger), *Lasius niger* (L.), *Leptothorax unifasciatus* (Latreille), *L. humile*, *Monomorium carbonarium* (F. Smith), *P. longicornis*, *Ph. megacephala*, *Tetramorium bicarinatum* (Nylander) (formerly identified as *Tetramorium guineense* (Bernard)), *Tetramorium caespitum* (L.), and *Tetramorium simillimum* (Smith) (updated taxonomy following Bolton 1977, 1995). We used Yarrow's (1967) analysis as a starting point.

Seifert (1992) examined nine *Lasius* specimens from two sites in the Azores and determined them all to be *Lasius grandis* Forel. Based on our collections, we concur with this change in identification (considered further below). Heinze (1986) reported additional ant records from the Azores: *P. longicornis* from São Miguel and *T. caespitum* from São Miguel and Terceira. Heinze (1986) wrote, concerning the ants of the Azores, "of the only 12 species recorded so far not more than seven can be called abundant or well established on the islands, the others seem to be very rare or have been recorded only once." Although Heinze (1986) did not list the ant species he collected, nor which he considered common, we concur with his overall assessment that not more than seven ant species are common in the Azores (see below).

In the present paper, we examined additional ant specimens from the Azores, both previously and newly collected. Our records include new records for two ant species, raising the total number of ants known from the Azores to 14 species.

METHODS

XE examined previously collected specimens of Azores ants from two sources: 1) 54 single species samples collected in 1987 and 1989 by N.P. Ashmole and P. Oromí from caves and recent (<500 yo) lava flows (published in Ashmole *et al.* 1996); 2) 159 pinned ant specimens from the Azores in the collection of the Smithsonian Institution Museum of Natural History (SI).

From 5-18 July 2002, JKW and ALW collected ants on São Miguel (11 days) and JKW collected ants on Terceira (2 days) through visual search and sifting soil and litter in a wide variety of habitats. We sampled most

intensively in disturbed areas searching for *L. humile* for a genetic and behavioral study (Vogel *et al.*, in prep.). We classified collection sites as follows: U = urban, N = relatively natural, G = garden, B = beachfront, A = agricultural. Collection sites on São Miguel: 1 = Ponta Delgada, youth hostel garden (G); 2 = W side of Lagoa Verde (N); 3 = Vista do Rei (N); 4 = Relva overlook (N); 5 = Ponta Delgada, waterfront, (U); 6 = Ponta Delgada, Praça Vasco da Gama (G); 7 = Ponta Delgada, near Piscinas San Pedro (G); 8 = Ribeirinha, under garbage bags (U); 9 = Ponta Delgada, Jardim António Borges (G); 10 = Cabouco, forest (N); 11 = Cabouco, field (A); 12 = Ribeira Grande, town park (G); 13 = Ribeira Grande, beachfront (B); 14 = 1 km E of Ribeirinha (N); 15 = Baía de Santa Iria (N); 16 = Furnas, Terra Nostra Garden (G); 17 = Caldeiras, vent area by Lagoa das Furnas (N); 18 = Ponta Delgada, Univ. of the Azores campus (G); 19 = Caloura, beachfront (B); 20 = Ilhéu da Vila (B); 21 = Vila Franca do Campo, town garden (G); 22 = Povoação, town zoo (G); 23 = Pica Verde (N); 24 = Miradouro da Tronqueira (N); 25 = Nordeste, school garden (G); 26 = Ponta Delgada, Jardim Antero Quental (G); 27 = Ponta Delgada, Jardim Sena de Freitas (G); 28 = Ponta Delgada, Castelo São Braz (U); 29 = Fajã de Cima, tennis club (G); 30 = Rosto do Cão (N); 31 = Ramalho, airport parking lot (U); 32 = Bretanha, coast road (U); 33 = Serra Gorda, northeast side (A); 34 = Rabo de Peixe, quinta (A); 35 = Santa Bárbara (U); 36 = Santa Bárbara, road to highlands (N); 37 = Miradouro da Comeira (N); 38 = Ribeira Grande, urban wall (U); 39 = Caldeira Velha, parking lot (U); 40 = Lagoa do Fogo, overlook (N); 41 = Ponta Delgada, Jardim José do Canto (G); 42 = Ponta Delgada, agricultural station (G); 43 = Ponta Delgada, alleyway behind Rua Gonçalo (U); 44 = Ponta Delgada, Rua Mãe Deus (U); 45 = Ponta Delgada, Alfandega, breakwater (U); 46 = Fajã de Baixo, pineapple plantation (A); 47 = Gorreana, tea plantation (A); 48 = Salga, Miradouro Salto da Fairinha (N); 49 = Ponta Delgada, Park Hotel garden (G); 50 = Lomba da Maia, town (U); 51 = Ponta Delgada, yard (U); 52 = Ponta Delgada, sugar factory garden (G); 53 = Lagoa das Furnas, S side beachfront (B); 54 = Ribeira Quente, alleyway (U). Collection sites on Terceira: 55 = Cabo da Praia (B); 56 = Praia da Vitória, by beach (UB); 57 = Terceira Golf Club, under grass on top of wall (G); 58 = Algar do Carvão, on lava rock wall near cave entrance (N); 59 = Furnas do Enxofre, among fumaroles (N); 60 = Altares, field (A); 61 = Porto Judeu, fishing port (UB); 62 = Praia da Vitória, public garden (G); 63 = Quatro Canadas, field (A); 64 = Angra de Heroísmo, vacant lot near dock (U); 65 = Angra de Heroísmo, dock (U); 66 = Angra de Heroísmo, municipal garden (G); 67 = Angra de Heroísmo, Rua de São Pedro (U); 68 = Monte Brasil, N end of fortress wall (UA); 69 = Monte Brasil, road to Pico das

