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RESEARCH ARTICLE

Interactions between ants and diaspores in a Brazilian hotspot: an overview of trends and gaps in literature

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Abstract

Ants are present in terrestrial ecosystems nearly worldwide and participate in several ecological interactions that result in essential ecosystem functions, such as seed dispersal. In these interactions, ants collect fruits and seeds and move them to safe sites, preventing pathogen proliferation and increasing seedling establishment. Some ant species play a key role in these interactions, enhancing seed dispersal efficiency in areas where they occur. However, species loss due to land-use changes threatens these interactions and the ecosystem functions they support. The Atlantic Forest is among the most critically endangered hotspots in the world, making studies that support conservation strategies urgent. To address this, we compiled 26 years of research on ant-diaspore interactions in the Atlantic Forest to assess the current state of knowledge and encourage future studies. Most research has focused on three Brazilian states, revealing large knowledge gaps across the biome. Additionally, many studies have only evaluated the quantitative aspects of seed dispersal by ants. We identified six key ant species responsible for diaspore removal (e.g., *Pachycondyla striata*, *Odontomachus chelifer* and *Atta sexdens*), but no key species were found for diaspore cleaning. Also, we found that seed size and lipid content influence interaction types. Finally, we highlighted priority locations for future sampling based on environmental characteristics, emphasizing specific ecoregions of the Brazilian Atlantic Forest. This information is crucial for advancing the discussion on ant species and their ecological interactions in the Atlantic Forest and guiding further research on their role in seed dispersal.

Keywords Atlantic forest · Ecosystem functions · Ant-plant interactions · Seed removing ants · Secondary dispersal.

Introduction

Interactions between ants and plants play a significant role in tropical and temperate terrestrial ecosystems (Beattie 1985; Jolivet 1992). Studies suggest that ant-plant interactions emerged during the Cretaceous period and evolved into several different mutualisms (Buckley 1982; Beattie 1985; Huxley and Cutler 1991; Jolivet 1996; Rico-Gray and Oliveira 2007). In these mutualistic relationships, ants provide crucial services to plants and are rewarded in many ways. For instance, ants can protect plants against herbivores and other threats, in return for food resources (Passos and Leal 2019) and nesting sites within plants (Longino 1991; Coley and Barone 1996). Additionally, ants can pollinate some plants by using them as foraging substrates and patrolling grounds (Beattie 1985). Ants also interact with fruits through a process called myrmecochory, which occurs in at least 4.5% of plant species worldwide (Lengyel et al. 2009). Myrmecochory is typically characterized by the presence of fleshy, lipid-rich appendages called elaiosomes

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that attract ants. This strategy is especially common in temperate forests and shrublands but also found in tropical ecosystems (Lengyel et al. 2010). In tropical forests, ants also interact with fallen fruits on the ground, removing and using lipid-rich arils as food (Pizo and Oliveira 2001; Passos and Oliveira 2004; Miller et al. 2020). Experimental evidence shows that the consumption of lipid-rich arils enhances larval development and colony fitness in primarily carnivorous ants, which reinforces the mutualistic nature of these ant-plant interactions (Bottcher and Oliveira 2014). These mutualistic interactions form a complex network of interactions involving multiple species and ecological processes, playing a crucial role in maintaining biodiversity and supporting ecosystem functioning.

Seed dispersal by ants is one of the most extensively studied ant-plant interactions, given its pivotal role in ecosystems (Buckley 1982; Beattie 1985; Handel and Beattie 1990; Rico-Gray and Oliveira 2007; Penn and Crist 2018). In this interaction, ants rapidly collect diaspores (i.e., dispersal units) and transport them to safe sites (e.g., nests), preventing seed exposure to predators (Van der Pijl 1982; Beattie 1985). Moreover, ant nests are microsites enriched with ant residues and crucial and often limiting nutrients such as nitrogen and phosphorus, and increase cations levels without affecting soil pH (Beattie 1985; Frouz and Jilková 2008; Farji-Brener and Werenkraut 2017). Diaspore dispersal away from the parent plant prevents competition for resources and nutrients, potentially enhancing seed dispersal success (Howe and Smallwood 1982; Beattie 1985; Fernandes et al. 2020). Ants also play a role in cleaning diaspores, preventing the proliferation of pathogens that could compromise the seeds (Beattie 1985; Oliveira et al. 1995; Passos and Oliveira 2002; Ohkawara and Akino 2005). Following the cleaning process, inside the nests, ants deposit the clean, intact seed in a refuse pile within or outside the nest, potentially increasing germination rates (Beattie 1985). In contrast, very small ant species unable to move diaspores may consume the attractive part of the seeds on-site, reducing the chances of the seeds being dispersed by other ants or alternative dispersal agents (Bronstein 2001).

In general, ecosystems with high species richness tend to have high functional redundancy, promoting critical ecological functions performed by multiple species (Fonseca and Ganade 2001). However, the specific importance of certain species in mutualist interactions, which contribute to functions such as seed dispersal, is poorly studied (Christian 2001; Gove et al. 2007; Leal et al. 2014b; Warren and Giladi 2014). For example, even though plant species may engage with multiple ant partner species, certain ant species have been identified as key species for seed dispersal (Horvitz and Beattie 1980; Buckley 1982; Ness 2004; Heithaus et al. 2005; Gove et al. 2007; Leal et al. 2014a; Fontenele and Schmidt 2021). In ant-diaspore interactions, a key ant species plays a more essential role than its density would suggest (Gove et al. 2007). This highlights the relevance of ants' contribution to seed dispersal, especially focal species that act more efficiently in plant species dynamics. However, ecosystems undergoing anthropogenic changes have experienced a decline in ant species that play a key role in seed dispersal (Fontenele and Schmidt 2021), which can affect the effectiveness of this ecological function.

