



RESEARCH ARTICLE - ANTS

Divergence of Ant Communities Over Time in a Fragmented Atlantic Rain Forest Landscape

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Abstract

Habitat fragmentation changes biological communities and its spatiotemporal dynamics – which may lead to either biotic homogenization or heterogenization along time and space. Both processes can occur by addition, replacement or loss of species within communities, altering compositional similarity across the landscape. We investigated which of these two processes (biotic homogenization or heterogenization) occurs, and its possible underlying mechanism, over 15 years in an Atlantic Forest landscape using ants as model organisms. We sampled ants in 17 forest fragments across three different years, compared their composition similarity, species richness, and species richness of groups classified according to their habitat preferences. We sampled a total of 132 ant species. Ant communities in fragments diverged over time, suggesting they experienced an idiosyncratic structuring process. This biotic heterogenization occurred through an additive process, as ant species richness increased over time, mainly due to an increase of generalist ant species, and a decrease of forest specialist ant species. These changes occurred despite the higher forest cover in the landscape along years. Since different species can perform different functions in ecosystems, this biotic heterogenization may have implications for ecosystem functioning. Investigating how disturbances structure biological communities over time, especially those performing important ecosystem functions, can shed light to our understanding of possible changes in ecosystem functions and consequently for forest regeneration.

Introduction

Metacommunities are a set of local communities that are linked by dispersal of multiple interacting species (Wilson, 1992). Local metacommunities are shaped by speciation, dispersal, abiotic conditions, biotic interactions, and ecological drift processes (Vellend, 2010; 2016). Such processes, which shape the structure and dynamics of local communities, may occurs as a result of habitat fragmentation (Chase et al., 2020). Habitat fragmentation isolate natural habitats, change their abiotic conditions, resource availability and quality (Arroyo-Rodríguez et al., 2017; 2020; Fahrig, 2003; Schmidt et al., 2013; Sobrinho et al., 2003; Sobrinho & Schoereder, 2007). Communities from isolated habitats

have smaller populations, different migration patterns and distribution, and richness and composition (Arroyo-Rodríguez et al., 2020; Bender et al., 1998; Fahrig, 2019; Lasmar et al., 2021; Madureira et al., 2012; Sobrinho & Schoereder, 2007; Vellend, 2010). These changes in species dynamics within fragments, may lead communities to become either more similar among each other or more dissimilar – i.e., they can cause a biotic homogenization (McKinney & Lockwood 1999) or biotic heterogenization, respectively (Laurance et al., 2007; Socolar et al., 2016).

Biotic homogenization may occur due to two mechanisms: additive and subtractive. Additive homogenization occurs when new species immigrate from other regions and become present in most fragments in the landscape.



Subtractive homogenization occurs when particular species with a distribution restricted to a few fragments disappear from all of them and consequently from the landscape (Socolar et al., 2016). Therefore, biotic homogenization occurs through immigration and extinction, which in turn impact species distribution and abundance across local sites (Olden, 2006). Lower connectivity in landscapes after fragmentation benefits species with a high dispersal ability, that can establish in isolated fragments and contribute to biotic homogenization (Chase et al., 2020). Changes in resource availability due to habitat fragmentation can benefit species that have more similar needs and are more adapted to disturbances (generalist species), altering local species composition due to invasion and extinction (McKinney & Lockwood, 1999; Olden et al., 2004; Tabarelli et al., 2012).

Biotic heterogenization may also occur due to species introduction (additive mechanisms) or species loss (subtractive mechanisms) (Socolar et al., 2016). Contrary to homogenization, heterogenization is likely driven mainly by idiosyncratic events, and if so local communities diverge along time after disturbance (Audino et al., 2014; Laurance et al., 2007; Socolar et al., 2016). For instance, additive heterogenization occurs when each fragment experiences a unique successional pattern, being colonized by different species from neighbouring fragments (Arroyo-Rodríguez et al., 2013) which depends on landscape connectivity and dispersal ability of organisms (Mouquet & Loreau, 2003). Subtractive heterogenization occurs if certain species are more prone to extinction due to new abiotic conditions, different biotic interactions and stochastic events, favouring different species across fragments (Socolar et al., 2016). In this case, changes in species groups - which represent the role that species play in the ecosystem - can also occur due to specialist species extinction and/or generalist species invasion (Tabarelli et al., 2012).

Habitat fragmentation can thus shape community structure across space and time by changing migration and extinction patterns, and local conditions and resources (Chase et al., 2020; Dornelas et al., 2014; Solar et al., 2015). To better conserve and restore impacted communities it is necessary to understand how and why community structuring vary over time (Arroyo-Rodríguez et al., 2013; Chase et al., 2020), but it is still unclear how biotic homogenization and heterogenization contribute to shape biological communities in human-driven fragmented landscapes (Arroyo-Rodríguez et al., 2020; Chase et al., 2020). Available studies suggest that metacommunities can suffer both processes in human-altered landscapes (Chase et al., 2020), and as a demand for conservation, it is necessary to understand how these processes contribute to community structuring in tropical forests, which are under high anthropogenic pressure. Additionally, anthropic pressure can favor non-native species invasion and exclude native species in forests, which first leads to biotic heterogenization, as initially species invades few fragments, but these species

spread and can lead to biotic homogenization (McKinney & Lockwood, 1999).