Cruzinhas (UG); 70 = Monte Brasil, hiking trail to Pico das Cruzinhas (N); 71 = Angra de Heroísmo, W side (U); 72 = Lagoa das Patas, forest (N); 73 = São Mateus da Calheta, beachfront (B); 74 = Ponta das Cinco (B); 75 = Salgueiros, beach campground (B); 76 = Ponta dos Biscoitos, by swimming holes (B); 77 = Quatro Ribeiros, lookout (N); 78 = Vila Nova, port (B); 79 = Vila Nova, road (A); 80 = Caldeira, beachfront (B);

From 15-19 June 2003, SGMC collected ants on Santa Maria using visual search. Collection sites: 1 = Pico Alto (N); 2 = Barreiro da Faneca (N); 3 = Feteiras de Cima (U); 4 = Feteiras de Cima, garden (G); 5 = Vila do Porto, garden (G); 6 = Vila do Porto, wall (U); 7 = Paul (G); 8 = Vila do Porto, municipal garden (G); 9 = Florestal de Vila do Porto (GN); 10 = Anjos, chapel (U); 11 = Anjos, vineyard (A); 12 = Anjos, cave (N); 13 = São Pedro (G); 14 = Feteiras de Cima, orchard (A); 15 = Ilhéu de Vila do Porto (N); 16 = Bananeiras (N); 17 = Fátima, chapel garden (G); 18 = Mata dos Piquinhos, forest (N); 19 = Milgares, chapel (U); 20 = Pico do Facho (N); 21 = Praia Formosa, beach (B); 22 = Praia Formosa, vineyard (A); 23 = Sul (NA); 24 = Ponta do Castelo (N); 25 = Maia, vineyard (A); 26 = Maia, beach (B); 27 = Fontinhas (GN); 28 = São Lourenço (U); 29 = Estação Lourã Norte (U).

Species found in relatively undisturbed environments in the Azores, the neighboring archipelago of Madeira, and the Mediterranean area, but not widely distributed beyond this region, we considered native to the Azores (i.e., predating human arrival). Species found only in highly disturbed environments in the Azores and distributed around the world through human commerce, we considered exotic.

XE identified all specimens. Voucher specimens will be deposited at the Museum of Comparative Zoology in Cambridge, Massachusetts and the SI.

RESULTS

Ashmole's *et al.* (1996) collection included six species of ants; the SI collection included four ant species (Table 1, site records below). JKW and ALW collected 12 ant species at 54 sites on São Miguel, JKW collected seven ant species at 20 sites on Terceira, and SGMC collected five species at 29 sites on Santa Maria (Table 1).

Two species, *Solenopsis* sp. and *Plagiolepis schmitzii* are new records for the Azores, the first new ant records from the Azores since the earliest collection of *Hypoponera punctatissima* in 1957 (Yarrow 1967). In total, we recorded 14 ant species from the Azores (Table 1), including new specimens for 13 species. We did not collect any new specimens for one species previously recorded from the Azores, *Aphaenogaster senilis*; instead, we examined specimens collected by others.

Table 1. Native and exotic ant records from the Azores, ranked according to total number of collection site records. Islands: Mi = São Miguel, Pi = Pico, Te = Terceira, Jo = São Jorge, Fa = Faial, Fl = Flores, Ma = Santa Maria, Gr = Graciosa, Co = Corvo. Records: a = André (1896), b = Wheeler (1908), c = Emery (1908), d = Santschi (1933), e = Donisthorpe (1936), f = Wellenius (1949), g = Carthy (1955), h = Yarrow (1967), i = Krauss (unpublished, see results), j = Bolton (1977), k = Heinze (1986), m = Ashmole et al. (1996), underlined = # of collection sites in present study (Ilhéu da Vila included with Mi; Ilhéu Vila do Porto included with Ma). East Atlantic island range (from North to South): Z = Azores, M = Madeira, C = Canary Islands, V = Cape Verde, A = Ascension, H = Saint Helena. Origin: E = Macaronesian endemic, M = Mediterranean, A = African, P = Palearctic, S = South American, O = Asian.

