Journal of Tropical Ecology

www.cambridge.org/tro

Nest density of *Atta sexdens* (Linnaeus, 1758) in Atlantic Forest restoration sites depends on the surrounding landscape

Jéssica Magon Garcia, Géssi de Sousa Gonzaga, Alexandre Mello Bordignon and José Marcelo Domingues Torezan

Universidade Estadual de Londrina, Laboratório de Biodiversidade e Restauração de Ecossistemas e Programa de Pós-Graduação em Ciências Biológicas, Rodovia Celso Garcia Cid, – PR 445 Km 380 –Campus Universitário, 86057-970 Londrina, PR, Brasil

Research Article

Cite this article: Garcia JM, Gonzaga GS, Bordignon AM, and Torezan JMD (2023). Nest density of *Atta sexdens* (Linnaeus, 1758) in Atlantic Forest restoration sites depends on the surrounding landscape. *Journal of Tropical Ecology*. **39**(e9), 1–6. doi: https://doi.org/10.1017/S0266467422000517

Received: 20 January 2022
Revised: 12 December 2022
Accepted: 19 December 2022

Keywords:
ecological filter; herbivory; leaf-cutting ants; Semi-deciduous Seasonal Forest; top-down control

Author for correspondence:
José Marcelo Domingues Torezan,
Email: torezan@uel.br

Abstract

Herbivory is an important ecological filter, affecting plant establishment in restoration sites. One group of herbivores whose abundance has been increasing with environmental changes are the leaf-cutting ants (LCA). Here we evaluated the influence of the surrounding landscape on *Atta sexdens* nest density in restoration sites, by testing the hypothesis that sites farthest from forest fragments or with less surrounding habitat cover have higher nest density. The study was conducted in eleven reforestations with native species, amidst an agricultural matrix in southern Brazil. For each site, we estimated LCA nest density (active, inactive and total) and landscape metrics (distance to nearest forest fragment, surrounding habitat area and an index combining both distance and surrounding habitat area, the Proximity Index). There were negative relationships between active and total nest density and surrounding habitat area. These results suggest that increased isolation from forest fragments is a factor contributing to the relaxation of top-down control. Therefore, the increase in *A. sexdens* population density in restoration sites is a result, at least in part, of low pressure from natural enemies, since LCA are not limited by resource availability.

Introduction

Habitat fragmentation drives changes in landscape functioning, biota composition and interactions among species (Filgueiras *et al.* 2019). In South America, increases in the abundance of leaf-cutting ants (LCA) have been reported in forest fragments, being attributed to increases in resource availability and smaller predation pressure (Almeida *et al.* 2008, Rao 2000, Rao *et al.* 2001, Terborgh *et al.* 2001). However, there is an overall lack of long-term monitoring data and few studies dealing with the drivers of LCA abundance.

LCA are species from *Atta* Fabricius (1804) and *Acromyrmex* Mayr (1865) genus (Hymenoptera, Formicidae, Myrmicinae, tribe Attini), known as *saúvas* and *quenquéns*, respectively. In their nests, they cultivate, on fresh vegetal material, a 'garden' of fungi from which they feed (Leal *et al.* 2014). These are herbivores abundant in the Neotropical region and considered as generalists, for being capable of gathering around 50% of the plant species (Wirth *et al.* 2003) and up to 20% of the vegetation in their foraging zones (Urbas *et al.* 2007). Their dispersion occurs through the nuptial flight when, after copulating, females search for places to establish new nests, which they found alone. Predation by insectivores is more efficient as population control if these females are captured in flight or right after it, when their nests are still incipient (Helms *et al.* 2016, Vieira-Neto & Vasconcelos 2010).

In forest landscapes subjected to fragmentation and converted to agriculture, there may be an increase in the density of fast-growing plants in the fragments, which are part of an impoverishment process called 'secondarization' (Joly *et al.* 2014). These plants, together with many agricultural crops such as soybean, have been described as favourite resources for LCA (Rao *et al.* 2001, Urbas *et al.* 2007), contributing to higher nest density and herbivory rate and smaller foraging areas in forest fragments (Rao *et al.* 2001, Urbas *et al.* 2007) and other landscape elements, such as forest plantations (Zanetti *et al.* 2014).

