Systematics and Biodiversity

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tsab20

Ants of Brazil: an overview based on 50 years of diversity studies

Rodrigo M. Feitosa, Gabriela P. Camacho, Thiago S. R. Silva, Mônica A. Ulysséa, Natalia Ladino, Aline M. Oliveira, Emília Z. Albuquerque, Fernando A. Schmidt, Carla R. Ribas, Anselmo Nogueira, Fabrício B. Baccaro, Antônio C. M. Queiroz, Wesley Dáttilo, Rogério R. Silva, Jean C. Santos, Ananza M. Rabello, Maria Santina De C. Morini, Yves P. Quinet, Kleber Del-Claro, Ana Y. Harada, Karine S. Carvalho, Tathiana G. Sobrinho, Aline B. Moraes, André B. Vargas, Helena Maura Torezan-Silingardi, Jorge Luiz P. Souza, Tatianne Marques, Thiago Izzo, Denise Lange, Iracenir A. Santos, Larissa Nahas, Lucas Paolucci, Stela A. Soares, Cinthia B. Costa-Milanez, Eduardo Diehl-Fleig, Renata B. F. Campos, Ricardo Solar, Tiago Frizzo & Wesley Darocha

To cite this article: Rodrigo M. Feitosa, Gabriela P. Camacho, Thiago S. R. Silva, Mônica A. Ulysséa, Natalia Ladino, Aline M. Oliveira, Emília Z. Albuquerque, Fernando A. Schmidt, Carla R. Ribas, Anselmo Nogueira, Fabrício B. Baccaro, Antônio C. M. Queiroz, Wesley Dáttilo, Rogério R. Silva, Jean C. Santos, Ananza M. Rabello, Maria Santina De C. Morini, Yves P. Quinet, Kleber Del-Claro, Ana Y. Harada, Karine S. Carvalho, Tathiana G. Sobrinho, Aline B. Moraes, André B. Vargas, Helena Maura Torezan-Silingardi, Jorge Luiz P. Souza, Tatianne Marques, Thiago Izzo, Denise Lange, Iracenir A. Santos, Larissa Nahas, Lucas Paolucci, Stela A. Soares, Cinthia B. Costa-Milanez, Eduardo Diehl-Fleig, Renata B. F. Campos, Ricardo Solar, Tiago Frizzo & Wesley Darocha (2022) Ants of Brazil: an overview based on 50 years of diversity studies, Systematics and Biodiversity, 20:1, 1-27, DOI: 10.1080/14772000.2022.2089268

To link to this article: https://doi.org/10.1080/14772000.2022.2089268

View supplementary material

Published online: 20 Jul 2022.

Submit your article to this journal

Article views: 569

View related articles

View Crossmark data

Citing articles: 4 View citing articles

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=tsab20

Systematics and Biodiversity (2022), **20(1)**: 2089268

Taylor & Francis
Taylor & Francis Group

Research Article

Check for updates

Ants of Brazil: an overview based on 50 years of diversity studies

RODRIGO M. FEITOSA[1], GABRIELA P. CAMACHO[2,3], THIAGO S. R. SILVA[4], MÔNICA A. ULYSSÉA[3], NATALIA LADINO[1], ALINE M. OLIVEIRA[4], EMÍLIA Z. ALBUQUERQUE[5,6], FERNANDO A. SCHMIDT[7], CARLA R. RIBAS[8,9], ANSELMO NOGUEIRA[10], FABRÍCIO B. BACCARO[11], ANTÔNIO C. M. QUEIROZ[8], WESLEY DÁTTILO[12], ROGÉRIO R. SILVA[13], JEAN C. SANTOS[14], ANANZA M. RABELLO[15], MARIA SANTINA DE C. MORINI[16], YVES P. QUINET[17], KLEBER DEL-CLARO[18], ANA Y. HARADA[19], KARINE S. CARVALHO[20], TATHIANA G. SOBRINHO[21], ALINE B. MORAES[22], ANDRÉ B. VARGAS[23], HELENA MAURA TOREZAN-SILINGARDI[18], JORGE LUIZ P. SOUZA[24], TATIANNE MARQUES[25], THIAGO IZZO[26], DENISE LANGE[27], IRACENIR A. SANTOS[28], LARISSA NAHAS[18], LUCAS PAOLUCCI[29], STELA A. SOARES[30], CINTHIA B. COSTA-MILANEZ[31], EDUARDO DIEHL-FLEIG[32], RENATA B. F. CAMPOS[33], RICARDO SOLAR[34], TIAGO FRIZZO[35] & WESLEY DAROCHA[36,37]

[1]Laboratório de Sistemática e Biologia de Formigas, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
[2]Center for Integrative Biodiversity Discovery, Museum für Naturkunde, Berlin, Germany
[3]Laboratório de Hymenoptera, Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil
[4]The Insect Biodiversity and Biogeography Laboratory, School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China
[5]AntLab, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
[6]Rabeling Lab, School of Life Sciences, Arizona State University, Tempe, AZ, USA
[7]Laboratório de Ecologia de Formigas, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Acre, Brazil
[8]Laboratório de Ecologia de Formigas, Departamento de Ecologia e Conservação, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil
[9]Lancaster Environment Centre, Lancaster University, Lancaster, UK
[10]Laboratório de Interações Planta-Animal, Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, São Bernardo do Campo, São Paulo, Brazil
[11]Departamento de Biologia, Universidade Federal do Amazonas, Manaus, Amazonas, Brazil
[12]Red de Ecoetología, Instituto de Ecología AC, Xalapa, Veracruz, Mexico
[13]Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil
[14]Laboratório de Ecologia & Biodiversidade, Departamento de Ecologia, Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil
[15]Instituto de Estudos do Xingu, Universidade Federal do Sul e Sudeste do Pará, São Félix do Xingu, Pará, Brazil
[16]Laboratório de Mirmecologia do Alto Tietê, Núcleo de Ciências Ambientais, Universidade de Mogi das Cruzes, Mogi das Cruzes, São Paulo, Brazil
[17]Laboratório de Entomologia, Departamento de Biologia, Universidade Estadual do Ceará, Fortaleza, Ceará, Brazil
[18]Laboratório de Ecologia Comportamental e de Interações, Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil
[19]Coordenação em Zoologia, Museu Paraense Emilio Goeldi, Belém, Pará, Brazil
[20]Laboratório de Ecologia, Departamento de Ciências Naturais, Universidade Estadual do Sudoeste da Bahia, Vitória da Conquista, Bahia, Brazil
[21]Laboratório de Sistemática e Ecologia de Insetos, Departamento de Ciências Agrárias e Biológicas, Universidade Federal do Espírito Santo, São Mateus, Espírito Santos, Brazil
[22]Prefeitura Municipal de Novo Hamburgo, Novo Hamburgo, Rio Grande do Sul, Brazil
[23]Centro Universitário de Volta Redonda, UniFOA, Volta Redonda, Rio de Janeiro, Brazil
[24]Instituto Nacional da Mata Atlântica, INMA, Santa Teresa, Espírito Santo, Brazil

Correspondence to: Rodrigo M. Feitosa. E-mail: rsmfeitosa@gmail.com

ISSN 1477-2000 print / 1478-0933 online
© The Trustees of the Natural History Museum, London 2022. All Rights Reserved.
https://dx.doi.org/10.1080/14772000.2022.2089268

Published online 20 Jul 2022

[25]Laboratório de Ecologia Aplicada e Citogenética, Instituto Federal do Norte de Minas Gerais – IFNMG, Salinas, Minas Gerais, Brazil
[26]Laboratório de Ecologia de Comunidades, Departamento de Botânica e Ecologia, Universidade Federal do Mato Grosso, Cuiabá, Mato Grosso, Brazil
[27]Universidade Tecnológica Federal do Paraná, Santa Helena, Paraná, Brazil
[28]Centro de Formação Interdisciplinar, Universidade Federal do Oeste do Pará, Santarém, Pará, Brazil
[29]Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil
[30]Secretaria Estadual de Educação de Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil
[31]Departamento de Biologia, Instituto de Ciências Exatas e Biológicas, Universidade Federal de Ouro Preto, Ouro Preto, Minas Gerais, Brazil
[32]In Memoriam. São Leopoldo, Rio Grande do Sul, Brazil
[33]Laboratório de Ecologia, Ambiente e Território, PPG Gestão Integrada do Território, Universidade Vale do Rio Doce, Governador Valadares, Minas Gerais, Brazil
[34]Centro de Síntese Ecológica e Conservação, Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil
[35]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília, Brasília, Distrito Federal, Brazil
[36]Laboratório de Mirmecologia (CPDC), Centro de Pesquisa do Cacau (CEPEC), Ilhéus, Bahia, Brazil
[37]Laboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

(Received 23 December 2021; accepted 9 June 2022)

Despite the historical efforts to list and organize the taxonomic knowledge about the Brazilian ant fauna, the most diverse in the world, several gaps regarding species distribution data and sampling coverage persist. In an attempt to fill some of these gaps, we here apply a scientometric approach to provide an updated overview of the ants of Brazil based on formal publications on ant diversity in the Brazilian territory. In the last 50 years, ant diversity studies in Brazil revealed 1130 species, corresponding to around 70% of the species known to occur in the country. The Brazilian biomes with the highest number of described species recorded were, respectively, the Amazon Forest (716 species), Atlantic Forest (657 species), Cerrado (389 species), Caatinga (185 species), Pantanal (143 species), and Pampa (86 species). Considering the number and frequency of unidentified species, the genera *Azteca*, *Hypoponera, Pheidole,* and *Solenopsis* represent the main knowledge frontiers regarding taxonomic resolution, with more than 80% of their records associated with morphospecies codes in diversity studies in Brazil. Moreover, around 7.5% of the papers presented inconsistences in their species lists regarding the validity of taxonomic names, and we found studies for which some taxa records are geographically implausible. Besides demonstrating the importance of ecological publications to the ant diversity knowledge in Brazil, our findings highlight a strong sampling bias in ant occurrence data in the country, with species records unevenly distributed across Brazilian biomes. In short, our results constitute valuable information for future projects on ant taxonomy and surveying in Brazilian natural areas.

Key words: ant taxonomy, biological surveys, Brazilian biomes, conservation ecology, fauna inventories, Neotropical Region, taxonomic validation

Introduction

Brazil is the fifth largest country in the world, with more than 8.5 million km^2. Its territory extends along most of the eastern coast of South America and occupies much of the continent's interior. The Brazilian diversity of geological formations and vegetation cover types is equally impressive, with six official biomes (or phytogeographic domains) currently recognized, namely the Amazon Forest, Atlantic Forest, Cerrado (Brazilian savanna), Caatinga (seasonal tropical dry forest), Pantanal (wetlands), and Pampa (subtropical grasslands) (MMA, 2020). Despite being considered geographic and ecological units by the government's environmental agencies, the Brazilian biomes encompass a remarkable heterogeneity in climate, vegetation, topography, soil, and hydrography (Ab'Saber, 2003; IBGE, 2012).

This heterogeneity of tropical and subtropical habitats is reflected in the species diversity known to Brazil, considered the highest in the world (CBD, 2021; Lewinsohn & Prado, 2005; Moura & Jetz, 2021). However, as observed for different tropical areas globally, Brazilian biodiversity faces an unprecedented threat represented mainly by the impact of human actions in the environment (Giam, 2017; Rosa et al., 2012; UN, 2021). In this scenario, effective conservation initiatives are urgently needed to measure and protect biodiversity. On the other hand, such efforts are highly dependent on surveys and analyses of the species composition of natural systems on different spatial and temporal scales, a task broadly based on local diversity studies (Heberling et al., 2021; Lortie & Svenning, 2015).

When it comes to the study of Brazilian biodiversity, ants (Formicidae), stands out. With their origin estimated at around 110 million years ago, ants have become the most speciose and ecologically diverse group of social insects (Borowiec, 2019). Along with termites, ants represent about 2% of the insect species described to date but can comprise more than 50% of the insect biomass in the world's tropical forests (Wilson & Hölldobler, 2005). Over the past 140 years, the ecological, economic, and sanitary importance of ants in the Brazil's diverse natural and anthropic environments has been extensively studied by a remarkable number of specialists (Formigas do Brasil, 2021; Lucky et al., 2020), which have greatly improved our knowledge on ant diversity in the country. Currently, Brazil is the most diverse country in the world regarding the number of ant species, with previous studies showing that about one-third of the described genera (117 out of 345) and one-tenth of the described species of the planet (about 1500 out of 14000) (Bolton, 2022; Dunn et al., 2007) occur in the country. As an ecologically dominant group in any ecosystem on Earth, from tundra to tropical forests (Kaspari, 2005), ants maintain ecological interactions with many other organisms and, consequently, are fundamental in the functional processes of those ecosystems, such as regulating the abundance of other arthropods, dispersing seeds, and promoting changes in the physical structure of environments (Elizalde et al., 2020; Folgarait, 1998). Not surprisingly, community ecology is the main research topic involving ants in Brazil (Schmidt et al., 2022).

Pioneering ant inventories in Brazil date back from the end of the XIX century (Emery, 1888; Mayr, 1878), with an exponential increase by the second half of the XX century and the first decades of the XXI century (Schmidt et al., 2022). With the rise in the number of projects involving ant surveys in Brazil, our understanding of the taxonomic diversity of this group in different Brazilian ecosystems has also greatly improved (Baccaro et al., 2015). However, despite the recent efforts to list and organize the taxonomic information about ant species in different regions and ecosystems of the country (e.g., Albuquerque et al., 2021; Dröse et al., 2017; Jory & Feitosa, 2020; Leal et al., 2018; Prado et al., 2019; Schmidt et al., 2020; Silva et al., 2022), knowledge about ant distribution and diversity is largely incomplete for a significant part of the Brazilian territory (Divieso et al., 2020; Guénard et al., 2012). This scenario hampers the advance in our understanding of drivers and spatial patterns of ant biodiversity and precludes the improvement of the taxonomic resolution, especially in areas where ant diversity is considerably high.

Here we summarize the occurrence data of all ant species recorded in Brazil based on a comprehensive data set formed by papers containing any aspect of ant diversity in the country. Based on this information, we aimed to explore to what extent the number of ant taxa formally recorded for Brazil in ant diversity studies contributes to the knowledge of the species described for the country and, consequently, to the world. Also, we identify the most common taxa (genera and species) recorded in the biomes of Brazil in the last five decades and explore the main frontiers of taxonomic knowledge for Brazilian ants based on the proportion between the taxa nominally identified and those treated as morphospecies.

The records gathered here hold essential information on the distribution of ants in the Brazilian biomes and, as far as we know, comprise the largest data set temporally organized on ant occurrences in a country explicitly based on ant surveys. Our findings can stimulate projects on poorly studied localities in Brazil, especially those under imminent risk of habitat loss, helping formulate conservation strategies. Moreover, by revealing the knowledge gaps about the taxonomic resolution of ants in Brazil, this study can guide new proposals of taxonomic investigation on neglected ant taxa and the formation of future generations of Brazilian myrmecologists in the regions where they are most needed.

Material and methods

Literature searching

This survey considered papers explicitly dealing with ant diversity in the Brazilian biomes (Amazon Forest, Atlantic Forest, Cerrado, Caatinga, Pantanal, and Pampas) as defined by the Brazilian Ministry of Environment (MMA, 2021). We considered 'ant diversity' in a broad sense, as proposed by Schmidt et al. (2022), including myrmecological surveys; ant checklists in ecoregions, conservation units and geopolitical provinces (states and municipalities); ecological interactions; behavior biology; studies on ant sampling techniques; and ecological aspects of ant assemblages (community, population, evolutionary, and conservation ecology). The keywords used on searches included 'ant + Brazil' or '*formiga* + *Brasil*' (in Portuguese). We also performed additional searches employing these same keywords followed by the name of the Brazilian biome both in Portuguese and English. The articles were then sorted according to their sampling localities, and classified in a particular biome when conducted strictly within its boundaries. For those ant diversity studies whose sampling was carried in more than one biome and in transition areas between biomes we applied the category 'multibiome'. Our papers classification system resulted in seven categories regarding the location where the samplings or experiments were carried out (see Supplemental Material Table S1).

