Received: 7 February 2022 | Revised: 26 July 2022 | Accepted: 24 August 2022

DOI: 10.1111/btp.13158

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

REVIEW

Ant diversity decreases during the dry season: A meta-analysis of the effects of seasonality on ant richness and abundance

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Funding information
Companhia Energética de Minas Gerais/ Programa de Pesquisa e Desenvolvimento da ANEEL, Grant/Award Number: P&DGT0611; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 301383/2021-2, 3014495/2019-0, 305739/2019-0, 309552/2018-4, 312752/2018-0, 313007-2020/9, 313986/2020-7 and 434692/2018-2; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2012/21309-7, 2015/06485, 2018/11453-0, 2019/19544-7 and 2019/24810-8; National Science Foundation, Grant/ Award Number: DEB1654829

Associate Editor: Jennifer Powers

Handling Editor: Michael Staab

Abstract

Tropical studies traditionally describe insect diversity variation throughout the year. The temporally structured responses of insect assemblages to climate seasonality vary across ecosystems due to gradients of resource availability and limiting ecological factors. These idiosyncratic responses might be particularly true across the vast geographical range of the Brazilian territory, including various environments that harbor one of the most diverse ant faunas worldwide. This study addressed the relationship between ant diversity and climatic seasonality, performing a quantitative review of the published data on ant diversity collected in Brazil. We investigated the seasonality effect on ant abundance and richness described in the literature in 47 papers published between 2000 and 2018. These studies were developed mainly in the Atlantic Forest biome and collected ants with pitfall traps on the soil/litter stratum. We initially carried out a vote-counting procedure by comparing the number of significant results describing seasonal differences in the ant assemblage. We found that most papers described a similar pattern of ant abundance, richness, and species composition between seasons. However, when we performed a meta-analysis, we observed a clear pattern of higher ant abundance and richness in the wet/summer season compared with the dry/winter season. Our meta-analysis reveals that the ant diversity decreases in the dry season, strongly in the Cerrado biome. Additionally, we point out differences in the sampling effort across biomes, indicating the need for further investments in studies focused on temporal diversity patterns, including seasonal effects, on the insect assemblage in biomes less investigated so far.

Abstract in Portuguese is available with online material.

KEYWORDS
ants, Brazil, diversity, Formicidae, meta-analysis, seasonality, tropical biomes, wet-dry

1 | INTRODUCTION

Climatic conditions (e.g., fluctuations in temperature, humidity, and precipitation) are determinants of insect diversity in tropical and temperate ecosystems because they shape the levels of resources and ecological conditions available to species (Prather et al., 2012; Wolda, 1988). The predictable temporal patterns of resources and climate variation within the years are called seasonality (Schwartz et al., 2020; Wolda, 1978). In response to seasonality, the activities of organisms, including the insect assemblages and their biotic interactions, can change over time (Anjos et al., 2019; Costa et al., 2018; Neves et al., 2010; Wolda, 1978).

Many studies in tropical regions describe an increase in insect richness and/or abundance, as well as changes in species composition, during the wet/summer season (Grimbacher et al., 2018; Kishimoto-Yamada & Itioka, 2015; Munyai & Foord, 2015; Vasconcelos et al., 2010). In general, this increase is associated with more favorable conditions and increased availability of insect resources (Rico-Gray & Oliveira, 2007). However, some studies show the opposite temporal pattern, that is, lower insect richness and abundance in the wet/summer season (e.g., Gove et al., 2005; Marques et al., 2017). Additionally, there are some studies that show an absence of variation in insect diversity throughout the year (e.g., Grimbacher & Stork, 2009; Montine et al., 2014). These results pose the question of the more general pattern of variation in insect diversity throughout the year and whether climatic seasonality is associated with such variation.