	Islands								Atl Is		Origin
	Mi	Pi	Te	Jo	Fa	Fl	Ma	Gr	Co	Range	
Native species											
<i>Lasius grandis</i>	abdfhim ⁴⁴	efghim	dfhm ¹⁷	def	fghim	fh	hi ¹⁴	f		ZMC—	M
<i>Monomorium carbonarium</i>	bdfh ¹⁷	efg	f ¹¹	ef	fghi	fh	im ²⁰	f	f	ZM—	E
<i>Tetramorium caespitum</i>	bdefhk ³¹	ghm	km ¹⁶	h	afghm			f		Z—	M
<i>Hypoponera eduardi</i>	bdehi ²³	ehm	<u>7</u>		hm	h	<u>2</u>			ZMCV—	M
<i>Leptothorax unifasciatus</i>	dm ⁶	efg	em ³		hm					ZM—	M
<i>Plagiolepis schmitzii</i>							1			ZMC—	M
Exotic species											
<i>Linepithema humile</i>	dfnim ⁸	m	df ⁶	df		f	hi ¹⁰			ZMC—H	S
<i>Aphaenogaster senilis</i>		efg	adf		adfg			c		Z-C—	M
<i>Solenopsis</i> sp.	<u>8</u>									Z—	?
<i>Tetramorium bicarinatum</i>	dj ¹				f				f	ZMCV—	O
<i>Hypoponera punctatissima</i>	h ²		<u>1</u>							ZMCV-H	M
<i>Paratrechina longicornis</i>	k ²			e						ZMCVAH	O
<i>Tetramorium caldarium</i>	d ²									ZM-V-H	P
<i>Pheidole megacephala</i>	1	h			e					ZMCVAH	A
# of studies	10	6	7	4	5	2	4	2	1		
# of ant species	12	8	8	5	8	4	5	4	2		

SPECIMENS EXAMINED

Collectors: A = NP Ashmole and P Oromi; G = P Garcia; K = N Krauss; W = JK Wetterer and AL Wetterer; C = SGM Cabral; museum collection: SI = Smithsonian Institute's National Museum of Natural History. For

Wetterer records of species with more than ten site records on an island, we list only the site numbers (see Methods).

1. *Aphaenogaster senilis* Mayr

Terceira: Angra de Heroísmo (F Santschi; see Cagniant *et al.* 1991).

Faial: Horta (1930; Chopard; see Cagniant *et al.* 1991).

In addition to *A. senilis*, two other *Aphaenogaster* have been recorded from the Azores. Emery (1893, 1908), André (1896), and Wheeler (1927) listed *Aphaenogaster testaceopilosa* (Lucas) and Donisthorpe (1936) listed *Aphaenogaster gemella* (Roger). Yarrow (1967), however, concluded that all specimens were *A. senilis*. Cagniant *et al.* (1991) found that the *A. senilis* specimens from the Azores were not distinct in biometry and morphology from European and Canary Island populations. We therefore consider all *Aphaenogaster* records from the Azores as *A. senilis*.

Aphaenogaster senilis is known from four Azorean islands (Table 1), though we did not collect any specimens of this species. Although *A. senilis* appears to be of Mediterranean origin and is not considered a tramp species, we believe it to be exotic to the Azores for two reasons. First, it is known primarily from urban sites in the Azores, and second, the queens of *A. senilis* are micrapterous and cannot fly, making their unassisted arrival in the Azores unlikely. Yarrow (1967) reported that *A. senilis* is “abundant in Portugal, Spain and along the north side of the Mediterranean.” It is also known from the Canary Islands.

2. *Hypoponera eduardi* (Forel)

Azores: no site data (1953; SI); no site data (1953; Kamper & Roth; SI).

São Miguel: São Vicente (1962; K; SI); 22 sites: 3,6,9-13,16,18,22,25,26,29-32,34,37, 38,40,41,49 (2002; W).

Pico: Baía Cachorro, pahoehoe area (1987; A).

Terceira: 7 sites: 55-57,66,70-72 (2002; W).

Faial: Costa da Nau (1987; A); Vulcão dos Capelinhos, lava area (1987; A); Cabeço do Fogo (1987; A).

Santa Maria: Baneiras (2003; C); Estação Loura, Norte (2003; C).

Hypoponera eduardi is known from six Azorean islands (Table 1). This species is common, though not conspicuous, in natural areas and urban gardens on both São Miguel and Terceira. On São Miguel and Terceira, we usually collected it under rocks and in soil siftings. On Santa Maria, we did not collect using soil sifting and we found this species less often.

This species appears to be native to the Azores. Yarrow (1967) reported that *H. eduardi* is “a fairly common ant in the Canary Isles, Madeira and throughout the Mediterranean area.”