Here we investigated processes driving ant community composition in a fragmented Atlantic Forest landscape, a hotspot Brazilian biome that suffered a severe fragmentation process: there is about 15% of the original cover remaining, almost half of which is located < 100 m from the edge, and most remaining fragments are < 50 ha (Ribeiro et al., 2009). We studied ants (Hymenoptera: Formicidae) because they are highly sensitive to habitat fragmentation (Lasmar et al., 2021; Vasconcelos et al., 2006), reflect impacts on other animal and plant species (Majer et al., 1997), and constitute an important ecological group of insects in tropical forests due to their large biomass. Additionally, ants play important roles in several ecological processes such as seed dispersal, invertebrate predation, soil bioturbation and herbivory (Ribas et al., 2012). We studied 17 secondary fragments of Atlantic Forest in southeastern Brazil throughout a 15-year interval. We investigated whether ant communities across these forest fragments experienced homogenization or heterogenization (or if neither process occurred), and which underlying mechanism (subtractive or additive) was responsible for such changes. We also evaluated whether generalist ant species are responsible for possible changes in species composition, by investigating whether species proportion of this group is higher in fragments.

Materials and methods

Study site

We carried out this study in the Atlantic Forest of southeastern Brazil, in the municipality of Viçosa, Minas Gerais state (20°45'S, 42°50'W). According to landowners of the region and previous studies, the region was covered by forests up to the 19th century, but during the 1930's and 1940's an accelerated process of fragmentation has begun and lasted until the 1960's (Schmidt et al., 2013; Sobrinho & Schoereder 2007). Most current fragments in the region resulted from natural recovery, and are between 20 and 60 years old, although some are up to 100 years old (Ribon et al., 2003). We documented changes in land-use types in our study region to better understand how different land-use cover could influence our results. During the years in which the samples were collected, there was an overall increase in forest cover in the study region (Table 1: Supplementary Material; MapBiomass, 2020).

Ant sampling

We sampled ant species from 17 fragments (Figure 1) in three years: 1995, 1996 and 2010 at the same points in all years, and always in the rainy season (from November to March). Fragments varied in size from three to 300 hectares (detailed in Table 2: Supplementary Material). We used pitfall traps of 19 cm in diameter and 11 cm high buried at

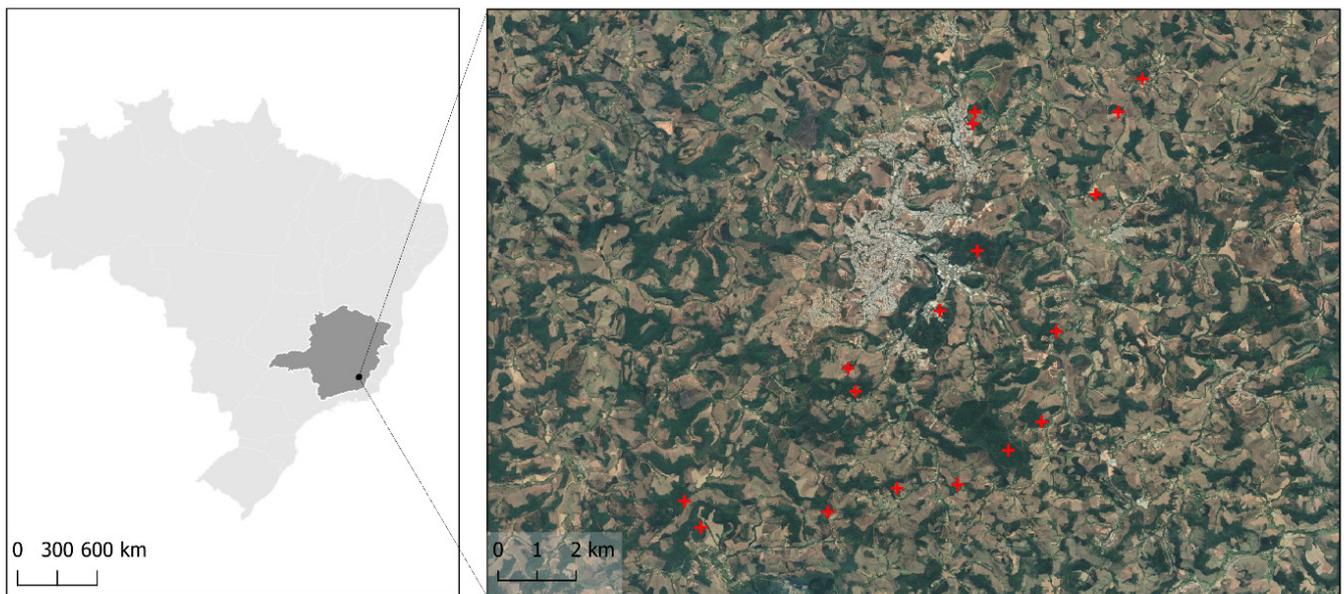


Fig 1. Map of sampled Atlantic rain forest fragments in Viçosa region, Minas Gerais state, Brazil. The red crosses show the location of the 17 fragments sampled in 1995, 1996 and 2010.