Among insects, ants are among the most diverse, abundant, and ecologically notable organisms on Earth. Also, like other insects, ants are positively influenced by temperature and precipitation (Gibb et al., 2015). These climatic filters affect different facets of ant assemblages, including ant activity, distribution, and diversity, because ant species exhibit specific tolerance limits (Barrow & Parr, 2008; Diamond et al., 2012). These tolerance limits can vary significantly between ant assemblages in different habitats and vegetation types (e.g., desert ants differ considerably from rainforest ants). However, climatic variations within habitats throughout the year generate variable responses in ant diversity patterns. Thus, changes in temperature and precipitation can directly or indirectly affect ant activity and influence the richness, abundance, and composition of ants as well as their biotic interactions (Cook et al., 2011; Costa et al., 2018; Lasmar et al., 2021; Nogueira et al., 2020; Nunes et al., 2020; Rico-Gray et al., 2006, 2012).

The Neotropical region has several biomes characterized by particular plant and animal life forms. The concept of biome is based on the vegetation physiognomy that is the primary determinant of plant formation (Mucina, 2019). In Brazil, there is an impressive diversity of geological formations and vegetation cover types 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, 2021). Despite being considered geographic and ecological units, the Brazilian biomes encompass a remarkable heterogeneity in climate, vegetation, topography, soil, and hydrography (Ab'Saber, 2003; IBGE, 2012). Many of these areas have marked climatic seasonality, and the wet and dry periods are mainly related to water availability that can change abruptly (Guan et al., 2015; Liebmann et al., 2012; Williams & Middleton, 2008). The current knowledge about the effects of climatic seasonality on ants came from studies focused on sampling sites that comprise a small area within these biomes. Additionally, these studies were carried out over short periods (e.g., Marques & Del-Claro, 2006; Gomes et al., 2014, studying savannas and tropical forests, respectively). However, we found no records of a single study attempting to compile information about the relationship between climatic seasonality and ant diversity across a broader range. As climatic seasonality varies widely within and among biomes (Lasmar et al., 2021), it is not clear whether there are systematic effects of seasonal climate variation on ant assemblages that are common across biomes.

This study addresses the relationship between ant diversity and seasonality with a systematic review composed of qualitative and quantitative syntheses (descriptive review and meta-analysis) (Figure 1). More specifically, in the meta-analysis, we investigated the general effect of the change of seasons on ant richness and abundance in six Brazilian biomes. We expected that ant assemblages show higher richness and abundance in the wet/summer season and different ant species composition between seasons. We also expected that more seasonal biomes (e.g., Cerrado and Caatinga) show a more marked difference in ant diversity between seasons. Because temporal biodiversity patterns (e.g., between seasons) are much less known than spatial patterns, this review becomes essential to close this gap, especially in tropical areas where land conversion is currently extremely fast. Moreover, the impact of climatic changes could be predicted if we knew the effects of seasonality on the diversity patterns including the extent of diversity reduction, if any, during drier months. We hope to provide information on biological diversity patterns to help manage and conserve the Neotropical biomes and their ecosystem functions.

2 | METHODS

We searched for papers regarding ant diversity and seasonality in Brazilian biomes using the database from the Ants of Brazil Project (Projeto Formigas do Brasil, http://www.formigasdobrasil.com) (Feitosa et al., 2022; Schmidt et al., 2022) and the search engines Web of Science, SciELO, and Scopus. Our search encompassed papers from 1945 to 2020. We used the following Portuguese and English keywords, as well as combinations of these words: “formiga”, “ant”, “sazonalidade”, “season”, “estação”, “Brasil”, and “Brazil”. We considered only studies with methods focused on sampling the ant assemblages, excluding studies of ant population ecology (focusing on one or a few ant species) and ant-plant or ant-trophobiont interactions.

