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The effects of two abundant ant species on soil nutrients and seedling recruitment in Brazilian Atlantic Forest

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ABSTRACT

Ants can influence soil fertility and the spatial distribution of seeds, with possible effects on seedling recruitment. The ant species *Pachycondyla striata* Fr. Smith, 1858 and *Odontomachus chelifer* (Latreille, 1802) co-occur in many forest areas in the Neotropics. We assessed soil fertility and seed bank structure in soil samples close and distant (control) from ant nests in forest fragments. We also assessed the richness and abundance of seedlings on nests and control sites. In soil samples from ant nests, the concentration of phosphorus and potassium were respectively 55.6% and 36% higher than in control sites. Aluminium was 11–15% lower in soil samples from ant nests. In the greenhouse, soils from ant nests had higher plant abundance and species richness, but the same species composition in comparison with control sites. Although more plants emerged from soil samples of *O. chelifer* nests, in the field, the density and richness of seedlings were similar for the two ant species studied. Seedlings in the nest sites were, on average, 1.8 times more abundant and 1.6 times richer in species than in control sites. Our results showed that ant species can play a key role in seedling recruitment in forest fragments, where other animals with equivalent and positive effects, such as mammals, are missing.

Introduction

Seed dispersal and the availability of suitable sites for seedling germination and growth affect the seedling recruitment process (Leck and Parker, 2008). The availability of suitable sites depends on several abiotic factors, such as temperature, light, water, and soil nutrient concentration (Bruna, 2002; Salinas-Peba et al., 2014), as well as biotic factors, such as seed predators, herbivores, pathogens, and soil bioturbators (Augspurger and Kelly, 1984; Brussaard, 1997; Benitez-Malvido et al., 1999; Zamora and Matias, 2014). Many animals move seeds from parent plants or soil surface to better sites for germination and to seed banks (Chambers and MacMahon, 1994). In soil seed banks, viable seeds remain buried and protected from predators for some time, waiting for favourable conditions to germinate (Escobar and Cardoso, 2015). Therefore, the digging and burrowing activities of animals that use fruits and seeds, such mammals and ants, can be positive for plant recruitment through the accumulation and protection of seeds in seed banks (O'Grady et al., 2013; Pires and Galetti, 2013).

The ants are abundant organisms in tropical forests (Fittkau and Klinge, 1973) and can directly and indirectly affect the process of seedling recruitment, thus, contributing to forest successional dynamics (Folgarait, 1998). By carrying fruits and seeds to the nests, ants act as important seed dispersers (Passos and Oliveira, 2004), improving the movement of seeds to suitable and protected sites. Ants can also affect the physical structure and chemical composition of soils (Farji-Brener and Werenkraut, 2017). During the construction of nests, a large amount of soil particles is moved, altering soil physical structure and forming biopores that increase water infiltration rates (Lobry De Bruyn and Conacher, 1994). There is evidence that the soil near ant nests has a higher nutrient concentration than adjacent soils (Farji-Brener and Ghermandi, 2000; Cammeraat et al., 2002; Folgarait et al., 2002; Passos and Oliveira, 2002, 2004). This increase in soil fertility is probably due to the behaviour of ants carrying plant material to the nest (Briese, 1982). Thus, the effects of ants on soil characteristics and plant community may vary according to food preferences, nest population characteristics, and nest structure, which vary among ant species.

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Pachycondyla striata Fr. Smith, 1858 and *Odontomachus chelifer* (Latreille, 1802) are abundant and ecologically important species in Neotropical forests (Almeida et al., 2013; Almeida and Queiroz, 2015). They have similar body sizes (head width: ca. 2.7 mm; Almeida et al., 2013). *Pachycondyla striata* makes nests composed of several shallow chambers, whereas *O. chelifer* makes deep nests (Bottcher et al., 2016). Although both ant species are classified as ground-dwelling generalist predators (Groc et al., 2013), *O. chelifer* has a greater propensity to interact with fruits (Bottcher et al., 2016). Both species can transport whole fruits or their fleshy portions to the nest and discard seeds intact (Passos and Oliveira, 2002; Pizo and Oliveira, 2000). The mature nests of *O. chelifer* usually shows a larger number of individuals than those of *P. striata* (Medeiros 1997; Guimarães et al., 2018), which can result in more activity of transportation of animal and plant parts to the nests of *O. chelifer*.

In the present study, we tested two hypotheses about the relationship among ants, plants, and soil composition in forest fragments of Atlantic Forest, south-eastern Brazil. (1) Soil fertility and species abundance and richness of seed and seedling banks are higher on nests than in adjacent areas. (2) Soil fertility and plant community variables are higher on nests of *O. chelifer* than on those of *P. striata*, due to differences in food preferences and colony characteristics. To investigate these hypotheses, we assessed information on soil fertility, soil seed bank, and seedling density in areas close to and distant from nests of *P. striata* and *O. chelifer*.