the ground level, containing water and detergent. Traps were baited with human feces and cattle carrion, and remained in the field for 48 h. These baits were used because, in addition to ants, samples were also intended to collect other invertebrates. Although the use of bait is not common in ant community studies, it is known that at least 60% of total ant species are captured using this method (Przybyszewski et al., 2020). Furthermore, the same method was repeated in all sampled and years. Each sampling point was constituted by a set of two traps, each with one bait type, three meters apart. According to Schoereder et al. (2004a), we used a sampling effort proportional to each fragment size: in fragments larger than 93 hectares, 48 traps were placed, totaling 24 sampling points; in fragments between 30 and 61 hectares, 24 traps in 12 sampling points were used; and in fragments between 3 and 9 hectares, 8 traps at 4 sampling points were used. Traps were placed at least 20 m from the edge of the fragments, and the distance between each sampling point was at least 30 m. Ant species were identified to the smallest possible level and deposited in the ant collection of the Laboratório de Sistemática e Biologia de Coleoptera of the Universidade Federal de Viçosa, Brazil.

To investigate whether different groups of ant species are responsible for possible changes in species composition, we categorized sampled ant species as generalists, forest specialists, open-habitat specialists or unclassified, according to environments in which species are typically found. Accordingly, forest specialist species rarely or never occur in savanna, and open-habitat specialists rarely or never occur in forest. Generalist species frequently occur in both types of habitats. This classification was only attributed for species where enough information is available. An ant taxonomist (Julio M.C. Chaul) provided the classifications.

Statistical analysis

To test whether ant communities in the studied fragments experienced a process of biotic homogenization or heterogenization, we first compared species composition similarity across all pairs of fragments from each year separately, using the Jaccard similarity index. Afterwards we compared the average similarity across years using a GLMM (Generalized Mixed Model), with fragment pair identity as a random effect, and the year of sampling as a fixed effect. As we expected larger changes in the mean similarity indices between the years 1995 - 2010 than between 1995 - 1996, the years were included in the model as a continuous variable. We used a binomial error distribution because these data are strictly bounded which values are between 0 and 1 (Crawley, 2013), and a contrast analysis to check if ant composition similarity differed among years.

We also investigated whether the found process (i.e., biotic homogenization or heterogenization process) was driven by species addition or subtraction mechanisms by analyzing changes in ant species richness over time across fragments. Changes in ant species composition driven by an increase in ant species richness in fragments suggest an additive mechanism. Alternatively, a decrease in ant species richness in each fragment suggests a subtractive mechanism. For that, we built a GLMM with Poisson error distribution, using fragments as a random effect and the sampling year as a fixed effect. We used a contrast analysis to check for differences among years.

We used the proportion of ant species richness from each group (generalists, forest specialists and open-habitat specialists species) as a response variable to test whether changes in ant species richness of these groups could have

caused biotic homogenization or heterogenization, through additive or subtractive mechanisms. The proportion of ant species from each group was obtained by dividing the number of species from each group by the total number of species sampled in each fragment and year. We adjusted a GLMM with a Binomial error distribution, using proportion of ant species richness from each group as the response variable, forest fragments as a random effect, and year as a fixed effect. We also used a contrast analysis to check for species richness differences among years.

We used the R software (R-core team 2021) to perform all analyzes. We used the packages *vegan* 2.5-6 (Oksanen et al., 2019) for species composition, *lme4* 1.1-26 (Bates et al., 2015) to perform GLMMs, and *DHARMA* 0.3.3.0 (Hartig, 2020) to perform residual analysis, check model suitability and distribution.

Results

We sampled a total of 132 ant species, distributed in eight subfamilies: Dolichoderinae; Dorylinae; Ectatomminae; Formicinae; Heteroponerinae; Myrmicinae; Ponerinae and Pseudomyrmicinae (Table 3: Supplementary Material). Subfamilies Dorylinae and Heteroponerinae was the only subfamily that decreased the species number in the year 2010, when compared to 1995 and 1996. Dorylinae had only one species, *Neivamyrmex alfaroi*, which was sampled in 1995 and 1996. Only two species were from the Heteroponerinae: *Heteroponera dolo*, which was sampled in all years, and *Heteroponera dentinodis*, sampled only in 1996. Subfamily Myrmicinae had the highest number of species in all years, representing 44% of total species.

