Introduction

Ants and plants interact in a variety of ways, from parasitism to mutualism (Beattie, 1985), including interactions with diaspores (i.e.: dispersal unit) that can result in seed dispersal (Anjos et al., 2020; Luna et al., 2021). Seed dispersal is a fundamental process for plant fitness because it determines the location in which seeds arrive and whether they will be able to develop and reach future stages in that location (Wenny, 2001). Ants can interact with non-myrmecochorous diaspores (without elaiosomes), in which the pulp and aryl work as an attraction for them (Rico-Gray & Oliveira, 2007). Several ant species have already been reported to disperse non-myrmecochorous diaspores across the globe (Anjos et al., 2020). Pizo and Oliveira (2000), for instance, observed more than 800 interactions between 56 species of non-myrmecochorous plants and 36 species of ants from monthly samplings in the Atlantic Forest over two years.

The interactions between several ant and plant species can be represented by complex ecological networks at the community level, in which species are represented as nodes, and interactions, as links. The use of the network approach...
allows visualizing multiple interactions between partners and how they are shaped by the community context, in addition to joining different research fields (Bascompte, 2007). Most studies on ant-plant networks have focused on the interactions between ants and plants with extrafloral nectaries (EFN), and only 6% have studied ant-seed networks (Del-Claro et al., 2018). Furthermore, the majority of such studies have been performed in a few regions, such as the Amazon and Neotropical Savanna, both in Brazil, and on the coast of the Gulf of Mexico (Del-Claro et al., 2018). In interactions between ants and EFN-bearing plants, studies show nested networks (Del-Claro et al., 2018), in which interactions are organized around a central core, and the interactions of less central species are a sub-set of the most generalist species (Bascompte et al., 2003). Studies on mutualistic and predation networks between diaspores and ants also have networks with a nested pattern (Guimarães et al., 2007; Anjos et al., 2018, 2019; Luna et al., 2018), showing that species do not interact randomly. In addition, Anjos et al. (2018) showed that removal and consumption networks are not modular in the Brazilian savanna. Network specialization, vulnerability and robustness were network metrics that were not affected by habitat and exclusion of the main disperser under study in the Mediterranean landscape (Timóteo et al., 2016). Several factors have been pointed out to explain the origin and maintenance of structural patterns of ant-plant networks, such as temperature and precipitation (Rico-Gray et al., 2012), soil characteristics (Dátilo et al., 2013b) and plant phenology (Lange et al., 2013; Anjos et al., 2018). Regarding the latter, as fruiting is seasonal, dry and rainy periods show differences in fruiting plant species, and this can affect the organization of interaction networks.

In addition to a network approach, in order to understand whether plants gain advantages in interactions with ants – such as escape from areas with a high mortality rate, colonization of new areas, and deposition in suitable areas for development (Wenny, 2001; Rico-Gray et al., 2007) –, approaches at the plant-population level are necessary. These approaches allow learning about the effective dispersers, which maximize the number of new adult plants by their dispersal activity, considering the quantitative and qualitative components (Schupp et al., 2010). The number of seeds dispersed represents the quantitative component, and the distance and removal destination represent the qualitative component. Diaspore removal rates by ants – quantitative component – may differ among different plant species, due to diaspore mass and chemical content (Pizo & Oliveira, 2000; Pizo & Oliveira, 2001). The lipid content of diaspores plays an important role in attracting ants for interaction. Small, lipid-rich diaspores (>60%) are highly attended by ants, quickly removed and moved over long distances (>10m) (Rico-Gray et al., 2007). However, ants can also consume diaspore resources locally or remove parts and take them to the nest, which promotes diaspore cleaning (Christianini et al., 2007; Christianini & Oliveira, 2010; Gallegos et al., 2014). Diaspore cleaning ensures germination rates approximately 20 to 60% higher than control tests (Leal & Oliveira, 1998; Pizo & Oliveira, 1998; Silva et al., 2019), but not for all plant species (Christianini et al., 2007). In addition, diaspore cleaning can increase the germination speed of some species (Pizo & Oliveira, 1998; Silva et al., 2019). Therefore, even without removal, diaspores have an advantage in interacting with ants.

Apart from the number of diaspores removed, the destination and removal distance are important to ensure that seeds are reaching places with improved conditions for seedling establishment and growth. Thus, destination and dispersal distance are part of the qualitative dispersal component (Schupp et al., 2010). The destination of ant-removed diaspores is frequently the ants’ nest (Rico-Gray et al., 2007), where they are cleaned and deposited in ant dumps, which are located in subterranean chambers or on the surface (Farji-Brener & Medina, 2000; Giladi, 2006; Luna et al., 2018). Outer dumps are potentially important for plants, as the soil around the nest has different edaphic and micromolecular conditions from those in regular soil, as well as higher nutrient content (Farji-Brener & Medina, 2000). These conditions favour germination in ants’ nesting soils for some plant species (Passos & Oliveira et al., 2002; Leal et al., 2007). Diaspore removal generally occurs at short distances, with a global mean dispersal distance of 2.39 m for non-myrmecochorous diaspores (Anjos et al., 2020). Removal distance depends on ants’ nest density and on diaspore disposition in relation to the nests. Furthermore, rainforest ecosystems have shorter removal distances than do savanna ecosystems (Anjos et al., 2020). Longer distances and the nest as a destination are more advantageous results for plants (Anjos et al., 2020; Ortiz et al., 2021).

Considering the different behaviors of ant species when interacting with diaspores, the aim of our study was to describe the network structure of ant-diaspore interactions and their temporal variation in the Atlantic Forest in south-eastern Brazil, seeking to understand several aspects of ants’ role in the interactions. In order to do so, we attempted to answer the following questions: (1) what is the structure of the ant-diaspore network in the study area? And does this network structure vary between dry and rainy seasons? We expected nested and non-modular networks to be observed, since they seem to be a pattern in mutualistic networks and a variation in this structure according to the season, due to the direct and indirect effect via plant phenology; (2) which ant behavior (removal or cleaning) is more common with diaspores in the community? As cleaning is a behavior with lower energy cost and performed by a wide variety of ant species, we expected it to be more common than removal; (3) what are the removal rates, distances and destinations of the diaspores carried by ants? Finally, we used a series of experiments to study various aspects of the ant-diaspore interaction in four species of plants. Our goal was to learn about the food preference of ants that remove diaspores in the study area, thus revealing their diaspore preferences and the role played by ants in the
quantitative and qualitative components of dispersal. We expected to find different removal rates, removal distances and destinations for different plant species.

**Methods**

*Study Area*

We carried out the present study in a secondary forest located on Marambaia Island (23° 02’ S; 43° 35’ W), on a part of the area known as Restinga de Marambaia and located within the municipalities of Rio de Janeiro, Itaguai, and Mangaratiba, in the Sepetiba Bay, south-eastern Brazil. Although it is called an island, the area corresponds to an enlarged portion of land (ca. 6 km) connected to the continent by a narrow sand strip. The northern part of the island faces the Sepetiba Bay and the southern part faces the Atlantic Ocean (Conde et al., 2005).

Marambaia Island shelters different vegetation types. This diversity of vegetation types is related to the geological processes that formed the island and originated soils with different levels of water saturation (Menezes & Araújo, 2005). Among the most common vegetation types are mangrove, restinga (coastal shrub land on sandy soils), and the sloped Atlantic Forest (Conde et al., 2005). The area was farmed from the 17th to the 19th centuries and had most of its forest removed, which is now under secondary succession (Goës et al., 2005). The soil has high leaf deposition, slow decomposition and higher nutrient levels on the surface layer (Pereira et al., 2008).

The regional climate is classified as Aw (Tropical Rainy Climate), according to the Köppen system, with average monthly temperatures above 20 °C. The coldest period occurs from June to August (average minimum temperature around 18 °C), and the warmest period occurs from December to March (average maximum temperature around 30 °C; (Mattos, 2005). Rainfall has an annual average above 1,000 mm. The rainy season consists of November to March, when rainfall indices are above 100 mm (Mattos, 2005).

