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

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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 inconsistencies 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 km². 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.webof-knowledge.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 reassessed 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 sub-specific 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
<i>Tatuidris</i>	0	2	0	0	0	0	0
Amblyoponinae	48	16	6	1	0	2	3
<i>Fulakora</i>	30	2	4	0	0	2	1
<i>Prionopelta</i>	18	14	2	1	0	0	2
Dolichoderinae	243	263	111	52	8	16	90
<i>Azteca</i>	24	22	9	2	0	4	4
<i>Dolichoderus</i>	56	185	25	4	0	3	17
<i>Dorymyrmex</i>	19	17	23	29	2	1	27
<i>Forelius</i>	2	3	13	8	2	1	9
<i>Gracilidris</i>	0	4	3	0	0	1	3
<i>Linepithema</i>	120	11	33	7	4	5	24
<i>Tapinoma</i>	22	21	5	2	0	1	6
Dorylinae	130	220	43	13	2	9	36
<i>Acanthostichus</i>	5	11	0	1	0	0	2
<i>Cheliomyrmex</i>	0	2	0	1	0	0	0
<i>Cylindromyrmex</i>	4	0	0	0	0	0	0
<i>Eciton</i>	23	64	3	1	0	2	9
<i>Labidus</i>	64	63	24	6	2	5	16
<i>Leptanilloides</i>	0	1	0	0	0	0	0
<i>Neivamyrmex</i>	11	48	12	3	0	1	6
<i>Neocerapachys</i>	15	7	1	0	0	1	1
<i>Nomamyrmex</i>	3	24	3	1	0	0	2
<i>Sphinctomyrmex</i>	5	0	0	0	0	0	0
Ectatomminae	390	351	193	58	12	24	95
<i>Acanthoponera</i>	3	2	3	2	0	0	3
<i>Alfaria</i>	9	9	0	0	0	0	3
<i>Bazboltonia</i>	5	0	0	0	0	0	0
<i>Ectatomma</i>	139	136	160	36	7	20	53
<i>Gnamptogenys</i>	41	120	16	9	2	2	13
<i>Heteroponera</i>	80	0	1	1	2	0	2
<i>Holcoponera</i>	68	62	12	10	1	1	16
<i>Poneracantha</i>	17	15	0	0	0	0	4
<i>Typhlomyrmex</i>	28	7	1	0	0	1	1
Formicinae	597	486	405	108	41	49	210
<i>Acropyga</i>	28	9	0	0	0	0	5
<i>Brachymyrmex</i>	83	35	15	6	5	3	18
<i>Camponotus</i>	399	376	374	95	32	41	158
<i>Gigantiops</i>	0	28	0	0	0	0	3
<i>Myrmelachista</i>	32	2	7	2	2	0	10
<i>Nylanderia</i>	33	27	2	2	2	4	12
<i>Paratrechina</i>	22	9	7	3	0	1	4
Myrmicinae	1840	1780	690	191	148	87	554
<i>Acanthognathus</i>	38	6	3	0	0	0	1
<i>Acromyrmex</i>	136	32	37	17	67	5	42
<i>Allomerus</i>	0	28	0	0	0	0	0
<i>Amoimyrmex</i>	0	0	0	0	9	0	2
<i>Apterostigma</i>	21	35	1	0	0	3	4
<i>Atta</i>	45	44	37	14	2	4	30
<i>Basicros</i>	23	5	0	1	0	1	4
<i>Blepharidatta</i>	1	19	3	0	0	0	4
<i>Cardiocondyla</i>	17	4	5	1	0	1	6
<i>Carebara</i>	28	25	8	0	0	1	7
<i>Cephalotes</i>	111	131	161	43	1	17	64
<i>Crematogaster</i>	131	323	68	27	8	11	52
<i>Cryptomyrmex</i>	5	2	0	0	0	1	0
<i>Cyatta</i>	0	0	3	0	0	0	0
<i>Cyphomyrmex</i>	76	73	19	13	2	3	13
<i>Daceton</i>	0	16	0	0	0	0	2

(continued)

Table 1. Continued.

