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Front cover: *Solenopsis geminata* major worker. © Henri W. Herrera.

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Distribution and habitat preferences of Galápagos ants (Hymenoptera: Formicidae)

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Abstract

We present the first comprehensive review of the ant taxa of the Galápagos archipelago. The review is based on data gathered during literature searches, field surveys, and the revision of museum specimens, and includes information on the distribution, habitat, and ecology of 47 species. At least nine of these species are assumed to be native or endemic to the islands and at least 32 species have been introduced through human-associated pathways. The status of the remaining six species is unknown. The information compiled in this study will allow us to better understand the ecological role of indigenous species and their potential as indicators of ecosystem health. Baseline information on the distribution of introduced ants will be indispensable for assessing impact and spread within the archipelago.

Keywords: Formicidae, Galápagos Islands, habitat preference.

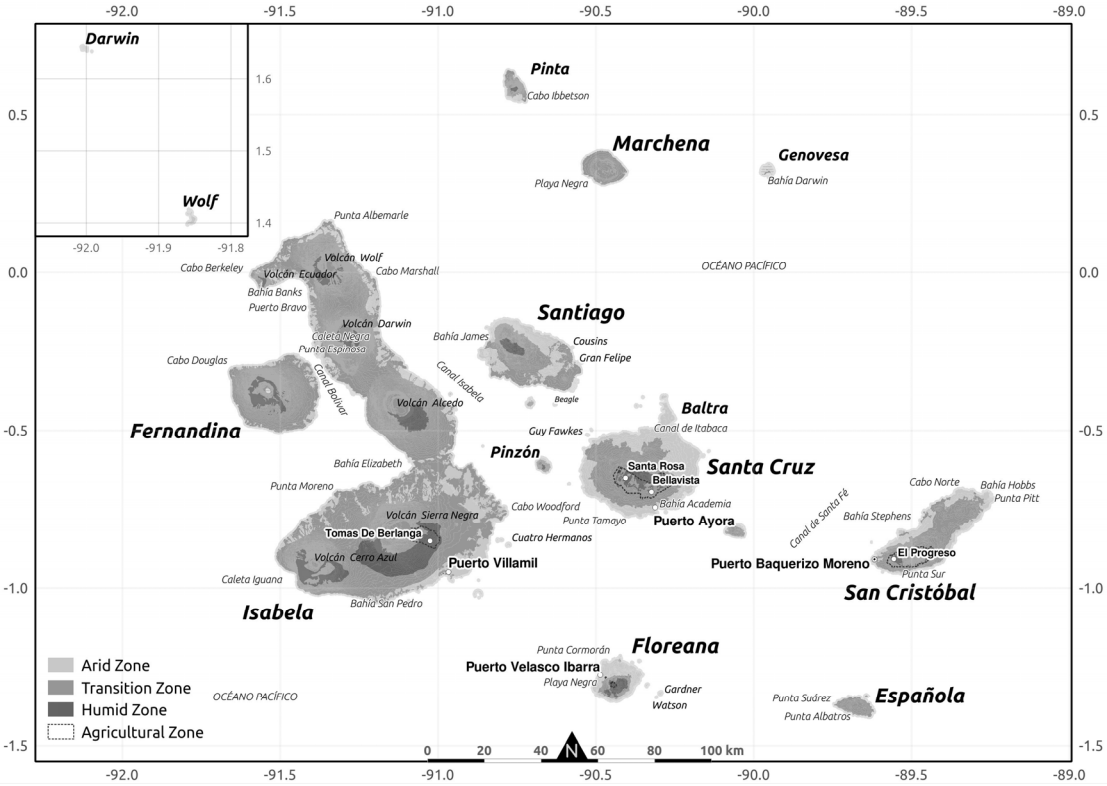
Introduction

Ants are a potential tool for monitoring ecosystem health in the Galápagos Islands, however, little is still known about their distribution and the role that they play in maintaining ecosystem processes (BRANDÃO & PAIVA, 1994; UNDERWOOD & FISHER, 2006; CAUSTON & HERRERA, 2014). Between 1835, the first collection of insects by Charles Darwin, and 2019, more than 46 entomological expeditions have surveyed the terrestrial invertebrate fauna in the archipelago (e.g. LINSLEY & USINGER, 1996; BAERT *et al*., 2008; PECK, 2001). However, none of these inventories focused on ants only. During early explorations of Galápagos (1835-1932), a few introduced and native species were collected from arid areas (GUNTHER, 1877; HOWARD, 1890; AGASSIZ, 1892; HELLER, 1903; BEEBE, 1923; SLEVIN, 1931; CROCKER, 1933), those taxa were published by SMITH (1877), EMERY (1893), WHEELER (1919, 1924), STITZ (1932) and WHEELER (1933). All known ant species and subspecies were summarized for the first time by LINSLEY & USINGER in 1966.

Later studies on the impact of two invasive ant species, *Solenopsis geminata* (Fabricius, 1804) and *Wasmannia auropunctata* (Roger, 1863), on the fragile Galápagos ecosystems, contributed to the detection of newly introduced ant species (PAZMIÑO, 1977; CLARK *et al*., 1982; LUBIN, 1984; 1985; WILLIAMS & WHELAN, 1991; ABEDRABBO, 1994; ROQUE–ALBELO *et al*., 2000; CAUSTON *et al*., 2005; CAUSTON *et al*., 2006; VON AESCH, 2006; HERRERA & CAUSTON, 2008;

HERRERA & LONGINO, 2008; HERRERA & CAUSTON, 2010; HERRERA *et al*., 2013; HERRERA *et al*., 2014; WAUTERS *et al*., 2014; WAUTERS *et al*., 2016). In spite of these studies, little is still known about ant diversity in Galápagos. Baseline data are needed for an ecological monitoring program and for the identification and management of invasive species (CAUSTON *et al*., 2012). Based on field studies and revisions of museum and bibliographic material, we present for the first time an overview of the distribution and habitat preferences of 47 taxa established on the Galápagos Islands.

The Galápagos Archipelago consists of 123 islands of various sizes (SNELL *et al*., 1996) (Map. 1). These islands are isolated from the South American mainland and lie at a distance of between 960 and 1180 km from the Ecuadorian coast. The islands are spread over an area of 304 km east to west and 341 km north-west to south-east. The total land area is about 7,856 km² spread over 45,000 km² of sea (JACKSON, 1985; PECK, 2006). All the islands are volcanic in origin and arose from the Nazca Plate. Their maximum emergence age is estimated between 4 (Isla San Cristóbal) and 0.07 (Isla Fernandina) million years ago (GEIST *et al*., 2014). The islands are situated at the edge of the Central Pacific Dry Zone. There are two seasons: (i) the rainy–warm season from about December to May, characterized by daytime temperatures of approximately 29°C with occasional short thunderstorms and (ii) the dry–cool season, also called "garua" – a wet fog–drip environment– from about May to December with an average August daytime temperature of about 22°C (WIGGINS & PORTER, 1971; PECK, 2001; TRUEMAN & D'OZOUVILLE, 2010). The prevailing winds and rain that originate from the south make the northern slopes much dryer. Some years are associated with exceptionally high rainfall due to warm water currents coming from the east. This phenomenon is called "El Niño" and occurs at irregular times. The average archipelago rainfall at sea level is less than 75mm per year, but in "El Niño" years it can easily exceed 3200 mm (JACKSON, 1985; SNELL & REA, 1999; PECK, 2006; TRUEMAN & D'OZOUVILLE, 2010).



Map 1. Galápagos archipelago with terrestrial ecological zones. The largest island Isabela is composed of six volcanoes.

According to WIGGINGS & PORTER (1971), there are seven vegetation zones categorized according to altitude and exposure: i) the Littoral or Coastal zone with its mangroves, sandy beaches and dunes with creeping vines, grasses, succulent shrubs and saltbushes; ii) the Arid or Dry zone with deciduous trees such as *Bursera graveolens* (Kunth) Triana and Planch., shrubs such as *Croton scouleri* Hook. f. and cacti (*Opuntia* sp. and *Jasminocereus* sp.); iii) the Transition zone, a deciduous woodland dominated by the endemic *Pisonia floribunda* Hook. f. and *Psidium galapageium* Hook. f. and with abundant epiphytes, lichens and mosses; iv) the *Scalesia* zone, a cloud–forest dominated by the composite *Scalesia* (*Scalesia pedunculata* Hook. f. or *Scalesia cordata* Stewart), with abundant epiphytes such as mosses, liverworts, ferns, orchids, peperonias and bromeliads; v) the *Zanthoxylum* or Brown zone that was deeply modified by humans in inhabited islands, transformed into agricultural fields, pastures and orchards; vi) the *Miconia* zone, a dense shrubby belt of *Miconia robinsoniana* Cogn., vii) the Fern sedge zone or Pampa zone with ferns, grasses, sedges and with some *Sphagnum* patches (WIGGINS & PORTER, 1971; JACKSON, 1985; MCMULLEN, 1999). Zones of *Scalesia*, *Zanthoxylum*, *Miconia and* Fern sedge are included as subdivisions of the Humid zone (TYE & ORTEGA, 2011). These zones in inhabited areas have been modified by human activities and by introduced feral grazing animals.

The altitudinal boundaries of these vegetation zones differ strongly between southern and northern slopes due to the drier conditions along the northern slopes (JACKSON, 1985; PECK, 2006). The vegetation types are developed most clearly on Santa Cruz, but are to a large degree also present on the other major islands. Islets and lower islands in contrast mainly consist of the dry zone only. The highest Isabela volcanoes and the island of Fernandina have an inversion zone situated around 1200m, a cloudy region above which there is an arid summit zone with vegetation similar to the arid zone (LAURELLE, 1965; WIGGINS & PORTER, 1971; JOHNSON & RAVEN, 1973; VAN DER WERFF, 1979; JOHNSON & RAVEN, 1973; TYE & ORTEGA, 2011; ZIEMEK, 2014) (Table 1). Five islands have human settlements: Isabela, Santa Cruz, Floreana, San Cristóbal and Baltra (WATSON *et al*., 2010); additionally, Santiago was inhabited briefly between the1920's and 1960's (LUNDH, 2001).

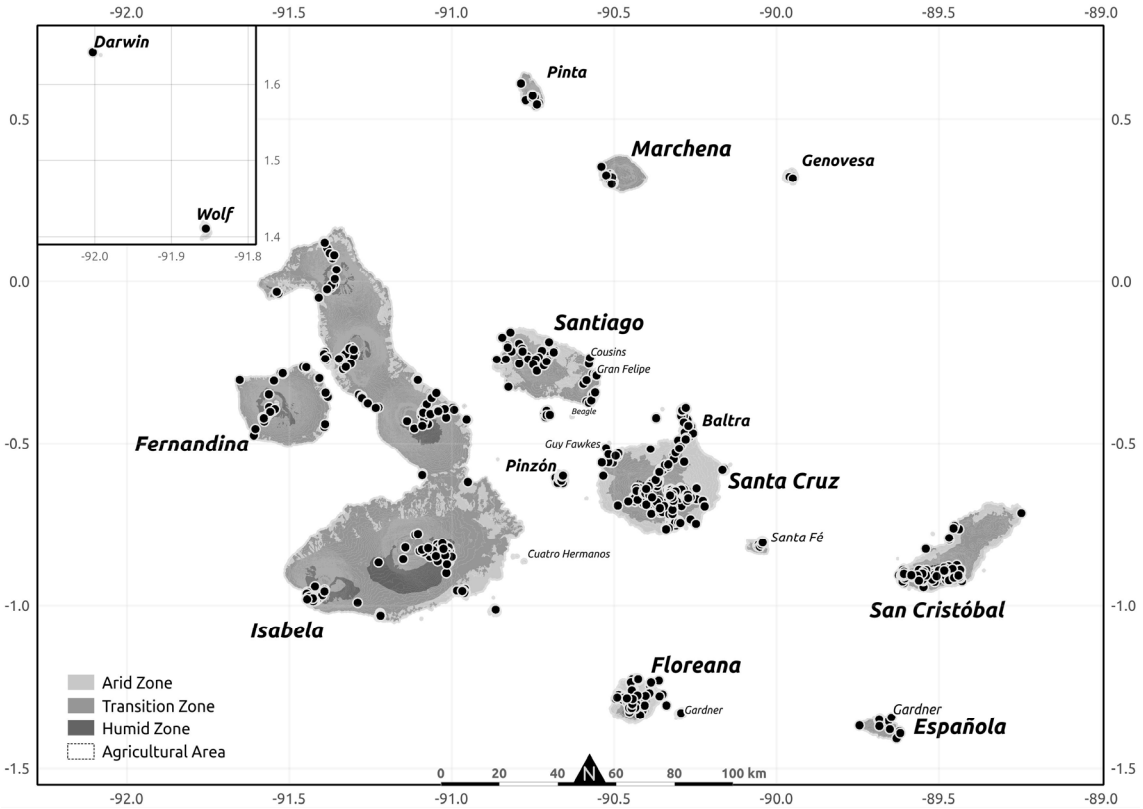
Materials & methods

The present study is based on 382,023 specimens deposited in the Terrestrial Invertebrates Collection of the Charles Darwin Research Station (ICCDRS) and The Royal Belgian Institute of Natural Sciences (RBINS), enriched with collections by the first author (2001–2014), ants sampled by expeditions conducted by the third and last author (2009, 2010, 2012 and 2014); the second author, Jean–Pierre Maelfait and Konjev Desender (1982, 1986, 1988, 1991, 1996, 1997, 1998, 2000, 2002 and 2009) as well as several CDRS-collaborators who have been able to collect ants in the archipelago. All geographical positions of sampling localities and ecological zones where ants were collected are depicted on Map 2.

Distribution maps of the species were obtained from coordinates written on labels attached to the individuals studied in the museums, as well as from field notes and surveys carried out by the first author. If coordinates were absent, coordinates of the name of the sampling site were used. This information was compiled into a GIS database. Records where the geographical position could not be traced with sufficient accuracy (e.g. records made by SMITH (1877); EMERY (1893); WHEELER (1919, 1924); STITZ (1932) and WHEELER (1933)), are depicted by triangles in the center of the island. Information on ant ecology and habitat preference was obtained from observations in the field as well as from the literature. Plant nomenclature in the paper follows WIGGINS & PORTER (1971) and the Galápagos Species Checklist (BUNGARTZ *et al*., 2009). For some taxa, scientific names are accompanied by common names. Photomontage images for all taxa are available on AntWeb, Galapágos ants (www.antweb.org).

Table 1. Classification of the vegetation and terrestrial ecological zones in the Galápagos archipelago, based on A) JOHNSON & RAVEN (1973); TYE & ORTEGA (2011); ZIEMEK (2014); B) WIGGINS & PORTER (1971) and VAN DER WERFF (1979). S-SIDE is the South-side, N-SIDE is the North-side of the island.

TERRESTRIAL ECOLOGICAL ZONES OR VEGETATION ZONES OF THE GALÁPAGOS ARCHIPELAGO				
		ALTITUDE (m.a.s.l.)		
ZONING		**S-SIDE**	**N-SIDE**	**VEGETATION**
A	B			
Littoral (Coastal) zone	Littoral (Coastal) zone	0 – 10	0 – 10	Mangroves, sandy beaches and dunes, creeping vines, grasses, succulent shrubs and saltbushes
Dry or arid zone	Dry or arid zone	10 – 80 (150)	10 – 200 (300)	Deciduous trees, shrubs and cacti
Transition zone	Transition zone	80 – 180 (200)	200 – 500 (600)	Deciduous and semi-deciduous woodland
Humid zone	Agriculture zone	180 – 1200	550 – 1000	Often mossy evergreen forest, scrub or non-wooded evergreen pampa
	Scalesia zone			
	Miconia zone			
	Pampa zone			
Inversion zone	High-altitude transition zone	1200 – 1300	–	Semi-deciduous woodland just above cloud layer
	High-altitude dry zone	> 1300	–	Open scrub. Well above cloud layer



Map 2. Localities where ants have been collected in the Galápagos archipelago.

Results

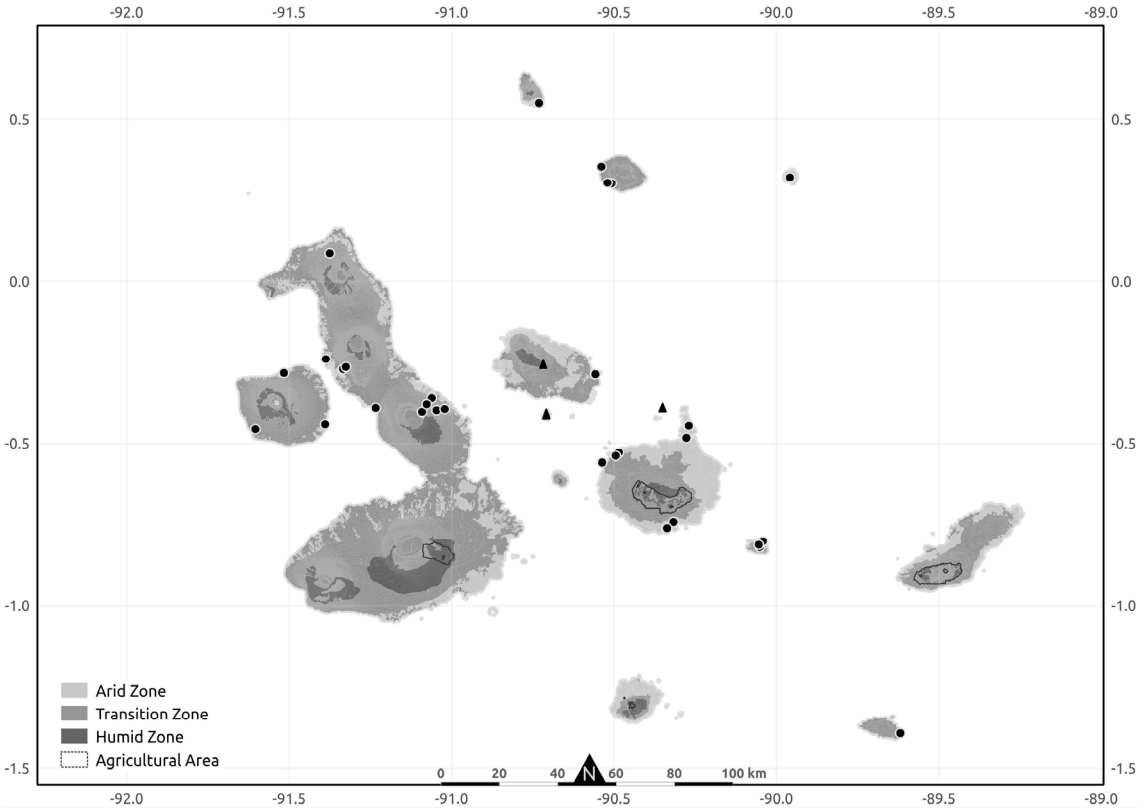
Overview of the species

SUBFAMILY DOLICHODERINAE

***Dorymyrmex pyramicus albemarlensis* Wheeler, 1919**
(ANTWEB: CASENT0173213). (Map 3)

This species is possibly endemic (LUBIN, 1984; F. Cuezzo pers. comm., XI.2009). It is distributed on 14 islands and is associated with natural areas. The first specimens were collected in 1898 on Isabela (WHEELER, 1919). This species builds nests in the soil, on sandy beaches, open areas between vegetation and lava (WHEELER, 1924; LUBIN, 1984), or in sandy patches within lava fields near the coast, surrounded by the occasional grass, trees of *B. graveolens* and *Opuntia cacti*.

Dorymyrmex pyramicus albemarlensis apparently prefers dry zones, where it feeds on extrafloral nectaries of the giant endemic cacti *Opuntia echios* Howell and *Jasminocereus thouarsii* (F.A.C. Weber) Backeb (Meier, 1994). The species can be found occasionaly in the Transition zone and rarely in humid areas. It has been collected in stands of *Cryptocarpus pyriformis* Kunth, under trees of *Hippomane mancinella* L., in forests of *B. graveolens* that also include *Zanthoxylum fagara* (L.) Sarg, *Macraea laricifolia* Hook. f., *Cordia* sp, *Waltheria ovata* Cav., *C. scouleri*, *Darwiniothamnus lancifolius* (Hook. f.) Harling, *Alternanthera filifolia* (Hook. f.) J.T. Howell and grasses. *Dorymyrmex pyramicus albemarlensis* is also recorded in areas with *Scalesia affinis* Hook. f., *Castela galapageia* Hook. f., *Opuntia insularis* Stewart,

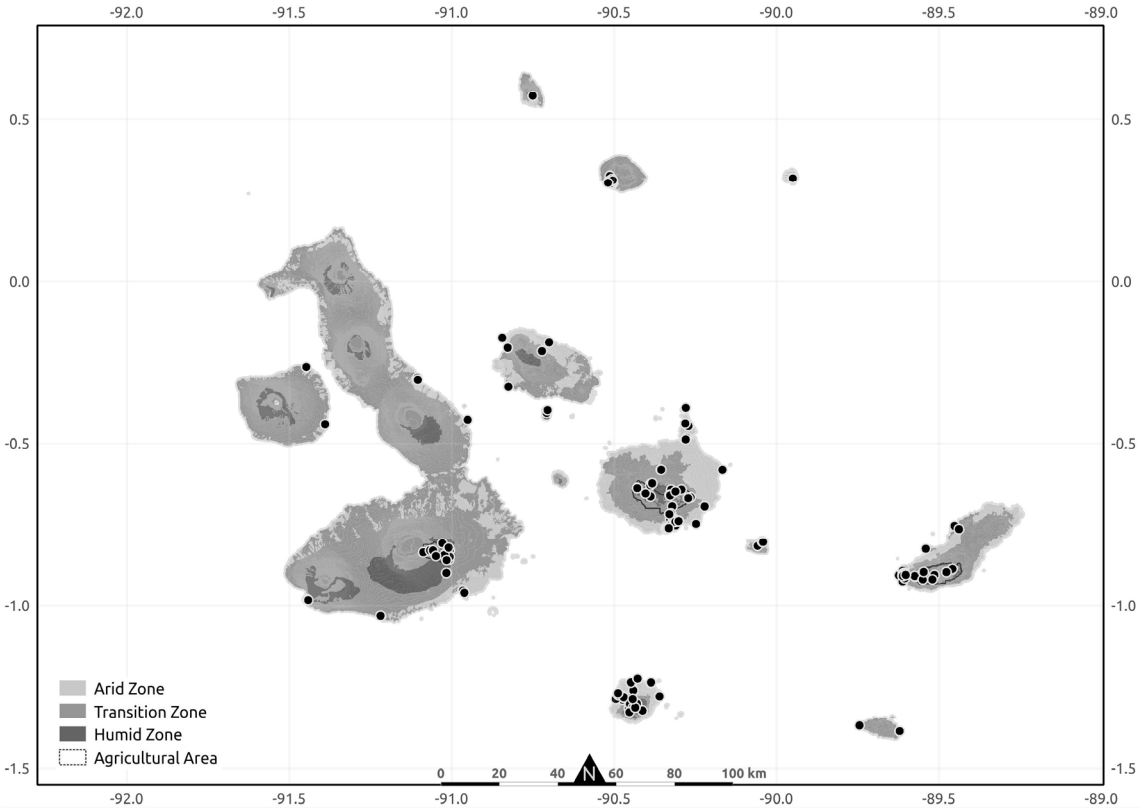


Map 3. Distribution of *Dorymyrmex pyramicus albemarlensis* Wheeler, 1919.

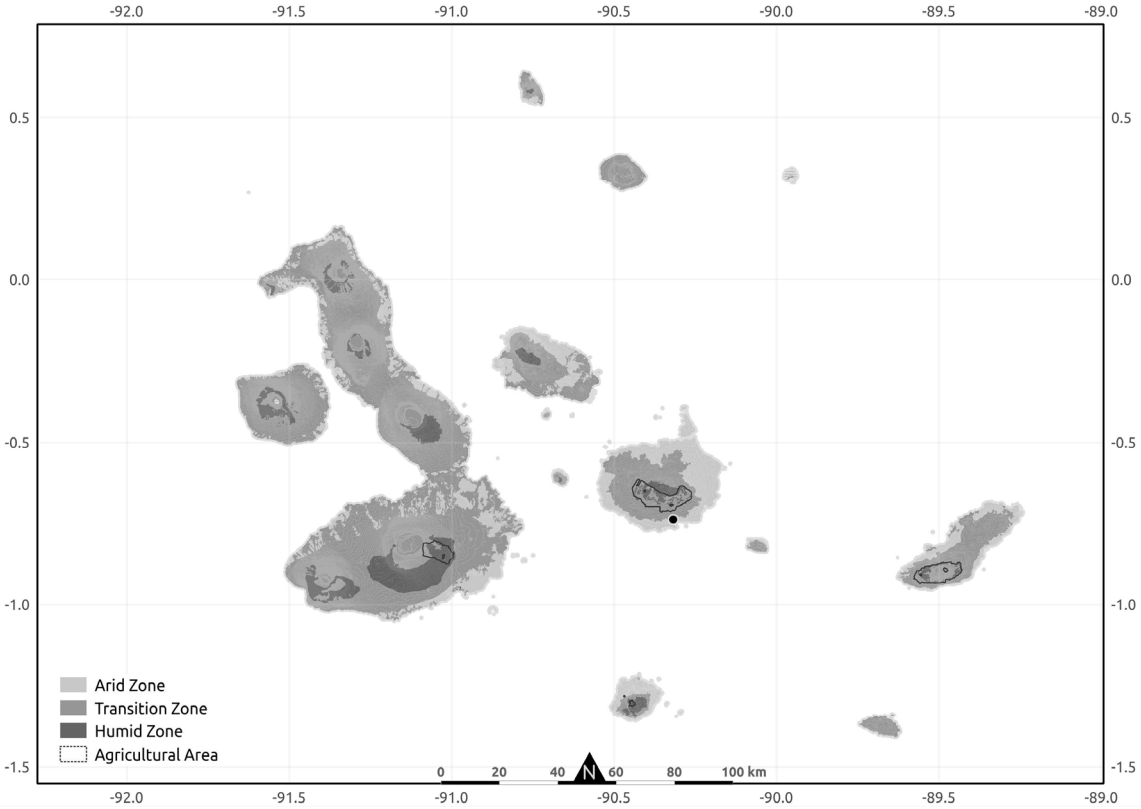
Cordia leucophlyctis Hook. f. and dry grass. Other records are from vegetation composed of *Opuntia helleri* K. Schum., *C. scouleri, Cordia lutea* Lam., *Lantana peduncularis* Andersson and dry litter. In the humid zone of Alcedo volcano (Isabela Island) workers were collected in a closed woodland of *P. floribunda*. *Dorymyrmex pyramicus albemarlensis* is preyed upon by *Tmarus stolzmanni* Keyserling, 1880, a crab-spider (Thomisidae) distributed in the arid and transition zones (LUBIN, 1983; BAERT, 2008). The invasive ants *W. auropunctata* and *S. geminata* could have displaced *D. pyramicus albemarlensis* on the islands of Santa Cruz and Baltra where it was once common (WHEELER, 1924).

***Tapinoma melanocephalum* (Fabricius, 1793)**
Ghost Ant (DEYRUP *et al.*, 2000)
(ANTWEB: CASENT0173215). (Map 4)

A cosmopolitan ant, widespread in the tropics, subtropics and temperate regions (KEMPF, 1972; BOLTON *et al.,* 2006; WETTERER, 2015). *Tapinoma melanocephalum* is a tramp species introduced through trade to many parts of the world (PASSERA, 1994; WETTERER, 2009a). It was collected for the first time in 1891 on San Cristóbal Island (EMERY, 1893; WHEELER, 1919). It is widely distributed in Galápagos on 17 islands and islets and found often in the Dry Zone in natural as well as disturbed habitats. Nests are found under and inside dead branches of *B. graveolens* abandoned by termites (WHEELER, 1924), under rocks, rotten logs, bark of dead–dry trees and house walls. This species has been collected in trunks of *B. graveolens* and several plant species, such as *Parkinsonia aculeata* L. and *Psidium guajava* L. *Tapinoma melanocephalum* is a diurnal species (LUBIN, 1984) that has been observed feeding on nectar from flowers of *Catharanthus roseus* (L.) G. Don. and extrafloral nectaries of *O. echios* and *J thouarsii* (MEIER, 1994). Visit flowers of *Avicennia germinans* (L.), *Ipomoea habeliana* Oliv., *O. helleri, Prosopis juliflora* (Sw.) DC. and *Scalesia atractyloides* Arn. Workers were



Map 4. Distribution of *Tapinoma melanocephalum* (Fabricius, 1793)



Map 5. Distribution of *Tapinoma* sp. hh07.

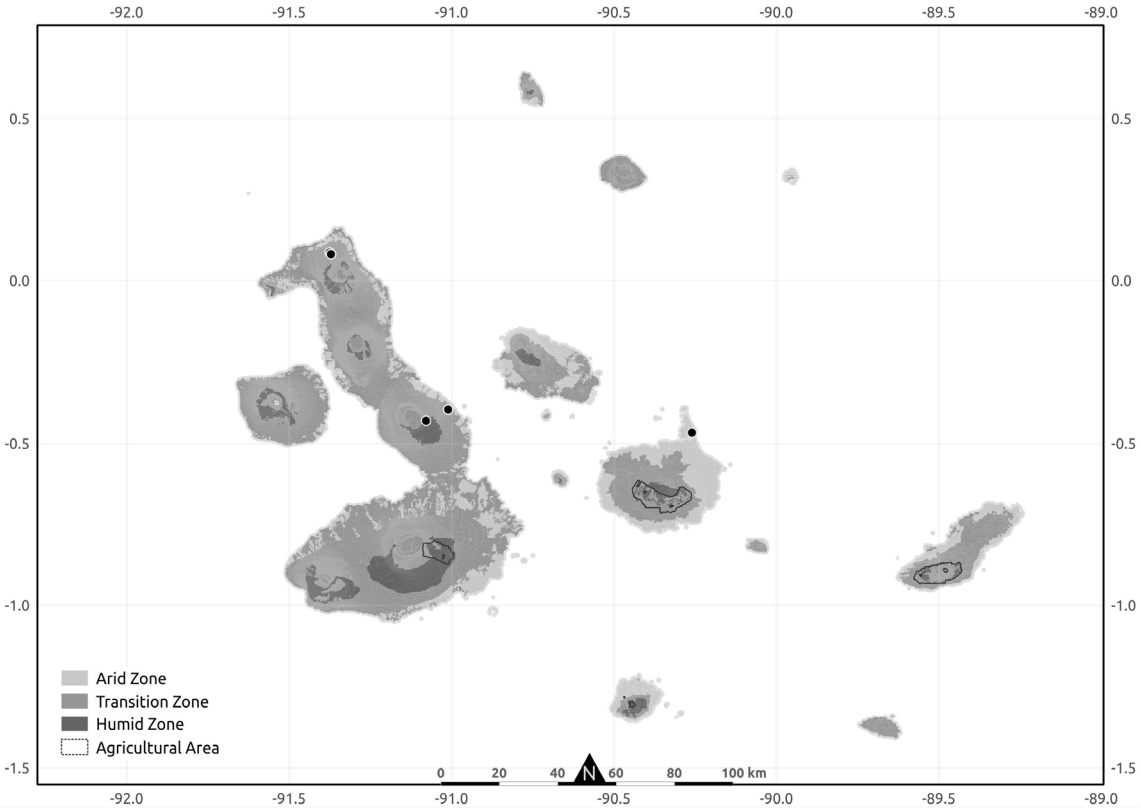
observed transferring pollen of *C. lutea* flowers (MCMULLEN, 1986, 1990, 1993, 2009; Chamorro *et al.,* 2012). *Tapinoma melanocephalum* can be common in the agricultural areas where it can attend Hemiptera species for honeydew, e.g on *Brassica oleracea* var. *italic* Plenck. It is common in human settlements.