*Ant-plant interactions*

This study was conducted in a transect with 0.5 km in length, in a secondary rainforest, and the procedures were performed monthly, from January 2012 to December 2013. We established 50 observation stations every 10 m. This distance is sufficient to preserve independence between ant colonies (Byrne & Levey, 1993; Kaspari, 1993). Each observation station consisted of diaspores on filter paper (10 × 10cm) to facilitate ant visualizing. We collected mature diaspores from trees or which just fallen on the ground. We provided diaspores monthly according to their availability and abundance, ranging from one to 10 diaspores of a single plant species per station. The diaspores made available each month, as well as the total number and stations are presented in supplementary material (Table S1). The diaspores were intercalated among stations in cases of availability of more than one species on the same day. We set up the stations at 8 a.m. and observed the interactions between diaspores and ants from 9 a.m. to 5 p.m., with two-hour intervals. The lack of nocturnal observations limits this experiment’s results, because there are species with nocturnal activity, such as Odontomachus chelifer, which are known to remove diaspores (Raimundo et al., 2009). Thus, some species may appear less important in the networks when the interactions actually occur at another time. We recorded the date, time, ant behavior (removal or cleaning) and plant species, as well as collected worker ants for identification. We considered the visualization of any ant species in contact with the surface of the diaspore to be an interaction, as long as the ant was not only walking on the diaspore or touching it with its antennae. Ants of the same species found in the same station at different times of the same day were considered to be the same interaction. The ant specimens were deposited in the Costa Lima Entomological Collection, of Universidade Federal Rural do Rio de Janeiro (UFRJR). The plant exsiccates were included in the herbarium collection of the Botany Department of UFRJR (herbarium RBR).

*Network Analysis*

Considering all observed interactions (removal and cleaning), we constructed interaction matrices A, where \( a_{ij} = 1 \) when ant species \( i \) was observed interacting with diaspore species \( j \), and using \( a_{ij} = 0 \) where there was no interaction. We built three matrices: one for the whole observation time (referred to here as total network); one for only the dry months (April to October), and one for only the rainy months (November to March). We analyzed the connectance, nestedness, modularity and specialization network metrics. Connectance is the proportion of links made by the total number of possible links in the network (Jordanó, 1987). Connectance was obtained by the number of observed connections divided by the number of possible connections, calculated by the formula: \( C = I / AP \), where \( C \) is connectance; \( I \) is the number of observed interactions; \( A \) is the number of ant species, and \( P \) is the number of plant species (Mello et al., 2011). Nestedness evaluates whether species with few interactions tend to interact with highly interactive species (i.e., generalist species) (Bascompte et al., 2003; Almeida-Neto et al., 2007). We estimated the nestedness value by the NODF index in the ANINHADO software (Guimarães-Jr & Guimarães, 2006). NODF values range from 0 (non-nested) to 100 (perfectly nested). We tested nestedness with 1,000 networks generated by the null model II (Bascompte et al., 2003). Such null model assumes that the probability of an interaction to occur is proportional to the observed number of interactions of both ant and plant species (Bascompte et al., 2003).

In addition, we also evaluated modularity. Modular networks are those in which species interact more frequently with a group than with species outside that group. We estimated modularity in the network by the M index in the MODULAR
software (Marquitti et al., 2013), based on a simulated annealing algorithm (Guimerà & Amaral, 2005). The M Index ranges from 0 (no modules) to 1 (totally separated modules). We used 1,000 randomized networks by the null model II with fixed total margins (Bascompte et al., 2003).

Aiming at a more conservative approach (Dáttilo et al., 2016), and counting on the availability of more data in the literature for comparison, we used binary data. Also, it was considered that quantitative and binary data, with the latter defining the fundamental niche of species (Fründ et al., 2016), can answer different questions. However, in order to measure specialization at the network level, we used quantitative data, where each cell in matrix $A$ was filled with the frequency of interaction between the ant species $i$ and the diaspora species $j$. We used the $H_2^*$ index, which ranged from 0 (completely generalist network, total overlap of interactions) to 1 (completely specialized network, without overlap of interactions). This index is robust to changes in sampling effort and network size (Blüthgen et al., 2006). We simulated 1,000 null networks from each network, using Patefield’s algorithm (Patefield, 1981) to evaluate the significance of the $H_2^*$ index. We estimated 1,000 $H_2^*$ values from the null networks, and then we compared if the observed $H_2^*$ value differed from those of the null model.

To test the differences between the dry and rainy periods, we calculated the absolute difference of the $H_2^*$ index between the dry and rainy networks, and then compared it with the absolute difference of the same metric for the networks generated by the null models. For NODF and M, which are metrics affected by the network size, we used the methodology adopted by Carvalho et al. (2021), where the observed and randomized values were standardized using z-scores. The transformed Z-score is defined: $Z = (x - μ) / σ$, where $x$ is the observed index value, $μ$ is the mean of the values from the null networks, and $σ$ is the standard deviation of the values from the null networks (Almeida-Neto et al., 2008). We used the calculated values of NODF and M for the null networks obtained on ANINHADO and MODULAR, respectively. We estimated the significance of the difference in the metrics between the dry and rainy networks using z-scores with values greater than 2 (Dormann & Strauss, 2014).

Moreover, we defined whether the species were central or peripheral in the networks by the formula: $G_c = (K_i - K_{mean}) / σ_c$, where $K_i$ is the mean number of connections for a given ant or diaspora species; $K_{mean}$ is the mean number of connections for all ant or diaspora species (connectance), and $σ_c$ is the standard deviation of the number of connections for ant or diaspora species (Dáttilo et al., 2013a). $G_c > 1$ values indicated central species in the network, with a large number of connections. $G_c < 1$ values indicated peripheral species in the network, with few connections. With the exception of nestedness and modularity, all other analyses cited were performed using the ‘bipartite’ package (Dormann et al., 2019) implemented in R v.4.0.2 (R Development Core Team, 2020).

**Diaspore removal rate**

We selected four species of plants with high abundance of individuals and a large number of fruits in the study area: *Inga edulis* Mart., *Miconia calvescens* DC., *M. prasina* (Sw.) DC. And *Psychotria leioarpa* Cham. & Schltdl. (Table 1). From June to October 2013, we picked 15 stations at random where we placed dias pores protected by screen fences ($20 \times 20 \times 12$ cm; 2-cm gap) fixed on the ground by 2-cm wires, so as to allow ant access and prevent disturbance by vertebrates. We then placed four dias pores of a single species in each station. We marked the diaspo res with a small dot using a marker pen to identify the fruits utilized in the experiment. We set up the experiment at 07:00 a.m. and then checked it after 24 h, when we recounted the number of dias pores. We considered a dias pore removed if we did not find it in a radius of 30 cm around the cage (Passos & Oliveira, 2002). We repeated the experiment during the fruiting period of each evaluated dias pore species and while there were enough dias pores to perform the experiment. We used GLMM with the Poisson family to test for differences in the number of removals between dias pore species. We considered the number of removals to be the dependent variable; dias pore species, the fixed factor; and stations, a random factor. The analyses were performed using the ‘lme4’ (Bates et al., 2019) and ‘multcomp’ (Hothorn et al., 2008) packages implemented in R v.4.0.2 (R Development Core Team, 2020).

**Destination and distance of dias pore removal**

From June to October 2013, we selected one fruiting individual of each plant species selected in the previous experiment (Table 1), and established three radial stations underneath it at approximately 1 m from each other, in which we assessed the dias pore destination and distance. Each station was composed of filter paper ($10 \times 12$ cm) used as substrate, and received two dias pores. Thus, each observed plant had a total of six dias pores. We monitored the stations for ant removal from 8:00 a.m. to 5:00 p.m. with one-hour pauses between observations, for a total of 5 observation hours per day. Observations were suspended during rain. The total hours observed in each species are shown in Table 1. When a removal event took place, we followed the ants to their nests or until they disappeared in the leaf litter, and then measured the removal distance with a measuring tape. We replaced each dias pore after removal.