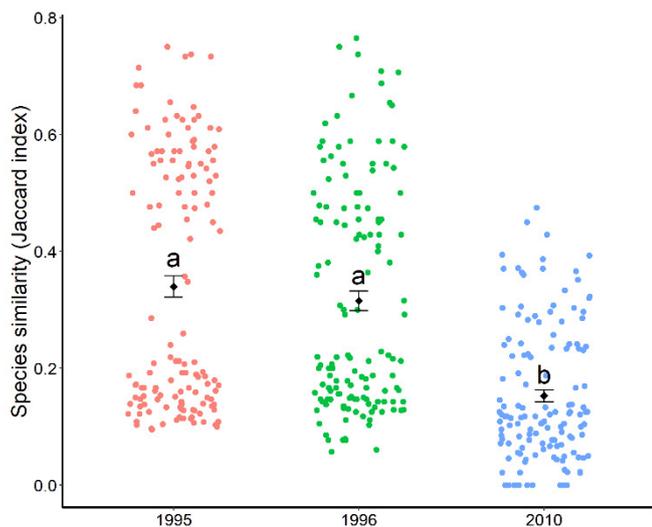


Fig 2. Average similarity of ant species composition across studied fragments, located in southeastern Brazilian Atlantic rain forest. Each point represents a pairwise comparison between fragments using the Jaccard similarity index. To compare averages, we used a mixed model considering each forest fragment identity as a random effect (see main text). The black lozenges represent the average, and the bars represent the standard error. Different letters represent significant differences at $\alpha = 0.05$.

The average similarity of ant species composition among fragments differed over time ($\chi^2 [2, N = 17] = 72.036, p < 0.001$, Figure 2). Ant species richness was higher in 2010 than in 1995 and 1996 ($\chi^2 [1, N = 17] = 9.13, p = 0.002$, Figure 3), which did not differ each other. Among the species sampled, 28% were classified as generalist, 34% forest specialist, 3% open-habitat specialist, and 35% of the species could not be classified into the three categories.

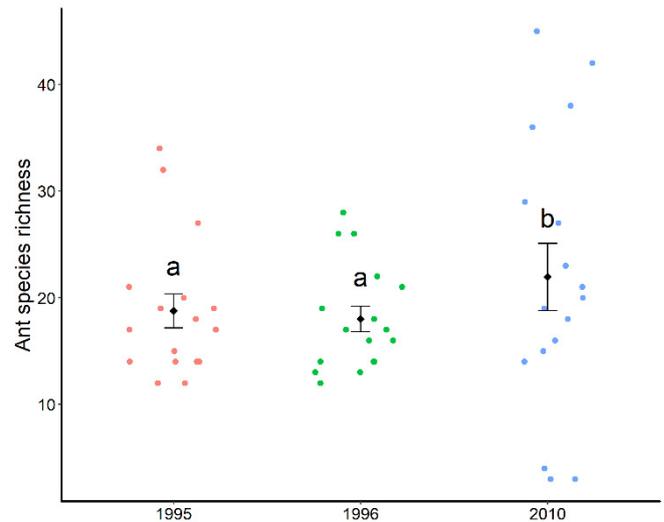


Fig 3. Average ant species richness across studied fragments, located in southeastern Brazilian Atlantic rain forest. In 2010, ant species richness was higher than in 1995 and 1996 ($p = 0.002$). Each point represents a fragment sampled in the correspondent year. The black lozenges represent the average and the bars represent the standard error. Different letters represent significant differences at $\alpha = 0.05$.

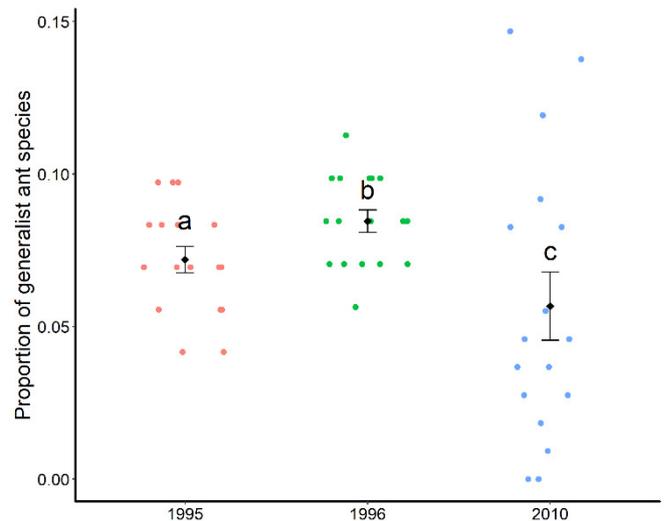


Fig 4. Average proportion of generalist ant species richness across studied fragments, located in southeastern Brazilian Atlantic rain forest. In 2010 it was higher than when compared to 1995 and 1996 ($p = 0.01$). Points represent the proportion of generalist ant species from each fragment in each year. The black lozenges represent the average and the bars represent the standard error. Different letters represent significant differences at $\alpha = 0.05$.