***Tapinoma* sp. hh07**
(ANTWEB: CASENT0625421). (Map 5)

Known only from Santa Cruz Island, its origin is unknown. It was collected for the first time in 2005 in the Dry Zone on Santa Cruz Island (HERRERA *et al.,* 2014). *Tapinoma* is a genus widely distributed in the world. Approximately 95 species have been described, 21 of them found in the Neotropical region (SHATTUCK, 1995).

SUBFAMILY DORYLINAE
***Cylindromyrmex whymperi* (Cameron, 1891)**
(ANTWEB: CASENT0173212). (Map 6)

A neotropical species whose origin in Galápagos is uncertain (KEMPF, 1972; LUBIN, 1982; DE ANDRADE, 1998, 2001; BOLTON *et al.,* 2006). Collected for the first time on Santa Cruz in 1906 (WHEELER, 1919), it has now been found on five islands. Little is known about *C. whymperi* in the archipelago. Nests can be found in dead branches (*Maytenus octogona* (L. Hér.) DC.). The species also uses galleries constructed by termites (possibly *Incisitermes pacificus* (Banks, 1901)) (WHEELER, 1924). In the Transition Zone of Wolf volcano on Isabela, workers were collected inside a rotten trunk next to nests of the ants *Camponotus macilentus* Smith, 1877 and *Camponotus planus* Smith, 1877. In the Dry Zone one worker was collected in an open forest



Map 6. Distribution of *Cylindromyrmex whymperi* (Cameron, 1891).

of *B. graveolens*. On a recent ant survey on the summit of Alcedo volcano on Isabela, one winged female was observed on leaves of *Scalesia microcephala* B.L. Rob. This is the first record from the pampa zone at higher altitudes. On Fernandina and in the Littoral Zone of Floreana specimens have not been collected since the first records of STITZ (1932) and SILBERGLIED (1972).

Cylindromyrmex whymperi appears to have been displaced by the invasive ant *W. auropunctata* on Santa Cruz Island (SILBERGLIED, 1972). This could be the case also for Floreana and Baltra Islands where *S. geminata* and the "destructive trailing ant" *Trichomyrmex destructor* (Jerdon, 1851) have invaded large areas of the islands (VON AESCH, 2006; HERRERA & CAUSTON, 2010; HERRERA unpublished data).

SUBFAMILY FORMICINAE

***Brachymyrmex heeri* Forel, 1874**

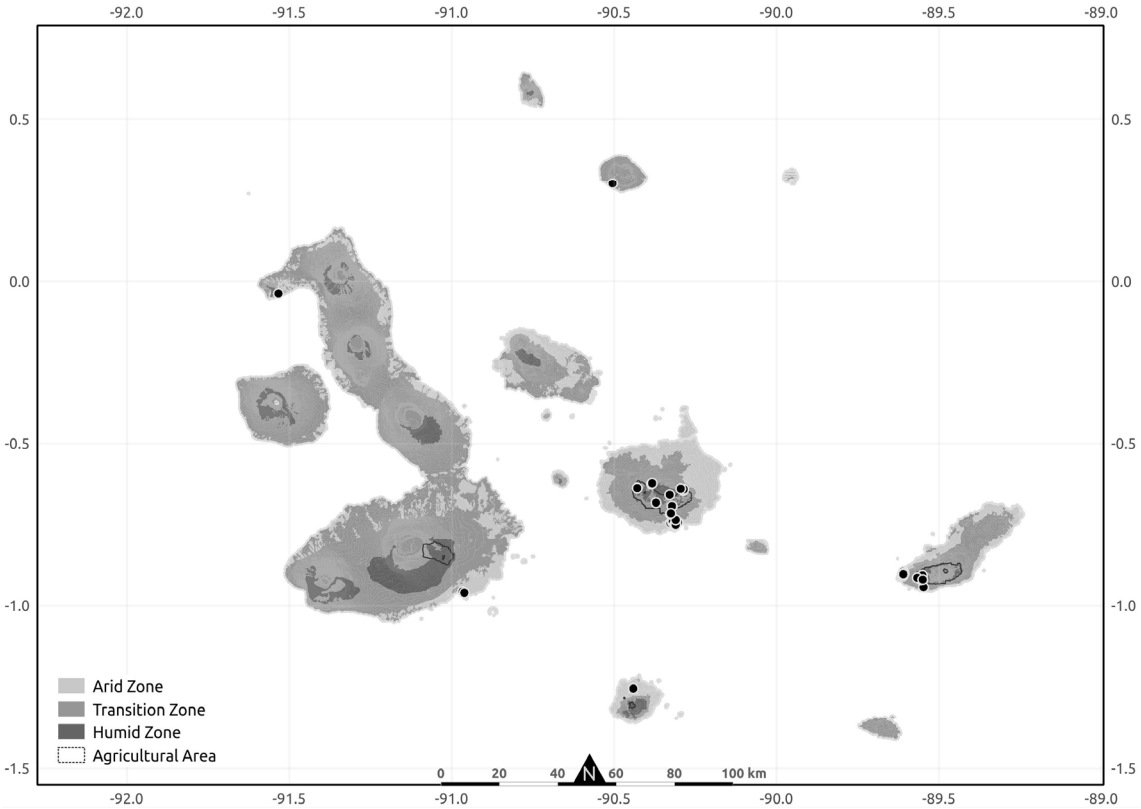
(ANTWEB: CASENT0173228). (Map 7)

Distributed in Central, South America and the Antilles (KEMPF, 1972; BOLTON *et al.,* 2006). *Brachymyrmex heeri* is an introduced species that was collected for the first time in 2001 (HERRERA & LONGINO, 2008). Often found in the dry areas, it is distributed on five islands in disturbed and natural environments. Nests have been found in roots of *C. roseus*, sidewalks of streets, and under rocks and rotten trunks in *Scalesia* and *Miconia* areas. It has been reported visiting flowers of *Gossypium darwinii* G. Watt, *C. roseus*, potted plants and other ornamental plants in gardens. It has also been reported on crops such as coffee (*Coffea arabica* L.), citrus and bananas. Other records are available from *Piscidia carthagenensis* Jacq. forests. Workers have been collected on *Opuntia megasperma* J. T. Howell, *G. darwinii*, *Malus pumila* (L.) Mill. and plants of *Hibiscus rosa–sinensis* L., *Ricinus communis* L., *Spondias purpurea* L., *Mangifera indica* L., *Carica papaya* L., *C. lutea*, *M. octogona* and *Cocos nucifera* L. Mutualistic interactions with scale insects like *Coccus viridis* (Green), the invasive cottony cushion scale *Icerya purchasi* (Maskell, 1878), and unidentified aphids (CAUSTON *et al.,* 2006; VELASCO *et al.,* 2010), could contribute to their spread. *Brachymyrmex heeri* is considered a minor threat to Galápagos ecosystems (HERRERA & LONGINO, 2008).

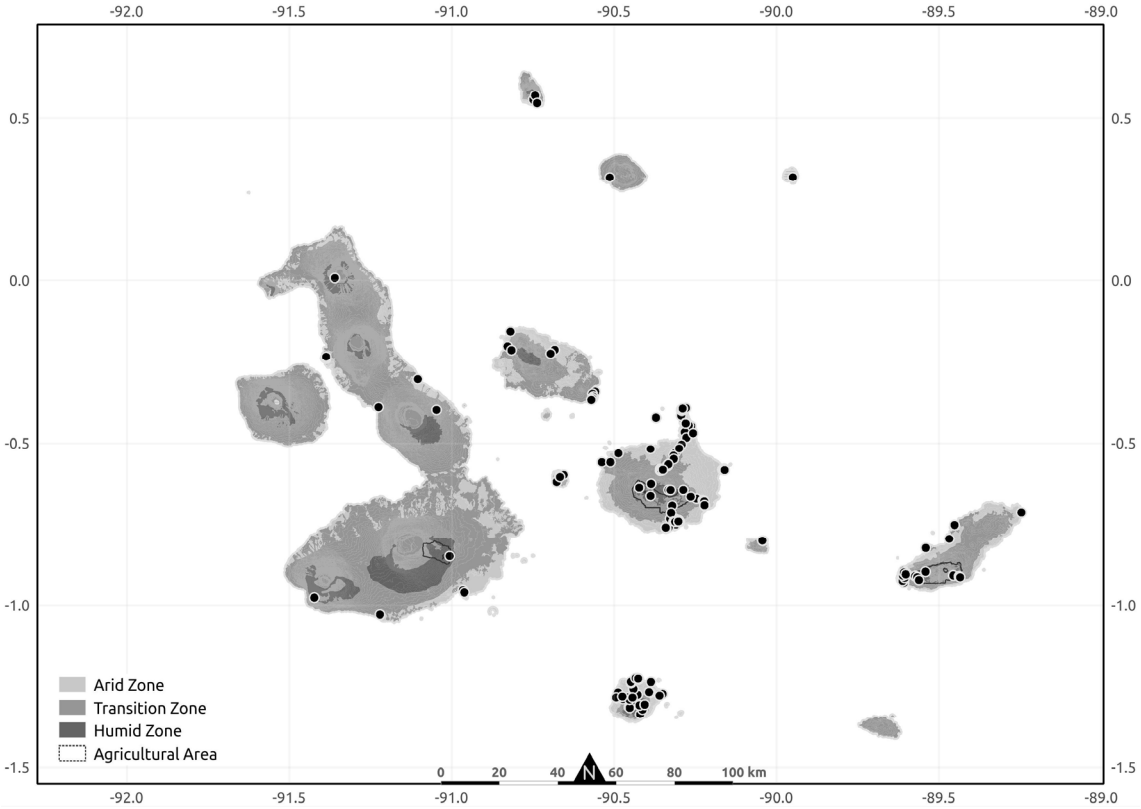
***Camponotus conspicuus zonatus* Emery, 1894**

(ANTWEB: CASENT0173224). (Map 8)

Known from Central America (Costa Rica) and South America (Brazil and Ecuador) (BOLTON *et al.,* 2006; ANTWEB, 2019). This introduced species is widely dispersed in Galápagos and occurs on 24 islands and islets from the littoral to humid zones. The first specimens were collected in 1975 in the Arid Zone of Santa Cruz Island. *Camponotus conspicuus zonatus* is a polygyne species that nests under rocks, rotten logs, and in and around buildings. It has been observed visiting flowers of *Tournefortia rufo–sericea* Hook. F, *C. lutea*, *C. pyriformis* and *Clerodendrum molle* Kunth. Reports also exist of tending of *I. purchasi* for honeydew (HODDLE *et al.,* 2013). It is common in populated areas of inhabited islands, and can be collected all year round. In the lowlands it can be observed foraging on sandy beaches, between mangrove leaf litter, in branches of *C. pyriformis* and in patches of *Sesuvium* spp. It has also been collected in areas with *M. octogona*, *A. germinans*, *Laguncularia racemosa* (L.) C.F. Gaertn) and in forests of *B. graveolens* with *Scutia spicata* (Humb.& Bonpl. ex Schult.) Weberb. It has been collected on *Passiflora suberosa*, *C. scouleri, J. thouarsii, B. graveolens*, *O. echios*, *H. mancinella. Ipomoea triloba* L., *M. laricifolia* and *Parkinsonia aculeata* L. Specimens have been registered in the agricultural zone in crops *Solanum lycopersicum* L., *B. oleracea var. italica*, *Musa acuminata* Colla, *Citrus* x *sinensis* (L.) Osbeck, *C. papaya* and *Cucumis sativus* L.



Map 7. Distribution of *Brachymyrmex heeri* Forel, 1874.



Map 8. Distribution of *Camponotus conspicuus zonatus* Emery, 1894.

Camponotus conspicuus zonatus is a nocturnal species, common in urban and disturbed zones. It is often confused with *C. macilentus* (HERRERA unpublished data) and has quickly invaded natural areas in the archipelago. *Camponotus conspicuus zonatus* appears to have replaced the endemic species *C. macilentus* in many localities of the archipelago. Collections of this ant from cargo docks, cargo ships and aircrafts suggest several reintroductions to Galápagos.

***Camponotus macilentus* Smith, 1877**
(ANTWEB: CASENT0173216). (Map 9)

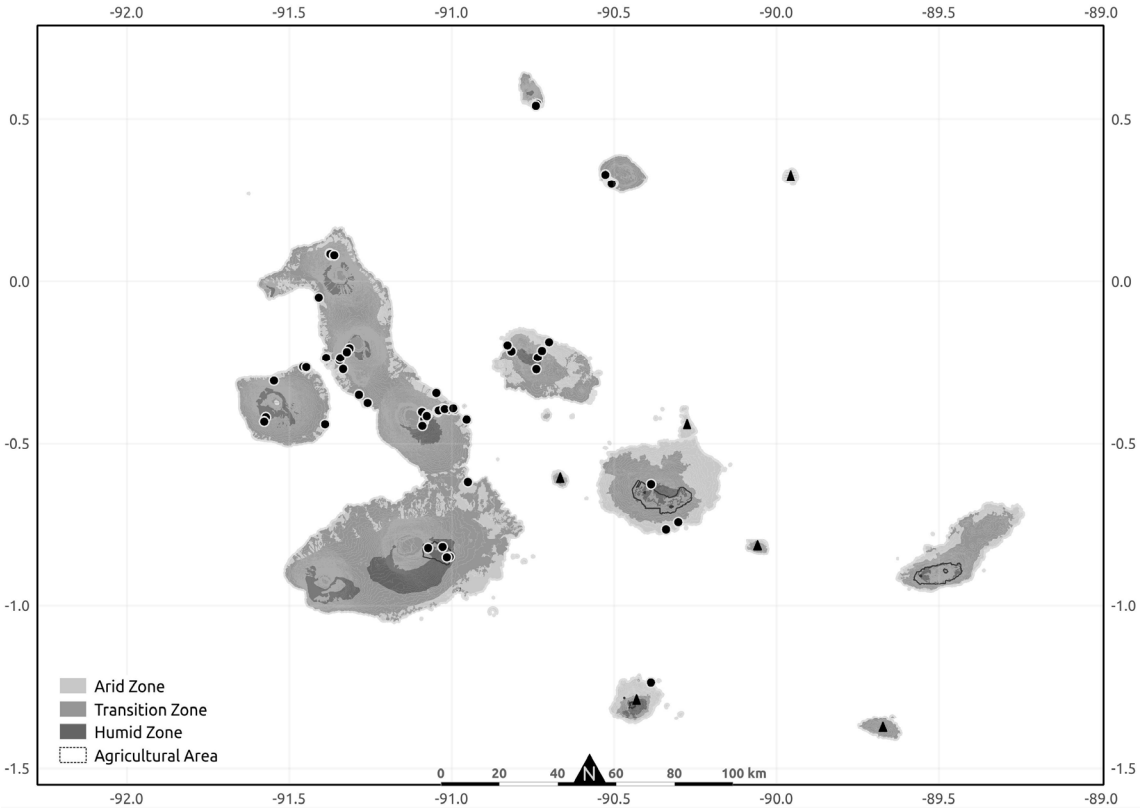
This endemic and nocturnal species is uncommon in the archipelago. It was collected for the first time by Charles Darwin in 1835 (SMITH, 1877; WHEELER, 1919; LUBIN, 1984). It is known mainly from dry areas and is rarely found in the humid zones. It is distributed on 13 islands and is known to nest under rocks, and in hollow twigs in dry branches of *B. graveolens* and *M. octogona* previously inhabited by termites (WHEELER, 1919, 1924). It has been observed collecting honeydew from scale insects on the trunks and stems of *Scalesia gordilloi* O. Hamann & Wiumand and it has been reported visiting flowers of *C. lutea*, *C. molle*, *S. cordata* and extrafloral nectaries of *O. echios* and *J. thouarsii* (MEIER, 1994; BOADA, 2005; MCMMULLEN, 2011, 2012). *C. macilentus* has been collected from mangroves (*Rhizophora mangle* L., *L. racemosa*), *B. graveolens*, *C. galapageia*, under trees of *H. mancinella*, and in undergrowth (like *I. triloba*) and ferns. It has also been collected in areas dominated by *Psychotria rufipes* Hook. f., *Z. fagara*, *S. microcephala*, *C. pyriformis* and *P. juliflora*. *Camponotus macilentus* apparently is strongly associated with forests of *B. graveolens* (HWH, pers. obs.).

Recent sampling (on volcanoes Alcedo and Darwin) show that the species is abundant in better conserved areas. *Camponotus macilentus* could be threatened by invasive species on Baltra, Floreana, Española and Santa Cruz islands. It was collected for the last time on Santa Cruz in the Littoral Zone in 1996 and in the Humid Zone in 2001 and has not been found since then despite intensive collections in all vegetation zones (using a large number of collecting methods) over the last 12 years. LUBIN (1985) suggested a probable displacement of *C. macilentus* due to the invasion of *Tetramorium bicarinatum* (Nylander, 1846) during the Niño event of 1982–1983 on Española. *Camponotus macilentus* is extremely shy and prefers to escape fast when threatened. In natural habitats it is preyed upon by *T. stolzmanni*, a crab–spider present in littoral, dry and transition zones, especially in shrubs of *C. galapageia* (LUBIN, 1983). *Camponotus macilentus* is a complex of at least 12 subspecies (WHEELER, 1919, 1924, 1933), that requires further study.

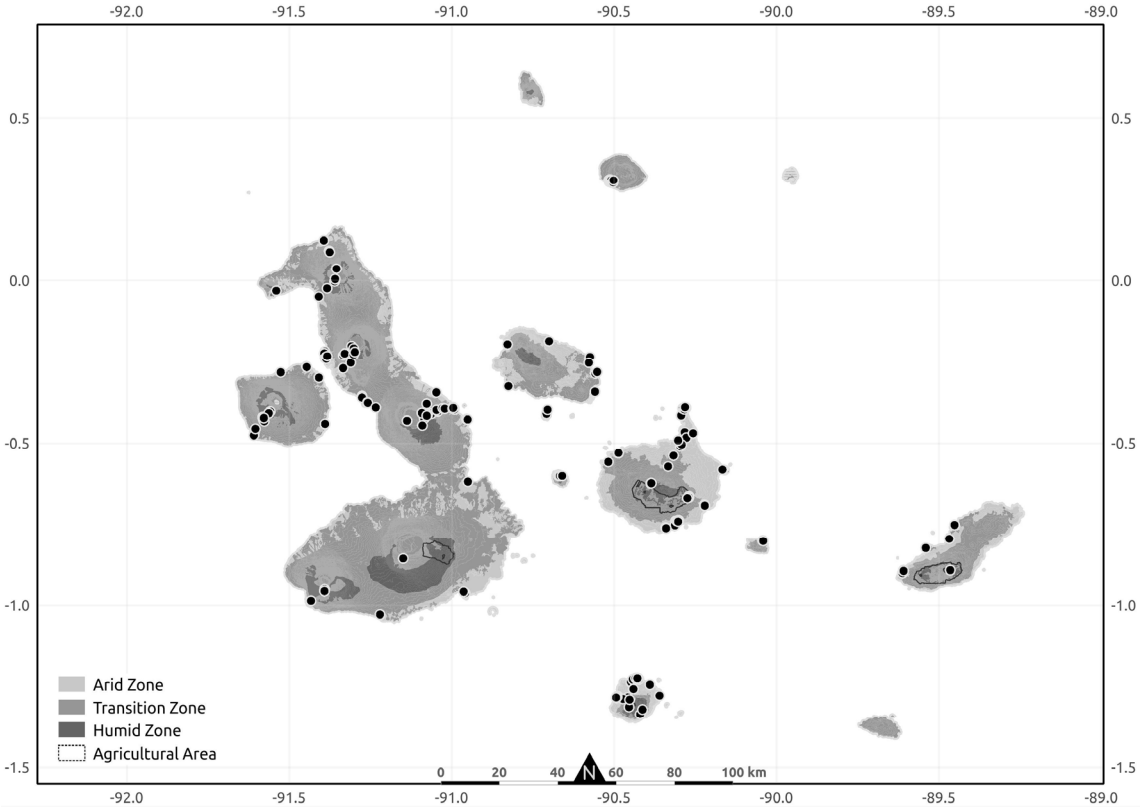
***Camponotus planus* Smith, 1877**
(ANTWEB: CASENT0173221). (Map 10)

Camponotus planus is an endemic diurnal species (WHEELER, 1924; MEIER, 1994). It was collected for the first time by Charles Darwin in 1835 and so far it is recorded on 17 islands. It is common in the Littoral Zone and mangrove patches (foraging between the leaf litter), and it can also be found in dry areas. It is not common in the humid highland zones. It nests in the roots of trees, shrubs, *Opuntia* sp. (WHEELER, 1924), under rocks, and in dry branches of *B. graveolens* and rotten logs. *Camponotus planus* has been recorded feeding on extrafloral nectaries of *O. echios*, visiting flowers of *J. thouarsii* (MEIER, 1994; JARAMILLO *et al.,* 2010), tending mealy bugs on stems of *S. atractyloides*, *S. gordilloi* and visiting flowers of *C. lutea* (WHEELER, 1924; BOADA, 2005).

Workers have been collected in areas with *C. scouleri*, *S. microcephala*, *M. laricifolia*, *B. graveolens*, *Z. fagara*, *C. lutea* and *W. ovata*, *P. rufipes*, *D. lancifolius*, *T. rufosericea*, *H. mancinella*, *M. octogona*, *P. floribunda*. *Camponotus planus* has also been found on sandy



Map 9. Distribution of *Camponotus macilentus* Smith, 1877.



Map 10. Distribution of *Camponotus planus* Smith, 1877.

beaches with *Sesuvium edmondstonii* Hook. f. and *C. pyriformis*, in the shrub layer dominated by *Dodonaea viscosa* Jacq. and *O. insularis*, in fern zones (like *Polypodium tridens* Kunze, *Doryopteris pedata* var. *palmata* (Willd) Hicken), on shrubs of *L. peduncularis*, in grasses covered with *I. triloba*, and herbs of *Sida salviifolia* C. Presl. *Camponotus planus* is also common in branches and leaves of mangroves (*A. germinans*, *L. racemosa*, *R. mangle*).

Camponotus planus reacts quickly when the nest is disturbed. In natural areas it can be preyed upon by *T. stolzmanni*, a crab–spider (LUBIN, 1983). Males and queens can be abundant in the hot–rainy season (December–May), especially near the coast, where nuptial flights occur. It can also be found during the cold season (June–November), though it is less active (WHEELER, 1924). Males and queens can be collected around lights of lamps in the streets, houses and on ships. *Camponotus planus* has been found traveling on tourist boats suggesting that they play a role in species transfer between islands (LOMAS, 2008). Despite its wide distribution in the archipelago *C. planus* has not been collected on Pinta, Genovesa and Española, however the ant fauna of these islands is poorly studied. *Camponotus planus* is a complex of at least nine subspecies (WHEELER, 1919, 1924, 1933), that requires further study.

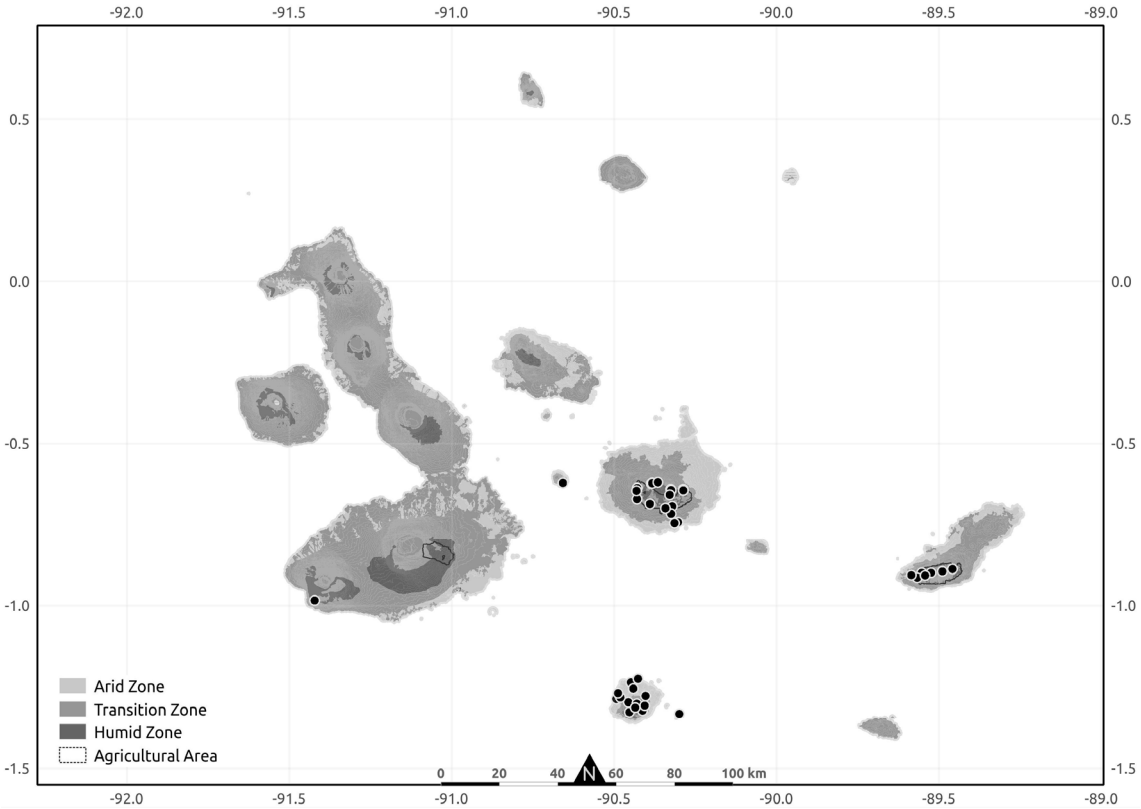
***Nylanderia steinheili* (Forel, 1893)**
(ANTWEB: CASENT0173233). (Map 11)

This species is found in tropical areas of Central, South America and some Caribbean islands (KEMPF, 1972; BRANDÃO, 1991; BOLTON *et al.,* 2006). *Nylanderia steinheili* was likely introduced to the Galapagos Islands 20-30 years ago. It was collected for the first time in 2003 in the Humid Zone of Santa Cruz (HERRERA *et al.,* 2014). Since then it has been found in the dry and humid areas and on six islands in the archipelago including in areas that are invaded by *W. auropunctata* and *S. geminata*. It has been found nesting under stones, logs, and rotten trunks. Workers were collected in gardens, *P. guajava* forest and open areas of urban, natural and cultivated zones. *Nylanderia steinheili* is also reported from shade–grown coffee zones and associated with anthropogenic areas. Its behavior in other parts of the world suggests that it is not a threat for the fauna of the archipelago (VARGAS *et al.,* 2006; MCGLYNN & KIRKSEY, 2000; REYES, 2010; KALLAL & LAPOLLA, 2012; HERRERA *et al.,* 2014), however a monitoring program is suggested.

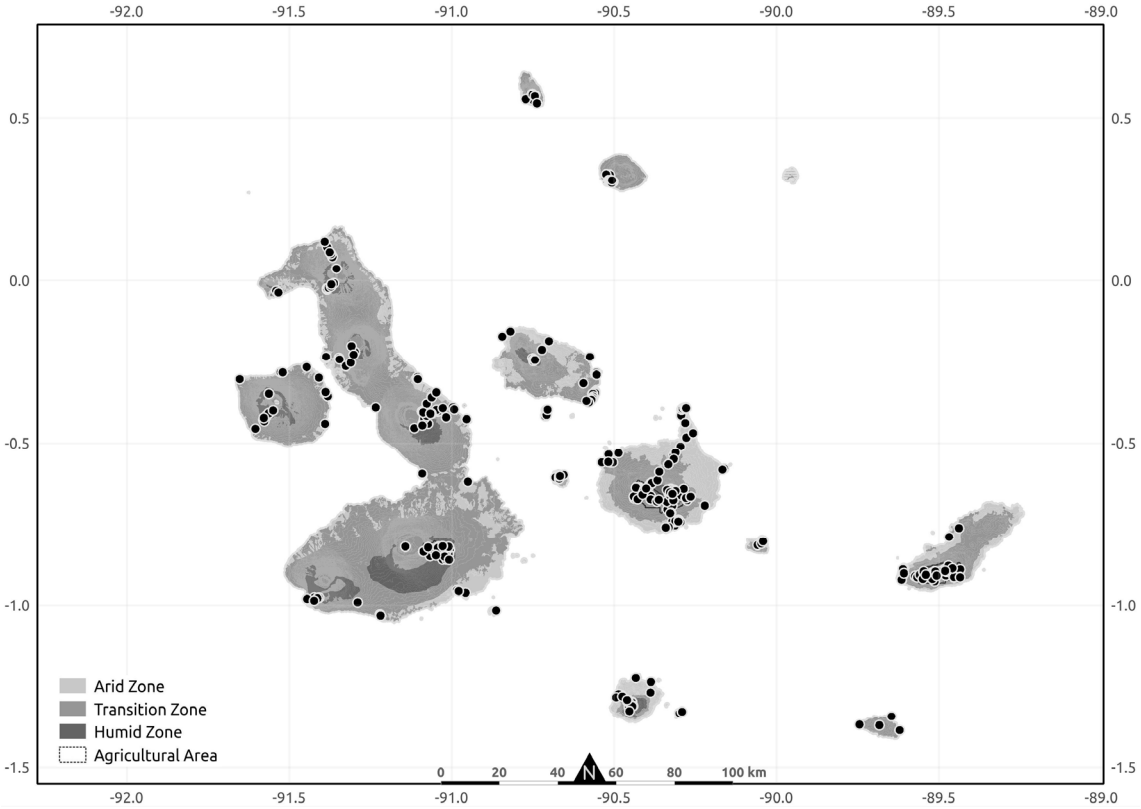
***Nylanderia* spp.** (Map 12)

Nylanderia is a widely distributed genus in all vegetation zones in Galápagos, but its taxonomy is not yet clearly understood and awaits a detailed revision. With the exception of *N. steinheili*, three other species have previously been recorded in Galápagos (WHEELER, 1919, 1924, 1933; CLARK, 1982), but the identity and taxonomical status of these records is uncertain.