Besides the known damages in agriculture, silviculture and fragmented habitats, LCA have been described as important factors in ecological restoration sites (Ferreira 2015, Garcia *et al.* 2020, Massad 2012, Massad *et al.* 2011, Montagnini *et al.* 1995). In reforestations with native species, these ants may increase costs during the implantation phase (Montagnini *et al.* 1995). Moreover, high abundance of LCA is still recorded in subsequent phases (Garcia *et al.* 2020, Massad 2012, Massad *et al.* 2011, Montagnini *et al.* 1995). LCA herbivory can negatively influence plants in all life cycle stages, from establishment to reproduction (Leal *et al.* 2014), changing the diversity and composition of plant species (Wirth *et al.* 2003), then the successional

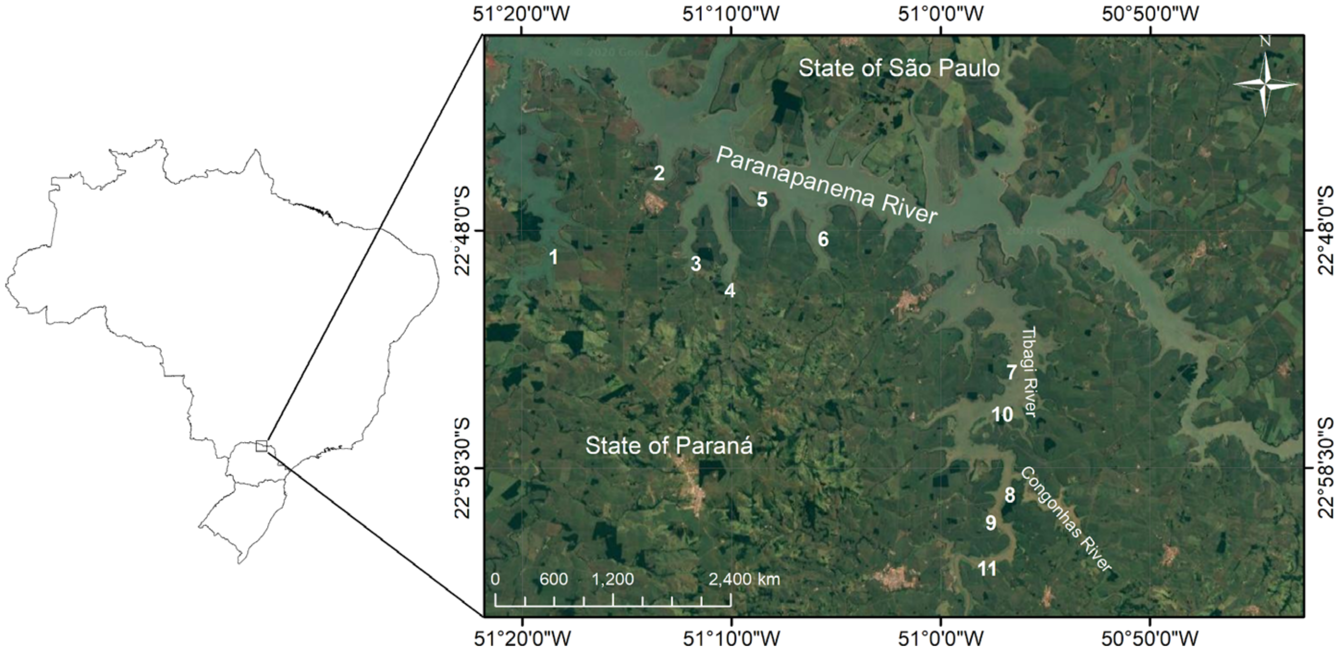

Figure 1. Location of study sites in Brazil, Paraná state, at the Capivara hydroelectric power plant reservoir (light green), in the Paranapanema river. The white numbers (same numbers used in Table 1) indicate the sampled restoration sites (reforestations with native species ageing 9-12 years). Dark green patches are Atlantic Forest fragments.

trajectory and acting as an ecological filter, as suggested by Costa *et al.* (2016) in forest fragments. Ferreira (2015) and Garcia *et al.* (2020) suggested that the herbivory rate of *Atta sexdens* (Linnaeus, 1758) in restoration sites varies among plant species, affecting the survival and development of some species, making LCA an important ecological filter.

In restoration sites, often dominated by pioneer species, and particularly in those situated amidst agricultural landscapes, there is an increased availability of food, which points to a release in the bottom-up control (Garcia *et al.* 2020). Still, the top-down control, exerted mainly by insectivores and parasites, may also have been relaxed in isolated restoration sites. Many groups of organisms that affect ants have their populations decreased in fragmented habitats, including mammals (Rao 2000), insectivore birds (Anjos *et al.* 2019) and parasite insects (Almeida *et al.* 2008, Barrera *et al.* 2017). This reduction in abundance may occur through habitat loss (Barrera *et al.* 2017, Terborgh *et al.* 2001), due to the influence of edge effects (Almeida *et al.* 2008) or less permeable matrices (Anjos *et al.* 2019).