Materials and methods

Site descriptions

The study plots were located in three areas of semi-deciduous tropical forest near the city of Vassouras, state of Rio de Janeiro, south-eastern Brazil. The first plot was located in a 6 ha forest fragment (22° 27′ 41″ S; 43° 38′ 57″ W); the second had an area of 36 ha (22° 27′ 3″ S; 43° 38′ 40″ W), and the third, 780 ha (22° 27′ 11″ S; 43° 39′47″ W). Native forests correspond to approximately 28% of the study region (Pereira et al., 2017). The average temperature is 18 °C in the coldest month and 23 °C in the warmest month. The average annual rainfall is 1280 mm (Francelino et al., 2012). The average altitude is 600 m a.s.l., and the regional climate is classified as CWa, according to the Köppen system (Alvares et al., 2013). The main soil type in the region is Haplic Cambisol (Pereira et al., 2017).

Data collection

We selected ten mature nests (i.e., with a considerable amount of soil excavated outside and high ant activity) of each ant species (*O. chelifer* and *P. striata*) in each of the three forest fragments. We collected soil samples to measure soil chemical properties and make a germination experiment, and recorded seedling density and richness in a paired design, comparing nests with control sites 10 m distant from the nest.

Soil chemical analysis

In each nest or control site (10 m distant from the nest), we collected six subsamples of 5 cm in diameter and 10 cm in depth (193 cm^3), extracted with a hollow metallic structure. Then, we transferred three subsamples to plastic bags in the field and took them to the laboratory for chemical analysis. We measured soil pH, the concentration of available Al, Ca, K, Mg, and P, and the percentage of organic carbon and saturation with bases (V%), which is considered a proxy for soil fertility (Fialho et al., 2006), following EMBRAPA (1997).

Seed bank and germination experiment

To study the relationship between ants and soil seed bank, the remaining three subsamples collected from nests of *O. chelifer* and *P. striata*, and their respective control sites, were combined and spread on plastic trays arranged at random in a greenhouse. The tray containing nest soil was placed beside the tray with soil from its control site. In the greenhouse, we monitored 120 samples for 14 consecutive weeks. During this period, we recorded species abundance and richness of the plants germinated per sample. Every ten days, we randomly changed the position of the trays on the bench of the greenhouse. To facilitate plant identification, we transplanted some individuals to larger pots, and monitored their development there. We also compared germinated plants with specimens of the local herbarium (Herbarium of the Department of Botany of the Federal Rural University of Rio de Janeiro).

Seedling community

We recorded seedling density and richness (5–30 cm tall) in 50 × 50-cm plots placed over the nests of the two ant species and their respective paired control sites (N = 10 for each ant species per forest fragment).

Monitoring ant activity

Ant activity is important because more activity implies more seeds coming to the nest, resulting in differences between nests. We observed for 10 min the number of ants attracted to biscuit/sardine baits in the morning (9:00–12:00) and afternoon (13:00–16:00) in the same marked nests. The baits were set at 15 cm from the nest entrance. We used the mean number of ants found in the morning and afternoon as an estimation of ant activity in the sampled nests.

Statistical analyses

As our data have a nested structure (i.e., the soil from nests and control sites was sampled in pairs and replicated in three different forest sites), we used mixed-effects models. We built a total of 12 models, changing the dependent variable but maintaining the same independent variables and the random structure. The independent variables were soil type (nest or control), ant species (*P. striata* or *O. chelifer*), their interaction, and ant activity. We included dependent variables related to soil chemistry and plant community. For the soil chemistry, we used aluminium concentration, soil pH, percentage of saturation with bases, calcium, magnesium, phosphorus, potassium, and organic carbon concentration as dependent variables in separate models. We used plant species richness and abundance of seedlings to test the effect of ant nests on seedlings and the soil seed bank (in the field), as well as for the soil seed bank (greenhouse experiment). Logarithmic or square-root transformations of dependent variables were used when necessary to normalize model residuals.

The random structure included soil type (nest or control), nested within forest fragments. The model selection followed Zuur et al. (2009), i.e., we started with a model in which the fixed component contained all the explanatory variables to find the optimal structure of the random component. In case we found the optimal random structure, we selected the fixed-effect components in the model, using likelihood ratio tests (Zuur et al., 2009).

For analysing species composition of the germinated seeds in the greenhouse experiment, we used PERMANOVA, as implemented in the Adonis routine of the vegan library (Oksanen et al., 2013), according to soil type (nest vs control) or ant species (*O. chelifer* vs *P. striata*), separately for each forest fragment. We also analysed the absolute frequency of the most common plant species in soils from

Table 1
Results of mixed effect models for soil chemical composition and the plant community parameters in the samples of *Pachycondyla striata* and *Odontomachus chelifer* nests as well as control sites; †Control soil is the reference; **Odontomachus* is the reference.