The proportion of generalist species increased over time ($\chi^2 [2, N = 17] = 9.0914, p = 0.01$, Figure 4). However, the proportion of forest specialist species was higher in 1995 compared to 1996 and 2010 ($\chi^2 [2, N = 17] = 32.264, p < 0.001$, Figure 5), while open-habitat specialist species was similar among years ($\chi^2 [2, N = 17] = 1.76, p = 0.41$, Figure 6).

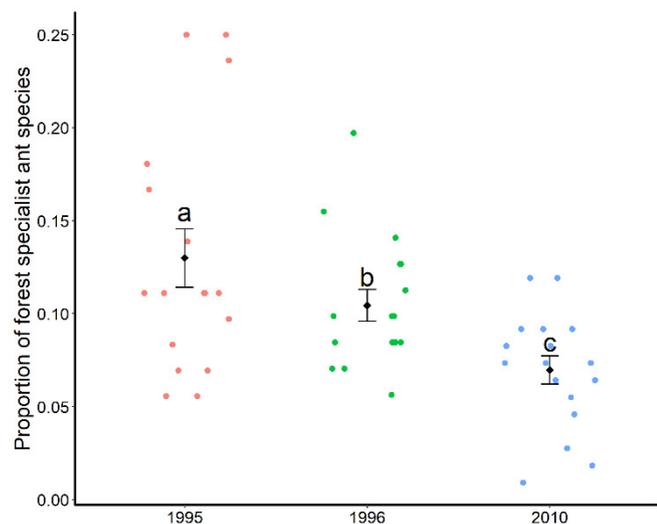


Fig 5. Average proportion of forest specialist ant species richness across studied fragments, located in southeastern Brazilian Atlantic rain forest. In 1995 it was higher when compared to 1996 and 2010 in fragments located in southeastern Brazilian Atlantic rain forest ($p < 0.001$). Points represent the proportion of forest specialist ant species from each fragment sampled in each year. The black lozenges represent the average and the bars represent the standard error. Different letters represent significant differences at $\alpha = 0.05$.

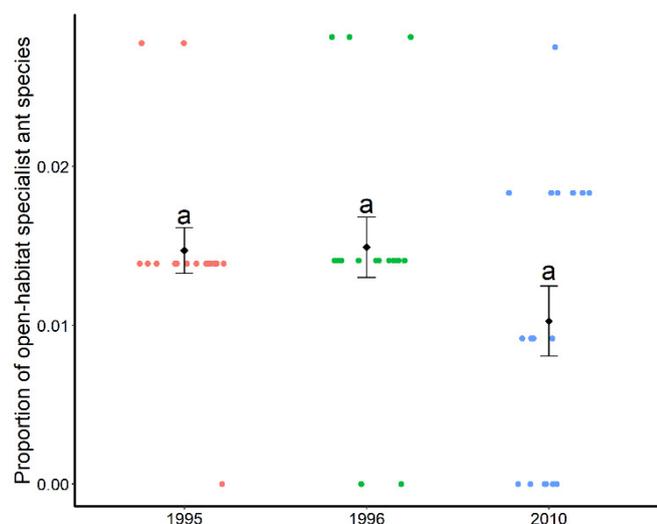


Fig 6. Average proportion of open-habitat specialist ant species richness across studied fragments, located in southeastern Brazilian Atlantic rain forest. Open-habitat specialist species was similar among years in fragments located in southeastern Brazilian Atlantic rainforest ($p = 0.41$). Points represent the proportion of open-habitat specialist ant from each fragment sampled in each year. The black lozenges represent the average and the bars represent the standard error. Different letters represent significant differences at $\alpha = 0.05$.

Discussion

Here we documented a 15-year long biotic heterogenization of ant communities across a fragmented rain forest landscape, suggesting ant communities experienced an idiosyncratic structuring process. The average ant species richness in fragments increased over time, so this biotic heterogenization probably occurred through an additive mechanism. Important implications for conservation biology emerge from this idiosyncrasy, since each fragment may contain a different set of species, including those with key roles in the ecosystem, interactions, and also invasive species (Laurance et al., 2007).

Biotic heterogenization occurred due to an increase of ant species richness in 2010, which was ~20% higher in comparison to 1995. In the same period, the forested area in our study landscape increased by 3% and agricultural area decreased by 4.2% (Table S.2: Supplementary Material). Habitat structure can be an environmental filter strongly related to changes in ant richness and composition in forest fragments (Castro et al., 2020). The increase of forest cover probably causes a higher habitat availability and quality for ant species in our study region (Schmidt et al., 2013; Sobrinho et al., 2003), which in turn reduces the extinction risk to forest species, and allows species to establish across fragments. Furthermore, forest recovery likely contributed to the biotic heterogenization we observed because it increased the proportion of different habitat (i.e., forest and agriculture) available in the landscape. As ant communities markedly differ across habitat types in our study region (Schmidt et al., 2013), some ant species from agriculture can enter forest remnants (Thomas, 2020) and alter their species composition (Sobrinho et al., 2003).