We postulate that both the position amidst palatable crops all year and the high proportion of native pioneer tree species in the restoration sites leads to a relaxation of bottom-up control, making nest density depend mostly on top-down control. Thus, we seek to test the prediction that restoration sites closer to Atlantic Forest remnants or with higher habitat cover in their surroundings have lower LCA nest density, in response to higher abundance of insectivores and parasites.

Methods

Study site

Eleven restoration sites (reforestations with native species) were selected, located at the margins of the Capivara reservoir, on the Paranapanema river, between the states of Parana and São Paulo (Figure 1; Supplementary Material 1). These sites are included in the long-term ecological research site 'Mata Atlântica do Norte do Paraná' (PELD MANP), established since 2014. This site is composed by a set of Atlantic Forest fragments and restoration sites scattered in an agricultural landscape in north of Parana state, southern Brazil.

According to Nitsche *et al.* (2019), region climate is Köppen's Cfa, with annual average temperature between 22ºC and 23ºC, winter temperature below 18ºC and summer temperature above 22ºC. Summers are hot, frosts are rare, and rain is concentrated in summer season, but with no marked dry season. Average annual rainfall ranges from 1,400 to 1,600 mm, and potential evapotranspiration is greater than 1,200 mm (Nitsche *et al.* 2019). Soils are Eutroferric Red Nitosols and Latosols, of great natural fertility. Original vegetation was a seasonal form of Atlantic Forest, now reduced to forest fragments totalling less than 3% in the studied area (Pereira *et al.* 2013), with a high level of fragmentation. The current landscape is dominated by monocultures of soybeans (planted and harvested in summer) and corn (with both summer and winter cultivars). In exception for the restoration project (see below), land use and cover have been the same for the last 30 years, showing a high level of land occupancy by agriculture, with almost no spare lands.

Selected restoration sites are in the Capivara hydroelectric power plant reservoir buffer strips, which are of mandatory preservation. Restoration activities were carried out by the power plant company, with aid of a municipality consortium and university staff. All restoration sites are reforestations with about 45 native tree species, with a high proportion of pioneer tree species (usually $> 50\%$, see Supplementary Material 2), and were of similar ages (9–12 years) when sampling was carried out (see Supplementary Material 3). Given the landscape structure, all sites are close to agricultural sites but are situated at different distances from Atlantic Forest remnants.

Seedlings were planted with 2 × 3 m spacing. Before planting the seedlings, the land was ploughed; mechanized mowing and chemical control of LCA (using fipronil ant killer baits) were held for two years after planting; other pesticides were not used. No fertilizers were applied.

Density of *LCA* nests

The density of LCA nests was estimated at each restoration site by two 250 m length and 40 m wide transects (1 ha per transect, 2 ha of sampling area per restoration site). Transects were placed at least 10 m from the site edge and at least 50 m from the other transect in the same site. The transect method was adapted from that described by Jaffe and Vilela (1989) and Wirth *et al.* (2003) and was sampled in June and July 2014. In each transect, the nests were located and georeferenced with GPS. The nests were classified as active (living) or inactive (dead), and the active nests were further classified into juvenile/adult and new nests. Those whose mound of soil had up to 2 m^2 and did not have the defence caste (soldiers) (Autuori 1941) were considered as new colonies, and the rest were considered juvenile/adult colonies. New nests are vulnerable to several biotic (e.g. control by microorganisms) and abiotic factors (e.g. heavy and abundant rainfall and soil attributes) that cause high mortality of colonies (Meyer *et al.* 2009, Vieira-Neto & Vasconcelos 2010). Therefore, only established colonies (juvenile/adult) were included in the analysis, as is commonly done when studying colonies of LCA (Meyer *et al.* 2009, Wirth *et al.* 2003).

Ten workers, preferably soldiers, were collected from each active nest sampled in the transects for species identification. All the collected materials were packaged in properly labelled bottle and filled with 70% alcohol. Ant samples were identified with the help of specialists and belong to the species *A. sexdens*.

All elements of the analysed landscapes (forest fragments, rural residences, rural roads, restoration sites themselves) are possible sources of post-flight queens for the foundation of new nests in the restoration sites. As the restoration sites are between 9 and 12 years old, the adult nests themselves contained in them serve as a source for new nests.

Characterization of the surrounding landscape

A polygon around the two transects was drawn for the estimation of surrounding landscape metrics. The distance from the polygon border to the nearest forest fragment with at least one hectare was estimated as a straight line (D), simulating the trajectory of natural enemies (such as birds and parasitoids) crossing the matrix (Pereira *et al.* 2013; see Supplementary Material 4). The distance to the nearest fragment was also calculated using a pathway through native vegetation corridors (D_V); for this purpose, we considered as native vegetation any forest vegetation, including forest remnants, secondary succession and restoration sites (Pereira *et al.* 2013), aiming to simulate the trajectory of natural enemies that avoid plantations and aquatic environments, such as armadillos or lizards (see Supplementary Material 4).