More than three morphospecies of *Nylanderia* occur in the archipelago (HERRERA unpublished data). Workers forage in the soil, between leaf litter in mangrove areas, on shrubs on beaches and between lava near to beaches. Ants have been observed nesting under stones and bark of rotten trunks as well as in small, humid patches of vegetation located in ravines that cross extensive fields of lava on Fernandina. Specimens are commonly collected in Winkler samples in the transition and humid zones (in natural and disturbed areas), in forests of *P. floribunda, B. graveolens*, *Cedrela odorata* L., *M. robinsoniana, Cinchona pubescens* Vahl, in areas covered with *Pteridium* spp., and the *S. pedunculata* forest in los Gemelos on Santa Cruz. Workers have also been collected on leaves and stems of *Conocarpus erectus* L., *Calandrinia galapagosa* H. St. John, *S. microcephala*, *S. cordata*, *A. germinans*, under trees of *H. mancinella*, visiting flowers of *C. lutea*, *I. habeliana*, *Plumbago scandens* L., and collecting nectar from *T. rufo–sericea* (MCMULLEN, 1986, 1993; BOADA, 2005; MCMULLEN, 2009). In the agricultural zone, workers were present in crops of *Ananas comosus* (L.) Merr., *Brassica*



Map 11. Distribution of *Nylanderia steinheili* (Forel, 1893).

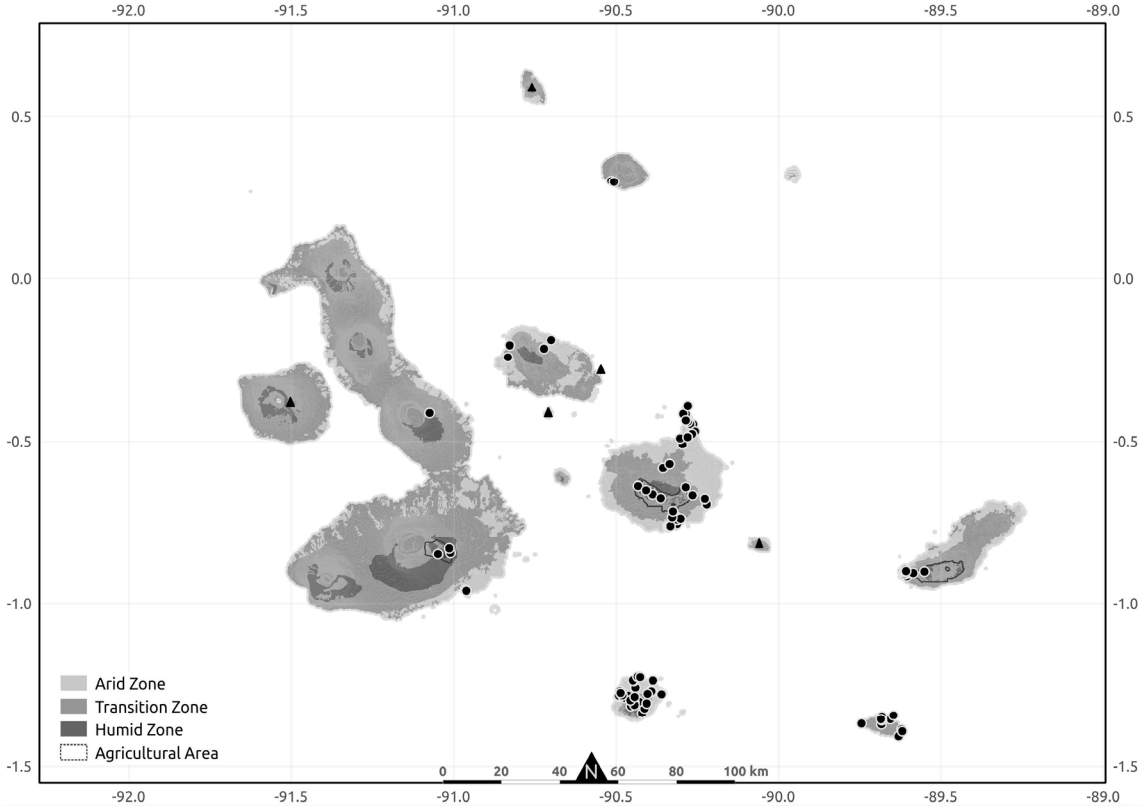


Map 12. Distribution of *Nylanderia* spp.

oleracea var. *capitata* L., *Allium cepa* L.*, B. oleracea var. italica*, *C. papaya*, *Capsicum annuum* L., *Citrullus lanatus* (Thunb.) Matsun. & Nakai, *C. sinensis*, *C. arabica*, *Manihot esculenta* Crantz, *Musa* × *paradisiaca* L., *M. acuminata*, *Persea americana* Mill., *Phaseolus vulgaris* L., *P. guajava*, *Paspalum* sp., *Saccharum officinarum* L., *Solanum betaceum* Cav., *S. lycopersicum*, *Solanum quitoense* Lam. and *Zea mays* L. *Nylanderia* spp. have been recorded visiting *I. purchasi* and other aphids for honeydew. In populated areas, *Nylanderia* spp., are common in gardens, disturbed areas and cargo docks. On San Cristóbal, specimens were found during inspections carried out in the holds of aircrafts arriving from mainland Ecuador.

***Paratrechina longicornis* (Latreille, 1802)**
Longhorn Crazy Ant (WETTERER, 2008)
(ANTWEB: CASENT0173232). (Map 13)

Paratrechina longicornis is a tramp species spread by human activities in tropical, subtropical and temperate areas around the world (KEMPF, 1972; BOLTON, 2006; WETTERER, 2015). Distributed over 16 islands and islets it was collected for the first time in Galápagos on Floreana Island between 1905–1906 (WHEELER, 1919). It nests between leaf litter, dead trunks and under stones. It is common in mangroves (*R. mangle*, *A. germinans, C. galapagosa*) and is a scavenger and opportunistic diurnal species also invading natural areas (MEIER, 1994). *Paratrechina longicornis* is very well adapted to all vegetation zones in Galápagos. An entomological survey carried out in 1991 on Española Island showed that *P. longicornis* was abundant in dry areas (with *Oxalis dombeyi* A. St.–Hil, *Physalis galapagoensis* Waterf., *B. graveolens*, *P. juliflora*, *C. lutea*, *I. triloba*, *Pennisetum pauperum* Nees ex Steud., *Mentzelia aspera* L., *Desmodium procumbens* (Mill.) Hitchc., *C. leucophlyctis*, *Alternanthera echinocephala* (Hook. f.) Christoph., *C. scouleri*, *L. pedunculares*, *P. aculeata*, *S. spicata*, *M. octogona* and *O. megasperma*).



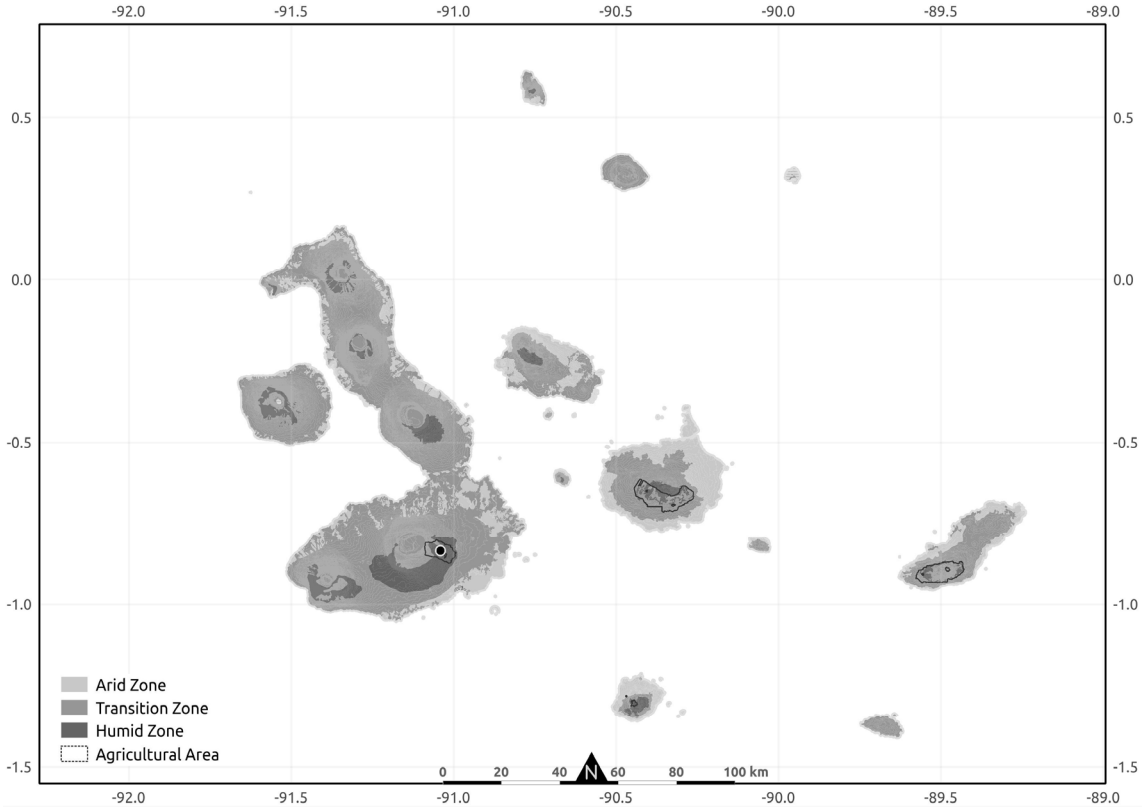
Map 13. Distribution of *Paratrechina longicornis* (Latreille, 1802).

Paratrechina longicornis has been recorded visiting flowers of *G. darwinii*, *A. germinans*, *C. molle*, *C. lutea*, and extrafloral nectaries of giant endemic cacti *O. echios* and *J. thouarsii* (MCMULLEN, 1990, 1993; MEIER, 1994; CHAMORRO *et al.,* 2012). It was collected on plants of *G. darwinii*, *M. octogona*, *O. megasperma*, *Annona cherimola* Mill., *R. communis* and *C. lutea*. It has been reported feeding on honeydew from *I. purchasi* and *Ceroplastes* spp. WETTERER (2008) mentions a possible case of mutualism with *Coluocera maderae* Wollaston, 1854, a beetle also recorded from Galapágos (PECK, 1993, 2005). *Paratrechina longicornis* is common in urban zones, inhabits flowerpots, buildings and streets. In gardens it can be found in plants of *C. nucifera*, *C. papaya*, *Annona muricata* L. and grass. It is present in agricultural areas of the inhabited islands of Floreana, Isabela, San Cristóbal and Santa Cruz where it is reported from crops of *P. vulgaris*, *M. esculenta* and *C. sinensis*.

Paratrechina longicornis is invasive in many parts of the world (WETTERER, 2008) and has probably been introduced several times to the islands. In Galápagos it is considered an invasive ant with a high potential to disperse and colonize new natural areas (CAUSTON *et al.,* 2006). It is common in ports and airports and has been intercepted in commercial aircraft during quarantine inspections of products from mainland Ecuador (in *A. comosus)* in Baltra. The species was also found in cargo and on tourist ships (LOMAS, 2008; HERRERA, 2011), that probably facilitate its spread to and within Galápagos.

SUBFAMILY MYRMICINAE
***Adelomyrmex longinoi* Fernández, 2003**
(ANTWEB: CASENT0173239). (Map 14)

An introduced species known from Central America; from Guatemala to Costa Rica (FERNÁNDEZ, 2003; LONGINO, 2012). It was collected in Galápagos for the first time in 2003



Map 14. Distribution and ecological zone registered for *Adelomyrmex longinoi* Fernández, 2003.

and is only known from the Humid Zone of Isabela Island (HERRERA & LONGINO, 2008, misidentified as *A. myops*). A few specimens have been collected in litter in mature forests of *Inga edulis* Mart. and *P. guajava* in disturbed and cultivated areas. Additional Berlese or Winkler sampling throughout other islands of the archipelago might reveal more records of this species and help us understand its distribution and habitat preferences.

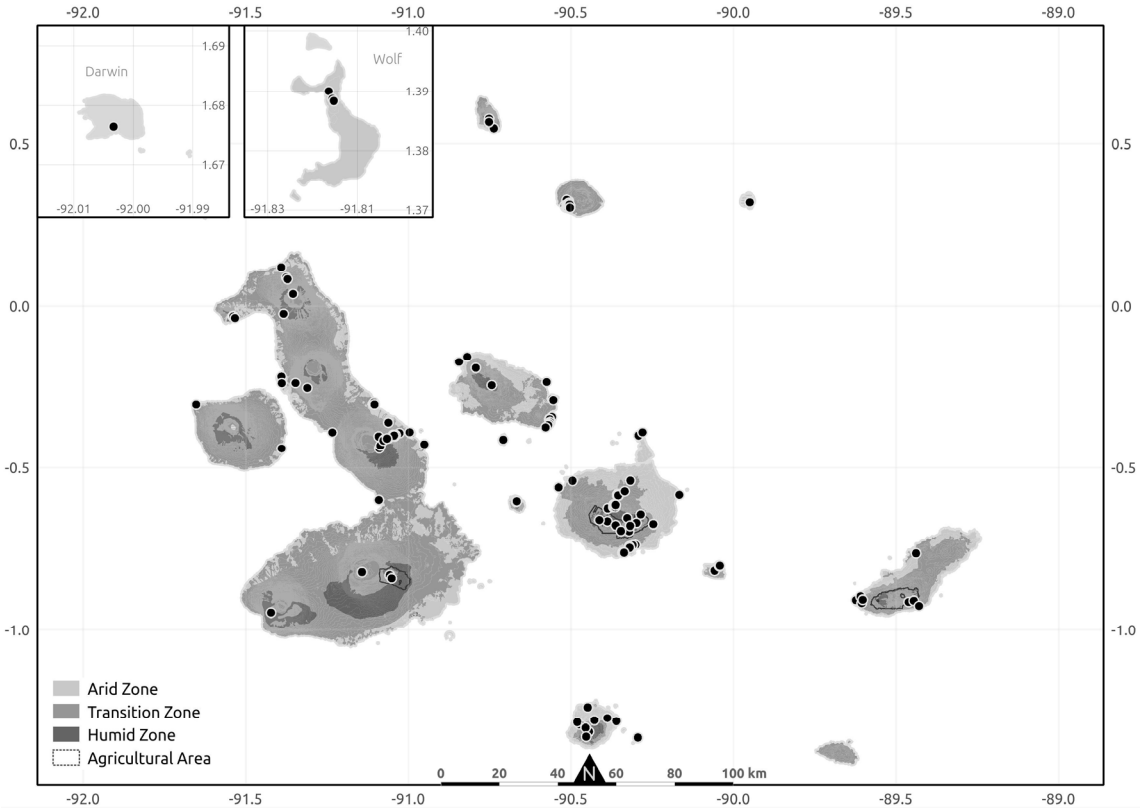
***Cardiocondyla emeryi* Forel, 1881**
Emery's Sneaking Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173259). (Map 15)

A tramp ant, widely distributed throughout tropical, subtropical and temperate areas (KEMPF, 1972; BOLTON *et al.,* 2006; WETTERER, 2012). It is found in 30 islands and islets of the archipelago. It was recorded for the first time in 1984 (LUBIN, 1984). Nests have been found in branches of *S. pedunculata*, under rocks, in the ground and in rotten logs. It is present from the littoral to humid zones, and has been found in mangroves and forests of *S. pedunculata*, *P. floribunda*, *P. galapageium* and *B. graveolens.* Some specimens were collected in closed woodlands dominated by *P. floribunda*, *Z. fagara*, *C. scouleri* and *P. galapageium*. It is a conspicuous species of arid and transition zones (LUBIN, 1984), and was collected in fields of *Paspalum* sp., branches of *S. pedunculata*, trees of *B. graveolens* and dry areas composed of *C. lutea* and *W. ovata*. In cultivated areas it is reported from crops of *M. paradisiaca*, *Bambusa vulgaris* var. *vulgaris* Schrad ex Wendle, *Cucumis melo* L. and *P. vulgaris*. In urban areas it is present in gardens where it has been found on grass (*Zoysia matrella* var. *pacifica* Goudwaard), *C. lanatus* and *C. nucifera*.

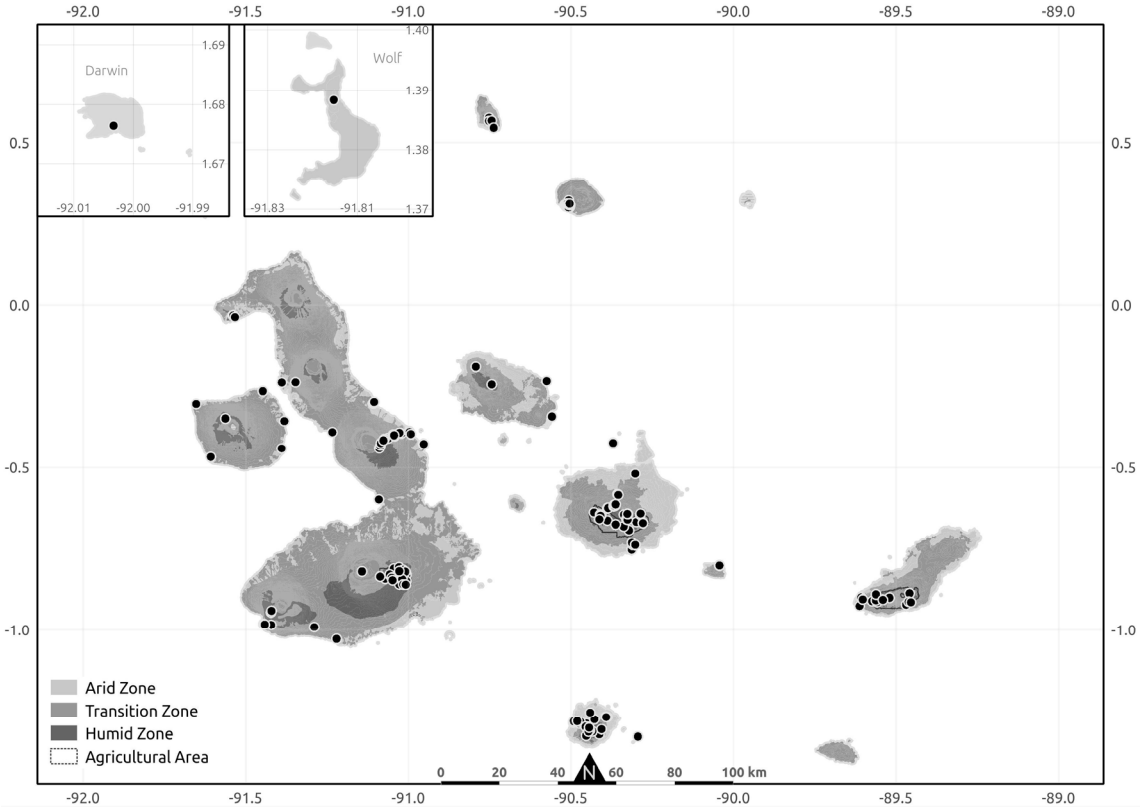
Cardiocondyla emeryi visits flowers and has been reported collecting nectar from *T. rufo–sericea* (MCMULLEN, 2007). In disturbed environments *C. emeryi* was collected in landfills, stone and gravel quarries, near electricity plants, urban areas and roads. *Cardiocondyla emeryi* is not considerated an agressive species in other parts of the world (WETTERER, 2014a), however in Galápagos it has colonized pristine areas, which suggests that it could have an impact on native biota (CAUSTON *et al.,* 2006).

***Cardiocondyla minutior* Forel, 1899**
(ANTWEB: CASENT0173261). (Map 16)

Cited in previous publications as *Cardiocondyla nuda* (WETTERER, 2014), *C. minutior* is a cosmopolitan tramp species introduced by human activities throughout the tropics and subtropics as well as to oceanic islands (SEIFERT, 2003; BOLTON *et al.,* 2006; HEINZE *et al.,* 2006, WETTERER, 2014b). It was collected for the first time in 1975 in the Humid Zone of Santa Cruz. It is a conspicuous ant of the Arid and Transition Zones (LUBIN, 1984; SEIFERT 2003, HEINZE *et al.,* 2006) and has been recorded on 16 islands. *Cardiocondyla minutior* visits flowers of *P. scandens* (MCMULLEN, 1993), trees of *B. graveolens*, *S. pedunculata,* shrubs of *T. rufo–sericea* and ferns in arid and humid zones of Santa Cruz. Specimens have also been collected in *P. floribunda* forests, under rocks and in mangrove litter. In the Littoral Zone of Fernandina, specimens were found along a small laguna under tidal influence; an area dominated by *Sporobolus virginicus* (L.) Kunth and grasses covered with *I. triloba*. *Cardiocondyla minutior* was collected along Black Beach (Bahía Urvina–Isabela Island) dominated by dry vegetation (*C. lutea*, *W. ovata* and *S. spicata*). In the Humid Zone of San Cristóbal, Santa Cruz, Floreana and Isabela, it is reported from cultivated areas in crops of *A. comosus, Solanum tuberosum* L., *S. lycopersicum*, *M. paradisiaca*, *C. papaya*, *S. quitoense*, *C. sativus*, *Z. mays*, *Lactuca sativa* L.*, P. vulgaris*, *A. cepa*, *B. oleracea var. capitata*. *Cardiocondyla minutior* is less common than *C. emeryi* and can be found in urban areas, tourist sites, landfills, electricity stations and quarries. In Galápagos it is considered an invasive ant with potential to disperse and colonize



Map 15. Distribution and ecological zone registered for *Cardiocondyla emeryi* Forel, 1881.



Map 16. Distribution of *Cardiocondyla minutior* Forel, 1899.

new natural areas (CAUSTON *et al.,* 2006). Although its impact on other Pacific Islands is considered to be minor (WETTERER, 2014a), it is possible that *C. minutior* could have a negative influence on native species in the natural areas of the Galapagos Islands.

***Crematogaster* JTL – 022**
(ANTWEB: ICCDRS0002584). (Map 17)

Probably distributed in the Andean regions of Colombia to southern Perú (HERRERA *et al.,* 2014). *Crematogaster* JTL –022 is an uncommon species recently introduced to the islands and only known from the Littoral and Transition Zone on San Cristóbal. It was recorded for the first time in 2007 in urban area near the coast of Puerto Baquerizo Moreno (HERRERA *et al.*, 2014). *Crematogaster* JTL–022 is a species that closely resembles *Crematogaster obscurata* Emery, 1895 (HERRERA *et al.,* 2014). It was found nesting in small dead branches in sunny habitats. It was collected in *C. pyriformis* and visiting flowers of *O. megasperma* and *G. darwinii*. This ant is considered a peripheral species in the pollination networks in Galápagos (TRAVESET *et al.,* 2011). *Crematogaster* JTL–022 is also know from Orellana and Sucumbios provinces on the mainland of Ecuador (Longino pers. comm., XI.2015).

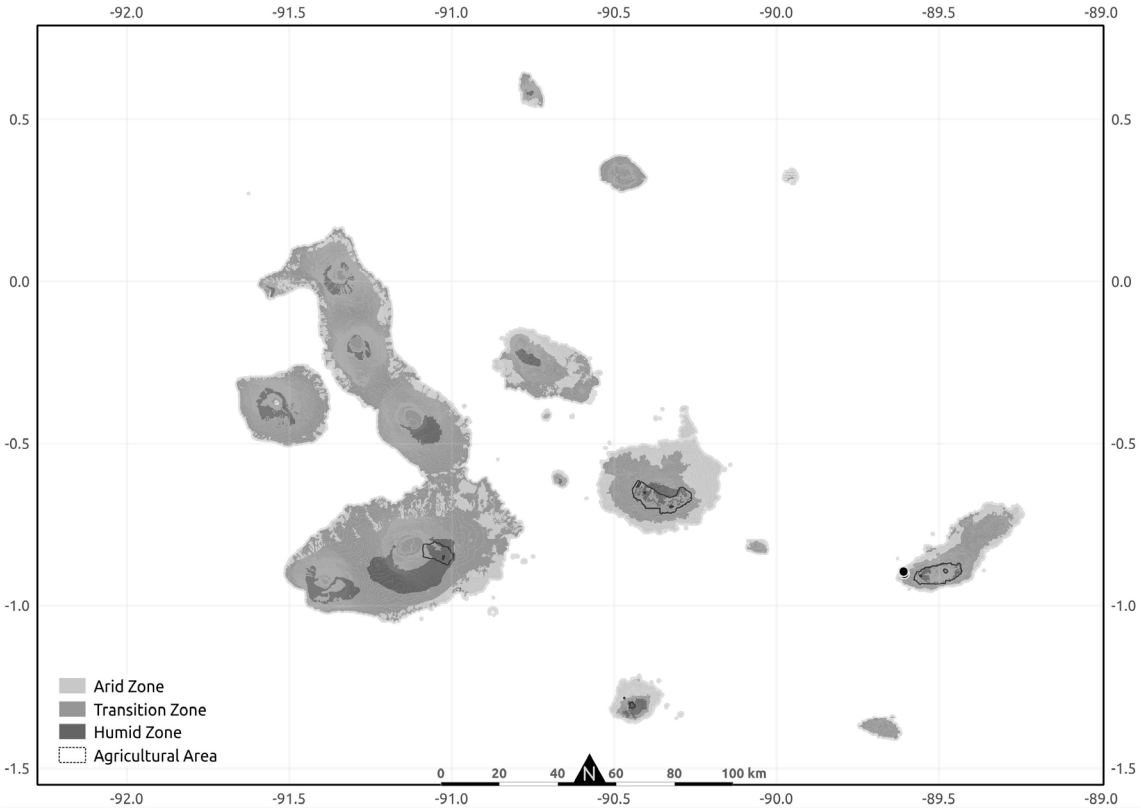
***Cyphomyrmex nesiotus* Snelling and Longino, 1992**
(ANTWEB: JTLC000009386). (Map 18)

Only known from Galápagos this ant species is probably endemic to Galapagos (SENLLING & LONGINO, 1992). It only occurs in the Humid Zone of Isabela. Workers were collected for the first time in 1982 (SNELLING & LONGINO, 1992), in secondary forests near agricultural areas, where it was observed foraging between the leaf–litter. *Cyphomyrmex nesiotus* is one of the two species of fungus–growing ants recorded in Galápagos.

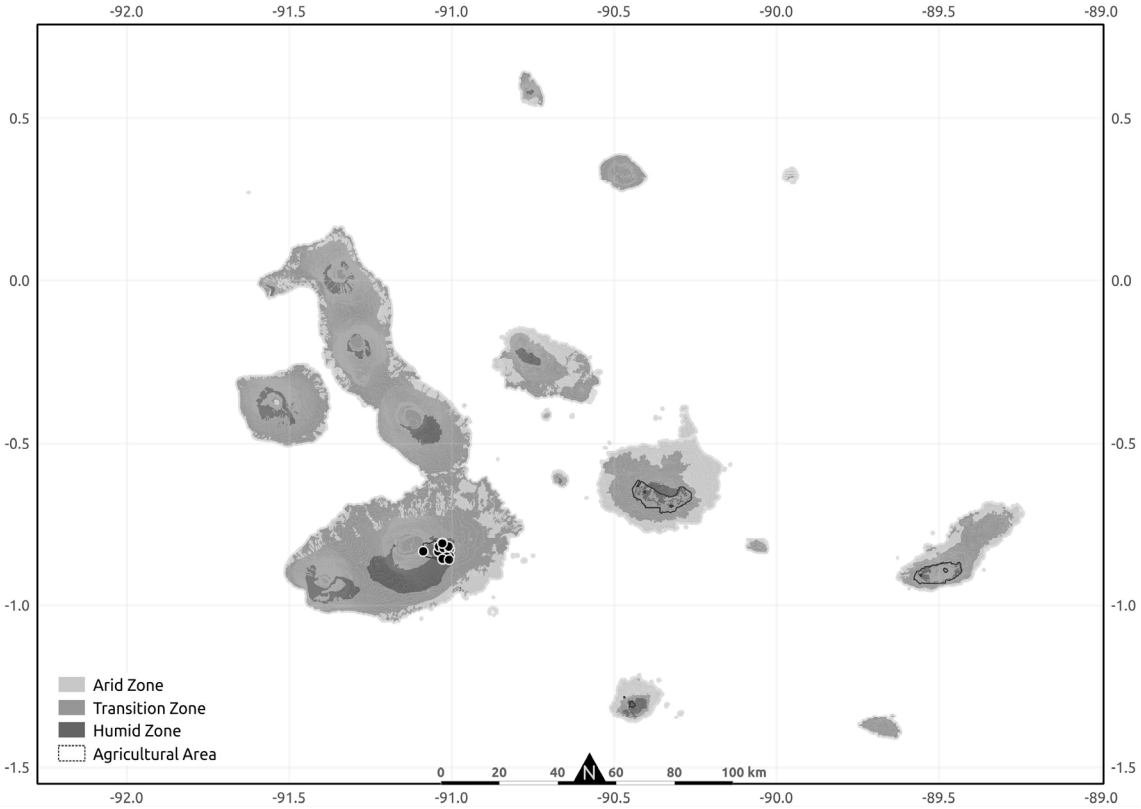
***Cyphomyrmex rimosus* Spinola, 1851**
Larger Little Fungus Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173243, CASENT0173246).
Light morph (Map 19a) and dark morph (Map 19b)

Widespread from southern U.S.A. to northern Argentina (SNELLING & LONGINO, 1992; BOLTON *et al.,* 2006; HERRERA & LONGINO, 2008). *C. rimosus* is thought to have been introduced by humans to Galapagos. It was reported for the first time on Santa Cruz Island in 2008 (HERRERA & LONGINO, 2008). Since then it has been recorded on five islands. It nests under rocks and bark of rotten trunks (*S. pedunculata*). It is common in the humid areas (landfills, stone and sand quarries) as well as in the Transition Zone, being almost completely absent in the Littoral and Dry Zone. HERRERA & LONGINO (2008) distinguish a light and a dark form of *C. rimosus* in Galápagos and they refer to them as sympatric forms as occurs in Florida, where a native form (*C. minutus*) is sympatric with an introduced form, the darker *C. rimosus fuscus* from southern South America.