Despite higher forest area in 2010, forest specialist ant species richness decreased over time. Specialist ant species are more vulnerable to disturbed environments (Andersen, 2019), and our results showed that these species were not reestablished in our fragments across the years. Contrarily, the number of generalist species increased about 254% in 2010 compared to 1995 – for instance, species usually found in disturbed savannas as *Ectatomma planidens* and *Linepithema humile* (Ramos et al., 2003) were sampled only in 2010, suggesting that generalist species and from open areas invaded fragment forests along years, despite the higher forest cover. This result supports recent findings that edge and matrix effects can increase ant species richness in local scales due to an invasion of generalist ant species (Lasmar et al., 2021), which are less vulnerable to impacts due to their wider use of resources (Andersen, 2019). Invasions of ant species from open areas into forests can occur after other anthropogenic disturbances, as due to recurrent forest fires and consequent canopy opening (Paolucci et al., 2017). In the studied fragments, one of the explanations for the invasion of generalist species in small fragments is the similarity between

these fragments and the surrounding matrix (Schoereder et al., 2004b), and here we show that such invasions can contribute to a biotic heterogenization of ant communities.

We did not test what were the consequences of additive biotic heterogenization for the ecosystem functions performed by ants in this landscape, although the loss of functions due to changes in ant species composition has been found before (Del Toro et al., 2012). What we do know is that the environmental filters imposed by habitat fragmentation can change ant taxonomic diversity, but not necessarily the functional diversity (Castro et al., 2020). Thus, even if biotic heterogenization occurs in the fragments, ecosystem functions promoted by ants can still be maintained, but this is an area for further investigations.

Our results have important implications for decisions regarding rain forests conservation, since ants are an ecologically dominant group, that play several ecosystem functions, and also bioindicators that can represent changes in other taxonomic groups (Andersen & Majer, 2004). Forest fragments under a natural recovery process can experience idiosyncratic trajectories regarding environmental conditions, human pressure and thus colonization / extinction of plant species (Laurance et al., 2007), and our results point to a parallel process for the associated fauna. The knowledge about ant species composition changes in remaining fragments and also about how these can impact ecosystem functions performed by ants are important to understand natural forest recovery, given several functions performed by ants relate to this process, as seed dispersal, herbivory and predation of insect herbivores. In addition, we hope that identifying empirically that fragmentation drives communities divergence leads to further investigations on other types of disturbances and their consequences for biological communities over time.

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Authors contribution

All authors contributed in the stages of: conceptualization, methods, validation, formal analysis, writing, review and editing, visualization, supervision.

J.H. Schoereder was responsible for research, resources and procurement of funding.

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Supplementary Material

Table S1. Area size in hectare and percentage of total area (in parentheses) showing changes in land uses in Viçosa municipality -MG, Brazil, classified in 1995, 1996 and 2010.

Class / Year	1995	1996	2010
Forest	6874.023 (22.96%)	6844.791 (22.86%)	7782.602 (25.99%)
Agriculture	22046.48 (73.64%)	22040.04 (73.61%)	20794.64 (69.45%)
Unvegetated area	997.3359 (3.33%)	1033.261 (3.45%)	1340.006 (4.48%)
Water	22.10562 (0.07%)	21.85455 (0.07%)	22.69341 (0.08%)
Size total		29939.95 (100%)	

Source: MapBiomias

Table S2. Proportional size in hectare of fragments area, number of traps installed and points sampled in Viçosa, state of Minas Gerais, Brazil.

Geographic coordinates	Fragment size	Fragment size 1995	Fragment size 2010	Traps	Points
20°48'22.2"S/42°51'10.9"W	> 93 hectares	298.92	350.14	48	24
20°49'31.0"S/42°55'44.5"W	> 93 hectares	93.37	88.52	48	24
20°45'24.2"S/42°51'38.8"W	30 to 61 hectares	60.52	79.57	24	12
20°47'29.5"S/42°53'26.9"W	30 to 61 hectares	46.16	51.12	24	12
20°46'17.6"S/42°52'11.7"W	30 to 61 hectares	39.21	100.47	24	12
20°47'56.9"S/42°50'41.3"W	30 to 61 hectares	30.13	36.90	24	12
20°44'34.0"S/42°49'53.3"W	3 to 9 hectares	8.57	9.24	8	4
20°49'17.0"S/42°53'51.4"W	3 to 9 hectares	4.05	4.72	8	4
20°48'55.9"S/42°52'49.9"W	3 to 9 hectares	3.15	9.98	8	4
20°49'07.3"S/42°55'58.9"W	3 to 9 hectares	4.99	4.15	8	4
20°46'36.2"S/42°50'28.2"W	3 to 9 hectares	8.00	6.58	8	4
20°43'20.2"S/42°51'40.7"W	3 to 9 hectares	7.72	7.19	8	4
20°43'30.9"S/42°51'42.5"W	3 to 9 hectares	7.97	5.66	8	4
20°43'20.3"S/42°49'33.3"W	3 to 9 hectares	6.91	5.09	8	4
20°42'50.7"S/42°49'11.6"W	3 to 9 hectares	5.56	6.44	8	4
20°47'08.8"S/42°53'33.4"W	3 to 9 hectares	4.21	6.12	8	4
20°48'52.7"S/42°51'56.0"W	3 to 9 hectares	5.77	2.32	8	4

