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Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest

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Abstract Ants are a dominant faunal group in tropical forests, but their responses to human disturbances remain poorly investigated. Here we examine the relative effects of habitat fragmentation (fragment size and amount of forest cover retained in the surrounding landscape) and habitat structure (tree density and richness) on ant species and functional composition in the Atlantic forest of northeast Brazil. Our study was carried out in 19 fragments ranging in size from 10 to 3,500 ha. We recorded 146 ant species from 41 genera. Fragment size and tree density were the most important variables predicting species richness and functional diversity. Additionally, fragment area and tree density also explained the richness of a range of global functional groups (Cryptic Species, Specialists Predators and Tropical-climate Specialists) and Atlantic forest functional groups (Cryptic Predators, Cryptic Omnivores, Epigaeic Predators and Epigaeic Omnivores). Taxonomic composition was influenced by fragment area and tree richness, while functional composition responded to forest cover and tree density. Overall variation of global functional groups was also affected by tree richness. Our results suggest that specialist ants (especially cryptic species, specialist predators and climate specialists) are particularly sensitive to forest fragmentation. Such functional groups would make useful indicators of ant responses to forest fragmentation.

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Introduction

Extensive land clearing remains a major threat to biodiversity globally, and typically results in the transformation of original habitat into small and isolated fragments surrounded by an often inhospitable matrix (Saunders et al. 1991). Habitat fragments experience a wide range of threatening processes, relating both directly to fragmentation (including small size and isolation) and to reduced habitat quality through increased disturbance, human exploitation, and invasion by exotic species (Cochrane and Laurance 2002; Tabarelli et al. 2004). These threatening processes operate simultaneously and synergistically (Tabarelli et al. 2004).

Habitat fragmentation not only influences species richness, but can result in persistent changes in ecological function (Laurance et al. 2006). For example, forest fragments not just have a reduced number of tree species (Oliveira et al. 2004; Santos et al. 2008), but have disproportionately fewer canopy and emergent trees (Laurance et al. 2000), shade-tolerant, edge-sensitive (Oliveira et al. 2004; Laurance et al. 2006; Santos et al. 2008) taxa, species pollinated by vertebrates (Lopes et al. 2009), and large-seeded trees dispersed by medium to large-bodied frugivores (Melo et al. 2006). Fragmentation can similarly result in important functional changes in vertebrate assemblages (Peres 2001; Becker et al. 2007). The effects of fragmentation on the functional composition of invertebrates, however, have been poorly studied, despite them mediating many key ecological processes such as nutrient recycling, herbivory, pollination and seed dispersal (e.g. Didham et al. 1996; Wirth et al. 2008).

Ants are a dominant faunal group in most terrestrial ecosystems and mediate many key ecological processes (Folgarait 1998). They are sensitive to a range of threatening processes, such as logging (Vasconcelos et al. 2000), fire (Andersen et al. 2006), mining (Majer et al. 1984) and agriculture (Silva et al. 2009), and are considered useful indicators of broader ecological change (e.g. Andersen and Majer 2004). There have been relatively few studies of the effects of fragmentation on ant species and functional diversity in tropical forests. Fragment size has been shown to have an important effect on ant species richness in both mesic and dry tropical forests (e.g. Brühl et al. 2003; Vasconcelos et al. 2006; Debuse et al. 2007). Highly specialised functional groups, such as army ants, are particularly sensitive to small fragment size (Petters et al. 2011). Ant assemblages are also influenced by edge effects (Carvalho and Vasconcelos 1999); for example, the abundance of leaf-cutting ants is strongly promoted by forest edges (Wirth et al. 2007; Dohm et al. 2011). As previous studies have addressed the response of particular ant-community attributes to particular environmental variables we still lack a more general view about ant response to forest fragmentation (but see Gomes et al. 2010).

Here we investigate how ant assemblages respond to fragment and landscape metrics and habitat structure in an aging and hyper-fragmented sector of the Brazilian Atlantic forest. More specifically, we sought to determine whether ant richness and species composition of both whole assemblage and functional groups are influenced by fragment area, isolation (amount of forest cover retained in the surrounding landscape), tree density and tree species richness. We predict that smaller and more isolated fragments, which tend to have lower tree density and species richness, support a lower abundance of specialised

functional groups. We use our results to identify particular functional groups for ongoing monitoring of biotic responses to forest conversion in human-modified landscapes.