Ant Taxa/Biome	Atlantic Forest	Amazon Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome
<i>Diaphoromyrma</i>	1	0	0	0	0	0	0
<i>Eurhopalothrix</i>	13	5	0	0	0	0	2
<i>Hylomyrma</i>	55	29	4	4	0	1	7
<i>Kalathomyrmex</i>	0	2	3	1	0	0	2
<i>Lachnomyrmex</i>	11	8	0	1	0	0	0
<i>Megalomyrmex</i>	66	74	6	1	0	2	3
<i>Monomorium</i>	33	24	4	1	0	1	11
<i>Mycetagroicus</i>	0	0	4	0	0	0	0
<i>Mycetarotes</i>	12	8	9	0	0	0	3
<i>Mycetomoellerius</i>	21	29	23	1	2	0	10
<i>Mycetophylax</i>	33	9	8	0	0	2	4
<i>Mycocepurus</i>	43	29	31	0	1	4	7
<i>Myrmicocrypta</i>	4	3	3	0	0	0	0
<i>Nesomyrmex</i>	21	15	19	5	0	0	8
<i>Ochetomyrmex</i>	4	46	8	0	1	1	7
<i>Octostruma</i>	79	42	12	4	0	4	6
<i>Oxyepoecus</i>	55	7	3	0	0	0	8
<i>Paratrachymyrmex</i>	7	31	4	0	0	0	3
<i>Phalacromyrmex</i>	3	0	0	0	0	0	0
<i>Pheidole</i>	191	228	74	14	35	8	109
<i>Pogonomyrmex</i>	11	12	15	3	5	1	9
<i>Procryptocerus</i>	34	21	1	0	0	0	6
<i>Rhopalothrix</i>	1	0	0	0	0	0	0
<i>Rogeria</i>	42	41	4	1	0	2	12
<i>Sericomyrmex</i>	9	9	6	0	0	0	6
<i>Solenopsis</i>	94	70	24	26	7	6	32
<i>Stegomyrmex</i>	8	2	0	0	0	0	1
<i>Strumigenys</i>	241	202	41	3	2	5	34
<i>Tetramorium</i>	10	6	1	1	0	0	4
<i>Tranopelta</i>	4	8	5	0	0	0	3
<i>Trichomyrmex</i>	1	0	0	0	0	0	0
<i>Wasmannia</i>	101	73	33	9	6	3	26
<i>Xenomyrmex</i>	0	4	0	0	0	0	0
Paraponerinae	1	22	2	0	0	0	2
<i>Paraponera</i>	1	22	2	0	0	0	2
Ponerinae	632	807	188	49	18	25	122
<i>Anochetus</i>	47	90	11	3	0	1	12
<i>Centromyrmex</i>	1	14	3	0	0	0	2
<i>Cryptopone</i>	3	3	1	0	0	0	1
<i>Dinoponera</i>	5	10	7	13	0	1	6
<i>Hypoponera</i>	47	9	4	0	5	1	7
<i>Leptogenys</i>	23	47	0	0	0	0	2
<i>Mayaponera</i>	26	53	1	0	0	0	4
<i>Neoponera</i>	134	218	59	8	5	8	32
<i>Odontomachus</i>	173	203	62	18	2	9	26
<i>Pachycondyla</i>	132	101	31	4	6	3	23
<i>Platythyrea</i>	1	13	0	1	0	0	3
<i>Pseudoponera</i>	11	14	3	0	0	0	3
<i>Rasopone</i>	13	14	2	0	0	2	1
<i>Simopelta</i>	5	9	0	0	0	0	0
<i>Thaumatomyrmex</i>	11	9	4	2	0	0	0
Proceratiinae	35	15	0	0	0	1	2
<i>Discothyrea</i>	29	15	0	0	0	0	2
<i>Probolomyrmex</i>	0	0	0	0	0	1	0
<i>Proceratium</i>	6	0	0	0	0	0	0
Pseudomyrmecinae	173	127	132	46	8	18	61
<i>Myrcidris</i>	0	2	0	0	0	0	0
<i>Pseudomyrmex</i>	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
<i>Tatuidris</i>	2	0	0	2	0	0.0
Amblyoponinae	76	2	31	109	33	30.3
<i>Fulakora</i>	39	0	16	55	16	29.1
<i>Prionopelta</i>	37	2	15	54	17	31.5
Dolichoderinae	783	50	912	1745	962	55.1
<i>Azteca</i>	65	12	252	329	264	80.2
<i>Dolichoderus</i>	290	13	130	433	143	33.0
<i>Dorymyrmex</i>	118	11	188	317	199	62.8
<i>Forelius</i>	38	1	23	62	24	38.7
<i>Gracilidris</i>	11	0	0	11	0	0.0
<i>Linepithema</i>	204	12	203	419	215	51.3
<i>Tapinoma</i>	57	0	109	166	109	65.7
Dorylinae	453	7	212	672	219	32.6
<i>Acanthostichus</i>	19	0	19	38	19	50.0
<i>Cheliomyrmex</i>	3	0	0	3	0	0.0
<i>Cylindromyrmex</i>	4	0	1	5	1	20.0
<i>Eciton</i>	102	0	26	128	26	20.3
<i>Labidus</i>	180	0	50	230	50	21.7
<i>Leptanilloides</i>	1	0	0	1	0	0.0
<i>Neivamyrmex</i>	81	5	91	177	96	54.2
<i>Neocerapachys</i>	25	1	0	26	1	3.8
<i>Nomamyrmex</i>	33	0	14	47	14	29.8
<i>Sphinctomyrmex</i>	5	0	2	7	2	28.6
Ectatomminae	1123	30	389	1542	419	27.2
<i>Acanthoponera</i>	13	0	7	20	7	35.0
<i>Alfaria</i>	21	0	0	21	0	0.0
<i>Bazboltonia</i>	5	0	0	5	0	0.0
<i>Ectatomma</i>	551	3	109	663	112	16.9
<i>Gnamptogenys</i>	203	12	218	433	230	53.1
<i>Heteroponera</i>	86	0	34	120	34	28.3
<i>Holcoponera</i>	170	10	0	180	10	5.6
<i>Poneracantha</i>	36	3	0	39	3	7.7
<i>Typhlomyrmex</i>	38	1	21	60	22	36.7
Formicinae	1896	84	2523	4503	2607	57.9
<i>Acropyga</i>	42	2	40	84	42	50.0
<i>Brachymyrmex</i>	165	10	577	752	587	78.1
<i>Camponotus</i>	1475	52	1342	2869	1394	48.6
<i>Gigantiops</i>	31	0	3	34	3	8.8
<i>Myrmelachista</i>	55	3	115	173	118	68.2
<i>Nylanderia</i>	82	16	208	306	224	73.2
<i>Paratrechina</i>	46	1	217	264	218	82.6
Myrmicinae	5290	303	8958	14551	9261	63.6
<i>Acanthognathus</i>	48	0	10	58	10	17.2
<i>Acromyrmex</i>	336	11	134	481	145	30.1
<i>Allomerus</i>	28	1	7	36	8	22.2
<i>Amoimyrmex</i>	11	0	0	11	0	0.0
<i>Apterostigma</i>	64	19	195	278	214	77.0
<i>Atta</i>	176	1	64	241	65	27.0
<i>Basiceros</i>	34	0	31	65	31	47.7
<i>Blepharidatta</i>	27	0	11	38	11	28.9
<i>Cardiocondyla</i>	34	0	10	44	10	22.7
<i>Carebara</i>	69	8	97	174	105	60.3
<i>Cephalotes</i>	528	9	192	729	201	27.6
<i>Crematogaster</i>	620	50	749	1419	799	56.3
<i>Cryptomyrmex</i>	8	0	0	8	0	0.0
<i>Cyatta</i>	3	0	0	3	0	0.0

