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Check list of ground-dwelling ant diversity (Hymenoptera: Formicidae) of the Iguazú National Park with a comparison at regional scale

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Abstract

We describe the ant fauna of Iguazú National Park (INP), a region of high biodiversity and endemism in northeastern Argentina that includes the southernmost protected area of the Atlantic Forest (AF). Ants were sampled over seven periods from 1998 to 2011 using a variety of techniques. We also surveyed museum collections and the scientific literature to obtain additional records of ants from INP. In addition to providing a species list, we compare ant composition of INP to other sites in the Upper Paraná, Serra do Mar Coastal Forest and Araucaria ecoregion of AF. A total of 172 ant species belonging to 56 genera are reported; 56 species are new records for Misiones Province and 39 species are reported from Argentina for the first time. Alto Paraná and Canindeyú departments in Paraguay present the most similar ant fauna to INP. Serra da Bodoquena in Brazil and Pilcomayo in Argentina showed higher similarity with the Upper Paraná AF ecoregion, despite that Serra da Bodoquena is composed of a mix of ecoregions. Ant diversity was lower in Upper Paraná than in Serra do Mar Coastal Forest ecoregion. This difference may result from higher primary productivity and a greater altitudinal variation in the coastal region.

Introduction

The Atlantic Forest (AF) of South America houses 7% of the world's species making it one of the most diverse ecosystems on the planet (Quintela, 1990 in Stevens & Husband, 1998). In addition to its high biodiversity, the AF is also characterized by high levels of endemism placing it among the world's highest priorities for conservation (Myers et al., 2000; Galindo-Leal & Câmara, 2003). The AF is considered one of the most endangered tropical rainforests because habitat loss and fragmentation due to agriculture and urbanization which has resulted in a drastic reduction in area (Olson & Dinesteirn, 2002; Di Bitetti et al., 2003; Ribeiro et al., 2009). Presently, only 6% of its original extent of 1,000,000 km^2 remains along the east coast of Brazil, in Misiones province in northeastern Argentina, and in eastern Paraguay (Galindo-Leal & Câmara, 2003). However, this may be an underestimate; if secondary forest and small fragments are also included, approximaly 11.7% of original AF still remains (Ribeiro et al., 2009).

The Upper Paraná Atlantic Forest ecoregion (UPAF) is located at the southernmost extent of this forest. This region is an area of ecological transition among biomes including: the Cerrado woodlands and savannas to the north, the Pantanal and the Humid Chaco to the west, the Campos and Esteros ecoregion dominated by grasslands to the South, and finally to the east, it intermingles with Araucaria Forests, part of the AF ecoregion complex (Di Bitetti et al., 2003). Also, components of UPAF extend south into Argentina along the Paraná and Uruguay rivers. Next to the Araucaria Forest is the Serra do Mar coastal forest ecoregion that includes one of the two largest remnants of the AF. The second one is the protected area within the UPAF (more than 10,000 km^2) located across the Paraná state (Brazil) and Misiones province (Argentina): The Iguaçu (Br) and Iguazú (Ar) National Parks (Galindo-Leal & Câmara, 2003). These parks are connected to the south with other areas of conservation and sustainable use given place to what is known as the Misiones green corridor (García Fernández, 2002). These two big remnants and the Misiones province green corridor play an important role in the conservation of AF flora and fauna at a regional scale (Di Bitetti et al., 2003; Galindo-Leal & Câmara, 2003) because fragmented, poor connected areas or secondary forests cannot hold complete species assemblages sustained over time (e.g. Chiarello, 2000; Silva et al., 2007; Bihn et al., 2010). Given the unique nature of these areas, they are priorities for research for understanding the diversity and conservation value and the maintaining or restoring connectivity among them via land-use planning and restoration of other areas (Ribeiro et al., 2009).

Insects, and particularly ants, are a valuable tool for conservation and restoration purposes as a result of the ecological services they provide (Del-Toro et al., 2012; Small et al., 2013) and their use as environmental, ecological, or biodiversity indicators (see Ribas et al., 2012). Ants are considered as a key component of terrestrial ecosystems, directly or indirectly providing ecological services including seed dispersion control of herbivore populations, acceleration of forest recovery or plant succession, organic matter decomposition and nutrient cycling in the soil through their nest building and maintenance (Folgarait, 1998; Wilson & Hölldobler, 2005; Trager et al., 2010; Del-Toro et al., 2012). Measures of ant species richness and functional composition are often used to understand community structure or as indicators of restoration success following great disturbance or environmental change (e.g. Andersen & Majer, 2004; Underwood & Fisher, 2006; Bihn et al., 2010; Pais & Varanda, 2010; Ribas et al., 2012). Conversely, a few ant species that are native in AF (e.g. *Linepithema humile, Nylanderia fulva, Solenopsis invicta, Wasmannia auropunctata*) have become invasive species around the world causing significant economic and ecological damage (Holway et al., 2002; Del-Toro et al., 2012). Documenting the distribution, ecology, and behavior of native populations of introduced ant species may provide insight for their control and guide monitoring programs for preventing invasions.

Studies on the biogeography and diversity of ants are of particular interest for effective conservation planning at multiple scales. In a global scale, due to ecological relevance and standardized samplings methods, ants are an ideal group to study diversity patterns along continents (Dunn et al., 2007). At a regional scale, while vertebrates tend to persist only in larger forest remnants, invertebrates such as ants are valuable at identifying the conservation value of smaller remnants (Kremen et al., 2008). In the AF, butterflies and birds exhibit species richness peaks in coastal areas of Brazil from 15º to 23°S (Brown & Freitas, 2000; Galindo-Leal & Câmara, 2003). While some work has been done on the effects of forest loss on local ant assemblages in AF (Silva et al., 2007; Bihn et al., 2008; Bihn et al., 2010) we have little knowledge of ant diversity and its patterns across the AF ecoregion complex. Silva and Brandão (2014) found a weak inverse latitudinal pattern in species richness with richer ant communities in higher than in lower latitudes. Iguazú National Park (INP) in northeastern Argentina represents the southernmost protected area of the AF, however, it remains poorly studied from the perspective of ants; only 5% of all studies conducted in the INP on biodiversity involved ants (http://www2.sib.gov.ar). The main objective of this work was to study the ant diversity in the INP in terms of species richness and species composition and compare these parameters with those from other protected areas located within and around the Atlantic Forest.

Materials and methods

Study site

The study was carried out in semi-deciduous subtropical forest within INP, which is located in the northwestern of the Misiones Province, Argentina (25°40'48.54''S, 54°27'15.09''W). The park was created in 1934 and covers more than 67,000 ha. The climate is subtropical humid without a defined dry season; annual rainfall ranges between 1800 and 2000 mm, and humidity between 70 and 90%. Mean monthly temperatures range from 15°C (winter) to 26°C (summer). The topography of this region is undulating as a result of the erosion of a network of rivers with elevation running from 0 to 500 m (Devoto & Rothkugel, 1936; Srur et al., 2007). Variations in the local environment and soil properties allow a variety of plant communities to occur including: gallery forests, bamboo forests, palmito (*Euterpe edulis*) forests, and Araucaria forests (Di Bitetti et al., 2003; Srur et al., 2007).