The surrounding forest habitat area (V) was estimated by the proportion of the landscape occupied by forest fragments, and the proximity index (PI) was estimated as the ratio between the total area of surrounding habitat inside a given search radius and the sum of the squared distances between the polygon containing the transects and the included forest patches (McGarigal & Marks 1995). PI combines a measure of isolation (in the same way as D) and surrounding habitat area (in the same way as V). Restoration and early succession sites were not considered in V and PI calculations; only Atlantic Forest remnants (hereafter, forest fragments) were considered. Because ant natural enemies include heterogeneous groups, the V and PI were estimated for each polygon using 500 and 1,000 m search radii. The 500 m measure represents a local landscape scale; 1,000 m was the highest distance with no sample overlap.

Forest area and distances for V and PI estimations were calculated using a thematic map based on 10 m resolution orbital images (bands 2, 3, 4 and 8 of the Multispectral Sensor Instrument, Sentinel-2 satellite), from 19 to 29 November 2019. The free software QGIS 3.12.0 was used to process the images. The variables D and D_v were estimated using '*Google Earth Pro*' with aid of field observations, when necessary.

Data analysis

The size of the restoration sites was not included in the analysis. Restoration sites form almost continuous land strips along hydroelectric power plant reservoir margins, so site size is not ecologically meaningful. The width of restoration sites was analysed and does not show any significant correlation with other variables (Supplementary Material 5).

The landscape metrics, as expected, are highly correlated (Supplementary Material 5). Thus, in order to find the metric that most influence nest density (active, inactive and total), we performed stepwise forward regression, using the Akaike Information Criterion (AIC) as a tool for selection of the best model. In a second step, we performed simple linear regressions (Zar 2010) to clarify the influence of selected landscape metric on nest density.

The homogeneity of the variances was verified by the Levene's test and normality by the Shapiro-Wilk test. All variables were transformed using log $(x + 1)$, because of the excess of zero values and also to meet the assumptions of data normality and variance homogeneity (Zar 2010). All analyses were done in the program R version 3.5.3 (R Core Team 2019).

All analyses were performed in the vegan package (Oksanen *et al.* 2022) in the program R version 3.5.3 (R Core Team 2019).

Results

In the eleven restoration sites, we sampled 93 active nests, ranging from no nest to ten nests per hectare (Table 1). The density of active nests was negatively influenced by proximity of forest fragments (PI_{1000}, Figure 2; see also Supplementary Material 6). The closer and larger the forest fragments are in the surrounding landscape, the lower the density of nests present in restoration sites.

Inactive nests ranged from none to 13.5 nests per hectare (Table 1), and there was no relationship with the landscape metrics; thus, the null model showed the smallest AIC (-19.15; see Supplementary Material 7). However, total nest density (active + inactive) showed a negative relationship with the surrounding habitat area (V_{1000}, Figure 2).

Discussion

Our results showed that restoration sites located further away from forest fragments and with less forest in their surroundings presented higher density of nests of the genus *Atta*. These results indicate a positive influence of both habitat loss and isolation on the population of LCA on restoration sites. This is possibly a result of negative effect of habitat loss and isolation on the dynamics of natural enemies of LCA such as anteaters, armadillos, lizards, insectivore or omnivore birds and other arthropods and parasitoids (Barrera *et al.* 2017, Camacho *et al.* 2012,

Table 1. Density of active (N_A) and inactive (N_I) nests of *Atta sexdens*, distance in a straight line (D) and through vegetation corridors (D_V) between the restoration sites and the nearest forest fragment, proximity index (PI) and forest habitat area (V), for search radius of 500 and 1,000 m, in eleven restoration sites (reforestations with native species ageing 9–12 years) located at Capivara hydroelectric power plant reservoir margins, Parana state, Brazil

Restoration sites	N_A (nest/ha)	N_I (nest/ha)	D (m)	D_V (m)	PI_{500}	V_{500} (ha)	PI_{1000}	V_{1000} (ha)
1	3.5	0	1,555	4,392	0	0	0	0
2	3	0	976	1,229	0	0	0.19	18
3	2	4	10	10	13,092	131	13,092	131
4	4	1	20	20	0.77	18	0.35	53
5	5.5	3.5	1,747	5,540	0	0	0	0
6	10	2	3,313	4,206	0	0	0	0
7	7.5	4	1,400	1,509	0	0	0	0
8	0	0	5	5	42,060	105	42,060	105
9	4.5	13.5	1,690	1,877	0	0	0	0
10	3.5	0	5	5	12,886	32	0.84	36
11	3	5	557	705	0	0	0.18	5