Three online databases were used for the literature surveying, specifically Web of Science (http://www.webofknowledge.com), SciELO (https://scielo.org/), and Scopus (https://www.scopus.com). Papers fitting our broad concept of 'ant diversity' from personal databases of authors that were not retrieved in the searches were manually included in the data set. At the end of the searches in each online and personal database, a round of verification for papers adequacy and redundancy was performed. Uncorrected proofs, online first versions of accepted articles, and preprints were replaced by the final versions of papers whenever possible. Books, book chapters, event presentations, technical reports, taxonomic papers, data papers, studies on a single focal taxon, and graduate dissertations were excluded from the final database.

Ant species surveying

Different coauthors performed a literature search in different moments from 2012 to 2021. These authors were also responsible for extracting the taxonomic information from the papers obtained, including the ant taxa names listed therein. In other words, the data presented here refer only to those diversity papers that provided a list including ant genera or species names. We considered a list as 'present' in the cases in which the species were included in a taxonomic table, either in the main text or supplementary material, or were simply mentioned sequentially in the text.

Since different coauthors performed searches over the nine years of the survey, inconsistencies in taxa retrieving and databasing were expected. To eliminate such potential conflicts, we went through different rounds of cross-validation of the data set performed by six ant taxonomists: R. M. Feitosa, G. P. Camacho, T. S. R. Silva, M. A. Ulysséa, N. Ladino, and A. M. Oliveira, all authors of the present paper. In the first evaluation round, papers published from 1970 (the first year represented in our data set) to 2012 were individually reassessed by three of these taxonomists. The taxonomic data entries were then compared, and all mismatches corrected. Later, the first author re-assessed the papers published from 2012 to 2021 and corrected any eventual discrepancy in the resulting spreadsheet. Lastly, these six taxonomists individually inspected the final version of the resulting taxa list and discussed how to deal with putative uncertainties until consensus was achieved.

For purposes of compatibility between the species lists of studies published in the survey interval (since 1970), the taxonomic names for the nominally identified ant species were updated based on the most current classification (Bolton, 2022), so that all names in our final species list are taxonomically accurate. Regarding the records classified into morphospecies in the articles, it was not possible to retrieve accurate information regarding the species records of some genera, since historical changes in the taxonomic status of some taxa prevent species not identified in the literature from being assigned to currently valid genera. This occurred mainly in cases where recent works have reclassified species from some genera by proposing new combinations in different valid, new, or revived genera (e.g., Camacho et al., 2022; LaPolla et al., 2010; Schmidt & Shattuck, 2014; Solomon et al., 2019; Sosa-Calvo et al., 2017).

For the transcription of taxon names from the surveyed articles to our final species list, small typos (in the original articles, not in our spreadsheets) were disregarded. If the taxon name had a spelling error due to a single altered letter, present or absent, the spelling was corrected in our final spreadsheet. This is because minor typos may have been introduced during the review process of articles or proofs and do not affect the correct identification of names. Writing errors in scientific names that exceeded one letter or names that referred to non-existent taxa were noted. The same was done for geographically spurious records. That is, genera and species that could in no way have been reported to Brazil, based on their current distribution validated by the most recent taxonomic literature for each genus or species. This filtering based on geographic occurrence allowed us to draw up the list of taxa that should be disregarded from the Brazilian genera and species record in the literature. The spurious records identified here were eliminated from our list of taxa occurrence and richness as well as the scientific names related to them.

To assess the taxonomic resolution of species lists in works involving ant diversity in Brazil, we created three categories of scientific names: (1) 'nominal species', including all the taxa identified to the specific or subspecific level in the papers surveyed; (2) 'species associated with valid names', including those species not formally named but considered similar to extant valid species or belonging to species groups, and usually recognized by traditional taxonomic abbreviations (e.g., aff., cf., pr., nr., and gr.); and (3) 'morphospecies', comprising the species for which identification to the specific level was not reached and are usually characterized by sequential codes (numbers or letters) in the original papers. Although the species associated with valid names are in practice 'morphospecies', they represent an additional level of taxonomic 'confidence' on the part of the identifier/author, and this data can be informative according to the purpose of the studies that will use the information provided by these lists (Silva et al., 2022). The final data set with nominal species, species associated with valid names and morphospecies per article surveyed can be consulted in Supplemental Material Tables S2–S4)

The richness of ant genera and species for each Brazilian biome considers only those studies in our survey which sampling was carried entirely within the boundaries of a single biome. This limitation occurred because studies with extensive collections included the data of two or more biomes (i.e. multibiome category) in a unique pooled species list, with taxa not necessarily classified by biomes, preventing us from accurately assessing this information. To individually access the species list of studies with extensive samplings in Brazil see the multibiome category in our Supplemental Material Tables S2–S4.

Finally, we are aware that some records listed here may not have accurately validated taxa identity. Different publications on ant species occurrences have dealt with taxonomic inaccuracy under distinct criteria for the record validation (e.g., Albuquerque et al., 2021; Franco et al., 2019; Silva et al., 2022). Although it is undoubtedly fundamental to interrupt the transmission of imprecise occurrence data in the literature by correcting historical errors involving taxa distribution, that effort is beyond this work. We could not individually check each taxa identification in the species lists due to the time expended in the present survey and the number of papers gathered. Thus, for all purposes, the names listed in our final data set are of total responsibility of the original authors. Still, taxonomically inexistent names and records of taxa not previously recorded for Brazil or neighboring countries were explicitly discussed here.

Analyses

To visualize the patterns of ant diversity in Brazil we used basic analytic procedures frequently employed in descriptive statistics. We calculated the absolute numbers for each category described in the previous section, based on the data retrieved from the bibliographic collection (see Supplemental Material.) and plotted the results obtained in trend graphs. Analysis and plotting were performed in an open-source spreadsheet management system. A heatmap depicting the number of genera, number of species, number of species records and number of publications recorded for each of the six biomes in Brazil was created using the function 'heatmap' natively provided in R v.3.6.3 (R Core Team, 2021).

Results

A total of 491 papers on Brazilian ant diversity was retrieved both from online repositories and personal databases, published from 1970 to 2021. The cross-validation rounds excluded 22 papers from our data set (Supplemental Material Table S5). From the 469 remaining papers, 402 (86%) presented an ant taxa list (including subfamilies, genera, species, and subspecies) from which we extracted the occurrence data analyzed in this study. To access the complete non-taxonomic data, including geographical information, from the papers surveyed here (from 1970 to 2020, including the studies excluded from this paper), see the supporting information in Schmidt et al. (2022).

Brazilian ant diversity

In total, 27525 ant records were obtained from the taxa lists of the papers surveyed here. From these, 12 109 (44%) refer to nominal species (Table 1), 542 (2%) are records of species associated with valid names, and 14874 (54%) represent taxa identified as morphospecies. Species richness per paper as defined by the number of species/morphospecies in each study varied from two to 526. Studies on Brazilian ant diversity revealed a total of 1130 nominal species and eight subspecies distributed in 106 genera and 11 subfamilies (Supplemental Material Table S2).

Considering the number of records by taxa (including nominal and unidentified species) (Table 2), the most frequently recorded subfamily was Myrmicinae (14551 records; 52.8%), followed by Formicinae (4503; 16.3%), Ponerinae (3148; 11.4%), Dolichoderinae (1745; 6.3%), Ectatomminae (1542; 4.1%), Pseudomyrmecinae (1108; 4%), Dorylinae (672; 2.5%), and Amblyoponinae (109; 0.4%), while Proceratiinae, Paraponerinae, and Agroecomyrmecinae appear with less than 100 records each (Fig. 1). Within nominal species (morphospecies excluded), Myrmicinae was again the richest subfamily in the data set (612 species/subspecies), followed by Formicinae (131), Ponerinae (120), Dolichoderinae (82), Ectatomminae (72), Pseudomyrmecinae (49), Dorylinae (47), Amblyoponinae (8), and Proceratiinae (7), while Agroecomyrmecinae and Paraponerinae appear with one species each (Table 3).

Among the 106 ant genera listed in Brazilian ant diversity studies, *Pheidole* (4617 records), *Camponotus* (2869), *Solenopsis* (1674), *Crematogaster* (1419), *Pseudomyrmex* (1102), *Strumigenys* (907), *Hypoponera* (854), *Brachymyrmex* (752), *Cephalotes* (729), and *Ectatomma* (663), are the ten most frequent (including nominal species and morphospecies), accounting for 56% of all records (Fig. 2). Regarding the number of species (morphospecies excluded), the richest genus was *Pheidole*, with 124 recorded species. Genera with more than 20 recorded species/subspecies included *Camponotus* (87), *Strumigenys* (71), *Crematogaster*

Table 1. Nominal (unidentified species excluded) ant records (frequency of occurrence) by subfamily and genera in diversity studies in the Brazilian biomes over the last 50 years.

Ant Taxa/Biome	Atlantic Forest	Amazon Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome
Agroecomyrmecinae	0	2	0	0	0	0	0
Tatuidris	0	2	0	0	0	0	0
Amblyoponinae	48	16	6	1	0	2	3
Fulakora	30	2	4	0	0	2	1
Prionopelta	18	14	2	1	0	0	2
Dolichoderinae	243	263	111	52	8	16	90
Azteca	24	22	9	2	0	4	4
Dolichoderus	56	185	25	4	0	3	17
Dorymyrmex	19	17	23	29	2	1	27
Forelius	2	3	13	8	2	1	9
Gracilidris	0	4	3	0	0	1	3
Linepithema	120	11	33	7	4	5	24
Tapinoma	22	21	5	2	0	1	6
Dorylinae	130	220	43	13	2	9	36
Acanthostichus	5	11	0	1	0	0	2
Cheliomyrmex	0	2	0	1	0	0	0
Cylindromyrmex	4	0	0	0	0	0	0
Eciton	23	64	3	1	0	2	9
Labidus	64	63	24	6	2	5	16
Leptanilloides	0	1	0	0	0	0	0
Neivamyrmex	11	48	12	3	0	1	6
Neocerapachys	15	7	1	0	0	1	1
Nomamyrmex	3	24	3	1	0	0	2
Sphinctomyrmex	5	0	0	0	0	0	0
Ectatomminae	390	351	193	58	12	24	95
Acanthoponera	3	2	3	2	0	0	3
Alfaria	9	9	0	0	0	0	3
Bazboltonia	5	0	0	0	0	0	0
Ectatomma	139	136	160	36	7	20	53
Gnamptogenys	41	120	16	9	2	2	13
Heteroponera	80	0	1	1	2	0	2
Holcoponera	68	62	12	10	1	1	16
Poneracantha	17	15	0	0	0	0	4
Typhlomyrmex	28	7	1	0	0	1	1
Formicinae	597	486	405	108	41	49	210
Acropyga	28	9	0	0	0	0	5
Brachymyrmex	83	35	15	6	5	3	18
Camponotus	399	376	374	95	32	41	158
Gigantiops	0	28	0	0	0	0	3
Myrmelachista	32	2	7	2	2	0	10
Nylanderia	33	27	2	2	2	4	12
Paratrechina	22	9	7	3	0	1	4
Myrmicinae	1840	1780	690	191	148	87	554
Acanthognathus	38	6	3	0	0	0	1
Acromyrmex	136	32	37	17	67	5	42
Allomerus	0	28	0	0	0	0	0
Amoimyrmex	0	0	0	0	9	0	2
Apterostigma	21	35	1	0	0	3	4
Atta	45	44	37	14	2	4	30
Basiceros	23	5	0	1	0	1	4
Blepharidatta	1	19	3	0	0	0	4
Cardiocondyla	17	4	5	1	0	1	6
Carebara	28	25	8	0	0	1	7
Cephalotes	111	131	161	43	1	17	64
Crematogaster	131	323	68	27	8	11	52
Cryptomyrmex	5	2	0	0	0	1	0
Cyatta	0	0	3	0	0	0	0
Cyphomyrmex	76	73	19	13	2	3	13
Daceton	0	16	0	0	0	0	2

(*continued*)

Table 1. Continued.

Ant Taxa/Biome	Atlantic Forest	Amazon Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome
Diaphoromyrma	1	0	0	0	0	0	0
Eurhopalothrix	13	5	0	0	0	0	2
Hylomyrma	55	29	4	4	0	1	7
Kalathomyrmex	0	2	3	1	0	0	2
Lachnomyrmex	11	8	0	1	0	0	0
Megalomyrmex	66	74	6	1	0	2	3
Monomorium	33	24	4	1	0	1	11
Mycetagroicus	0	0	4	0	0	0	0
Mycetarotes	12	8	9	0	0	0	3
Mycetomoellerius	21	29	23	1	2	0	10
Mycetophylax	33	9	8	0	0	2	4
Mycocepurus	43	29	31	0	1	4	7
Myrmicocrypta	4	3	3	0	0	0	0
Nesomyrmex	21	15	19	5	0	0	8
Ochetomyrmex	4	46	8	0	1	1	7
Octostruma	79	42	12	4	0	4	6
Oxyepoecus	55	7	3	0	0	0	8
Paratrachymyrmex	7	31	4	0	0	0	3
Phalacromyrmex	3	0	0	0	0	0	0
Pheidole	191	228	74	14	35	8	109
Pogonomyrmex	11	12	15	3	5	1	9
Procryptocerus	34	21	1	0	0	0	6
Rhopalothrix	1	0	0	0	0	0	0
Rogeria	42	41	4	1	0	2	12
Sericomyrmex	9	9	6	0	0	0	6
Solenopsis	94	70	24	26	7	6	32
Stegomyrmex	8	2	0	0	0	0	1
Strumigenys	241	202	41	3	2	5	34
Tetramorium	10	6	1	1	0	0	4
Tranopelta	4	8	5	0	0	0	3
Trichomyrmex	1	0	0	0	0	0	0
Wasmannia	101	73	33	9	6	3	26
Xenomyrmex	0	4	0	0	0	0	0
Paraponerinae	1	22	2	0	0	0	2
Paraponera	1	22	2	0	0	0	2
Ponerinae	632	807	188	49	18	25	122
Anochetus	47	90	11	3	0	1	12
Centromyrmex	1	14	3	0	0	0	2
Cryptopone	3	3	1	0	0	0	1
Dinoponera	5	10	7	13	0	1	6
Hypoponera	47	9	4	0	5	1	7
Leptogenys	23	47	0	0	0	0	2
Mayaponera	26	53	1	0	0	0	4
Neoponera	134	218	59	8	5	8	32
Odontomachus	173	203	62	18	2	9	26
Pachycondyla	132	101	31	4	6	3	23
Platythyrea	1	13	0	1	0	0	3
Pseudoponera	11	14	3	0	0	0	3
Rasopone	13	14	2	0	0	2	1
Simopelta	5	9	0	0	0	0	0
Thaumatomyrmex	11	9	4	2	0	0	0
Proceratiinae	35	15	0	0	0	1	2
Discothyrea	29	15	0	0	0	0	2
Probolomyrmex	0	0	0	0	0	1	0
Proceratium	6	0	0	0	0	0	0
Pseudomyrmecinae	173	127	132	46	8	18	61
Myrcidris	0	2	0	0	0	0	0
Pseudomyrmex	173	125	132	46	8	18	61
Formicidae	30	0	1	0	0	0	0
Total	**4089**	**4089**	**1770**	**518**	**237**	**231**	**1175**

Table 2. Ant records (frequency of occurrence) including unidentified species (species associated with valid names and morphospecies) in Brazilian diversity studies over the last 50 years, with the proportion (%) of unidentified species per ant taxa.