			Nest vs control soil†			Ant species*			Ant activity		
Dependent variable	Transformation used	Intercept	Parameter	L.Ratio	P-value	Parameter	L. Ratio	P-value	Parameter	L. Ratio	P-value
Aluminium	none	1.72	−0.19	4.92	0.03	—	—	> 0.05	—	—	> 0.05
Magnesium	sqrt	1.06	0.14	6.44	0.01	—	—	> 0.05	—	—	> 0.05
Calcium	log	0.28	0.07	7.67	0.006	—	—	> 0.05	—	—	> 0.05
% base saturation (V)	sqrt	5.03	—	—	> 0.05	—	—	> 0.05	—	—	> 0.05
Phosphorous	log	0.79	0.11	8.08	0.005	—	—	> 0.05	—	—	> 0.05
Potassium	log	1.67	0.1	13.9	< 0.001	—	—	> 0.05	—	—	> 0.05
pH	log	0.54	—	—	> 0.05	—	—	> 0.05	—	—	> 0.05
Organic carbon	sqrt	1.6	—	—	> 0.05	—	—	> 0.05	—	—	> 0.05
Seedling richness	log	0.83	0.17	50.01	< 0.001	—	—	> 0.05	—	—	> 0.05
Seedling abundance	log	9.97	2.44	32.33	< 0.001	—	—	> 0.05	0.2	12.07	< 0.001
Seed richness	sqrt	1.86	0.3	11.42	< 0.001	—	—	> 0.05	—	—	> 0.05
Seed abundance	log	0.81	0.15	8.65	0.003	−0.11	5.23	0.02	—	—	> 0.05

ant nests and control sites in the greenhouse experiment using a Chi-square test.

Statistical analyses and graphics were carried out in the statistical software R (R Development Core Team, v. 3.3.1) using nlme, vegan, and ggplot2 packages.

Results

Samples from ant nests had different chemical properties, except soil pH, percentage of saturation with bases, and organic carbon percentage (Table 1). The concentration of calcium, magnesium, phosphorus, and potassium were higher in ant nest soils than in control sites. Aluminium content, though, was significantly higher in control sites (Table 1, Figs. 1 and 2). The concentration of phosphorus and magnesium were 64% and 32% higher, respectively, in *O. chelifer* nests than in control sites. Potassium and magnesium were 36% and 30% higher, respectively, in *P. striata* nests than in control sites. On the other hand, aluminium was 15% and 11% lower, respectively, in *O. chelifer* and *P. striata* nests than in control sites. Differences between ant species in the concentration of chemical elements were not statistically significant (Table 1). Differences in ant activity between *P. striata* and *O. chelifer* were not statistically significant (Wilcoxon rank sum test; $W = 399.5$; $P = 0.573$).

The analysis of the seed bank in ant nests and control sites resulted in the germination of 980 seeds of 46 plant species. We counted a total of 509 seedlings, with a minimum of 1 and a maximum of 23 per sample. Seedling species richness per sample varied from 1 to 6. The median seedling abundance and richness were, respectively, 66% and 50% higher in ant nests than in control sites. However, differences in seedling abundance and richness between nests of the two ant species were not statistically significant. We found a positive and significant relationship between ant activity and seedling abundance, but not for species richness (Table 1).

Seedling abundance in *P. striata* nests was 59% higher than in control sites, and in *O. chelifer* nests, it was 29% higher than in control sites. Plant species richness and number of germinating plants were significantly higher in ant nest soils (Table 1). Differences between ant species were not statistically significant for plant species richness, but were significant for abundance, due to a higher abundance of germinated seeds in samples from nests of *O. chelifer* (Table 1, Fig. 2).

Plant species composition, analysed with a PERMANOVA, did not differ between nest and control soil or ant species in the three forest fragments ($P > 0.05$). Among the seven most common plant species recorded in the seed bank (80% of seedlings), only one was significantly more frequent in samples from control sites, whereas three predominated in samples from ant nests (Chi-squared test; Table 2).

Discussion

We found strong support to our hypothesis that poses differences on the soil characteristics and plant community between nest and control sites. However, we only found partial support to our hypothesis posing that these differences would be dependent on ant species. Soil characteristics were similar in nests of *O. chelifer* and *P. striata*, with a higher concentration of calcium, magnesium, phosphorus, and potassium, and a lower concentration of aluminium than in control sites. In addition, the abundance and richness of seedlings were higher on ant nests than in control sites, and similar for both ant species, according to the data collected in the field. Plant richness was similar in nests of both ant species, according to data obtained from the seed bank. However, corroborating our second hypothesis, we found differences in seed bank abundance between ant species. Samples from *O. chelifer* nests showed significantly more seedlings emerging in the greenhouse experiment than samples from *P. striata* nests. However, plant species richness and composition in the seed bank did not differ between soil samples from the two ant species.