In the face of the escalating biodiversity loss and the disruption of ecological interactions, studies that actively assist in planning conservation strategies are urgently needed. The Atlantic Forest, a biodiversity hotspot of global significance, exemplifies this urgency with less than 3% of its original primary vegetation remaining due to centuries of deforestation and exploitation, this biome harbors extraordinary levels of species richness, endemism, and ecological complexity, making it a vital yet critically threatened ecosystem (Myers et al. 2000; Joly et al. 2014; Rezende et al. 2018; Vancine et al. 2024). Although the Atlantic Forest is not considered a global hotspot for myrmecochory, ants play a key role in dispersing diaspores beyond the so-called "true" myrmecochorous plants, often moving seeds on the forest floor of species that lack specialized traits for ant dispersal (Pizo and Oliveira 2001; Passos and Oliveira 2004). This non-specialized dispersal can significantly influence seed survival, germination, and seedling establishment, especially in disturbed and fragmented landscapes where other dispersers (e.g., birds and mammals) have declined (Harrison et al. 2013; Vidal et al. 2013). Given the pervasive defaunation in tropical forests, including the Atlantic Forest, which has drastically reduced populations of large vertebrate frugivores (Dirzo et al. 2014), ants may become increasingly important for determining seed fate and plant recruitment, particularly for small-seeded species (Christianini et al. 2014). Therefore, compiling decades of research on ant and diaspore interaction in this biome is crucial to reveal the extent and ecological significance of this process, identify knowledge gaps, and guide future studies.

In this study, we conducted a comprehensive survey of studies focused on the interactions between ants and diaspores, systematically compiling data for the Brazilian Atlantic Forest. Our objective was to provide a qualitative overview of the central aspects addressed in the published literature and to reveal key aspects that shape ant-diaspore interactions in the Atlantic Forest. Initially, we described the main ant and plant interacting species, and subsequently, evaluated the predominant types of interactions (cleaning and/or removal) that are often observed or studied. Specifically, we provide a list of key ant species that participate in these interactions and point out which traits (size and lipid concentration) influence the type of ant-diaspore

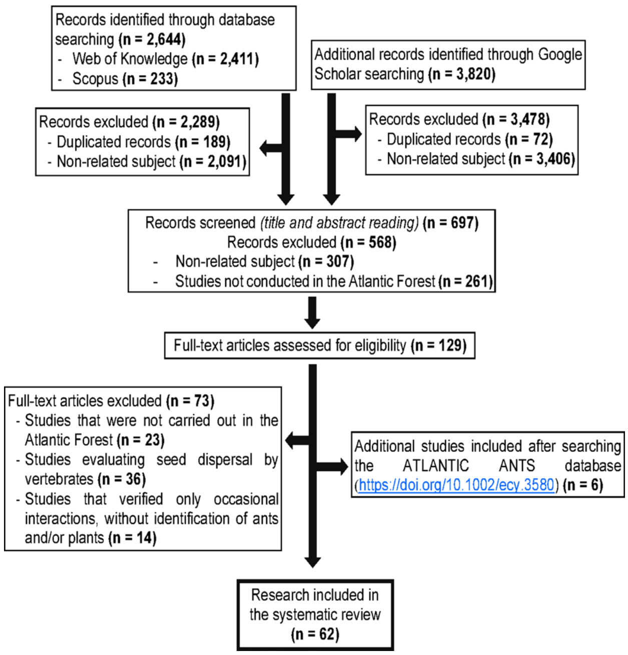

Fig. 1 Flow diagram showing the selection procedure to identify the studies on ant-diapore interactions included in the systematic review, which was performed in the dataset selection of our study

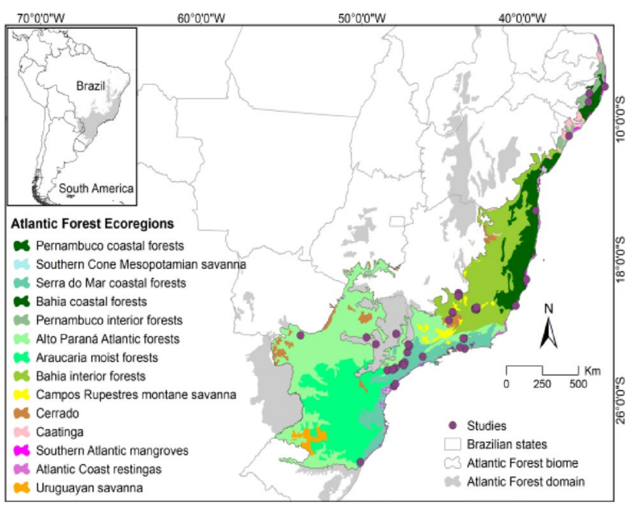

Fig. 2 Geographic distribution of studies on ant-diaspore interactions in the Brazilian Atlantic Forest included in the systematic review. The limits of the Atlantic Forest domain were defined by Ribeiro et al. 2009 and Muylaert et al. 2018. The ecoregions that encompass the Atlantic Forest biome are based on the Terrestrial Ecoregions of the World (TEOW) classification proposed by Olson et al. (2001), and all regional names used in our study strictly follow this classification

interactions. In addition, we present priority sites in the Atlantic Forest, considering their ecoregions, for future research on ants and their interactions with diaspores.