Taxa	Nominal species	Species associated with valid names	Morphospecies	Total	Total unidentified	% unidentified
Agroecomyrmecinae	2	0	0	2	0	0.0
Tatuidris	2	0	0	2	0	0.0
Amblyoponinae	76	2	31	109	33	30.3
Fulakora	39	0	16	55	16	29.1
Prionopelta	37	2	15	54	17	31.5
Dolichoderinae	783	50	912	1745	962	55.1
Azteca	65	12	252	329	264	80.2
Dolichoderus	290	13	130	433	143	33.0
Dorymyrmex	118	11	188	317	199	62.8
Forelius	38	1	23	62	24	38.7
Gracilidris	11	0	0	11	0	0.0
Linepithema	204	12	203	419	215	51.3
Tapinoma	57	0	109	166	109	65.7
Dorylinae	453	7	212	672	219	32.6
Acanthostichus	19	0	19	38	19	50.0
Cheliomyrmex	3	0	0	3	0	0.0
Cylindromyrmex	4	0	1	5	1	20.0
Eciton	102	0	26	128	26	20.3
Labidus	180	0	50	230	50	21.7
Leptanilloides	1	0	0	1	0	0.0
Neivamyrmex	81	5	91	177	96	54.2
Neocerapachys	25	1	0	26	1	3.8
Nomamyrmex	33	0	14	47	14	29.8
Sphinctomyrmex	5	0	2	7	2	28.6
Ectatomminae	1123	30	389	1542	419	27.2
Acanthoponera	13	0	7	20	7	35.0
Alfaria	21	0	0	21	0	0.0
Bazboltonia	5	0	0	5	0	0.0
Ectatomma	551	3	109	663	112	16.9
Gnamptogenys	203	12	218	433	230	53.1
Heteroponera	86	0	34	120	34	28.3
Holcoponera	170	10	0	180	10	5.6
Poneracantha	36	3	0	39	3	7.7
Typhlomyrmex	38	1	21	60	22	36.7
Formicinae	1896	84	2523	4503	2607	57.9
Acropyga	42	2	40	84	42	50.0
Brachymyrmex	165	10	577	752	587	78.1
Camponotus	1475	52	1342	2869	1394	48.6
Gigantiops	31	0	3	34	3	8.8
Myrmelachista	55	3	115	173	118	68.2
Nylanderia	82	16	208	306	224	73.2
Paratrechina	46	1	217	264	218	82.6
Myrmicinae	5290	303	8958	14551	9261	63.6
Acanthognathus	48	0	10	58	10	17.2
Acromyrmex	336	11	134	481	145	30.1
Allomerus	28	1	7	36	8	22.2
Amoimyrmex	11	0	0	11	0	0.0
Apterostigma	64	19	195	278	214	77.0
Atta	176	1	64	241	65	27.0
Basiceros	34	0	31	65	31	47.7
Blepharidatta	27	0	11	38	11	28.9
Cardiocondyla	34	0	10	44	10	22.7
Carebara	69	8	97	174	105	60.3
Cephalotes	528	9	192	729	201	27.6
Crematogaster	620	50	749	1419	799	56.3
Cryptomyrmex	8	0	0	8	0	0.0
Cyatta	3	0	0	3	0	0.0

(*continued*)

Table 2. Continued.

Taxa	Nominal species	Species associated with valid names	Morphospecies	Total	Total unidentified	% unidentified
Cyphomyrmex	199	16	275	490	291	59.4
Daceton	18	0	1	19	1	5.3
Diaphoromyrma	1	0	0	1	0	0.0
Eurhopalothrix	20	0	14	34	14	41.2
Hylomyrma	100	5	76	181	81	44.8
Kalathomyrmex	8	0	3	11	3	27.3
Lachnomyrmex	20	0	12	32	12	37.5
Megalomyrmex	152	5	103	260	108	41.5
Monomorium	74	0	25	99	25	25.3
Mycetagroicus	4	0	1	5	1	20.0
Mycetarotes	32	0	22	54	22	40.7
Mycetomoellerius	86	7	12	105	19	18.1
Mycetophylax	56	6	18	80	24	30.0
Mycocepurus	115	0	55	170	55	32.4
Myrmicocrypta	10	5	89	104	94	90.4
Nesomyrmex	68	12	70	150	82	54.7
Ochetomyrmex	67	0	14	81	14	17.3
Octostruma	147	2	59	208	61	29.3
Oxyepoecus	73	3	56	132	59	44.7
Paratrachymyrmex	45	7	11	63	18	28.6
Phalacromyrmex	3	0	0	3	0	0.0
Pheidole	659	91	3867	4617	3958	85.7
Pogonomyrmex	56	0	19	75	19	25.3
Procryptocerus	62	4	57	123	61	49.6
Rhopalothrix	1	0	15	16	15	93.8
Rogeria	102	4	117	223	121	54.3
Sericomyrmex	30	1	137	168	138	82.1
Solenopsis	259	17	1398	1674	1415	84.5
Stegomyrmex	11	1	4	16	5	31.3
Strumigenys	528	16	363	907	379	41.8
Tetramorium	22	0	9	31	9	29.0
Tranopelta	20	0	1	21	1	4.8
Trichomyrmex	1	0	0	1	0	0.0
Wasmannia	251	2	174	427	176	41.2
Xenomyrmex	4	0	10	14	10	71.4
Paraponerinae	27	0	2	29	2	6.9
Paraponera	27	0	2	29	2	6.9
Ponerinae	1841	29	1278	3148	1307	41.5
Anochetus	164	2	57	223	59	26.5
Centromyrmex	20	2	6	28	8	28.6
Cryptopone	8	0	1	9	1	11.1
Dinoponera	42	1	8	51	9	17.6
Hypoponera	73	3	778	854	781	91.5
Leptogenys	72	2	60	134	62	46.3
Mayaponera	84	2	1	87	3	3.4
Neoponera	464	10	17	491	27	5.5
Odontomachus	493	4	121	618	125	20.2
Pachycondyla	300	1	194	495	195	39.4
Platythyrea	18	2	4	24	6	25.0
Pseudoponera	31	1	3	35	4	11.4
Rasopone	32	0	2	34	2	5.9
Simopelta	14	0	5	19	5	26.3
Thaumatomyrmex	26	0	19	45	19	42.2
Proceratiinae	53	1	31	85	32	37.6
Discothyrea	46	1	26	73	27	37.0
Probolomyrmex	1	0	2	3	2	66.7
Proceratium	6	0	3	9	3	33.3
Pseudomyrmecinae	565	36	507	1108	543	49.0
Myrcidris	2	0	2	4	2	50.0
Pseudomyrmex	563	36	503	1102	539	48.9
Formicidae	0	31	31	31	31	100.0
Total	**12109**	**542**	**14874**	**27525**	**15416**	**56.0**

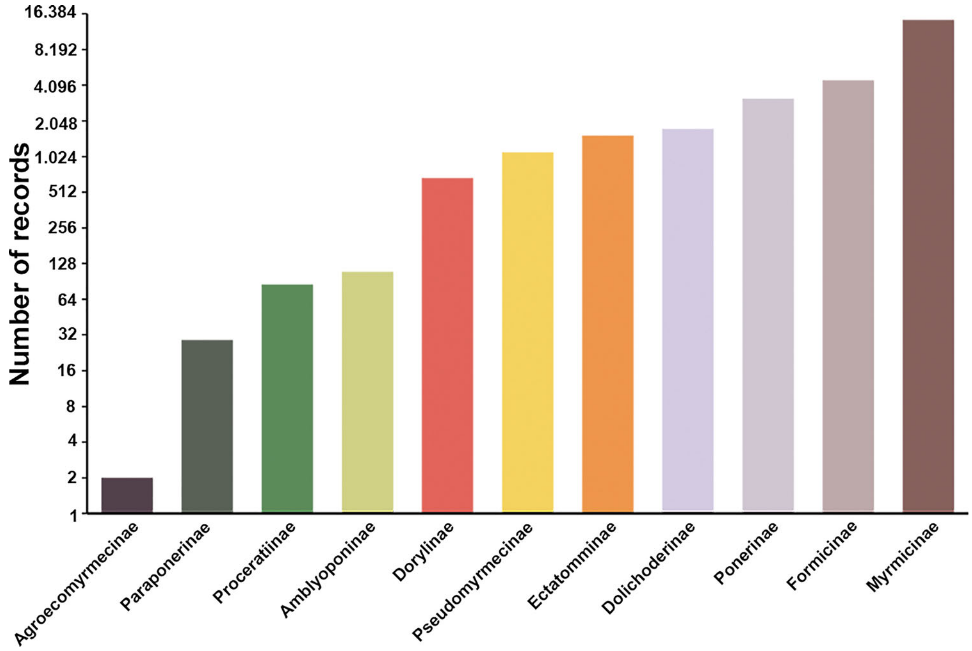

Fig. 1. Bar plot depicting the number of species records per subfamily in Brazilian ant diversity studies. Absolute numbers were converted to a logarithmic scale (base 2) for better visualization.

(50), *Cephalotes* (48), *Pseudomyrmex* (47), *Neoponera* (30), *Dolichoderus* (32), *Acromyrmex* (24), *Solenopsis* (23), and *Neivamyrmex* (21) (Fig. 3).

The ten most frequently recorded species were *Camponotus crassus* Mayr, 1862 (162 records), *Wasmannia auropunctata* (Roger, 1863) (150), *Ectatomma edentatum* Roger, 1863 (133), *Camponotus rufipes* (Fabricius, 1775) (122), *Cephalotes pusillus* (Klug, 1824) (118), *Atta sexdens* (Linnaeus, 1758) (114), *Pachycondyla striata* Smith, 1858 (114), *Pachycondyla harpax* (Fabricius, 1804) (112), *Ectatomma tuberculatum* (Olivier, 1792) (104), and *Pseudomyrmex gracilis* (Fabricius, 1804) (104) (Fig. 4). Together, these species account for slightly more than 10% of all ant records in the studies. On the other hand, 269 species and three subspecies were represented by a single record in the data set.

A total of 15 species listed in the studies about ant diversity in the last 50 years are non-native elements of the Brazilian ant fauna and are here considered exotic. Furthermore, ten species recorded here are included in the Brazilian Red List of Threatened Species, six under the ‘vulnerable’ status and five as ‘endangered species’ (ICMBio, 2018) (Table 4).

Distribution of ant diversity across the Brazilian biomes

From the 402 papers in the data set that provided a taxa list, 142 are studies carried out in the Atlantic Forest, 88 in the Amazon Forest, 87 in the Cerrado, 29 in the Caatinga, 19 in the Pampa, 13 in the Pantanal, and 24 studies performed their ant samplings in more than one biome and are here classified as ‘multibiome’ papers (Fig. 5*d*).

Studies on ant diversity in the Atlantic Forest revealed 10071 ant records, representing 36.6% of all records in the data set. The subfamily Myrmicinae was the most frequent in this biome (5560 records) followed by Formicinae (1493), Ponerinae (1295), Ectatomminae (582), Dolichoderinae (480), Pseudomyrmecinae (312), Dorylinae (194), Amblyoponinae (68), Proceratiinae (56), and Paraponerinae (1). From the 92 ant genera recorded in the Atlantic Forest, *Pheidole* was the most frequent (1774 records) followed by *Camponotus* (789), *Solenopsis* (726), *Hypoponera* (509), *Strumigenys* (450), *Crematogaster* (404), *Brachymyrmex* (343), and *Pseudomyrmex* (312). A total of 657 ant species were listed for the Atlantic Forest (Table 3). The five most frequent ant species were *Pachycondyla striata* (72 records), *Wasmannia auropunctata* (59), *Ectatomma edentatum* (56), *Odontomachus chelifer* (Latreille, 1802) (53), and *Odontomachus meinerti* Forel, 1905 (51) (Fig. 6). The richest subfamily was Myrmicinae, with 359 species, followed by Formicinae (82) and Ponerinae (73). Genera with more than 20 recorded species/subspecies included *Pheidole* (59), *Camponotus* (52), *Strumigenys* (43), *Pseudomyrmex* (27), and *Crematogaster* (25) (Table 3).

Table 3. Number of nominal ant species listed in Brazilian diversity studies per biome over the last 50 years, with the proportion of species recorded in diversity studies in relation to the total number of species formally reported for Brazil per ant taxa.

Taxa/Biome	Atlantic Forest	Amazon Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome	Total	Species in Brazil
Agroecomyrmecinae	0	1	0	0	0	0	0	1	1
Tatuidris	0	1	0	0	0	0	0	1	1
Amblyoponinae	7	5	2	1	0	2	3	8	15
Fulakora	5	2	1	0	0	2	1	5	8
Prionopelta	2	3	1	1	0	0	2	3	7
Dolichoderinae	42	57	33	19	3	12	39	82	149
Azteca	11	10	5	2	0	3	4	17	67
Dolichoderus	11	28	8	3	0	3	13	32	38
Dorymyrmex	4	7	8	5	0	1	8	13	15
Forelius	2	3	2	3	1	1	3	3	6
Gracilidris	0	1	1	0	0	1	1	1	1
Linepithema	12	5	8	5	2	2	9	12	13
Tapinoma	2	3	1	1	0	1	1	4	7
Dorylinae	18	35	17	8	1	5	20	47	111
Acanthostichus	2	4	0	1	0	0	2	5	11
Cheliomyrmex	0	1	0	1	0	0	0	2	2
Cylindromyrmex	1	0	0	0	0	0	0	1	6
Eciton	4	9	2	1	0	1	6	9	17
Labidus	3	4	3	2	1	2	3	4	6
Leptanilloides	0	1	0	0	0	0	0	1	6
Neivamyrmex	5	13	10	2	0	1	6	21	55
Neocerapachys	1	1	1	0	0	1	1	1	1
Nomamyrmex	1	2	1	1	0	0	2	2	2
Sphinctomyrmex	1	0	0	0	0	0	0	1	3
Ectatomminae	45	48	22	15	5	12	28	72	83
Acanthoponera	1	2	1	1	0	0	1	2	4
Alfaria	2	4	0	0	0	0	2	5	6
Bazboltonia	1	0	0	0	0	0	0	1	1
Ectatomma	9	9	10	6	2	8	10	11	12
Gnamptogenys	10	15	6	4	1	2	6	19	21
Heteroponera	7	0	1	1	1	0	1	7	7
Holcoponera	7	9	3	3	1	1	4	12	13
Poneracantha	4	6	0	0	0	0	3	9	11
Typhlomyrmex	4	3	1	0	0	1	1	5	9
Formicinae	82	88	57	28	14	21	64	131	245
Acropyga	7	4	0	0	0	0	2	7	6
Brachymyrmex	13	9	6	3	2	2	9	20	30
Camponotus	52	65	46	20	10	16	41	87	169
Gigantiops	0	1	0	0	0	0	1	1	1
Myrmelachista	6	2	3	2	1	0	6	8	27
Nylanderia	3	6	1	2	1	2	4	7	11
Paratrechina	1	1	1	1	0	1	1	1	1
Myrmicinae	359	349	189	82	51	63	269	612	813
Acanthognathus	3	2	2	0	0	0	1	3	5
Acromyrmex	19	9	15	7	14	4	16	24	30
Allomerus	0	4	0	0	0	0	0	4	6
Amoimyrmex	0	0	0	0	1	0	1	1	2
Apterostigma	12	10	1	0	0	3	4	18	19
Atta	5	3	2	3	1	1	7	8	9
Basiceros	3	1	0	1	0	1	3	4	6
Blepharidatta	1	1	1	0	0	0	1	3	4
Cardiocondyla	5	3	2	1	0	1	2	5	5
Carebara	6	6	2	0	0	1	3	11	18
Cephalotes	19	28	27	15	1	10	20	48	65
Crematogaster	25	34	24	14	4	7	26	50	61
Cryptomyrmex	2	1	0	0	0	1	0	2	2
Cyatta	0	0	1	0	0	0	0	1	1
Cyphomyrmex	11	12	4	4	1	2	6	13	13

(*continued*)

Table 3. Continued.