Ants transport to their nest chambers animal and plant parts (leaves, flowers, fruits, and seeds) that will increase soil fertility once they decompose (Cammeraat et al., 2002; Moutinho et al., 2003; Farji-Brener and Werenkraut, 2017). Moreover, physical and chemical effects emerging from ant colony activities can accelerate litter decomposition inside chambers (Wang et al., 2017). Therefore, although we do not have specific information on nest-site selection by the species of our study system, we assume that the differences in soil parameters close to nests result from soil bioturbation and food accumulation inside them caused by ant activities. The concentration of aluminium can decrease in nest soils by the release of organic acids by plant materials inside nest chambers (Madureira et al., 2013). Despite differences among ant species, chemical characteristics of nest soil samples were not species dependent. Therefore, these data do not corroborate our second hypothesis. However, it is possible that soil sampling at only one depth prevented the detection of differences in species effects (Wang et al., 2017).

We found higher abundance and diversity of plants in seed bank samples from ant nests, but plant species composition was similar in soil samples close and distant from ant nests. The fact that plant species composition did not differ suggests that both ant species collect fruits and seeds according to the availability of these resources in the environment rather than in a selective

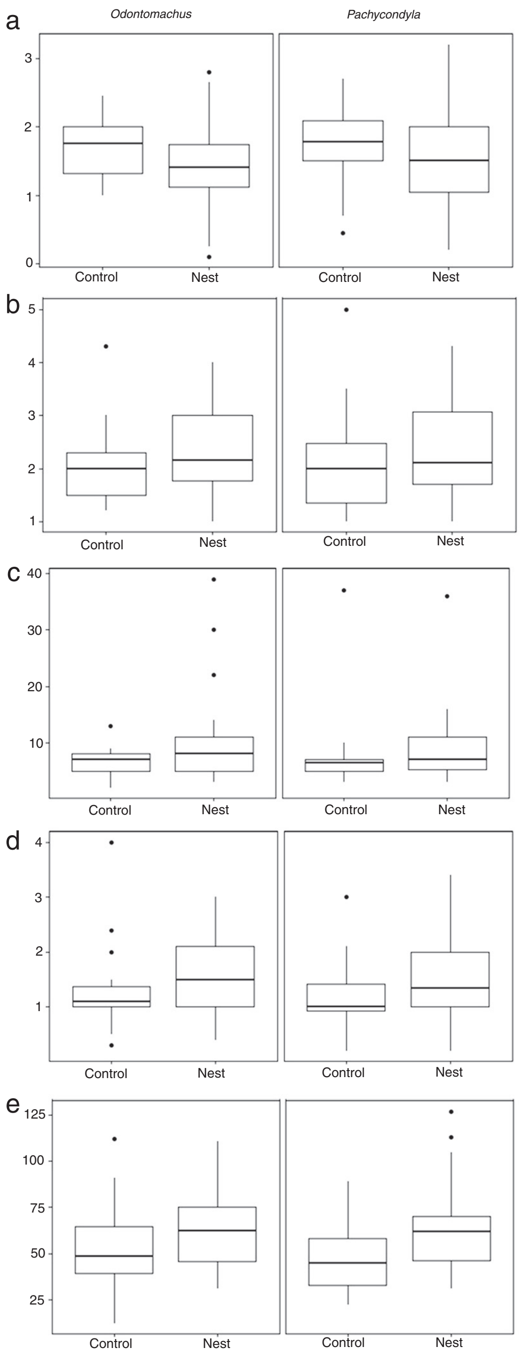

Fig. 1. Chemical elements in soil samples from ant nests and control sites. Concentration of (a) Aluminium, (b) Calcium, (c) Phosphorus, (d) Magnesium, and (E) Potassium. Al, Ca, and Mg are given in Cmolc/Kg, whereas P and K are given in mg/Kg. Solid horizontal black lines in the boxes indicate the median values; the whiskers represent the smallest and largest non-outlier observations; dots represent outlying data points.