(continued)

Table 2. Continued.

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

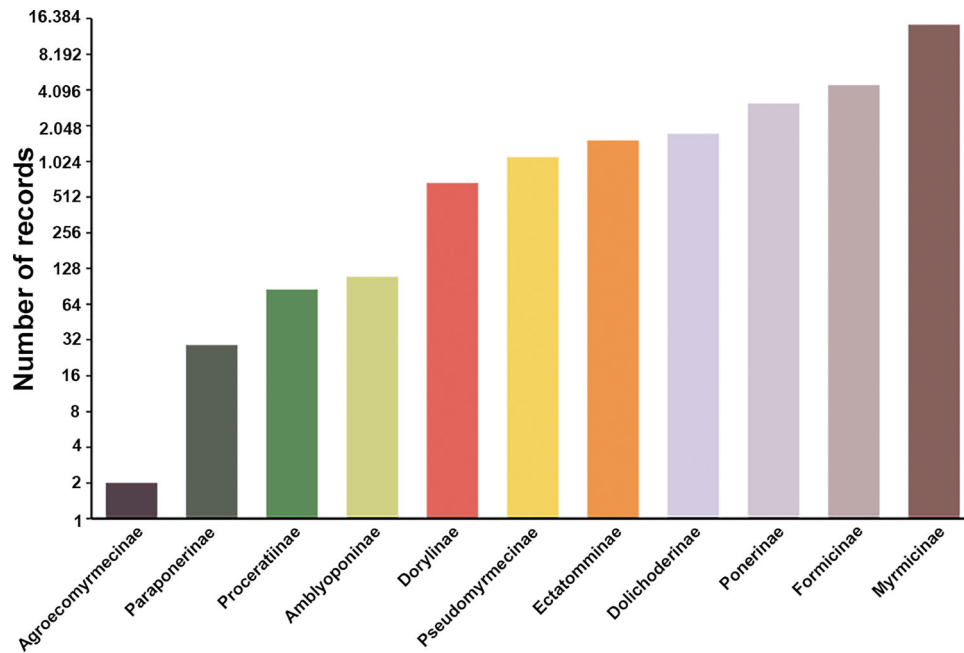


Fig. 1. Bar plot depicting the number of species records per subfamily in Brazilian ant diversity studies. Absolute numbers were converted to a logarithmic scale (base 2) for better visualization.

(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. 5d).