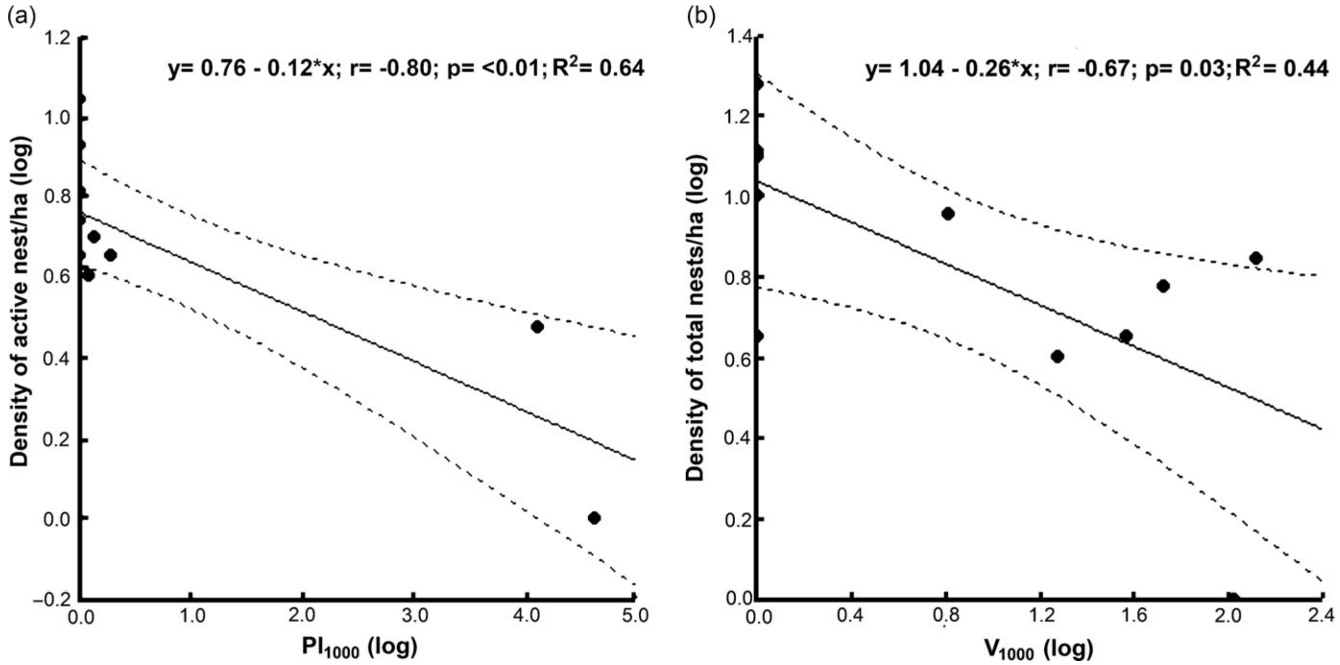

Figure 2. Relationship between landscape metrics and density of *Atta sexdens* active and total nest density (in number of nests per ha), recorded in restoration sites (reforestations with native species ageing 9–12 years) located at Capivara hydroelectric power plant reservoir margins, Parana state, Brazil. PI_{1000} – proximity index, and V_{1000} – proportion of the landscape occupied by forest fragments, estimated for 1,000 m neighbourhoods.

Terborgh *et al.* 2001), once that, for all sampled sites, resource availability for ants (palatable plants in crop fields and restoration sites) is uniformly high. Thus, an increase in isolation or a lower quantity of forest habitat in the surrounding landscape may contribute to relax the top-down control.

Data were sampled in restoration sites containing high abundance of pioneer species (see Supplementary Material 2) and surrounded by an agricultural matrix. As both native pioneer species and cultivated plants have less structural and chemical quantitative defences and higher nutritional value than non-pioneer species (Massad 2012), restoration sites offer more resources to the LCA. This, in association with the proximity to agricultural crops, which are palatable to the LCA, results in high quantity and quality of available resources for foraging and thus represents a relaxation of the bottom-up control (Terborgh *et al.* 2001, Urbas *et al.* 2007). Furthermore, *A. sexdens* presents a more generalist foraging behaviour when compared to other species of the same genus, foraging opportunistically and adapting to many habitat types (Garcia *et al.* 2020, Rao *et al.* 2001, Sousa-Souto *et al.* 2008).