We used GLMM with the Binomial family to test for differences in destination between dias pore species. We considered the destination the dependent variable; dias pore species, the fixed factor; and data and time, random factors. To test differences in removal distance between dias pore species, we used GLMM with the Gaussian family. We considered the removal distance the dependent variable; dias pore species, the fixed factor; and data and time, random factors. The analyses were performed using the ‘lme4’ (Bates et al., 2019) and ‘multcomp’ (Hothorn et al., 2008) packages implemented in R v.4.0.2 (R Development Core Team, 2020).
Sociobiology 68(3): e7104 (September, 2021)

Table 1. Plant species used in the removal-rate, destination and removal-distance experiments. Observation hours refer to the total time of removal-distance experiments.

| Plant species | Diaspore size (cm) | Observation hours |
|---------------|--------------------|-------------------|
| Inga edulis Mart. | $1.20 \pm 0.17 \times 0.77 \pm 0.13$ | 5 |
| Miconia calvuscas DC. | $0.42 \pm 0.05 \times 0.37 \pm 0.04$ | 25 |
| Miconia prasina (Sw.) DC. | $0.51 \pm 0.04 \times 0.42 \pm 0.04$ | 25 |
| Psychotria leiocarpa Cham. & Schltdl. | $0.57 \pm 0.09 \times 0.49 \pm 0.06$ | 26.5 |

Results

Ant-plant interactions

We recorded a total of 1,032 interactions among 49 ant species (22 genera belonging to six subfamilies) (Table 2) and 25 plant species belonging to 17 families (Table 3). Myrmicinae was the subfamily of ants with the largest number of species (S = 36 spp.; 73.47%), followed by Ponerinae (S = 4 spp.; 8.16%) and Formiciniae (S = 4 spp.; 8.16%). For plants, the Melastomataceae, Meliaceae and Rubiaceae families equated to over 50% of the interactions.

We observed 1,016 diaspore cleaning interactions (98.45%) versus 16 diaspore removal interactions (1.55%). However, 275 diaspores disappeared from the observation area and may have been removed by the ants. We have included these diaspores as removals in Table 3, which, therefore, has a different total number of removals from that shown here. Considering these disappearances to be removals, the total number of removals was 291 (22.26% of interactions). The inclusion of such data overestimates removal by ants; however, the specific removal experiments (results in the topic below) showed that the removal was greater than 1.55%. The true percentage of diaspore removal by ants in the community must be between these two values (1.55% and 22.26%). Ants that removed diaspores were Acromyrmex subterraneus, Atta sexdens rubropilosa, Cyphomyrmex sp. 1, Ectatoma edentatum, E. permagnum, Neoponera apicalis, Pachycondyla striata, Pheidole sigillata and Sericomyrmex sp. 1.

Table 2. Ant species recorded in this study on Marambaia Island (RJ) interacting with diaspore species.

| Sub-family / Species | Code |
|----------------------|------|
| **Dolichoderinae**   |      |
| 1. Lineepithema sp. 1 | Linep1 |
| **Ectatomminae**     |      |
| 2. Ectatomma edentatum Roger, 1863 | E_ede |
| 3. Ectatomma permagnum Forel, 1908 | E_per |
| **Formicinae**       |      |
| 4. Brachymyrmex sp. 1 | Brach1 |
| 5. Brachymyrmex sp. 2 | Brach2 |
| 6. Camponotus sp. 1  | Campo1 |
| 7. Myrmelachista sp. 1 | Myrme1 |
| **Myrmicinae**       |      |
| 8. Acromyrmex subterraneus Forel, 1893 | A_sub |
| 9. Atta sexdens rubropilosa Forel, 1908 | A_sex |
| 10. Carebara urichi (Wheeler, 1922) | C_uri |
| 11. Carebara bicolor Emery, 1906 | Careb1 |
| 12. Crematogaster sp. 1 | Crema1 |
| 13. Cyphomyrmex sp. 1 | Cypho1 |
| 14. Mycocepurus sp. 1 | Mycc1 |
| 15. Octotruma rugifera (Mayr, 1887) | O_rug |
| 16. Pheidole diligens (Smith, 1858) | Ph_dil |
| 17. Pheidole sigillata Wilson, 2003 | Ph_sig |
| 18. Pheidole sp. 3 | Phied3 |
| 19. Pheidole transversostriata Mayr, 1887 | Ph_tr |
| 20. Pheidole pedana Wilson, 2003 | Ph_ped |
| 21. Pheidole subarmata Mayr, 1884 | Ph_sub |
| 22. Pheidole sp. 7 | Phied7 |
| 23. Pheidole tijucana Borgmeier, 1927 | Ph_tij |
| 24. Pheidole sp. 9 | Phied9 |
| 25. Pheidole sp. 10 | Phied10 |
| 26. Pheidole puttemansi Forel, 1911 | Ph_put |
| 27. Pheidole lucaris Wilson, 2003 | Ph_luc |
| 28. Pheidole sp. 13 | Phied13 |
| 29. Pheidole sp. 14 | Phied14 |
| 30. Pheidole sensitiva Borgmeier, 1959 | PhSen |
| 31. Pheidole sp. 16 | Phied16 |
| 32. Pheidole sp. 17 | Phied17 |
| 33. Sericomyrmex sp. 1 | Serie1 |
| 34. Solenopsis sp. 1 | Solen1 |
| 35. Solenopsis sp. 2 | Solen2 |
| 36. Solenopsis sp. 3 | Solen3 |
| 37. Solenopsis sp. 4 | Solen4 |
| 38. Solenopsis sp. 5 | Solen5 |
| 39. Solenopsis sp. 6 | Solen9 |
| 40. Trachymyrmex sp. 1 | Trach1 |
| 41. Trachymyrmex sp. 2 | Trach2 |
| 42. Wasmannia auropunctata (Roger, 1863) | W_aur |
| 43. Wasmannia sp. 2 | Wasm2 |
| **Ponerinae**        |      |
| 44. Odontomachus chelifer (Latreille, 1802) | O_che |
| 45. Odontomachus meinerti Forel, 1905 | O_mei |
| 46. Neoponera apicalis (Latreille, 1802) | N_api |
| 47. Pachycondyla striata Fr. Smith, 1858 | P_str |
| **Pseudomyrmecinae** |      |
| 48. Pseudomyrmex sp. 1 | Pseud1 |
| 49. Pseudomyrmex sp. 2 | Pseud2 |
Table 3. Diaspore species explored by ants in this study on Marambaia Island (RJ) with the total number of interactions recorded and ant species with which they interacted (see code in Table 2).