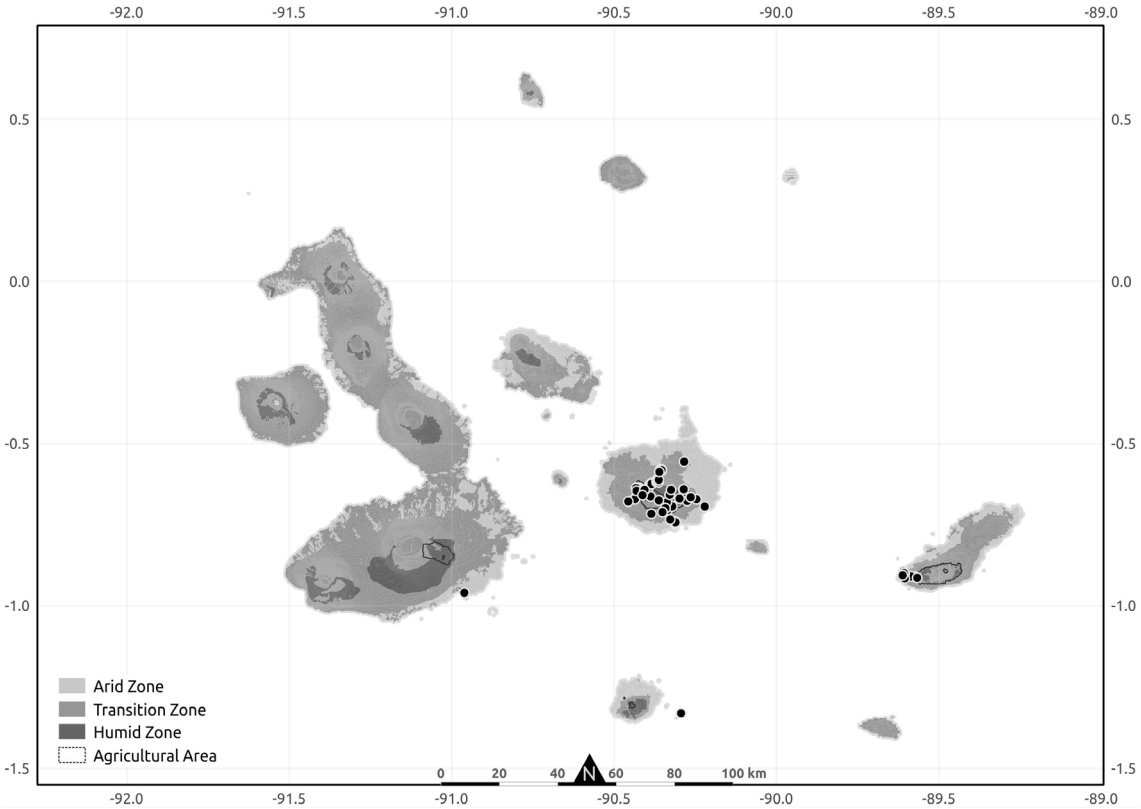
On Santa Cruz Island, *C. rimosus* is a common inhabitant of forests of *S. pedunculata*, *C. odorata* in the Humid Zone and is also found in the lower part of the *Miconia* zone. In cultivated areas it is reported in crops of *A. comosus, B. oleracea* var. *italica*, *M. paradisiaca*, *M. esculenta, C. annuum*, *P. vulgaris*, *Z. mays*, *C. arabica*, *B. oleracea* var. *capitata* and *P. guajava*. It has been recorded in disturbed areas of inhabited islands such as in landfills, and stone and sand quarries. In urban areas the species is present in gardens, where workers can build nests and cultivate fungus under rocks or between sidewalk borders, especially in small humid areas covered with grass and ornamental plants. *C. rimosus* profits from flowers, fruits, nectar and sap which it uses as substrates for growing fungi (LEAL & OLIVEIRA, 2000). In the highlands of Santa Cruz, San Cristóbal and Isabela Islands, *C. rimosus* inhabits areas that are



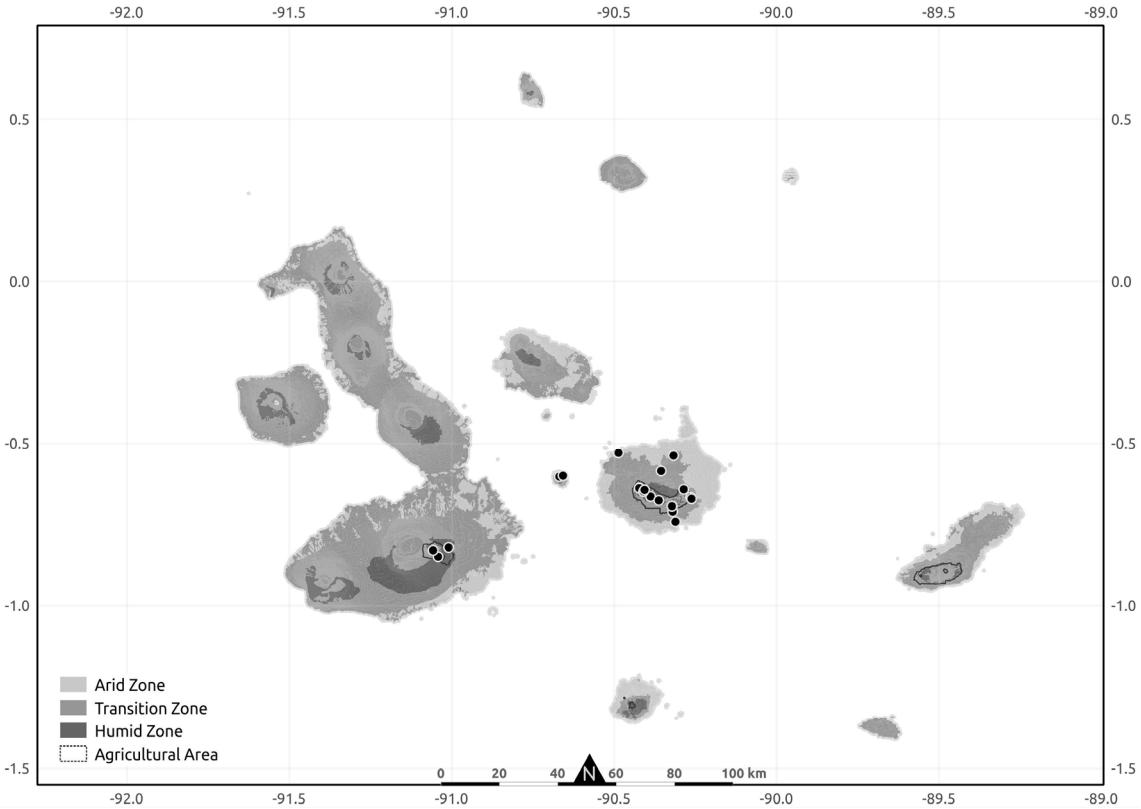
Map 17. Distribution and ecological zone registered for *Crematogaster* JTL-022.



Map 18. Distribution of *Cyphomyrmex nesiotus* Snelling & Longino, 1992.



Map 19a. Distribution of *Cyphomyrmex rimosus* Spinola, 1851. (Ligth morph).



Map 19b. Distribution of *Cyphomyrmex rimosus* Spinola, 1851. (Dark morph).

invaded by *W. auropunctata*, where it seems to be tolerant of the little fire ant. This behavior was also observed by GRAINER *et al.* (2017) in French Guyana.

***Monomorium floricola* (Jerdon, 1851)**
Bicolored Trailing Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173274). (Map 20)

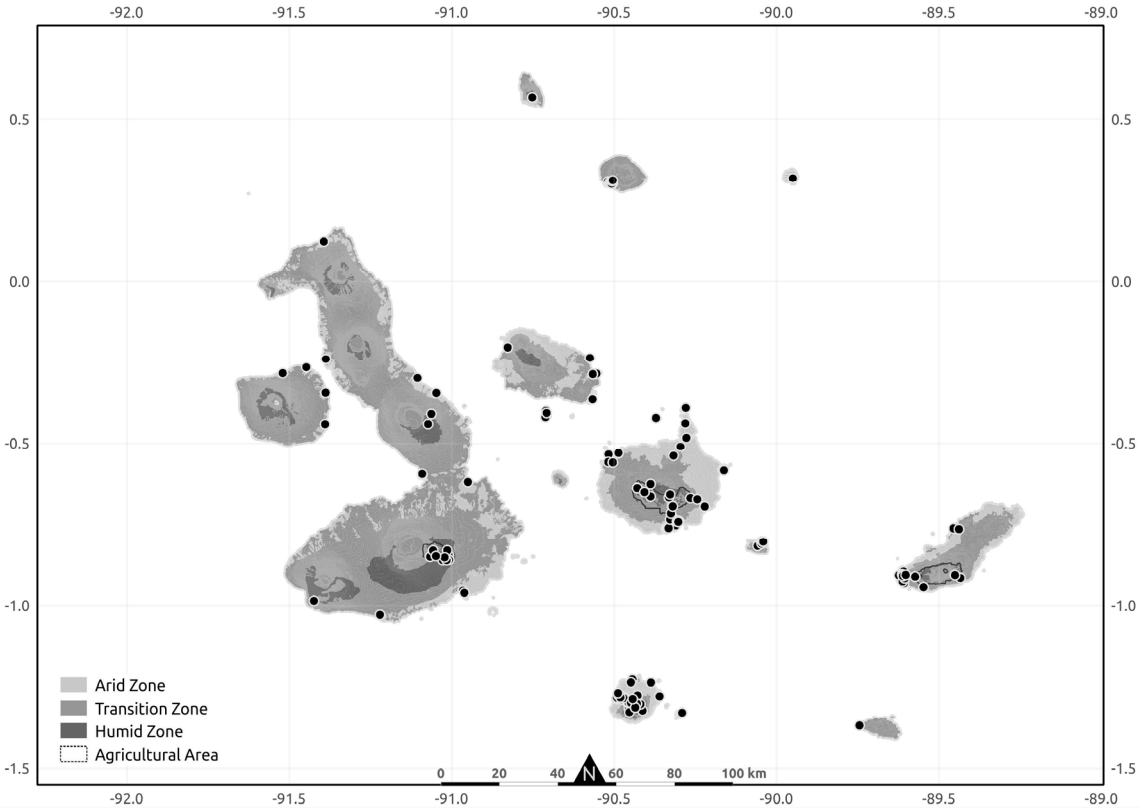
This pantropical species is a tramp ant (KEMPF, 1972; BOLTON *et al.,* 2006; WETTERER, 2010a) and was introduced to Galapagos via human activities. It is now found on 26 islands where many islets are included. *Monomorium floricola* typically occurs in littoral and dry zones in natural and disturbed environments as well as in agricultural areas. It was collected for the first time on Genovesa Island in 1923 nesting in dead twigs of *B. graveolens* (WHEELER, 1924). It has also been observed to nest in branches of *M. octogona* and rotten logs. *Monomorium floricola* is diurnal (LUBIN, 1984) and can be found in leaf–litter and foraging between rocks and plants in humid and dry forests. This species has been recorded visiting flowers of *Plumeria rubra* L., *O. helleri*, *S. pedunculata, S. gordilloi*, nectaries of *O. echios*, *O. helleri, J. thouarsii* and *C. lutea*, and tending *I. purchasi* in return for honeydew (WHEELER, 1924; MCMULLEN, 1993; MEIER, 1994; BOADA, 2005; CHAMORRO *et al.,* 2012, HODDLE *et al.,* 2013). This species was also collected in branches of *Scalesia baurii* Rob. & Greenm., *S. cordata*, *B. graveolens* (BOADA, 2005). In agricultural areas it has been found on *Citrus spp.*, *Z. mays* and *A. comosus.* It can be found near houses, in abandoned lots, docks and airports. In gardens it was found on *C. papaya*, *B. graveolens*, *A. cherimola*, *Tamarindus indica* L., *C. lutea*, *Acacia nilotica* (L.) Willd. Ex Delile, *S. purpurea*, *Z. matrella* var. *pacifica* and *C. nucifera*. In Galápagos *M. floricola* is considered an invasive ant with a high potential to disperse and colonize new natural areas (CAUSTON *et al.,* 2006).

***Monomorium pharaonis* (Linnaeus, 1758)**
Pharaoh's Trailing Ant (DEYRUP *et al.,* 2000)
(ANTWEB: ICCDRS0013052). (Map 21)

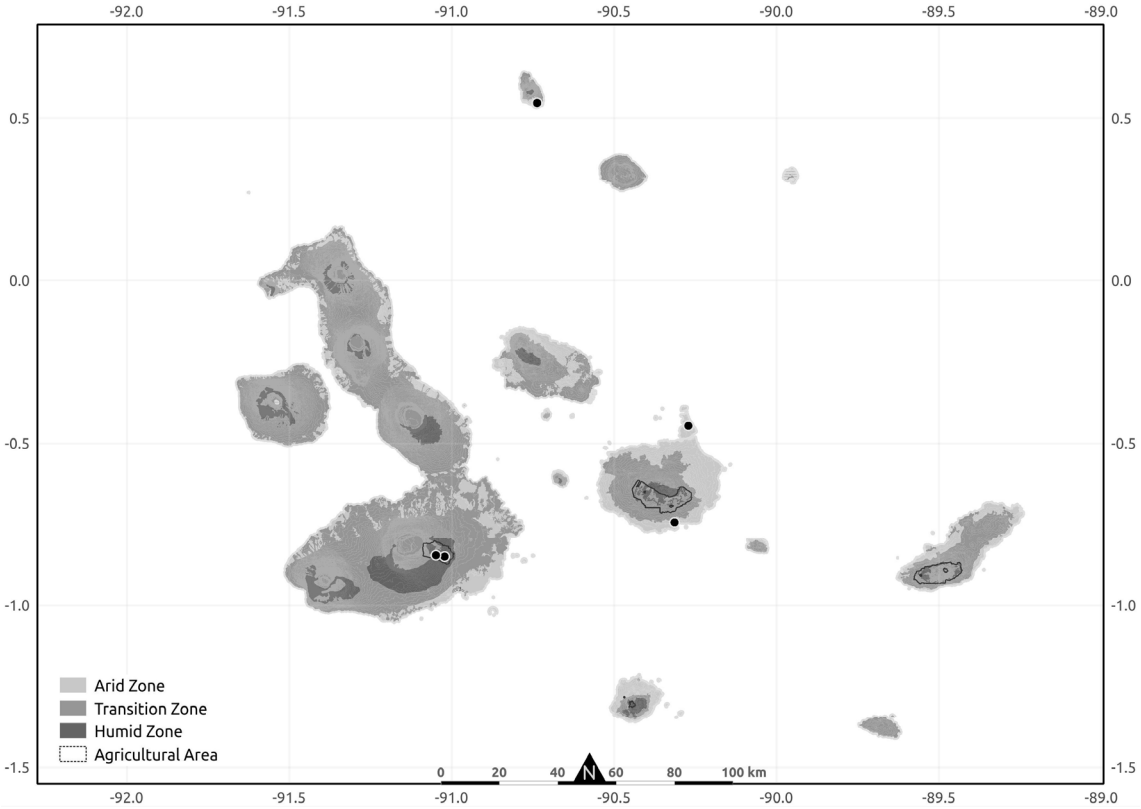
A tramp ant with worldwide distribution (WETTERER, 2015). It was collected for the first time in Galápagos in 1905 on Santa Cruz and Pinta by WHEELER (1919). *Monomorium pharaonis* is distributed on four islands in dry and humid zones. Specimens have primarily been collected from disturbed areas; Baltra airport, agricultural areas of Isabela, Puerto Ayora on Santa Cruz Island, as well as on aircrafts coming from mainland Ecuador. The only known case of *M. pharaonis* in natural areas is on Pinta Island, where specimens were collected in 1982 and 2006 in the littoral zone. *Monomorium pharaonis* is considered a moderately invasive species in Galápagos (CAUSTON *et al.,* 2006).

Monomorium* sp. nr. *pharaonis
(ANTWEB: CASENT0173275). (Map 22)

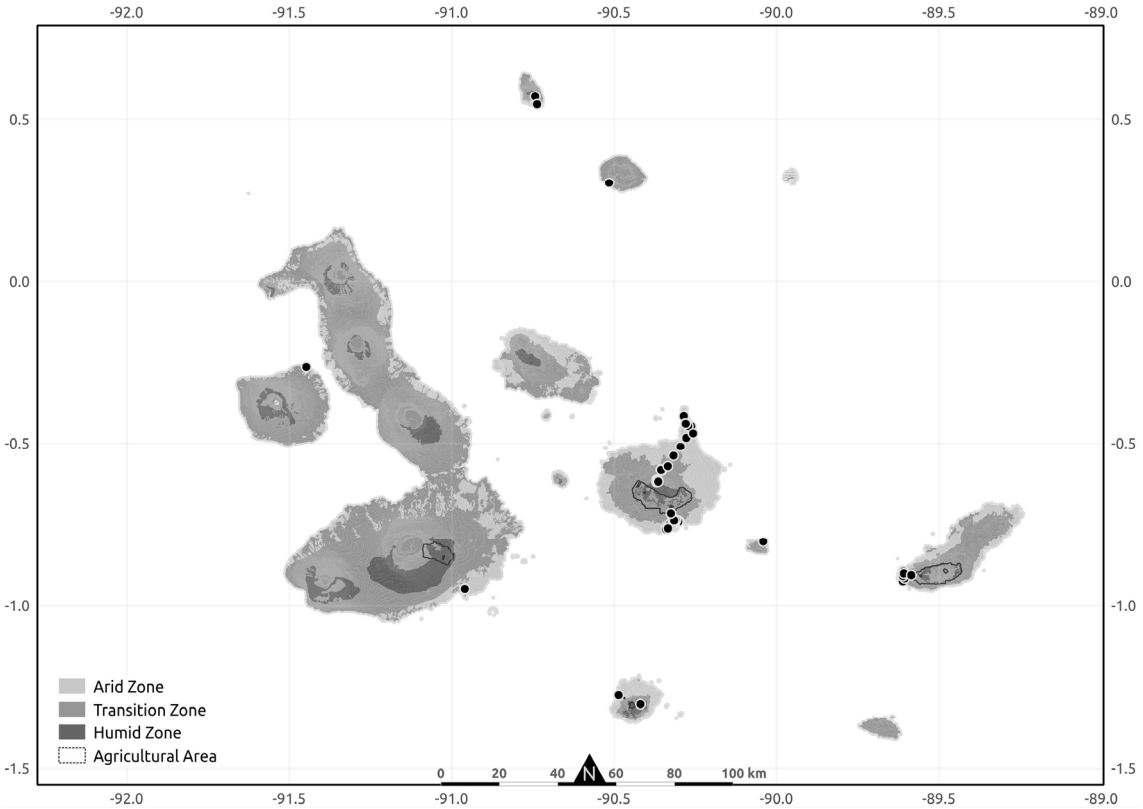
Only known from India, southeast Asia, California (US) and Galápagos (WARD, 2005; HERRERA & CAUSTON, 2010; Bolton pers. comm., XI.2009. Evidence suggests that this species was introduced to Galapagos by humans. It was first collected in 1992 on Baltra Island (HERRERA & CAUSTON, 2010) and since then has been recorded on nine islands. It is found in natural, urban and disturbed habitats from dry to humid zones. *Monomorium* sp. nr. *pharaonis* has been collected in plants of *C. lutea*, *A. nilotica*, *Z. matrella* var. *pacifica*, *R. communis*, *G. darwinii*, *T. indica*, *B. graveolens*, *C. pyriformis*., *M. nr pharaonis* was observed competing with other introduced ants (e.g. *P. longicornis*) for honeydew produced by *I. purchasi* on branches of *P. aculeata*. This species has been collected in open areas, leaf litter, fruits and branches of *Citrus* x *limon* (L.) Osbeck. *Monomorium* sp. nr *pharaonis* is often collected in the docks and cargo holds of airports in Galápagos. Studies carried out in disturbed landfills and



Map 20. Distribution of *Monomorium floricola* (Jerdon, 1851).



Map 21. Distribution of *Monomorium pharaonis* (Linnaeus, 1758).



Map 22. Distribution of *Monomorium* sp. nr. *pharaonis*.

stone quarries show that it can be abundant in these habitats (HERRERA unpublished data). This species was also found on baits used to control the tropical fire ant *S. geminata*.

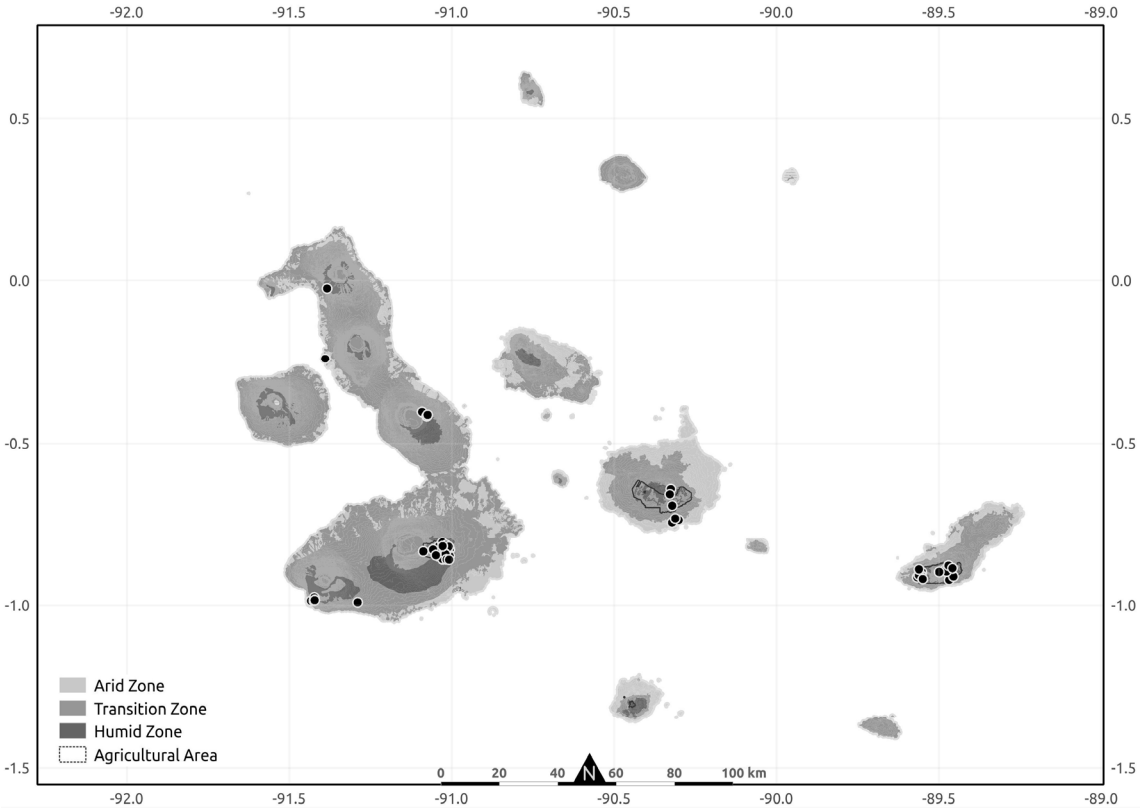
***Pheidole flavens* Roger, 1863**
Yellow Big–Headed Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173263). (Map 23)

Widespread in the Neotropics (KEMPF, 1972; WILSON, 2003; BOLTON *et al.,* 2006). *Pheidole flavens* is an introduced species which is found on three islands in natural and disturbed areas. Mostly found in humid zones, it was recorded in Galápagos for the first time in 1888 from Isabela Island (WHEELER, 1919). In 1982 it was recorded on Santa Cruz (CLARK, 1982). Nests have been found in rotten trunks in moist areas and bark of dead trunks of *B. graveolens*. Workers have been collected in litter in secondary forests as well as in closed woodland dominated by *P. floribunda*, *Z. fagara*, *C. scouleri*, *P. galapageium* and *Scalesia* forest. *Pheidole flavens* has been recorded in crops of *C. arabica*, *S. officinarum*, *A. cepa*, *M. paradisiaca*, *P. guajava*, *C. annuum* and *S. lycopersicum*. It was collected on trees of *C. papaya* in Puerto Ayora. So far, there is no evidence that *P. flavens* should be considered an invasive species in Galápagos.

***Pheidole megacephala* (Fabricius, 1793)**
Pantropical Big–Headed Ant
(DEYRUP *et al.,* 2000)
(ANTWEB: ICCDRS0003685). (Map 24)

Distributed in tropical and subtropical areas (WETTERER, 2015), *P. megacephala* is an invasive species and is considered a threat to the native fauna in many parts of the world (PERKINS, 1913; VANDERWOUDE *et al.,* 2000; BASKIN, 2002; HOLWAY *et al.,* 2002; WETTERER & O'HARA,

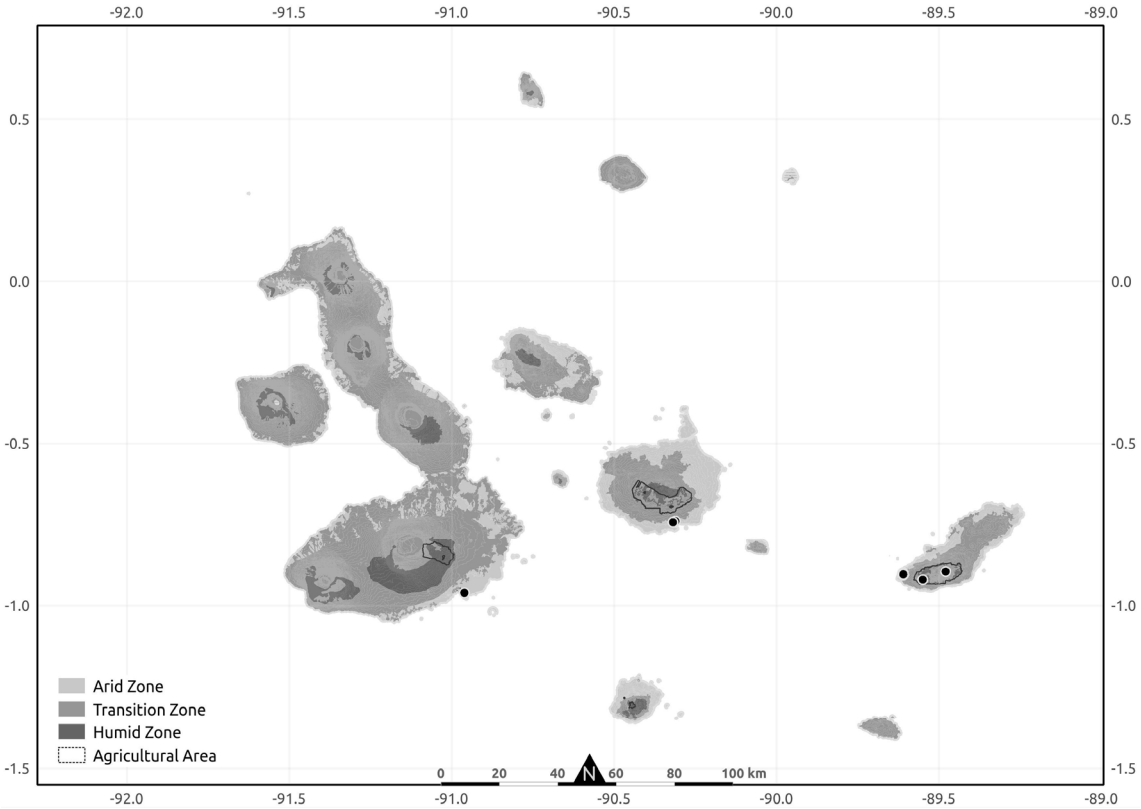
2002; WETTERER, 2015). In Galápagos the first specimens were collected in San Cristóbal Island in 2006 (HERRERA *et al.,* 2013). Currently it is present in the dry areas on three islands: it is widespread in urban zones in Puerto Ayora (Santa Cruz), Puerto Baquerizo Moreno (San Cristóbal) and Puerto Villamil (Isabela). *Pheidole megacephala* is a pest in houses in Galápagos and can invade gardens where it is known to forage and hide under grass (*Z. matrella* var. *pacifica*), visit flowers of *H. rosa–sinensis* and attend Homoptera species on introduced plants (e.g. *C. roseus*). Although the impact of *P. megacephala* has not yet been evaluated in Galápagos, similar problems to those recorded on other Pacific Islands can be expected (WETTERER, 2007; HERRERA *et al.,* 2013). In mainland Ecuador specimens of *Pheidole megacephala* were collected in Guayaquil, the main port for cargo boats that travel to Galapagos (Herrera unpublished data).



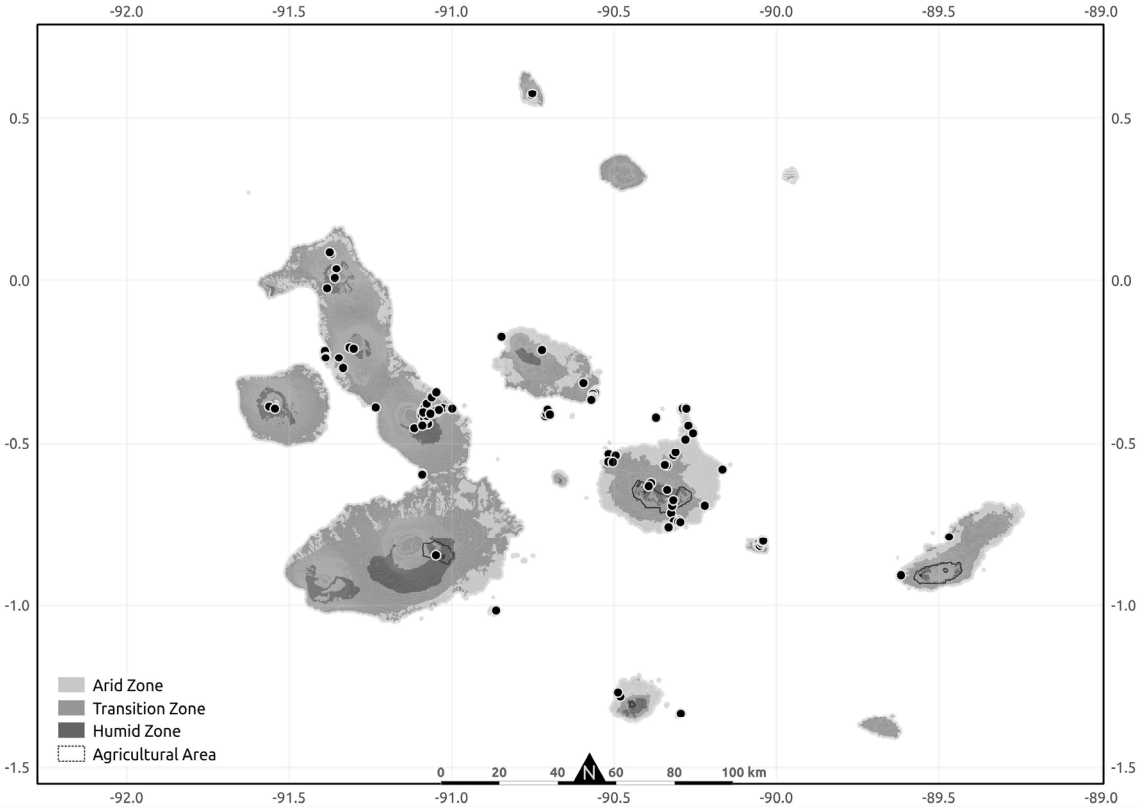
Map 23. Distribution of *Pheidole flavens* Roger, 1863.