3. *Hypoponera punctatissima* (Roger)

São Miguel: Povoação, zoo (2002; W); Gorreana, tea plantation (2002; W).

Terceira: Monte Brasil, north end of Castelo wall (2002; W).

Hypoponera punctatissima is known only from São Miguel and Terceira (Table 1). At Povoação we found a trail of *H. punctatissima* foraging above ground, while our other two records came from litter sifting. This species had been collected only once before in the Azores, on São Miguel in 1957 (Yarrow 1967). *Hypoponera punctatissima* is almost certainly an exotic in the Azores. It is a well-known tramp species distributed throughout the tropics and subtropics.

4. *Lasius grandis* Forel

São Miguel: Ribeiro Grande (1962; K; SI); Furnas (1972; K; SI); Mistério de Rabo de Peixe (1989; A); Gruta do Pico da Cruz (1989; A); 42 sites: 2-5,7-16,18,19,21-29,31-37,39-42,45-48,50-53 (2002; W).

Pico: Magdalena (1972; K; SI); Baía do Cachorro, pahoehoe area (1987; A); Mistério da Silveira (1987; A).

Terceira: Mistério Negro, kipuka area (1987; A); Pico do Fogo (1987; A); 17 sites: 55,58-60,63, 65,66,68,70,72-75, 77-80 (2002; W).

Faial: Horta (1972; K; SI); Pedro Miguel (1972; K; SI); Costa da Nau (1987; A); Cabeço do Fogo (1987; A); Vulcão dos Capelinhos, base of cliff (1989; A).

Santa Maria: airport (1962; K; SI), mountains (1962; K; SI), Vila do Porto (1972; K; SI); 14 sites: 2,3,4,5,6,9,11,12,14,20,23,25,27,28 (2003; C).

There has been some debate over which species of *Lasius* occurs in the Azores. André (1896), Wheeler (1908), Santschi (1933), Wellenius (1949), Carthy (1955), and Yarrow (1967) all reported *Lasius niger* from the Azores. Santschi (1933) and Donisthorpe (1936) also reported *L. grandis*. Yarrow (1967) concluded that all specimens were probably *L. niger*, writing that “Santschi’s record of var. *grandis* probably refers only to a large aberration of *niger*,” and that “I have seen two dealate females from Faial named by Donisthorpe as var. *grandis* both of which are quite normal *L. niger*.” Wilson (1955), in his revision of the genus *Lasius*, examined *Lasius* specimens from the Azores and Madeira, and although he identified them as *L. niger*, he noted that their allometry

was different than *L. niger* from other regions. More recently, Seifert (1992) examined *Lasius* specimens from the Azores and Madeira and identified them all as *L. grandis*. Although XE had earlier identified the Azores specimens of Ashmole *et al.* (1996) as *L. niger*, based on further analysis, we consider all records from the Azores as *L. grandis*.

Some *L. grandis* workers from the Azores appear to differ somewhat from those of Madeira. We found that the *Lasius* in Madeira were uniform in color, whereas some *Lasius* workers in the Azores were distinctly bicolor, though we found uniform and bicolor workers from the same colony. Earlier authors (Wellenius 1949, Yarrow 1967, Seifert 1992) also noted bicolor *Lasius* in the Azores.

Lasius grandis is known from eight of nine islands of the Azores (Table 1), and is the most common and conspicuous ant on São Miguel and Terceira. It seems likely that this species is native to the Azores. It is also the most common ant on the island of Madeira, occurring in all but driest habitats from sea level to the highest peaks (Wetterer *et al.* in prep.). In addition, this species is known from the Canary Islands, the Iberian Peninsula, the Balearic Islands, and the Maghreb of northwest Africa.

5. *Leptothorax unifasciatus* (Latreille)

São Miguel: Mistério de Rabo de Peixe (1989; A); Ponta Delgada, Jardim António Borges (2002; W); Furnas, Terra Nostra Garden (2002; W); Vila Franca do Campo, town garden (2002; W); Rabo da Peixe, quinta (2002; W); Serra Gorda, pasture wall on northeast side (2002; W); Salga, Miradouro Salto da Fairinha (2002; W).

Terceira: Pico do Fogo (1987; A); Angra de Heroísmo, municipal garden (2002; W); Monte Brasil, north end of fortress wall (2002; W), Algar do Carvão, on lava rock wall near cave entrance (2002; W).

Faial: Cabeço do Fogo (1987; A).

Donisthorpe (1936) listed *Leptothorax tuberum* (Fabricius) from the Azores, but at the time, *L. unifasciatus* was considered a race of this species.

Leptothorax unifasciatus is known from four islands of the Azores (Table 1). We found it in only a few places on São Miguel and Terceira, always near lava rocks. At both Jardim António Borges and Algar do Carvão, we witnessed workers entering a hole in a piece of lava, where we presume the colony was nesting. *L. unifasciatus* is probably native to both the Azores and Madeira. It is abundant throughout Southern and Central Europe, from Portugal to the Caucasus and from southern Italy to northern Germany and Poland.