| Family / Species | Unit of dispersal | Number of interactions | Number of removals | Ant species |
|------------------|-------------------|------------------------|--------------------|-------------|
| **Araceae**      |                   |                        |                    |             |
| 50. *Monstera adansonii var klotzschiana* (Schott) Madison | Fruit | 4 | 1 | 18-19; 34; 38 |
| **Burseraceae**  |                   |                        |                    |             |
| 51. *Protium brasiliense* Engl. | Seed | 61 | 41 | 3; 16-21; 25-26; 33-38; 42; 44; 47 |
| **Erythroxylaceae** |                   |                        |                    |             |
| 52. *Erythroxylum pulchrum* A. St.-Hil. | Fruit | 74 | 19 | 12; 16-21; 25-27; 29-30; 34-36; 38-42; 47 |
| **Fabaceae**     |                   |                        |                    |             |
| 53. *Inga edulis* Mart. | Seed | 23 | 2 | 1; 3; 12; 16-19; 25; 40-41; 46-47 |
| **Lauraceae**    |                   |                        |                    |             |
| 54. *Ocotea schottii* (Meisn.) Mez | Fruit | 89 | 1 | 1-2; 4-5; 14; 16-22; 25; 33-35; 38-40; 42; 48 |
| **Malpighiaceae**|                   |                        |                    |             |
| 55. *Niedenzuela acutifolia* (Cav.) W.R. Anderson | Fruit | 1 | 1 | 42 |
| **Melastomataceae** |               |                        |                    |             |
| 56. *Clidemia hirta* (L.) D. Don | Fruit | 26 | 17 | 16-21; 35; 40; 42-43; 47 |
| 57. *Miconia calvensis* DC. | Fruit | 70 | 30 | 1; 4; 8; 12; 16-21; 23; 25; 34; 38; 42 |
| 58. *Miconia prasina* (Sw.) DC. | Fruit | 193 | 93 | 1; 3-4; 12; 16-21; 23; 25; 28; 33; 35; 38; 40-41; 43; 46; 49 |
| **Meliaceae**    |                   |                        |                    |             |
| 59. *Guarea guidonia* (L.) Sleumer | Seed | 132 | 35 | 2-3; 10; 12; 16-27; 34; 36-38; 42-43; 45-47 |
| **Moraceae**     |                   |                        |                    |             |
| 60. *Ficus insipida* Willd. | Fruit | 78 | 0 | 1; 3; 7; 10; 12; 16-21; 25; 33-38; 40; 42-44; 47 |
| **Nyctaginaceae**|                   |                        |                    |             |
| 61. *Guapira opposita* (Vell.) Reitz | Fruit | 7 | 0 | 16; 18-19; 25; 36; 47 |
| **Passifloraceae**|                   |                        |                    |             |
| 62. *Passiflora edulis* Sims | Seed | 18 | 1 | 14; 16-20; 35-36; 42 |
| **Piperaceae**   |                   |                        |                    |             |
| 63. *Piper amplum* Kunth | Fruit | 2 | 0 | 6; 19 |
| 64. *Piper anisum* (Spreng.) Angely | Fruit | 3 | 0 | 16; 40; 42 |
| 65. *Piper caldense* C. DC. | Fruit | 5 | 0 | 9; 13; 19; 43 |
| **Rubiaceae**    |                   |                        |                    |             |
| 66. *Coccocypselum cordifolium* Nees & Mart. | Fruit | 17 | 0 | 16-22; 36; 42 |
| 67. *Psychotria cf. hoffmannseggiana* (Schult.) Müll. Arg. | Fruit | 14 | 1 | 1; 16-22; 31 |
| 68. *Psychotria deflexa* DC. | Fruit | 37 | 10 | 11-12; 16-20; 36; 40; 42-43; 47 |
| 69. *Psychotria leiocarpa* Cham. & Schltdl. | Fruit | 58 | 14 | 16-22; 28; 32; 34; 36; 40-43 |
| **Sapindaceae**  |                   |                        |                    |             |
| 70. *Paulinia micrantha* Cambess. | Seed | 33 | 6 | 9; 11; 16-21; 25; 33; 36; 40; 42 |
| 71. *Urvillea sp.* | Fruit | 3 | 0 | 18; 20 |
| **Siparunaceae** |                   |                        |                    |             |
| 72. *Siparuna guianensis* Aubl. | Seed | 17 | 17 | 16-19; 29; 42 |
| **Solanaceae**   |                   |                        |                    |             |
| 73. *Solanum pseudochina* Spreng. | Fruit | 21 | 0 | 10; 16-20; 22; 36; 40; 47 |
| **Verbenaceae**  |                   |                        |                    |             |
| 74. *Citharexylum myrianthum* Cham. | Fruit | 46 | 2 | 1; 15-21; 25; 34-36; 40; 42-43; 47 |
**Network analysis**

The complete network between ants and diaspores (removal and cleaning interactions) showed a connectance of 0.237; it was significantly nested (NODF = 33.74; $p < 0.001$), not significantly modular (M = 0.23; $p = 1.00$; Fig 1), and it had a higher level of specialization than the null models ($H^*_2 = 0.099$; $p < 0.001$). *Pheidole* species (Species 16-21 – Table 2), *Solenopsis* sp. 3, *Trachymyrmex* sp. 1 and *Wasmannia auropunctata* species were present in the core ant species. In plants, the species observed in the central core were *Erythroxylum pulchrum* (Erythroxylaceae), *Ocotea schottii* (Lauraceae), *Miconia prasina* (Melastomataceae), *Guarea guidonia* (Meliaceae) and *Ficus insipida* (Moraceae).

**Fig 1.** Network of interactions between diaspores and ant species. Plants are represented by triangles, and ants by circles. Lines represent ant-diaspore interactions. (a) Dry-season network. (b) Rainy-season network. (c) Total network. The ant codes are in Table 2. Cmyr = *Citharexylum myrianthum*; Chir = *Clidemia hirta*; Ceor = *Coccocypselum cordifolium*; Epul = *Erythroxylum pulchrum*; Fins = *Ficus insipida*; Gopp = *Guapira opposita*; Ggui = *Guarea Guidonia*; Iedu = *Inga edulis*; Mcal = *Miconia calvescens*; Mpra = *Miconia prasina*; Mada = *Monstera adansonii*; Nacu = *Niedenzuella acutifolia*; Osch = *Ocotea schottii*; Pedu = *Passiflora edulis*; Pmic = *Paulinia micrantha*; Pamp = *Piper amplum*; Pani = *Piper anisum*; Pcal = *Piper caldense*; Pbra = *Protium brasiliense*; Phof = *Psychotria cf. hoffmannseggiana*; Pdef = *Psychotria deflexa*; Plei = *Psychotria leiocarpa*; Sgui = *Siparuna guianensis*; Spse = *Solanum pseudochina*; Urv1 = *Urvillea* sp.
Diaspore removal rate, destination and distance of diaspore removal

*Miconia calvescens, M. prasina* and *Inga edulis* showed the highest removal rates (65.8%, 58.3% and 40.0%, respectively), whereas *P. leiocarpa* showed a low removal rate (2.1%; deviance = 310.03; d.f = 3; p < 0.001, Fig 2a).

In the experiments on destination and distance of diaspore removal, we observed 137 removals for *M. calvescens*, 14 for *M. prasina* and 17 for *I. edulis*. No removals were observed for *P. leiocarpa*. The ants that removed diaspores were *A. sexdens rubropilosa* and poneromorph species (*Pachycondyla* and *Ectatomma* species). The *A. sexdens rubropilosa* species removed the most diaspores of *M. calvescens* (95.62%; n = 131), whereas the poneromorph species removed the most diaspores of *M. prasina* (92.86%; n = 13). The *A. sexdens rubropilosa* species removed all the diaspores of *I. edulis*. The removal distance varied between 5 and 473 cm. The average removal was 107.50 cm for *M. calvescens*, 104.57 cm for *M. prasina* and 300.55 cm for *I. edulis*. The diaspores of *I. edulis* were removed farther than *Miconia* diaspores (deviance = 1945.3; d.f. = 3; p < 0.001). Ants carried most of the diaspores of *M. calvescens* and *I. edulis* to their nests (83.94% and 94.12%, respectively; Fig 2b). In most *M. prasina* removals, ants did not reach the nests and abandoned the diaspores in the leaf litter (92.86%; deviance = 134.02; d.f = 2; p < 0.001; Fig 2b). We observed pieces of *M. calvescens* fall to the ground along the path of *A. sexdens*. We did not observe any subsequent discards by *A. sexdens* for any plant species after they entered the nest.