Table S3. Ant species sampled in the years of 1995, 1996 and 2010. The letter G represents the species classified as generalists, letters FS as forest specialist and letters OH those species classified as open-habitat specialist. Species that do not have any letter were unclassified.

Subfamily / species	1995	1996	2010	Subfamily / species	1995	1996	2010
Dolichoderinae				Formicinae			
<i>Dolichoderus attelaboides</i> ^{FS}	X	X	X	<i>Camponotus atriceps</i> ^G	X	X	X
<i>Linepithema humile</i> ^G			X	<i>Camponotus crassus</i> ^{OH}		X	X
<i>Linepithema iniquum</i> ^{FS}	X	X	X	<i>Camponotus genatus</i> ^G	X	X	X
<i>Linepithema leucomelas</i> ^{FS}	X	X		<i>Camponotus melanoticus</i> ^G	X	X	X
<i>Linepithema</i> sp.1			X	<i>Camponotus novogranadensis</i> ^G		X	X
<i>Linepithema</i> sp.2			X	<i>Camponotus rufipes</i> ^G	X	X	X
<i>Linepithema</i> sp.5	X		X	<i>Camponotus</i> sp.2		X	X
<i>Linepithema</i> sp.6			X	<i>Camponotus</i> sp.7	X	X	X
<i>Linepithema</i> sp.7			X	<i>Camponotus</i> sp.10	X	X	X
<i>Linepithema</i> sp.8			X	<i>Nylanderia fulva</i> ^G	X	X	X
<i>Linepithema</i> sp.9			X	<i>Nylanderia</i> sp.1	X	X	X
<i>Linepithema</i> sp.10			X	<i>Nylanderia</i> sp.2			X
Dorylinae				Heteroponerinae			
<i>Neivamyrmex alfaroi</i> ^{FS}	X	X		<i>Heteroponera dentinodis</i> ^G		X	
Ectatomminae				<i>Heteroponera dolo</i> ^{FS}	X	X	X
<i>Ectatomma edentatum</i> ^G	X	X	X	Myrmicinae			
<i>Ectatomma permagnum</i> ^{FS}	X	X	X	<i>Acanthognathus rudis</i> ^G	X		X
<i>Ectatomma planidens</i> ^{OH}			X	<i>Acromyrmex niger</i> ^G	X	X	X
<i>Ectatomma</i> sp.3	X	X	X	<i>Acromyrmex rugosus</i> ^G			X
<i>Ectatomma</i> sp.4			X	<i>Acromyrmex subterraneus</i> ^G	X	X	X
<i>Ectatomma</i> sp.5			X	<i>Acromyrmex</i> sp.2 ^G			X
<i>Gnamptogenys acuminata</i> ^{FS}			X	<i>Acromyrmex</i> sp.3 ^G			X
<i>Gnamptogenys horni</i> ^{FS}	X	X	X	<i>Acromyrmex</i> sp.4 ^G			X
<i>Gnamptogenys mina</i> ^{FS}	X	X	X	<i>Acromyrmex</i> sp.5 ^G			X
<i>Gnamptogenys regularis</i> ^{FS}			X	<i>Acromyrmex</i> sp.7 ^G			X
<i>Gnamptogenys striatula</i> ^G	X	X	X	<i>Acromyrmex</i> sp.10 ^G	X	X	
<i>Gnamptogenys</i> sp.3	X	X		<i>Acromyrmex</i> sp.15 ^G			X
<i>Gnamptogenys</i> sp.4	X	X		<i>Acromyrmex</i> sp.21 ^G			X
<i>Gnamptogenys</i> sp.8			X	<i>Apterostigma jubatum</i> ^{FS}	X	X	X
<i>Gnamptogenys</i> sp.9			X	<i>Apterostigma</i> sp.3 ^{FS}	X	X	X
Formicinae				<i>Apterostigma</i> sp.4 ^{FS}	X	X	X
<i>Brachymyrmex depilis</i> ^G		X	X	<i>Apterostigma</i> sp.7 ^{FS}			X
<i>Brachymyrmex</i> sp.1 ^G			X	<i>Atta sexdens</i> ^{OH}	X	X	X
<i>Brachymyrmex</i> sp.2 ^G			X	<i>Basiceros disciger</i> ^{FS}	X		
<i>Brachymyrmex</i> sp.4 ^G			X	<i>Basiceros</i> sp.1 ^{FS}	X	X	X
<i>Brachymyrmex</i> sp.5 ^G			X	<i>Cardiocondyla emeryi</i> ^{OH}	X	X	
<i>Brachymyrmex</i> sp.6 ^G			X	<i>Cephalotes atratus</i> ^{FS}	X	X	X
<i>Brachymyrmex</i> sp.8 ^G			X	<i>Cephalotes ustus</i>		X	