Taxa/Biome	Atlantic Forest	Amazon Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome	Total	Species in Brazil
Daceton	0	1	0	0	0	0	1	1	1
Diaphoromyrma	1	0	0	0	0	0	0	1	1
Eurhopalothrix	6	1	0	0	0	0	2	7	9
Hylomyrma	5	9	2	2	0	1	7	10	12
Kalathomyrmex	0	1	1	1	0	0	1	1	1
Lachnomyrmex	3	4	0	1	0	0	0	5	5
Megalomyrmex	12	13	4	1	0	2	3	18	19
Monomorium	3	2	2	1	0	1	2	3	6
Mycetagroicus	0	0	1	0	0	0	0	1	4
Mycetarotes	3	3	4	0	0	0	1	4	4
Mycetomoellerius	10	6	10	1	1	0	7	19	24
Mycetophylax	10	3	2	0	0	2	4	13	14
Mycocepurus	3	2	3	0	1	2	2	3	4
Myrmicocrypta	4	2	1	0	0	0	0	5	8
Nesomyrmex	5	5	5	4	0	0	7	10	14
Ochetomyrmex	2	2	1	0	1	1	2	2	2
Octostruma	5	8	2	4	0	4	4	8	8
Oxyepoecus	11	4	3	0	0	0	7	15	17
Paratrachymyrmex	1	5	2	0	0	0	1	5	7
Phalacromyrmex	1	0	0	0	0	0	0	1	1
Pheidole	59	61	32	7	19	7	64	124	184
Pogonomyrmex	2	2	2	1	3	1	5	5	5
Procryptocerus	11	8	1	0	0	0	4	16	30
Rhopalothrix	1	0	0	0	0	0	0	1	1
Rogeria	14	13	3	1	0	2	8	19	20
Sericomyrmex	3	4	3	0	0	0	5	6	8
Solenopsis	13	18	5	6	1	3	9	23	49
Stegomyrmex	2	2	0	0	0	0	1	2	3
Strumigenys	43	44	12	3	1	4	23	71	86
Tetramorium	3	2	1	1	0	0	2	3	4
Tranopelta	1	2	1	0	0	0	1	2	2
Trichomyrmex	1	0	0	0	0	0	0	1	1
Wasmannia	10	6	5	3	2	2	6	10	8
Xenomyrmex	0	2	0	0	0	0	0	2	2
Paraponerinae	1	1	1	0	0	0	1	1	1
Paraponera	1	1	1	0	0	0	1	1	1
Ponerinae	73	96	41	17	9	17	55	120	173
Anochetus	9	8	3	2	0	1	8	12	14
Centromyrmex	1	3	2	0	0	0	1	3	3
Cryptopone	1	1	1	0	0	0	1	2	4
Dinoponera	2	4	3	1	0	1	4	5	10
Hypoponera	8	7	1	0	3	1	5	10	29
Leptogenys	8	11	0	0	0	0	2	15	24
Mayaponera	2	2	1	0	0	0	2	2	3
Neoponera	19	26	14	5	3	6	14	30	38
Odontomachus	7	14	8	4	1	4	8	16	17
Pachycondyla	5	5	4	3	2	2	5	5	9
Platythyrea	1	4	0	1	0	0	2	4	5
Pseudoponera	2	2	2	0	0	0	2	2	3
Rasopone	2	2	1	0	0	2	1	2	2
Simopelta	2	3	0	0	0	0	0	5	5
Thaumatomyrmex	4	4	1	1	0	0	0	7	7
Proceratiinae	3	5	0	0	0	1	1	7	13
Discothyrea	2	5	0	0	0	0	1	5	6
Probolomyrmex	0	0	0	0	0	1	0	1	5
Proceratium	1	0	0	0	0	0	0	1	2
Pseudomyrmecinae	27	31	27	15	3	10	24	49	80
Myrcidris	0	1	0	0	0	0	0	1	1
Pseudomyrmex	27	30	27	15	3	10	24	47	79
Total	**657**	**716**	**389**	**185**	**86**	**143**	**504**	**1130**	**1684**

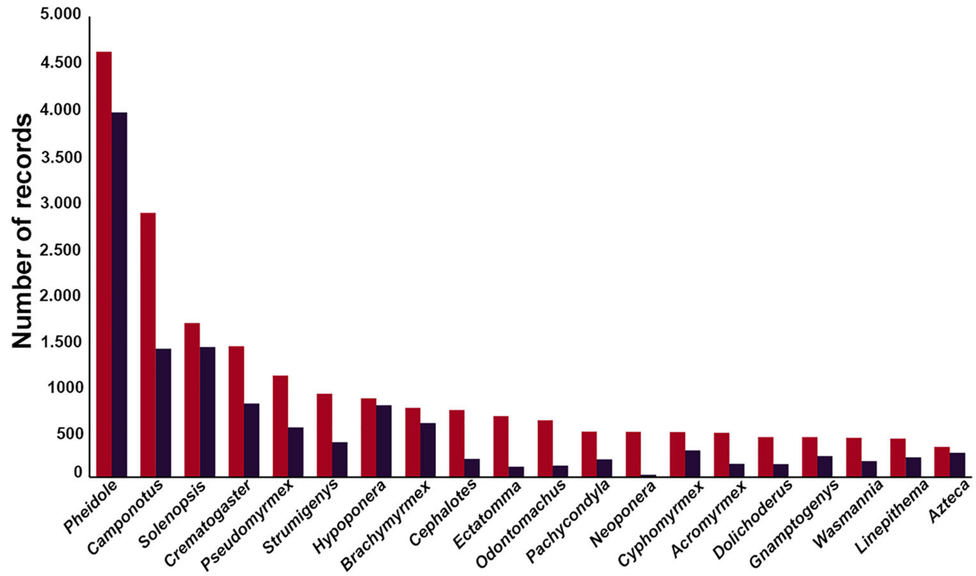

Fig. 2. Bar plot depicting the absolute number of species records for each of the 20 most frequently recorded ant genera in Brazilian ant diversity studies. Red bars show the total number of records per genera (nominal and unidentified); purple bars show the number of unidentified records per genera.

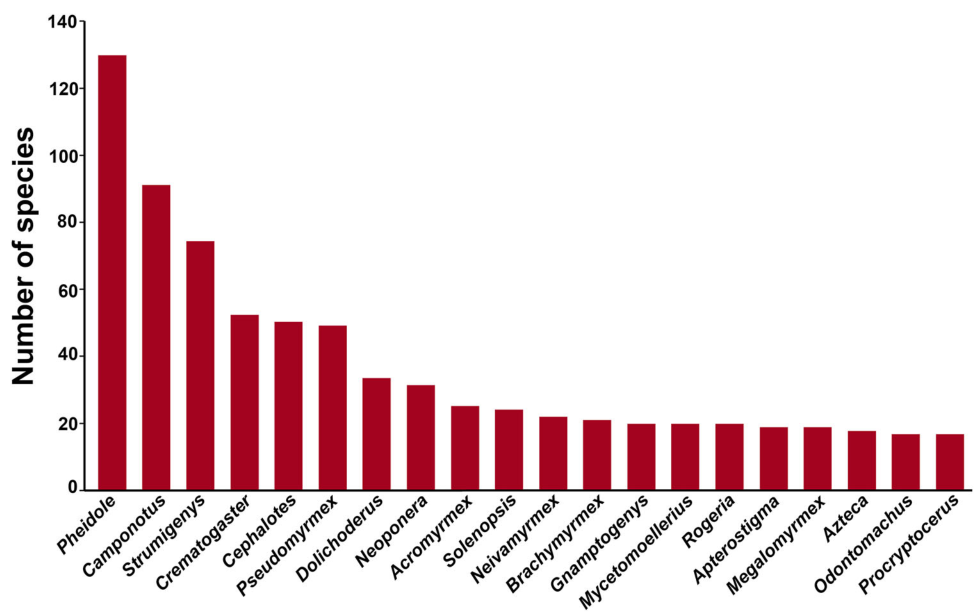

Fig. 3. Bar plot depicting the number of species recorded for the 20 most diverse ant genera in ant diversity studies in Brazil.

The Amazon Forest had the second-highest number of ant records in Brazil, 8279, accounting for 30% of the records in Brazilian ant studies. Again, Myrmicinae was the most frequent subfamily (4382 records), followed by Ponerinae (1150), Formicinae (1061), Dolichoderinae (561), Ectatomminae (470), Pseudomyrmecinae (300), Dorylinae (289), Proceratiinae (25), Paraponerinae (24), Amblyoponinae (21), and Agroecomyrmecinae (2). In total, 93 ant genera were recorded in the Amazon biome. *Pheidole* was the most frequent genus (1446 records), followed by *Camponotus* (666), *Crematogaster* (511), *Solenopsis* (367), *Strumigenys* (312), *Pseudomyrmex* (298), *Dolichoderus* (280), *Odontomachus* (249), and *Neoponera* (230). The Amazon Forest was the most diverse biome in Brazil, with 716 species recorded (Table 3). The five most frequently sampled ant species include *Odontomachus haematodus* (Linnaeus, 1758) (40 records), *Pachycondyla harpax* (40), *Wasmannia auropunctata* (38), *Mayaponera constricta* (Mayr, 1884) (37), and

Fig. 4. In frontal and lateral view, workers of the six most frequent species recorded in the ant diversity studies in Brazil, in order of frequency. (A) *Camponotus crassus* (CASENT0173407), (B) *Wasmannia auropunctata* (CASENT0178173), (C) *Ectatomma edentatum* (CASENT0173376), (D) *Camponotus rufipes* (CASENT0173444), (E) *Cephalotes pusillus* (CASENT0173703), (F) *Atta sexdens* (CASENT0173817). Images by April Nobile, available from www.antweb.org.

Pachycondyla crassinoda (Latreille, 1802) (36) (Fig. 6). Myrmicinae was the richest subfamily in the Amazon Forest, with 349 species, followed by Ponerinae (96) and Formicinae (88). Nine genera had more than 20 ant species/subspecies recorded, namely *Camponotus* (65), *Pheidole* (61), *Strumigenys* (44), *Crematogaster* (34), *Pseudomyrmex* (30), *Cephalotes* (28), *Dolichoderus* (28), and *Neoponera* (26) (Table 3).

In the Cerrado, we gathered 4497 ant records, representing 16.3% of the records in the data set. Myrmicinae accounted for nearly half of the records in this biome (2155), followed by Formicinae (1073), Dolichoderinae (326), Ponerinae (326), Ectatomminae (262), Pseudomyrmecinae (261), Dorylinae (82), Amblyoponinae (9), and Paraponerinae (2). Seventy-eight ant genera were recorded in the Cerrado, with *Camponotus* as the most frequent (835 records), followed by *Pheidole* (639), *Pseudomyrmex* (259), *Crematogaster* (249), *Solenopsis* (236), *Cephalotes* (218), *Ectatomma* (201), and *Brachymyrmex* (141). A total of 389 ant species was listed for the Cerrado in ant diversity studies (Table 3). The most frequent species were *Camponotus crassus* (55 records), *Cephalotes pusillus* (51), *Camponotus rufipes* (42), *Ectatomma brunneum* Smith, F., 1858 (33), and *Ectatomma tuberculatum* (32) (Fig. 6). The subfamily with the highest number of species was Myrmicinae, with 189 species, followed by Formicinae (57), and Ponerinae (41). Genera with more than 20 ant species recorded comprise *Camponotus* (46), *Pheidole* (32), *Cephalotes* (27), *Pseudomyrmex* (27), and *Crematogaster* (24) (Table 3).

The Caatinga had 1192 records, totaling 4.3% of the ant occurrences in Brazilian diversity papers. Myrmicinae was the most frequent subfamily (608 records), followed by Formicinae (238), Dolichoderinae (107), Ponerinae (77), Pseudomyrmecinae (74), Ectatomminae (65), Dorylinae (21), and Amblyoponinae (2). A total of 54 ant genera were recorded in Caatinga. *Pheidole* was once again the most representative genus, with 203 records, followed by *Camponotus* (158), *Solenopsis* (110), *Pseudomyrmex* (74), *Crematogaster* (73), *Cephalotes* (59), *Dorymyrmex* (52), and *Brachymyrmex* (38). One hundred eighty-five species were sampled in the Caatinga biome (Table 3). *Ectatomma muticum* Mayr, 1870 was the most frequent ant species, with 18 records, followed by *Camponotus*

Table 4. Ecological and conservation status of the ant species listed in Brazilian diversity studies per biome (0 = absent, 1 = present) over the last 50 years, with exotic species and those included in the Brazilian Red List of Threatened Species as 'vulnerable' or 'endangered' (ICMBio, 2018).

Ant species	Status	Atlantic Forest	Amazon Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome
Anochetus oriens Kempf, 1964	Vulnerable	1	0	0	1	0	0	0
Atta robusta Borgmeier, 1939	Vulnerable	1	0	0	0	0	0	0
Brachymyrmex micromegas Santschi, 1923	Endangered	1	0	0	0	0	0	0
Cardiocondyla emeryi Forel, 1881	Exotic	1	1	1	1	0	0	1
Cardiocondyla minutior Forel, 1899	Exotic	1	1	0	0	0	0	0
Cardiocondyla nuda (Mayr, 1866)	Exotic	1	0	0	0	0	0	0
Cardiocondyla obscurior Wheeler, 1929	Exotic	1	1	0	0	0	1	1
Cardiocondyla wroughtonii (Forel, 1890)	Exotic	1	0	1	0	0	0	0
Diaphoromyrma sofiae Fernández, Delabie & Nascimento, 2009	Endangered	1	0	0	0	0	0	0
Dinoponera lucida Emery, 1901	Endangered	1	0	0	0	0	0	0
Lachnomyrmex nordestinus Feitosa & Brandão, 2008	Vulnerable	1	0	0	0	0	0	0
Monomorium delabiei Fernández, 2007	Vulnerable	1	0	0	0	0	0	0
Monomorium floricola (Jerdon, 1851)	Exotic	1	1	1	1	0	1	1
Monomorium pharaonis (Linnaeus, 1758)	Exotic	1	1	1	0	0	0	1
Mycetomoellerius atlanticus (Mayhé-Nunes & Brandão, 2007)	Vulnerable	1	0	0	0	0	0	0
Mycetophylax simplex (Emery, 1888)	Vulnerable	0	0	0	0	0	0	1
Paratrechina longicornis (Latreille, 1802)	Exotic	1	1	1	1	0	1	1
Pheidole megacephala (Fabricius, 1793)	Exotic	1	1	1	0	0	0	1
Rhopalothrix plaumanni Brown & Kempf, 1960	Endangered	1	0	0	0	0	0	0
Strumigenys emmae (Emery, 1890)	Exotic	1	1	0	0	0	0	0
Tapinoma melanocephalum (Fabricius, 1793)	Exotic	1	1	1	1	0	1	1
Tetramorium bicarinatum (Nylander, 1846)	Exotic	1	1	0	0	0	0	1
Tetramorium lucayanum Wheeler, 1905	Exotic	1	0	0	0	0	0	0
Tetramorium simillimum (Smith, 1851)	Exotic	1	1	1	1	0	0	1
Trichomyrmex destructor (Jerdon, 1851)	Exotic	1	0	0	0	0	0	0

crassus (17 records), *Dorymyrmex thoracicus* Gallardo, 1916 (16), *Camponotus blandus* (Smith, F., 1858) (14), *Dinoponera quadriceps* Kempf, 1971 (13), *Camponotus atriceps* (Smith, F., 1858) (11), *Pseudomyrmex gracilis* (11), and *Cephalotes pusillus* (10) (Fig. 6). Myrmicinae was the richest subfamily (82 species), followed by Formicinae (28), and Ponerinae (17). Four genera had more than ten ant species recorded, namely *Camponotus* (20), *Cephalotes* (15), *Pseudomyrmex* (15), and *Crematogaster* (14) (Table 3).

Studies on ant diversity in the Pampa biome revealed a total of 615 ant records, representing 2.2% of the records in the data set. Myrmicinae was the most frequently registered, with 334 records, followed by Formicinae (134), Ponerinae (53), Dolichoderinae (40), Pseudomyrmecinae (29), Ectatomminae (15), and Dorylinae (10). Thirty ant genera were recorded in the Pampa. *Pheidole* was the most frequent genus in samples, with 115 records, followed by *Camponotus* (83), *Solenopsis* (49), *Brachymyrmex* (29), *Crematogaster* (28), *Pseudomyrmex* (27), and *Hypoponera* (24). The Pampa registered the lowest species richness among Brazilian biomes, with only 86 species listed in diversity papers (Table 3). Many of the most frequent ant species in the Pampa belong to the leaf-cutter ant genus *Acromyrmex*, of which *Acromyrmex lundii* (Guérin-Méneville, 1838) was the most frequent, with 11 records, followed by *Camponotus rufipes* (10), *Acromyrmex heyeri* (Forel, 1899) (9), *Amoimyrmex striatus* (Roger, 1863) (9), *Acromyrmex ambiguus* (Emery, 1888) (8), *Acromyrmex crassispinus* (Forel, 1909) (8), *Acromyrmex laticeps* (Emery, 1905) (7), and *Solenopsis invicta* Buren, 1972 (7) (Fig. 6). The richest subfamily was Myrmicinae, with 51 species, followed by Formicinae (14), and Ponerinae (9). The most diverse genera in the Pampas regarding the number of species were *Pheidole* (19), *Acromyrmex* (14), *Camponotus* (10), *Crematogaster* (4), *Hypoponera*, *Neoponera*, *Pogonomyrmex*, and *Pseudomyrmex* with three species each (Table 3).