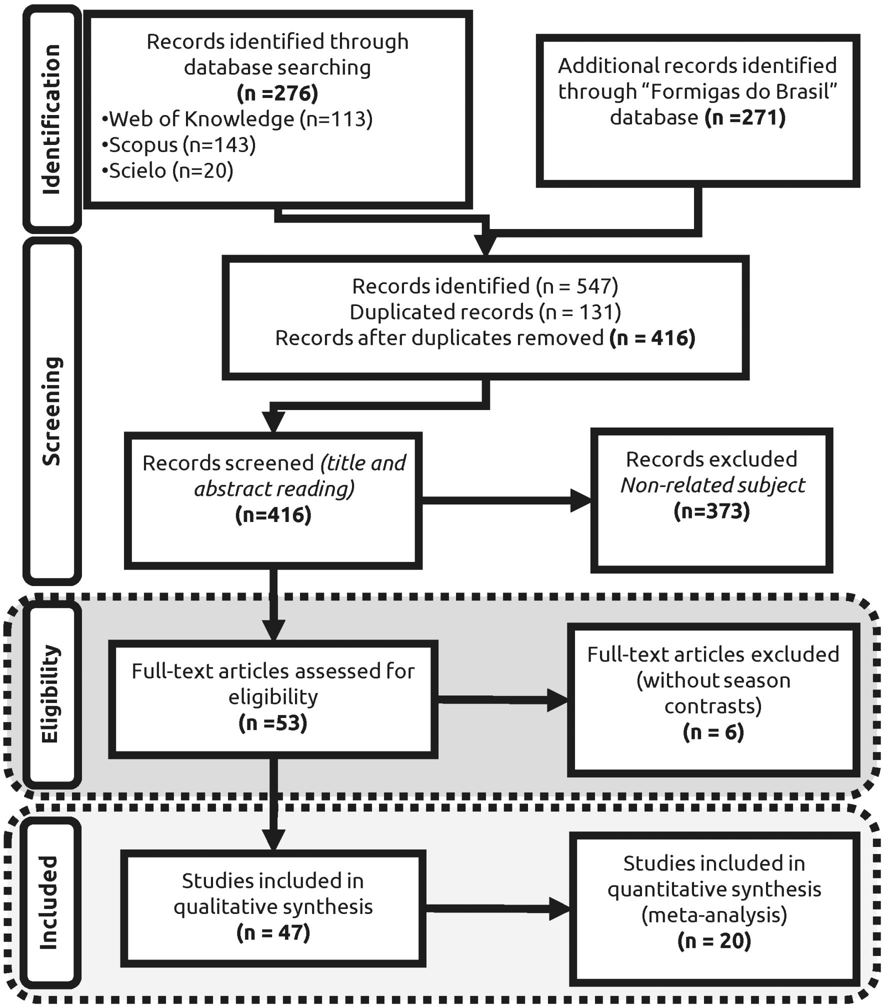

FIGURE 1 Diagram flow of the different phases of a systematic review with the qualitative and quantitative (meta-analysis) syntheses investigating the patterns of ant diversity associated with the seasonal changes in Brazilian Biomes. The image was based on the PRISMA model (Page et al., 2021)

2.1 | Seasonality in Brazil

Two well-defined seasons occur in Brazil: wet summers and dry winters. The wet season is concentrated between October and April in the Amazon Forest (Costa & Pires, 2010). In the Cerrado (Malheiros, 2016), Pampas (Rubert et al., 2018), and Pantanal (Prance & Schaller, 1982), the wet season happens from October to March. There is a more complex seasonal pattern in the Atlantic Forest as in its southern portion the wet season happens from October to March (Oliveira et al., 2016), whereas in the northern portion, between April and August (Oliveira et al., 2017; Piotto et al., 2019; Rao et al., 1993). The Caatinga, on the contrary, has an irregular rainfall system that varies from the border to the interior. In this biome, there is a concentration of rainfall during a few months of the year, from November to January and from February to April, depending on the infiltration and origin of wet masses, with seven to 8 months of drought (Leal et al., 2003).

2.2 | Qualitative review

From the studies collated in our database, we obtained the following information: year of publication, journal, impact factor (for the 2019 year), language, aims' relevance (if the paper specifically evaluated the relationship between ant diversity and seasons, see the categorization below), contrast between seasons (wet/summer vs. dry/winter), geographical coordinates, biome or transition between two biomes (e.g., Cerrado-Caatinga), diversity estimates, ant sampling methods, strata sampled, number of seasons sampled, analyses, and results found (Queiroz et al., 2022). After obtaining this information, we examined and summarized the most frequent patterns of ants' responses to seasonal changes.