***Pheidole williamsi* (Wheeler, 1919)**
(ANTWEB: CASENT0173266). (Map 25)

Pheidole williamsi is possibly endemic to Galápagos (WILSON, 2003). The first records originate from Santa Cruz Island (WHEELER, 1919). Currently it is distributed on 25 islands and islets and often it is found in natural areas in littoral, dry and transition zones. It nests on sandy beaches (WHEELER, 1924), under rocks below shrubs, dry trunks of *C. sinensis* and dry branches of *B. graveolens*. It has been observed foraging between litter of mangroves in the littoral zone on Isabela Island (Playa Tortuga Negra). *Pheidole williamsi* was also observed on rocky soils with little leaf litter, in forests of *S. pedunculata*, closed woodland and from arid to moist habitats represented by *Tournefortia psilostachya* Kunth, *W. ovata*, *Commicarpus tuberosus* (Lam.) Standl., *Acacia* sp., *S. affinis*, *C. galapageia*, *O. insularis*, *C. leucophlyctis*, *P. floribunda*, *Z. fagara, C. scouleri*, *P. galapageium*, *Psychotria* sp., *Verbena townsendii*



Map 24. Distribution of *Pheidole megacephala* (Fabricius, 1793).

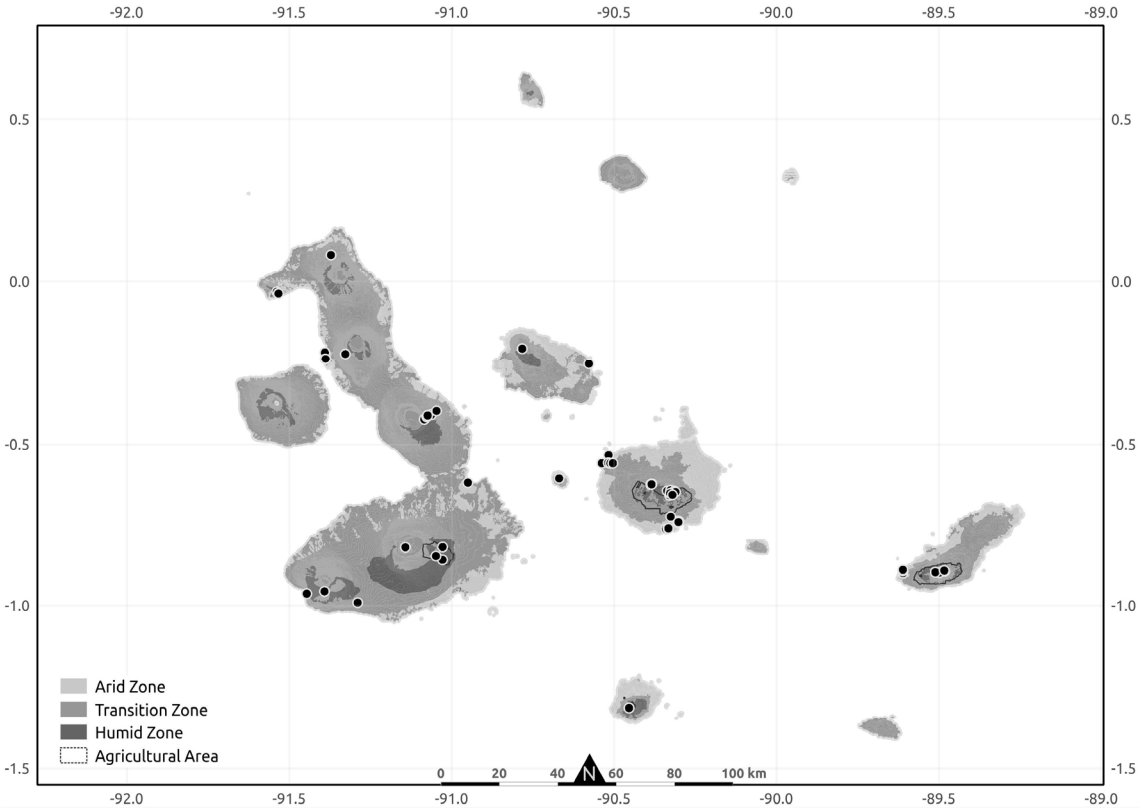


Map 25. Distribution of *Pheidole williamsi* (Wheeler, 1919).

Svenss., *Pennisetum* sp. and *Baccharis gnidiifolia* Kunth. This species was also recorded in vegetation composed of sedges (like *Cyperus anderssonii* Boeck.), grasses (*P. pauperum, Setaria setosa* (Sw.) P. Beauv.), herbs (*Rhynchosia minima* (L.) DC.) and shrub layers represented by *O. echios* and *M. laricifolia*. *Pheidole williamsi* is a common visitor to baits used for monitoring rats in islets located near to the west coast of Santiago Island. On Santiago island, ants were attacked by the fungus *Myrmiciniosporidium durum* Hölldobler, 1933 (ESPADALER, 1997). Workers of *P. williamsi* were identified from material collected in holds of aircrafts in Galápagos, suggesting a possible transfer of this species from Galápagos to mainland Ecuador.

***Pheidole* sp. hh01**
(ANTWEB: CASENT0173268). (Map 26)

Pheidole sp. hh01 is a rather rare ant that is similar to *Pheidole nana* Emery 1894, known from types from Matto Grosso–Brazil (HERRERA *et al.,* 2014). *Pheidole* sp. hh01 is found mainly in dry and humid zones on nine islands and its origin is uncertain. Specimens have been collected under trees of *Sapindus saponaria* L., in the fern zone (*Pteridium* sp.), in forests of *H. mancinella*, *M. robinsoniana* and *C. pubescens*. On Cerro Azul volcano (Isabela Island), we found some specimens in xerophylic open vegetation composed of very short grasses and herbs dominated by *Muhlenbergia microsperma* (DC.) Trin., *S. setosa*, *Borreria laevis* (Lam.) Griseb., ferns, *Darwiniothamnus* species, *Opuntia saxicola* Howell, and trees of *S. cordata*. *Pheidole* sp. hh01 has been collected mainly from natural areas. The only information related to the nesting habits of *Pheidole* sp. hh01 comes from an observation of some queens and dimorphic workers nesting at the base of small shrubs on Darwin volcano on Isabela Island. Attraction to toxic baits (Hydramethylnon) suggests that *Pheidole* sp. hh01 might possibly be affected by control programs against other ant species (CAUSTON *et al.,* 2005).



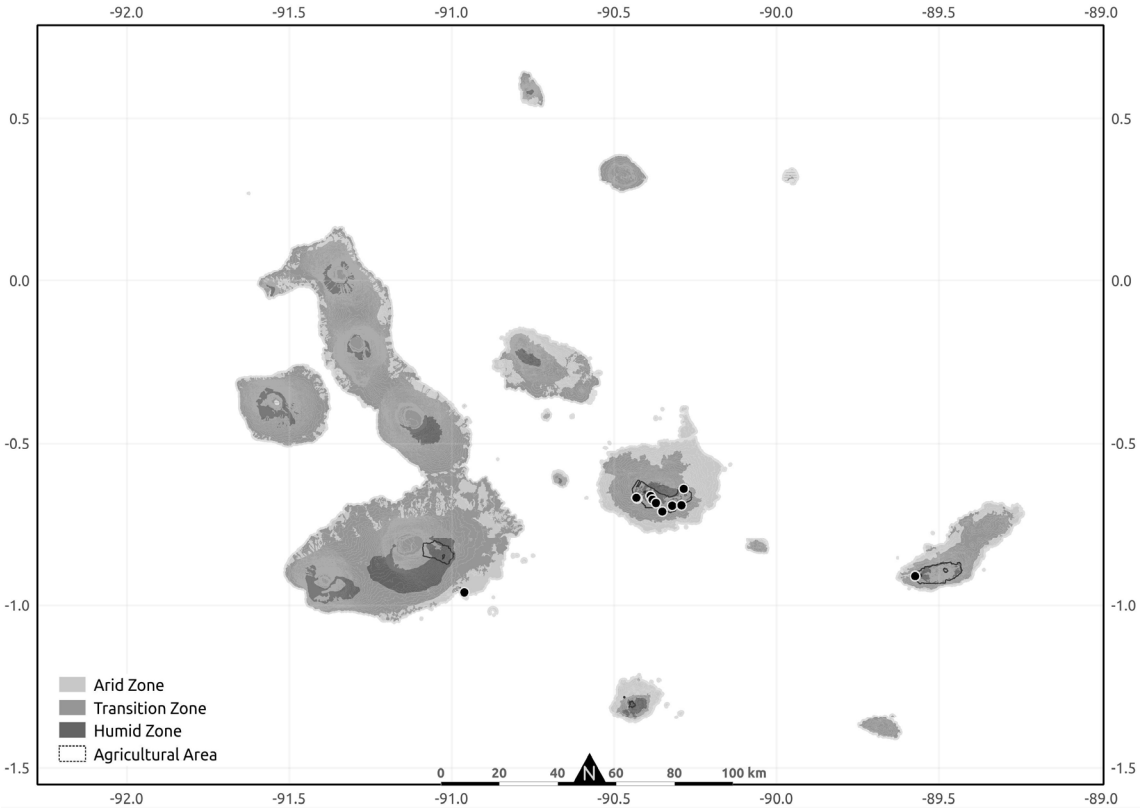
Map 26. Distribution of *Pheidole* sp. hh01.

***Rogeria curvipubens* Emery, 1894**
(ANTWEB: CASENT0173282). (Map 27)

This neotropical species occurs on some Caribbean islands and in Central and South America (KEMPF, 1972; KUGLER, 1994; FERNÁNDEZ & SENDOYA, 2004; HERRERA & LONGINO, 2008). *Rogeria curvipubens* is a cryptic species introduced to Galápagos. It was reported for the first time in the Humid Zone of Santa Cruz Island in 2008 (HERRERA & LONGINO, 2008). However, recent revisions of museum material showed that it was also collected in the Transition Zone of San Cristóbal Island in 1992. To date, it has been found on three inhabited islands in the Galápagos archipelago and is found in human settlements and protected areas. It has been collected from leaf litter in secondary successional forest. We observed a nest of *R. curvipubens* under attack from *Wasmannia auropunctata*. This species was collected with Winkler traps and using visual searches in *C. arabica* planted under *S. pedunculata*.

***Solenopsis geminata* (Fabricius, 1804)**
Tropical Fire Ant (TABER, 2000)
(ANTWEB: CASENT0173278). (Map 28)

Solenopsis geminata is an invasive ant transported by humans. It was collected for the first time in San Cristóbal in 1891 (EMERY, 1893). *Solenopsis geminata* is found on 20 islands and islets having invaded natural as well as fragmented habitats, successional forest, human settlements and agricultural zones. It is widely distributed along all ecological zones in the archipelago from littoral to humid zones. The species is commonly present in open areas and has been collected in stands of *S. pedunculata*, *P. guajava*, *S. cordata*, *P. floribunda, B. graveolens*, *S. gordilloi*, *C. leucophlyctis*, *Homolepis glutinosa (*Sw.) Zuloaga & Soderstr.*, H. mancinella*,



Map 27. Distribution of *Rogeria curvipubens* Emery, 1894.

Gossypium barbadense L. and areas composed by ferns (*Pteridium aquilinum* (L.) Kuhn), grasses (*Eragrostis pilosa* (L.) P. Beauv. *S. setosa*, *Cynodon* sp.) and herbs (*Centella asiatica* (L.) Urb. in Mart.). It can be found in mangrove litter, near lagoons, sandy dunes, beaches and wetlands.

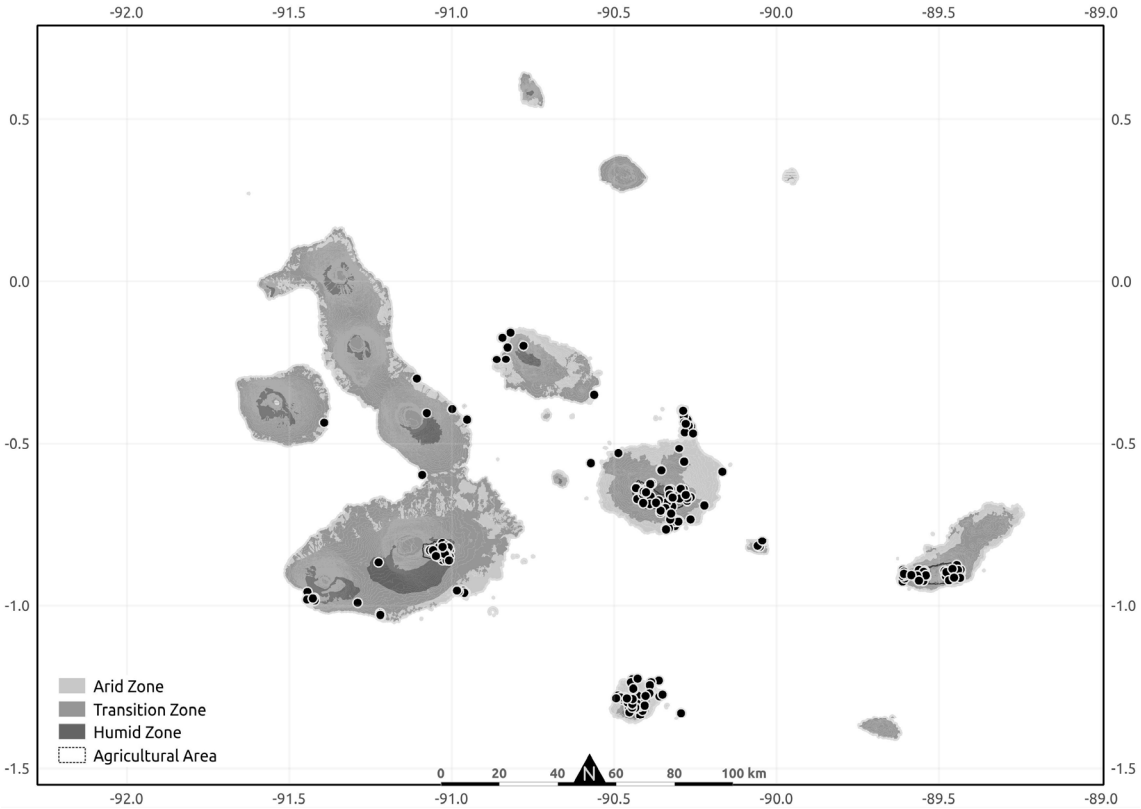
Solenopsis geminata visits flowers of *C. galapagosa*, extrafloral nectaries of *O. echios* and *J. thouarsii* (MEIER, 1994), plant species infested by *I. purchasi* where it feeds on the honeydew produced by the scale insect (LINCANGO *et al.,* 2010; HODDLE *et al.,* 2013), as well as other plants like *Senna alata* (L.) Roxb., A. *muricata* and *Acacia* spp. infested by other Hemiptera species. The tropical fire ant has invaded all agricultural zones in the inhabited islands of the archipelago. It has been reported from the crops *M. esculenta, A. comosus, M. acuminata*, *S. lycopersicum*, *S. tuberosum*, *Brassica oleracea* var. *botrytis* L., *Coriandrum sativum*, *S. betaceum*, *C. lanatus, M. paradisiaca*, *C. papaya*, *C. annuum*, *C. sativus*, *Z. mays*, *L. sativa, P. vulgaris*, *C. melo*, *Citrus* spp., *B. oleracea* var. *italica*, *A. cepa*, *S. officinarum*, *C. arabica*, and *M. acuminata*.

In urban areas it is a pest in houses and was collected in gardens, trash cans, stands of *G. darwinii*, *C. sinensis, A. cherimola*, *S. purpurea*, *R. communis*, *C. limon*, *B. graveolens*, *M. paradisiaca*, and mangroves. Nests of *Solenopsis geminata* occur in soil, on rocks, in open areas, on the edges of the roads, under stones, and in rotten trunks and roots of plants (e.g. *Hyptis pectinata* (L.) Doit. and *Hyptis sidifolia* (L'Hér.) Briq). This species often builds galleries on the bark of orange trees in agricultural areas, and constructs small tunnels under soil. *Solenopis geminata* is considered one of the most invasive species in Galápagos and a major threat to the terrestrial fauna (WILLIAMS & WHELAN, 1991; TAPIA, 1997; CAUSTON *et al.,* 2006; WETTERER, 2011a; WAUTERS *et al.,* 2014). It has been the target of several control programs (CAUSTON *et al.,* 2012). The species is probably continuously reintroduced into Galápagos, as it has been intercepted in cargo holds of aircrafts arriving from Quito and Guayaquil and on several occasions from cargo holds of ships coming from the Guayaquil ports (ABG, personal communication). Ants have been collected from tourist boats traveling between the islands (LOMAS, 2008).

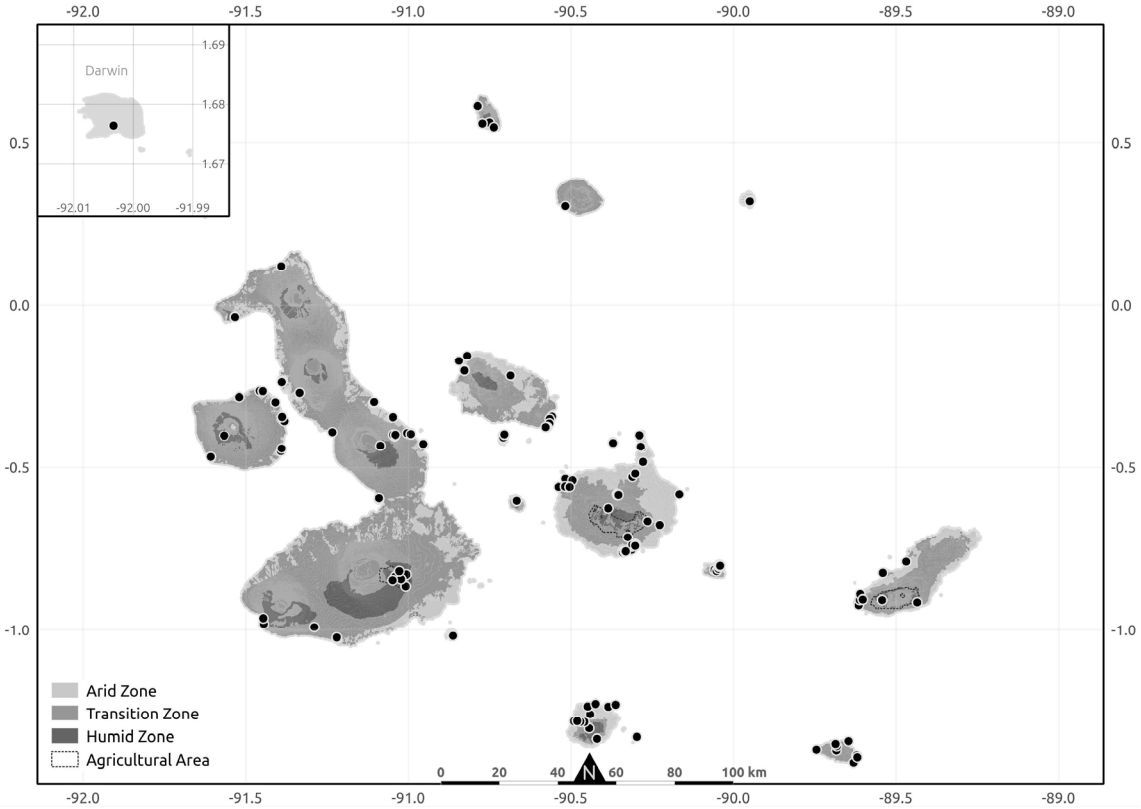
***Solenopsis globularia* Smith, 1858**
(ANTWEB: CASENT0173279). (Map 29)

An ant reported from southeastern United States, Central America, Caribbean islands and parts of South America (PACHECO & MACKAY, 2013). *Solenopsis globularia* is a species of uncertain origin in Galápagos. The first specimens were collected in 1899 in Española, Genovesa and Isabela islands (WHEELER, 1919, 1924). Now present on 34 islands and islets, it is the most widely distributed ant in all vegetation zones of the archipelago – though it seems to prefer natural, dry habitats. *Solenopsis globularia* has rarely been found in urban areas. Nests can be found under rocks and under small logs on sandy beaches. It has been found feeding on extrafloral nectaries of *O. echios* and *J. thouarsii* (WHEELER, 1924; MEIER, 1994). It has also been recorded visiting flowers of *O. megasperma* and *C. lutea* (BOADA, 2005).

This species has been collected in natural and dry areas, open dry deciduous forest dominated by *B. graveolens*, rocky soil with little leaf litter covered with herbs, under piles of leaves of *R. mangle*, *A. germinans*, *C. pyriformis* and between patches of *Sesuvium portulacastrum* (L.) L. *Solenopsis globularia* was also found in areas dominated by *C. scouleri*, *Acacia rorudiana* Christoph., herbs layer (*P. pauperum, M. aspera, Oxalis* sp., *P. galapagoensis*, *D. procumbens*), shrubs (*P. juliflora*, *C. lutea*, *C. leucophlyctis*, *A. echinocephala*), and in areas with *S. virginicus* and *I. triloba* along small lagunas under tidal influence (coast of Fernandina). In the humid highlands, all records are from areas cultivated with *B. oleracea var. italica* or *C. annuum*.



Map 28. Distribution of *Solenopsis geminata* (Fabricius, 1804).



Map 29. Distribution of *Solenopsis globularia* Wheeler, 1919.

***Solenopsis gnoma* Pacheco, Herrera & Mackay, 2007**
(ANTWEB: CASENT0104994, CASENT0104995). (Map 30)

This species of thief ant is probably endemic to Galápagos and is found on eight islands. It is usually collected in the Transition and the Humid zone. Museum records date back to 1986 on Sierra Negra volcano on Isabela. Nests have been observed in rotten logs, rotten branches and in nests of the introduced ant *T. bicarinatum* (PACHECO *et al.,* 2007). On Santa Cruz Island, *Solenopsis gnoma* is primarily an inhabitant of humid areas, being found in litter of *Scalesia* forests, ferns, secondary successional forests, *Miconia* zone and patches of *Sphagnum*. Specimens were collected in urban areas on *B. graveolens*, *C. pyriformis*, *C. lutea* and on grasses. In agricultural areas it is known from the crops *S. tuberosum*, *M. esculenta,* and *C. arabica* planted under *S. pedunculata* trees.

***Solenopsis* sp. hh06 (cf. *basalis*)**
(ANTWEB: ICCDRS0012776). (Map 31)

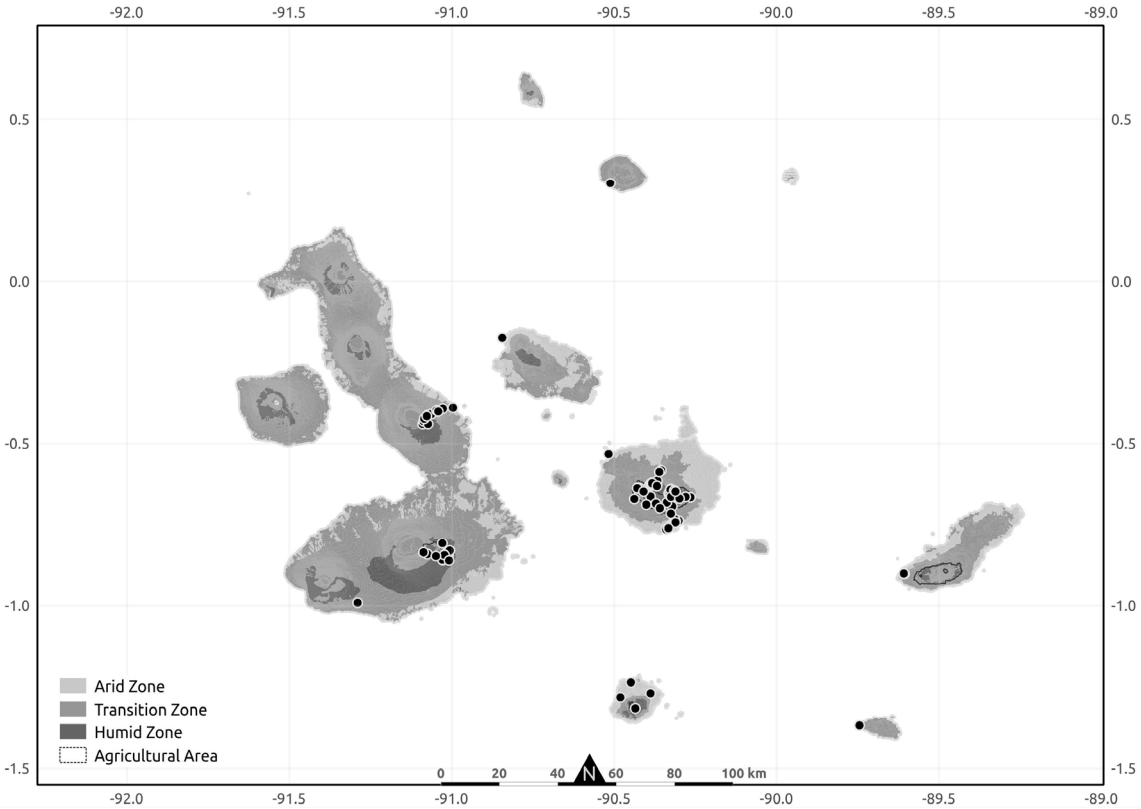
This is a rare species whose distribution outside Galápagos is unknown. Workers were collected for the first time in 2008 in the Arid Zone of Santa Cruz Island (HERRERA *et al.,* 2014). *Solenopsis* sp. hh06 is found on three islands and is similar to *Solenopsis basalis* Forel, 1895 from Brazil and Argentina (HERRERA *et al.,* 2014). The few records come from material collected in transition zones, including areas with human settlements. This species is probably also present in the agricultural area; one specimen was collected in *M. esculenta. Solenopsis* sp. hh06 (cf. *basalis*) is a new record of a thief ant in Galápagos. Thief ants are often found near the tunnels of nests of larger ants, of which they are presumed to steal brood or food items (CREIGHTON, 1950; MACKAY & BRADLEIGH, 1989; PACHECO *et al.,* 2007).

***Strumigenys eggersi* (Emery, 1890)**
Egger's Pygmy Snapping Ant (DEYRUP *et al.,* 2000)
(AntWeb: CASENT0625428, CASENT 0625429). (Map 32)

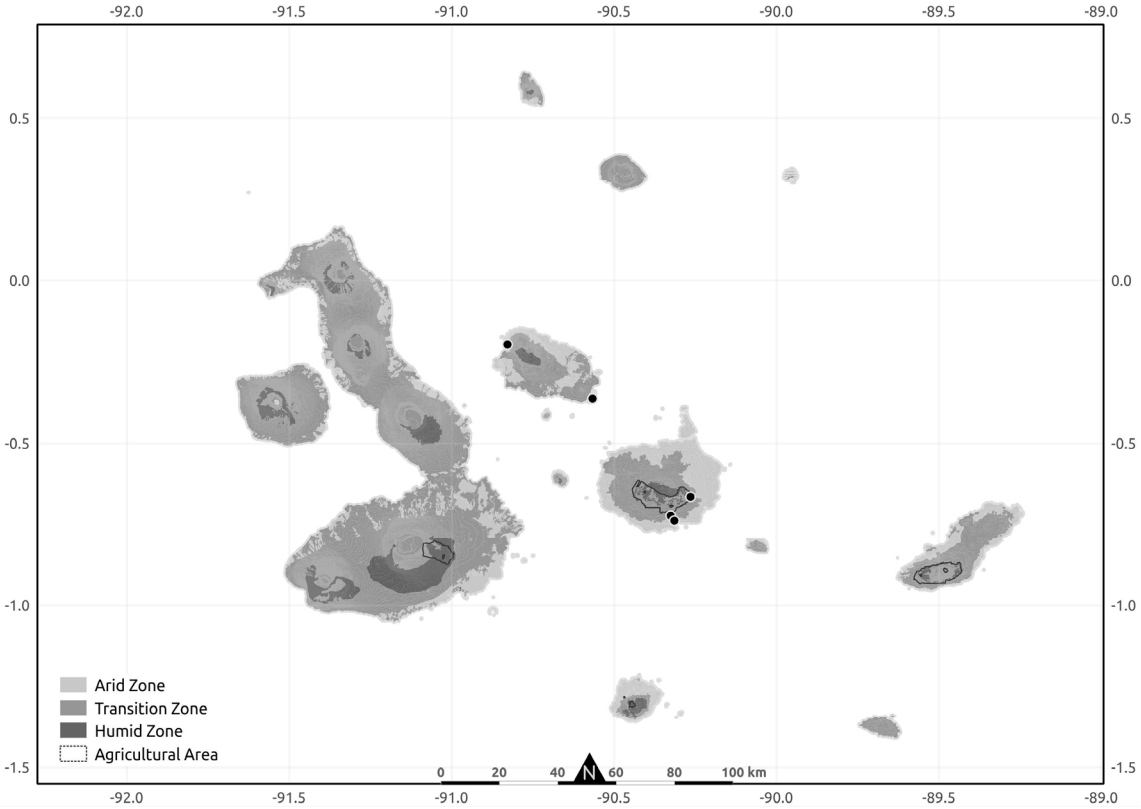
A neotropical species found throughout Central and northern South America, numerous in the Caribbean islands and in Florida, U.S.A. (KEMPF, 1972; BOLTON *et al.,* 2006). This introduced ant was collected for the first time in 2011 and is known only from the Humid Zone of Santa Cruz Island (HERRERA *et al.,* 2014). The record in the Galápagos Islands of *S. eggersi* in crops of *M. paradisiaca* is the first for an archipelago in the Pacific Ocean (HERRERA *et al.,* 2014). Little is known about its ecology in Galápagos. In other parts of the world, *Strumigenys eggersi* is an important predator of Collembola fauna and can be abundant in secondary forests or seasonally dry habitats. Records of *S. eggersi* in other localities originate from leaf litter, compost heaps, rotten twigs, gardens, coffee plantations and low epiphytes in second–growth forests (WEBER, 1952; BROWN, 1962; MCGLYNN, 1999; LATTKE & GOITÍA, 1997; DEYRUP *et al.,* 2000). It is known to nest in leaf litter, hollow twigs, or nuts within the litter (DEYRUP *et al.,* 2000). It is also reported from the mainland of Ecuador in the Orellana province in the Amazon region (MERTL *et al.,* 2012).