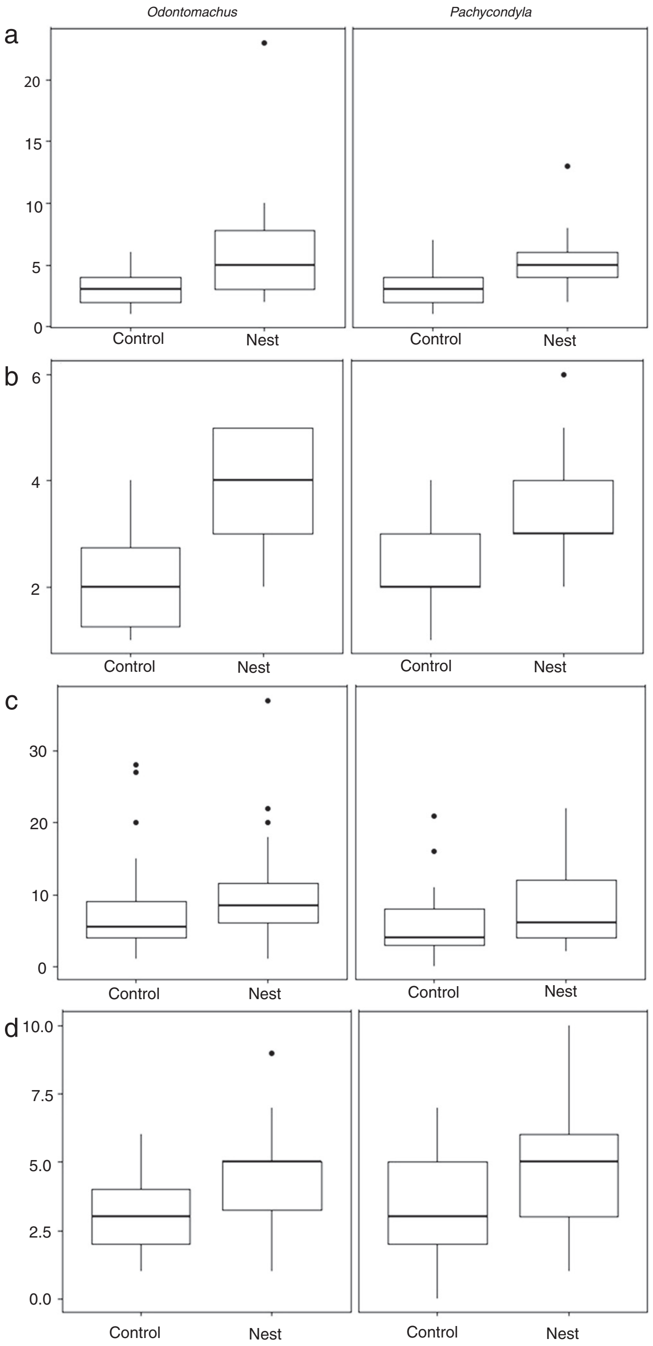

Fig. 2. Seedling abundance (a) and richness (b) on nest sites and control sites; seed bank abundance (c) and richness (d) in the greenhouse experiment. Solid horizontal black lines in the boxes indicate the median values; the whiskers represent the smallest and largest non-outlier observations; dots represent outlying data points.

way (Horvitz and Beattie, 1980; King, 1977; Farji-Brener and Silva, 1996).

Clidemia hirta (L.) D. Don and *Miconia calvescens* DC. (Melastomataceae), two of the most abundant species in the greenhouse experiment, had higher frequencies in samples from ant nests. *Clidemia hirta* is zoochoric, important for birds, and commonly found in early succession forests (Leitao et al., 2010). The high number of germinated seeds of *M. calvescens* in the greenhouse experiment is related to the high abundance of its diaspores in the habitats studied (pers. obs.) and their usual collection by ant species (Dalling and Wirth, 1998; Farji-Brener and Medina, 2000; Christianini et al., 2007). The only plant species that showed an opposite pattern in nest and control sites, with a lower abundance near nest soil, was *Panicum pilosum* SW, a non-forest grass species. We suggest that *P. pilosum* seeds are less attractive because of their small size in comparison with other seeds, and the lack of fleshy tissue, which seems to be preferred by both ant species (Pizo and Oliveira, 2000). It is also possible that the low number of *P. pilosum* plants in nest samples is related to allelopathic effects of other seeds in the soil of ant nests, as it was already described for another species of *Panicum* (Martins et al., 2006).

Table 2
Most common plant species and number of seeds germinating from samples taken from nests (N) of *Odontomachus chelifer* (Latreille) and *Pachycondyla striata* Fr. (N) or control sites (C). * Probabilities for the Chi-square test of the plant species frequencies in ant-nest vs control sites.

Taxa	*O. chelifer*		*P. striata*		Total	P*
	N	C	N	C		
Miconia calvescens DC.	80	57	58	25	220	0.0001
Panicum pilosum SW	46	73	29	45	193	0.0019
Clidemia hirta (L.) D. Don	51	34	47	26	158	0.0025
Mikania lanuginosa DC	20	12	18	11	61	0.0547
*Piptocarpha brasiliana*Cass.	22	14	16	6	58	0.0181
Cecropia pachystachya Trec.	13	8	16	10	47	0.1086
Casearia sylvestris Swartz	11	10	16	7	44	0.1317

The higher density and diversity of seedlings emerging in soil samples from ant nests in the greenhouse experiment is no guarantee of higher seedling recruitment compared to sites without nests in forest fragments. Density-dependent mortality factors could act on nest areas and reduce seedling recruitment (Alvarez-Loayza and Terborgh, 2011). However, in the field, seedlings in the nest sites were, on average, 1.8 times more abundant and 1.6 times richer in species than control sites. Therefore, even if density-dependent mortality factors were operating, they were not enough to reduce the number of seedlings in nest areas to the same level of control sites. Besides, seedling survival in nest areas may be higher due to better conditions of ant nest soils, e.g., higher soil fertility.