Materials and methods

Study site

The study was carried out at Usina Serra Grande (Fig. 1), a large (667 km^2) sugar-cane company estate in the Alagoas State, northeastern Brazil (8°30′S, 35°52′W). The site contains 109 forest fragments (range in size: 1.67–3,500 ha), which represent ca. 9 % of its original Atlantic forest cover, belonging to the Pernambuco Center of Endemism (Santos et al. 2007). Although aging and hyper-fragmented, the landscape of Usina Serra Grande includes the Coimbra forest—the largest (3,500 ha) and best-preserved patch of Atlantic forest in northeastern Brazil (Pôrto et al. 2006). The forest remnants of Usina Serra Grande are situated on a low altitude plateau (300–400 m above sea level) covered by two similar classes of dystrophic and clay-laden soils: yellow–red latosol and yellow–red podzol (IBGE 1985). Annual rainfall is ∼2,000 mm, with a 3-month dry season (<60 mm per month) from November to January, and the natural vegetation is lower montane rain forest (Veloso et al. 1991). The families with the highest richness of trees are Leguminosae, Lauraceae, Sapotaceae, Chrysobalanaceae, Euphorbiaceae and Lecythidaceae (Pôrto et al. 2006). All remnants are embedded in a >60 year-old, homogeneous matrix of sugar-cane fields, with its edge dominated by pioneer species with impoverished shade-tolerant, vertebrate pollinated, and large-seeded vertebrate dispersed trees (Oliveira et al. 2004; Melo et al. 2006; Lopes et al. 2009).

We conducted our surveys in 19 forest fragments, ranging from 10 ha to 3,500 ha in size (Fig. 1). All fragments are located in the hillsides and tops because the more fertile valleys have been used for sugar-cane-plantation since the 19th century (Galindo-Leal and Câmara 2003). We estimated the amount of forest cover retained in the surrounding landscape as a measure of patch isolation (Gorresen and Willig 2004) and therefore availability of source populations. It was defined as the percentage of forest within 1-km of the fragment perimeter. The area of fragments and the amount of forest cover retained in the surrounding landscape were quantified using two GIS packages (ArcView 3.2 and Erdas Imagine 8.4) on the basis of: (1) three Landsat and Spot images (years 1989, 1998, 2003) and (2) a set of 160 aerial photos (1:8,000) taken from helicopter overflights commissioned in April 2003 (provided by Conservation International do Brasil). We also measured the vegetation structure at all sites where all trees with diameter at breast high (dbh) >10 cm were surveyed on permanent plots of 0.1 ha (10 × 100 m) established in the centre of fragments between 2002 and 2006. Trees were identified to species level with the help of a local expert and through comparisons with specimens deposited (1) at the UFP Herbarium (vouchers n° 34,445–51,604 for the study site) and (2) at the Plant Ecology Laboratory (Serra Grande tree collections) of the Universidade Federal de Pernambuco, Brazil. A checklist of Serra Grande flora is available in www.cepan.org.br and in Pôrto et al. (2006).