The Brazilian biome with the lowest number of diversity studies was the Pantanal, which summed 610 ant records, representing 2.2% of the occurrences in our data set. Myrmicinae was the most frequent subfamily with 301 records, followed by Formicinae (104), Ponerinae (60), Dolichoderinae (51), Ectatomminae (36), Pseudomyrmecinae (35), Dorylinae (18),

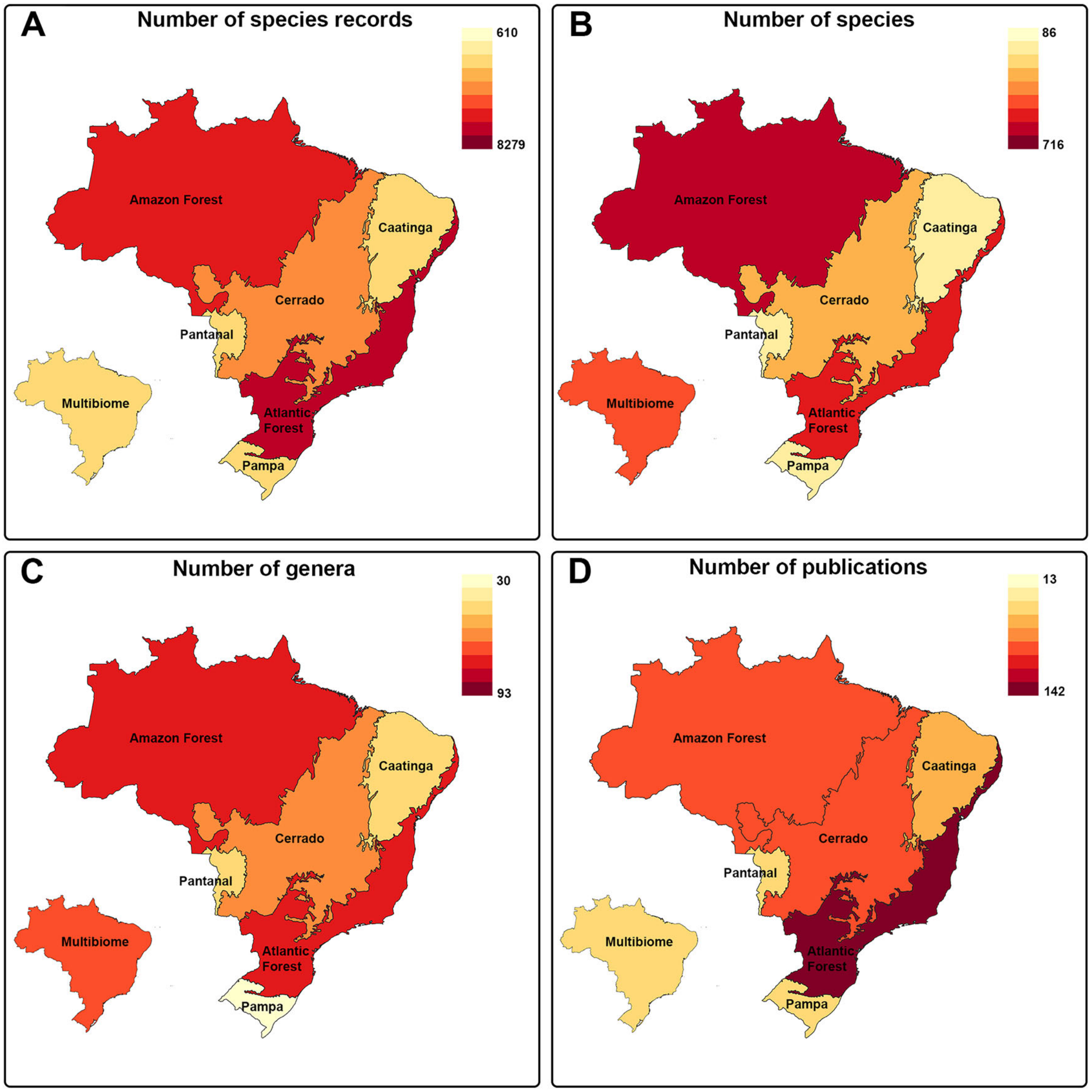

Fig. 5. Heatmap depicting the ant species records, the number of genera and species, the publications on ant diversity and their distribution across Brazilian biomes. (A) Number of ant species records (including nominal and unidentified species); (B) Number of ant species (morphospecies excluded); (C) Number of genera; (D) Number of ant diversity studies. More intense red (hot) colors indicate biomes with higher occurrence density, although color scales are not equivalent between heatmaps. The maximum and the minimum occurrence density values of each map is available above to clarify the amplitude variation across biomes.

Amblyoponinae (3), and Proceratiinae (2). In total, 53 ant genera were recorded in the Pantanal, with *Pheidole* as the most frequent (70 records), closely followed by *Camponotus* (68), *Solenopsis* (47), *Crematogaster* (40), *Pseudomyrmex* (35), *Cephalotes* (28), *Ectatomma* (26), and *Hypoponera* (26). One hundred forty-three ant species were sampled in diversity studies carried out in Pantanal (Table 3). *Camponotus crassus* and *Camponotus melanoticus* Emery, 1894 were the most frequent species in the biome, with seven records each, followed by *Ectatomma brunneum*, *Camponotus rufipes* and *Pseudomyrmex gracilis* (6 records each), *Cephalotes atratus* (Linnaeus, 1758) and *Odontomachus bauri* Emery, 1892 (5 records each) (Fig. 6). The subfamily with the highest number of species was Myrmicinae, with 63 species, followed by Formicinae (21), and Ponerinae (17). The richest ant genera were *Camponotus* (16 species), *Cephalotes* (10), *Pseudomyrmex* (10), *Ectatomma* (8), *Crematogaster* (7), *Pheidole* (7), and *Neoponera* (6) (Table 3).

Finally, 24 studies sampled more than one biome or transition zones between biomes (ecotones), some of which did not indicate the precise occurrence of the taxa in their lists or main text. Thus, we here list the

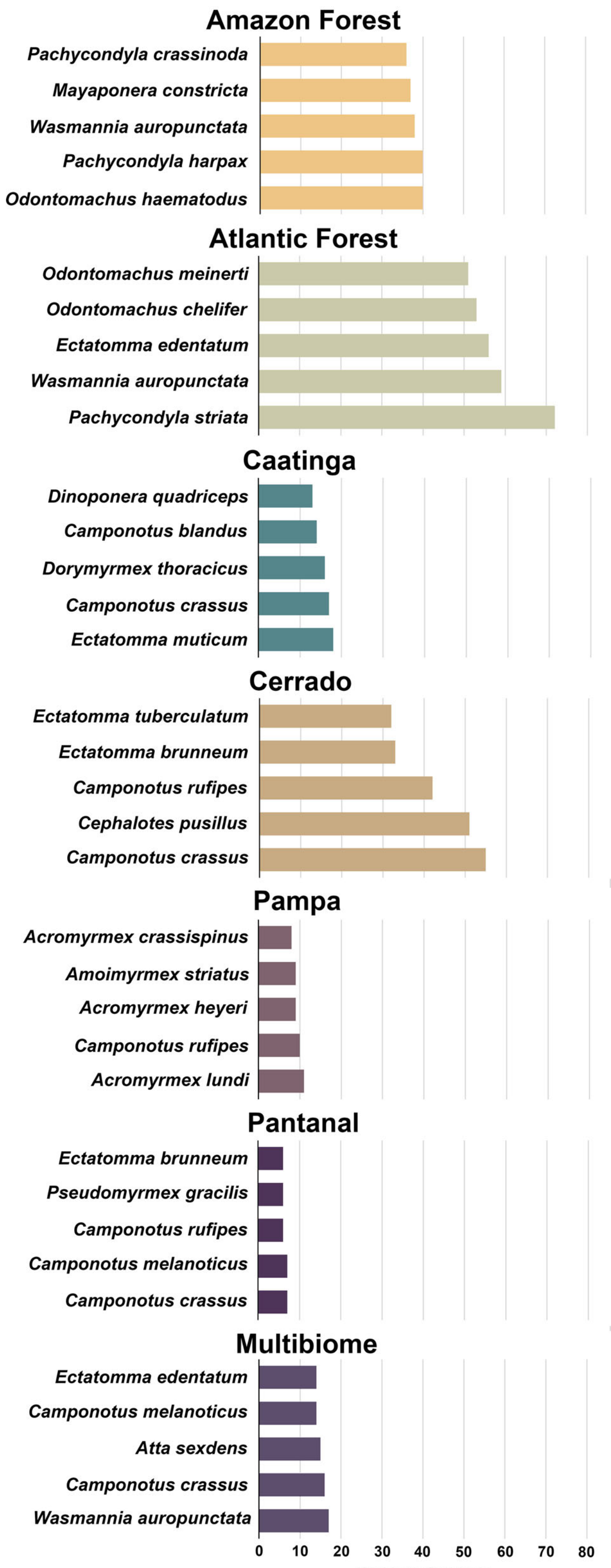

Fig. 6. Bar plots depicting the number of records for each of the five most frequently collected species in each of the six biomes occurring in Brazil and for the multibiome category.

taxa information of these multibiome papers as a data set separated from the official Brazilian biomes. Multibiome studies revealed 2262 ant records, which account for 8.2% of all records in the papers surveyed. As expected, giving the general pattern for the country, Myrmicinae was the most frequent subfamily with 1211 records, followed by Formicinae (401), Ponerinae (187), Dolichoderinae (186), Ectatomminae (112), Pseudomyrmecinae (97), Dorylinae (58), Amblyoponinae (6), Paraponerinae, and Proceratiinae (2 each). A total of 85 ant genera was recorded in the multibiome papers. Also, as noted for the overall tendency for the country, *Pheidole* was the most frequently sampled genus, with 370 records, followed by *Camponotus* (270), *Solenopsis* (139), *Crematogaster* (114), *Pseudomyrmex* (97), *Cephalotes* (71), *Acromyrmex* (67), *Brachymyrmex* (62), *Dorymyrmex* (59), and *Ectatomma* (57). Multibiome papers listed 504 species (Table 3), and *Wasmannia auropunctata* was the most often recorded (17 records), followed by *Camponotus crassus* (16), *Atta sexdens* (15), *Ectatomma edentatum* (14), *Camponotus melanoticus* (14), *Camponotus rufipes* (13), *Cephalotes pusillus* (11), *Pseudomyrmex termitarius* (Smith, F., 1855) (11), *Camponotus atriceps*, and *Holcoponera striatula* (Mayr, 1884) (10 each) (Fig. 6). Myrmicinae was the subfamily with the highest number of species, 269, followed by Formicinae (64) and Ponerinae (55). Six genera had 20 or more species recorded, *Pheidole* with 64 species, *Camponotus* (41), *Crematogaster* (26), *Pseudomyrmex* (24), *Strumigenys* (23), and *Cephalotes* (20) (Table 3).

Taxonomic resolution in Brazilian ant diversity studies

In our final database, 15416 records refer to taxa not nominally identified in the studies, including those taxa associated with valid names (542 records) and morphospecies (14874 records). Therefore, 56% of occurrence data in Brazilian ant diversity studies come from unidentified specimens. For 67 records in the data set, authors were not able to identify their ants to the generic level and associated the morphospecies with the family Formicidae (31 records), subfamilies (35 records) or tribe (1 record) (Supplemental Material Table S4).

Among ant subfamilies, unidentified records were higher than nominal records in Myrmicinae (9261 vs. 5290; 63.6%), Formicinae (2607 vs. 1896; 57.9%), and Dolichoderinae (962 vs. 763; 55.1%). For 26 ant genera in the data set, the number of unidentified species was higher than the number of nominal species. Genera for which the number of morphospecies was more than 80% higher than the number nominal species include

Table 5. Spurious ant records listed in Brazilian diversity studies over the last 50 years, including the biome, reference source, and type of error. Names of ant taxa are listed here exactly as in the original papers (*ipsis litteris*).

Taxa	Biome	Source	Error
Allomerus auripunctata	Amazon	Fonseca and Ganade (1996)	Invalid name
Allomerus prancei	Amazon	Fonseca and Ganade (1996)	Invalid name
Anoplolepis sp.	Pampa	Bolico et al. (2012)	Misidentification
Brachymyrmex pyramica	Caatinga	Soares et al. (2003)	Invalid name
Camponotus eurynota	Amazon	Adis et al. (1998)	Invalid name
Camponotus leyoligi	Atlantic Forest	Sobrinho et al. (2003)	Invalid name
Camponotus temoralus	Amazon	Nogueira et al. (2020)	Invalid name
Cephalotes grandispinosus	Atlantic Forest	Campos-Farinha et al. (1997)	Invalid name
Crematogaster elevans	Cerrado	Rabello et al. (2021)	Invalid name
Crematogaster micropilosa	Amazon	Nogueira et al. (2020)	Invalid name
Dolichoderus burtoni	Amazon	Souza et al. (2018)	Invalid name
Dorymyrmex alticanis	Cerrado, Atlantic Forest	Pacheco and Vasconcelos (2007), Munhae et al. (2009)	Invalid name
Dorymyrmex guianensis	Amazon	Vasconcelos and Vilhena (2006)	Invalid name
Iridomyrmex sp.	Cerrado	Almeida et al. (2014)	Misidentification
Monomorium panamanus	Amazon	Souza et al. (2012)	Invalid name
Monomorium stollii	Amazon	Souza et al. (2012)	Invalid name
Nomamyrmex espinodiz	Amazon	Peixoto et al. (2010)	Invalid name
Odontomachus mayri	Amazon	Marini-Filho (1999)	Invalid name
Odontonanchus blandus	Atlantic Forest	Haddad et al. (2011)	Invalid name
Pachycondyla clavata	Atlantic Forest	Chinarelli et al. (2021)	Invalid name
Pachycondyla evexa	Cerrado	Andrade et al. (2007)	Invalid name
Pachycondyla rapax	Amazon	Nogueira et al. (2020)	Invalid name
Patagonomyrmex angustus	Atlantic Forest	Lutinski et al. (2018)	Misidentification
Pheidole escoliolips	Cerrado	Nogueira et al. (2020)	Invalid name
Plagiolepis sp.	Atlantic Forest	Campos-Farinha et al. (1997), Sobrinho et al. (2003), Ribas et al. (2005)	Misidentification
Ponera sp.	Caatinga, Cerrado, Atlantic Forest	Bihn et al. (2008), Oliveira et al. (2017), Ribeiro-Neto et al. (2016), Costa et al. (2015)	Misidentification
Prenolepis sp.	Amazon, Atlantic Forest	Kalif et al. (2001), Assis et al. (2018)	Misidentification
Rhytidoponera strigosa	Atlantic Forest	Campos-Farinha et al. (1997)	Misidentification
Solenopsis molestans	Atlantic Forest	Assis et al. (2018)	Invalid name
Strumigenys mandibulata	Caatinga, Atlantic Forest	Carvalho et al. (2014)	Invalid name
Syscia augustae	Amazon	Souza et al. (2016), Fernandes & Sousa (2018)	Misidentification

Rhopalothrix (15 vs. 1; 93.7%), *Hypoponera* (781 vs. 73; 91.4%), *Myrmicocrypta* (94 vs. 10; 90.4%), *Pheidole* (3958 vs. 659; 85.7%), *Solenopsis* (1415 vs. 259; 84.5%), *Sericomyrmex* (138 vs. 30; 82.1%), and *Azteca* (264 vs. 65; 80.2%) (Fig. 2). On the other hand, ten genera had all their species nominally identified in 100% of the papers surveyed, including *Tatuidris, Gracilidris, Cheliomyrmex, Leptanilloides, Amoimyrmex, Cryptomyrmex, Cyatta, Diaphoromyrma, Phalacromyrmex*, and *Trichomyrmex*. Not surprisingly, most of these genera are monotypic or have no more than four species formally recorded in Brazil. Also, these genera together are represented in the data set by only 44 records.

Finally, during data surveying and assembling, we detected a series of taxonomic imprecisions involving the writing of ant taxa names and identification accuracy by authors of ant diversity studies. A total of 25 records in the data set refer to 24 inexistent species whose names have never been formally proposed in ant taxonomy. Also, 17 records are related to obvious misidentifications since they are attributed to nine ant taxa restricted to different biogeographical regions that do not include Brazil or even the Neotropical Region (Table 5).

Discussion

Our study was the first to apply a scientometric approach to evaluate how ecological publications contribute to the ant diversity knowledge in Brazil. Our data set is entirely comprised of records from ecological surveys published since 1970 and does not include ant occurrence data from taxonomic papers or entomological collections. Even so, the number of taxa listed here is considerably close to the total ant diversity formally recorded for the country, about 67% of the species known for Brazil and 90% of the genera currently recorded for the country. We list a total of 1130 species/subspecies in 106 ant genera, while the current numbers are 1684 species and 117 genera (Bolton, 2022). As for the ant subfamilies, the ecological surveys recorded 11 of the 12 subfamilies occurring in the country so far, except for Martialinae, which is composed of a single rarely collected ant species (Boudinot, 2015; Rabeling et al., 2008).