Methods

Literature review

In July 2021, we conducted a systematic literature review focused on studies investigating interactions between ants and diaspores (e.g., removal behaviors, cleaning, inspection, handling, or access to diaspores within nests) throughout the Brazilian Atlantic Forest. Searches were performed in the following databases: SCOPUS (https://www.scopus.com*)*, ISI Web of Knowledge (https://www.webofknowledge*)*, and Google Scholar (http://scholar.google.com.br*)* to complement the dataset with theses and dissertations. We used the following search terms: "ant + seed" OR "ant + diaspore" AND "Atlantic Forest"; and "formiga + semente" OR "formiga + diásporo" AND "Mata Atlântica" (the same terms in Portuguese). In order to build our database, we included studies that assessed either ant or plant communities interacting, as well as those that focused on a single ant species or a single plant species. After the screening process, we remained with 62 studies (Fig. 1), including theses and dissertations, encompassing all ecoregions of the Brazilian Atlantic Forest (Fig. 2).

Studies information

We extracted the following information from each study: publication year, study type (published article or thesis/dissertation), journal, language, geographical coordinates, the focus of the study (population or community study), and data collection method (laboratory or field study). Additionally, we gathered specific information on both ant and diaspore species, including ant and plant species identification to report the type of interaction investigated, morphological information, and when available, chemical information for diaspores. Morphospecies were treated as study-specific operational taxonomic units. Identical morphospecies labels (e.g., "*Pheidole* sp. 1") reported in different studies were not assumed to correspond to the same species and were therefore not pooled across studies. To enhance our database on diaspore characteristics, we used data collected from studies covering a significant amount of plants known to attract fauna elements of the Atlantic Forest (Cazetta 2008; Bello et al. 2017).

Identification of key ant species

To classify ant species, we focused only on those species involved in seed removal or cleaning, as these behaviors are the most well studied in the context of ant-diaspore interactions. Thus, to determine the existence of key ant species that remove or clean diaspores, we conducted Wilcoxon tests using the "wilcox.test" function from the essential R package (R Core Team 2023). This test allows pairwise comparisons of different data generated from the same original dataset (Wilcoxon 1946). To do this, we constructed two global matrices (original matrices) with the total frequency of ants that removed diaspores and ants that cleaned diaspores in each study. Subsequently, we subtracted the number of appearances of each ant species from each global value (total frequency), without altering the values for locations where the species was absent. We performed this procedure for all identified ant species in each type of interaction (removal and/or cleaning). Thus, the global matrix, both for diaspore removal and cleaning, was compared to the matrix of the remaining frequency of each species in each study. A species was considered key when the comparison between the matrix with their absence showed a significant difference ($p \leq 0.05$) from the original matrix (global matrix). To account for multiple comparisons and control the false discovery rate, we applied the Benjamini-Hochberg correction (Benjamini and Hochberg 1995) to all pairwise Wilcoxon tests for both diaspore removal and cleaning. Furthermore, for this analysis, we included only ant taxa identified at the species level to ensure taxonomic consistency across studies. All morphospecies or records identified only at the genus level were excluded. This approach aimed to reduce uncertainty associated with highly diverse and taxonomically challenging groups, such as *Pheidole* and *Solenopsis*, which may otherwise distort species-level frequency estimates.

Morphological and nutritional attributes of diaspores

To determine whether diaspore traits determine the type of ant-diaspore interaction, we used diaspore length (mm), lipid content (low, medium, and high), and interaction type (removal or cleaning) as predictor variables, and the proportion of diaspores removed or cleaned in each study as the response variable. Based on lipid concentration we classified diaspore as low (0 to 10%), medium (>10 to 20%), and high lipid concentration (>20%), following Bello et al. (2017). Subsequently, we constructed Generalized Linear Mixed Models (GLMM) (O'Connell 1993), including interaction type (removal or cleaning) as a fixed effect and plant species as a random effect to account for the non-independence of observations within species. This model specification allowed us to directly test whether diaspore traits (lipid content and size) influence the likelihood of each interaction type. We tested for interaction effects between lipid content and diaspore size, but this interaction was not significant ($\chi^2 = 0.77$, df = 2, $p = 0.679$). Models were fitted using the "glmmPQL" function from the MASS package (Ripley et al. 2023) in the R software (R Core Team 2023). We employed a binomial error distribution and adjusted the distribution using the quasibinomial distribution to correct data overdispersion (Crawley 2012).