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), *Hypoconera* (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
<i>Tatuidris</i>	0	1	0	0	0	0	0	1	1
Amblyoponinae	7	5	2	1	0	2	3	8	15
<i>Fulakora</i>	5	2	1	0	0	2	1	5	8
<i>Prionopelta</i>	2	3	1	1	0	0	2	3	7
Dolichoderinae	42	57	33	19	3	12	39	82	149
<i>Azteca</i>	11	10	5	2	0	3	4	17	67
<i>Dolichoderus</i>	11	28	8	3	0	3	13	32	38
<i>Dorymyrmex</i>	4	7	8	5	0	1	8	13	15
<i>Forelius</i>	2	3	2	3	1	1	3	3	6
<i>Gracilidris</i>	0	1	1	0	0	1	1	1	1
<i>Linepithema</i>	12	5	8	5	2	2	9	12	13
<i>Tapinoma</i>	2	3	1	1	0	1	1	4	7
Dorylinae	18	35	17	8	1	5	20	47	111
<i>Acanthostichus</i>	2	4	0	1	0	0	2	5	11
<i>Cheliomyrmex</i>	0	1	0	1	0	0	0	2	2
<i>Cylindromyrmex</i>	1	0	0	0	0	0	0	1	6
<i>Eciton</i>	4	9	2	1	0	1	6	9	17
<i>Labidus</i>	3	4	3	2	1	2	3	4	6
<i>Leptanilloides</i>	0	1	0	0	0	0	0	1	6
<i>Neivamyrmex</i>	5	13	10	2	0	1	6	21	55
<i>Neocerapachys</i>	1	1	1	0	0	1	1	1	1
<i>Nomamyrmex</i>	1	2	1	1	0	0	2	2	2
<i>Sphinctomyrmex</i>	1	0	0	0	0	0	0	1	3
Ectatomminae	45	48	22	15	5	12	28	72	83
<i>Acanthoponera</i>	1	2	1	1	0	0	1	2	4
<i>Alfaria</i>	2	4	0	0	0	0	2	5	6
<i>Bazboltonia</i>	1	0	0	0	0	0	0	1	1
<i>Ectatomma</i>	9	9	10	6	2	8	10	11	12
<i>Gnamptogenys</i>	10	15	6	4	1	2	6	19	21
<i>Heteroponera</i>	7	0	1	1	1	0	1	7	7
<i>Holcoponera</i>	7	9	3	3	1	1	4	12	13
<i>Poneracantha</i>	4	6	0	0	0	0	3	9	11
<i>Typhlomyrmex</i>	4	3	1	0	0	1	1	5	9
Formicinae	82	88	57	28	14	21	64	131	245
<i>Acropyga</i>	7	4	0	0	0	0	2	7	6
<i>Brachymyrmex</i>	13	9	6	3	2	2	9	20	30
<i>Camponotus</i>	52	65	46	20	10	16	41	87	169
<i>Gigantiops</i>	0	1	0	0	0	0	1	1	1
<i>Myrmelachista</i>	6	2	3	2	1	0	6	8	27
<i>Nylanderia</i>	3	6	1	2	1	2	4	7	11
<i>Paratrechina</i>	1	1	1	1	0	1	1	1	1
Myrmicinae	359	349	189	82	51	63	269	612	813
<i>Acanthognathus</i>	3	2	2	0	0	0	1	3	5
<i>Acromyrmex</i>	19	9	15	7	14	4	16	24	30
<i>Allomerus</i>	0	4	0	0	0	0	0	4	6
<i>Amoimyrmex</i>	0	0	0	0	1	0	1	1	2
<i>Apterostigma</i>	12	10	1	0	0	3	4	18	19
<i>Atta</i>	5	3	2	3	1	1	7	8	9
<i>Basiceros</i>	3	1	0	1	0	1	3	4	6
<i>Blepharidatta</i>	1	1	1	0	0	0	1	3	4
<i>Cardiocondyla</i>	5	3	2	1	0	1	2	5	5
<i>Carebara</i>	6	6	2	0	0	1	3	11	18
<i>Cephalotes</i>	19	28	27	15	1	10	20	48	65
<i>Crematogaster</i>	25	34	24	14	4	7	26	50	61
<i>Cryptomyrmex</i>	2	1	0	0	0	1	0	2	2
<i>Cyatta</i>	0	0	1	0	0	0	0	1	1
<i>Cyphomyrmex</i>	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
<i>Daceton</i>	0	1	0	0	0	0	1	1	1
<i>Diaphoromyrma</i>	1	0	0	0	0	0	0	1	1
<i>Eurhopalothrix</i>	6	1	0	0	0	0	2	7	9
<i>Hylomyrma</i>	5	9	2	2	0	1	7	10	12
<i>Kalathomyrmex</i>	0	1	1	1	0	0	1	1	1
<i>Lachnomyrmex</i>	3	4	0	1	0	0	0	5	5
<i>Megalomyrmex</i>	12	13	4	1	0	2	3	18	19
<i>Monomorium</i>	3	2	2	1	0	1	2	3	6
<i>Mycetagroicus</i>	0	0	1	0	0	0	0	1	4
<i>Mycetarotes</i>	3	3	4	0	0	0	1	4	4
<i>Mycetomoellerius</i>	10	6	10	1	1	0	7	19	24
<i>Mycetophylax</i>	10	3	2	0	0	2	4	13	14
<i>Mycocepurus</i>	3	2	3	0	1	2	2	3	4
<i>Myrmicocrypta</i>	4	2	1	0	0	0	0	5	8
<i>Nesomyrmex</i>	5	5	5	4	0	0	7	10	14
<i>Ochetomyrmex</i>	2	2	1	0	1	1	2	2	2
<i>Octostruma</i>	5	8	2	4	0	4	4	8	8
<i>Oxyepocus</i>	11	4	3	0	0	0	7	15	17
<i>Paratrachymyrmex</i>	1	5	2	0	0	0	1	5	7
<i>Phalacromyrmex</i>	1	0	0	0	0	0	0	1	1
<i>Pheidole</i>	59	61	32	7	19	7	64	124	184
<i>Pogonomyrmex</i>	2	2	2	1	3	1	5	5	5
<i>Procryptocerus</i>	11	8	1	0	0	0	4	16	30
<i>Rhopalothrix</i>	1	0	0	0	0	0	0	1	1
<i>Rogeria</i>	14	13	3	1	0	2	8	19	20
<i>Sericomyrmex</i>	3	4	3	0	0	0	5	6	8
<i>Solenopsis</i>	13	18	5	6	1	3	9	23	49
<i>Stegomyrmex</i>	2	2	0	0	0	0	1	2	3
<i>Strumigenys</i>	43	44	12	3	1	4	23	71	86
<i>Tetramorium</i>	3	2	1	1	0	0	2	3	4
<i>Tranopelta</i>	1	2	1	0	0	0	1	2	2
<i>Trichomyrmex</i>	1	0	0	0	0	0	0	1	1
<i>Wasmannia</i>	10	6	5	3	2	2	6	10	8
<i>Xenomyrmex</i>	0	2	0	0	0	0	0	2	2
Paraponerinae	1	1	1	0	0	0	1	1	1
<i>Paraponera</i>	1	1	1	0	0	0	1	1	1
Ponerinae	73	96	41	17	9	17	55	120	173
<i>Anochetus</i>	9	8	3	2	0	1	8	12	14
<i>Centromyrmex</i>	1	3	2	0	0	0	1	3	3
<i>Cryptopone</i>	1	1	1	0	0	0	1	2	4
<i>Dinoponera</i>	2	4	3	1	0	1	4	5	10
<i>Hypoponera</i>	8	7	1	0	3	1	5	10	29
<i>Leptogenys</i>	8	11	0	0	0	0	2	15	24
<i>Mayaponera</i>	2	2	1	0	0	0	2	2	3
<i>Neoponera</i>	19	26	14	5	3	6	14	30	38
<i>Odontomachus</i>	7	14	8	4	1	4	8	16	17
<i>Pachycondyla</i>	5	5	4	3	2	2	5	5	9
<i>Platythyrea</i>	1	4	0	1	0	0	2	4	5
<i>Pseudoponera</i>	2	2	2	0	0	0	2	2	3
<i>Rasopone</i>	2	2	1	0	0	2	1	2	2
<i>Simopelta</i>	2	3	0	0	0	0	0	5	5
<i>Thaumatomyrmex</i>	4	4	1	1	0	0	0	7	7
Proceratiinae	3	5	0	0	0	1	1	7	13
<i>Discothyrea</i>	2	5	0	0	0	0	1	5	6
<i>Probolomyrmex</i>	0	0	0	0	0	1	0	1	5
<i>Proceratium</i>	1	0	0	0	0	0	0	1	2
Pseudomyrmecinae	27	31	27	15	3	10	24	49	80
<i>Myrcidris</i>	0	1	0	0	0	0	0	1	1
<i>Pseudomyrmex</i>	27	30	27	15	3	10	24	47	79
Total	657	716	389	185	86	143	504	1130	1684