**Discussion**

This study recorded a large number of interactions in an Atlantic Forest area on Marambaia Island, with diaspore cleaning being the main interaction. The networks analysed cleaning and removal interactions together, and the network of only dry months showed a connectance of 0.271; it was significantly nested (NODF = 34.34; p < 0.001), not significantly modular (M = 0.25; p = 0.99), and it had a higher level of specialization than the null models (H2' = 0.123; p < 0.001). The ant species in the central core were *Pheidole* species (Species 16-20 – Table 2) and *W. auropunctata*. The diaspores in the central core were *O. schottii* (Lauraceae), *M. prasina* (Melastomataceae) and *G. Guidonia* (Meliaceae). The network of only rainy months showed a connectance of 0.279; it was significantly nested (NODF = 36.03; p < 0.001), not significantly modular (M = 0.25; p = 0.99), and it had no higher level of specialization than the null models (H2' = 0.118; p = 0.086). The ant species in the central core were *Pheidole* species (Species 16-21 – Table 2), *Solenopsis* sp. 3, *W. auropunctata* and *P. striata*. The diaspores in the central core were *Protium Guidonia brasiliense* (Burseraceae), *E. pulchrum* (Erythroxylaceae) and *G. guidonia* (Meliaceae).

**Ant-plant interactions**

Diaspore cleaning was the most common ant behavior in the recorded interactions, being 3.5 times more frequent than diaspore removal. This result opposes to that found in ant-fruit interaction networks in the Brazilian *Cerrado*, where diaspore removal was more common than diaspore cleaning (Anjos et al., 2018). Despite not presenting values for comparison, Pizo and Oliveira (2000) report that the behavior...
of removing pieces and collecting liquids is more common than removing diaspores in the Atlantic Forest. In addition, Passos and Oliveira (2003) justify their systematic sampling in a restinga area by pointing the high speed of diaspore removal by large ponerines, which makes it difficult for them to be seen during active search. Moreover, ants remove diaspores at longer distances in savanna areas than in rainforests (Anjos et al., 2020). In addition to the distance, the removal rate may also be lower in rainforests. Moreover, impacted areas of the Atlantic Forest and in secondary succession had lower removal rates when compared to undisturbed areas (Zwiener et al., 2012; Almeida et al., 2013; Bieber et al., 2014). Poneromorph species are the ant species that most remove in Atlantic Forest areas, and they are less often observed in impacted areas than in undisturbed areas (Almeida et al., 2013; Bieber et al., 2014). The fact that the study area was in the process of secondary succession explains the low removal rate. In addition, most interacting ant species were small and did not remove diaspores. An ant’s body size is also a key trait for removal (Camargo et al., 2019).

Diaspore cleaning plays an important role in plant recruitment, since it increases germination rates in most plant species whose diaspores are cleaned by ants (Christianini et al., 2007; Camargo et al., 2016), and it may also decrease germination time (Lima et al., 2013). In addition, diaspore cleaning decreases the chances of attacks by pathogens such as fungi, providing conditions for germination and seedling development (Pizo & Oliveira, 1998; Passos & Oliveira, 2002). For example, Guarea guidonia, whose diaspores are cleaned by ants, is benefited by this interaction (Silva et al., 2019). Therefore, although there is no removal, diaspore cleaning brings benefits to the plants.

The M. prasina species was the most frequent in the interaction records, followed by G. guidonia. Miconia species are classified as ornitochoric and usually have high water and sugar content (Silveira et al., 2012). The compounds present in these fruits serve as a resource for the ants and should promote the high number of interactions found for that species. Guarea guidonia is an ornitochoric species whose seeds are covered with a red sarcotesta, a similar compound to aryl, usually rich in lipids (Van Der Pijl, 1972). The presence of resources such as pulp is important for ant attraction (Rico-Gray & Oliveira, 2007).

Network analysis

The networks showed low connectance, a nested pattern, absence of significant modules and low specialization. These results indicate low interaction between diaspores and ants and with some species of plants and ants dominating most interactions. Other studies have shown that mutualistic networks between ants and diaspores were also nested (Guimarães et al., 2007; Anjos et al., 2018). In our study, we observed that some species of ants (e.g., Pheidole species) and plants (e.g., G. guidonia, M. prasina) concentrated most of the interactions. This result agrees with those by Palacio et al. (2016), which showed that generalist species play a central role in highly diverse plant-frugivorous networks. In addition, the specialization values of the networks were very low (although the total and dry season networks were more specialized than the null models). This indicates that ants that explore diaspores are generalists and interacting with any diaspore type, just as plant species (diaspores) interact with several ant species. This is probably the result of opportunistic interactions (Anjos et al., 2018), and it is common in relationships with frugivorous insects (Passos & Oliveira, 2003), where most frugivorous species have generalist and opportunistic behavior and whose spectrum of fruits visited by different ant species commonly overlaps (Blüthgen, 2011). In the case of frugivorous vertebrates, specialization varies among dispersal groups and it is influenced by fruit characteristics (Donatti et al., 2011; Garcia et al., 2018). The absence of differences in the values of nestedness, modularity and specialization between the rainy and dry networks indicates that ant-diaspore interactions remain stable despite differences in climate in our study area. Thus, species of ants and plants interact throughout the year, regardless of seasonal variation. In line with our results, Ruzi et al. (2017) found that the removal rate by ants for 12 species of neotropical pioneer trees was not affected by seasonality.

The core of generalist species was stable throughout the years. The Pheidole transversostriata, Pheidole sp3, P. diligens, P. sigillata, P. pedana and Wasmannia auropunctata species are almost always present in the generalist core, which makes them important species in the general structure of the network and within the community because they promote diaspore cleaning and removal. Core species are known to be competitively superior and to monopolize resources in interactions between ants and EFN-bearing plants (Dättilio et al., 2013a; Dättilio et al., 2014a, 2014c). A stable core appears to be robust to annual fluctuations, and core species tend to belong to lineages that are less volatile and/or generate multiple species in a short time span (Burin et al., 2021). Regarding the ant species in the core species in this study, Pheidole species are extremely competitive, and they monopolize the resources that they explore, being considered dominant omnivores (Silvestre et al., 2003), and W. auropunctata shows massive recruitment, which facilitates the control of the diaspore stations (Delabie et al., 2003; Silvestre et al., 2003). Species of the Pheidole and Wasmannia genera can remove seeds, although that is not frequent (Christianini et al., 2010). Thus, a core of interactions composed by such species may indicate high diaspore cleaning rates, which corroborates our results, as well as potential for removing diaspores. The presence of P. striata in the core of central species in the rainy season network may indicate an increase in removal by that species during rainy period, since it removes seeds (Christianini et al., 2010; Christianini et al., 2012). This idea should be evaluated in future studies.
Diaspore removal rate, destination and distance of diaspore removal

We observed high removal rates for two Miconia species and I. edulis, but not for P. leiocarpa. Differences in secondary removal rates occur among plant species (Christianini et al., 2012; Ruzi et al., 2017; Ortiz et al., 2021). The presence of several attractive resources for ants is one of the causes for such differences (Christianini et al., 2012; Ruzi et al., 2017; Clemente & Whitehead, 2019; Ortiz et al., 2021). The presence of secondary compounds, as occurs in Psychotria fruits, can reduce the ant recruitment and result in low removal rates (Cazetta et al., 2008; Santana et al., 2013). As a result, diaspores ‘preferred’ by ants have greater removal (e.g., M. calvescens = 65.8% of removal), and ‘non-preferred’ diaspores are rarely or not removed (e.g., P. leiocarpa = 2.1% of removal). This had already been observed in granivory by ants (Willot et al., 2000).

The studied ants removed diaspores to short distances. Removal distances are in accordance with data reported by Anjos et al. (2020), in which rainforests ecosystems show shorter removal distances by ants than savanna ecosystems. Hence, even at short distances diaspore removal decreases diaspore aggregation and helps the local plant population (Gorb & Gorb, 2000), as it may promote recruitment through a reduction in competition among seeds and a decrease in attacks by predators (Guimarães-Jr & Cogni, 2002). Despite their larger sizes (Table 1), I. edulis diaspores were removed for longer distances than those of Miconia. Diaspore size is also a key trait influencing removal rates (Pizo & Oliveira, 2001). Therefore, the high rates of removal of a large diaspore must have occurred due to the chemical composition of the fleshy portion. It is known that ants look for more fleshy fruits (Passos & Oliveira, 2003; Rico-Gray & Oliveira, 2007), and the composition of these fruits can also be an important factor (Pizo & Oliveira, 2001; Christianini et al., 2012).