Priority sites for future samplings

To identify priority sites for future studies, we did not rely on the number of existing studies per region but instead divided the Atlantic Forest into 3-km^2 areas and assessed environmental differences between sampled and unsampled locations based on geographical coordinates provided in each study. To assess environmental dissimilarity, we used data from sample locations, considering eight variables relevant to ant studies based on Schmidt et al. (2020). The variables included altitude, soil type, and six bioclimatic variables: annual precipitation, precipitation in the wettest month, precipitation in the driest month, mean annual temperature, maximum temperature in the hottest month, and minimum temperature in the coldest month (Schmidt et al. 2020). We also included the Atlantic Forest ecoregion as an environmental variable, as ecoregions represent land units with distinct communities and species, often aligning with the original extent of natural communities before significant land use changes (Olson et al. 2001). Moreover, these biogeographic units are crucial for conservation planning as they may reflect species and community distributions more accurately (Olson et al. 2001). Raster layers for all variables were obtained from the AmbData website (for soil types and altitude (Amaral et al. 2013) and WorldClim (for bioclimatic variables (Fick and Hijmans 2017). To obtain the raster layer for Atlantic Forest ecoregions, we rasterized the shapefile available on the World Wildlife Fund (WWF) website (http://www.worldwildlife.org).

We standardized all continuous variables (bioclimatic variables) using z-scores. This procedure is essential to avoid biases due to variables with larger values (Legendre and Legendre 2012). Subsequently, we calculated the mean environmental dissimilarity of the sampled locations (Schmidt et al. 2020) for each 3-km^2 area throughout the Atlantic Forest biome, based on Gower's distance (Legendre and Legendre 2012). Finally, we normalized all values from 0 to 1 using Min-Max normalization (Patro and Sahu 2015), so that values close to 0 represented environmentally similar areas, while values close to 1 represented environmentally different areas from those where existing studies in literature were sampled. This resulted in a raster containing a gradient of sampling relevance for ant-diaspore interactions in the Atlantic Forest biome. The same procedure was performed for ecoregions. Finally, we assessed the sampling relevance of each ecoregion of the Atlantic Forest. For the analysis, we used the R software version 4.3.0 (R Core Team

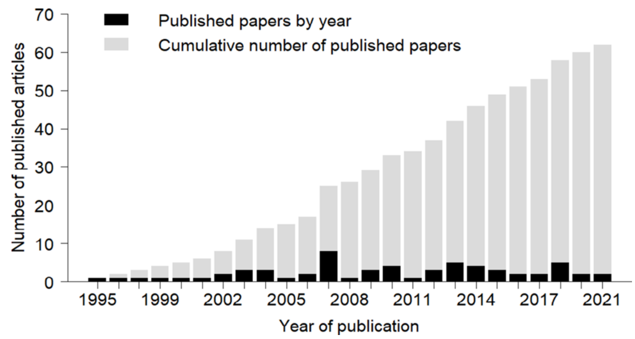

Fig. 3 Number of published articles and cumulative number of published articles from 1995 to 2021 on ant-diaspore interactions in the Brazilian Atlantic Forest

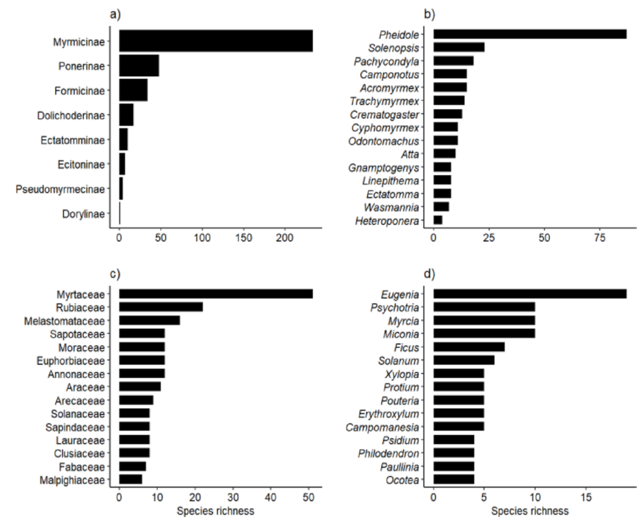

Fig. 4 Subfamilies (**a**) and the top 15 ant genera (**b**), plant families (**c**) and plant genera (**d**) with the highest number of species found in the 62 studies on ant-diaspore interactions in the Atlantic Forest

2023) with the 'vegan' (Oksanen et al. 2019), 'raster' (Hijmans et al. 2023), and 'rgdal' (Bivand et al. 2017) packages.

Results

General aspects of literature

We found 62 studies assessing interactions between ants and diaspores in the Brazilian Atlantic Forest, spanning a 26-year period (1995–2021). Although the number of studies published per year fluctuated over time, the cumulative number of publications on ant-diaspore interactions in the Atlantic Forest increased steadily throughout the study period (Fig. 3). Among these 62 studies, 50 were published articles (80.6% of the total), five theses (8.1%), and seven dissertations (11.3%). The published studies were distributed across 24 journals, with Sociobiology (eight), Journal of Tropical Ecology (six), and Biotropica (six) being prominent (Figure S1). The theses and dissertations were accessible in five open-access academic repositories (Figure S2). Most of the studies were published in English (83.9%), and 16.1% in Portuguese. Geographically, the studies primarily focused on three states – São Paulo, Minas Gerais, and Rio de Janeiro, which highlights knowledge gaps in ant-diaspore interactions in other regions of the Atlantic Forest (Figure S3).

In general, most of the studies used the method of actively collecting ants interacting with diaspores. Additionally, only 10 studies (16.1% of the studies) employed random active search for ant-diaspore interaction, while the remaining studies used predetermined diaspore species as bait for provoking ant-diaspore interactions (Table 1). Regarding the focus of the studies, 12 studies (19.4% total) specifically evaluated a single ant species interacting with diaspores, while 50 studies (80.6% total) assessed ant communities (Table 1). Finally, five studies (8.1% total) were conducted partially or entirely in a controlled laboratory environment, with the remaining taking place in the field.