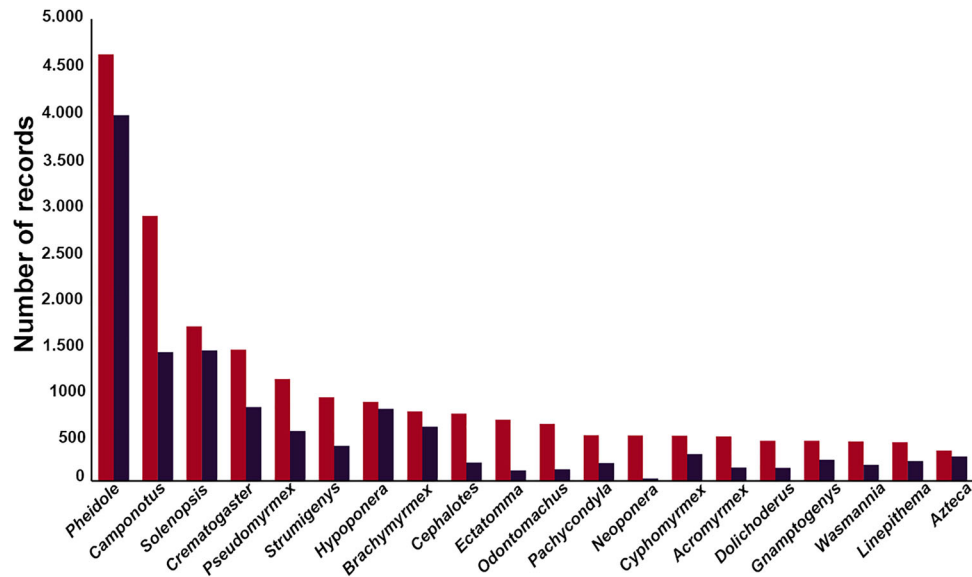


Fig. 2. Bar plot depicting the absolute number of species records for each of the 20 most frequently recorded ant genera in Brazilian ant diversity studies. Red bars show the total number of records per genera (nominal and unidentified); purple bars show the number of unidentified records per genera.