Most of the removals of I. edulis and M. calvescens were to the nest, which is advantageous for seedling development (Farji-Brener & Medina, 2000). However, the arrival of many seeds in the nest can increase competition (Spiegel & Nathan, 2012). Therefore, behaviors in which ant species take some diaspores to the nest and abandons others can be advantageous for plants (Ortiz et al., 2021). In removals by Atta sexdens, nest deposition without subsequent seed discard may indicate that the diaspores serve as a substrate for the fungus and, therefore, dispersal does not occur. In the case of M. calvescens, in which the dispersal unit is the fruit with multiple seeds, some of them are abandoned along the way and can benefit from the removal distance. However, in I. edulis, in which the dispersal unit is the seed, A. sexdens may be acting as a predator.

General conclusions

In the Atlantic Forest, interactions between ants and diaspores are frequent and generalised, with ants playing an important role in dispersal stages. In general, ants interact with diaspores by cleaning them, and some species also remove them. Ant-diaspore networks are generalist, nested and remain stable throughout the seasons. Thus, we can conclude that diaspore cleaning and removal occur continuously. The removal distance and final destination of diaspores depend on the diaspore species and on the ant species that remove them. Ants are good secondary dispersers for only some plant species, depending on their behavior and the identity of the ant species (Christianini et al., 2012; Clemente & Whitehead, 2019). For most plants, ants would play a more important role in cleaning and promoting germination (Pizo & Oliveira, 1998).

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References

Almeida, F.S., Mayhé-Nunes, A.J. & Queiroz, J.M. (2013). The Importance of Poneromorph Ants for Seed Dispersal in Altered Environments. Sociobiology, 60: 229-235. doi: 10.13101/sociobiology.v60i3.229-235
Almeida-Neto, M., Guimarães-Jr, P.R., Lewinsohn, T. (2007). On nestedness analyses: rethinking matrix temperature and anti-nestedness. Oikos, 116: 716-722. doi: 10.1111/j.0030-1299.2007.15803.x
Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117: 1227-1239. doi: 10.1111/j.0030-1299.2008.16644.x
Anjos, D., Dáttilo, W. & Del-Claro, K. (2018). Unmasking the architecture of ant-diaspore networks in the Brazilian Savanna. PLoS ONE, 13: e0201117. doi: 10.1371/journal.pone.0201117
Anjos, D.V., Luna, P., Borges, C.C.R., Dáttilo, W. & Del-Claro, K. (2019). Structural changes over time in individual-based networks involving a harvester ant, seeds, and invertebrates. Ecological Entomology, 44: 753-761. doi: 10.1111/een.12764.
Anjos, D.V., Leal, L.C., Jordano, P. & Del-Claro, K. (2020). Ants as diaspore removers of non-myrmecochorous plants: a meta-analysis. Oikos, 129: 775-786. doi: 10.1111/oik.06940.
Baccaro, F.B., Feitosa, R.M., Fernández, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P. & Solar, R. (2015). Guia para os géneros de formigas do Brasil. Manaus: INPA, 388 p.
Bascompte, J. (2007). Networks in ecology. Basic and Applied Ecology, 8: 485-490. doi: 10.1016/j.baae.2007.06.003
Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. PNAS, 100: 9383-9387. doi: 10.1073/pnas.1633576100

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R., Singmann, H., et al. (2019). Package ‘lme4’.

Beattie, A.J. (1985). The evolutionary ecology of ant-plant mutualisms. Cambridge: Cambridge University Press, 182 p

Bieber, A.G.D., Silva, P.S.D., Sendoya, S.F. & Oliveira, P.S. (2014). Assessing the impact of deforestation of the Atlantic rainforest on ant-fruit interactions: A field experiment using synthetic fruits. PLoS ONE, 9: e90369. doi: 10.1371/journal.pone.0090369

Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialisation in species interaction networks. BMC Ecology 6, 1. doi: 10.1186/1472-6785-6-9

Blüthgen, N. (2011). Interações planta-animais e a importância funcional da biodiversidade. In K. Del-Claro Blüthgen, N. (2011). Interações planta-animais e a especialisation in species interaction networks. BMC Ecology 6, 1. doi: 10.1186/1472-6785-6-9

Byrne, M.M. & Levey, D.J. (1993). Removal of seeds from frugivore defecations by ants in a Costa Rican rain forest. Vegetatio, 107: 363-374. doi: 10.1007/BF00052235

Camargo, P.H.S.A., Martins, M.M., Feitosa, R.M. & Christianini, A.V. (2016) Bird and ant synergy increases the seed dispersal effectiveness of an ornithochoric shrub. Oecologia, 181: 507-518. doi: 10.1007/s00442-016-3571-z

Camargo, P.H.S.A., Rodrigues, S.B.M., Piratelli, A.J., Oliveira, P.S. & Christianini, A.V. (2019). Interhabitat variation in diplochory: Seed dispersal effectiveness by birds and ants differs between tropical forest and savanna. Perspectives in Plant Ecology, Evolution and Systematics, 38: 48-57. doi: 10.1016/j.ppees.2019.04.002

Carvalho, R. L., Anjos, D. V., Fagundes, R., Luna, P., & Ribeiro, S. P. (2021). Similar topologies of individual-based plant-herbivorous networks in forest interior and anthropogenic edges. Austral Ecology, 46: 411-423. doi: 10.1111/aec.13001

Cazetta, E., Schaefer, H.M. & Galetti, M. (2008). Does attraction to frugivores or defense against pathogens shape fruit pulp composition? Oecologia, 155: 277-286. doi: 10.1007/s00442-007-0917-6

Christianini, A.V., Mayhê-Nunes, A.J. & Oliveira, P.S. (2007). The role of ants in the removal of non-myrmecochorous diaspires and seed germination in a neotropical savanna.

Journal of Tropical Ecology, 23: 343–351. doi: 10.1017/S0266467407004087

Christianini, A.V., Mayhê-Nunes, A.J. & Oliveira, P.S. (2012). Exploitation of Fallen Diaspores by Ants: Are there Ant-Plant Partner Choices? Biotropica, 44: 360-367. doi:10.1111/j.1744-7429.2011.00822.x

Christianini, A.V. & Oliveira, P.S. (2010). Birds and ants provide complementary seed dispersal in a neotropical savanna. Journal of Ecology, 98: 573-582. doi: 10.1111/j.1365-2745.2010.01653.x

Clemente, S. & Whitehead, S.R. (2020). Ant seed dispersal of a non-myrmecochorous neotropical shrub. Biotropica, 52: 90-100. doi: 10.1111/btp.12728

Conde, M.M.S., Lima, H.R.P. & Peixoto, A.L. (2005). Aspectos florísticos e vegetacionais da Marambaia, Rio de Janeiro, Brasil. In L.F.T. Menezes, A.L. Peixoto & D.S.D. Araújo (Eds.), História Natural da Marambaia (pp. 133-168). Seropédica: EDUR.