Ant and diaspore species

In the 62 studies, we identified 356 ant species/morphospecies interacting with diaspores, distributed across eight Formicidae subfamilies and 49 genera. Of this total, 140 (39.3%) ant species were identified at the species level, while 216 (60.7%) were identified at the genus level only. The most abundant subfamily was Myrmicinae (Fig. 4a), and the genera with the highest number of species were *Pheidole*, *Solenopsis*, and *Pachycondyla* (Fig. 4b). Among the 15 ant genera with the highest number of species, morphospecies identifications exceeded nominal species in *Pheidole* (65 vs. 22), *Camponotus* (8 vs. 7), *Trachymyrmex* (9 vs. 5), *Solenopsis* (19 vs. 4), *Crematogaster* (9 vs. 4), and *Wasmannia* (4 vs. 3) (Figure S4).

Table 1 Description of the methods used, the level of biological organization, and the seed dispersal component evaluated, along with the number of studies in each category, across the 62 studies on ant-diaspore interactions

		Number of studies
Method for ant-diaspore interactions collection	Active search on trails	10
	Diaspores as attraction traps	52
Level of biological organization	Ant population	12
	Ant community	50
Evaluated seed dispersal component	Quantitative component	44
	Qualitative component	18

Regarding diaspore species, we identified 334 species (~1.55% of the total known plant species in the Atlantic Forest (21,573) (Brasil 2025) distributed across 83 plant families and 181 genera. Among these, 248 (74.3%) were identified at the species level, 85 (25.4%) at the genus level, and a single (0.3%) at the family level (Sapotaceae). The most abundant family was Myrtaceae (Fig. 4c), and *Eugenia*, *Psychotria*, and *Myrcia* were the genera with the highest number of species (Fig. 4d). Among the 15 plant genera with the larger number of species, morphospecies identifications exceeded nominal species only in *Ficus* (5 vs. 2) (Figure S5). Furthermore, ants interacted primarily with diaspores from tree species, followed by shrubs (see more details about plant species in Table S3).

Main objectives of the studies

The studies primarily focused on the quantitative component of the seed dispersal framework (n=44, 71% of the total), with a higher interest in quantifying removal and cleaning rates (n=28, 63.6%), removal only (n=13, 29.5%), or diaspore cleaning (n=3, 6.8%). In contrast, fewer studies assessed the qualitative component of the seed dispersal framework (n=18, 29% of the total). Among these, diaspore dispersal distance (n=8, 44.4%) and diaspore deposition in ant nests (n=3, 16.7%) appeared most frequently. Additionally, three studies (16.7%) examined the effects of ant nests on seedling establishment, evaluating the distance from the nest or the relationship of soil components around specific ant nests to plant seedling richness or abundance (e.g., Passos and Oliveira 2004; Almeida et al. 2019). Concerning seed germination, only two studies (11.1%) evaluated germination rates after ant manipulation (e.g., Passos and Oliveira 2002; Peternelli et al. 2003). It is worth noting that studies that consider manual removal of seeds from the pulp were excluded from the analyses. Finally, two studies (11.1%) covered the entire process of seed dispersal by ants, from removal and cleaning to germination (Camargo et al. 2019; Fernandes et al. 2019).

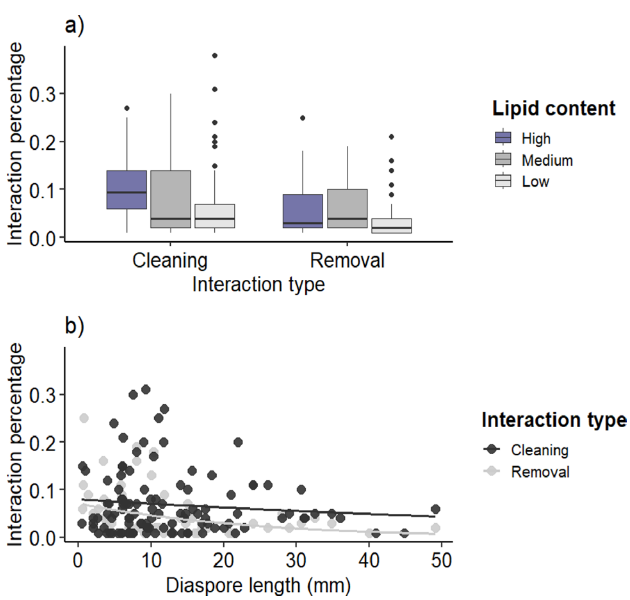

Fig. 5 Percentages of removal and cleaning based on diaspore lipid content (**a**) and diaspore size (**b**) in the Atlantic Forest (n=248 plant species; cleaning: n=146; removal: n=102)

Regarding ant behavior towards diaspores, ants showed diverse responses upon encountering fallen diaspores on the ground. In addition to diaspore removal and cleaning, observed ant behaviors included worker recruitment, removal attempts, fluid collection from seed appendages, inspection, and instances where ant species ignored the diaspores (Passos and Ferreira 1996; Christianini et al. 2012; Camargo et al. 2016). Notably, some studies did not specify ant behavior (four studies), while others only partially specified it (four studies).