We compared ant composition of INP to four previously studied areas at similar latitude within the AF: Alto Paraná Department (Wild, 2007), Rio Cachoeira (Bihn et al., 2008), Parque Estadual da Ilha do Cardoso (PEIC), and Parque Estadual do Pau Oco (PEPO) (Silva & Brandão, 2014). We also compared our surveys to the Canindeyú Department where a special sampling effort was made in the Mbaracayú forest reserve, a 65,000 ha fragment of AF (Wild, 2007), and Seara municipality in Santa Catarina (South of Brazil) as a represent of the Araucaria Forest ecoregion (Silva & Silvestre, 2004). Finally, we included three other regions neighboring the AF: Serra da Bodoquena National Park (Silvestre et al., 2012), Pilcomayo National Park (Leponce et al., 2004), and Iberá Nature Reserve (Calcaterra et al., 2010). Iberá NR located in Corrientes Province (Argentina) has four main natural habitats (savanna, dry woodlands, gallery forest, and floating islands), but we only included the gallery forest habitat in this study, which share an important vegetation components with the AF (Fig 1). Additional information about the study sites is provided in Table 1.

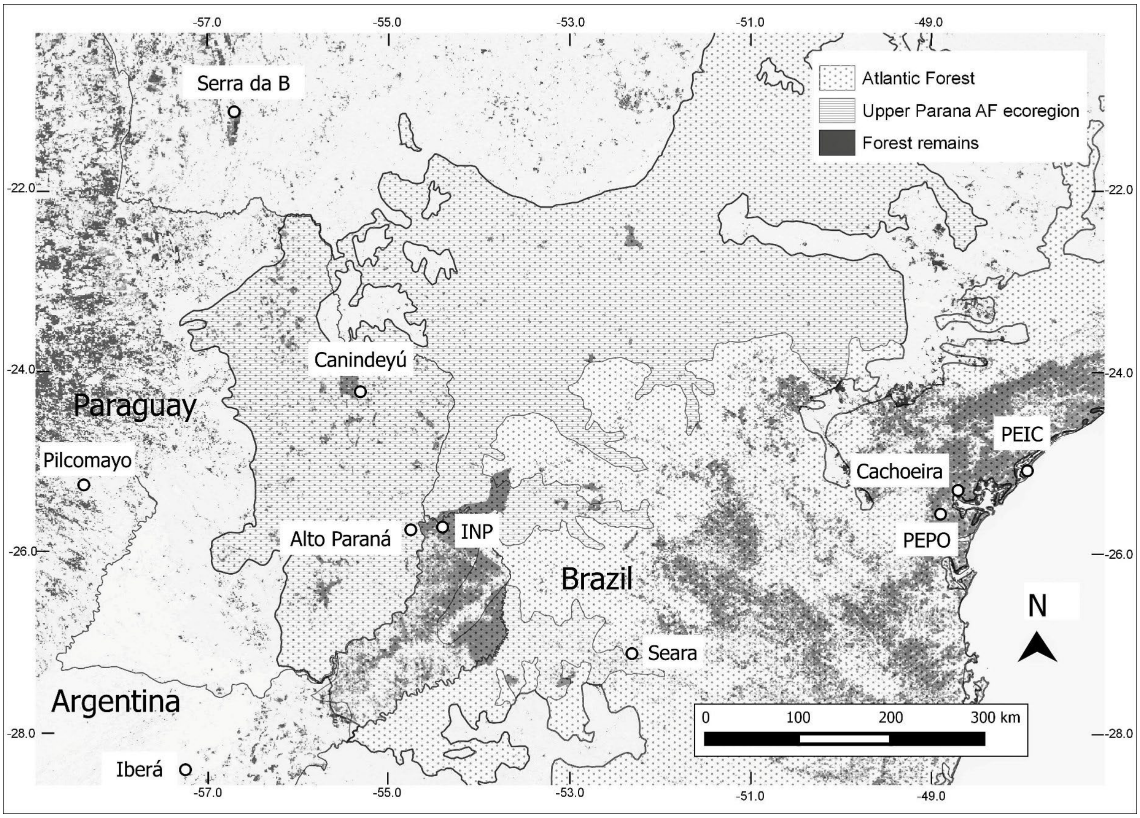

Fig 1. Locations of sampled areas in Paraguay, Brazil and Argentina used to compare myrmecological fauna against Iguazú National Park. Atlantic Forest is delimited by dotted areas meanwhile Upper Paraná ecoregion is shown with straight lines. Within both regions remnants of forest are shown in grey.

Table 1. Ant sampling sites used in this study, coordinates, habitat components and sampling information. More information in Hanisch (2013), Calcaterra et al. (2010), Wild (2007), Bihn et al. (2008), Silva and Brandão (2014), Silva and Silvestre (2004), Silvestre et al. (2012) and Leponce et al. (2004).

	Latitude	Longitude	Ecoregion	Sampling protocol (t = no. sampling sites; n = no. samples)
Iguazú NP	25°40'48.54''S	54°27'15.09''W	Upper Paraná AF	Pitfall traps (t = 9; n=78); Winkler sacs (t = 12; n=118); ground baits (t = 10; n=228); subterranean baits (t=6; n=57) and no systematic hand collecting.
Alto Paraná	25°44'56.84''S	54°44'34.60''W	Upper Paraná AF	No systematic: hand-collection, blacklighting, Malaise traps, Berlese funnels and ground baits.
Canindeyú	24° 9'20.86''S	55°26'9.98''W	Upper Paraná AF and Cerrado	No systematic: hand-collection, blacklighting, Malaise traps, Berlese funnels and ground baits.
Iberá NR	28°24'0.00''S	57°14'0.00''W	Gallery forest (Upper Paraná AF)	Pitfall traps (t = 20; n=100), Ground baits (t = 4; n=40), Berlese funnels (t = 2; n=12) and Winkler sacs (t = 2; n = 12)
Pilcomayo NP	25°04'06''S	58°05'36''W	Wet Chaco	Winkler sacs (t = 2; n=180)
Serra da Bodoquena	21°07'16'' S	56°28'55''W	Cerrado, Atlantic Forest, Amazonian Forest and Pantanal	Winkler sacs (t = 10; n=262)

Ant surveys

Ant surveys were conducted during 1998, 1999, 2003, 2005, 2008, 2009, and 2011 at 21 sites in INP (Fig 2). Surveys were performed mostly in spring and summer months and combined 72, 48, and 24 hours pitfalls traps (n=78), 48 and 24 hours Winkler sacs of 1m^2 plot (n=118), one hour ground (n=228) and 72 (n=48) and 92 hours (n=9) subterranean baits, and opportunist hand collecting. Collections were primarily made along areas of relatively easy access and the distance between sampling stations varied from 0.2 to 28 km (Fig 2). More detailed information about our collecting protocols can be found in Hanisch (2013). Collections by Leponce in 1998 followed the A.L.L. protocol in term of spatial design and sampling techniques (Agosti et al., 2000). Vouchers of all specimens collected are deposited in the Museo Argentino de Ciencias Naturales (MACN) Bernardino Rivadavia (numbers: MACN_En17408 to MACN_En17721), the Royal Belgian Institute of Natural Sciences (RBINS), the University of Illinois (numbers: AVS 705-798, 2344-2367, 2870-2912, 3053-3070, 4035-4066), the Institute and Museum Miguel Lillo (IMML) and the Bohart Museum at UC Davis (genus *Pseudomyrmyex*). For specimens stored in RBINS, SEM images are available at: http://www.sciencesnaturelles.be/cb/ants/collections/Argentina%20Ants/index.html.