6. *Linepithema humile* (Mayr)

Azores: no site data (1940; Shemin *et al.*; SI).

São Miguel: Ponta Delgada (1972; K; SI); Água de Pau, on shore and at cave threshold (1989; A); Ponta Delgada, University of Azores campus, along wall (2002; W); Rabo de Peixe, quinta (2002; W); Ribeira Grande, urban wall (2002; W); Ponta Delgada, Agricultural station (2002; W); Ponta Delgada, Rua da Mãe Deus, along base of a wall (2002; W); Fajã de Baixo, Arruda Açores pineapple plantation (2002; W); Rabo de Peixe, quinta (2002; G).

Pico: Baía do Cachorro, pahoehoe area (1987; A).

Terceira: Angra de Heroísmo, waterfront, east end of town, by port (2002; W); Angra de Heroísmo, waterfront, west end of town (2002; W); Angra de Heroísmo, Rua de São Pedro, along base of wall (2002; W); Angra de Heroísmo, Rua Ciprião Figueiredo, on wall (2002; W); Monte Brasil, by road to Pico das Cruzinhas (2002; W); Porto Judeu, fishing port (2002; W); Praia da Vitória, storefronts in town center (2002; W); Praia da Vitória, town garden (2002; W).

Ilhéu da Vila (south of São Miguel): all parts of the islet (2002; W).

Santa Maria: no site data (1960; K; SI); airport (1962; K; SI); Vila do Porto (1972; K; SI); 10 sites: 2, 10, 13, 18, 19, 22, 24, 26, 28, 29 (2003; C).

Linepithema humile, the Argentine ant, is known from five Azorean islands (Table 1), plus the small Ilhéu da Vila. Although Suarez *et al.* (2001) listed the 1940 record above as the earliest record of this species in the Azores, Santschi (1933) listed specimens collected in 1930 from three Azorean islands, and Wellenius (1949) listed specimens collected in 1938 from four islands. On São Miguel, Terceira, and Santa Maria, we found this species in only a few places where it was locally abundant. On Ilhéu da Vila, a small, heavily disturbed islet off São Miguel that is a popular destination for day trips, we found it in extremely high densities in all parts of the islet, apparently excluding all other ant species. *L. humile* was abundant in some urban areas where there was little vegetation present. We also found it occasionally in agricultural areas. Where we found *L. humile* in high densities, we usually found no other ant species. This species appears to be more common on Santa Maria, the driest island. On Madeira, *L. humile* is also more common in drier areas (Wetterer *et al.*, in prep.).

Linepithema humile is native to South America but has been spread to many temperate and subtropical locales around the world through human commerce.

7. *Monomorium carbonarium* (F. Smith)

São Miguel: Ponta Delgada (1907, WM Wheeler; SI); 16 sites:

5,9,12,16,18,19,21,28,29,

31-35,41,48,51 (2002; W); Rabo de Peixe, quinta (2002; G).

Terceira: 11 sites: 55,56,60,66,68,73-77, 80 (2002; W).

Faial: Horta (1972; K; SI);

Santa Maria: airport (1962; K; SI); Vila do Porto (1972; K; SI); Grutas dos Anjos, threshold of cave (1989; A); Furnas Velhas, threshold of cave (1989; A); 20 sites: 1,3,4,5,6,7,

8,9,11,12,13,15,17,19,20,21,23,24,27,28 (2003; C).

Monomorium carbonarium is the only ant species known from all nine Azorean islands (Table 1). It was common on São Miguel, Terceira, and Santa Maria, particularly in urban sites, though not very conspicuous due to its small size. Although earlier researchers considered this species to be an exotic from the Neotropics, Yarrow (1967) considered it a Macaronesian endemic found only in the Azores and Madeira. Specimens from the Neotropics, once identified as *M. carbonarium*, are now recognized as a separate species, *Monomorium ebeninum* Forel (Kempf 1972).

8. *Paratrechina longicornis* (Latreille)

São Miguel: Ponta Delgada, Praça Vasco da Gama (2002; W); Ponta Delgada, Jardim Antero Quental (2002; W).

Paratrechina longicornis, the crazy ant, is known from two Azorean islands (Table 1). Because *Paratrechina longicornis* is conspicuous and easy to recognize, the absence of additional records suggests that this species is rare in the Azores. *Paratrechina longicornis* is a major pest species spread throughout the tropics and subtropics by human commerce, and certainly exotic to the Azores. Yarrow (1967) wrote that this species “once established might be expected to become abundant but this evidently has not happened.” It appears that the Azores may be at the latitudinal limit for this species. The sites in the Azores, “Villa Velhas” (= Velas), São Jorge (38.68°N; Donisthorpe 1936) and Ponta Delgada, São Miguel (37.73°N; Heinze 1986 & this study), are the highest latitude outdoor populations recorded for this species, surpassing records from Almería, Spain (36.83°N; Tinaut & Año 2000), St. George’s, Malta (35.93°N; Schembri & Collingwood 1981) and Gwardamangia and Msida, Malta (35.89°N; Schembri & Collingwood 1995).