Ant nests may also improve the reception and transmission of water from the soil surface to the subsoil for plant usage (Lobry de Bruyn and Conacher, 1994). This is particularly relevant in forest fragments where poor soil conditions, in combination with high temperatures, reduce drought tolerance of seedlings (Zambrano et al., 2014). Seedlings can also benefit from ant protection against natural enemies (Passos and Oliveira, 2004).

In addition to some niche differences between *O. chelifer* and *P. striata*, such as nest architecture, characteristics of colonies and feeding strategies (Bottcher et al., 2016), the only significant difference between ant species was the higher abundance of plants germinating in soil samples from *O. chelifer* nests. This result may be due to the higher use of fruits by *O. chelifer*, as demonstrated by Bottcher et al. (2016). Despite that, field data did not confirm a higher abundance of seedlings on *O. chelifer* nests, suggesting that density-dependent mortality may occur. Therefore, our results indicate that the species studied may be functionally similar to forest ecosystems. Due to the high abundance of *O. chelifer* and *P. striata* in forest fragments (Almeida and Queiroz, 2015), the population dynamics of the two species may be coupled by competition (Medeiros and Oliveira, 2009). Hence, if they have similar functional roles, the decrease in one species can be functionally compensated for by an increase in the other. This compensation effect is predicted by the “insurance hypothesis”, which links biodiversity to ecosystem stability (Yachi and Loreau, 1999).

Small and large mammals disperse seeds of species of the genus *Miconia* (Magnusson and Sanaiotti, 1987; Groenendijk et al., 1996). Mammals are important for seedling recruitment because they bury seeds (Pires and Galetti, 2013), protecting them against seed predators. Besides, some mammal species promote soil movement and contribute to its fertility (Clark et al., 2018), but they can be absent from small forest fragments (Redford, 1992; Turner, 1996). The absence of mammals from forest fragments, as is the case of the fragments studied (A. Pires, unpublished data), can affect plant recruitment. We suggest that in this scenario, plant recruitment can be highly influenced by ants, such as *O. chelifer* and *P. striata*, which are abundant and can protect the seeds from predation by taking them inside or near their nests. They may also facilitate plant growth due to improved soil conditions. In the forest fragments studied, *O. chelifer* and *P. striata* are the most frequent ant species removing seeds from the forest floor (Almeida et al., 2013). Due to their widespread occurrence in Neotropical forests, *O. chelifer* and *P. striata* may have a strong influence on plant community, not only in relatively well-preserved tropical forests (Passos and Oliveira, 2002, 2004), but also in forest fragments with the absence of other animal species with similar ecological roles, but more vulnerable to habitat fragmentation.

Conflicts of interest

The authors declare no conflicts of interest.

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References

Almeida, F.S., Queiroz, J.M., 2015. Formigas poneromorfas como engenheiras de ecossistemas: impactos sobre a biologia, estrutura e fertilidade dos solos. In: Delabie, J.H.C., Feitosa, R.M., Serrão, J.E., Mariano, C.S.F., Majer, J.D. (Eds.), As Formigas Poneromorfas Do Brasil. Editus, Ilhéus, pp. 437–446.

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, http://dx.doi.org/10.13102/sociobiology.v60i3.229-235.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes, G., Leonardo, J., Sparovek, G., 2013. Koppen's climate classification map for Brazil. Meteorol. Z. 22, 711–728, http://dx.doi.org/10.1127/0941-2948/2013/0507.

Alvarez-Loayza, P., Terborgh, J., 2011. Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? J. Ecol. 99, 1045–1054, http://dx.doi.org/10.1111/j.1365-2745.2011.01835.x.

Augspurger, C.K., Kelly, C.K., 1984. Pathogen mortality of tropical tree seedlings - experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61, 211–217, http://dx.doi.org/10.1007/BF00396763.

Benitez-Malvido, J., García-Guzmán, G., Kossmann-Ferraz, I.D., 1999. Leaf-fungal incidence and herbivory on tree seedlings in tropical rainforest fragments: an experimental study. Biol. Conserv. 91, 143–150, http://dx.doi.org/10.1016/S0006-3207(99)00090-7.

Bottcher, C., Peixoto, P.E., Silva, W.R., Pizo, M.A., 2016. Drivers of spatial variation in the role of ants as secondary seed dispersers. Environ. Entomol. 45, 930–937, http://dx.doi.org/10.1093/ee/nvw058.

Briese, D.T., 1982. The effect of ants on the soil of a semi-arid saltbush habitat. Ins. Soc. 29, 375–386, http://dx.doi.org/10.1007/BF02228765.

Bruna, E., 2002. Effects of forest fragmentation on *Heliconia acuminate* seedling recruitment in central Amazonia. Oecologia 132, 235–243, http://dx.doi.org/10.1007/s00442-002-0956-y.

Brussaard, L., 1997. Biodiversity and ecosystem functioning in soil. Ambio 26, 563–570.

Cammeraat, L.H., Willott, S.J., Compton, S.G., Incoll, L.D., 2002. The effects of ants'nest on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. Geoderma 105, 1–20, http://dx.doi.org/10.1016/S0016-7061(01)00085-4.