***Strumigenys emmae* (Emery, 1890)**
Bow–Jawed Pygmy Snapping Ant
(DEYRUP *et al.,* 2000) (ANTWEB: CASENT0173254). (Map 33)

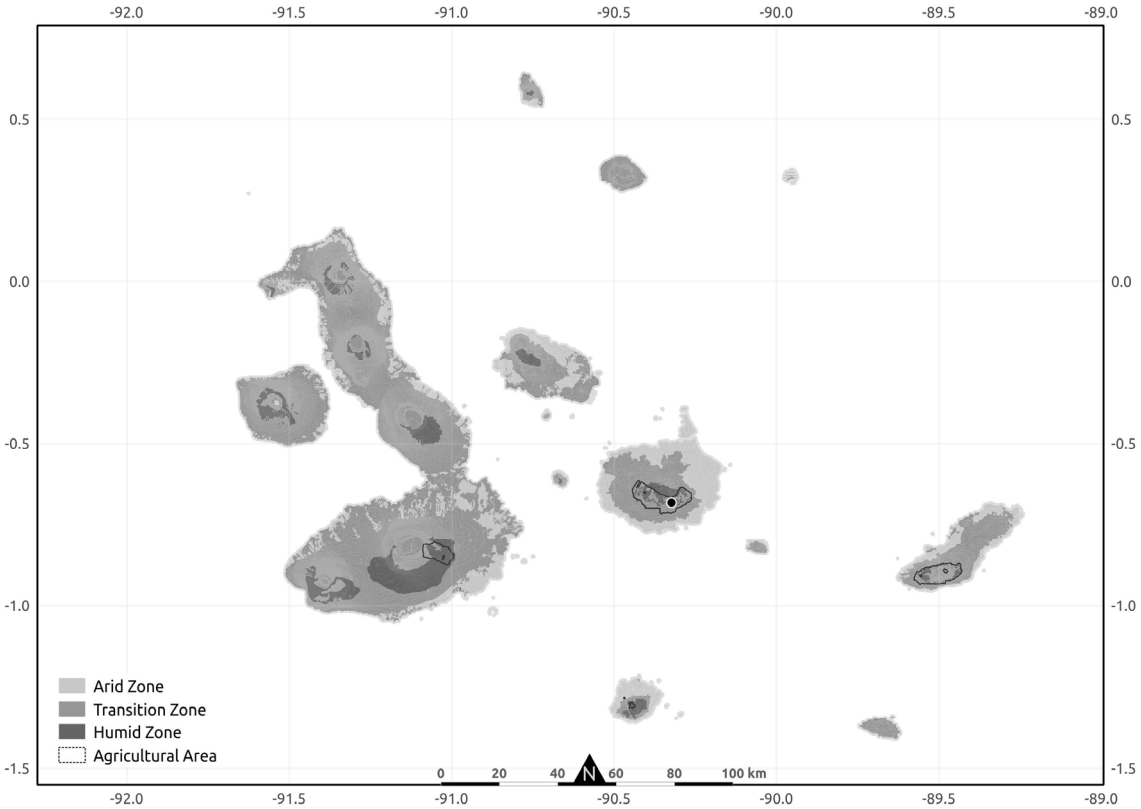
This Pantropical species (KEMPF, 1972; BROWN, 1949; BOLTON, 1983, BOLTON *et al.,* 2006) is a tramp ant, which was introduced to Galápagos and has now been collected from four islands. It was reported for the first time in 1997 from a natural area in the Humid Zone of Floreana Island (PEZZATTI *et al.,* 1998). *Strumigenys emmae* is an inhabitant of leaf litter in moist habitats. On Alcedo volcano, however, it was found in dry habitats near *S. affinis*, *B. graveolens*,



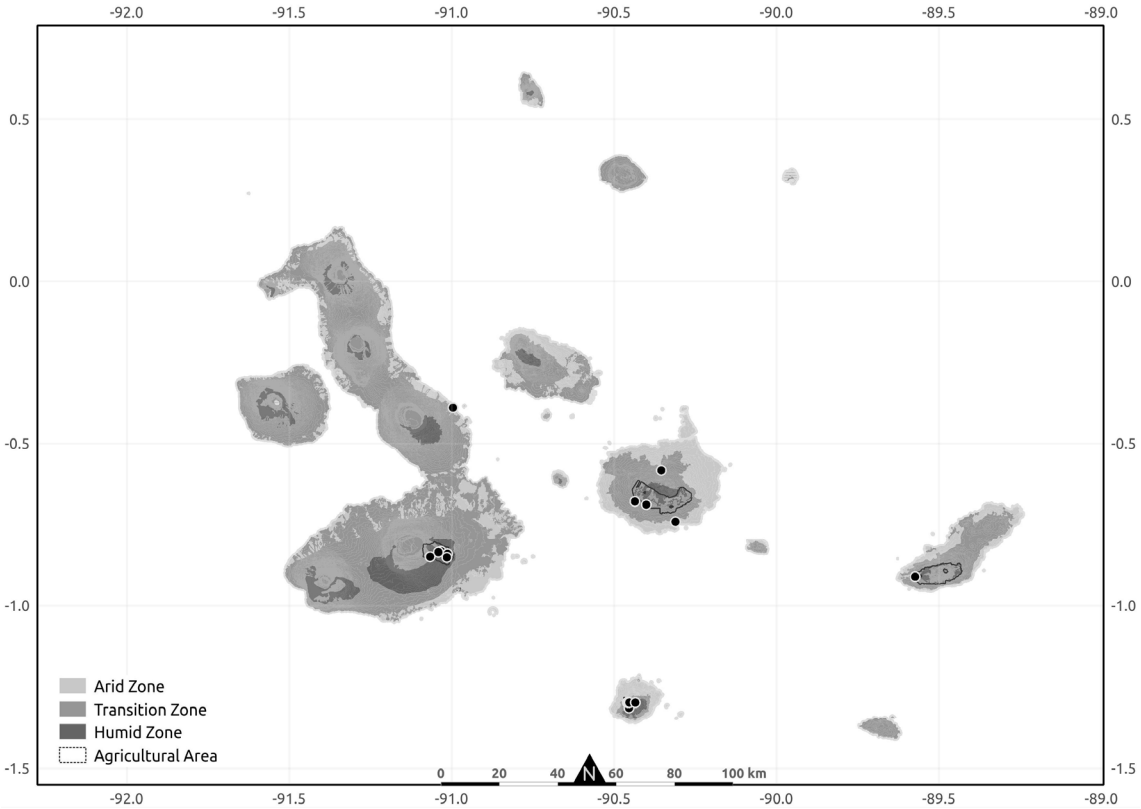
Map 30. Distribution of *Solenopsis gnoma* Pacheco, Herrera & Mackay, 2007.



Map 31. Distribution of *Solenopsis* sp. hh06 (cf. *basalis*).



Map 32. Distribution of *Strumigenys eggersi* (Emery, 1890).



Map 33. Distribution of *Strumigenys emmae* (Emery, 1890).

W. ovata and *Bastardia viscosa* (L.) Kunth). This species can be found in urban areas (gardens mainly) and disturbed and cultivated areas. *Strumigenys emmae* has received very little attention in Galápagos, however it is a good colonizer and could be affecting terrestrial invertebrate (DEYRUP *et al.,* 2000; CAUSTON *et al.*, 2006).

Strumigenys louisianae Roger, 1863
(ANTWEB: CASENT0173257). (Map 34)

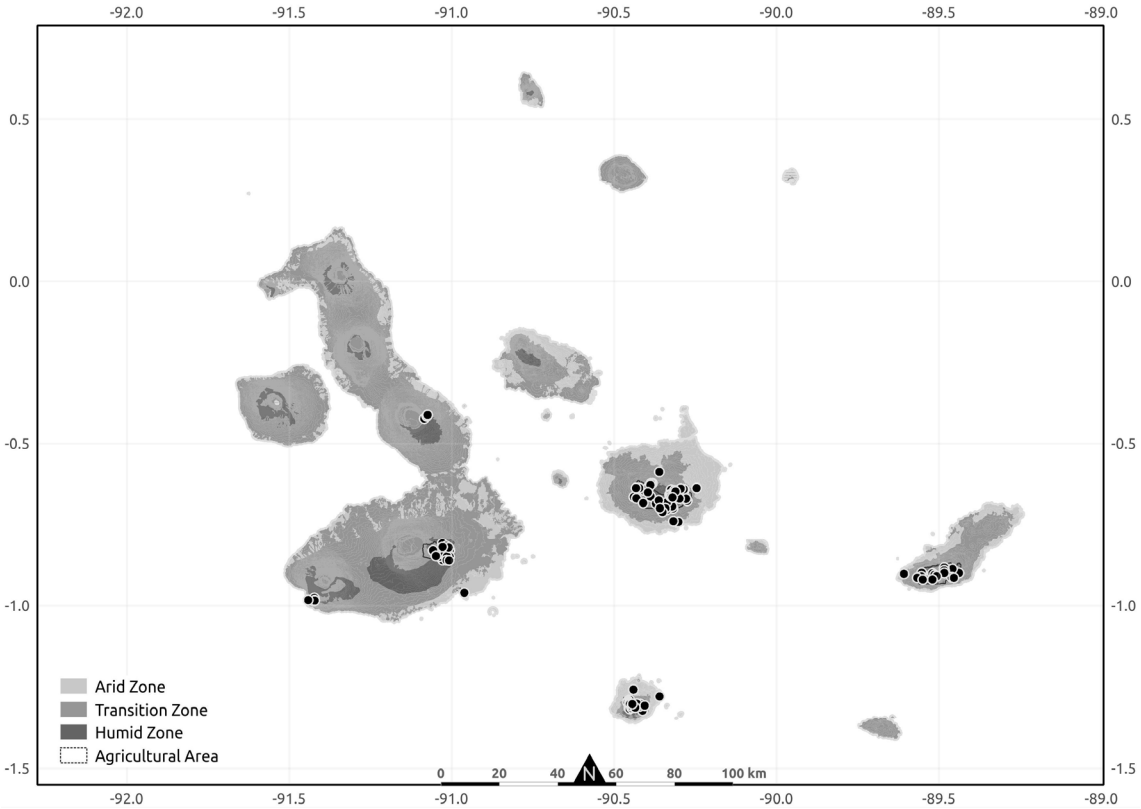
Widespread in the Americas, from Southern United States to Argentina (BROWN, 1961; BROWN, 1962; KEMPF, 1972; BRANDÃO, 1991; BOLTON *et al.,* 2006; WETTERER 2014b). *Strumigenys louisianae* is an introduced ant that is only recorded on the inhabited islands. It was recorded for the first time in 1981–1982 on Santa Cruz (Lubin, 1984). Nests can be found under soil and rotten wood. It is the most common *Strumigenys* species collected in the Transition and Humid Zone. In the Humid Zone it usually occurs in leaf litter where it preys on Collembola (LUBIN, 1984; DEYRUP *et al.,* 2000). *Strumigenys louisianae* also inhabits disturbed areas including gardens in human settlements. Other records come from forests of *S. pedunculata*, *P. galapageium, M. robinsoniana* and *P. guajava*. In cultivated areas it was found on the crops *P. americana*, *C. arabica, B. oleracea* var. *capitata*, *Z. mays, A. comosus, S. betaceum, M. paradisiaca, S. quitoense, S. lycopersicum*, *Paspalum* sp. and *M. esculenta*. According to LUBIN (1984), *S. louisianae* is one of the few species that is not affected by *W. auropunctata*. Nevertheless, recent observations from farms of Bellavista Village (Santa Cruz Island), revealed that nests of *S. louisianae* can be preyed upon by *W. auropunctata*. This ant is a predator of small arthropods, but little is known about its impact in Galapagos (WILSON, 1953; CAUSTON *et al*., 2006).

Strumigenys membranifera (Emery, 1869)
Bare Pygmy Snapping Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173252). (Map 35)

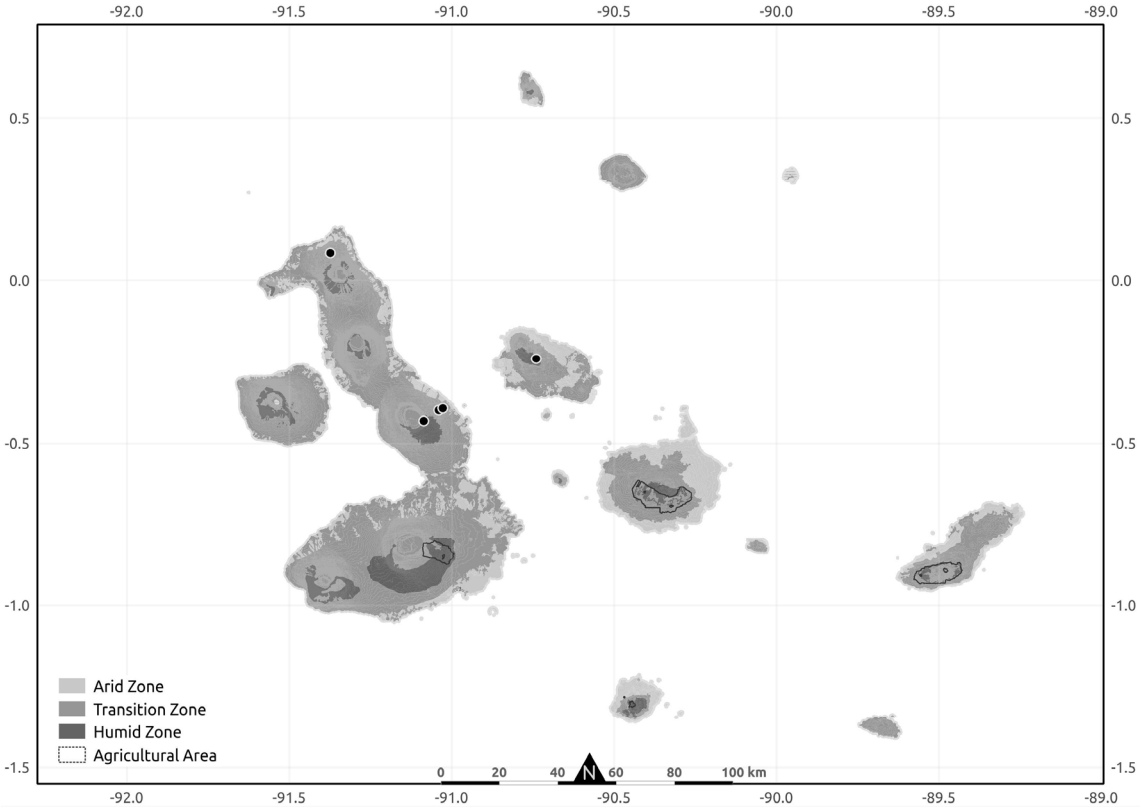
A pantropical ant, but also found in some subtropical and temperate areas (KEMPF, 1972; BOLTON *et al.,* 2006; WETTERER 2011b). *Strumigenys membranifera* is a tramp ant which was introduced to Galápagos through human activities. It is known from a few localities on Isabela and Santa Cruz Islands in the Transition and Humid Zone. It was recorded for the first time in 2008. Elsewhere it is known to feed on Collembola and Campodeidae species (WILSON, 1953; DEYRUP *et al.,* 2000; HERRERA & LONGINO, 2008). Workers were recorded in areas with *B. graveolens*, *W. ovata*, *M. laricifolia*, *O. insularis*, *Paspalum conjugatum* Bergius, *Verbena litoralis* Kunth, *T. rufo–sericea*, *Kyllinga brevifolia* Rottb., ferns (*Pteridium arachnoideum* (Kaulf.) Maxon) and *Commelina diffusa* Burm. f. This species of ant may be impacting small soil arthropods in Galápagos, as found in other parts of the world (WETTERER, 2011b).

Tetramorium bicarinatum (Nylander, 1846)
Penny ant (WETTERER, 2009c)
(ANTWEB: CASENT0173284). (Map 36)

A tramp ant widespread throughout tropical, subtropical and temperate regions in the world (WETTERER, 2009c). This introduced species is found in all vegetation zones and most islands and islets of the Galápagos archipelago. *Tetramorium bicarinatum* occurs in natural and disturbed areas from the coast to the high–altitude Dry Zone. It was recorded for the first time in 1891 on San Cristóbal Island (EMERY, 1893). It makes nests under rocks, in small holes in the soil, in bark, dry mangrove trunks, rotten logs and roots (e.g. *B. graveolens*). It has been recorded visiting flowers of *O. helleri* (CHAMORRO *et al.,* 2012) and flowers and extrafloral nectaries of *O. echios* and *J. thouarsii* (Meier, 1994). Although it is well known as a predator



Map 34. Distribution of *Strumigenys louisianae* Roger, 1863.



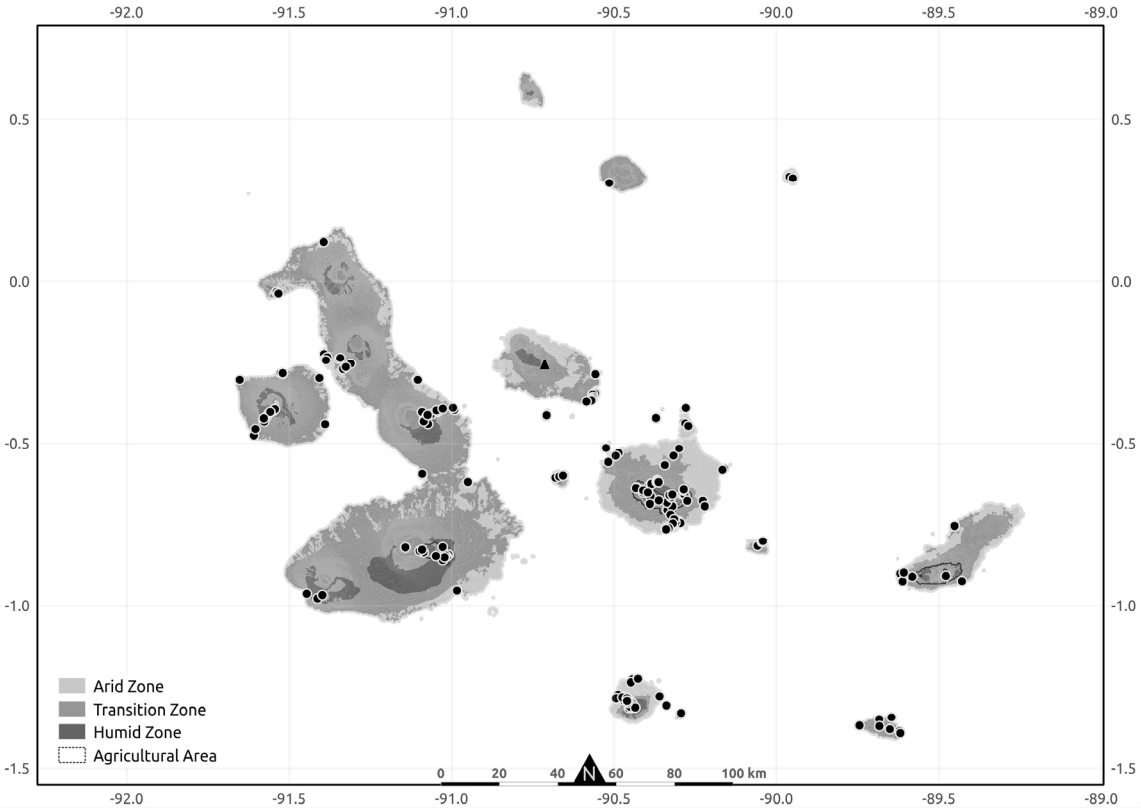
Map 35. Distribution of *Strumigenys membranifera* (Emery, 1869).

of insects (WETTERER, 2009c) it also feeds on dead animals, like dead lizards, in arid environments (e.g. on Daphne Major Island). WHEELER (1924) reports workers of *T. bicarinatum* exploring the foliage of bushes where a great numbers of frigate birds and boobies were nesting. Specimens were collected from bare lava soil with few grasses and sedges, between litter in the crevices of rocks where seabirds rest, stands of *C. pyriformis*, mangrove leaf litter, areas with grass along sandy dunes and beaches (in Puerto Villamil), forests of *B. graveolens* (with *Z. fagara*, *M. laricifolia*, *Cordia* sp., *W. ovata*, *C. scouleri*, *D. lancifolius*, *A. filifolia* and grasses) as well as in deciduous steppe forest of *H. mancinella,* herbs (*P. conjugatum*, *H. glutinosa, E. pilosa, Aristida subspicata* Trin. & Rupr., *Rhynchospora* sp., *C. asiatica*, *R. minima* and *S. setosa*), ferns (*P. aquilinum*, *P. tridens*, *Doryopteris palmata* (Willd.) J. Sm., *S. salviifolia*) mosses, sedges (*C. anderssonii*), grasses (*P. pauperum, S. setosa*), plants of *B. graveolens*, *Chloris* sp, *Merremia* sp. *Exodeconus miersii* (Hook. f.) D'Arcy and *Scalesia villosa* Stewart. In cultivated areas it attends scale insects and is reported in crops of *S. officinarum*, *A. comosus, S. betaceum, Z. mays, M. acuminata*, *S. quitoense*. In urban areas it was collected in gardens, trees of *C. papaya*, soil and leaf litter. It can easily be collected with pitfall traps, or tuna and honey baits.

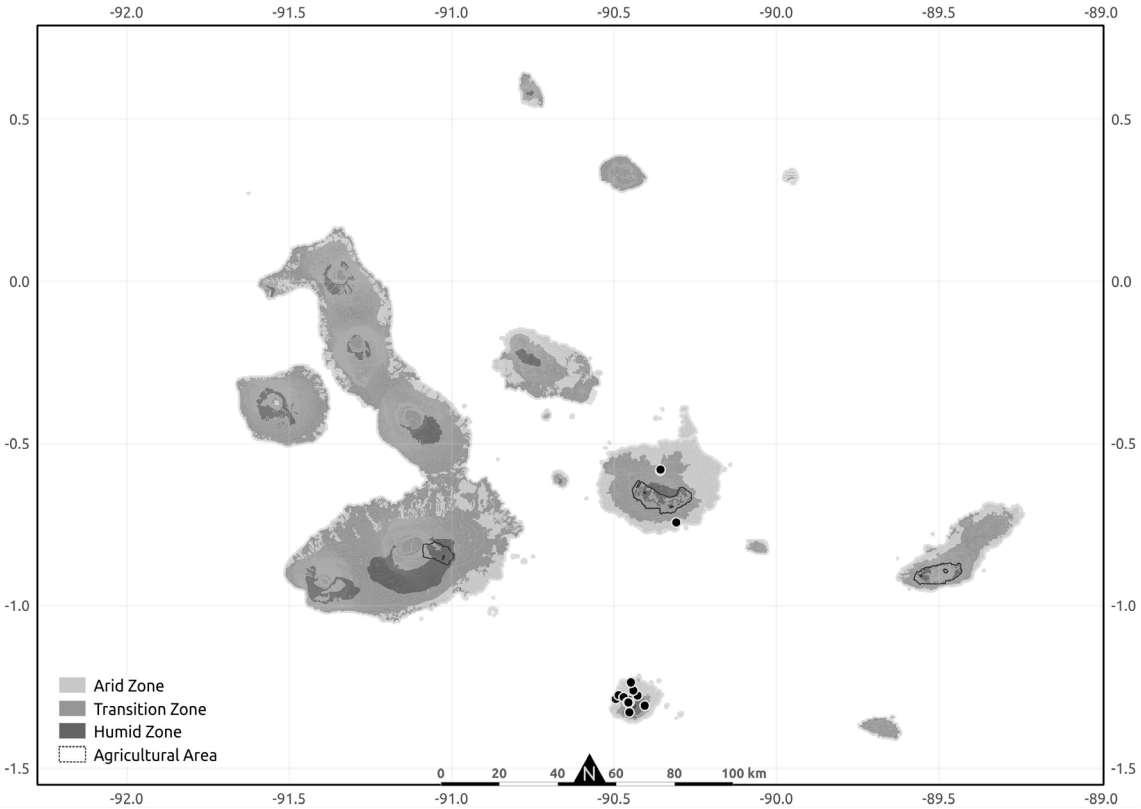
Tetramorium bicarinatum is an introduced species impacting natural environments. In Galápagos it was identified as the probable cause of the extinction of *C. macilentus* on Española Island (LUBIN, 1985). Recent expeditions by the authors to Fernandina Island show that it is probably the main competitor of the endemic ant *C. planus*, having invaded extensive areas around the trail to the summit. This suggests that its invasiveness potential is greater than previously thought (CAUSTON *et al.,* 2006). This species has been recorded in ports, airports and tourist boats, suggesting continuous reintroductions to and within the archipelago.

***Tetramorium caldarium* (Roger, 1857)**
Confused Groove Headed Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173287). (Map 37)

An uncommon species in Galápagos, known from tropical and temperate zones (KEMPF, 1972; BOLTON, 1979; BOLTON *et al.,* 2006; BHARTI & KUMAR, 2012). This tramp ant occurs in natural and inhabited areas of dry and humid zones on Santa Cruz and Floreana. It was reported for the first time in 1998 (PEZZATTI *et al.,* 1998). Revisions at ICCDRS showed it was already collected around 1992. *Tetramorium caldarium* can be found in dense forests of *S. pedunculata* in the highlands (areas also occupied by *C. scouleri*, *T. rufo–sericea*, *Z. fagara*, *M. laricifolia*, *Chiococca alba* (L.) Hitchc.) and open shrublands (composed of *M. laricifolia* and *W. ovata*). In the transition area it is present in forests of *P. galapageium*, *C. scouleri* and *Z. fagara*. *Tetramorium caldarium* is also present in herbaceous vegetation (*Phyla strigulosa* (M. Martens & Galeotti) Moldenke) and occasionally in grasses. This species can also be found in open forest (composed of *P. juliflora*, *S. spicata* with occasional trees of *B. graveolens*) and cultivated areas. On Santa Cruz, *T. caldarium* was collected near a landfill area located in a deciduous forest of *B. graveolens*. *Tetramorium caldarium* has been collected in boats transporting tourists to other islands and it is likely that other areas in Galápagos have been invaded by this ant (LOMAS, 2008). According to WETTERER & HITA–GARCIA (2015) there is no evidence that *T. caldarium* has a significant ecological impact on native fauna in other parts of the world and it is possible that its invasive rating in Galápagos is too high (CAUSTON *et al*., 2006).



Map 36. Distribution of *Tetramorium bicarinatum* (Nylander, 1846).



Map 37. Distribution of *Tetramorium caldarium* (Roger, 1857).

***Tetramorium lanuginosum* Mayr, 1870**
Wooly Groove–Headed Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173289). (Map 38)

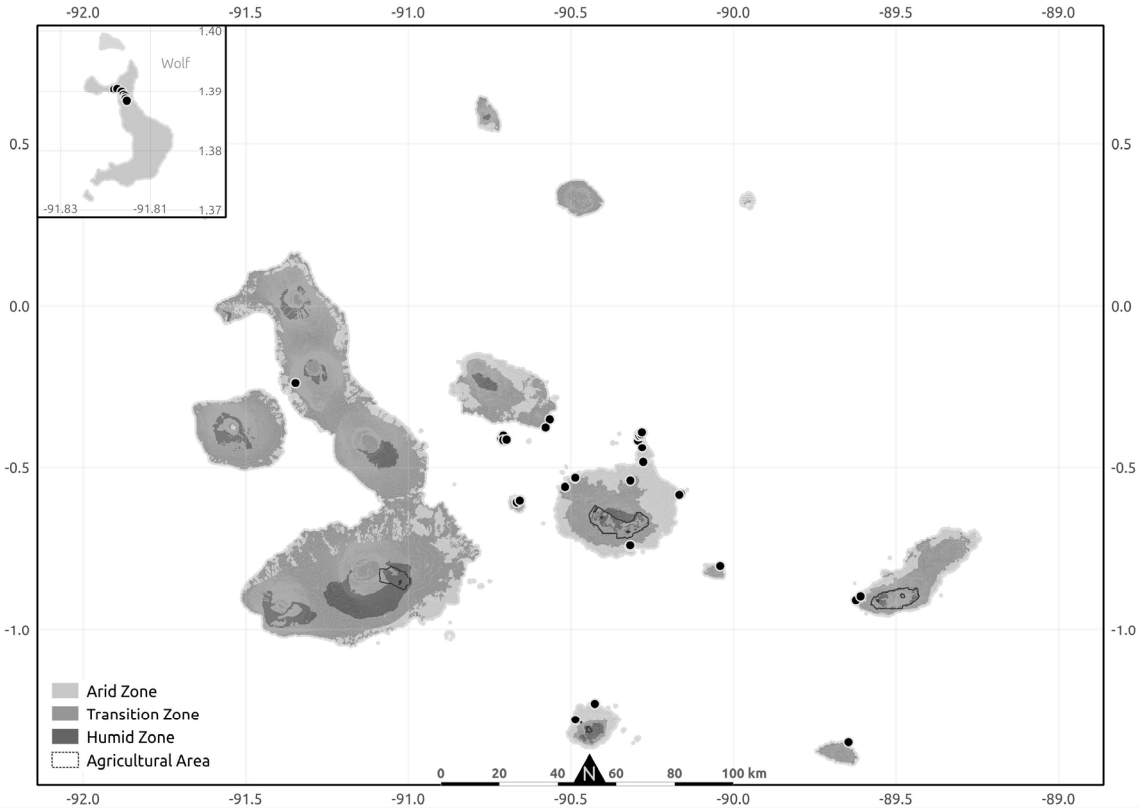
An ant known from some states in the south of the United States, Caribbean islands, Central America, East Asia, Australia, Oceania and the western Old World (WETTERER, 2010b). *Tetramorium lanuginosum* is a tramp ant previously only known from Floreana Island (PEZZATTI *et al.,* 1998). It is currently recorded on 15 islands. Recent collections and revisions of museum material show it to be distributed in natural and disturbed areas, including human settlements and places visited by tourists. Nests can be found under rocks and in soil. The species is mainly established in dry areas of Galápagos and has been collected under mangrove plants and stones, on beaches, on dry shrubs, and visiting flowers of *O. megasperma*. *Tetramorium lanuginosum* was the only ant species collected on Wolf Island during an intensive survey (more than 5 hours) and it may outcompete other ant species on some of the smaller islands. Although *T. lanuginosum* is not considered invasive in other parts of the world, it has potential to impact island ecosystems (CAUSTON *et al.* 2006; WETTERER, 2010b; WETTERER & HITA–GARCIA, 2015).