2.3 | Meta-analysis

We analyzed the effects of seasonality on ant abundance and richness in the different Brazilian biomes by systematically reviewing the published literature and computing effect sizes between contrasting seasons of the year. Of the 53 studies found, 20 papers (Figure 1; Queiroz et al., 2022) met the criteria of statistics reported (data of means, sample size, and measurement of variance separately for seasons, such as wet/summer and dry/winter) and were included in our meta-analyses. We gathered from the text, tables, and figures, using the software ImageJ (Rasband, 2006), response mean values (X_{dry},

X_{wet}), standard deviations (SD_{dry}, SD_{wet}), and sample size (N_{dry}, N_{wet}) in each study to compare ant abundance and richness on both seasons. Ant abundance encompassed data on counts (number of workers) and density (frequency of occurrence), and ant richness was described as the number of ant species. To address the effects of seasonality on ant assemblages, we used the standardized mean difference between dry and wet to calculate Hedge's d for each variable extracted in each study. The cumulative overall Hedge's d effect size was calculated using a weighing method with the reciprocal of the sampling variance (see Mengersen et al., 2013). Negative Hedge's d values indicate a decrease in ant richness or abundance during the dry season. Firstly, we ran an overall random model, including a publication level random effect to account for the dependence among outcomes from the same study (see Nakagawa et al., 2017). Levels were included to incorporate non-independence among studies (level 1), among registers within the same study (level 2), and error (level 3) (see Appendix S1). Second, we ran a mixed-model meta-analysis, incorporating the Brazilian biomes as sources of heterogeneity in effect sizes and the moderator seasonality described as two categorical levels (wet/summer vs. dry/winter). Heterogeneity (total, between biomes and within biomes) of effect sizes was evaluated through Q-statistics using a chi-square distribution with n-1 degrees of freedom, where n equals the number of comparisons. The robustness of the meta-analysis was evaluated through funnel plots and the calculation of the Rosenthal fail-safe number (Jennions et al., 2013).

3 | RESULTS

3.1 | Qualitative review

After identifying and screening (Figure 1), we assessed 53 full-text papers for eligibility, including qualitative and quantitative descriptors related to seasonal diversity patterns (Figure S1). Among the 53 papers, we excluded six mainly due to the absence of quantitative estimates of the seasonal pattern of ant diversity. We remained with 47 studies for the qualitative review of the seasonality effect on ant diversity patterns.

The 47 studies were published from 2000 to 2018. The authors conducted ant surveys in all six Brazilian biomes and the transition between Cerrado and Caatinga (Figure S2). Most papers were published in English (74% vs. 26% in Portuguese). The main journals were Sociobiology (18), Neotropical Entomology (four), and “Revista Brasileira de Entomologia” (three). Finally, the journals that met our criteria and have helpful information on seasonal patterns involving ants had an average impact factor of 0.75 ± 0.60 ($\bar{x} \pm$SD).

There is a greater concentration of papers from the Atlantic Forest (16), twice the second most investigated biome, Cerrado (8). These studies are concentrated in the southeast region of Brazil (24). Pitfall trapping was the most common method of collecting ants in 21 studies analyzed, followed by baiting (13) and active search (9), and the most sampled stratum was soil/litter (29), followed by vegetation (22) (Figure S3).

On average, the time frame used in these studies was 1.30 years $\pm$ 0.50 ($\bar{x} \pm$SD), including eight samplings over time, usually covering both seasons (wet/summer and dry/winter). Thirty-four studies sampled ants in different seasons over 1 year, 12 collected samples over 2 years, and only one collected samples over 3 years. These studies evaluated richness (41; 87.2%), composition (33; 70.2%), and abundance (18; 38.3%) as ant diversity descriptors. Among those that evaluated richness (41), 19 studies observed no differences between seasons (46.3%), whereas 19 observed higher richness during the wet/summer season (46.3%). In contrast, higher species richness in the dry/winter season was rarely observed (3 studies; 7.4%). Among the 33 studies that investigated ant composition, changes in composition between seasons were found only in 36.4% (12). Most studies (21; 63.6%) did not find changes in ant species composition between seasons. For ant abundance, only six out of the 18 studies showed differences between seasons, five with higher abundance in the wet/summer season (27.8%) and only one with higher abundance in the dry/winter season (6%).