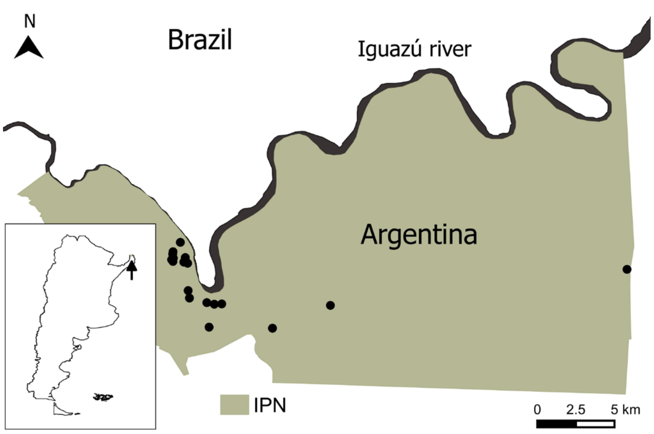

Fig 2. Area comprised by the National Park of Iguazú (INP) in grey within Misiones province, Argentina pointed by the arrow. Survey points during years 1998, 1999, 2003, 2005, 2008, 2009, and 2011 are shown in black dots.

Our surveys were supplemented by examining previous collections and published records including: IMML, MACN, and Antweb.org (California Academy of Sciences).We assessed if any ants could be qualified as new records for INP or the country of Argentina based on the absence of the species in the main catalogs of Neotropical and Argentinean ant species listed in Appendix.

Ant identification

Ants were sorted to species using available taxonomic keys. To confirm identifications, we sent samples to specialists of each genus when possible. As with other studies conducted in the Neotropics, many individuals from taxonomically difficult genera remain unidentified to species. These individuals were sorted to morphospecies, and when possible, compared across sample periods by PEH and RA (samples from the PEH, CIP and AVS collections). Synonyms and trinomial names were updated following Bolton (2014).

Data analysis

Species richness was compared between INP and those sites of the Serra do Mar Coastal Forest where a similar sampling methodology (e.g. Winkler) was employed. We performed occurrence-based rarefaction curves for incidence data, this allows a standardization removing biases linked for example to ant activity (higher in good climatic conditions) (Gotelli & Colwell, 2001). An occurrence by species incidence matrix was produced for each sites and year of collection using EstimateS 9.0 (Colwell, 2013). We only used the Winkler data set (including morphospecies) from collections made in INP in 1998 and 2008 when the leaf-litter remained 24 and 48 hours in the Winkler, respectively. Winkler extraction is the best technique for capturing ants inhabiting leaf-litter (Agosti et al., 2000; Delabie et al., 2000; Hanisch, 2013), the forest strata usually containing the most ant species.

To evaluate the similarity in the species composition of known ant assemblages among our sites, we performed Non-metric Multi Dimensional Scaling (NMDS) based on a Jaccard index in a matrix containing presence-absence data. NMDS is an appropriated method for non-normal data and does not assume linear relationships among variables (Mac Cune & Mefford, 1999). We used Jaccard index as a measure of similarity, as this index gives the same weight to mismatches (0,1 or 1,0) and matches (1,1) of presence/absence of species between two sites. Due to unresolved taxonomy, most studies included contain a high number of morphospecies in known diverse genera (e.g. *Pheidole*, *Hypoponera,* and *Solenopsis*). We excluded these genera so our comparisons were not compromised by different estimates of undescribed species in diverse but unresolved groups. We also excluded exclusively arboreal genera (e.g. *Cephalotes*) because nearly all studies focused on litter and soil ants. This allowed us to compare the ant community among sites based on common sampling techniques and taxa for which the taxonomy was best resolved, but without having to rely solely on common species. Analyses were performed using PC-ORD 4.0 software (Mac Cune & Mefford, 1999). We also performed a cluster analysis in R (R Core Team, 2014) using Jaccard index and UPGMA method with the vegan (Oksanen et al., 2014) and cluster (Maechler et al., 2014) packages. Cutting level was defined as the maximum dissimilarity value between nodes height. To test if groups obtained with the cluster analyses were different of those expected by chance, we performed a non-parametric Analysis of Similarity (ANOSIM) with PAST v.3.04 software (Hammer et al., 2001).

Results

Ant Diversity

After pooling all collection events between 1998 and 2011, we recorded 172 ant species belonging to 56 genera and 10 subfamilies for INP: Amblyoponinae (2 species), Dolichoderinae (14), Dorylinae (10), Ectatomminae (7), Formicinae (21), Heteroponerinae (4), Myrmicinae (85), Ponerinae (21), Proceratiinae (1), Pseudomyrmecinae (7). Among them, 56 were new to province and 39 new to country (Appendix). Including unidentified morphospecies not shown in Appendix, the total number of species increased to 203 species: *Brachymyrmex* (1), *Hypoponera* (1), *Nesomyrmex* (1), *Nylanderia* (1), *Pheidole* (8), *Solenopsis* (18) and *Pseudomyrmex* (1)

Of the 172 species recorded in INP, 141 species (82%) were captured during our surveys, while the remaining species were recorded from museum or personal collections. Eighty seven of these 141 species (61%) were captured using Winkler, 39 (28%) in pitfall traps, 26 (18%) were attracted to baits placed above the ground, and 17 (12%) were attracted to subterranean baits. Concerning the strata, 66 species (47%) were collected on the soil surface using pitfall traps, baits and hand collecting, 86 (61%) in the leaf-litter, 22 (15%) in the soil (using subterranean bait and soil sieving), and 14 (10%) on the vegetation. The most diverse genera were *Pheidole* with 19 species followed by *Camponotus* with 15 species.

Species density and composition

Rarefaction curves based on Winkler sampling suggested that the Serra do Mar Coastal Forests (PEPO and PEIC) located at the same latitude of INP are richer in ground-dwelling ant species than INP (Fig 3). The estimated richness was clearly higher in PEPO than in INP (both years), based conservatively on non-overlapping confidence intervals. PEPO and 2008 INP sampling showed higher values over PEIC and 1998 INP respectively, however, these values are within the overlap in confidence intervals (Fig 3).