Key ant species

A total of 386 interaction events between ants and diaspores were recorded, involving 284 unique ant species. This total includes all types of ant-diaspore interactions reported in the studies, such as inspection, handling, removal, cleaning, attempt to remove, manipulate and access to diaspores within nests. Among these, diaspore removal and cleaning were the most frequently studied. A total of 102 species engaged in both cleaning and removal behaviors, while 101 species were observed exclusively removing diaspores, and 81 species exclusively cleaning them. We identified six key ant species (out of 73 analyzed) playing an essential role in diaspore removal (Table S1), but no key species were found for diaspore cleaning (out of 51 species analized). Overall, key ant species involved in removal and cleaning interacted with a wide diversity of diaspore species. Among the key diaspore-removing ant species, those interacting with the highest number of diaspore species were *Pachycondyla striata* (95 species), *Odontomachus chelifer* (59 species), and *Atta sexdens* (45 species).

Attributes of diaspores

We found that the type of interaction was affected by both diaspore size (χ^2 = 6.99, df=1, p=0.0082) and lipid content (χ^2 = 14.35, df=2, p=0.00077). The percentage of diaspore cleaning and removal by ants decreased with increasing diaspore size (t = -2.61, df=47, p=0.0122; Fig. 5a). Diaspores with low lipid content were less frequently cleaned and removed than those with high lipid content (t = -3.62, df=47, p=0.0007), while diaspores with medium lipid content showed intermediate values, not significantly different from those with high lipid content ($p = 0.17$; Fig. 5b).

Relevance for future sampling of ant-diaspore interactions

The spatial analysis of environmental dissimilarity revealed several knowledge gaps regarding ant-diaspore interactions across the ecoregions of the Atlantic Forest (Fig. 6). Most studies occurred in São Paulo, Minas Gerais and Rio de Janeiro states, located in the southern and southeastern regions of Brazil (Figure S3). Consequently, most areas within these states showed low environmental dissimilarity to previously sampled sites and were ranked as lower priority in our analysis. Other ecoregions (e.g., Caatinga, Pernambuco interior forests, Southern Atlantic mangroves) were less represented among previous studies, making them highly relevant for future research (Figure S6). Most of the Atlantic Forest ecoregions had dissimilarity values higher than 0.6 (Figure S6), meaning they are higher priorities for future research sites.

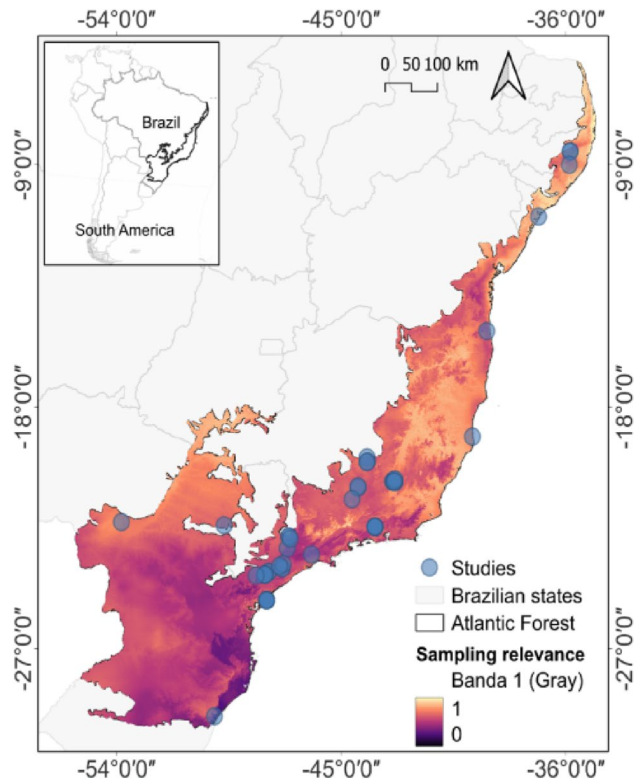

Fig. 6 Map of relevant areas for future sampling of ant-diaspore interactions in the Atlantic Forest. The locations with values closer to 1 have higher environmental dissimilarity, indicating greater relevance for future studies

Discussion

Our study provides a comprehensive overview of ant-diapore interactions, based on a thorough review of 26 years of literature (1995–2021). We found that the vast majority of studies are concentrated in the southeastern region, which hosts major research centers and exhibits higher socioeconomic development. This geographic bias highlights the urgent need for financial investments and human resources to advance research in underrepresented regions of the Atlantic Forest. Furthermore, we revealed that the primary focus of ant-diaspore interaction studies in the Atlantic Forest is seed dispersal by ants. However, our results showed that most of these studies assess only the quantitative component of the seed dispersal framework, leaving substantial gaps in our understanding of the broader ecological role of ants. Additionally, we identified ant species that play a key role in diaspore removal and cleaning and found that diaspore size and lipid content can determine the type of interaction. Finally, we propose priority areas for future sampling based on environmental characteristics, including ecoregions of the Brazilian Atlantic Forest. This information is essential for advancing research on ant species and their ecological interactions as a mean to guide conservation efforts in the Atlantic Forest.

General aspects of literature

In 26 years of studies on ant-diaspore interactions, we found that the vast majority were published in journals accessible to the whole scientific community. This is significant as it facilitates international discussions on ant-plant interactions. Our findings indicate a relatively consistent interest in ants and their interactions with diaspores in the Atlantic Forest over time, underscoring the continued relevance of the topic. However, most studies are concentrated in three Brazilian states, specifically near major research centers. This can be explained by the fact that these states are part of the southeastern region of Brazil, which has higher socioeconomic development, and consequently more investments in research (Schmidt et al. 2022). These trends underscore the importance of broadening research efforts to encompass other regions of the Atlantic Forest, ensuring a more comprehensive understanding of ant-plant interactions within this ecosystem.