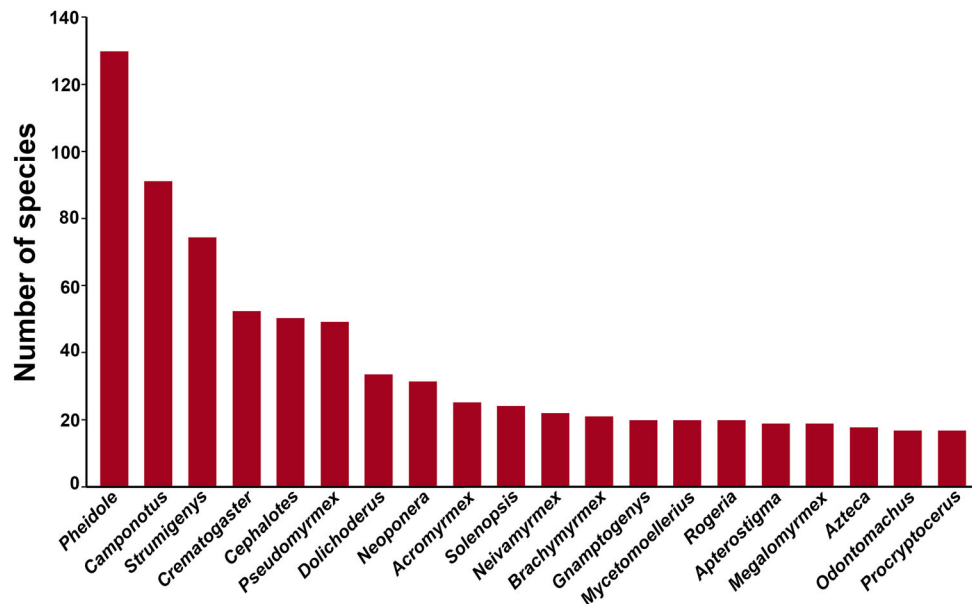


Fig. 3. Bar plot depicting the number of species recorded for the 20 most diverse ant genera in ant diversity studies in Brazil.

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 Amazon						
		Forest	Forest	Cerrado	Caatinga	Pampa	Pantanal	Multibiome
<i>Anochetus oriens</i> Kempf, 1964	Vulnerable	1	0	0	1	0	0	0
<i>Atta robusta</i> Borgmeier, 1939	Vulnerable	1	0	0	0	0	0	0
<i>Brachymyrmex micromegas</i> Santschi, 1923	Endangered	1	0	0	0	0	0	0
<i>Cardiocondyla emeryi</i> Forel, 1881	Exotic	1	1	1	1	0	0	1
<i>Cardiocondyla minutior</i> Forel, 1899	Exotic	1	1	0	0	0	0	0
<i>Cardiocondyla nuda</i> (Mayr, 1866)	Exotic	1	0	0	0	0	0	0
<i>Cardiocondyla obscurior</i> Wheeler, 1929	Exotic	1	1	0	0	0	1	1
<i>Cardiocondyla wroughtonii</i> (Forel, 1890)	Exotic	1	0	1	0	0	0	0
<i>Diaphoromyrma sofiae</i> Fernández, Delabie & Nascimento, 2009	Endangered	1	0	0	0	0	0	0
<i>Dinoponera lucida</i> Emery, 1901	Endangered	1	0	0	0	0	0	0
<i>Lachnomyrmex nordestinus</i> Feitosa & Brandão, 2008	Vulnerable	1	0	0	0	0	0	0
<i>Monomorium delabiei</i> Fernández, 2007	Vulnerable	1	0	0	0	0	0	0
<i>Monomorium floricola</i> (Jerdon, 1851)	Exotic	1	1	1	1	0	1	1
<i>Monomorium pharaonis</i> (Linnaeus, 1758)	Exotic	1	1	1	0	0	0	1
<i>Mycetomoellerius atlanticus</i> (Mayhé-Nunes & Brandão, 2007)	Vulnerable	1	0	0	0	0	0	0
<i>Mycetophylax simplex</i> (Emery, 1888)	Vulnerable	0	0	0	0	0	0	1
<i>Paratrechina longicornis</i> (Latreille, 1802)	Exotic	1	1	1	1	0	1	1
<i>Pheidole megacephala</i> (Fabricius, 1793)	Exotic	1	1	1	0	0	0	1
<i>Rhopalothrix plaumanni</i> Brown & Kempf, 1960	Endangered	1	0	0	0	0	0	0
<i>Strumigenys emmae</i> (Emery, 1890)	Exotic	1	1	0	0	0	0	0
<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	Exotic	1	1	1	1	0	1	1
<i>Tetramorium bicarinatum</i> (Nylander, 1846)	Exotic	1	1	0	0	0	0	1
<i>Tetramorium lucayanum</i> Wheeler, 1905	Exotic	1	0	0	0	0	0	0
<i>Tetramorium simillimum</i> (Smith, 1851)	Exotic	1	1	1	1	0	0	1
<i>Trichomyrmex destructor</i> (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 quadricaps* 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 *Hypoconera* (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-Ménéville, 1838) was the most frequent, with 11 records, followed by *Camponotus rufipes* (10), *Acromyrmex heyeri* (Forel, 1899) (9), *Acromyrmex 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), *Hypoconera*, *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),