We also show that ant richness patterns strongly vary among Brazilian biomes. This is in part related to the considerable differences in the sampling effort applied among them in the last 50 years, represented in our data set by the number of ant diversity publications per biome (Fig. 5*d*). The number of ant surveys in Atlantic Forest that provided a taxa list is eleven times higher than the number of similar studies carried out in the Pantanal (142 vs. 13). The reasons are both historical and logistical. Brazil's socioeconomic development took place from the coast, covered by the Atlantic Forest. In contrast, the interior had the least investigated natural areas. This explains the higher concentration of research centers and universities, as well as ant diversity studies, in the Atlantic Forest (Schmidt et al., 2022). In this sense, the position of the Amazon Forest as the second best sampled biome in our survey, despite the logistical challenges involved in sampling ants in this vast and largely unexplored region, is largely due to the work of researchers based at Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, at Amazonas state, and Museu Paraense Emilio Goeldi in Belém (MPEG), at Pará state, two Amazonian research institutions that stand out for their myrmecological scientific productivity (Fernandes & Oliveira, 2020; Prado et al., 2020).

However, contrary to the general perception that species richness would be proportional to the number of surveys carried out in each biome, we here show that, based on ecological surveys in the last 50 years, the most diverse Brazilian biome regarding ant species is not that with the highest number of diversity studies. We recorded 142 diversity studies in the Brazilian Atlantic Forest against 88 in the Amazon Forest. Yet, the Atlantic Forest contributed with 657 ant species to the entire data set, while the Amazon Forest revealed a richness of 716 species (Table 3, Fig. 5). Nevertheless, this apparent contradictory pattern is related to the significant differences between biomes regarding their total area, conservation status, environmental heterogeneity, and latitudinal patterns in rainfall and therefore in plant productivity, which strongly affect ant diversity (Silva & Brandão, 2014; Vasconcelos et al., 2018). In fact, besides the number of diversity studies, the vegetation types could also play an important role in the ant richness of biomes observed here. The Atlantic Forest and the Amazon Forest, two predominantly forested Brazilian biomes, presented a substantially higher ant richness when compared to the Cerrado (389 species), an extensive savanna, even considering that the Amazon and the Cerrado had basically the same number of diversity studies recorded in our survey (88 vs. 87, respectively). Therefore, the comparatively lower ant richness of the shrublands and grasslands of the Caatinga, Pantanal, and Pampa (Table 3, Fig. 5) is somewhat expected given the relatively simplified vegetation structure and shorter territorial extension of these biomes (Ab'Saber, 2003).

Besides the remarkable differences in the historical sampling effort among Brazilian biomes, the ant occurrence patterns greatly vary in the prevalence of different taxonomic categories, especially among genera and species. Overall, a clear pattern readily emerged in relation to the most frequent ant subfamilies, with Myrmicinae, Formicinae, and Ponerinae as the most common and speciose taxa in almost all Brazilian biomes, usually in this very sequence (Fig. 1). In fact, ant surveys carried out in tropical regions worldwide, constantly include the statement 'Myrmicinae was the richest ant subfamily in the study'. This is a classic pattern among ant subfamilies, explained by the remarkable species diversity and prevalence of Myrmicinae, which comprises almost 50% of all ant species known (Bolton, 2022). In addition, myrmicine ants have high ecological disparity, occupying all habitat strata of most terrestrial ecosystems, except maybe by the temperate and structurally simplified areas of the globe, where Dolichoderinae and Formicinae predominate (Andersen, 1997).

Regarding the prevalence of ant genera and species in the Brazilian biomes, the patterns are slightly more irregular than those observed for subfamilies. *Pheidole* (Myrmicinae) tends to be the most frequent and diverse genus in almost all Brazilian biomes, followed by *Camponotus* (Formicinae) (Fig. 2). In the predominantly forested biomes of the country, represented by the Atlantic Forest and the Amazon Forest, the prevalence of *Pheidole* is substantial, exceeding the number of records for *Camponotus* by more than twice. However, these proportions decrease when considering the biomes dominated by shrublands and grasslands. Indeed, the Brazilian Cerrado is the only biome where *Camponotus* surpasses *Pheidole* both in number of records (835 vs. 639) and species richness (46 vs. 32). Therefore, despite the ubiquity of *Pheidole* in most Brazilian biomes, *Camponotus* species tend to be comparatively more frequent in hot, open, and structurally simple environments, a pattern also observed in other regions of the world (Andersen, 1995). Once again, hyperdiversity may explain the patterns observed here. *Pheidole* is the most diverse genus among ants globally, with 1171 species described, followed by *Camponotus* with 1089 species (Bolton, 2022). Different authors have postulated that *Pheidole*'s remarkable diversity may result from behavior-related traits (Mertl et al., 2010) or that the wide occupation of niches in *Pheidole* would have as its primary cause the dimorphism between its workers, with major workers being specialized individuals related to specific tasks within the colonies. These specialized tasks may vary interspecifically, highly improving the ecological plasticity of the genus (Casadei-Ferreira et al., 2021; Wilson, 2003). A similar morphology-based explanation could be given for *Camponotus*, another hyperdiverse genus of which most species have different degrees of polymorphism (Blaimer et al., 2015). Besides *Pheidole* and *Camponotus*, the genera *Crematogaster, Pseudomyrmex,* and *Solenopsis* can also be considered dominant elements of the Brazilian ant fauna, given their frequency and species richness in all biomes of the country (Tables 1 and 3).

The highest variation in ant occurrence patterns among Brazilian biomes was observed at the species level. In most biomes, except for two, a distinct ant species prevailed as the most frequent based on diversity studies (Fig. 6). Interestingly, in most cases, these species represented not only distinct genera, but distinct subfamilies. Ponerinae stands out in the Atlantic Forest for the higher frequency of *Pachycondyla striata* and in the Amazon Forest with *Odontomachus haematodus* and *Pachycondyla harpax*. Ectatomminae is represented by *Ectatomma muticum* in the Caatinga, and the Pampa biome has the myrmicine *Acromyrmex lundii* as its most frequent species. The only species recorded as the most frequent in two distinct biomes was *Camponotus crassus*, whose records exceeded that of the other species in the Cerrado and Pantanal. Once again, the vegetation cover could play an important role in the frequency and abundance of ants in Brazilian biomes. In these cases, forested biomes (Atlantic Forest and Amazon Forest) would favor primarily predatory ponerine ants; opened shrubland biomes (Caatinga, Cerrado, and Pantanal) would favor generalist/opportunist species; and, finally, opened grasslands of Pampa would favor a higher abundance of leaf-cutting ants. These patterns are similar to those of different ant checklists and ecological surveys individually carried out in the Brazilian biomes (Albuquerque et al., 2021; Dröse et al., 2017; Leal et al., 2018; Martins et al., 2021; Silva et al., 2022; Vasconcelos et al., 2018), reinforcing that ant occurrence data extracted from ant diversity studies under a scientometric approach has the potential to reveal ecological patterns.

Another major outcome from our results is that most of the ants recorded in diversity studies in Brazil were not identified and assigned to a described species name. Instead, researchers tend to assign ants to morphospecies, and each research group tends to adopt its own morphospecies coding system or even a separate coding system for each study case, limiting the comparison between studies (Delabie et al., 2012). However, the use of morphospecies as surrogates for nominal species is not exclusive to Brazilian myrmecologists. This practice has been proposed as an alternative to overcome identification difficulties associated with many invertebrate groups, particularly in large-scale biodiversity surveys (Derraik et al., 2010). However, we observed that in 2% of the cases, authors of ant diversity studies were able to classify unidentified species in species groups (or species complexes) and even to associate morphospecies to a valid extant species name by applying traditional taxonomic abbreviations as 'nr.' (='near' in English), 'pr.' (='*próximo*' in Portuguese) or 'aff.' (='*affinis*' in Latin), all of them meaning 'near to'. Although morphospecies cannot be considered nominal species, classification into groups or the association with valid names represents a higher level of taxonomic resolution on the part of identifiers than the morphospecies codes associated exclusively with the ant genera. In general, the associations with valid names are usually performed by taxonomists or other experienced ant identifiers consulted by authors, which increases the taxonomic resolution of studies (R.M. Feitosa pers. obs.). Additionally, our data show that unidentified species were most frequent in the commonly collected ant subfamilies Myrmicinae, Formicinae, and Dolichoderinae (Fig. 2). This limitation is expected since these subfamilies have an impressive species richness and a considerably taxonomic complexity for several genera (Baccaro et al., 2015). The most concerning situations involve genera for which we have a combination of high diversity, ecological prevalence, and low taxonomic resolution. This is mainly the case of *Hypoponera* (Ponerinae), *Pheidole*, *Solenopsis* (Myrmicinae), and *Azteca* (Dolichoderinae), all of them with more than 80% of records represented by morphospecies in our data set (Table 2).

Since the monumental monograph on the *Pheidole* of the New Word by Wilson (2003), a single paper on the taxonomy of the Brazilian species including identification tools was published, although restricted to the fauna from the southern grasslands (Casadei-Ferreira et al., 2020). So, considering the remarkable number of species in the genus, the knowledge of *Pheidole* diversity in Brazil is still incomplete, and accurate species identification is considerably difficult. Despite the lower species diversity compared to *Pheidole*, the situation of *Solenopsis* is no better. Three revisionary studies deal with the taxonomy of Brazilian species in this genus (Pacheco & Mackay, 2013; Pitts et al., 2018; Trager, 1991). However, some *Solenopsis* species are polymorphic (*saevissima* species-group), and the precise identification is largely dependent on the major workers, which in most cases are absent from samples. Another drawback is that workers of monomorphic species of *Solenopsis* have subtle and continuous morphological differences along geographical gradients, making the accurate identification based on external morphology virtually impossible in some cases. So far, the taxonomic resolution for most species in *Hypoponera* and *Azteca* can be considered hopeless for opposite reasons. While *Hypoponera* species are desperately homogeneous morphologically and restricted to the crevices of wet forests leaf-litter, *Azteca* species are highly polymorphic in many cases and dominant vegetation components in both forest and savanna environments in Brazil. In addition, both genera can be considered the nightmare of myrmecologists in the neotropics due to the high frequencies in samples and absence of formal taxonomic studies (Fernández et al., 2021). Despite being considered taxonomically challenging by the high species diversity in Brazilian biomes and the high polymorphism of some species, the most common species of *Camponotus* are traditionally identified with a reasonable level of accuracy by comparison with museum specimens or even with high-resolution images available in online repositories (e.g., AntWeb.org).

Considering the discrepancies in the proportion of nominal and unidentified ant species in Brazilian diversity studies, another concern that emerges from our data is related to the highly variable levels of difficulty for species identification in different ant genera or subfamilies. In this scenario, although species estimation based on morphospecies appear to have a relatively low error rate, delimitation errors involving morphospecies of taxonomically complex taxa and the precise identification of more friendly groups may be balancing each other out. In this case, morphospecies in different groups could be wrongly used as surrogate for valid taxonomic species in studies involving the Brazilian ant fauna (Souza et al., 2018; Vasconcelos et al., 2014). Therefore, based on our findings, morphospecies as diversity surrogates must be adopted only for selected and reliable target groups under specific criteria of taxonomic accuracy (Derraik et al., 2010).

Regarding the exotic species recorded, there is a clear prevalence of three species in Brazil. *Monomorium floricola* (Jerdon, 1851) (52 records), *Tapinoma melanocephalum* (Fabricius, 1793) (50), and *Paratrechina longicornis* (Latreille, 1802) (46) were found in all Brazilian biomes, except for the Pampa (Table 4). This pattern is an expected outcome due to the invasive potential of these three species and the long history of introduction worldwide, from their native distributions in Southeast Asia (Wong et al., 2021). On the other hand, three exotic species have been recorded only once or twice in the last 50 years in studies on ant diversity in Brazil: *Cardiocondyla nuda* (Mayr, 1866) (2 records), *Tetramorium lucayanum* Wheeler, 1905 (2), and *Trichomyrmex destructor* (Jerdon, 1851) (1) were found exclusively in the Atlantic Forest. Moreover, the Atlantic Forest had the highest number of records of exotic species (117), being the only biome with all the invasive species recorded in Brazil. This concentration of exotic species is largely due to the high number of studies carried out in this biome, predominantly located on the Brazilian coast. The cargo ports widely distributed on the coast are historically the entry route for invasive species in the country (Bueno et al., 2017), explaining the prevalence of exotic ant species in the Atlantic Forest.

Around 7% of the ant diversity studies in Brazil had some taxonomic imprecision regarding the spelling of scientific names or identification accuracy of the taxa (Table 5). Some of these flaws can be attributed to small typing errors, with no major consequences for interpreting the results or conclusions of the studies. However, the presence of non-existent taxonomic names (i.e., name combinations of genera and epithets that were never formally proposed) is extremely worrying. In some cases, the authors have changed the specific epithet of the species of a given genus for another genus, probably due to a lack of awareness when preparing the species lists. However, these taxonomically spurious names can be propagated by subsequent studies, causing a non-existent species to compose local lists of taxa or even to support conclusions about patterns of ant diversity, with very negative consequences (Murray et al., 2017). Nevertheless, perhaps the greatest concern regarding the errors in ant diversity studies analyzed here refers to the record of ant species and even genera in Brazil unrelated to the Neotropical ant fauna. Examples of problems caused by misidentifications and spurious records are frequent in literature, including severe economic and sanitary consequences (Bortolus, 2008). Thus, it is extremely important that authors, editors, and reviewers of scientific journals are aware of and committed to good taxonomic practices in ecological studies.

Although we recognize that the Brazilian ant fauna is higher than the 1130 species/subspecies listed in our study, the ant diversity publications analyzed here revealed almost 70% of the total species richness known in Brazil. This diversity is a significant proportion of the ant species described worldwide, around 8% (Bolton, 2022). However, sampling and listing the already described Brazilian ant species is the first result, but not the only one from ant diversity studies. Extensive surveys based on different sampling methods in unexplored places revealed many new species in Brazil. As a recent example, the first standardized inventory of ant fauna in native grasslands of Paraná state, southern Brazil (Franco et al., 2021), revealed six new species of the genus *Pheidole* (Casadei-Ferreira et al., 2020). Even species surveys in highly anthropized regions of Brazil, close to large urban centers, have proven effective in revealing a previously unknown ant diversity. For example, the species *Leptogenys academica* López-Muñoz et al., 2018, was recently described from a small fragment of Atlantic Forest on the campus of the Universidade Federal do Paraná, in Curitiba, after an unpretentious local sampling with didactic purposes (López-Muñoz et al., 2018).

The current number of described ant species is around 14000 worldwide (Bolton, 2022). However, different informal estimates indicate that this number could reach 20000 species (Krapf, 2018). Considering the existing sampling gaps in the planet's tropical areas, including Brazil (Guénard et al., 2012; Schmidt et al., 2022), it is easy to conclude that a large proportion of the undescribed contingent of ant species inhabit natural areas distributed on different Brazilian biomes. In this scenario, even the large number of unidentified species in diversity studies can be fundamental for advancing our taxonomic knowledge about ants. Based on the number of unidentified species in Brazilian ant inventories, it is likely that a great part of the ant diversity that remains to be described is currently lying in the cabinets of myrmecological collections under morphospecies codes. Still, regarding the limitations in identifying ant species in Brazil, our study shows an urgent need to invest in training specialists and adopt integrative methodological tools to improve the species delimitation in genera that represent frontiers of taxonomic knowledge for the ant fauna in the country.

Finally, our findings suggest a sampling bias in the patterns of ant occurrence in Brazil, with records unevenly distributed between and within Brazilian biomes (from 231 in the Pampa to more than 4000 in the Amazon and Atlantic Forest). Given this incomplete knowledge about ant distribution patterns and the increasing rates of habitat loss in the country (Divieso et al., 2020), future ant surveys to be carried out in areas that are both poorly studied and are under high risk of habitat loss are urgently needed.