The NMDS ordination and cluster analyses of the different regions show the same visual grouping among sites except within the UPAF sites (Table 1, Fig 4a,b). The dendrogram obtained by hierarchical methods identified six groups (Fig 4a) that were concordant in general with the belonged ecoregion of each site (Table 1). However, these visual differences among groups were marginally not significant (ANOSIM, R=0.90, p=0.06). Visual grouping suggested that Canindeyú and Alto Paraná Departments were the most similar sites to INP. Moreover, UPAF was more similar to Serra da Bodoquena and Pilcomayo than to Serra do Mar coastal forests and Araucaria Forest ecoregion (Cachoeira, PEPO, PEIC and Seara municipality). However, the percent of species shared with INP was very similar among these

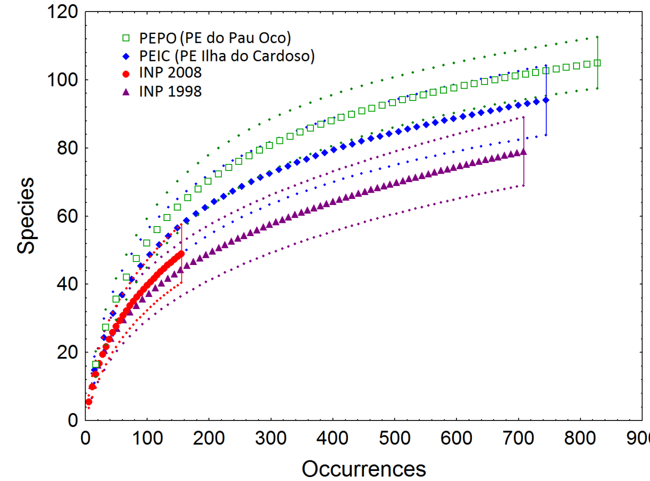

Fig 3. Occurrence-based interpolation (rarefaction) based on species/morphospecies obtained with Winkler litter samples from three sites on the Atlantic Forest with 95% unconditional confidence intervals (dashed lines). Squares represents PE do Pau Oco (n= 50; Sobs=105), diamons PE da Ilha do Cardoso (n= 50; Sobs=94), circles INP 2008 (n=28, Sobs=49) and triangles INP 1998 (n= 69; Sobs=79) samplings. Maximum species richness is found at PE do Pau Oco site, exceeding the species density at both INP collection years based in non overlapping confidence intervals.

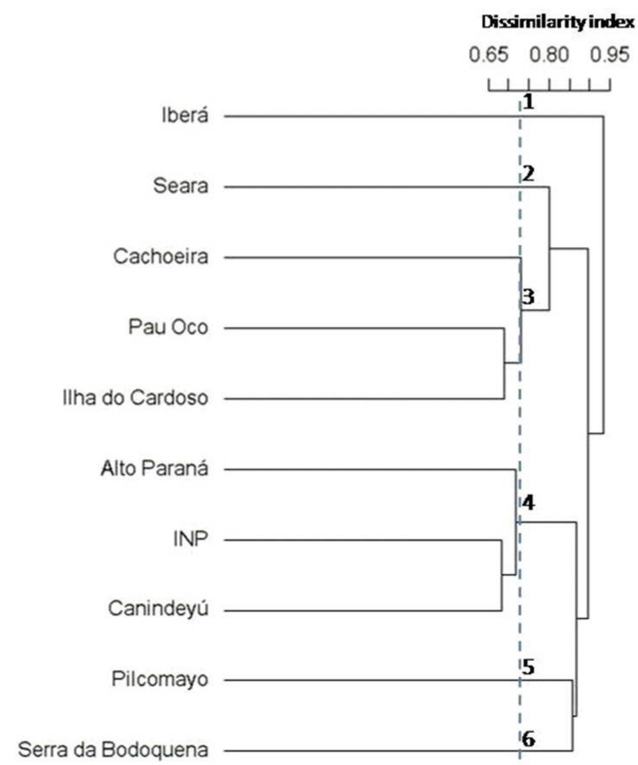

Fig 4a. Six clusters were defined according to the similarity found in the presence-absence matrix of 261 ant species among 10 sites. Cluster analysis based on Jaccard index and UPGMA as linkage method. Cophenetic correlation=0.93. Dashed line shows the level of cut used to group sites. We applied maximum dissimilarity value between node height as criteria for cutting level of dendrogram.

Supplementary material available at: http://periodicos.uefs.br/ojs/index.php/sociobiology/rt/suppFiles/724/0
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regions (between 37-48% with Serra do Mar Costal Forest sites, 54 % with Seara and 43% with Serra da Bodoquena, Fig 5). Despite the short geographic distance between Seara and UPAF ecoregion (Fig 1), the ant community of Seara was more similar to that from Serra do Mar Coastal Forests (Fig 4a, b). Finally, Iberá showed to be the most different site according species incidence (Fig 4a, b), despite that they shared near 66% of their species with INP (Fig 5).

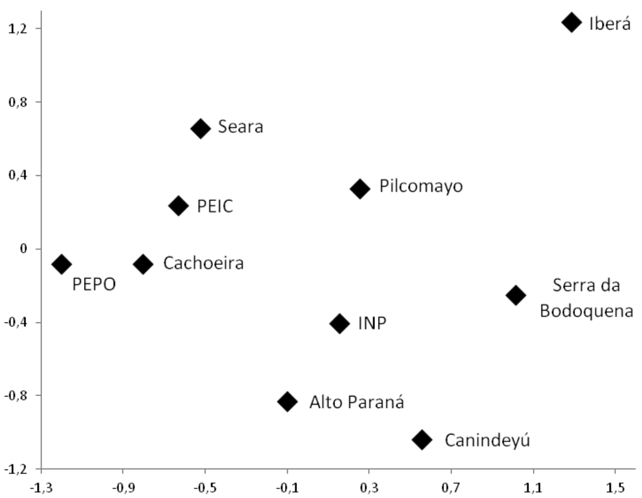

Fig 4b. Ordination of sites according to NMDS analysis, based on Jaccard index. Stress = 0.11 Presence-absence matrix of 261 species.