3.2 | Meta-analysis: effects of seasonality across study cases

Among the studies selected in the previous steps, 20 published studies were included in our meta-analysis. These studies were published between 2006 and 2017 and assessed the seasonal effects on ant diversity descriptors in five Brazilian biomes and the transition between Cerrado and Caatinga. They enabled 52 independent comparisons or outcomes (number of effect sizes), evaluating ant richness (36) and abundance (16) in Brazil's dry and wet seasons.

Our analysis of the effects of season on ants indicated an overall and significant reduction of ant richness and abundance during the dry season (E++ = −0.478, CI = −0.74 to −0.20, df = 51) (Figure 2a). Additionally, the effects of seasonality were stronger for ant richness than abundance. Overall, the effects of seasonality were not strongly influenced by all biomes together (Q_w = 7.97, P = .157) (Figure 2b), but ant richness was significantly lower in the dry season for the Cerrado biome (E++ = −0.549, CI = −1.06 to −0.03, df = 13), and marginally significant for the Atlantic Forest. Fail-safe numbers for both the random model (209) and the mixed model (211) were around 5 k+10, where k is the number of comparisons, indicating the results' robustness.

4 | DISCUSSION

We found a significant reduction of ant diversity during the dry season in Brazilian biomes in the meta-analysis, although the qualitative review (i.e., the vote-counting approach) showed a variable pattern between studies and much less conclusive patterns. This is an intriguing result that could be explained at least partially by the different sets of studies used in each approach (47 studies in the qualitative review and 20 in the meta-analysis). This sampling