Ant species and diaspores

Less than half of the ant species found were identified until the species level. Accurate identification of ant species is very important for precise data analysis and ecological pattern recognition (Feitosa et al. 2023). While genus-level identification is efficient in predicting variations in ant assembly structure (Souza et al. 2016), our findings highlight the need for increased collaboration with taxonomists. Such collaboration, for both specimen identification and review of ants identified based on guides and keys, is vital in making results more robust and accurate (Feitosa et al. 2023).

Most of the ant species found in the studies belong to the subfamilies Myrmicinae and Ponerinae. Myrmicinae ants are highly capable of occupying the whole strata of tropical ecosystems, which is a pattern commonly observed in ant studies (Feitosa et al. 2022). Our findings support this pattern for myrmicine ants interacting with diaspores in the Atlantic Forest, likely due to the high generalist diet of these species. Similarly, the high number of ponerine ants found is not surprising, as fallen fruits and seeds on the ground are an important resource for poneromorph ants in Brazil (Delabie et al. 2015). However, unlike myrmicines, ponerine ants are highly sensitive to habitat disturbances, highlighting the need for conservation plans for these seed-dispersing ant species (See Leal et al. 2014a, b).

Regarding diaspores, the most abundant families in ant-diaspore interactions consist of species primarily dispersed by other agents, especially birds (e.g., Myrtaceae (Bello et al. 2017). These findings corroborate the contribution of ants to the dispersal of seeds, including species also dispersed by birds in the Atlantic Forest (Christianini et al. 2007; Camargo et al. 2016), potentially shaping the spatial distribution of seedlings. Ants are capable of rapidly reshaping more than half of the seed shadow generated during bird dispersal by quickly rescuing seeds fallen beneath parent plants or defecated by birds (Camargo et al. 2016). They also contribute substantially to increasing seedling survival rates due to the location where they deposit the seeds (Camargo et al. 2016). This evidence demonstrates the important role of ants in both the quantitative and qualitative aspects of seed dispersal, even for seeds not adapted to attract ants (i.e., seeds containing elaiosomes), which are relatively fewer in tropical biomes (Lengyel et al. 2010). All of this underscores the important role of ant-diaspore interactions in maintaining, together with vertebrate frugivores, the functionality of terrestrial ecosystems in the Atlantic Forest.

Main objectives of studies

Our findings showed that studies on ant-diaspore interactions in the Atlantic Forest primarily focused on assessing seed dispersal by ants. This is highly valuable, as the seed dispersal performed by ants still has many knowledge gaps in tropical regions. The substantial loss of large seed dispersers due to deforestation and defaunation in the Atlantic Forest (Vellend et al. 2006; Gardner et al. 2019) makes it increasingly necessary to understand the role of ants as potential mitigating agents (Anjos et al. 2020). Despite the progress in this field over 26 years of research, there are still several aspects to be investigated and explored. For example, we found that most of the studies only measure the quantitative component of the seed dispersal framework (*sensu* Schupp 1993) (e.g., removal and cleaning rates). While revealing quantitative patterns of seed dispersal aids in monitoring the initial phases of plant regeneration, qualitative aspects need also to be analyzed to uncover the effectiveness of the process (Schupp 1993). Furthermore, evaluating qualitative aspects of seed dispersal can indicate how efficient the dispersal agents are in seed dispersal (Jordano and Schupp 2000; Schupp et al. 2010). In this regard, behavioral and morphological characteristics of ants, diaspore fate, and the probability of a seed surviving and producing a new adult individual should be considered in future studies on seed dispersal by ants (See Martins et al. 2006; Gallegos et al. 2014; Camargo et al. 2019).

We found that most studies rely on using one to five preselected diaspore species as bait to attract ants, rather than surveying naturally fallen diaspores on the forest floor. This approach likely reflects the challenges of conducting extensive searches for natural ant-diaspore interactions across large areas in such a taxonomically complex and megadiverse biome as the Atlantic Forest. Additionally, for fruit and diaspore sampling to represent the community accurately, plant phenology must be taken into account, increasing the costs and time required for sampling. This lack of information on ant-diaspore interactions without the use of attractive baits (selected diaspores) can lead to important omissions regarding the plants that naturally attract ants in the Atlantic Forest. Moreover, information on the architecture of ant-diaspore interactions in the biome and how different anthropogenic impacts shape the structure of these interaction networks remains unknown (but see Laviski et al. 2021). Therefore, aside from knowledge gaps in several states within the Brazilian Atlantic Forest, our findings point to data deficiencies that are necessary for a better understanding of some ecological processes.