Dátillo, W., Guimarães, P.R. & Izzo, T.J. (2013). Spatial structure of ant-plant mutualistic networks. Oikos, 122: 1643-1648. doi: 10.1111/j.1600-0706.2013.00562.x

Dátillo, W., Izzo, T.J., Vasconcelos, H.L. & Rico-Gray, V. (2013) Strength of the modular pattern in Amazonian symbiotic ant-plant networks. Arthropod-Plant Interactions, 7: 455-461. doi: 10.1007/s11829-013-9256-1

Dátillo, W., Rico-Gray, V., Rodrigues, D.J. & Izzo, T.J. (2013). Soil and vegetation features determine the nested pattern of ant-plant networks in a tropical rainforest. Ecological Entomology, 38: 374-380. doi: 10.1111/eet.12029

Dátillo, W., Diaz-Castelazo, C. & Rico-Gray, V. (2014). Ant dominance hierarchy determines the nested pattern in ant-plant networks. Biological Journal of the Linnean Society, 113: 405-414. doi: 10.1111/bij.12350

Dátillo, W., Fagundes, R., Gurka, C.A.Q., Silva, M.S.A., Vieira, M.C.L., Izzo, T.J., Diaz-Castelazo, C., Del-Claro, K. & Rico-Gray, V. (2014). Individual-based ant-plant networks: diurnal-nocturnal structure and species-area relationship. PLoS One, 9: e99838. doi:10.1371/journal.pone.0099838

Dátillo, W., Marquitti, F.M.D., Guimarães, P.R. & Izzo T.J. (2014). The structure of ant-plant ecological networks: is abundance enough? Ecology, 95: 475-485. doi: 10.1890/12-1647.1

Dátillo, W., Lara-Rodriguez, N., Jordano, P., Guimarães, P.R., Thompson, J.N., Marquis, R.J., Medeiros, L.P., Ortiz-Pulido, R., Marcos-Garcia, M.A. & Rico-Gray, V. (2016). Unravelling Darwin’s entangled bank: architecture and robustness of mutualistic networks with multiple interaction types. Proceedings of the Royal Society B, 283: 1-9. doi: 10.1098/rspb.2016.1564
Del-Claro, K., Lange, D., Torezan-Silingardi, H.M., Anjos, D.V., Calixto, E.S. & Dáttilo, W. (2018). The complex ant-plant relationship within tropical ecological networks. In W. Dáttilo & V. Rico-Gray (Eds), Ecological Networks in the Tropics, An Integrative Overview of Species Interactions From Some of the Most Species-Rich Habitats on Earth (pp. 59-71). Berlin, Heidelberg: Springer.

Delabie, J.H.C., Ospina, M. & Zaba, G. (2003). Relaciones entre hormigas y plantas. In F. Fernandez (Ed.), Introducción a las hormigas de la región Neotropical (pp. 167-180). Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Diaz-Castelazo, C., Sánchez-Galván, I.R., Guimarães-Jr, P.R., Raimundo, R.L.G & Rico-Gray, V. (2013). Long-term temporal variation in the organization of an ant-plant network. Annals of Botany, 111: 1285-1293. doi:10.1093/aob/mct071

Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D. & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. Ecology Letters, 14: 773-781. doi: 10.1111/j.1461-0248.2011.01639.x

Dormann, M., Fruend, J. & Gruber, B. (2019). Visualising bipartite networks and calculating some (Ecological) indices. Bipartite Reference Manual.

Dormann, C.F. & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. Methods in Ecology and Evolution, 5: 90-98. doi: 10.1111/2041-210X.12139

Farji-Brener, A.G. & Medina, C.A. (2000). The importance of where to dump the refuse: seed banks and fine roots in nests of the leaf-cutting ants Atta cephalotes and A. colombica. Biotropica, 32: 120-126. doi:10.1111/j.1744-7429.2000.tb00454.x

Fedriani, J.M. & Wiegand, T. (2014). Hierarchical mechanisms of spatially contagious seed-dispersal networks. Ecology, 95: 514-526. doi: 10.1890/13-0718.1

Fründ, J., McCann, K.S. & Williams, N.M. (2016). Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. Oikos, 125: 502-513. doi: 10.1111/oik.02256

Gallegos, S.C., Hensen, I. & Schleuning, M. (2014). Secondary dispersal by ants promotes forest regeneration after deforestation. Journal of Ecology, 102: 659-666. doi:10.1111/j.1365-2745.12226

García, D., Donoso, I. & Rodríguez-Pérez, J. (2018). Frugivore biodiversity and complementarity in interaction networks enhance landscape-scale seed dispersal function. Functional Ecology, 32: 2742-2752. doi: 10.1111/1365-2435.13213

Giannini, T.C., Garibaldi, L.A., Acosta, A.L., Silva, J.S., Maia, K.P., Saraiva, A.M., Guimarães, P.R. & Kleinert, A.M.P. (2015). Native and non-native supergeneralist bee species have different effects on plant-bee networks. PLoS ONE, 10: e0137198. doi: 10.1371/journal.pone.0137198

Giladi, I. (2006). Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos, 112: 481-492. doi: 10.1111/j.0030-1299.2006.14258.x

Goés, M.H.B., Silva, J.X., Rodrigues, A.F., Cavalcante, M.S.G., Roncarati, H., Cravo, C.D., Menezes, L.F.T., Anjos, L.H., Valadares, G.S. & Pereira, M.G. (2005). Modelo digital para a restinga e paleoilha da Marambaia, Rio de Janeiro. In L.F.T. Menezes, A.L. Peixoto & D.S.D. Araújo (Eds.), História Natural da Marambaia (pp. 231-284). Seropédica: EDUR.

Gómez, C. & Espadaler, X. (2013). An update of the world survey of myrmecochorous dispersal distances. Ecography, 36: 1193-1201. doi: 10.1111/j.1600-0587.2013.00289.x

Gorb, E. & Gorb, S. (2000). Effects of seed aggregation on the removal rates of elaiosome-bearing Chelidonium majus and Viola odorata seeds carried by Formica polyctena ants. Ecological Research, 15: 187-192. doi:10.1046/j.1440-1703.2000.00338.x

Guimarães-Jr, P.R. & Cogni, R. (2002). Seed cleaning of Cupania vernalis (Sapindaceae) by ants: edge effect in a highland forest in south-east Brazil. Journal of Tropical Ecology, 18: 303-307. doi: 10.1017/S0266474X02002213

Guimarães-Jr, P.R. & Guimarães, P. (2006). Improving the analyses of nestedness for large sets of matrices. Environmental Modelling & Software, 21: 1512-1513. doi:10.1016/j.envsoft.2006.04.002

Guimarães-Jr, P.R., Rico-Gray, V., Oliveira, P.S., Izzo, T.J., Reis, S.F. & Thompson, J.N. (2007). Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. Current Biology, 17: 1797-1803. doi: 10.1016/j.cub.2007.09.059

Guimerá, R. & Amaral, L.A.N. (2005). Cartography of complex networks: modules and universal roles. Journal of Statistical Mechanics, P02001: P02001-1–P02001-13. doi:10.1088/1742-5468/2005/02/P02001

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. Biometrical Journal, 50: 346-363.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. The American Naturalist, 104: 501-528.

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. American Naturalist, 129: 657-677.

Kaspari, M. (1993). Removal of seeds from Neotropical frugivore droppings: Ant responses to seed number. Oecologia, 95: 81-88. doi: 10.1007/BF00649510.
Lange, D., Dáttilo, W., Del-Claro, K. (2013). Influence of extrafloral nectary phenology on ant-plant mutualistic networks in a neotropical savanna. Ecological Entomology, 385: 463-469. doi: 10.1111/een.12036.

Leal, I.R. & Oliveira, P.S. (1998). Interactions between Fungus-Growing Ants (Attilini), Fruits and Seeds in Cerrado Vegetation in Southeast Brazil. Biotropica, 30: 170-178. doi: 10.1111/j.1744-7429.1998.tb00052.x

Leal, I.R., Wirth, R. & Tabarelli, M. (2007). Seed Dispersal by Ants in the Semi-arid Caatinga of North-east Brazil. Annals of Botany, 99: 885-894. doi: 10.1093/aob/mcm017

Lima, M.H.C., Oliveira, E.G. & Silveira, F.A.O. (2013). Interactions between Ants and Non-myrmecochorous Fruits in Miconia (Melastomataceae) in a Neotropical Savanna. Biotropica, 45: 217-223. doi:10.1111/j.1744-7429.2012.00910.x

Luna, P., García-Chávez, J.H. & Dáttilo, W. (2018). Complex foraging ecology of the red harvester ant and its effect on the soil seed bank. Acta Oecologica, 86: 57-65. doi: 10.1016/j.actao.2017.12.003.