***Tetramorium simillimum* (Smith, 1851)**
Similar Groove–Headed Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173291). (Map 39)

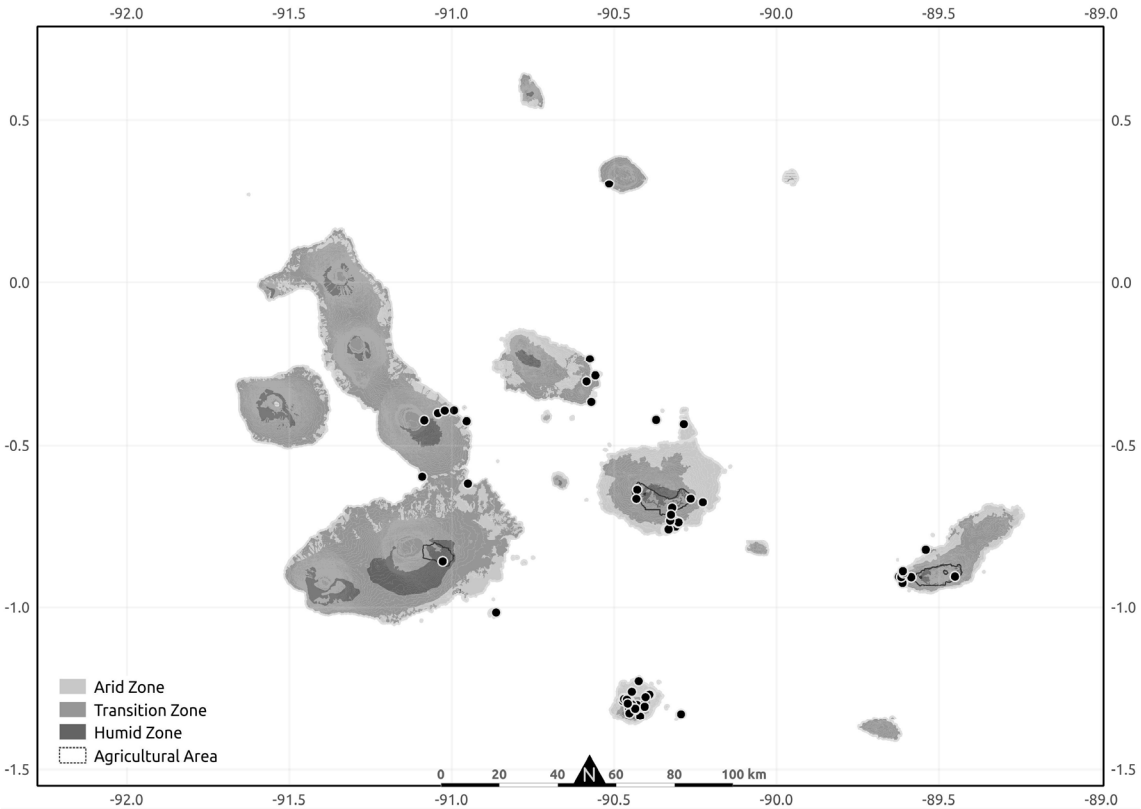
A widespread species in the tropics (KEMPF, 1972; BOLTON, 1979; BRANDÃO, 1991; BOLTON e*t al.,* 2006). This introduced ant was first collected around 1900 from Floreana Island (WHEELER, 1919). Now it is recorded from 13 other islands. Nests can be found under rocks, soil and rotten wood. Workers were observed foraging on sandy beaches in plants of *C. pyriformis*, in leaf litter in dry and humid areas in secondary growth forest, and natural areas such as the *Scalesia* forest in the highlands of Santa Cruz. *Tetramorium simillimum* is a common species in cultivated areas of Santa Cruz, Floreana and San Cristóbal being reported in crops of *C. annuum* and *M. esculenta.* In urban areas it was observed foraging between grass, under trees of *M. octogona*, in branches of *Citrus x aurantiifolia* (Christm.) Swingle, *M. acuminata*, *C. nucifera*, *A. cherimola*, *S. purpurea*, *C. lutea* and *H. rosa–sinensis*. It is frequently collected in landfill and waste treatment areas, ports and airports. It has a minor ecological impact in places where it has been introduced (WETTERER & HITA–GARCIA, 2015). It is rated to have low invasive potential in Galápagos (CAUSTON *et al.,* 2006).

***Tetramorium lucayanum* Wheeler, 1905**
Ebony Ant (WETTERER, 2011c)
(ANTWEB: CASENT0625424). (Map 40)

An uncommon species in Galápagos, it is known from Neotropical (Antilles and Brazil), Paleartic (Italy and Irland) and Afrotropical regions (KEMPF, 1972; BRANDÃO, 1991; BOLTON *et al.,* 2006; WETTERER, 2011c). This tramp species is dispersed by human commerce (FONTELA, 1995; MCGLYNN, 1999; WETTERER, 2011c). *Tetramorium lucayanum* is only known from the littoral and humid zones on Isabela Island. A few specimens were collected in 1986 during the dry season in a deciduous steppe forest of *H. mancinella* (HERRERA *et al.,* 2014). In other parts of the world it inhabits a wide range of habitats and nests have been found under stones, beneath bark of trees and near termite nests (SMITH, 1936; MANN, 1920; DEJEAN *et al.,* 1996).



Map 38. Distribution of *Tetramorium lanuginosum* Mayr, 1870.



Map 39. Distribution of *Tetramorium simillimum* (Smith, 1851).

***Trichomyrmex destructor* (Jerdon, 1851)**
Destructive Trailing Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173269). (Map 41)

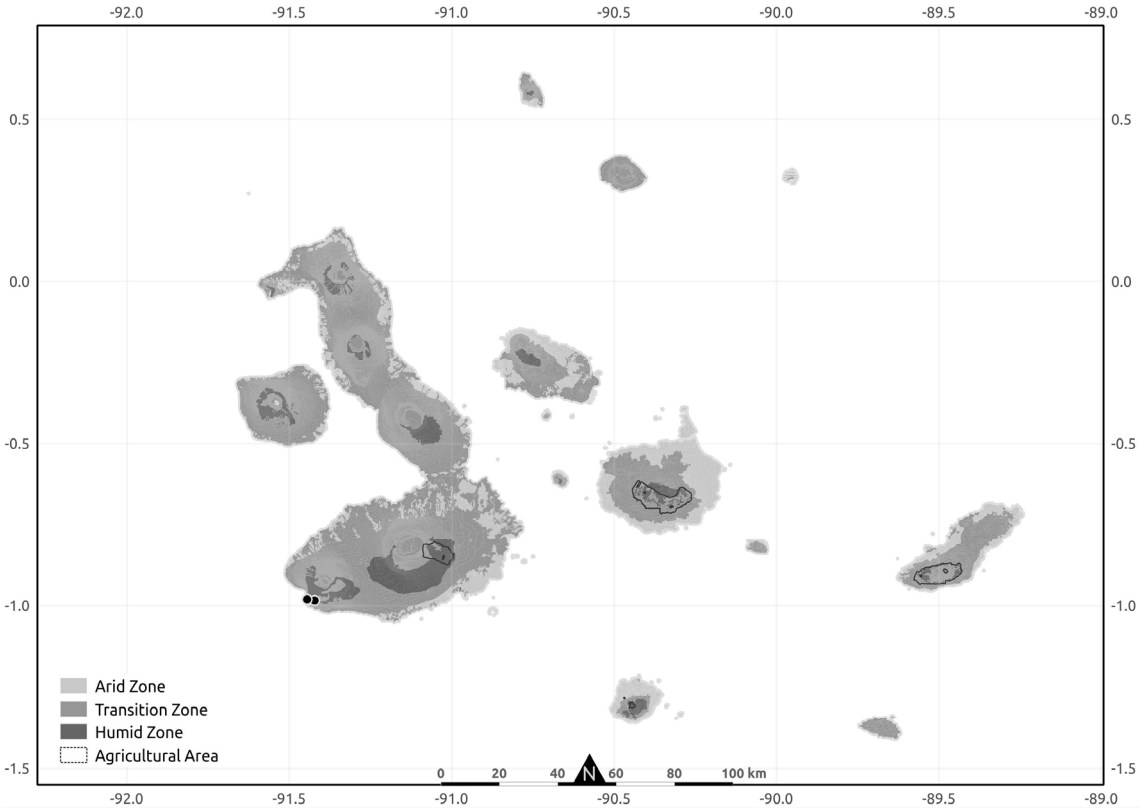
A cosmopolitan species and a tramp ant (WILSON & TAYLOR, 1967; ESPADALER, 2005; WETTERER, 2015). This invasive ant was recorded for the first time in 1998 on Floreana (PEZZATTI *et al.,* 1998), however, studies of museum material showed it was already collected in 1992 from Baltra. *Trichomyrmex destructor* is a scavenger species found in dry and humid areas and distributed on four islands of the archipelago. It is abundant in the disturbed places of Baltra as well as in the urban zone and surrounding area in Floreana (PEZZATTI *et al.,* 1998; VON AESCH & CHERIX 2005; HERRERA & CAUSTON, 2010). Workers have been observed feeding on insects, birds and dead animals in the arid zone of Baltra Island. Nests can be found under rocks where long columns of workers transport the food. *Trichomyrmex destructor* was observed attending *Ceroplastes* spp., and aphids on plants of *Sida ciliaris* L. On Baltra it was observed monopolizing honeydew produced by *I. purchasi* and displacing other introduced ants like *P. longiconris* and *T. melanocephalum* from branches of *Acacia insulae–iacobi* Riley and *P. aculeata*.

Recently, *T. destructor* was collected from the humid agricultural area of Isabela in leaf–litter under trees of *I. edulis*, and on Floreana in crops of *A. comosus* and *M. esculenta*. *Trichomyrmex destructor* is considered a pest in tropical and subtropical areas of the old world (WETTERER, 2009b), and is considered a threat for the insect fauna of the Galápagos Islands (VON AESCH & CHERIX 2005; CAUSTON *et al.,* 2006, HERRERA & CAUSTON, 2010).

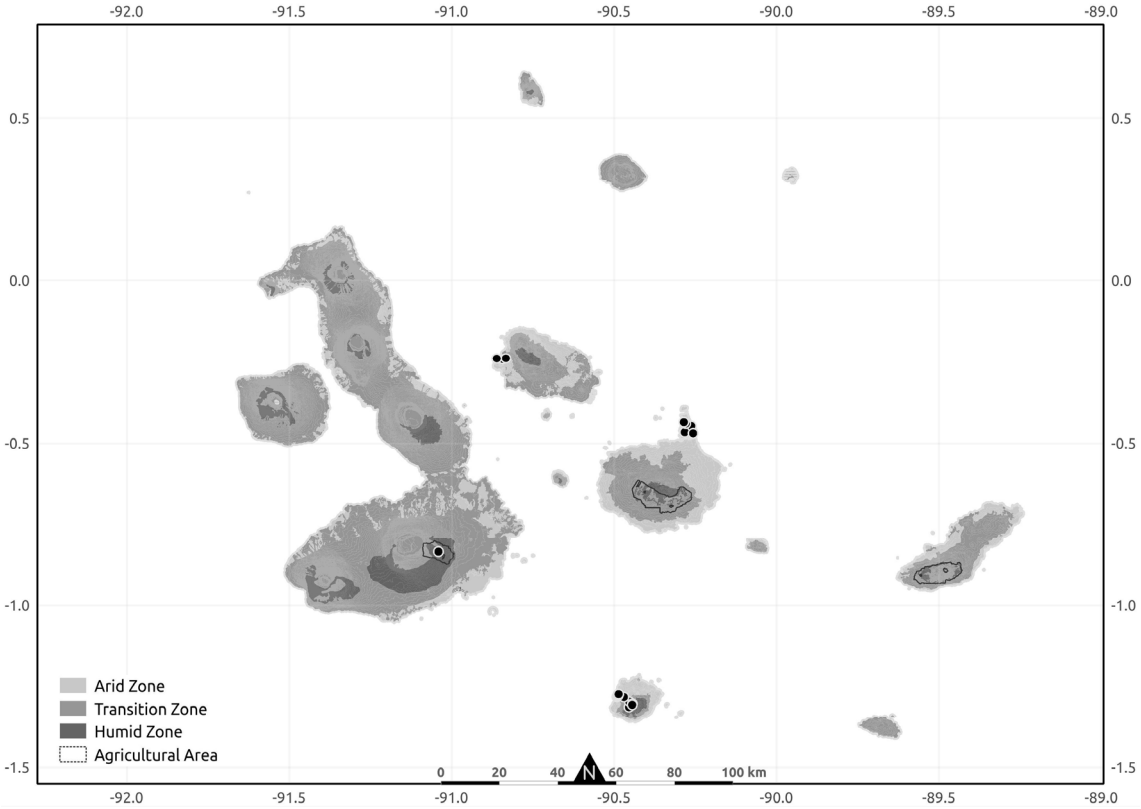
***Wasmannia auropunctata* (Roger, 1863)**
Little Fire Ant (DEYRUP *et al.,* 2000)
(ANTWEB: CASENT0173249). (Map 42)

This cosmopolitan ant (WETTERER & PORTER, 2003; LONGINO & FERNÁNDEZ, 2007; WETTERER, 2015), is an invasive species which has been spread by human commerce. It is thought to have established in Galápagos 114 years ago (SILBERGLIED, 1972; HERRERA & CAUSTON, 2008). It is known from 21 islands and islets and is present in natural and disturbed enviroments of the dry, transition and humid areas of inhabited and uninhabited islands. Nests can be found in leaf litter, rotten trunks, the base of trees (*P. guajava, B. graveolens, P. carthagenensis*), under mosses in branches of *C. sinensis* or *P. guajava*, under bark of rotten trunks (*C. odorata* and *B. graveolens*), under stones, and in hollow twigs. *Wasmannia auropunctata* is a polyphagous and opportunistic species (ULLOA–CHACON, 1990; MEIER, 1994), that forages on trees, leaf litter and soil. It tends the cottony cushion scale *I. purchasi* for honeydew. In dry areas it visits extrafloral nectaries of giant endemic cacti *O. echios* and *J. thouarsii* (MEIER, 1994). It was collected on stems of *M. robinsoniana* (BOADA, 2005), in mangrove areas, on plants of *C. pyriformis, C. alba*, *H. mancinella*, *Paspalum* sp., *W. ovata* and *A. filifolia*. It visits flowers of *Capsicum frutescens* L., *C. molle*, *C. lutea*, *Cucurbita pepo* L., *Iochroma ellipticum* (Hook. f.) Hunz., *Justicia galapagana* Lindau, *Mormodica charantia* L., *P. scandens*, *Setaria parviflora* (Poir.) Kerguélen and collects nectar in flowers of *T. rufo–sericea* (MCMULLEN, 1986, 1990, 1993; BOADA, 2005; MCMULLEN, 2007, 2009, 2011; CHAMORRO *et al.,* 2012).

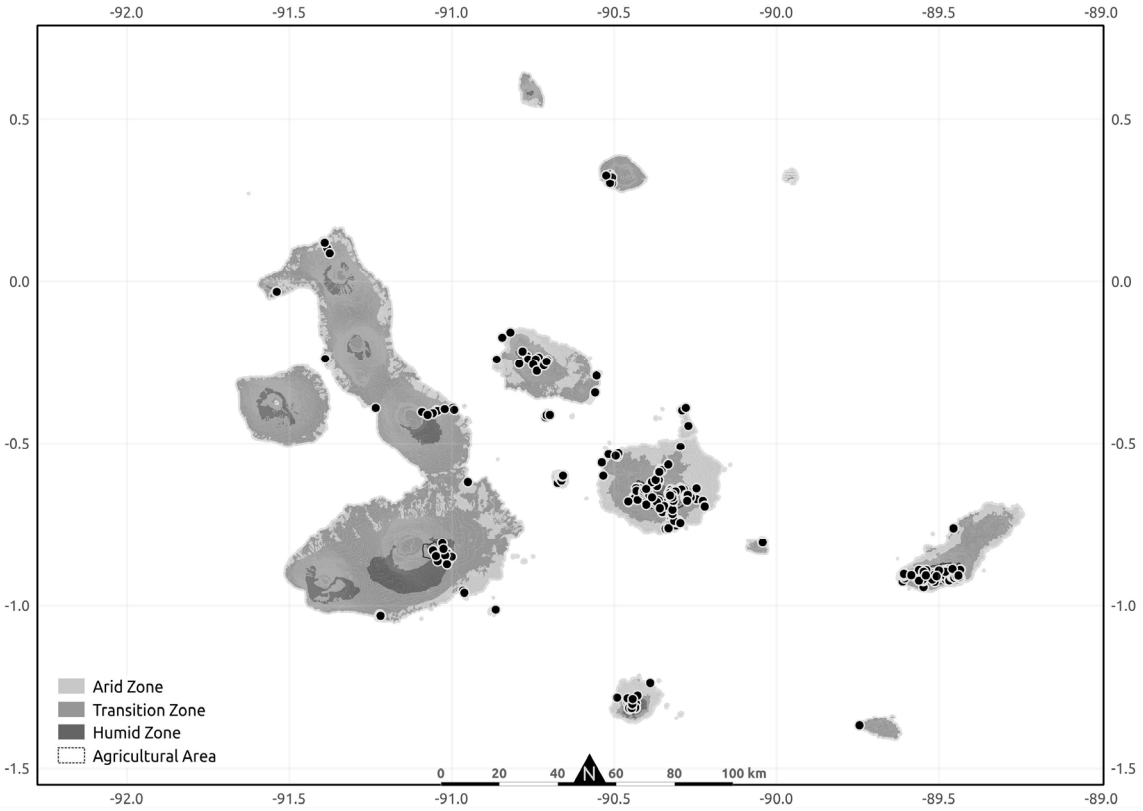
In cultivated areas *W. auropunctata* is present in crops of *S. officinarum*, *A. cepa*, *C. sativum*, *C. arabica*, *M. paradisiaca*, *B. oleracea*, *P. vulgaris*, *Z. mays*, *S. tuberosum*, *C. sativus*, *C. annuum*, *S. betaceum*, *S. lycopersicum*, *M. esculenta*, *Cajanus cajan* (L.) Millsp., *L. sativa*, *Brassica napus* L., *S. quitoense*, *S. tuberosum*, *C. papaya*, *A. comosus*, *C. lanatus*, *G. barbadense*, *Citrus reticulata* Blanco, *Paspalum* sp., *Cynodon dactylon* (L.) Pers.,



Map 40. Distribution of *Tetramorium lucayanum* Wheeler, 1905.



Map 41. Distribution of *Trichomyrmex destructor* (Jerdon, 1851).



Map 42. Distribution of *Wasmannia auropunctata* (Roger, 1863).

Pennisetum purpureum Schumach. and *P. americana*. In urban areas it is common in gardens and has been collected on plants of *A. muricata*, *H. rosasinensis*, *A. nilotica*, *M. indica*, *T. indica*, *C. nucifera*, *Ficus* sp., *C. lutea* and *B. graveolens*. It was also collected in parks, ports, airports and at sites frequented by tourists.

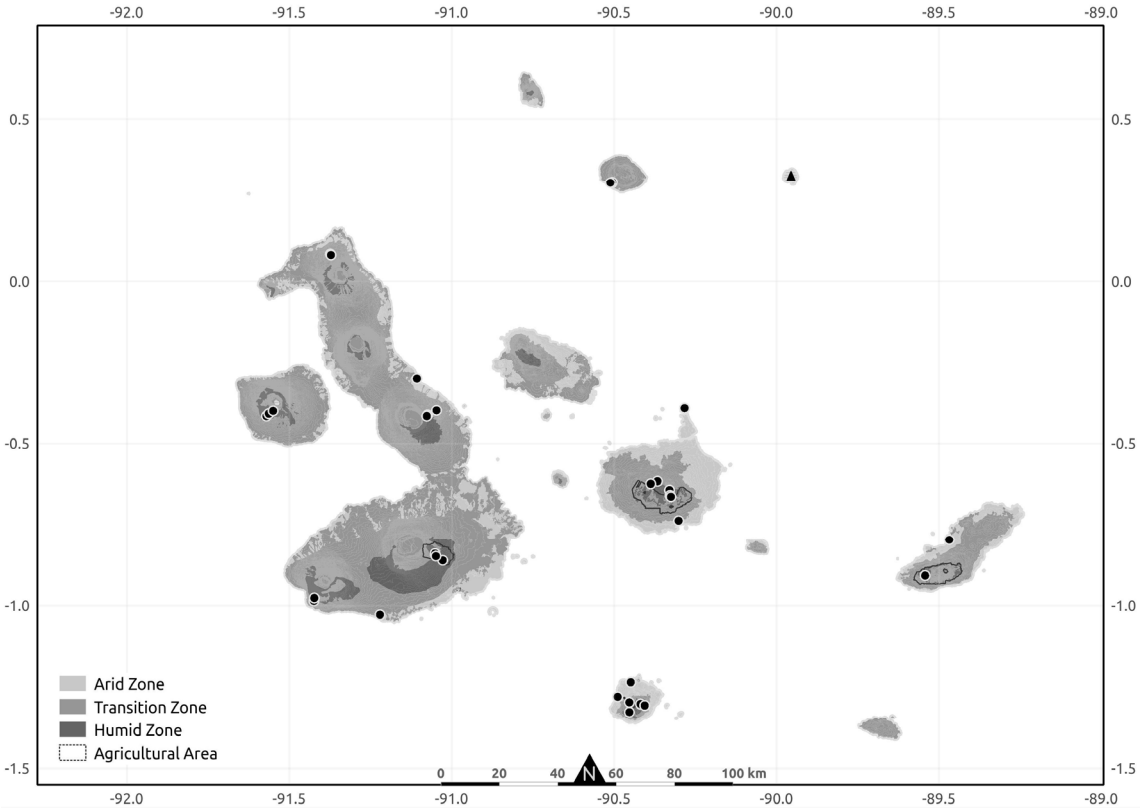
Wasmannia auropunctata has been collected from tourist boats traveling between the islands (LOMAS, 2008). The negative impact and consequences of the invasion of *W. auropunctata* in natural environments of Galápagos, as well as in other regions has been extensively documented (CLARK *et al.,* 1982; FABRES & BROWN, 1978; JOURDAN, 1997; LUBIN, 1984; ULLOA–CHACÓN & CHERIX, 1990; WILLIAMS & WHELAN, 1992; PASSERA, 1994; WETTERER & PORTER, 2003; CAUSTON *et al.,* 2006; LONGINO & FERNÁNDEZ, 2007; HERRERA & CAUSTON, 2008). *Wasmannia auropunctata* was the target of two successful eradication programs in Galápagos (ABBEDRABO *et al.,* 1994; CAUSTON *et al.,* 2005).

SUBFAMILY PONERINAE

***Hypoponera beebei* (Wheeler, 1924)**

(ANTWEB: CASENT0173306). (Map 43)

Only known from Galápagos (BOLTON *et al.,* 2006), *H. beebei* is found on eight islands in natural areas, humid zones and occasionally in the dry and littoral zones. It was collected for the first time in 1923 from Genovesa Island and could be endemic (WHEELER, 1924). In the littoral zones specimens have been collected under stones and on sandy beaches surrounded by *C. pyriformis*. It has been collected from leaf litter in the humid areas. On Fernandina a few specimens were collected in an area with ferns and grasses near the summit (1300 m).



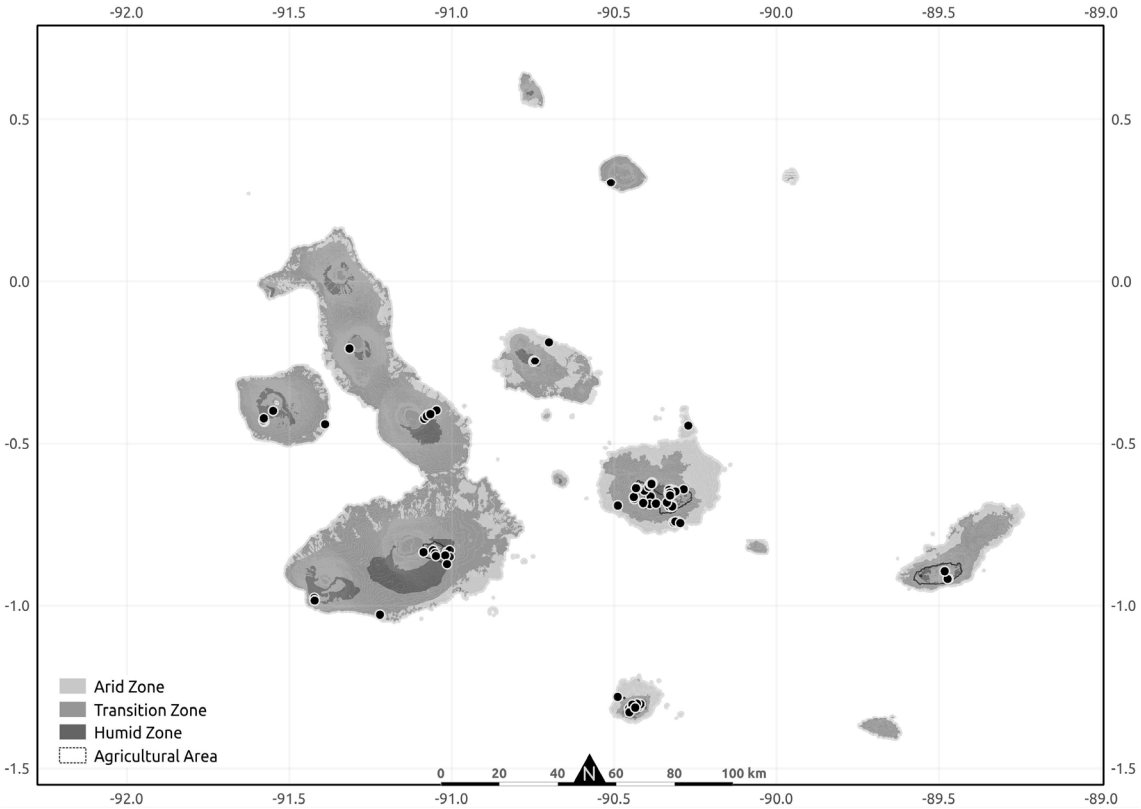
Map 43. Distribution of *Hypoponera beebei* (Wheeler, 1924).

***Hypoponera opaciceps* (Mayr, 1887)**
(ANTWEB: CASENT0173294). (Map 44)

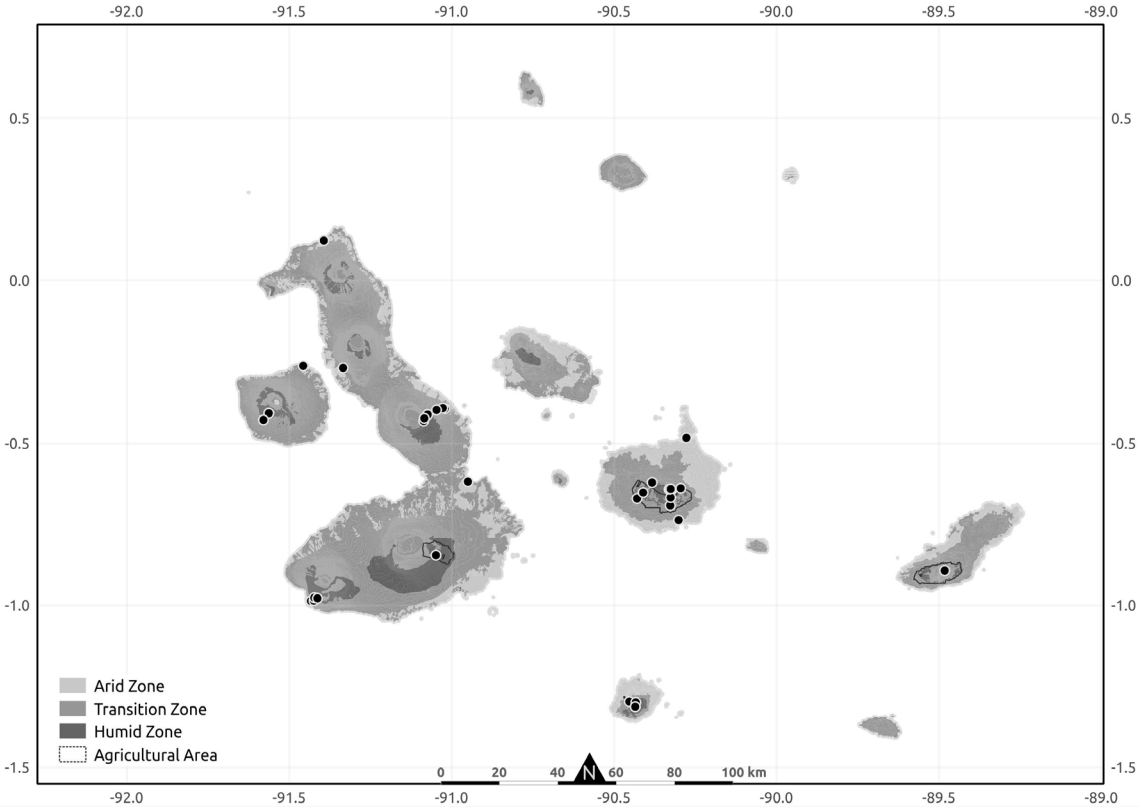
A pantropical species (KEMPF, 1972; BOLTON *et al.,* 2006; WETTERER & VARGO, 2003). This tramp ant was recorded for the first time in 1984 (LUBIN, 1984). It has been recorded from eight islands and it is found in both natural and disturbed zones. It is a common inhabitant of leaf litter and nests in rotten logs, under rocks, bases of trees and dead and humid stems of grass (*P. purpureum*). In natural areas it is registered from forests of *M. robinsoniana*, *C. pubescens*, *S. pedunculata* and *P. floribunda*. In the humid zone it is present in areas composed of herbs, grasses and ferns (*Galactia* sp., *Diodela radula* (Willd. & Hoffmanns. ex Roem. & Schult.). Delprete, *J. galapagana*, *S. setosa*, *Panicum* sp., *P. conjugatum* and *Pteridium* sp.) and patches of *Sphagnum*. In dry environments specimens were registered in litter collected from lava near the beach on Santiago Island while in Fernandina it was collected in a small woodland composed of ferns (*P. tridens, D. palmata*) and shrubs (*P. rufipes*, *D. lancifolius*, *T. rufo–sericea*). On Floreana Island some workers were collected near the beach under *C. pyriformis*. In cultivated areas *H. opaciceps* is known from leaf litter of *S. purpurea, M. acuminata*, *C. arabica*, and *M. esculenta*. In urban areas it can be found in gardens. *Hypoponera opaciceps* was recorded on tourist boats traveling between islands (LOMAS, 2008) and also from aircrafts coming from mainland Ecuador.