Natural enemies of the LCA act in different phases of the life cycle of the colony, from the nuptial flight (Camacho *et al.* 2012), foundation and establishment of the nest (Araújo *et al.* 2015, Erthal Jr & Tonhasca Jr 2001, Silveira *et al.* 2006, Travaglini *et al.* 2016) and during selection and foraging activity (Almeida *et al.* 2008, Barrera *et al.* 2017). These natural enemies encompass invertebrate predators as other species of ants, spiders, beetles and mites (Araújo *et al.* 2015, Erthal Jr & Tonhasca Jr 2001, Silveira *et al.* 2006); vertebrates as frogs, lizards, birds, armadillos and anteaters (Camacho *et al.* 2012, Rao 2000, Terborgh *et al.* 2001); parasitoids as flies from the family Phoridae and wasps (Almeida *et al.* 2008, Barrera *et al.* 2017) and soil microorganisms as bacteria and fungi (Travaglini *et al.* 2016). All of them are important to the maintenance of LCA population control in a wide range of ecosystems. Nevertheless, the efficiency of population control is higher in the initial phase, when females are predated during the nuptial flight, or on the soil, or inside a shallow, incipient nest (Helms *et al.* 2016, Vieira-Neto & Vasconcelos 2010), than after the establishment of the colony.

There is no specific survey on the LCA's natural enemies or on their potential for predation or parasitism conducted specifically on forest restoration sites. However, fauna surveys have been performed in the same restoration sites studied here, and potential enemy species have been identified. It is important to highlight that all these faunal samplings (Lima 2012, Lima 2018, Santos Jr *et al.* 2016, Silva 2016) were made in restoration sites that are adjacent to forest fragments, and it is not reasonable to expect that the fauna of the more distant restoration sites is similar to those of that connected ones, highlighting the importance of greater landscape connectivity for the biological control of LCA. Among those species were beetles from the genus *Canthon* Hoffmannsegg, 1818 (Silva 2016), which predate the queens to feed their larvae (Araújo *et al.* 2015, Silveira *et al.* 2006). Furthermore, many anuran species were listed as common in restoration sites, adjacent forest fragments and nearby lakes (Lima 2012), most of them being generalist insectivores. Lima (2018) registered *Dasypus novemcinctus* Linnaeus, 1758, nine-banded armadillo, which was considered abundant; *Euphractus sexcinctus* Linnaeus, 1758, six-banded armadillo and *Tamandua tetradactyla* Linnaeus, 1758, lesser anteater, both less abundant, both in forest fragments and adjacent restoration sites. Finally, among birds, there are insectivore and omnivore species that use the matrix for foraging (Anjos *et al.* 2019). In a study in the same region and including some of the restoration sites sampled in this study, Santos Jr *et al.* (2016) suggest that, at least until they reach 12 to 15 years of age, restoration sites support only open area or generalist forest bird species. Nevertheless, these birds may have a crucial role in the control of LCA in the nuptial flight phase, as they include animals that capture insects in flight or on the soil (Helms *et al.* 2016, Vieira-Neto & Vasconcelos 2010).

Apart from predators, flies from the family Phoridae, important parasitoids of LCA, occur in higher abundances under high levels of humidity and moderate temperatures, avoiding environments under edge effect or high disturbance (Almeida *et al.* 2008, Barrera *et al.* 2017). For this reason, it is possible that this group is absent or in low abundance at restoration sites, which hold drier and warmer microclimates when compared to forest fragments (Mota 2013).

Since they consist of linear buffer strips in the margin of a water reservoir, presenting similar sizes and shapes, the whole area of the restoration sites is likely under edge effects (Mota 2013). Considering also the high homogeneity of species composition, age, soil and other environmental features of those reforestations, the amount of surrounding forest habitat is possibly the more important factor affecting the natural enemies of LCA (Joly *et al.* 2014).

In synthesis, our results suggest that both distance from forest fragments and the amount of surrounding forest habitat are important factors to determine the abundance of *A. sexdens* nests. This is likely a consequence of (1) the low abundance of ant natural enemies which leads to a relaxation of top-down control in more isolate restoration sites and (2) the high resource availability which relax the bottom-up control. Thus, landscape fragmentation may be acting as an ecological filter, regulating the presence of many groups of organisms in successional habitats, not only plants (Pereira *et al.* 2013, Santos Jr *et al.* 2016) but also faunal groups, such as LCA's natural enemies, which in turn may indirectly affect plant populations in forest restoration sites, by increasing herbivory (Garcia *et al.* 2020). Thus, LCA represent an important factor influencing on long-term trajectories of restoration sites; plant composition in restoration sites far away from forest remnants is known for being affected by plant dispersal itself responding to landscape structure (Suganuma *et al.* 2017), and the effect of increased LCA presence on such isolated sites add uncertainty to long-term trends in vegetation development. This reinforces the importance of long-term studies in restoration sites, including the monitoring of LCA.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467422000517

Acknowledgments. Authors are also grateful to Odair do Carmo Pavão, Alba Cavalheiro and other members of LABRE team, for the help in the field and in the laboratory activities.