Acknowledgements

The nearly 500 publications gathered in this survey were almost entirely financed by Brazilian research development agencies in the form of fellowships to graduate students and grants to researchers and institutions. These same agencies have suffered drastic cuts in their budgets in recent governments, compromising the continuity of research programs and the training of young scientists in Brazil. No less worrying is the environmental policy imposed by the current Brazilian government. In the last few years, we have witnessed an alarming growth of deforestation rates in Brazilian natural areas and even the encouragement of illicit activities associated with environmental degradation in Brazil, such as mining, arsons, and illegal exploitation of natural resources in pristine ecosystems. We here register our deep gratitude to funding agencies, educational and research institutions and environmental inspection agents who have been fighting for the conservation of the massive Brazilian biodiversity.

Disclosure statement

The authors declare no competing interests and their organizations had no role in any steps of the development of this study, from its design to submission for publication.

Authors’ contributions

R. M. Feitosa designed the study, compiled, organized and analyzed the data, wrote the manuscript, discussed concepts, revised and approved its final version. G. P. Camacho, T. S. R. Silva, N. Ladino, A. M. Oliveira, and M. A. Ulysséa compiled, organized and analyzed the data, wrote the manuscript, discussed concepts, revised and approved its final version. C. R. Ribas and F. A. Schmidt designed the study, compiled data, revised and approved its final version. All the remaining coauthors compiled data, revised and approved the final version.

Supplemental material

Supplemental material for this article can be accessed here: http://dx.doi.org/10.1080/14772000.2022.2089268.

Funding

This study was supported by the National Council for Scientific and Technological Development (CNPq) through fellowships to R. M. Feitosa, T. J. Izzo, J. C. Santos, R. Solar, F. B. Baccaro, A. Nogueira, and J. L. P. Souza [grants 3014495/2019-0; 309552/2018-4; 312752/2018-0; 305739/2019-0; 313986/2020-7; 434692/2018, 302065/2021-0]; the São Paulo Research Foundation (FAPESP) through fellowships to M. A. Ulysséa and A. Nogueira [grants 2012/21309-7, 2015/06485-1, 2018/11453-0, 2019/21309-7]; the National Science Foundation and the Peter Buck Postdoctoral Fellowship at the Smithsonian Institution through fellowships to E.Z. de Albuquerque [grant DEB1654829]; and CEMIG—Companhia Energética de Minas Gerais S.A. through fellowship to A. C. M. Queiroz [project P&D 611—Descomissionamento da PCH Pandeiros: Uma experiência inédita na América do Sul].

ORCID

Rodrigo M. Feitosa http://orcid.org/0000-0001-9042-0129
Gabriela P. Camacho http://orcid.org/0000-0002-8792-7719
Thiago S. R. Silva http://orcid.org/0000-0002-4239-1500
Mônica A. Ulysséa http://orcid.org/0000-0001-7296-4659
Natalia Ladino http://orcid.org/0000-0001-8230-9439
Aline M. Oliveira http://orcid.org/0000-0002-1967-3294
Emília Z. Albuquerque http://orcid.org/0000-0002-2888-2864
Fernando A. Schmidt http://orcid.org/0000-0002-3722-5196
Carla R. Ribas http://orcid.org/0000-0002-9781-0450
Anselmo Nogueira http://orcid.org/0000-0002-8232-4636
Fabrício B. Baccaro http://orcid.org/0000-0003-4747-1857
Antônio C. M. Queiroz http://orcid.org/0000-0002-7434-9796
Wesley Dáttilo http://orcid.org/0000-0002-4758-4379
Rogério R. Silva http://orcid.org/0000-0002-0599-2155
Jean C. Santos http://orcid.org/0000-0001-6031-9193
Ananza M. Rabello http://orcid.org/0000-0003-4089-251X
Maria Santina De C. Morini http://orcid.org/0000-0002-1823-6703
Yves P. Quinet http://orcid.org/0000-0002-6245-8784
Kleber Del-Claro http://orcid.org/0000-0001-8886-9568
Karine S. Carvalho http://orcid.org/0000-0002-8689-9066
Tathiana G. Sobrinho http://orcid.org/0000-0003-1567-0122
André B. Vargas http://orcid.org/0000-0002-8340-8217
Helena Maura Torezan-Silingardi http://orcid.org/0000-0002-0393-869X
Jorge Luiz P. Souza http://orcid.org/0000-0003-4574-8111
Thiago Izzo http://orcid.org/0000-0002-4613-3787
Denise Lange http://orcid.org/0000-0002-5386-7252
Iracenir A. Santos http://orcid.org/0000-0002-8879-6650
Lucas Paolucci http://orcid.org/0000-0001-6403-5200
Renata B. F. Campos http://orcid.org/0000-0002-2046-3235
Ricardo Solar http://orcid.org/0000-0001-5627-4017

References

Ab’Saber, A. N. (2003). *Os domínios de natureza no Brasil: Potencialidades paisagísticas*. Ateliê Editorial.

Adis, J., Harada, A. Y., Fonseca, C. R. V., Paarmann, W., & Rafael, J. A. (1998). Arthropods obtained from the Amazonian tree species “cupiuba” (*Goupia glabra*) by repeated canopy fogging with natural pyrethrum. *Acta Amazonica*, *28*, 273–283. https://doi.org/10.1590/1809-43921998283283

de Albuquerque, E. Z., Prado, L. P. D., Andrade-Silva, J., DE Siqueira, E. L. S., DA Silva Sampaio, K. L., Alves, D., Brando, C. R. F., Andrade, P. L., Feitosa, R. M., DE Azevedo Koch, E. B., Delabie, J. H. C., Fernandes, I., Baccaro, F. B., Souza, J. L. P., Almeida, R. P. S., & Silva, R. R. (2021). Ants of the State of Par, Brazil: A historical and comprehensive dataset of a key biodiversity hotspot in the Amazon Basin. *Zootaxa*, *5001*, 1–83. https://doi.org/10.11646/zootaxa.5001.1.1

Almeida, M. F. B., Santos, L. R., & Carneiro, M. A. A. (2014). Senescent stem-galls in trees of *Eremanthus erythropappus* as a resource for arboreal ants. *Revista Brasileira de Entomologia*, *58*, 265–272. https://doi.org/10.1590/S0085-56262014000300007

Andersen, A. N. (1995). A classification of Australian ant communities based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, *22*, 15–29. https://doi.org/10.2307/2846070

Andersen, A. N. (1997). Functional groups and patterns of organization in North American ant communities: A

comparison with Australia. *Journal of Biogeography*, *24*, 433–460. https://doi.org/10.1111/j.1365-2699.1997.00137.x
Andrade, T., Marques, G. V., & Del-Claro, K. (2007). Diversity of ground dwelling ants in cerrado: An analysis of temporal variations and distinctive physiognomies of vegetation (Hymenoptera: Formicidae). *Sociobiology*, *50*, 121–134.
Assis, D. S., Santos, I. A., Ramos, F. N., Barrios-Rojas, K. E., Majer, J. D., & Vilela, E. F. (2018). Agricultural matrices affect ground ant assemblage composition inside forest fragments. *Public Library of Science One*, *13*, e0197697. https://doi.org/10.1371/journal.pone.0197697
Baccaro, F. B., Feitosa, R. M., Fernández, F., Fernandes, I. O., Izzo, T. J., Souza, J. L. P., & Solar, R. (2015). *Guia para os gêneros de formigas do Brasil*. INPA.
Bihn, J. H., Verhaagh, M., & Brandl, R. (2008). Ecological stoichiometry along a gradient of forest succession: Bait preferences of litter ants. *Biotropica*, *40*, 597–599. https://doi.org/10.1111/j.1744-7429.2008.00423.x
Blaimer, B. B., Brady, S. G., Schultz, T. R., Lloyd, M. W., Fisher, B. L., & Ward, P. S. (2015). Phylogenomic methods outperform traditional multi-locus approaches in resolving deep evolutionary history: A case study of formicine ants. *BioMedCentral Evolutionary Biology*, *15*, 271. https://doi.org/10.1186/s12862-015-0552-5
Bolico, C. F., Oliveira, E. A., Gantes, M. L., Dumont, L. F. C., Carrasco, D. S., & D'Incao, F. (2012). Mirmecofauna (Hymenoptera, Formicidae) de Duas Marismas do Estuário da Lagoa dos Patos, RS: Diversidade, Flutuação de Abundância e Similaridade como Indicadores de Conservação. *EntomoBrasilis*, *5*, 11–20. https://doi.org/10.12741/ebrasilis.v5i1.147
Bolton, B. (2022). An online catalog of the ants of the world. https://antcat.org
Borowiec, M. L. (2019). Convergent evolution of the army ant syndrome and congruence in big-data phylogenetics. *Systematic Biology*, *68*, 642–656. https://doi.org/10.1093/sysbio/syy088
Bortolus, A. (2008). Error cascades in the biological sciences: The unwanted consequences of using bad taxonomy in ecology. *Ambio*, *37*, 114–118. https://doi.org/10.1579/0044-7447
Boudinot, B. E. (2015). Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): A new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. *European Journal of Taxonomy*, *120*, 1–62. https://doi.org/10.5852/ejt.2015.120
Bueno, O. C., Campos, A. E. C., & Morini, M. S. C. (2017). *Formigas em ambientes urbanos no Brasil*. Canal 6.
Camacho, G. P., Franco, W., Branstetter, M. G., Pie, M. R., Longino, J. T., Schultz, T. R., & Feitosa, R. M. (2022). UCE phylogenomics resolves major relationships among ectaheteromorph ants (Formicidae: Ectatomminae, Heteroponerinae): A new classification for the subfamilies and the description of a new genus. *Insect Systematics and Diversity*, *6*, 5. https://doi.org/10.1093/isd/ixab026
Campos-Farinha, A. E. C., Bergmann, E. C., de Faria, A. M., & Lara, R. I. R. (1997). Mirmecofauna em cultura de seringueira (*Hevea brasiliensis*) no município de Ibitinga, São Paulo. *Arquivos Do Instituto Biológico de São Paulo*, *64*, 103–109.
Carvalho, K. S., Nascimento, I. C., Delabie, J. H. C., Zina, J., Souza, A. L. B., Koch, E. B. A., Carneiro, M. A. F., & Santos, A. S. (2014). Litter as an important resource determining the diversity of epigeic ants in the south-central part of Bahia state, Brazil. *Sociobiology*, *59*, 1375–1387. https://doi.org/10.13102/sociobiology.v59i4.512
Casadei-Ferreira, A., Friedman, N. R., Economo, E. P., Pie, M. R., & Feitosa, R. M. (2021). Head and mandible shapes are highly integrated yet represent two distinct modules within and among worker subcastes of the ant genus *Pheidole*. *Ecology and Evolution*, *11*, 6104–6118. https://doi.org/10.1002/ece3.7422
Casadei-Ferreira, A., Economo, E. P., & Feitosa, R. M. (2020). Additions to the taxonomy of *Pheidole* (Hymenoptera: Formicidae) from the southern grasslands of Brazil. *Revista Brasileira de Entomologia*, *64*, e20200068. https://doi.org/10.1590/1806-9665-rbent-2020-0068
CBD – Convention on Biological Diversity. (2021). *Brazil – Main details*. https://www.cbd.int/countries/profile/?country=br
Chinarelli, H. D., Pupe, A. E., & Leal, L. C. (2021). Peace, sweet peace: Ants become less aggressive when carbohydrates abound. *Ecological Entomology*, *46*, 273–282. https://doi.org/10.1111/een.12959
Costa, F. V., Mello, R., Lana, T. C., & Neves, F. S. (2015). Ant fauna in megadiverse mountains: A checklist for the rocky grasslands. *Sociobiology*, *62*, 228–245. https://doi.org/10.13102/sociobiology.v62i2.228-245
Delabie, J. H. C., Fernandez, F., & Majer, J. D. (2012). Advances in neotropical myrmecology. *Psyche: A Journal of Entomology*, *2012*, 1–3. https://doi.org/10.1155/2012/286273
Derraik, J. G., Early, J. W., Closs, G. P., & Dickinson, K. J. (2010). Morphospecies and taxonomic species comparison for Hymenoptera. *Journal of Insect Science (Online)*, *10*, 108. https://doi.org/10.1673/031.010.10801
Divieso, R., Rorato, A., Feitosa, R. M., Meyer, A. L. S., & Pie, M. R. (2020). How to prioritize areas for new ant surveys? Integrating historical data on species occurrence records and habitat loss. *Journal of Insect Conservation*, *24*, 901–911. https://doi.org/10.1007/s10841-020-00262-y
Dröse, W., Podgaiski, L. R., Cavalleri, A., Feitosa, R. M., & Mendonça Jr., M. (2017). Ground-dwelling and vegetation ant fauna in southern Brazilian Grasslands. *Sociobiology*, *64*, 381–392. https://doi.org/10.13102/sociobiology.v64i4.1795
Dunn, R. R., Sanders, N. J., Fitzpatrick, M. C., Laurent, E., Lessard, J. P., Agosti, D., Andersen, A. N., Brühl, C., Cerdá, X., Ellison, A., Fisher, B., Gibb, H., Gotelli, N., Gove, A., Guénard, B., Janda, M., Kaspari, M., Longino, J. T., Majer, J., … Vasconcelos, H. (2007). Global ant (Hymenoptera : Formicidae) biodiversity and biogeography – a new database and its possibilities. *Myrmecological News*, *10*, 77–83.
Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I. R., Lescano, M. N., Saez, A., Werenkraut, V., & Pirk, G. I. (2020). The ecosystem services provided by social insects: Traits, management tools and knowledge gaps. *Biological Reviews of the Cambridge Philosophical Society*, *95*, 1418–1441. https://doi.org/10.1111/brv.12616
Emery, C. (1888). Formiche della provincia di Rio Grande do Sûl nel Brasile, raccolte dal dott. Hermann von Ihering. *Bollettino Della Società Entomologica Italiana*, *19*, 352–366.
Fernandes, I. O., & Oliveira, M. L. (2020). A mirmecologia brasileira no século XXI: A coleção do Instituto Nacional

de Pesquisas da Amazônia. *Boletim Do Museu Paraense Emílio Goeldi - Ciências Naturais*, *15*, 257–264. https://doi.org/10.46357/bcnaturais.v15i1.292

Fernandes, I. O., & Souza, J. L. (2018). Dataset of long-term monitoring of ground-dwelling ants (Hymenoptera: Formicidae) in the influence areas of a hydroelectric power plant on the Madeira River in the Amazon Basin. *Biodiversity Data Journal*, *6*, e24375. https://doi.org/10.3897/BDJ.6.e24375

Fernández, F., Guerrero, R. J., & Sánchez-Restrepo, A. F. (2021). Systematics and diversity of Neotropical ants. *Revista Colombiana de Entomología*, *47*, 1–420. https://doi.org/10.25100/socolen.v47i1.11082

Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: A review. *Biodiversity and Conservation*, *7*, 1221–1244. https://doi.org/10.1023/A:1008891901953

Fonseca, C., & Ganade, G. (1996). Asymmetries, compartments and null interactions in an Amazonian ant-plant community. *The Journal of Animal Ecology*, *65*, 339–347. https://doi.org/10.2307/5880

Formigas do Brasil. (2021). *Mirmecólogos pelo Brasil*. https://formigasdobrasil.com/mirmecologia/mirmecologos-pelo-brasil/

Franco, W., Ladino, N. M., Delabie, J. C. H., Dejean, A., Orivel, J., Fichaux, M., Groc, S., Leponce, M., & Feitosa, R. M. (2019). First checklist of the ants (Hymenoptera: Formicidae) of French Guiana. *Zootaxa*, *4674*, zootaxa.4674.5.2–543. https://doi.org/10.11646/zootaxa.4674.5.2

Franco, W., Vasconcelos, H. L., & Feitosa, R. M. (2021). Patterns of ant diversity in the natural grasslands of Southern Brazil. *Neotropical Entomology*, *50*, 725–735. https://doi.org/10.1007/s13744-021-00886-y

Giam, X. (2017). Global biodiversity loss from tropical deforestation. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 5775–5777. https://doi.org/10.1073/pnas.1706264114

Guénard, B., Weiser, M. D., & Dunn, R. R. (2012). Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 7368–7373.