Chambers, J.C., Macmahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annu. Rev. Ecol. S. 25, 263–292.

Christianini, A.V., Mayhe-Nunes, A.J., Oliveira, P.S., 2007. The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a neotropical savanna. J. Trop. Ecol. 23, 343–351, http://dx.doi.org/10.1017/S0266467407004087.

Clark, K.L., Branch, L.C., Farrington, J., 2018. Bioturbation by mammals and fire interact to alter ecosystem-level nutrient dynamics in longleaf pine forests. PLoS One 13, e0201137, http://dx.doi.org/10.1371/journal.pone.0201137.

Dalling, J.W., Wirth, R., 1998. Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. J. Trop. Ecol. 14, 705–710, http://dx.doi.org/10.1017/S0266467498000492.

EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária, 1997. Serviço Nacional de levantamento e conservação de solos. In: Manual De Métodos De Análise De Solo. EMBRAPA, Rio de Janeiro.

Escobar, E.D.F., Cardoso, V.J.M., 2015. Longevity of seeds and soil seed bank of the Cerrado tree *Miconia chartacea* (Melastomataceae). Seed Sci. Res. 25, 386–394, http://dx.doi.org/10.1017/S0960258515000173.

Farji-Brener, A.G., Ghermandi, L., 2000. Influence of nests of leaf-cutting ants on plant species diversity in road verges of Northern Patagonia. J. Veg. Sci. 11, 453–460, http://dx.doi.org/10.2307/3236638.

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

Farji-Brener, A.G., Silva, J.F., 1996. Leaf cutter ants (*Atta laevigata*) aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna. J. Trop. Ecol. 12, 163–168, http://dx.doi.org/10.1017/S0266467400009378.

Farji-Brener, A.G., Werenkraut, V., 2017. The effects of ant nests on soil fertility and plant performance: a meta-analysis. J. Anim. Ecol. 86, 866–877, http://dx.doi.org/10.1111/1365-2656.12672.

Fialho, J.S., Gomes, V.F.F., Oliveira, T.S., Silva-Júnior, J.M.T., 2006. Indicadores da qualidade do solo em áreas sob vegetação natural e cultivo de bananeiras na Chapada do Apodi-CE. Rev. Ciênc. Agron. 37, 250–257.

Fittkau, E.J., Klinge, H., 1973. On biomass and trophic structure of the Central Amazonian rain forest ecosystem. Biotropica 5, 2–14, http://dx.doi.org/10.2307/2989676.

Folgarait, P.F., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers. Conserv. 7, 1221–1244, http://dx.doi.org/10.1023/A:1008891901953.

Folgarait, P.J., Perelman, S., Gorosito, N., Pizzio, R., Fernandez, J., 2002. Effects of *Camponotus punctulatus* ants on plant community composition and soil properties across land-use histories. Plant Ecol. 163, 1–13, http://dx.doi.org/10.1023/A:1020323813841.

Francelino, M.R., Rezende, E.M.C., Silva, L.D.B., 2012. Proposta para zoneamento ambiental de plantio de eucalipto. Cerne 18, 275–283, http://dx.doi.org/10.1590/S0104-77602012000200012.

Groc, S., Delabie, J.H.C., Fernández, F., Leponce, M., Orivel, J., Silvestre, R., Vasconcelos, H.L., Dejean, A., 2013. Leaf-litter ant communities (Hymenoptera: formicidae) in a pristine Guianese rainforest: stable functional structure versus high species turnover. Myrmecol. News 19, 43–51.

Groenendijk, J.P., Bouman, F., Cleef, A.M., 1996. An exploratory study on seed morphology of *Miconia* ruiz & Pavon (Melastomataceae), with taxonomic and ecological implications. Acta Bot. Neerl. 45, 323–344.

Guimarães, I.C., Pereira, M.C., Batista, N.R., Rodrigues, C.A.P., Antonialli Júnior, W.F., 2018. The complex nest architecture of the Ponerinae ant Odontomachus chelifer. PLoS One 13, e0189896, http://dx.doi.org/10.1371/journal.pone.0189896.

Horvitz, C.C., Beattie, A.J., 1980. Ant dispersal of *Calathea marantaceae* seeds by carnivorous ponerines (Formicidae) in a tropical rain-forest. Am. J. Bot. 67, 321–326, http://dx.doi.org/10.2307/2442342.

King, T.J., 1977. Plant ecology of ant-hills in calcareous grasslands.1. Patterns of species in relation to ant-hills in southern England. J. Ecol. 65, 235–256, http://dx.doi.org/10.2307/2259077.

Leck, M., Parker, T. (Eds.), 2008. Seedling Ecology and Evolution. Cambridge University Press, New York.

Leitao, F.H.M., Marques, M.C., Ceccon, E., 2010. Young restored forests increase seedling recruitment in abandoned pastures in the Southern Atlantic rainforest. Rev. Biol. Trop. 58, 1271–1282.