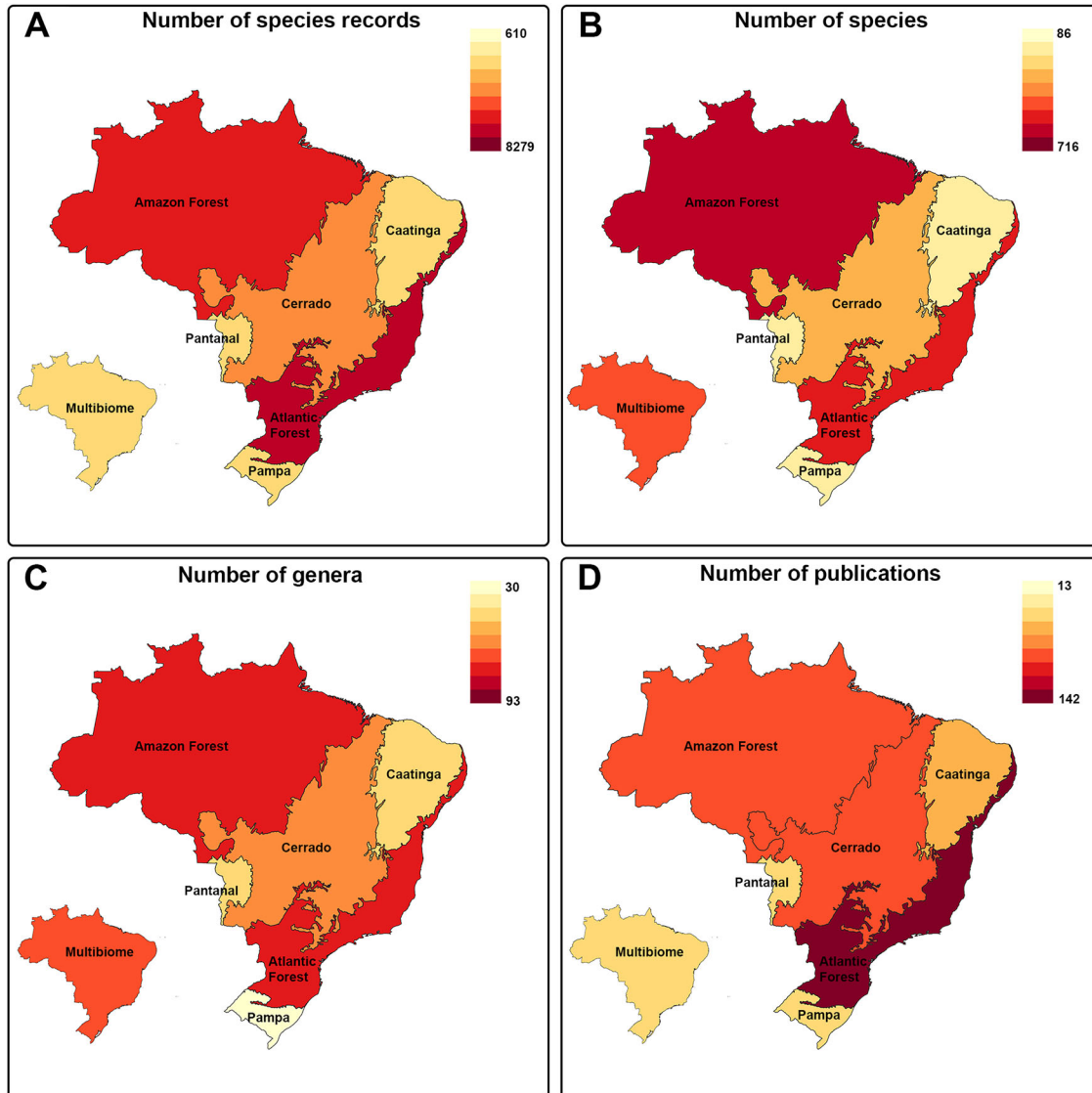


Fig. 5. Heatmap depicting the ant species records, the number of genera and species, the publications on ant diversity and their distribution across Brazilian biomes. (A) Number of ant species records (including nominal and unidentified species); (B) Number of ant species (morphospecies excluded); (C) 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