Key ant species for diaspore removal and cleaning

We found six key species of seed-removing ants in the Atlantic Forest. Our findings corroborate the importance of species such as *Ectatomma edentatum*, which has been reported as a key seed remover in specific Cerrado localities, such as the APA Pandeiros (Wilker et al. 2022). Several studies also highlight the substantial contribution of *Pachycondyla* *striata* and *Odontomachus chelifer* in diaspore removal, as well as the benefits of their nests for seedling establishment (Passos and Oliveira 2002; Bottcher and Oliveira 2014; Camargo et al. 2019). In general, these ant species have a medium to large body size (>4 mm), forage individually, and remove diaspores over long distances, characteristics that indicate high-quality seed dispersing ants (Leal et al. 2014b). Therefore, we suggest that *P. striata* and *O. chelifer* are high-quality seed-dispersal ants in the Atlantic Forest (see maximum removal distances and body size in Figure S7). This information can be useful in developing conservation plans for areas where these ants occur since they are important seed dispersers.

Other species, such as *Atta sexdens* and *Atta laevigata*, were also identified as key species for diaspore removal in the Atlantic Forest. Several studies have revealed that these interactions offer no benefits due to the behavior of these species (e.g., mass recruitment, seed cleaning around nests, and seed and seedling damage) (Carney et al. 2003; Knoechelmann et al. 2020). The presence of these ants as key species may indicate low-quality performance in diaspore removal by ants in the Atlantic Forest, likely due to habitat loss in the biome (Meyer et al. 2009).

Regarding diaspore cleaning, despite the absence of key species for this interaction, the commonest genera (Table S2) included small-bodied species that clean seeds without removing them far from the mother plant (it is the case of the genus *Pheidole* with nine ant species). Ants with this behavior are more associated with predation or cheating in mutualism by hindering the collection of diaspores by other ants (Bronstein 2001). Together, these fragments of information can be useful in evaluating whether ant-diaspore interactions are closer to seed dispersal or seed predation, particularly in areas affected by some form of disturbance.

Influence of diaspore characteristics on interaction type

The size and lipid content of diaspores affected the number of ant-diaspore interactions (removal, cleaning). We found that both diaspore removal and cleaning by ant species decreased inversely to diaspore size in the Atlantic Forest. Generally, in tropical environments, small-sized ants are responsible for the removal of the majority of diaspores (Pizo and Oliveira 2001), which may explain their preference for smaller diaspores. Due to the morphological limitations of ants, smaller diaspores have a higher probability of being removed (Anjos et al. 2020), whereas larger diaspores are more likely to be cleaned on-site after removal attempts. For example, larger diaspore species that had both types of interactions (e.g., *Eugenia cuprea* (length 17.7 mm) and *Copaifera langsdorffii* (length 17 mm) were removed by large ponerines and cleaned by small myrmicines (Costa and Leal 2007; Bottcher 2010). However, some ant species tend to exhibit innate behavior rather than this being a consequence of diaspores being difficult to transport (Gove et al. 2007).

We found that diaspores with lower lipid contents had lower removal and cleaning rates by ants. This pattern has previously been demonstrated for ant-diaspore interactions in some Atlantic Forest locations (Pizo and Oliveira 2001; Santana et al. 2013). Our findings show that this pattern can be observed throughout the biome, considering both the removal and cleaning by key ant species. Empirical evidence suggests that increased deforestation in the Atlantic Forest leads to a loss of functional plant diversity (Rocha-Santos et al. 2019), contributing to a decrease in the biomass, and nutritional quality of diaspores in these areas (Pessoa et al. 2016, 2017). Consequently, diaspores in deforested areas are nutritionally poorer (Pessoa et al. 2016). Therefore, ant-mediated seed dispersal may be compromised in areas under anthropogenic influence in the Atlantic Forest, as high-quality ants strongly prefer high-quality diaspores (Kaspari 1996; Leal et al. 2014a).

Relevance for future sampling of ant-diaspore interaction

We identified several relevant locations as priorities for future sampling of ant-diaspore interactions. The Atlantic Forest has a significant number of ant species survey studies, with 10,071 records and a total of 657 species, making it the second richest biome in Brazil in ant species (Feitosa et al. 2022). This results in a relatively low urgency index value for new ant fauna sampling, even in the face of high deforestation levels in the biome (Divieso et al. 2020). However, our findings showed that this does not reflect knowledge about ant-diaspore interactions. We identified a high relevance for future sampling in a large part of Atlantic Forest, even in areas very close to previously sampled sites, because they are in different ecoregions of the Atlantic Forest. It is important to note that we used environmental dissimilarity to highlight undersampled regions, this approach may underestimate the importance of some areas that already have more studies but still harbor a disproportionately high share of the Atlantic Forest's biodiversity. Thus, a low-priority classification may not necessarily indicate biological redundancy. Integrating biodiversity richness and sampling coverage across taxa with dissimilarity-based metrics would provide a more comprehensive view of research priorities for ant-diaspore interactions.

Empirical evidence suggests that ecoregional scales are important in structuring ant assemblages in Brazil (Marques and Schoereder 2014). This can be explained by the expressive number of distinct ecosystems with different degrees of environmental complexity and heterogeneity throughout the country (Olson et al. 2001). Generally, differences in floristics, microclimates, and soil types are some of the environmental attributes that affect ant assemblage structures (Ribas et al. 2012; Schmidt et al. 2013). However, too little is known about the role played by the different ecoregions in the Atlantic Forest in ant-diaspore interactions. Therefore, we emphasize the importance of further research considering the classification of ecoregions, as it will enhance the understanding of the factors shaping these interactions, especially seed dispersal by ants. This will enable fine-scale spatial actions to assess the need for creating new protected areas within the Atlantic Forest, as ants serve as a surrogate taxon reflecting patterns of other groups (Paknia and Pfeiffer 2011).

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