Lobry De Bruyn, L.A., Conacher, A.J., 1994. The effect of ant biopores on water infiltration in soils in undisturbed bushland and in farmland in a semi-arid environment. Pedobiologia 38, 193–207.

Madureira, M.S., Schoereder, J.H., Teixeira, M.C., Sobrinho, T.G., 2013. Why does *Atta robusta* (Formicidae) not change soil features around their nests as other leaf-cutting ants do? Soil Biol. Biochem. 57, 916–918, http://dx.doi.org/10.1016/j.soilbio.2012.11.005.

Magnusson, W.E., Sanaiotti, T.M., 1987. Dispersal of *Miconia* seeds by de rat *Bolomys lasiurus*. J. Trop. Ecol. 3, 277–278, http://dx.doi.org/10.1017/S0266467400002169.

Martins, D., Martins, C.C., Costa, N.V., 2006. Potencial alelopático de soluções de solo cultivado com *Brachiaria brizantha*: efeitos sobre a germinação de gramíneas forrageiras e plantas daninhas de pastagens. Planta Daninha 24, 61–70, http://dx.doi.org/10.1590/S0100-83582006000100008.

Medeiros, F.N.S., Oliveira, P.S., 2009. Season-dependent foraging patterns: case study of a neotropical forest-dwelling ant (*pachycondyla striata*; Ponerinae). In: Jarau, S., Hrncir, M. (Eds.), Food Exploitation by Social Insects: Ecological, Behavioral, and Theoretical Approaches. CRC Press, New York, pp. 81–95.

Medeiros, F.N.S., 1997. Ecologia comportamental da formiga *Pachycondyla striata* Fr. Smith (Formicidade: Ponerinae) em uma floresta do sudeste do Brasil. Tese (Mestrado em Ciências Biológicas), Universidade Estadual de Campinas.

Moutinho, P., Nepstad, D.C., Davidson, E.A., 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. Ecology 84, 1265–1276, http://dx.doi.org/10.1890/0012-9658(2003)084[1265:IOLANO]2.0.CO;2.

O'Grady, A., Breen, J., Harrington, T.J., Courtney, R., 2013. The seed bank in soil from the nests of grassland ants in a unique limestone grassland community in Ireland. Ecol. Eng. 61, 58–64, http://dx.doi.org/10.1016/j.ecoleng.2013.09.011.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., http://CRAN.R-project.org/package=vegan, 2013.

Passos, L., Oliveira, P.S., 2002. Ants affect the distribution and performance of *Clusia criuva* seedlings, a primarily bird-dispersed rain forest tree. J. Ecol. 90, 517–528, http://dx.doi.org/10.1046/j.1365-2745.2002.00687.x.

Passos, L., Oliveira, P.S., 2004. Interactions between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sand plain rain forest: ant effects on seeds and seedling. Oecologia 139, 376–382, http://dx.doi.org/10.1007/s00442-004-1531-5.

Pereira, M.P.S., Francelino, M.R., Queiroz, J.M., 2017. A cobertura florestal em paisagens do médio vale do Rio Paraíba do sul. Floresta & Ambiente 24, 1–11, http://dx.doi.org/10.1590/2179-8087.134115.

Pires, A., Galetti, M., 2013. The agouti *Dasyprocta leporina* (Rodentia: dasyproctidae) as seed disperser of the palm *Astrocaryum aculeatissimum*. Mastozool. Neotrop. 19, 147–153.

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.

Redford, K.H., 1992. The empty forest. BioScience 42, 412–422.

Salinas-Peba, L., Parra-Tabla, V., Campo, J., Munguía-Rosas, M.A., 2014. Survival and growth of dominant tree seedlings in seasonally tropical dry forests of Yucatan: site and fertilization effects. J. Plant Ecol. 7, 470–479.

Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Anim. Ecol. 33, 200–209, http://dx.doi.org/10.2307/2404743.

Wang, S., Wang, H., Li, J., Zhang, Z., 2017. Ants can exert a diverse effect on soil carbon and nitrogen pools in a Xishuangbanna tropical forest. Soil Biol. Biochem. 113, 45–52, http://dx.doi.org/10.1016/j.soilbio.2017.05.027.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Nati. Acad. Sci. 96, 1463–1468.

Zambrano, J., Coates, R., Howe, H.F., 2014. Effects of forest fragmentation on the recruitment success of the tropical tree *Poulsenia armata* at Los Tuxtlas, Veracruz, Mexico. J. Trop. Ecol. 30, 209–218, http://dx.doi.org/10.1017/S0266467414000108.

Zamora, R., Matias, L., 2014. Seed dispersers, seed predators, and browsers act synergistically as biotic filters in a mosaic landscape. PLoS One 9, e107385, http://dx.doi.org/10.1371/journal.pone.0107385.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R, Statistics for Biology and Health. Springer-Verlag, New York.