Ant surveys

In each fragment, surveys of leaf-litter ants were conducted along a 290 m transect running through the permanent plot, with 30 1-m^2 leaf litter samples collected at 10 m intervals. Ants were extracted using Berlese funnels active for a 48 h-period and preserved in 70 %
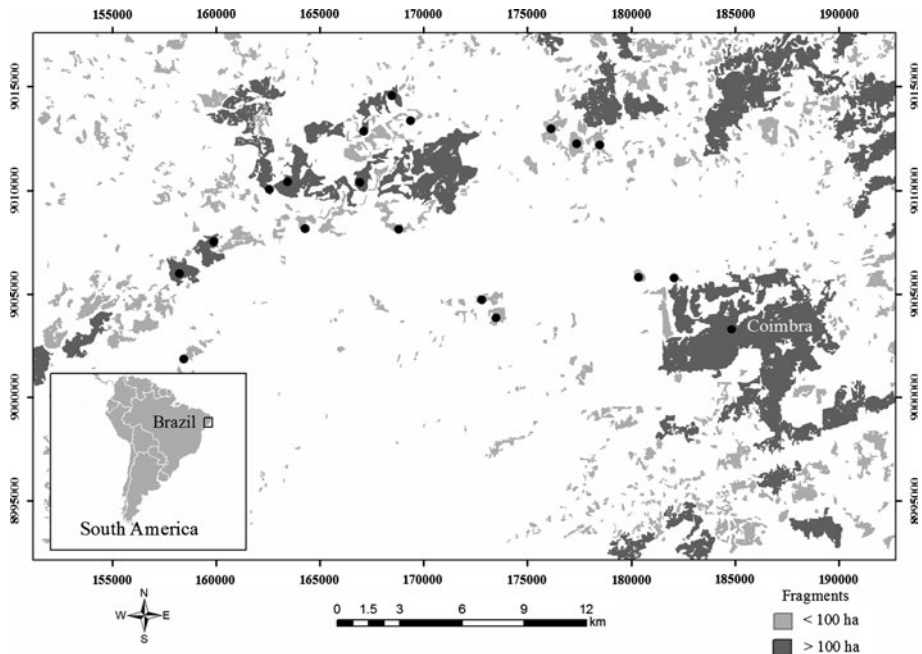
Fig. 1 Map of the Atlantic forest fragments remaining in Usina Serra Grande, Alagoas, northeastern Brazil. Forest fragments sampled ($n = 19$) are represented by *shaded polygons*: small fragments (<100 ha) and large fragments (>100 ha). *Blank spaces* represent uniform matrix of sugar-cane monoculture

alcohol. Sampling was conducted between September 2007 and March 2008. All ants collected were sorted to species level, and identified through comparison with specimens from the collection of the Plant-Animal Laboratory (Ant collection) of the Universidade Federal de Pernambuco, where voucher specimens of all species are deposited. A detailed description of ants from Serra Grande is given in Gomes et al. (2010).

Functional groups

We used two functional group classifications for ants. One of these was Andersen's (1995) widely used functional groups based on global-scale responses of ants to environmental stress and disturbance: Dominant Dolichoderinae; Generalised Myrmicinae; Opportunists; Subordinate Camponotini; Tropical-climate Specialists; Cryptic Species; and Specialist Predators. However, these groups are of limited use for local-scale analysis in regions where one functional group is particularly diverse both taxonomically and ecologically, such as Tropical-climate Specialists in lowland tropical rainforest (Andersen 2010). We therefore created a functional group classification specifically designed for Atlantic forest ant faunas, modified from Delabie et al. (2000). These groups were: (1) Cryptic Predators—small to minute species that nest primarily within the soil, leaf and rotting logs, where they specialise on living arthropods or their eggs; (2) Cryptic Omnivores—small to minute species nesting within the soil, leaf and rotting logs, where they are generalist predators and scavengers; (3) Epigaeic Predators—medium-to large-sized species that forage on the litter surface and are specialist predators of other arthropods; (4) Epigaeic Omnivores—medium-to large-sized species that forage on the litter surface and are

generalist predators and scavengers; (5) Arboreal Dominants—highly active and aggressive species with large colony sizes, nesting in trees; (6) Arboreal Subordinates—other tree-nesting species, (7) Opportunists—unspecialized and poorly competitive, ruderal species, (8) Army Ants—highly aggressive, nomadic species with legionary recruitment, (9) Leaf-cutting Attini—highly active and aggressive, polymorphic, species with large colony sizes that use leaves to cultivate a symbiotic fungus; and (10) Non leaf-cutting Attini—monomorphic, non-aggressive species with small colony sizes that use other organic material to cultivate a symbiotic fungus.

Data analyses

We used additive partitioning of total diversity (expressed by species richness) to identify patterns of beta diversity across fragmented landscape. We calculated the average number of species not present in each site (beta diversity) defined as $\beta = \gamma - \alpha$, where γ is the number of species sampled in the entire landscape (gamma diversity) and α is the average number of species present at a given site (alpha diversity) (Veech et al. 2002). We assessed the completeness of each sample by calculating the number of observed species as a percentage of the total richness, which was estimated based on the average of two abundance-based nonparametric estimators, Chao 1 and Jack 1 (Colwell 2009).