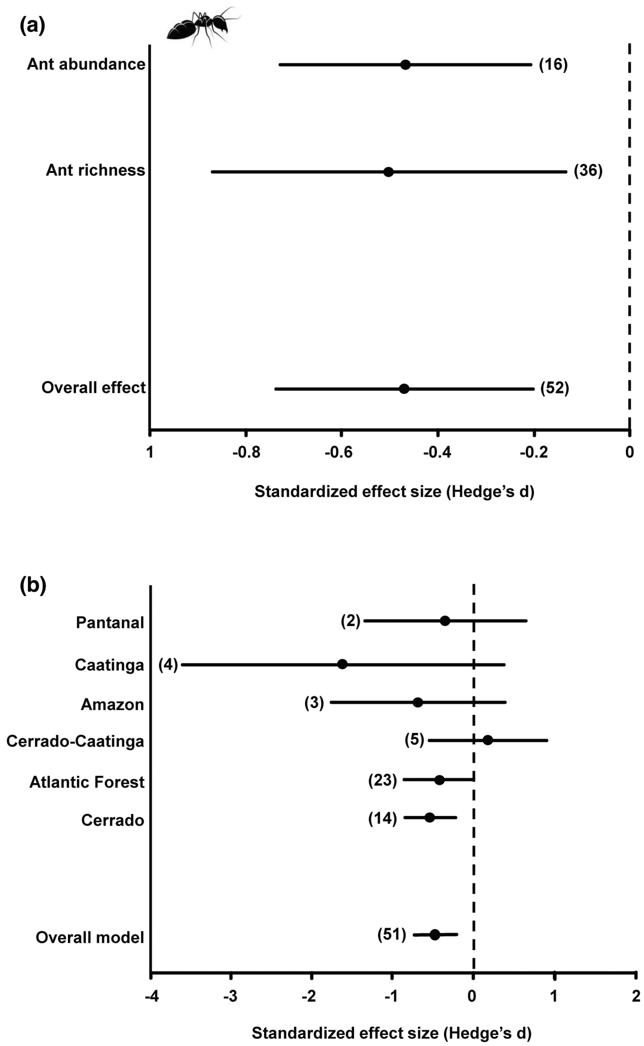

FIGURE 2 Negative effects (at the left of the horizontal dashed line) of seasonality on ant diversity (abundance and richness) during the dry season (a). Effects of seasonality on ant richness during the dry season by biome or transition between biomes (b). Dots represent the estimated mean effect size (Hedge's d), and the lines represent the 95% confidence interval. The cumulative effect size is reported with its 95% confidence interval. Numbers in parentheses indicate the number of effect sizes recovered in the literature, and the estimated mean effects are significant if confidence intervals do not overlap the vertical dashed line representing the null effect (zero)

difference may be at least the partial cause of the discrepancy, but it does not appear to be the only one. Effect sizes describe the magnitude of the ecological effects (Gurevitch et al., 2018). Therefore, when a particular case study does not show that ant diversity has decreased in the dry season, this can be caused by the low power of the test (e.g., small sample size), and the authors do not reject the null hypothesis in this case. Therefore, even when a qualitative review does not show a particular global effect, the meta-analysis can clarify this global effect as it quantitatively recovers the effect sizes observed here. However, fewer studies can be used in a meta-analysis due to the robust criteria for extracting effect sizes that are not carefully reported by many studies. Regardless, our main result shows that in the dry/winter season, the ant diversity (abundance and richness), more than the composition, changes and becomes smaller compared with the wet/warm season. This global pattern in the data is mainly generated by the effect sizes obtained in the Cerrado and Atlantic Forest biomes.

Analyses about seasonal effects on ants in large spatial scales (e.g., across all Brazilian biomes) are missing. We pointed out this gap in Brazil, a large country with different biomes. We highlight that the quantitative reviews about seasonality effects in other countries and continents could follow our effort, so we can take more robust conclusions about the response of ants to climatic changes and land conversion that affect resources and ecological conditions for ants. Most studies of ant diversity in Brazil are not focused on seasonality since only 47 out of 416 ant diversity studies have data about seasonal patterns. These studies were performed mainly in the Atlantic Forest biome, with pitfall trapping used to sample soil/litter ants. We did not find long-term studies, and other methodological limitations (e.g., lack of data publication) prevent broader conclusions about the relationship between ant diversity and seasonality. Therefore, studies about seasonality effects on ant diversity in Brazil are still incipient. The publication of these data on repositories is an initial step to reaching long-term projects with cooperation for an intercontinental approach depicting changes in resources, climatic conditions, and associated communities.

4.1 | Qualitative review

Although we observed an increase in the cumulative number of studies over time, the number of studies per year is similar, about five per year, demonstrating that seasonality effects on ants are not the main subject for ant diversity researchers in Brazil. The lower investment in temporal pattern investigations of biodiversity is probably due to financial and logistic limitations. Most papers evaluating seasonal patterns of ant diversity were carried out in the Atlantic Forest biome. This concentration is due to the Atlantic Forest biome holding the most significant proportion of the Brazilian population (~70% of 212 million inhabitants) (Marques et al., 2016; SOS Mata Atlântica, 2021). Furthermore, historically, there is a large concentration of higher education institutions (and graduate courses) in the Southeast Region (Sguissardi, 2006). Therefore, we expect some changes in these trends in the following years due to the scientific expansion from 2007 to 2015 that led many scientists to occupy other Brazilian regions.

Pitfall trapping is the most used technique for capturing ants. Pitfall traps are popular because they are inexpensive and, in terms of logistics, they can be easily used to collect terrestrial arthropods (Delabie et al., 2020; Morrill, 1975) and are efficient in obtaining information about ant assemblages (Bestelmeyer et al., 2000; Lopes & Vasconcelos, 2008; Souza et al., 2012). Besides, the soil/litter stratum is the commonly sampled habitat in studies that assess differences in ant assemblages in different seasons.