Haddad, G. Q., Cividanes, F. J., & Martins, I. C. F. (2011). Species diversity of myrmecofauna and araneofauna associated with agroecosystem and forest fragments and their interaction with Carabidae and Staphylinidae (Coleoptera). *Florida Entomologist*, *94*, 500–509. https://doi.org/10.1653/024.094.0314

Heberling, J. M., Miller, J. T., Noesgaard, D., Weingart, S. B., & Schigel, D. (2021). Data integration enables global biodiversity synthesis. *Proceedings of the National Academy of Sciences*, *118*, e2018093118. https://doi.org/10.1073/pnas.2018093118

IBGE – Instituto Brasileiro de Geografia e Estatística. (2012). *Manual técnico da vegetação brasileira* (2nd ed.). IBGE-Série Manuais técnicos em Geociências.

ICMBio – Instituto Chico Mendes de Conservação da Biodiversidade. (2018). *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção*, ICMBio/MMA. (Vol. VII).

Jory, T. T., & Feitosa, R. M. (2020). First survey of the ants (Hymenoptera, Formicidae) of Piauí: Filling a major knowledge gap about ant diversity in Brazil. *Papéis Avulsos de Zoologia*, *60*, e20206014. https://doi.org/10.11606/1807-0205/2020.60.14

Kalif, K. A. B., Azevedo-Ramos, C., Moutinho, P., & Malcher, S. A. O. (2001). The effect of logging on the ground-foraging ant community in Eastern Amazonia. *Studies on Neotropical Fauna and Environment*, *36*, 215–219. https://doi.org/10.1076/snfe.36.3.215.2119

Kaspari, M. (2005). Global energy gradients and size in colonial organisms: Worker mass and worker number in ant colonies. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 5079–5083. https://doi.org/10.1073/pnas.0407827102

Krapf, P. (2018). How many ant species are there on Earth? *Myrmecological News Blog*. https://blog.myrmecologicalnews.org/2018/06/15/how-many-ant-species-are-there-on-earth/

LaPolla, J. S., Cheng, C. H., & Fisher, B. L. (2010). Taxonomic revision of the ant (Hymenoptera: Formicidae) genus *Paraparatrechina* in the Afrotropical and Malagasy regions. *Zootaxa*, *2387*, 1–27. https://doi.org/10.11646/zootaxa.2387.1.1

Leal, I., Ribeiro-Neto, J. D., Arnan, X., Oliveira, A. F. M., Arcoverde, G. B., Feitosa, R. M., & Andersen, A. N. (2018). *Ants of the Caatinga: Diversity, biogeography, and functional responses to anthropogenic disturbance and climate change*. In J. M. C. Silva, I. R. Leal, & M. Tabarelli (Eds.), *Caatinga: The largest tropical dry forest region in South America* (pp. 65–95). Springer.

Lewinsohn, T. M., & Prado, P. I. (2005). Biodiversidade brasileira: Síntese do estado atual do conhecimento. In T. M. Lewinsohn & P. I. Prado (Eds.), *Síntese do conhecimento atual da biodiversidade brasileira* (pp. 21–112). Contexto.

López-Muñoz, R. A., Villarreal, E., & Lattke, J. E. (2018). Two new species of *Leptogenys* from southern Brazil (Hymenoptera: Formicidae). *Zootaxa*, *4410*, 559–566. https://doi.org/10.11646/Zootaxa.4410.3.9

Lortie, C. J., & Svenning, J. C. (2015). The diversity of diversity studies: Retrospectives and future directions. *Ecography*, *38*, 330–334. https://doi.org/10.1111/ecog.01646

Lucky, A., Atchison, R. A., Ohyama, L., Zhang, Y. M., Williams, J. L., Pinkney IV, J. L., Clancy, K. L., Nielsen, A. N., & Lippi, C. A. (2020). Myrmecology, gender, and geography: Changing demographics of a research community over thirty years. *Myrmecological News*, *30*, 187–199. https://doi.org/10.25849/myrmecol.news_030:187

Lutinski, J., Guarda, C., Lutinski, C., & Garcia, F. (2018). Fauna de formigas em áreas de preservação permanente de usina hidroelétrica. *Ciência Florestal*, *28*, 1741–1754. https://doi.org/10.5902/1980509835334

Marini-Filho, O. J. (1999). Distribution, composition, and dispersal of ant gardens and tending ants in three kinds of central Amazonian habitats. *Tropical Zoology*, *12*, 289–296. https://doi.org/10.1080/03946975.1999.10539395

Martins, M. F. O., Nickele, M. A., Feitosa, R. M., Pie, M. R., & Reis-Filho, W. (2021). Species list of ground-dwelling ants (Hymenoptera: Formicidae) in the Nhecolândia, Pantanal, Mato Grosso do Sul, Brazil. *Papéis Avulsos de Zoologia*, *61*, e202161. https://doi.org/10.11606/1807-0205/2021.61.81

Mayr, G. (1878). Formiciden. Gesammelt in Brasilien von Professor Trail. *Verhandlungen Der k.k. – Zoologisch-Botanischen Gesellschaft in Wien*, *27*, 867–878.

Mertl, A. L., Sorenson, M. D., & Traniello, J. F. A. (2010). Community-level interactions and functional ecology of major workers in hyperdiverse ground-foraging *Pheidole* (Hymenoptera, Formicidae) of Amazonian Ecuador. *Insectes Sociaux*, *57*, 441–452. https://doi.org/10.1007/s00040-010-0102-5

MMA – Ministério do Meio Ambiente. (2021). *Biomas*. https://antigo.mma.gov.br/biomas.html

Moura, M. R., & Jetz, W. (2021). Shortfalls and opportunities in terrestrial vertebrate species discovery. *Nature Ecology & Evolution*, *5*, 631–639. https://doi.org/10.1038/s41559-021-01411-5

Munhae, C. B., Bueno, Z. A. F. N., Morini, M. S. C., & Silva, R. R. (2009). Composition of the ant fauna (Hymenoptera: Formicidae) in public squares in southern Brazil. *Sociobiology*, *53*, 455–472.

Murray, B. R., Martin, L. J., Phillips, M. L., & Pyšek, P. (2017). Taxonomic perils and pitfalls of dataset assembly in ecology: A case study of the naturalized Asteraceae in Australia. *NeoBiota*, *34*, 1–20. https://doi.org/10.3897/neobiota.34.11139

Nogueira, A., Baccaro, F. B., Leal, L. C., Rey, P. J., Lohmann, L. G., & Bronstein, J. L. (2020). Variation in the production of plant tissues bearing extrafloral nectaries explains temporal patterns of ant attendance in Amazonian understory plants. *Journal of Ecology*, *108*, 1578–1591. https://doi.org/10.1111/1365-2745.13340

Oliveira, F., Ribeiro-Neto, J., Andersen, A., & Leal, I. (2017). Chronic anthropogenic disturbance as a secondary driver of ant community structure: Interactions with soil type in Brazilian Caatinga. *Environmental Conservation*, *44*, 115–123. https://doi.org/10.1017/S0376892916000291

Pacheco, J. A., & Mackay, W. P. (2013). *The systematics and biology of the New World thief ants of the genus Solenopsis (Hymenoptera: Formicidae)*. Edwin Mellen Press.

Pacheco, R., & Vasconcelos, H. L. (2007). Invertebrate conservation in urban areas: Ants in the Brazilian Cerrado. *Landscape and Urban Planning*, *81*, 193–199. https://doi.org/10.1016/j.landurbplan.2006.11.004

Peixoto, T., Praxedes, C., Baccaro, F., Barbosa, R., & Júnior, M. (2010). Composição e riqueza de formigas (Hymenoptera: Formicidae) em savana e ambientes associados de Roraima. *Revista Agro@Mbiente on-Line*, *4*, 1–10. https://doi.org/10.18227/1982-8470ragro.v4i1.345

Pitts, J. P., Camacho, G. P., Gotzek, D., Mchugh, J. V., & Ross, K. G. (2018). Revision of the fire ants of the *Solenopsis saevissima* species-group (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington*, *120*, 308–411. https://doi.org/10.4289/0013-8797.120.2.308

Prado, L. P., Favacho, C. A. C., Silveira, O. T., & Silva, R. R. (2020). Uma jornada científica na Amazônia: Revisitando os 121 anos do acervo de Formicidae (Insecta: Hymenoptera) do Museu Paraense Emílio Goeldi. *Boletim Do Museu Paraense Emílio Goeldi - Ciências Naturais*, *15*, 245–255. https://doi.org/10.46357/bcnaturais.v15i1.277

Prado, L. P., Feitosa, R. M., Triana, S. P., Gutierrez, J. A. M., Rousseau, G. X., Silva, R. A., Siqueira, G. M., Santos, C. L. C., Silva, F. V., Silva, T. S. R., Ferreira, A. C., Silva, R. R., & Andrade-Silva, J. (2019). An overview of the ant fauna (Hymenoptera: Formicidae) of the state of Maranhão. *Papéis Avulsos de Zoologia*, *59*, e20195938. https://doi.org/10.11606/1807-0205/2019.59.38

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rabeling, C., Brown, J. M., & Verhaagh, M. (2008). Newly discovered sister lineage sheds light on early ant evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 14913–14917. https://doi.org/10.1073/pnas.0806187105

Rabello, A. M., Parr, C. L., Queiroz, A. C. M., Braga, D. L., Santiago, G. S., & Ribas, C. R. (2021). Taxonomic and functional approaches reveal different responses of ant assemblages to land-use changes. *Basic and Applied Ecology*, *54*, 39–49. https://doi.org/10.1016/j.baae.2021.04.001

Ribas, C. R., Sobrinho, T. G., Schoereder, J. H., Sperber, C. F., Lopes-Andrade, C., & Soares, S. D. (2005). How large is large enough for insects? Forest fragmentation effects at three spatial scales. *Acta Oecologica*, *27*, 31–41. https://doi.org/10.1016/j.actao.2004.08.008

Ribeiro-Neto, J. D., Arnan, X., Tabarelli, M., & Leal, I. (2016). Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. *Biodiversity and Conservation*, *25*, 943–956. https://doi.org/10.1007/s10531-016-1099-5

Rosa, I. M. D., Souza, C., & Ewers, R. M. (2012). Changes in size of deforested patches in the Brazilian Amazon. *Conservation Biology: The Journal of the Society for Conservation Biology*, *26*, 932–937.

Schmidt, C. A., & Shattuck, S. O. (2014). The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa*, *3817*, 1–242. https://doi.org/10.11646/zootaxa.3817.1.1

Schmidt, F. A., Ribas, C. R., Feitosa, R. M., Baccaro, F. B., de Queiroz, A. C. M., Sobrinho, T. G., Quinet, Y., Carvalho, K. S., Izzo, T., de Castro Morini, M. S., Nogueira, A., Torezan-Silingardi, H. M., Souza, J. L. P., Ulysséa, M. A., Vargas, A. B., Dáttilo, W., Del-Claro, K., Marques, T., Moraes, A. B., … Martello, F. (2022). Ant diversity studies in Brazil: An overview of the myrmecological research in a megadiverse country. *Insectes Sociaux*, *69*, 105–121. https://doi.org/10.1007/s00040-022-00848-6

Schmidt, F. A., Costa, M. M. S., Martello, F., Oliveira, A. B., Menezes, A. S., Fontenele, L. K., Morato, E. F., & Oliveira, M. A. (2020). Ant diversity studies in Acre: What we know and what we could do to know more? *Boletim Do Museu Paraense Emílio Goeldi - Ciências Naturais*, *15*, 113–134. https://doi.org/10.46357/bcnaturais.v15i1.235

Silva, R. R., & Brandão, C. R. F. (2014). Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. *Public Library of Science One*, *9*, e93049. https://doi.org/10.1371/journal.pone.0093049

Silva, R. R., Martello, F., Feitosa, R. M., Silva, O. G. M., Prado, L. P., Brandão, C. R. F., Albuquerque, E. Z., Morini, M. S. C., Delabie, J. H. C., Santos Monteiro, E. C., Emanuel Oliveira Alves, A., Wild, A. L., Christianini, A. V., Arnhold, A., Casadei Ferreira, A., Oliveira, A. M., Santos, A. D., Galbán, A., Oliveira, A. A., … Ribeiro, M. C. (2022). ATLANTIC ANTS: A dataset of ants in Atlantic Forests of South America. *Ecology*, *103*, e03580. https://doi.org/10.1002/ecy.3580

Soares, I. M., Santos, A. A., Delabie, J. H. C., & Castro, I. (2003). Comunidades de formigas (Hymenoptera: Formicidae) em uma "Ilha" de floresta ombrófila serrana em região de Caatinga (BA, Brasil). *Acta Biologica Leopoldensia*, *25*, 197–204.

Sobrinho, T., Schoereder, J., Sperber, C., & Madureira, M. S. (2003). Does fragmentation alter species composition in ant communities (Hymenoptera: Formicidae)? *Sociobiology*, *42*, 329–342.

Solomon, S. E., Rabeling, C., Sosa-Calvo, J., Lopes, C. T., Rodrigues, A., Vasconcelos, H. L., Bacci, M., Jr., Mueller, U. G., & Schultz, T. R. (2019). The molecular phylogenetics of *Trachymyrmex* Forel ants and their fungal cultivars provide insights into the origin and coevolutionary history of 'higher-attine' ant agriculture. *Systematic Entomology*, *44*, 939–956. https://doi.org/10.1111/syen.12370

Sosa-Calvo, J., Ješovnik, A., Vasconcelos, H. L., Bacci, M., Jr., & Schultz, T. R. (2017). Rediscovery of the enigmatic fungus-farming ant "*Mycetosoritis*" asper Mayr (Hymenoptera: Formicidae): Implications for taxonomy, phylogeny, and the evolution of agriculture in ants. *Public Library of Science One*, *12*, e0176498. https://doi.org/10.1371/journal.pone.0176498

Souza, J. L., Baccaro, F. B., Landeiro, V. L., Franklin, E., & Magnusson, W. E. (2012). Trade-offs between complementarity and redundancy in the use of different sampling techniques for ground-dwelling ant assemblages. *Applied Soil Ecology*, *56*, 63–73. https://doi.org/10.1016/j.apsoil.2012.01.004

Souza, J. L., Baccaro, F. B., Landeiro, V. L., Franklin, E., Magnusson, W. E., Pequeno, P. A., & Fernandes, I. O. (2016). Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. *Diversity and Distributions*, *22*, 111–122. https://doi.org/10.1111/ddi.12371

Souza, J. L. P., Baccaro, F. B., Pequeno, P. A. C. L., Franklin, E., & Magnusson, W. E. (2018). Effectiveness of genera as a higher-taxon substitute for species in ant biodiversity analyses is not affected by sampling technique. *Biodiversity and Conservation*, *27*, 3425–3445. https://doi.org/10.1007/s10531-018-1607-x

Trager, J. C. (1991). A revision of the fire ants, Solenopsis geminata group (Hymenoptera: Formicidae: Myrmicinae). *Journal of the New York Entomological Society*, *99*, 141–198.

Vasconcelos, H. L., Frizzo, T. L., Pacheco, R., Maravalhas, J. B., Camacho, G. P., Carvalho, K. S., Koch, E. B., & Pujol-Luz, J. R. (2014). Evaluating sampling sufficiency and the use of surrogates for assessing ant diversity in a neotropical biodiversity hotspot. *Ecological Indicators*, *46*, 286–292. https://doi.org/10.1016/j.ecolind.2014.06.036

Vasconcelos, H. L., Maravalhas, J. B., Feitosa, R. M., Pacheco, R., Neves, K. C., & Andersen, A. N. (2018). Neotropical savanna ants show a reversed latitudinal gradient of species richness, with climatic drivers reflecting the forest origin of the fauna. *Journal of Biogeography*, *45*, 248–2258. https://doi.org/10.1111/jbi.13113

Vasconcelos, H. L., & Vilhena, J. M. S. (2006). Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: A Comparison of Forests and Savannas. *Biotropica*, *38*, 100–106.

Wilson, E. O. (2003). *Pheidole in the New World: A dominant, hyperdiverse ant genus*. Harvard University Press.

Wilson, E. O., & Hölldobler, B. (2005). Eusociality: Origin and consequences. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 13367–13371. https://doi.org/10.1073/pnas.0505858102

Wong, M. K. L., Economo, E. P., & Guénard, B. (2021). The global spread and invasion capacities of alien ants. *BioRxiv*, *11*, 19469299. https://doi.org/10.1101/2021.11.19.469299

UN – United Nations. (2021). *UN Report: Nature's dangerous decline 'unprecedented'; species extinction rates 'accelerating'*. https://go.nature.com/37O15pf

Associate Editor: Rosa Fernandez