***Hypoponera opacior* (Forel, 1893)**
(ANTWEB: CASENT0173297). (Map 45)

Found in the tropical and subtropical Americas (KEMPF, 1972; BRANDÃO,1991; BOLTON *et al*., 2006). It was possibly introduced to Galápagos through human commerce and now occurs on six islands (SALOMON & MICKHEYEV, 2005; HERRERA *et al.,* 2014). This species was reported



Map 44. Distribution of *Hypoponera opaciceps* (Mayr, 1887).



Map 45. Distribution of *Hypoponera opacior* (Forel, 1893).

for the first time in 2014 and is known from humid zones in natural and disturbed areas (HERRERA *et al.,* 2014). However, examinations of museum material showed that it was already collected in 1987 near the agricultural zone in Isabela Island. This species has been found in leaf litter in humid areas, in herb layers (composed of *P. conjugatum*, *H. glutinosa*, *E. pilosa, A. subspicata*, *Rhynchospora* sp., *C. asiática*, *S. setosa*), ferns (*P. aquilinum*) and mosses. Some samples have been collected from native forests of *P. floribunda* and invaded areas infested by *P. guajava*. In cultivated areas *H. opacior* is recorded on crops of *S. officinarum* and *M. paradisiaca.*

***Leptogenys santacruzi* Lattke, 2011**
(ANTWEB: CASENT0173299). (Map 46)

Only known from Galápagos (LATTKE, 2011), this ant is known from natural areas in the Littoral and Dry zone of Santa Cruz and Isabela Island (LATTKE, 2011). It was collected for the first time in 1984 on Santa Cruz Island and has only been collected infrequently since then. Most records are of winged individuals.

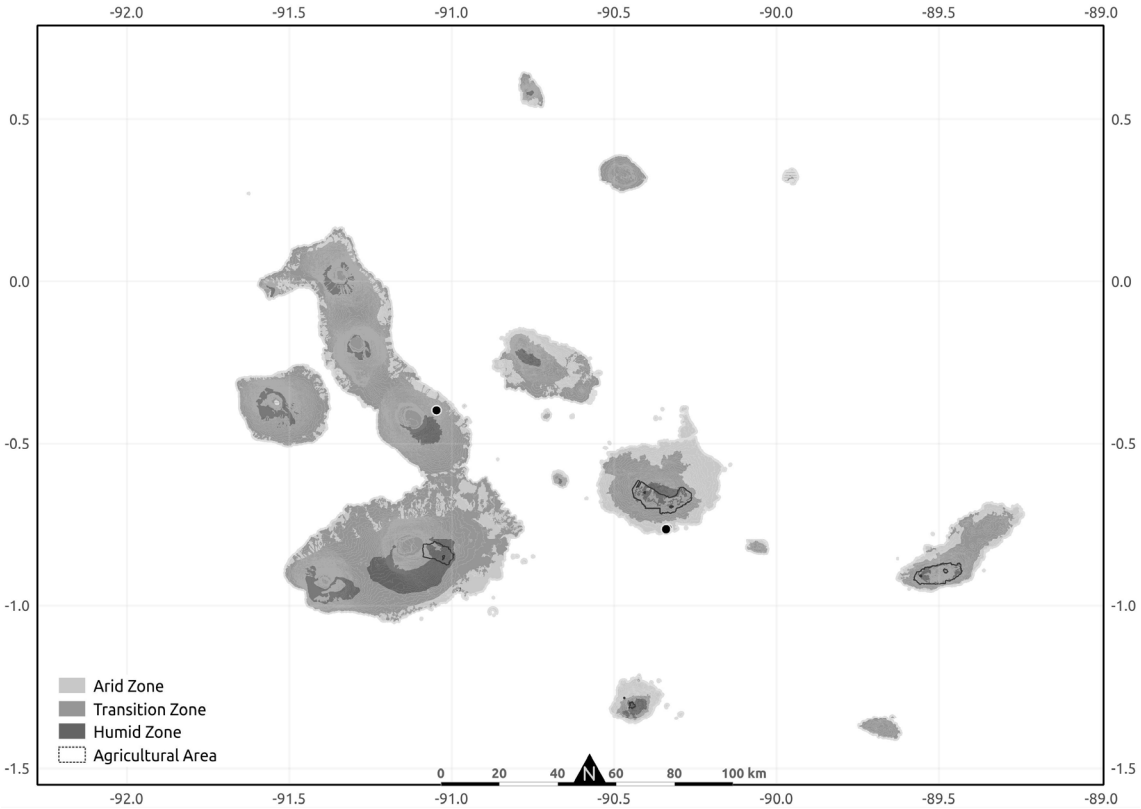
***Leptogenys* cf. *gorgona* (hh03)**
(ANTWEB: CASENT0173300). (Map 47)

An uncommon ant species collected for the first time in 2005 from Santa Cruz Island. Since then, it has only been collected in secondary and disturbed forests in humid areas. LATTKE (2011) mentions that *L.* cf. *gorgona* could be native to the archipelago. Nests have been observed under rocks.

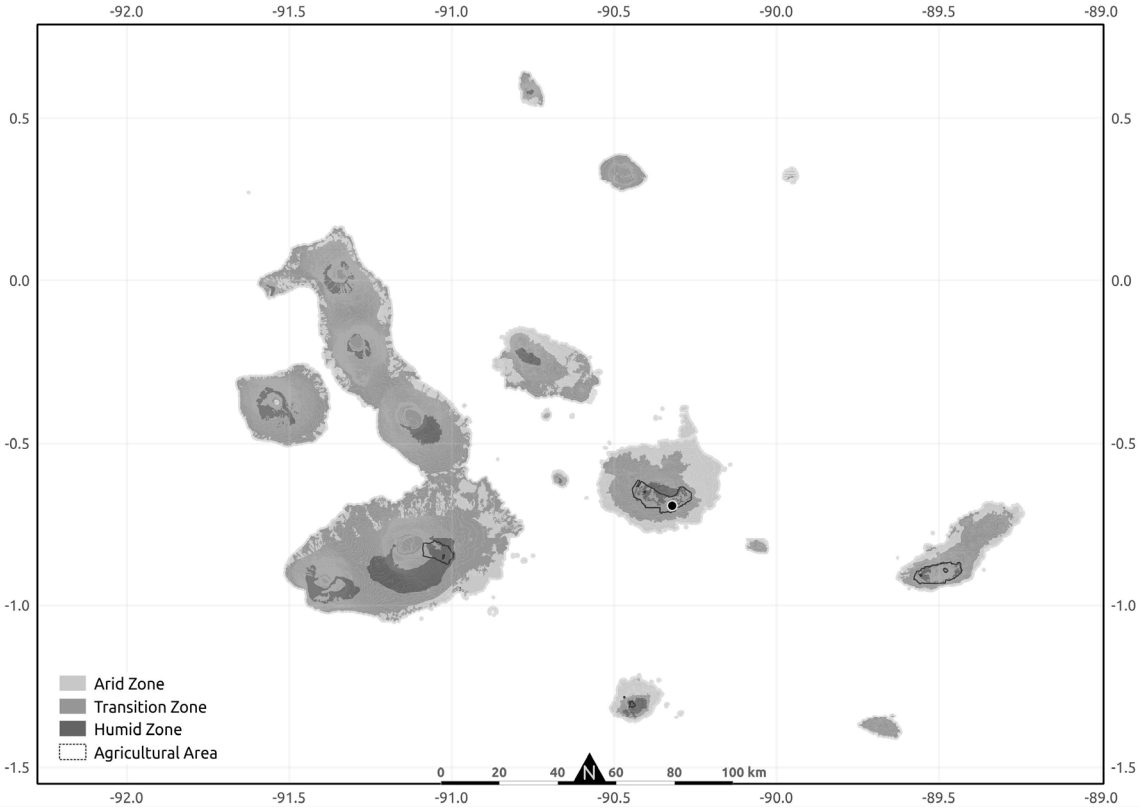
***Odontomachus bauri* Emery, 1892**
(ANTWEB: CASENT0173305). (Map 48)

This species is found on some Caribbean Islands as well as from south of Nicaragua down to Brazil (including the Galápagos Islands) (KEMPF, 1972; BROWN, 1976; BRANDÃO, 1991; BOLTON, 2006). It usually occurs in the humid areas of the inhabited islands of Galápagos. The first specimens were collected in 1891 on San Cristóbal Island (EMERY, 1893). This species was probably introduced to the archipelago through human activities (WHEELER, 1919; BROWN, 1976). Nests can be found under rocks in dry areas as well as in rotten logs at the base of dead trunks and roots. *Odontomachus bauri* can be found in natural areas near the coast hidden under the vegetation (*C. pyriformis* and mangroves) on sandy beaches, in forests of *S. pedunculata*, *P. floribunda* and *H. mancinella*, and in secondary succession forests of *P. guajava, C. odorata,* and *C. pubescens*. In the humid zone it is a visitor of leaf litter where it probably forages on invertebrates, especially ants and termites (EHMER & HÖLLDOBLER, 1995). This species has also been observed in vegetation composed of grasses (*H. glutinosa, E. pilosa*, *S. setosa*), ferns (*P. aquilinum*, *Asplenium* sp.) sedges and herbs (*P. conjugatum*, *Rhynchospora* sp., *S. salviifolia*, *C. asiatica*, *Galactia* sp.).

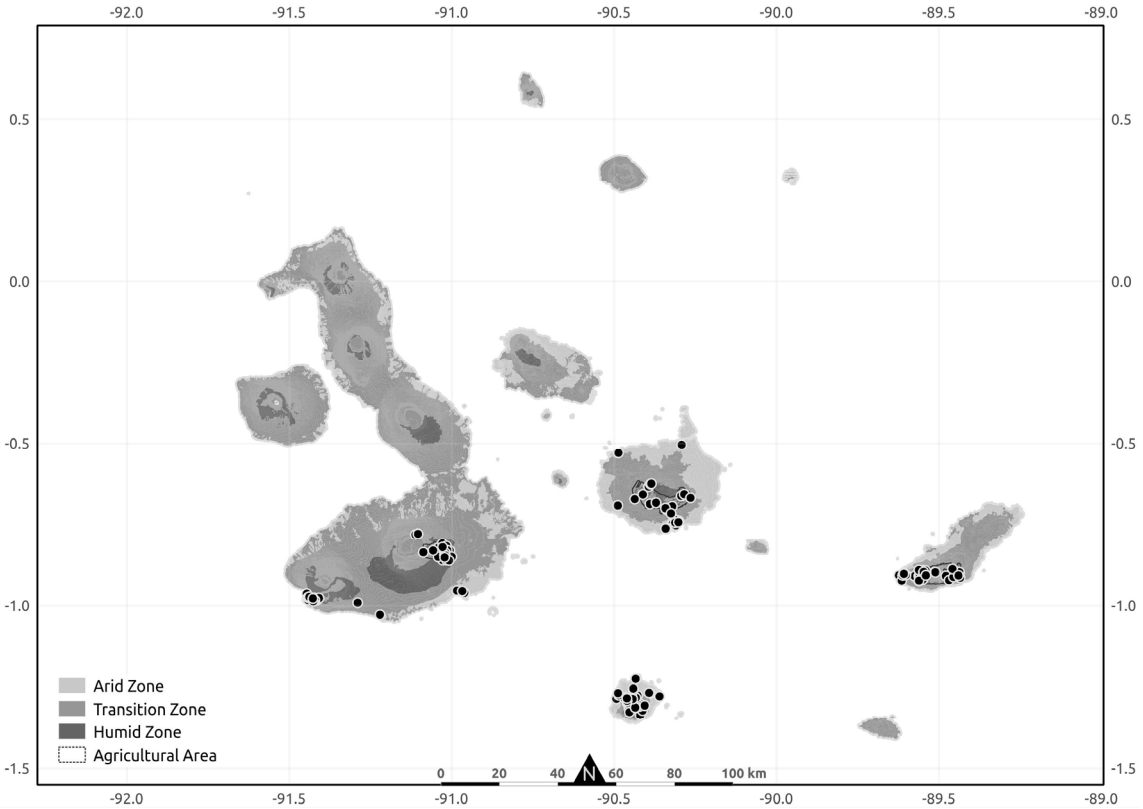
Odontomachus bauri has been collected in disturbed areas and is more common in the humid agricultural zones. It has been collected in crops of *C. arabica, A. cepa*, *S. betaceum*, *S. lycopersicum*, *M. esculenta*, *Z. mays*, *B. oleracea var. capitata*, *C. annuum*, *A. comosus, M. paradisiaca*, *B. oleracea* var. *botrytis* and *C. sativus*. In urban zones it can be observed in gardens foraging in grass (*Z. matrella var. pacifica*). It has been found building its nests at the base of trunks of *Acacia* sp., *O. megasperma*, *C. limon, S. purpurea*. Its presence on tour ships (LOMAS, 2008) suggests that this is a mechanism for its dispersal to other islands. It is considered a minor threat in the Galápagos (CAUSTON *et al*., 2006).



Map 46. Distribution of *Leptogenys santacruzi* Lattke, 2011.



Map 47. Distribution and ecological zone registered for *Leptogenys* cf. *gorgona.*



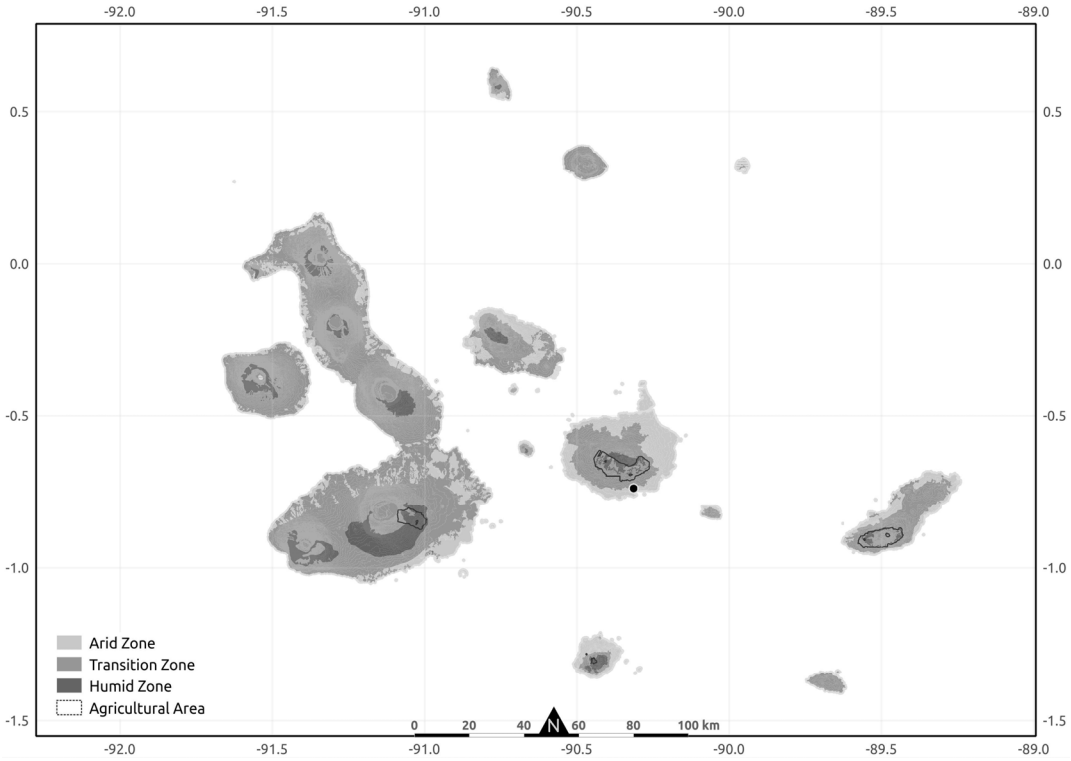
Map 48. Distribution of *Odontomachus bauri* Emery, 1892.

***Odontomachus ruginodis* Smith, 1937**
Rough–Node Snapping Ant (DEYRUP *et al.,* 2000)
(ANTWEB: ICCDRS0013038). (Map 49)

This species occurs in the northern neotropics, southeastern United States, Central America, and many Caribbean islands (KEMPF, 1972; BRANDÃO, 1991; BOLTON *et al.,* 2006). *Odontomachus ruginodis* is an introduced species, collected for the first time in Galápagos in 2008 in the urban area of Santa Cruz Island (HERRERA *et al.,* 2014). Since then it has become increasingly abundant. It nests in soil and under stones. Some specimens were found at the base and in the roots of *C. roseus*, an ornamental plant. *Odontomachus ruginodis* is common in disturbed areas, beaches, open woods and mangroves (DEYRUP *et al.,* 1988; DEYRUP *et al.,* 2000). Its invasive potential has yet to be evaluated, however its rapid colonization of areas and its predatory habits suggest that it should be monitored closely.

Species diversity

Of the 47 ant species recorded here, at least nine (19%) are assumed to be native or endemic to the islands and at least 32 (68%) species have been introduced by human-associated pathways. The status of the remaining six species is unknown. A summary of the number of ant species reported from each island and ecological zone can be found in Table 2 and Fig. 1. Overall, larger islands with a range of vegetation zones harbor a larger number of ant species (Fig. 2). The highest ant diversity was found on islands with extensive humid areas such as Santa Cruz, Isabela, San Cristóbal and Floreana.



Map 49. Distribution of *Odontomachus ruginodis* Smith, 1937.

The number of introduced ant species are considerably higher on inhabited islands, with Isabela (the largest island) having the greatest number of species, followed by Santa Cruz, San Cristóbal, Floreana and Baltra (Fig. 1). On these islands species are typically established in human-inhabited as well as in natural areas. The uninhabited islands Marchena, Santiago, Santa Fe, Fernandina and Española have a low number of native ant species and therefore are mainly characterized by introduced species (Table 1).

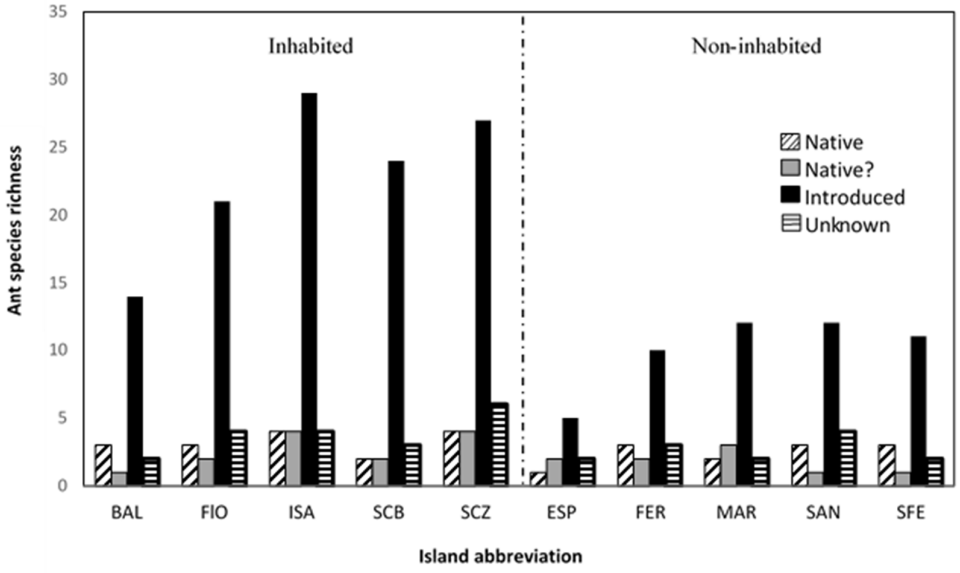


Fig. 1 – Composition of the ant fauna in some inhabited and uninhabited islands of the Galápagos archipelago: BAL = Baltra; ESP = Española; FER = Fernandina; FLO = Floreana; ISA = Isabela; MAR = Marchena; SAN = Santiago; SCB = San Cristóbal; SCZ = Santa Cruz; SFE = Santa Fé.

Table 2. Number of ant species found by Ecological Terrestrial Zones (ETZ) and Anthropized Areas (AA). * = inhabited islands; (—) = ETZ or AA absent; Litt = littoral zone; Tra = transition zone; Hum = humid zone; Urb = urban area; Agr = cultural area; Oth = Others Anthropized Areas; TT = total taxa register on the island and distributed indistinctly along ETA or AA; A = total island area in hectares (SNELL *et al.,* 1995).

ISLAND	ECOLOGICAL TERRESTRIAL ZONES				ANTHROPIZHED AREAS				
	Litt	Dry	Tra	Hum	Urb	Agr	Oth	TT	A
Albany		9	—	—	—	—	—	9	12.733
Bainbridge 1		10	—	—	—	—	—	10	11.421
Bainbridge 2		3	—	—	—	—	—	3	2.896
Bainbridge 3	7		—	—	—	—	—	7	18.336
Bainbridge 4		5	—	—	—	—	—	5	3.444
Bainbridge 5		8	—	—	—	—	—	8	4.072
Bainbridge 6		6	—	—	—	—	—	6	4.484
Bainbridge 7		1	—	—	—	—	—	1	0.796
Bainbridge 8		5	—	—	—	—	—	5	0.647
Baltra*	13	18	—	—	—	—	19	20	2619.6
Bartolomé	2	8	—	—	—	—	—	8	124.48
Bayas		3	—	—	—	—	—	3	2.070
Bowditch South		7	—	—	—	—	—	7	1.511
Caldwell		1	—	—	—	—	—	1	22.837
Champion		8	—	—	—	—	—	8	9.508
Cousin	5	4	—	—	—	—	—	6	0.858
Cuevas (Este)		2	—	—	—	—	—	2	0.130
Daphne Mayor		8	—	—	—	—	—	8	33.022
Darwin		3	—	—	—	—	—	3	106.3
Edén		8	—	—	—	—	—	8	23.020
Enderby		2	—	—	—	—	—	2	19.297
Española	7	8	—	—	—	—	—	10	6048.0
Fernandina	12	11	2	11	—	—	—	18	64248.0
Floreana*	19	22	21	25	12	17	12	29	17253.0
Gardner_Esp	5		—	—	—	—	—	5	58.038
Gardner_Flo		11	—	—	—	—	—	11	81.174
Genovesa	8	1	—	—	—	—	—	8	1410.8
Gran Felipe		3	—	—	—	—	—	3	0.039
Guy Fawkes		1	—	—	—	—	—	1	3.402
*Isabela	24	34	27	38	16	25	1	41	458812.0
Logie	2		—	—	—	—	—	2	0.200
Mao	6		—	—	—	—	—	6	1.250
Marchena	8	19	—	—	—	—	—	19	12996.0

Table 2. Continued. Number of ant species found by Ecological Terrestrial Zones (ETZ) and Anthropized Areas (AA). * = inhabited islands; (—) = ETZ or AA absent; Litt = littoral zone; Tra = transition zone; Hum = humid zone; Urb = urban area; Agr = cultural area; Oth = Others Anthropized Areas; TT = total taxa register on the island and distributed indistinctly along ETA or AA; A = total island area in hectares (SNELL *et al.,* 1995).

ISLAND	ECOLOGICAL TERRESTRIAL ZONES				ANTHROPIZHED AREAS				
	Litt	Dry	Tra	Hum	Urb	Agr	Oth	TT	A
Mariela grande		9	—	—	—	—	—	9	1.253
Mariela mediana		5	—	—	—	—	—	5	0.242
Mariela pequeña		1	—	—	—	—	—	1	0.067
Pinta	8	6	6	—	—	—	—	13	5940.0
Pinzon		11	—	—	—	—	—	11	1815.0
Plaza Norte		5	—	—	—	—	—	5	8.844
Plaza Sur	3	10	—	—	—	—	—	11	11.9
Rabida	2	10	—	—	—	—	—	12	499.312
San Cristóbal*	23	24	17	24	24	21	16	31	55808.6
Santa Cruz*	29	33	24	33	36	29	30	40	98555.0
Santa Fé	12	13	—	—	—	—	—	17	2413.0
Santiago	14	10	9	9	—	—	—	20	58465.0
Seymour Norte	14		—	—	—	—	—	14	183.887
Sombrero Chino	2		—	—	—	—	—	2	20.875
Tortuga	5		—	—	—	—	—	5	129.896
Wolf	3		—	—	—	—	—	3	134.4

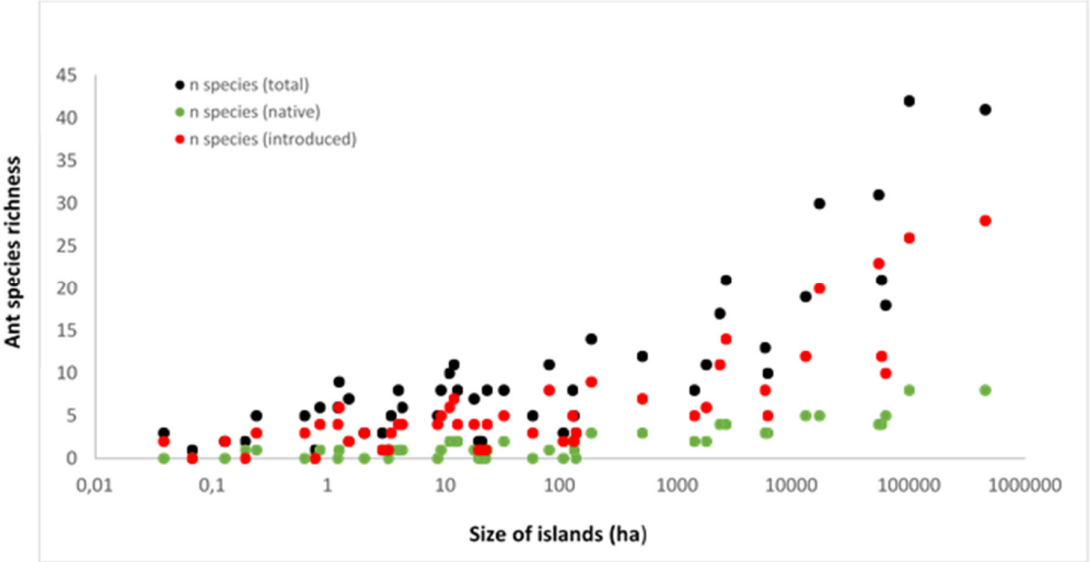


Fig. 2. Relationship between ant species richness and island size within the Galápagos archipelago. Species or morphospecies with unknown origin have been excluded here. Size of islands as reported in SNELL *et al.* (1995).

Discussion and conclusions

This study provides baseline information about the distribution and ecology of 47 ant taxa including nine possible endemic species and 32 introduced species. The endemic species include *C. macilentus, C. planus, C. nesiotus, Dorymyrmex p. albemarlensis, H. beebei*, *L. santacruzi, P. williamsi* and *S. gnoma*. However, due to the lack of taxonomic information about the ant fauna on mainland Ecuador, it is possible that some of these species will turn out to be native rather than strictly endemic to the islands. For some morphospecies that were rarely observed, such as *Crematogaster* sp. JTL-022, *Leptogenys* cf. *gorgona* (hh03), *Pheidole* sp. hh01, *Solenopsis* sp. cf. *basalis* (hh06) and *Tapinoma* sp. (hh07) and a dark form of *Cyphomyrmex* (HERRERA & LONGINO, 2018), their status in the Galapagos is still poorly understood. It is possible that some were recently introduced from the mainland and Galápagos is the first locality where they were discovered. Studies on mainland Ecuador are necessary to gain insight into the true number of endemic species.

Our study indicates that at least 14 introduced species have a wide distribution on the larger islands and at least 18 introduced ant species still have a restricted distribution in Galápagos. On the other hand, 15 species are limited to islands inhabited by humans and at least 17 species are shared with uninhabited islands, having a strong influence or may be having some impact on the Galápagos ecosystem.

Twenty-four ant species appear to occur in a wide range of habitats and ecological conditions. With the exception of the invasive species *S. geminata* and *W. auropunctata*, little is known about the impact of introduced ant species on native plants, arthropods and vertebrates. Most of the introduced ant species that were reviewed in this study could apparently be pollinators of flowers, including endemic species (HERRERA, unpublished data). TRAVESET *et al.* (2013) demonstrated that introduced species can replace the pollinator function of native species, with unpredictable consequences for the maintenance of native biodiversity. Introduced species can also have mutualistic relationships with introduced Hemiptera, defending and facilitating transfer between plants, in exchange for honeydew. As most species feed on invertebrates (with exception of the *C. rimosus,* a mycophagy ant (MURAKAMI & HIGASHI, 1997), most will be impacting the invertebrate fauna to some degree. Species of particular concern include *C. conspicuus zonatus*, which appears to have displaced the endemic ant *C. macilentus.* Also *T. bicarinatum* needs a follow-up as it is now found throughout the archipelago and has a wide ecological range, even in pristine islands. Amongst newly introduced species of concern *P. megacephala* requires an extensive survey. Although it has been reported from urban zones only, field trips suggest that it could already be established in natural areas of the islands Santa Cruz, San Cristóbal and probably Isabela.

The four inhabited islands (Isabela, Santa Cruz, San Cristóbal and Floreana), all which possess all major vegetation zones, have the highest number of introduced species of ants, Though, interestingly Baltra island, a small (2619.6 ha) island with xeric vegetation probably has the highest number of introduced ants/ha. This is the main port of entry of tourist and products and was previously a military base (ROJAS, 1993; HERRERA & CAUSTON, 2010). Introduced and invasive ants cause loss of diversity and it is very likely that these inhabited islands, which also are associated with the highest number of native and endemic arthropods (PECK, 1991; BAERT, 2013), are experiencing continuous changes in composition of faunas (CLARK *et al.,* 1982; LUBIN, 1984; HOLWAY *et al.,* 2002; TSUTSUI & SUAREZ, 2003; WAUTERS, 2014, 2016).

The rise in human activities in Galápagos, and hence pathways for introduced species is enabling new species of ants to reach Galápagos (TORAL *et al.,* 2017), and is also facilitating both introduced ant dispersal between islands. At least 17 introduced species are now found on

uninhabited islands, including two invasive species. Tourism, research and management activities likely all contribute accidentally to expanding the range of ants. Nine ant species have been found on tourist boats traveling between islands including introduced and endemic species (LOMAS, 2008; HERRERA, unpublished data). There is also evidence that ants are transported to new areas in Galápagos by natural vectors. PECK (1994a, 1994b) collected ants in aerial and sea surface nets set up on boats traveling between islands, including the introduced ants *M. floricola* and *H. opaciceps*.

The Galápagos Archipelago is a natural laboratory where islands with different geological ages represent replicas of ecological events, and where the isolation has facilitated speciation in some taxa. Systematic baseline data collection and monitoring is necessary to better understand the role of both indigenous and introduced ants in the archipelago. Such knowledge will aid in employing a science-based management approach to protect Galapágos biodiversity.

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