In order to test whether habitat fragmentation and vegetation structure alters ant functional diversity, we used functional evenness as response variable in our models. This index measures both the regularity of spacing between species along a functional trait gradient and evenness in the distribution of abundance across species (Villéger et al. 2008). Multiple linear regressions were used to detect the effects of fragment area, forest cover retained in the surrounding landscape and vegetation structure (i.e. tree density and richness) on the observed and estimated ant species richness, functional diversity and the richness of ant functional groups. The performance of multiple linear regressions was assessed using Akaike's Information Criterion (AIC). We used three measures associated with the AIC to determine the optimal model given the data: the ΔAIC ranks alternative models according to their AIC values; the AIC for each model (rescaled based on the best model) and wAICc—chance for the model to be selected, which varies from 0 to 1 (Burnham and Anderson 1998).

We performed a canonical correspondence analysis (CCA) to investigate whether explanatory variables explained species composition considering the composition of both species and functional groups (i.e. for the Globe and for the Atlantic forest) using frequency data (i.e. number of occurrences in 30 samples per fragment). In the stepwise forward selection we included only those environmental variables that proved significant ($P < 0.05$) in the final ordination. Explanatory variables were tested for independency with Pearson correlation (Appendix Table 4). Data on fragment area and tree richness were $\log_{10}$-transformed prior to analysis in order to meet the assumptions of normality. Normality and homoscedasticity of the residuals were checked with Lilliefors and Levene tests, respectively. All analyses were carried out using R 2.11.1 (R Development Core Team 2011).

Results

In total, we recorded 146 ant species (all native) from 41 genera. The richest genera were *Pheidole* (24 species), *Pachycondyla* (10), and *Hypoponera* and *Solenopsis* (9). Thirty-one

species (21.2 % of the total) were recorded in only one fragment, 22 (15 %) in two and 11 (7.5 %) in three. Species of *Pachycondyla* had particularly restricted distributions, with seven of the ten species occurring at only one site. Only seven species were found in all 19 fragments, including one species of *Nylanderia*, two of *Pheidole*, two of *Solenopsis* (*Diplorhoptrum*), and two of *Wasmannia*. The richest global functional group was Tropical-climate Specialists (43 species), followed by Cryptic Species (32 species) and Generalised Myrmicinae (31). Epigaeic Omnivores was by far the richest Atlantic forest functional group with 45 species, followed by Cryptic Omnivores (20 species) and Cryptic Predators (18; Table 1). Ant species richness varied markedly between fragments, from 29 (fragment area 45.9 ha) to 67 (Coimbra forest, 3500 ha). Almost half (46 %) of recorded species were present in Coimbra forest, with 4 % of all species being unique to this habitat (Table 2). The estimation of the total species number (26.7–46 %) indicated a moderate level of completeness (see Table 2). The gamma diversity of the entire landscape can be expressed in an additive form as: 146 [γ] = 59 [α] + 87 [β]. Beta diversity contributed 4.9 and 4.4 % of the total gamma diversity for small (<100 ha) and large fragments (>100 ha), respectively (Table 2).

The multi-model inference analysis indicated that a combination of fragment area and tree density represented the best-fit model predicting observed ant species richness and functional diversity (Table 3). For estimated ant species richness tree density alone was the most important explanatory variable (Table 3). Additionally, fragment area and tree density explained the richness of a range of global functional groups (Cryptic Species, Specialists Predators and Tropical-climate Specialists) and Atlantic forest functional groups (Cryptic Predators, Cryptic Omnivores, Epigaeic Predators and Epigaeic Omnivores Table 3). For Generalised Myrmicinae, ΔAICc comparisons supported a model with fragment area, tree density, tree richness and forest cover as predictor variables (ΔAICc = 0.04). For All Attini, the model showed forest cover as an important variable (ΔAICc = 0.00). On the other hand, the variance explained was low to both Opportunists and Arboreal Species (see Table 3) suggesting there may be other important predictors.