The most widely distributed species were *Strumigenys denticulata* (present in all sites but Serra da Bodoquena and Iberá) and *Odontomachus meinerti* (all sites but Seara and Iberá). Followed by *S. louisianae* (INP, Cachoeira, Iberá, Canindeyú, Alto Paraná, PEIC and Seara), *Strumigenys crassicornis* (INP, Cachoeira, PEPO, Canindeyú, Pilcomayo, Alto Paraná and Seara) and *Octostruma rugifera* (INP, PEPO, Canindeyú, Pilcomayo, Alto Paraná and Seara). Other species that were present in at least six sites include: the fungus growing ant *Apterostigma pilosum* (found in INP, Iberá, Canindeyú, Pilcomayo, Alto Paraná, and Serra da Bodoquena), *Basiceros disciger* (INP, PEPO, Alto

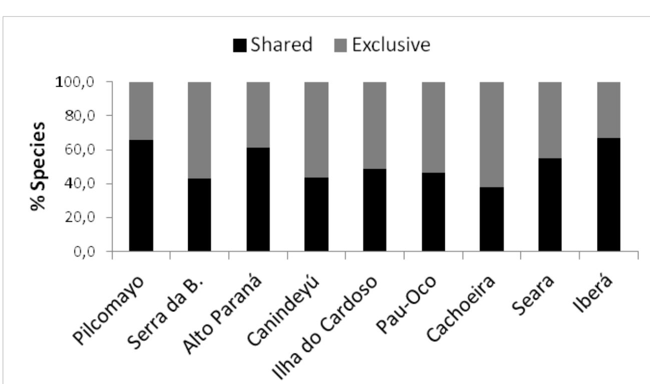

Fig 5. Percent of ant species of each site exclusive and shared with the Iguazú National Park recorded in Paraguay (Alto Paraná y Canindeyú departments), Brazil (Cachoeira NR, PE do Pau Oco, PE da Ilha do Cardoso, Serra da Bodoquena), and Argentina (Iberá NR and Pilcomayo NP).

Pananá, PEIC, Serra da Bodoquena and Seara), and the little fire ant, *W. auropunctata* (INP, Iberá, Canindeyú, Alto Paraná, PEIC, and Serra da Bodoquena). *Heteroponera mayri* and *Heteroponera microps* were only collected in the sites within the AF (INP, Cachoeira, PEPO, Alto Paraná, and PEIC) with the exception of Araucaria Forest ecoregion for *H. microps* (Supplementary material, Appendix 1). A record of *Azteca instabilis* from the IMML collection was not included because of a lack of enough individuals to confirm this identification. Our record for the rarely encountered *Anillindris bruchi* is in agreement with Schmidt et al.'s, (2013) assumption that rather than a locally uncommon species it is a broadly distributed but rarely collected species. Several ant genera/species, such as *Eurhopalothrix* (Ketterl et al., 2004) and *Eciton quadriglume* (Watkins, 1976), that were expected to be collected given their known distribution in the AF have not been found during this study.

Discussion

We report the first compilation of ant species identified for Iguazú National Park (172 species), 141 species registered only from our samplings and the remained species were retrieved from museum collections and literature. More ant species will be added to our list and results could change once the status of some morphospecies will be resolved. Fifty six species were new to province and 39 new to Argentina. The majority of morphospecies that we could not identify belonged to diverse ant genera that include many similar species and also lack taxonomic resources for the region (e.g *Solenopsis*, *Pheidole*). As in other Neotropical studies *Pheidole* was the most diverse genus with 19 species (Silva et al., 2007; Donoso & Ramón, 2009) followed by *Camponotus* (15 species). The most efficient technique to capture ant species was Winkler litter sampling, however, other methodologies including subterranean baits and hand collecting provided some unique records (e.g. *Linepithema neotropicum* and *Heteroponera microps*; Appendix). Because our methods concentrated on ground dwelling fauna, the list of canopy ant species is underestimated.

Due to the high heterogeneity of the AF (Galindo-Leal & Câmara, 2003) and the heterogeneous sampling efforts of the ant surveys, the estimated ant richness for the studied regions of the AF is very variable among sites. In Paraguay, Wild (2007) found a total of 285 species in Canindeyú Department (mostly found in Mbaracayú forest reserve), but only 89 species in Alto Paraná Department, which is the closest study site to the INP. This is probably due to the lower sampling effort used and the poorer conservation state of this latter department. Silva and Brandão (2014) studying the leaf-litter ant fauna found 94 and 105 species in PEIC and PEPO AF sites, respectively. In our case, employing the same methodology and similar sampling effort, we found 79 species for INP (1998 sampling) using only Winkler sacs (Fig 3). In Serra da Bodoquena, Silvestre et al. (2012) found 170 species over a four-year study. Despite that sampling was conducted in multiple years, sampling efforts concentrated on hand collection and systematic Winkler sampling and pitfall trapping in a sector of easy access of the INP close to the Iguazú river. Truly comprehensive faunal surveys take much more effort. For example, in a long term study (23 years) in the tropical forest of La Selva Biological Station, Costa Rica, Longino et al. (2002) found 437 ant species. La Selva station is a small area (1,500 ha) when compared with the INP (~67,000 ha) or the Cachoeira reserve (8,700 ha). Our survey covered only approximately 15 ha of INP (0.02% of its surface) in seven sampling opportunities using several sampling methods, where most sampling sites were clumped in an easy-access area of the Park (Fig 2). As a consequence, other habitat types present in the park were not sampled, which potentially may have increased our ant species list. Because Canindeyú Department represents so far the best studied area of UPAF and shows a similar ant species composition with INP (Fig 4a, b), ant richness in INP may be similar to that of Canindeyú (~300 ground-dwelling ant species; Wild 2007).

The diversity of ground-dwelling ant species in the AF seems to increase slightly with latitude along the Brazilian coast (Silva & Brandão, 2014) and to decrease with the distance from the coast (Fig 3). The longitudinal pattern found in this work is consistent with other taxa studied like birds and butterflies (Brown & Freitas, 2000; Galindo-Leal & Câmara 2003). Ribeiro et al. (2009) concluded that the northern AF is presently in more dire need of conservation compared to the southern part, with the exception of the large mosaic in the south of the Bahia region. This could mean that the observed latitudinal pattern in species richness could be a consequence of better conservation status in the southern AF. Also, a latitudinal gradient in primary productivity could be an alternative explanation for this pattern (Silva & Brandão, 2014; Kaspari et al., 2000).

In a large-scale leaf litter ant diversity study performed by Ward (2000), altitude and latitude alone account for 47% of the variance in ant species richness; species richness peaked at mid-elevations in the tropics. In the UPAF the elevation ranges from 0 to 500 m in contrast with those sites of Serra do Mar coastal ecoregion with montane and submontane forests (0 to 1000 m). Larger elevation ranges could lead to a greater diversification and niche availability, resulting in higher species richness in ants as in other organisms (Brown & Freitas, 2000). Also, Sanders (2002) showed that other parameters, often confounded with area, can also play an important role in determining species richness patterns along elevation gradients.

Our survey of the incidence of ant species at a regional scale suggests that the sites studied in the AF grouped according to each ecoregion (Fig 4a, b; Table 1). However, ant species composition was similar among all sites despite their strong environmental heterogeneity. Many widespread species were shared among the different sites. However, it is important to consider that these results were based on tractable taxonomic species (i.e., excluding morphospecies of difficult genera), limiting our interpretation of this pattern. Undoubtedly, these genera are characteristic components of the structure of local communities and the general pattern reported in this survey may change if more complete community compositions are estimated. Despite this limitation, we still found differences in ant composition among sites.