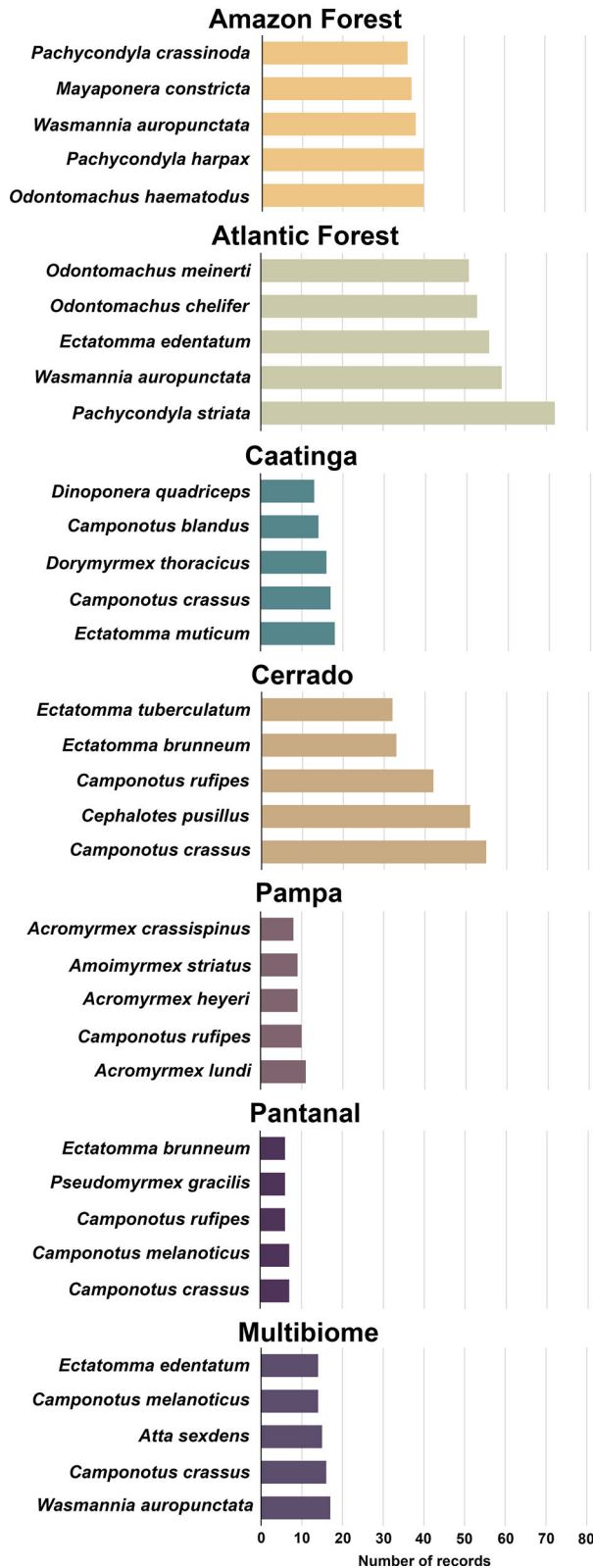


Fig. 6. Bar plots depicting the number of records for each of the five most frequently collected species in each of the six biomes occurring in Brazil and for the multi-biome category.

taxa information of these multi-biome papers as a data set separated from the official Brazilian biomes. Multi-biome 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 multi-biome 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). Multi-biome 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 *Holcaponera 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 morpho-species (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 of 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
<i>Allomerus auripunctata</i>	Amazon	Fonseca and Ganade (1996)	Invalid name
<i>Allomerus prancei</i>	Amazon	Fonseca and Ganade (1996)	Invalid name
<i>Anoplolepis</i> sp.	Pampa	Bolico et al. (2012)	Misidentification
<i>Brachymyrmex pyramica</i>	Caatinga	Soares et al. (2003)	Invalid name
<i>Camponotus eurynota</i>	Amazon	Adis et al. (1998)	Invalid name
<i>Camponotus leyoligi</i>	Atlantic Forest	Sobrinho et al. (2003)	Invalid name
<i>Camponotus temoralus</i>	Amazon	Nogueira et al. (2020)	Invalid name
<i>Cephalotes grandispinosus</i>	Atlantic Forest	Campos-Farinha et al. (1997)	Invalid name
<i>Crematogaster elevans</i>	Cerrado	Rabello et al. (2021)	Invalid name
<i>Crematogaster micropilosa</i>	Amazon	Nogueira et al. (2020)	Invalid name
<i>Dolichoderus burtoni</i>	Amazon	Souza et al. (2018)	Invalid name
<i>Dorymyrmex alticanis</i>	Cerrado, Atlantic Forest	Pacheco and Vasconcelos (2007), Munhae et al. (2009)	Invalid name
<i>Dorymyrmex guianensis</i>	Amazon	Vasconcelos and Vilhena (2006)	Invalid name
<i>Iridomyrmex</i> sp.	Cerrado	Almeida et al. (2014)	Misidentification
<i>Monomorium panamanus</i>	Amazon	Souza et al. (2012)	Invalid name
<i>Monomorium stollii</i>	Amazon	Souza et al. (2012)	Invalid name
<i>Nomamyrmex espinodiz</i>	Amazon	Peixoto et al. (2010)	Invalid name
<i>Odontomachus mayri</i>	Amazon	Marini-Filho (1999)	Invalid name
<i>Odontonachus blandus</i>	Atlantic Forest	Haddad et al. (2011)	Invalid name
<i>Pachycondyla clavata</i>	Atlantic Forest	Chinarelli et al. (2021)	Invalid name
<i>Pachycondyla evexa</i>	Cerrado	Andrade et al. (2007)	Invalid name
<i>Pachycondyla rapax</i>	Amazon	Nogueira et al. (2020)	Invalid name
<i>Patagonomyrmex angustus</i>	Atlantic Forest	Lutinski et al. (2018)	Misidentification
<i>Pheidole escoliolips</i>	Cerrado	Nogueira et al. (2020)	Invalid name
<i>Plagiolepis</i> sp.	Atlantic Forest	Campos-Farinha et al. (1997), Sobrinho et al. (2003), Ribas et al. (2005)	Misidentification
<i>Ponera</i> sp.	Caatinga, Cerrado, Atlantic Forest	Bihn et al. (2008), Oliveira et al. (2017), Ribeiro-Neto et al. (2016), Costa et al. (2015)	Misidentification
<i>Prenolepis</i> sp.	Amazon, Atlantic Forest	Kalif et al. (2001), Assis et al. (2018)	Misidentification
<i>Rhytidoponera strigosa</i>	Atlantic Forest	Campos-Farinha et al. (1997)	Misidentification
<i>Solenopsis molestans</i>	Atlantic Forest	Assis et al. (2018)	Invalid name
<i>Strumigenys mandibulata</i>	Caatinga, Atlantic Forest	Carvalho et al. (2014)	Invalid name
<i>Syscia augustae</i>	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. 5d). 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 Emílio 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 World 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 floridicola* (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.

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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

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