For the CCA analyses, the first two axes explained ca. 59 % of ant species composition. The most important variables predicting ant composition were fragment area and tree richness (Fig. 2a), explaining as much as all the other factors combined. On the other hand, in terms of functional groups the most important variables predicting ant composition were forest cover (%) and tree density (Fig. 2b, c). Total variation of global functional groups was also affected by tree richness (Fig. 2b). The first two axes of the ordination analyses explained ca. 14 % of the variation in the composition of Atlantic forest functional groups, and ca. 25 % for global functional groups.

Discussion

Our study investigated how patch and landscape metrics and habitat structure influence ant taxonomic and functional composition in a fragmented landscape of Atlantic forest. Our results indicated that ant assemblages exhibit a reduced spatial species turnover, but they respond to fragmentation-related and habitat structure metrics. Precisely, taxonomic composition responded to variation in fragment area and tree density, while tree species richness and forest cover retained in the surrounding landscape affected both ant species richness and the functional composition of ant assemblages inhabiting forest fragments. In addition, ants with specialised habits (especially cryptic species, specialist predators and climate specialists) were particularly sensitive to fragmentation. These findings highlight

Table 1 Numbers of species recorded per ant genus, classified according to a functional group scheme for Atlantic forest ants (modified from Delabie et al. 2000). Classifications according to Andersen's (1995) global functional groups in relation to environmental stress and disturbance are given in parentheses (*CS* Cryptic Species, *DD* Dominant Dolichoderinae, *GM* Generalised Myrmicinae, *OPP* Opportunists, *SC* Subordinate Camponotini, *SP* Specialist Predators, *TCS* Tropical-climate Specialists)

Functional group/Genus	Number of species
1. Cryptic Predators	12
Acanthognathus (CS)	1
Amblyopone (CS)	1
Octostruma (CS)	2
Prionopelta (CS)	1
Probolomyrmex (CS)	1
Pyramica (CS)	1
Strumigenys (CS)	3
Thaumatomyrmex (CS)	1
Typhlomyrmex (CS)	1
2. Cryptic Omnivores	20
Acropyga (CS)	1
Hypoponera (CS)	9
Myrmelachista (CS)	1
Oligomyrmex (CS)	1
Solenopsis (*Diplorhoptrum*) (CS)	8
3. Epigaeic Predators	18
Anochetus (SP)	2
Leptogenys (SP)	1
Odontomachus (SP)	5
Pachycondyla (SP)	10
4. Epigaeic Omnivores	46
Camponotus (part) (SC)	3
Gnamptogenys (TCS)	6
Hylomyrma (TCS)	5
Linepthema (DD)	1
Megalomyrmex (TCS)	4
Pheidole (GM)	24
Solenopsis (*Solenopsis*) (TCS)	1
Wasmannia (TCS)	2
5. Arboreal Dominants	4
Dolichoderus (DD)	4
6. Arboreal Subordinates	14
Camponotus (part) (SC)	3
Cephalotes (TCS)	1
Crematogaster (GM)	7
Pseudomyrmex (TCS)	3
7. Opportunists	10
Brachymyrmex (OPP)	2
Dorymyrmex (OPP)	1
Ectatomma (OPP)	3
Nylanderia (OPP)	4

Table 1 continued

Functional group/Genus	Number of species
8. Army Ants	2
Eciton (TCS)	1
Neivamyrmex (TCS)	1
9. Leaf-cutting Attini	4
Acromyrmex (TCS)	2
Atta (TCS)	2
10. Non Leaf-cutting Attini	16
Apterostgima (TCS)	3
Cyphomyrmex(TCS)	4
Mycocepurus (TCS)	1
Sericomyrmex (TCS)	5
Trachymyrmex (TCS)	3
Total no. species	146

Table 2 Species richness, sample completeness and beta diversity for ants sampled in fragments of Atlantic forest in northeastern Brazil