Most habitats within UPAF held a similar ant fauna (Fig 4). Canindeyú Department, despite belonging also to the Cerrado ecosystem, was similar in composition to INP (Fig 4a). Surprisingly, Serra da Bodoquena, a seasonal deciduous and semi deciduous forests with important influences of surrounding different biotas showed a closed relation with the UPAF. Cachoeira NR, PEIC, and PEPO are characterized by lowland and submontane forests, with vegetation adapted to the sea when approaching to the coast (e.g. mangroves and restinga) (Bihn et al. 2008). These vegetation differences together with the broader range of altitudes, probably increases the difference among ant communities of UPAF and Serra do Mar coastal forest ecoregion, making UPAF be more similar to Serra da Bodoquena. Of the total ant species found in the gallery forest of Iberá (15 species excluding morphospecies), a high proportion were shared with INP (Fig 5), including the most widespread species (e.g. *A. pilosum, Camponotus rufipes*, *Pachycondyla striata*, *S. louisianae*).

INP includes the native range of many ant species introduced in other regions of the world, including *L. humile, N. fulva*, *Pheidole obscurithorax, S. invicta* and *W. auropunctata* (McGlynn, 1999; Holway et al., 2002). However, most (if not all) source populations of these species are from further South along the corridor formed by the Paraná and Paraguay rivers from Buenos Aires to Formosa province (Calcaterra et al., 2015). Some of these species are not common within INP. For example, *L. humile* was collected in 1995 by J. M. Ramírez (IMML collection) but was not found in our surveys (Appendix). In fact, other species of *Linepithema* are much more common within the forest. *Solenopsis invicta* was often collected in open, disturbed environments in INP (e.g. near buildings and paths), but not collected in traps placed within the forest. Further ecological studies on these species in their native ranges could enlighten biological control methods for invaded areas and also help identify how abiotic and biotic factors select for traits that confer invasion success.

Our work contributes to the general knowledge of ant diversity in the extreme south of the AF (subtropical), one of their less studied regions, where we make a special effort identifying the majority of the capture species. Our results suggest that study sites between Upper Paraná and Serra do Mar Coastal Atlantic Forest ecoregion should be added to improve our knowledge of the longitudinal pattern and species turnover of ant species diversity in the AF. For INP, more dispersed collection sites would potentially targeted different habitat types, which would include unknown ant species. Regarding the conservation implications, the study of ant richness in UPAF is a valuable tool for the restoration and the sustainable development of non-protected areas of the Atlantic Forest in Misiones province, a region that offers real opportunities to preserve extensive areas and reserves connected by corridors, maintaining genetic exchange among different populations (Di Bitteti et al., 2003; Pais & Varanda, 2010).

Supplementary material:
http://periodicos.uefs.br/ojs/index.php/sociobiology/rt/suppFiles/724/0
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Appendix. Ant species collected from Iguazú National Park. Capture methodology is as follows: W (Winkler sacs), SB (subterranean baits), S (soil samples), HC (hand collecting), B (baits), P (pitfalls). Bibliography of species with previous records is provided. (*) new record only for Misiones province, (**) new record for Argentina. Abbreviations of entomological collections used in this study: MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; IMML the Institute and Museum Miguel Lillo, Tucumán Argentina; RBINS Royal Belgian Institute of Natural Sciences; LC Luis Calcaterra personal collection, Hurlingham, Buenos Aires, Argentina; AVS Andrew V. Suarez personal collection, University of Illinois, Urbana, USA; BMNH British Museum of Natural History, London, UK; CASC California Academy of Sciences, San Francisco, California, USA. Records collected by the authors and stored in the MACN are mark as MACN^A to make a distinction from old records review in the museum collection. The abbreviation cf. before species name that were not included in published taxonomic list, means proximity to that species but require more taxonomic research and were considered as a new record, but subjective to be test against literature.

	Source	Methodology	Collection
Amblyoponinae			
Amblyopone			
Prionopelta punctulata Mayr	Kempf 1972	W	IMML; RBINS
Stigmatomma elongatum Santschi *	Kusnezov 1953	W	AVS
Dolichoderinae			
Anillidris bruchi Santschi	Kempf 1972	HC	AVS
Azteca alfari Emery	Kempf 1972	HC	AVS;IMML
Azteca adrepens Forel **		B	MACN^A
Azteca lanuginosa Emery	Kusnezov 1978		IMML
Azteca luederwaldti Forel	Kempf 1972	W	IMML; RBINS
Dolichoderus bispinosus (Olivier)	Kempf 1959	HC, B	MACN^A; AVS
Dolichoderus lamellosus (Mayr)	Shattuck 1994		
Dorymyrmex brunneus Forel	Kempf 1972	HC	MACN^A
Linepithema humile (Mayr)	Cuezzo 1998		IMML
Linepithma iniquum (Mayr) **		P, HC, B	AVS; MACN^A
Linepithema micans (Forel)	Kempf 1972	P,W,SB,HC,B	AVS; IMML; LC; MACN^A
Linepithema neotropicum Wild **		HC	AVS
Linepithema pulex Wild	Wild 2007	W, SB, B	LC; MACN^A
Tapinoma atriceps Emery **		HC	AVS
Dorylinae			
Acanthostichus brevicornis Emery *	Kempf 1972	SB	MACN^A
Acanthostichus quadratus Emery	Brandão 1991	S	RBINS
Eciton dulcium Forel	Kempf 1972		IMML
Eciton vagans (Olivier)	Kusnezov 1978	HC	AVS; MACN^A
Labidus coecus (Latreille)	Kempf 1972	W, SB, HC	AVS, MACN^A; RBINS
Labidus praedator (Smith)	Kempf 1972	P, W, HC	LC, MACN^A
Labidus spininodis (Emery)*	Forel 1913	HC	AVS
Neivamyrmex punctaticeps (Emery)	Bruch 1914	HC	MACN, MACN^A
Neivamyrmex halidaii (Shuckard)	Borgmeier 1955		
Nomamyrmex esenbeckii (Westwood)	Kempf 1972		IMML
Ectatomminae			
Ectatomma edentatum Roger	Kempf 1972	P, W, HC, B	AVS; IMML; MACN^A
Ectatomma brunneum Smith	Kusnezov 1978		IMML
Gnamptogenys caelata Kempf **		W	RBINS
Gnamptogenys haenschi (Emery) **		HC	AVS
Gnamptogenys rastrata (Mayr) **		W, B	LC
Gnamptogenys striatula Mayr	Kempf 1972	P, W, HC, B, S	AVS; MACN^A; RBINS
Gnamptogenys sulcata (Smith)	Kusnezov 1978	HC	AVS; IMML

Appendix. Ant species collected from Iguazú National Park. Capture methodology is as follows: W (Winkler sacs), SB (subterranean baits), S (soil samples), HC (hand collecting), B (baits), P (pitfalls). Bibliography of species with previous records is provided. (*) new record only for Misiones province, (**) new record for Argentina. Abbreviations of entomological collections used in this study: MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; IMML the Institute and Museum Miguel Lillo, Tucumán Argentina; RBINS Royal Belgian Institute of Natural Sciences; LC Luis Calcaterra personal collection, Hurlingham, Buenos Aires, Argentina; AVS Andrew V. Suarez personal collection, University of Illinois, Urbana, USA; BMNH British Museum of Natural History, London, UK; CASC California Academy of Sciences, San Francisco, California, USA. Records collected by the authors and stored in the MACN are mark as MACN^A to make a distinction from old records review in the museum collection. The abbreviation cf. before species name that were not included in published taxonomic list, means proximity to that species but require more taxonomic research and were considered as a new record, but subjective to be test against literature (Cont.).