9. *Pheidole megacephala* (Fabricius)

São Miguel: Ribeira Quente, alleyway (2002; W).

Pheidole megacephala, the big-headed ant, is known from three Azorean islands (Table 1), but appears to be rare, and perhaps occurs

only in urban areas. *Pheidole megacephala* is an important pest ant spread throughout the tropic and subtropics by human commerce, and no doubt exotic to the Azores. It appears that the Azores may be at the latitudinal limit for this species as well. The Azorean population on Pico is the highest latitude outdoor record for this species: 1 km S of Areia Larga, Pico (38.52°N; Yarrow 1967). A population in Melbourne, Australia (37.83°S; Clark 1941) narrowly surpasses the population we found in Ribeira Quente, São Miguel (37.73°N). The only other *P. megacephala* population known from the Azores (from Horta, Faial; 38.53°N; Donisthorpe 1936), was found indoors.

10. *Plagiolepis schmitzii* Forel

Ilhéu Vila do Porto (2003; C).

Our record of this ant is the first for the Azores (Table 1). *Plagiolepis schmitzii* is known from only Ilhéu Vila do Porto, a small uninhabited islet next to Santa Maria, the warmest and driest island of the Azores. Ilhéu Vila do Porto is a "Special Protected Zone" of the European Union with restricted human access. *Plagiolepis schmitzii* is one of the two most common ants in Madeira, rivaling *L. grandis* in its ubiquity and abundance (Wetterer *et al.*, in prep.). It is found in and is probably native to the Azores, Madeira, the Canary Islands, and Morocco.

11. *Solenopsis (Diplorhoptrum) sp.*

São Miguel: Ponta Delgada, near Piscinas São Pedro (2002; W); Ponta Delgada, Jardim António Borges (2002; W); Ponta Delgada, University of Azores campus (2002; W); Ponta Delgada, Jardim Antero Quental (2002; W); Fajã de Cima, tennis club (2002; W); Ponta Delgada, Jardim José do Canto (2002; W); Ponta Delgada, Rua de São Gonçalo (2002; W); Rosto do Cão, sifted from soil in crevices (2002; W).

Workers of this species are monomorphic, yellow-orange in color, and usually have two clypeal teeth; rare individuals have two more poorly developed lateral teeth. They have well-developed black eyes with 3-5 ommatidia. Long and short hairs are abundant all over the body. Measurements: head length (hl) = 0.41-0.46 mm; head width (hw) = 0.30-0.34 mm; scape length (sl) = 0.25-0.30 mm; cephalic index (ci) = (hw * 100)/hl = 74-80; scape index (si = (sl * 100)/hl) = 61-66.

Queens are brown to dark brown, with the following measurements: hl = 0.54-0.61 mm; hw (eyes included) = 0.56-0.58; sl = 0.38-0.41; ci = 95-102; si = 67-70; Weber's length (distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum) = 1.05-1.17. Ocelli were large with the central ocellus separated from the lateral ocelli by a distance a bit larger than its diameter. The scutum hides the pronotum in dorsal view.

Our records of this small thief ant are the first for the Azores (Table 1). We found this species only at highly disturbed sites in Ponta Delgada and nearby Fajã de Cima and Rosto do Cão, almost exclusively in soil sift samples.

This species is indistinguishable from a common *Solenopsis* we collected in Madeira (Wetterer *et al.*, in prep.), but quite distinct from all *Solenopsis* known from the Canary Islands and Cape Verde (XE, pers. obs.). Its occurrence in highly disturbed areas around the largest city of the Azores suggest that this ant is an exotic introduction. Systematic work on thief ants is direly needed.

12. *Tetramorium bicarinatum* (Nylander)

São Miguel: Caldeiras, N side of Lagoa das Furnas, geothermal area (2002; W).

This ant is known from three islands of the Azores (Table 1).

Tetramorium bicarinatum is a tramp ant spread throughout the tropic and subtropics by human commerce, and is probably exotic to the Azores. Its known locales in the Azores are the highest latitude outdoor populations recorded for this species: Ribeira, Faial, (39.02°N; Wellenius 1949), Vila Nova, Corvo, (38.78°N; Wellenius 1949), Caldeiras, São Miguel (37.77°N; this study), Furnas, São Miguel, (37.77°N, Santschi 1933), Ponta Delgada, São Miguel, (37.73°N; Bolton 1977), surpassing records from Kanto District, Japan (36.25°N; <http://ant.edb.miyakyou-u.ac.jp/E/index.html>).