Luna, P., García-Chávez, J.H., Izzo, T., Sosa, V.J., Del-Claro, K., & Dáttilo, W. (2021). Neutral and niche-based factors simultaneously drive seed and invertebrate removal by red harvester ants. Ecological Entomology. doi: 10.1111/een.13018

Marquitti, F.M.D., Guimarães-Jr, P.R., Pires, M.M. & Bittencourt, L.F. (2013). MODULAR: Software for the Autonomous Computation of Modularity in Large Network Sets. Ecography, 37: 221-224. doi: 10.1111/j.1600-0587.2013.00506.x

Mattos, C.L.V. (2005). Caracterização climática da Restinga da Marambaia. In L.F.T. Menezes, A.L. Peixoto & D.S.D. Araújo (Eds.), História Natural da Marambaia (pp. 55-66). Seropédica: EDUR.

Mello, M.A.R., Marquitti, F.M.D., Guimarães, P.R., Kalko, E.K.V., Jordano, P. & Aguilar, M.A.M. (2011). The modularity of seed dispersal: differences in structure and robustness between bat-and bird-fruit networks. Oecologia, 167: 131-140. doi: 10.1007/s00442-011-1984-2

Menezes, L.F.T. & Araújo, D.S.D. (2005). Formações vegetais da Restinga da Marambaia. In L.F.T. Menezes, A.L. Peixoto & D.S.D. Araújo (Eds.), História Natural da Marambaia (pp. 67-120). Seropédica: EDUR.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007). The modularity of pollination networks. PNAS, 104: 19891-19896. doi: 10.1073/pnas.0706375104

Ortiz, D.P., Elizalde, L. & Pírk, G.I. (2021). Role of ants as dispersers of native and exotic seeds in an understudied dryland. Ecological Entomology, 46: 626-636. doi: 10.1111/een.13010

Palacio, R.D., Valderrama-Ardila, C. & Kattan, G.H. (2016). Generalist Species Have a Central Role In a Highly Diverse Plant-Frugivore Network. Biotropica, 48: 349-355. doi: 10.1111/btp.12290

Passos, L. & Oliveira, P.S. (2002). Ants affect the distribution and performance of seedlings of Clusia criuva, a primarily bird-dispersed rainforest tree. Journal of Ecology, 90: 517-528. doi: 10.1046/j.1365-2745.2002.00687.x

Passos, L. & Oliveira, P.S. (2003). Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil. Journal of Tropical Ecology, 19: 261-270. doi: 10.1017/S02664740303298

Patefield, W. M. (1981). Algorithm AS 159: an efficient method of generating random R× C tables with given row and column totals. Journal of the Royal Statistical Society. Series C (Applied Statistics), 30: 91-97.

Pereira, M.G., Menezes, L.F.T. & Schultz, N. (2008). Aporte e decomposição da serapilheira na Floresta Atlântica, Ilha da Marambaia, Mangaratiba, RJ. Ciência Florestal, 18: 443-454. doi: 10.5902/19805098428

Pizo, M.A. & Oliveira, P.S. (1998). Interactions between ants and seeds of a nonmyrmecochorous neotropical tree, Cabralea canjerana (Meliaceae), in the Atlantic forest of southeast Brazil. American Journal of Botany, 85: 669-674. doi: 10.2307/2446536

Pizo, M.A. & Oliveira, P.S. (2000). The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. Biotropica, 32: 851-861. doi: 10.1111/j.1744-7429.2000.tb00623.x

Pizo, M.A. & Oliveira, P.S. (2001). Size and lipid content of nonmyrmecochorous diasporas: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil. Plant Ecology, 157: 37-52. doi: 10.1023/A:1013735305100.

Plowman, N.S., Hood, A.S.C., Moses, J., Redmond, C., Novotny, V., Klimes, P. & Fayle, T.M. (2017). Network reorganization and breakdown of an ant-plant protection mutualism with elevation. Proceedings of the Royal Society of London B, 284: 20162564. doi: 10.1098/rspb.2016.2564

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

Raimundo, R.L.G., Freitas, A.V.L. & Oliveira, P. S. (2009). Seasonal Patterns in Activity Rhythm and Foraging Ecology in the Neotropical Forest-Dwelling Ant, Odontomachus chelifer (Formicidae:Ponerinae). Annals of the Entomological Society of America, 102: 1151-1157. doi: 10.1603/008.102.0625

Rico-Gray, V. & Oliveira, P.S. (2007). The ecology and evolution of ant-plant interactions. Chicago: University of Chicago Press, 331 p

Rico-Gray, V., Díaz-Castelazo, C., Ramírez-Hernández, A., Guimarães, P.R., Holland, J.N. (2012). Abiotic factors shape temporal variation in the structure of an ant-plant network. Arthropod Plant Interactions 6:289–295. doi: 10.1007/s11829-011-9170-3.
Ruzi, S.A., Roche, D.P., Zalamea, P.C., Robison, A.C. & Dalling, J.W. (2017). Species identity influences secondary removal of seeds of Neotropical pioneer tree species. Plant Ecology, 218: 983-995. doi: 10.1007/s11258-017-0745-7

Santana, F.D., Cazetta, E. & Delabie, J.H.C. (2013). Interactions between ants and non myrmecochorous diaspores in a tropical wet forest in southern Bahia, Brazil. Journal of Tropical Ecology, 29: 71-80. doi: 10.1017/S0266467412000715

Schupp, E.W., Jordano, P. & Gómez, J.M. (2010). Seed dispersal effectiveness revisited: a conceptual review. New Phytologist, 188: 333-353. doi: 10.1111/j.1469-8137.2010.03402.x

Silva, B.F., Azevedo, I.H.F., Mayhé-Nunes, A., Breier, T., Nunes-Freitas, A.F. (2019). Ants promote germination of the tree Guarea guidonia by cleaning its seeds. Floresta e Ambiente, 26: e20180151. doi: 10.1590/2179-8087.015118

Silveira, F.A.O., Mafia, P.O., Lemos-Filho, J.P. & Fernandes, G.W. (2012). Species-specific outcomes of avian gut passage on germination of Melastomataceae seeds. Plant Ecology and Evolution, 145: 350-355. doi: 10.5091/plecevo.2012.706

Silvestre, R., Brandão, C.R.F. & Silva, R.R. (2003). Grupos funcionales de hormigas: El caso de los gremios del Cerrado. In F. Fernandez (Ed.), Introducción a las hormigas de la región Neotropical (pp. 101-136). Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Spiegel, O. & Nathan, R. (2012). Empirical evaluation of directed dispersal and density-dependent effects across successive recruitment phases. Journal of Ecology, 100: 392-404. doi: 10.1111/j.1365-2745.2011.01886.x

Timóteo, S., Ramos, J.A., Vaughan, I.P. & Memmott, J. (2016). High resilience of seed dispersal webs highlighted by the experimental removal of the dominant disperser. Current Biology, 26: 910-915. doi: 10.1016/j.cub.2016.01.046

Van der Pijl, L. (1982). Principles of dispersal in higher plants. Berlin: Springer, 162 p

Watts, S., Dormann, C.F., González, A.M.M. & Ollerton, J. (2016). The influence of floral traits on specialization and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes. Annals of Botany, 118: 415-429. doi: 10.1093/aob/mcw114

Wenny, D.G. (2001). Advantages of seed dispersal: A re-evaluation of directed dispersal. Evolutionary Ecology Research, 3: 51-74.

Willott, S.J., Compton, S.G. & Incoll, L.D. (2000). Foraging, food selection and worker size in the seed harvesting ant Messor bouvieri. Oecologia, 125: 35-44. doi: 10.1007/PL00008889

Zwiener, V.P., Bihn, J.H. & Marques, M.C.M. (2012). Ant-diaspore interactions during secondary succession in the Atlantic forest of Brazil. Revista de Biología Tropical, 60: 933-942. doi: 10.15517/rbt.v60i2.4028