Financial support. This research was part of the long-term ecological research site PELD MANP, supported by CNPq (grant 441540/2016-3) and Fundação Araucária (41872.434.40722.27092013). CNPq also provided research grants for JMDT (309244/2015-3 and 447561/2014-6). CAPES provided a graduate scholarship for JMG ('Finance Code 001').

Conflicts of interest. The authors declare none.

References

Almeida WR, Wirth R and Leal IR (2008) Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic Forest. *Entomologia Experimentalis et Applicata* **129**, 251–257.

Anjos L, Bochio GM, Medeiros HR, Almeida BA, Lindsey BRA, Calsavara LC, Ribeiro MC and Torezan JMD (2019) Insights on the functional composition of specialist and generalist birds throughout continuous and fragmented forests. *Ecology and Evolution* **9**, 6318–6328.

Araújo MS, Rodrigues CA, Oliveira MA and Jesus FG (2015) Controle biológico de formigas-cortadeiras: o caso da predação de fêmeas de *Atta* spp. por *Canthon virens*. *Revista de Agricultura Neotropical* **2**, 8–12.

Autuori M (1941) Contribuição para o conhecimento da saúva (Atta sp. – Hymenoptera – Formicidae) I. Evolução do sauveiro (*Atta sexdens rubropilosa* Forel, 1908). *Arquivos do Instituto Biológico* **12**, 197–229.

Barrera CA, Becker EL, Elizalde L and Queiroz JM (2017) Parasitoid phorid flies of leaf-cutting ants are negatively affected by loss of forest cover. *Entomologia Experimentalis et Applicata* **164**, 1–12.

Camacho I, Honorato RS, Fernandes BC, Boechat RF, Filho CS and Kanegae MF (2012) Aves de rapina diurnas forrageando tanajuras (*Atta* sp.) em revoada em uma paisagem fragmentada de floresta atlântica, sudeste do Brasil. *Revista Brasileira de Ornitologia* **20**, 19–21.

Costa AN, Vasconcelos HL and Bruna EM (2016) Biotic drivers of seedling establishment in Neotropical savannas: selective granivory and seedling herbivory by leaf-cutter ants as an ecological filter. *Journal of Ecology* **105**, 132–141.

Erthal Jr M and Tonhasca Jr A (2001) *Attacobius attarum* Spiders (Corinnidae): myrmecophilous predators of immature forms of the leaf-cutting ant *Atta sexdens* (Formicidae). *Biotropica* **33**, 374–376.

Ferreira BZ (2015) *Herbivoria por Atta sexdens rubropilosa Forel, 1908 sobre espécies arbóreas em restauração florestal.* Master thesis. Universidade Estadual Paulista "Júlio de Mesquita Filho". Faculdade de Ciências Agronômicas.

Filgueiras BKC, Melo DHA, Andersen AN, Tabarelli M and Leal IR (2019) Cross-taxon congruence in insect responses to fragmentation of Brazilian Atlantic forest. *Ecological Indicators* **98**, 523–530.

Garcia JM, Bordignon AM, Gonzaga GS and Torezan JMD (2020) Tree seedling responses to leaf-cutting ants herbivory in Atlantic Forest restoration sites. *Biotropica* **52**, 884–895.

Helms JA, Godfrey AP, Ames T and Bridge ES (2016) Are invasive fire ants kept in check by native aerial insectivores? *Biology Letters* **12**, 1–4.

Jaffe K and Vilela E (1989) On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. *Biotropica* **21**, 234–236.

Joly CA, Metzger JP and Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytologist* **204**, 459–473.

Leal IR, Wirth R and Tabarelli M (2014) The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. *Biotropica* **46**, 516–528.

Lima FCM (2018) *Mamíferos de Médio e Grande Porte em Sítios de Restauração Ecológica da Mata Atlântica: Características da Paisagem e Diversidade Funcional.* Doctoral thesis. Departamento de Biologia Animal e Vegetal. Universidade Estadual de Londrina.

Lima MZ (2012) *Comparação da anurofauna em remanescentes florestais e em reflorestamentos no Reservatório Capivara, Rio Paranapanema, Paraná, Brasil.* Master thesis. Departamento de Biologia Animal e Vegetal. Universidade Estadual de Londrina.

Massad TJ (2012) Interactions in tropical reforestation – how plant defence and polycultures can reduce growth-limiting herbivory. *Applied Vegetation Science* **15**, 338–348.

Massad TJ, Chambers JQ, Rolim SG, Jesus RM and Dyer LA (2011) Restoration of pasture to forest in Brazil's Mata Atlântica – the roles of herbivory, seedling defenses, and plot design in reforestation. *Restoration Ecology* **19**, 257–267.