13. *Tetramorium caespitum* (L.)

São Miguel: 31 sites: 1,5-7,9,11-14,16,18,21,22,25-28,30,31,35,39-42,45-48,50,52,53 (2002; W).

Pico: Porto Cachorro (1987; A); Baía do Cachorro, pahoehoe area (1987; A); Mistério da Silveira (1987; A); Lajes, coast (1987; A).

Terceira: Praia da Vitória (1985; J Heinze); Porto Judeu, pahoehoe (1987; A); 16 sites: 55,57-59,63,65,66,71,73-80 (2002; W).

Faial: Costa da Nau (1987; A); Cabeço do Fogo (1987; A); Vulcão dos Capelinhos (1987; A); Vulcão dos Capelinhos, cliff (1989; A).

Several earlier authors, including André (1896), have reported *T. caespitum*, the pavement ant, from the Azores. Wheeler (1908) wrote “this species was represented by two varieties, one larger and darker, like the form common in rich moist soil in Europe, and the other smaller and redder, like the variety met with on xerothermic hillsides in Switzerland and Italy.” Yarrow (1967), however, noted “such variation can be detected in most nest samples of this species and apparently has no geographical significance.” We also noted such variation among

specimens we examined. Many specimens appear to be more like *Tetramorium impurum*, a species recently revived from synonymy with *T. caespitum* (Kutter, 1977; Cammaerts *et al.* 1985; Seifert, 1996). The distinction between these two species is best made using males, which have a well-differentiated morphology; queens and workers are less reliably distinguished. Unfortunately, no males have ever been collected in the Azores. One queen from Vulcão dos Capelinhos and two queens from Vulcão dos Capelinhos cliff (see above) have somewhat intermediate biometry: mesosoma length/head length = 2.09 (more like *caespitum*); postpetiole width/head width = 0.54 (more like *impurum*); scutellum width/scape length = 0.98 (*impurum*); distance between posterior ocelli/head width = 0.35 (*caespitum*). The mesonotum is longitudinally striate in its posterior half and the scutellum is next to completely smooth. The majority of worker specimens have very rugose petiole and postpetiole and brownish (not dark brown, not black) coloration, all characteristics of *T. impurum*. A few samples in our captures contain very small workers (often mixed with bigger and sculptured ones) whose postpetiole is more *caespitum*-like. Four very small workers collected by Heinze (see above) show the petiole sculpture of *T. caespitum*. It is possible that both *T. caespitum* and *T. impurum* are present in the Azores. Alternatively, the Azores populations may constitute a distinct species. We have elected to be conservative and retain *T. caespitum* as our identification for all specimens.

This ant is known from six Azores islands (Table 1).

Tetramorium caespitum is considered native to Europe, but has been widely introduced to temperate locales around the world. Because the intraspecific variation among Azores specimens of *T. caespitum* differs from what is found in introduced population elsewhere, we consider this species native to the Azores.

14. *Tetramorium caldarium* (Roger)

São Miguel: Ponta Delgada, Jardim António Borges (2002; W); Ponta Delgada, Jardim José do Canto (2002; W).

Santschi (1933) listed *Tetramorium simillimum* from São Miguel, but at that time *T. caldarium* was considered a junior synonym of *T. simillimum*. Bolton (1979) revived *T. caldarium* as a species separate from *T. simillimum*, and though he did not identify any specimens from the Azores, he placed all specimens he examined from Madeira and the Canary Islands in this species. We therefore expect that Santschi's (1933) specimens were also *T. caldarium*.

Tetramorium caldarium is known in the Azores from only one island (Table 1).

This species is a tramp ant spread throughout the tropic and subtropics by human commerce, and is probably exotic to the Azores.

DISCUSSION

Of the 14 ant species known from the Azores, seven appear to be common and/or widespread, known from at least four islands and collected in at least six separate studies (Table 1). In our surveys of three islands, we found that two of these species, *Lasius grandis* and *Tetramorium caespitum*, were very common and conspicuous in all habitat types on both São Miguel and Terceira. *Lasius grandis* was also ubiquitous on Santa Maria, but *T. caespitum* was not found on that island. Two other ant species, *Monomorium carbonarium* and *Hypoponera eduardi*, were very common in all habitat types on all three islands, but neither was very conspicuous, *M. carbonarium* due to its small size, and *H. eduardi* due to its subterranean habits. One ant species, *Linepithema humile*, was common in some urban areas with little vegetation and in some agricultural areas on all three islands. *Leptothorax unifasciatus* was common on São Miguel and Terceira only in areas with numerous lava rocks, including urban parks with lava rock walls. We did not find this species on Santa Maria. We did not collect *Aphaenogaster senilis* on any of the three islands we surveyed, but seven other studies have found it on four different islands, meeting our criteria for being considered “common and/or widespread.”