	Source	Methodology	Collection
Formicinae			
Brachymyrmex aphidicola Forel	Cuezzo 1998	P, W, SB, B	MACN^A
Brachymyrmex antennatus Santschi **		SB	MACN^A
Brachymyrmex cordemoyi Forel	Kempf 1972	W	MACN^A
Brachymyrmex cf. *depilis* Emery **		W	LC
Camponotus atriceps (Smith)	Kusnezov 1978	P	MACN^A
Camponotus cingulatus Mayr	Emery 1906	P, HC, B	IMML; MACN^A; RBINS
Camponotus crassus Mayr	Kempf 1972	W, B	IMML; MACN^A; RBINS
Camponotus depressus Mayr	WP Mackay record	HC	AVS; MACN^A
Camponotus cf. *landolti* Forel	WP Mackay record	P	MACN^A
Camponostus lespesii Forel	Kempf 1972	P	RBINS
Camponotus mus Roger	Kempf 1972	W	LC
Camponotus punctulatus andigenus Emery *	Kempf 1972	HC	RBINS
Camponotus renggeri Emery	Kempf 1972	P, HC	RBINS
Camponotus rufipes (Fabricius)	Kempf 1972	P, W, HC, B	AVS; IMML; LC; MACN^A; RBINS
Camponotus scissus Mayr	Kusnezov 1978	HC, P	MACN^A; RBINS
Camponotus sericeiventris (Guérin-Méneville)	Kempf 1972	P, HC, B	AVS; IMML; MACN^A; RBINS
Camponotus sexguttatus (Fabricius)			IMML
Camponotus substitutus Emery	Cuezzo 1998	HC	AVS
Camponotus trapezoideus Mayr	Kusnezov 1978	W	IMML; LC; RBINS
Myrmelachista cf.*nodifera* Mayr	Kusnezov 1978	HC	AVS
Nylanderia fulva (Mayr)	Bruch 1914	P, W, HC, B	AVS; MACN^A; LC
Heteroponerinae			
Heteroponera flava Kempf **		W, HC, P	AVS; MACN^A
Heteroponera dolo (Roger)	Kempf 1972	W, HC	IMML; MACN^A; RBINS
Heteroponera mayri Kempf **		P, W	LC; RBINS
Heteroponera microps Borgmeier **		SB	MACN^A
Myrmicinae			
Acromyrmex coronatus (Fabricius)	Kusnezov 1978	HC	AVS
Acromyrmex hispidus fallax Santschi	Kusnezov 1978	W, HC	RBINS
Acromyrmex laticeps (Emery)	Kempf 1972	HC, B	AVS; IMML; MACN^A
Acromyrmex niger (Smith)	Cuezzo 1998	P	MACN^A
Acromyrmex nigrosetosus (Forel) **		HC	MACN^A
Apterostigma pilosum Mayr	Kempf 1972	W	AVS; LC; RBINS
Atta sexdens (Linnaeus)	Kempf 1972	P, W, HC	AVS; IMML; MACN^A; RBINS
Basiceros disciger (Mayr) **		W	RBINS
Carebara cf. *brasiliana* Fernández**		W	AVS
Carebara brevipilosa Fernández **		P, W, SB	MACN^A

Appendix. Ant species collected from Iguazú National Park. Capture methodology is as follows: W (Winkler sacs), SB (subterranean baits), S (soil samples), HC (hand collecting), B (baits), P (pitfalls). Bibliography of species with previous records is provided. (*) new record only for Misiones province, (**) new record for Argentina. Abbreviations of entomological collections used in this study: MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; IMML the Institute and Museum Miguel Lillo, Tucumán Argentina; RBINS Royal Belgian Institute of Natural Sciences; LC Luis Calcaterra personal collection, Hurlingham, Buenos Aires, Argentina; AVS Andrew V. Suarez personal collection, University of Illinois, Urbana, USA; BMNH British Museum of Natural History, London, UK; CASC California Academy of Sciences, San Francisco, California, USA. Records collected by the authors and stored in the MACN are mark as MACN[A] to make a distinction from old records review in the museum collection. The abbreviation cf. before species name that were not included in published taxonomic list, means proximity to that species but require more taxonomic research and were considered as a new record, but subjective to be test against literature (Cont.).

	Source	Methodology	Collection
Myrmicinae (Continuation)			
Carebara urichi (Wheeler) **		W	AVS; RBINS
Cephalotes atratus (Linnaeus)	Kempf 1972		IMML; MACN
Cephalotes borgmeieri (Kempf)	Kempf 1951		
Cephalotes clypeatus (Fabricius)	Kempf 1972		IMML; MACN
Cephalotes depressus (Klug)	Kempf 1972		IMML
Cephalotes minutus (Fabricius)	Bruch 1914	W, HC	AVS; MACN[A]; RBINS
Cephalotes pusillus (Klug)	Kempf 1972	HC	AVS; IMML MACN[A]
Crematogaster arata Emery	Kempf 1972	HC	AVS
Crematogaster cisplatinalis Mayr			JTLC
Crematogaster corticicola Mayr	Kusnezov 1978		IMML
Crematogaster crinosa Mayr		HC	AVS;IMML; JTLC
Crematogaster erecta Mayr **		W, B	MACN[A]
Crematogaster nigropilosa Mayr **		P, W, B	AVS; MACN
Crematogaster montezumia Smith	Kempf 1972		IMML
Cyphomyrmex minutus Mayr **		P, W	AVS; MACN[A]
Cyphomyrmex olitor Forel *	Kempf 1972	W	LC
Cyphomyrmex rimosus (Spinola)	Kempf 1972	W, HC	AVS; RBINS
Hylomyrma balzani (Emery)	Kempf 1972	W	LC; MACN[A]
Hylomyrma reitteri (Mayr) **		W	LC; MACN[A]; RBINS
Lachnomyrmex plaumanni Borgmeier	Feitosa & Brandão 2008	W	RBINS
Megalomyrmex drifti Kempf **		W	LC; MACN
Megalomyrmex miri Brandão **		W	AVS
Megalomyrmex silvestrii Wheeler	Kempf 1972	W	RBINS
Monomorium pharaonis (Linnaeus)	Cuezzo 1998		IMML
Mycetarotes parallelus (Emery)	Kusnezov 1978 & Solomon et al. 2004	HC	AVS
Mycocepurus smithii (Forel)	Kusnezov 1978	P, W	MACN[A]
Myrmicocrypta foreli Mann *	Leponce et al. 2004	W	RBINS
Nesomyrmex asper (Mayr)	Kusnezov 1978		IMML
Nesomyrmex argentinus (Santschi) *	Kempf 1972	W	RBINS
Octostruma balzani (Emery)	Cuezzo 1999	P, W	AVS; MACN[A]
Octostruma iheringi (Emery) **		W, SB	AVS; MACN[A]
Octostruma rugifera (Mayr)	Kempf 1972	W	LC; RBINS
Oxyepoecus reticulatus Kempf *	Theunis et al. 2005	P, W	MACN[A]
Pheidole aberrans Mayr	Kempf 1972		MACN
Pheidole bergi Mayr *	Kempf 1972	W	LC; MACN
Pheidole bruchi Forel	Kempf 1972		MACN
Pheidole cf. *diligens* (Smith) **		B	MACN[A]