From the reviewed studies, few detected effects of climatic seasonality on the diversity and composition of ant assemblages in Brazilian biomes. Some authors found a higher ant richness and abundance in the wet/summer season and differences in species composition between seasons (e.g., Castilho et al., 2011; Costa-Milanez et al., 2015; Rosado et al., 2013; Santos et al., 2014). To explain these results, the authors suggested the influence of abiotic factors, such as temperature and precipitation, on ant foraging activity (Almeida et al., 2007; Levings, 1983; Nunes et al., 2020). Besides, few studies have reported the opposite effect of seasonality on ant assemblages, that is, higher richness and abundance of species in the dry/winter season (Costa-Milanez et al., 2015; Gomes et al., 2014; Marques et al., 2017). One of the common explanations for this pattern is the possible expansion of ant foraging areas due to the reduction in resource availability in the dry/winter season. This reduction would increase the chances of collecting species foraging in the environment. Since there are different patterns in the literature regarding the effects of seasonality on Brazilian ants, the meta-analysis helped us to reach more robust conclusions about these effects.

4.2 | Effect of seasonality across study cases: A meta-analysis

Our meta-analysis found a significant ant richness and abundance reduction during the dry season. This seasonal pattern of ant diversity is not new (Levings, 1983), but to our knowledge, we are the first to summarize the available literature to estimate the cumulative effect size that describes the seasonality effect on these components of the ant community in Brazilian biomes. Reductions in ant species richness during the dry season may be due to the modulation of foraging activities, as most ant species have relatively fixed and perennial colonies (Hölldobler & Wilson, 1990). In this case, colony behavior may buffer climatic changes in seasonal environments (Kaspari & Vargo, 1995). Droughts at certain times of the year become crucial in decreasing ant activity and their interactions with other organisms (Calixto et al., 2020; Lasmar et al., 2021; Levings, 1983). In addition, abiotic factors, such as temperature and precipitation, are hypothesized as direct causal factors on ant foraging activity (Almeida et al., 2007; Levings, 1983; Nunes et al., 2020). The argument is based on the thermophilic nature of ant species since their foraging behavior is associated with temperature and is usually distinct among seasons (Hölldobler & Wilson, 1990; Kaspari et al., 2003; Schutte et al., 2007). Indirectly, climate variation can also influence the quantity and quality of available resources (Nogueira et al., 2020; Speight et al., 2008).

Overall, biomes did not strongly modify the seasonality effect on ant diversity, although ant richness was significantly lower in the dry season for the Cerrado and marginally significant for the Atlantic Forest compared with the other biomes. The pronounced drought effect on the Cerrado vegetation is observed in plant deciduousness, with several plant species dropping their leaves during the dry season, reaching their peak between July and August (dry season) when water availability is minimal (Calixto et al., 2020; Lange et al., 2013). During the wet/summer season, the leaves on plants, and due to extrafloral nectaries across species in the vegetation, ants have more carbohydrate resources available on plants (Rico-Gray & Oliveira, 2007). We could expect more negative effects of the dry season for the Caatinga (Brazilian semi-arid biome) ants. Still, we did not see a homogeneous response from the few studies incorporated into our meta-analysis. In this biome, harsh environmental conditions may shape ant behavior, guaranteeing their survival and reproduction in other periods. It is important to point out that the number of entries (size effects) in the meta-analysis for different biomes, except for Atlantic Forest, was limited (between two and five effect sizes) and smaller than for the Cerrado and this could influence the results found. Indeed, this limitation prevents us from concluding clearer patterns for the Brazilian biomes that have been undersampled. We suggest that the intensity of the response of ant assemblages to climatic seasonality depends upon variation in climatic conditions (e.g., temperature and precipitation), availability of resources, and biotic integrity (impacted vs. non-impacted ecosystems). Our results on differences between biomes also indicate that we need to explore seasonal effects among vegetation types in each biome, concentrating studies in neglected areas (e.g., open environments).