Seven additional ant species in the Azores are relatively uncommon and/or with a restricted distribution, which we defined as known from three or fewer islands and collected in four or fewer separate studies. We collected *Solenopsis* sp. in soil sifts at eight different locales, all highly disturbed sites in and around Ponta Delgada. We found *Hypoponera punctatissima* at only three highly disturbed sites, two on São Miguel and one on Terceira. We collected *Paratrechina longicornis* and *Tetramorium caldarium* at two sites each, all within city parks of Ponta Delgada. We found *Pheidole megacephala* and *Tetramorium bicarinatum* once each. We collected *P. megacephala* workers foraging around the edge of buildings in back alleys devoid of vegetation and going down cracks in the concrete sidewalk in Ribeira Quente. We found *T. bicarinatum* only in a geothermal area near Lagoa das Furnas. It is possible that the warmth of this area is important to this species' survival at this site. We collected *P. schmitzii* only on a relatively pristine islet near Santa Maria, which appears to serve as a refuge for this and other native Azorean plants and animals.

The Azores have far fewer ant species than neighboring Madeira (27 species; Wetterer *et al.*, in prep.), no doubt related to the Azores'

younger age, higher latitude, and greater distance from continental source populations. Of the 14 ant species found in the Azores, 12 are also known from Madeira. Only *A. senilis* and *T. caespitum* are found in the Azores but not in Madeira.

The Azores hold the highest known latitude population of three ant species that are widespread and important pests in the tropics, *P. longicornis*, *P. megacephala*, and *T. bicarinatum*, probably a reflection of the relatively mild climate in the Azores due to the warming influence of the Gulf Stream.

NATIVE VERSUS EXOTIC

Some researchers (e.g., Wheeler 1908) considered all ants in the Azores to be exotics, introduced to the islands through human commerce. However, we believe, based on their distribution and ecology, that six ant species may be native to the Azores, i.e., predating human arrival. One, *M. carbonarium*, may be a Macaronesian endemic. Four others (*H. eduardi*, *L. grandis*, *L. unifasciatus*, and *P. schmitzi*) are all native to the Mediterranean region, but not known as tramp species. Finally, *T. caespitum*, a European native, has been widely introduced to temperate locales around the world, but we consider the Azorean populations to be probably native (see Results). All except *T. caespitum* are found on at least one other Macaronesian island group. None of these six species are found on the South Atlantic islands of Ascension and Saint Helena (Table 1).

Six of the eight ant species we consider exotics in the Azores are well-known tramp species spread worldwide through human commerce (*H. punctatissima*, *L. humile*, *P. longicornis*, *P. megacephala*, *T. bicarinatum*, and *T. caldarium*). Five of these six have also been introduced to the isolated South Atlantic island of Saint Helena (Table 1). *Solenopsis (Diplorhoptrum)* sp. may also be a widespread tramp species, but its distribution cannot be determined until the taxonomy of this species is properly evaluated. Finally, *A. senilis* is considered native to the Mediterranean and is not known as a tramp species; nonetheless it appears to be exotic to the Azores (see Results).

Although the ant species richness of the Azores is quite low, the native fauna appears fairly intact. Five of the seven most common ants appear to be native to the Azores. Exotic ant species that are known for their great impact elsewhere (e.g., *P. longicornis*, *P. megacephala*, and *L. humile*) do not seem to have had much impact in the Azores. The Azores may be near the latitudinal limit for many of the exotic ant species present (all except *L. humile*).

Natural areas in the Azores had low ant species richness, but usually all ants present we considered native species. Urban sites had higher ant species richness due to the presence of both native and exotic ant species. Thus, total ant species richness was not a useful indicator of habitat integrity. However, we found exotics only in highly disturbed habitats, primarily in urban areas. Thus, the presence of exotic ant species was an excellent indicator of human disturbance.

Future research

The number of ant species known from an Azorean (N) island is strongly correlated with island area (A in km²) ($N = 3.1 + 0.012 A$, $R^2 = 0.83$; $\log N = 0.25 + 0.44 \log A$, $R^2 = 0.86$). Species number, however, is even more strongly correlated with the number of studies reporting ants from that island (S) ($N = 1.5 + 1.0 S$, $R^2 = 0.95$; $\log N = 0.34 + 0.72 \log S$, $R^2 = 0.95$). We expect that thorough ant surveys may find that the six or seven most common species occur on all nine Azorean islands.

DNA analyses should be useful in evaluating the native versus exotic status of the ants in the Azores, e.g., to determine whether the *T. caespitum* populations are genetically distinct from exotic populations in other locales. Preliminary DNA and behavioral analyses of *L. humile* specimens we collected on São Miguel and Terceira indicate that both populations belong to the same supercolony group as the main exotic population in mainland Europe (V. Vogel, in prep.; see Giraud *et al.* 2002).

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