McGarigal K and Marks BJ (1995) *Fragstats: Spatial Patterns Analysis Program for Quantifying Landscape Structure.* Portland: USDA, Forest Service, Pacific Northwest Research Station.

Meyer ST, Leal IR and Wirth R (2009) Persisting hyper-abundance of Leaf-cutting Ants (*Atta* spp.) at the edge of an old Atlantic forest fragment. *Biotropica* **41**, 711–719.

Montagnini F, Gonzalez E, Porras C and Rheingans R (1995) Mixed and pure forest plantations in the humid neotropics – a comparison of early growth, pest damage and establishment costs. *Commonwealth Forestry Review* **74**, 306–314.

Mota MC (2013) *Efeitos da largura da mata ciliar em restauração sobre a comunidade vegetal.* Master thesis. Departamento de Biologia Animal e Vegetal. Universidade Estadual de Londrina.

Nitsche PR, Caramori PH, Ricce WS and Pinto LFD (2019) *Atlas climático do estado do Paraná.* Londrina: Instituto Agronômico do Paraná.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan, G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C and Weedon J (2022) Vegan: Community Ecology Package. R package version 2.6-2. Available at https://CRAN.R-project.org/package=vegan (accessed 15 October 2022).

Pereira LCSM, Oliveira CCC and Torezan JMD (2013) Woody species regeneration in Atlantic forest restoration sites depends on surrounding landscape. *Natureza & Conservação* **11**, 138–144.

R Core Team (2019) *R: A Language and Environment for Statistical Computing*: R Foundation for Statistical Computing. Available at https://www.R-project.org (accessed 15 July 2019).

Rao M (2000) Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation. *Journal of Tropical Ecology* **16**, 209–225.

Rao M, Terborgh J and Nunez P (2001) Increased herbivory in forest isolates: implications for plant community structure and composition. *Conservation Biology* **15**, 624–633.

Santos Jr PCA, Marques FC, Lima MR and Anjos L (2016) The importance of restoration areas to conserve bird species in a highly fragmented Atlantic forest landscape. *Natureza & Conservação* **14**, 1–7.

Silva BP (2016) *Comunidade de Scarabaeinae (Coleoptera: Scarabaeidae) em reflorestamentos e remanescentes de Mata Atlântica do Sul do Brasil.* Master thesis. Departamento de Biologia Animal e Vegetal. Universidade Estadual de Londrina.

Silveira FAO, Santos JC, Viana LR, Falqueto SA, Vaz-de-Mello FZ and Fernandes GW (2006) Predation on *Atta laevigata* (Smith 1858) (Formicidae Attini) by *Canthon virens* (Mannerheim 1829) (Coleoptera Scarabaeidae). *Tropical Zoology* **19**, 1–7.

Sousa-Souto L, Schoereder JH and Lima ER (2008) Why do leaf-cutting ants (Hymenoptera: Formicidae) change their foraging pattern? *Sociobiology* **52**, 645–654.

Suganuma MS, Torezan JMD, Durigan G (2017) Environment and landscape rather than planting design are the drivers of success in long term restoration of riparian Atlantic Forest. *Applied Vegetation Science* **21**, 76–84.

Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD and Balbas L (2001) Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1925.

Travaglini RV, Forti LC, Arnosti A, Camargo RS, Silva LC and Camargo-Mathias MI (2016) Mapping the adhesion of different fungi to the external integument of *Atta sexdens* rubropilosa (Forel, 1908). *International Journal of Agriculture Innovations and Research* **5**, 2319–2473.

Urbas P, Araújo Jr MV, Leal IR and Wirth R (2007) Cutting more from cut forests: edge effects on foraging and herbivory of leaf-cutting ants in Brazil. *Biotropica* **39**, 489–495.

Vieira-Neto EHM and Vasconcelos HL (2010) Developmental changes in factors limiting colony survival and growth of the leaf-cutter ant *Atta laevigata*. *Ecography* **33**, 538–544.

Wirth R, Beyschlag W, Herz H, Ryel RJ and Hölldobler B (2003) *The Herbivory of Leaf-Cutting Ants: A Case Study on Atta Colombica in the Tropical Rainforest of Panama.* Ecological Studies, 164. Berlin: Springer-Verlag.

Zanetti R, Zanuncio JC, Santos JC, Silva WLP, Ribeiro GT and Lemes PG (2014) An overview of integrated management of leaf-cutting ants (Hymenoptera: Formicidae) in Brazilian forest Plantations. *Forests* **5**, 439–454.

Zar JH (2010) *Biostatistical Analysis.* New Jersey: Prentice-Hall Inc.