4.3 | Findings and conclusions

As a result of climate changes, the frequency and periodicity of extreme climatic events, such as storms and severe droughts, are predicted to be higher, and precipitation and temperature variation are less predictable than in the past. Similarly, changes caused by land conversion modify the availability and predictability of resources and conditions. These changes can interfere with the patterns of biota diversity in the short and long term. In this sense, only long-term studies may be able to capture the influence of unstable climatic conditions on biodiversity over time. Thus, we encourage researchers to conduct long-term studies on ant diversity, including different biomes. This increase in the study time range will allow us to make more robust predictions about the distribution of ant assemblages in the context of climate change. One promising way forward might be establishing a scientific collaboration network to advance ant occurrence and distribution studies using standardized measurements. We, therefore, advocate that research groups implement similar experimental designs and methods across ecosystems, which will enable direct comparisons and reduction of study heterogeneity shortly (e.g., spatial and temporal replicates and diversity parameters such as richness, abundance, composition, and diversity indexes).

Our meta-analysis revealed that ant diversity decreases in the dry season, especially in the Cerrado biome. This biome is currently at risk due to land-use intensification (Colli et al., 2020). We hope our findings will be helpful to stimulate ant researchers to work with seasonal patterns, taking care of the aspects of their experimental design, and establishing partnerships with researchers across biomes. With a more robust database worldwide, we will be able to visualize different responses of ants to seasonal climatic filters. Consequently, if we know the spatial and temporal dynamics of ant assemblages in their environments, we can predict climatic changes and land conversion effects on ants and other insect groups regarding the influence of resources and climatic conditions.

AUTHOR CONTRIBUTIONS

ACMQ, CRR, FAS, RMF, and TGM conceptualized the manuscript. ACMQ, CRR, and TGM administrated the project. ACMQ, CRR, and TGC did the formal analysis. ACMQ, CRR, TGC, and TGM wrote the original draft. All authors collected the data, reviewed, and edited the manuscript.

ACKNOWLEDGMENTS

We thank the referees for their comments and suggestions on the previous version of the manuscript. We are most grateful for the support provided by F. Neves, R. Campos, J. Schoereder, J. Rosado, and M. Gonçalves with paper search and information survey. ACMQ received a postdoctoral fellowship from P&D GT0611 – "Descomissionamento da PCH Pandeiros: Uma experiência inédita na América do Sul" CEMIG/Programa de Pesquisa e Desenvolvimento da ANEEL. MAU acknowledges the FAPESP for the current postdoctoral fellowship (grant n° 2018/11453-0 and 2019/24810-8) and the previous fundings (grants n° 2012/21309-7 and 2015/06485-1). EZA acknowledges the support from the National Science Foundation (DEB1654829) and Peter Buck Postdoctoral Fellowship at the Smithsonian Institution. JLPS acknowledges the CNPq for the postdoctoral fellowship (grant n° 301383/2021-2). TI, JCS, RRCS, FBB, AN, RMF and TGC are supported by CNPq (309552/2018-4; 312752/2018-0; 305739/2019-0; 313986/2020-7; 434692/2018-2; 3014495/2019-0; 313007-2020/9). AN is also supported by the São Paulo Research Foundation (FAPESP) grant number 2019/19544-7.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from https://figshare.com at https://doi.org/10.6084/m9.figshare.19746946.v3

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Queiroz, A. C. M., Marques, T. G., Ribas, C. R., Cornelissen, T. G., Nogueira, A., Schmidt, F. A., Feitosa, R. M., Sobrinho, T. G., Quinet, Y., Baccaro, F. B., Ulysséa, M. A., Vargas, A. B., Morini, M. S. C., Souza, J. L. P., Paolucci, L. N., Dáttilo, W., Del-Claro, K., Lange, D., Santos, J. C. … Diehl-Fleig, E. (2023). Ant diversity decreases during the dry season: A meta-analysis of the effects of seasonality on ant richness and abundance. *Biotropica*, *55*, 29–39. https://doi.org/10.1111/btp.13158