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	Source	Methodology	Collection
Myrmicinae (Continuation)			
Pheidole fimbriata Roger	Kempf 1972	P, W, SB	IMML; MACN[A]
Pheidole cf. *flavens* Roger	Kusnezov 1952	P, S	RBINS
Pheidole gertrudae Forel	Kempf 1972	W	IMML; RBINS
Pheidole guilelmimuelleri Forel	Kempf 1972	W	RBINS
Pheidole cf. *inversa* Forel **		W	LC
Pheidole jelskii Mayr *	Bruch 1914	HC	AVS; MACN[A]
Pheidole mosenopsis Wilson **		P, W, SB	AVS; MACN[A]
Pheidole nubila Emery *	Kempf 1972	P, W	RBINS
Pheidole obscurithorax Naves *	Kempf 1972	W, B	LC
Pheidole radoszkowskii Mayr	Vittar 2008	B	LC
Pheidole subarmata Mayr	Cuezzo 1998	W, SB, B	AVS; MACN[A]
Pheidole cf. *subarmata*		SB, B	MACN[A]
Pheidole rugatula Santschi	Kempf 1972		MACN
Pheidole rudigenis Emery	Kempf 1972	W	AVS
Pheidole vafra Santschi	Kusnezov 1952		IMML
Pogonomyrmex naegelli Emery	Kempf 1972	HC	AVS; MACN[A]
Procryptocerus hylaeus Kempf **		HC	AVS; MACN[A]
Procryptocerus regularis Emery	Kempf 1972	HC	MACN[A]
Rogeria scobinata Kugler *	Leponce et al. 2004	W, S	MACN[A]; RBINS
Solenopsis clytemnestra Emery	Kusnezov 1978	W, S	RBINS
Solenopsis invicta Buren *	Brandão 1991	HC	AVS;IMML
Solenopsis solenopsidis (Kusnezov)	Kusnezov 1962		
Solenopsis tridens Forel	Kempf 1972		IMML
Stegomyrmex vizottoi Diniz			CASC
Strumigenys cf. *siagodens* (Bolton) **		W	MACN[A]
Strumigenys crassicornis Mayr	Kempf 1972	W	AVS; MACN[A]
Strumigenys denticulata Mayr	Kempf 1972 & Cuezzo 1999	P, W, HC	AVS; IMML; MACN[A]; RBINS
Strumigenys elongata Roger	Cuezzo 1999	W, SB	AVS; IMML; MACN[A]; RBINS
Strumigenys hindenburgi (Forel)	Cuezzo 1999		IMML
Strumigenys louisianae Roger	Kempf 1972	P, W	LC; MACN[A];
Strumigenys ogloblini Santschi	Kempf 1972	W	RBINS
Strumigenys silvestrii Emery	Kempf 1972 & Cuezzo 1999	W	AVS
Strumigenys splendens (Borgmeier)			BMNH
Strumigenys subedentata Mayr **		W	AVS
Strumigenys tanymastax (Brown) **		W	AVS

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	Source	Methodology	Collection
Myrmicinae (Continuation)			
Wasmannia auropunctata (Roger)	Kempf 1972	P, W, SB, B	AVS; LC; MACN^{A};
Wasmannia rochai Forel **		W	LC
Wasmannia sp. n. **		B, W	LC
Ponerinae			
Anochetus neglectus Emery*	Brandão 1991	W	MACN^{A}
Dinoponera australis Emery	Kempf 1972	P, W, HC, B	AVS; LC; MACN^{A}; RBINS
Hypoponera clavatula (Emery)	Kempf 1972	W	MACN^{A}; RBINS
Hypoponera distinguenda (Emery)	Kusnezov 1978	P, W	AVS; MACN^{A}; RBINS
Hypoponera schmalzi (Emery) **		W	AVS
Hypoponera foreli (Mayr) **		W, SB	MACN^{A}; RBINS
Hypoponera opaciceps (Mayr)	Kempf 1972		IMML
Hypoponera opacior (Forel)	Kempf 1972	W	IMML
Hypoponera trigona (Mayr)	Kempf 1972	W	MACN^{A}
Odontomachus chelifer (Latreille)	Kempf 1972	P, HC, B	AVS; IMML; LC, MACN^{A}; RBINS
Odontomachus meinerti Forel *	Leponce et al. 2004	P, W, SB	MACN^{A}; RBINS
Neoponera agilis (Forel)	Kusnezov 1969		IMML
Neoponera crenata (Roger)	Kempf 1972	W, HC	AVS; IMML; RBINS
Neoponera marginata (Roger)	Cuezzo 1998	HC	MACN^{A}
Neoponera moesta Mayr	MacKay & MacKay 2010	HC	AVS; MACN^{A}
Neoponera villosa (Fabricius)	Kempf 1972	HC	IMML; AVS
Pachycondyla constricticeps MacKay & MacKay	MacKay & MacKay 2010	P	IMML; MACN^{A};
Pachycondyla harpax (Fabricius)	Kusnezov 1978; MacKay & MacKay 2010	P, W	MACN^{A}
Pachycondyla striata Smith	Kempf 1972	P, W, HC, B, S	AVS; IMML; LC; MACN^{A}; RBINS
Rasopone lunaris (Emery) **		W	MACN^{A}
Thaumatomyrmex mutilatus Mayr **		W	RBINS
Proceratiinae			
Discothyrea neotropica Bruch	Kempf 1972	W	AVS; RBINS
Pseudomyrmecinae			
Pseudomyrmex gracilis (Fabricius)	Kempf 1972	HC	AVS; MACN^{A};
Pseudomyrmex kuenckeli (Emery)*	Kempf 1972	HC	RBINS
Pseudomyrmex lizeri (Santschi) **		HC	AVS
Pseudomyrmex phyllophilus (Smith)	Kempf 1972	HC	AVS; IMML
Pseudomyrmex rufiventris (Forel)			IMML
Pseudomyrmex schuppi (Forel)	Kempf 1972	HC	IMML
Pseudomyrmex simplex (Smith) **		HC	AVS