Table S3. Ant species sampled in the years of 1995, 1996 and 2010. The letter G represents the species classified as generalists, letters FS as forest specialist and letters OH those species classified as open-habitat specialist. (Continuation)

Subfamily / species	1995	1996	2010	Subfamily / species	1995	1996	2010
Myrmicinae				Ponerinae			
<i>Crematogaster distans</i> ^G			X	<i>Hypoponera foreli</i> ^G			X
<i>Crematogaster nigropilosa</i> ^G			X	<i>Hypoponera</i> sp.1	X	X	X
<i>Crematogaster ocuta</i> ^G		X		<i>Hypoponera</i> sp.2	X	X	X
<i>Crematogaster</i> sp.1 ^G			X	<i>Hypoponera</i> sp.3	X		X
<i>Crematogaster</i> sp.5 ^G			X	<i>Hypoponera</i> sp.4			X
<i>Eurhopalothrix</i> sp.1 ^{FS}	X			<i>Hypoponera</i> sp.6		X	X
<i>Hylomyrma balzani</i> ^{FS}	X	X	X	<i>Leptogenys</i> sp.1 ^{FS}	X	X	X
<i>Hylomyrma reitteri</i> ^{FS}	X	X	X	<i>Neoponera lenis</i> ^{FS}	X	X	X
<i>Hylomyrma</i> sp.1	X	X	X	<i>Neoponera magnifica</i> ^{FS}	X	X	X
<i>Megalomyrmex drifti</i> ^{FS}		X		<i>Neoponera metanotalis</i> ^{FS}	X	X	X
<i>Megalomyrmex gnomus</i> ^{FS}	X			<i>Neoponera venusta</i> ^{FS}			X
<i>Megalomyrmex goeldii</i> ^{FS}	X	X	X	<i>Neoponera</i> sp.4		X	X
<i>Megalomyrmex iheringi</i> ^{FS}	X	X	X	<i>Neoponera</i> sp.6			X
<i>Megalomyrmex incisus</i> ^{FS}	X		X	<i>Neoponera</i> sp.7	X	X	X
<i>Megalomyrmex modestus</i> ^{FS}	X	X		<i>Neoponera</i> sp.8	X		
<i>Megalomyrmex pusillus</i> ^{FS}	X	X		<i>Odontomachus chelifer</i> ^G	X	X	X
<i>Megalomyrmex</i> sp.2			X	<i>Odontomachus minutus</i> ^{FS}	X	X	X
<i>Octostruma rugifera</i> ^{FS}	X	X	X	<i>Odontomachus</i> sp.2	X		X
<i>Oxyepoecus plaumanni</i> ^{FS}	X			<i>Pachycondyla harpax</i> ^{FS}	X	X	X
<i>Oxyepoecus reticulatus</i> ^{FS}	X		X	<i>Pachycondyla impressa</i> ^{FS}	X	X	
<i>Procryptocerus convergens</i> ^{FS}	X			<i>Pachycondyla striata</i> ^{FS}	X	X	X
<i>Procryptocerus marginatus</i> ^{FS}	X	X	X	Pseudomyrmicinae			
<i>Procryptocerus</i> sp.2			X	<i>Pseudomyrmex tenuis</i> ^G	X		X
<i>Rogeria ciliosa</i> ^{FS}		X		<i>Pseudomyrmex</i> sp.1	X	X	X
<i>Rogeria</i> sp.1	X	X	X	<i>Pseudomyrmex</i> sp.2	X	X	X
<i>Rogeria</i> sp.2		X		<i>Pseudomyrmex</i> sp.3			X
<i>Strumigenys apreciatta</i> ^{FS}	X	X					
<i>Trachymyrmex aspersus</i> ^G	X	X					
<i>Trachymyrmex oetkeri</i> ^{FS}			X				
<i>Trachymyrmex</i> sp.1	X	X	X				
<i>Trachymyrmex</i> sp.2	X	X	X				
<i>Trachymyrmex</i> sp.4			X				
<i>Trachymyrmex</i> sp.5			X				
<i>Trachymyrmex</i> sp.6			X				
<i>Trachymyrmex</i> sp.7			X				
<i>Trachymyrmex</i> sp.8			X				