Fragments	Area (ha)	Species richness	Exclusive (%)[a]	Coverage (%)[b]	Completeness (%)[c]	Beta diversity (%)[d]	FEve[e]
1	10.17	49	0	34.02	33.56	5.1	0.1429
2	22.56	53	0	100	36.3	4.89	0.1400
3	24.93	57	0	36.31	39.04	4.68	0.1273
4	27.52	50	3	32.67	34.24	5.05	0.1429
5	30.55	49	1	31.61	33.56	4.89	0.1277
6	31.74	58	2	36.7	39.72	4.63	0.1250
7	37.03	59	0	38.97	40.41	4.57	0.1250
8	38.17	52	3	48.14	35.61	4.94	0.1429
9	45.92	29	0	19.59	19.86	6.15	0.1852
10	50.05	59	2	41.84	40.41	4.57	0.1250
11	79.64	50	0	40.44	34.24	5.05	0.1522
12	83.37	54	1	55.67	36.98	4.84	0.1346
13	83.63	39	0	28.46	26.71	5.63	0.1429
14	87.94	61	1	38.36	41.78	4.47	0.1207
15	91.16	48	0	41.37	32.87	5.15	0.1556
16	230.52	62	0	48.43	42.46	4.42	0.1167
17	295.76	56	1	68.29	38.35	4.73	0.1296
18	347.93	67	3	50.37	46	4.15	0.1231
Coimbra forest	3500	67	4	41.87	46	4.15	0.1077

[a] Number of species not found elsewhere as a percentage of landscape total

[b] Number of species observed as a percentage of the total estimated richness

[c] Number of species observed as a percentage of landscape total

[d] Beta diversity across the landscape

[e] Functional evenness: multidimensional functional diversity index

Table 3 Results of the best models (ΔAICc < 2) of multiple linear regression analysis for the effects of fragment area ($\log_{10}$-transformed), forest cover retained in the surrounding landscape (buffer of 1,000 m), tree density, and tree richness ($\log_{10}$-transformed) on observed and estimated ant species richness, functional diversity and richness of both global (Andersen 1995) and Atlantic forest functional groups collected in northeastern Brazil. To meet the assumptions of data normality, arboreal dominant and arboreal subordinate ants and Attini leaf-cutting and Attini non leaf-cutting ants were analyzed together. Army ants, Dominant Dolichoderinae and Subordinate Camponotini were not analyzed because there were few records and normality was not meet. Models are ranked from best to worst according to model ΔAICc. *K* the numbers of estimated parameters for each model, *AREA* Fragment area, *FC* forest cover, *TD* tree density, *TR* tree richness

Response variables	Models	ΔAICc	AICc	K	wAICc	R^2
Total observed richness	AREA + TD	0.00	138.21	4	0.42	0.40
	AREA	1.68	139.89	3	0.18	0.22
Total estimated richness[a]	TD	0.00	112.53	3	0.30	0.31
	TD + FC	1.44	113.97	4	0.15	0.38
Functional diversity[b]	AREA + TD	0.00	99.64	4	0.47	0.38
Global functional groups						
Cryptic Species	AREA + TD	0.00	104.53	4	0.39	0.36
	TD	1.33	105.86	3	0.20	0.19
Generalised Myrmicinae	AREA	0.00	97.40	3	0.19	0.20
	AREA + TD + FC + TR	0.04	97.43	6	0.19	0.55
	AREA + TR	0.58	97.68	4	0.14	0.30
Opportunists	TR	67.03	0.00	3	0.26	0.04
	AREA	67.26	0.22	3	0.23	0.03
	FC	67.93	0.90	3	0.17	0.05
Specialist Predators	AREA	60.21	0.00	3	0.44	0.38
	AREA + TD	61.79	1.58	4	0.20	0.43
Tropical-climate Specialists	AREA + TD	87.41	0.00	4	0.46	0.36
	AREA	89.37	1.96	3	0.17	0.16
Atlantic forest functional groups						
Cryptic Predators	AREA	0.00	61.08	3	0.32	0.23
	AREA + TD	1.15	62.23	4	0.18	0.31
	AREA + FC	1.37	62.45	4	0.16	0.30
Cryptic Omnivores	TD	0.00	98.23	3	0.35	0.21
	AREA + TD	0.97	99.20	4	0.22	0.30
Epigaeic Predators	TD	0.00	93.28	3	0.27	0.02
	TD + FC	1.69	94.97	4	0.12	0.04
Epigaeic Omnivores	AREA + TD	0.00	105.52	4	0.34	0.40
	AREA	1.03	106.55	3	0.20	0.24
	AREA + TD + FC + TR	1.28	106.80	6	0.18	0.58
All Arboreal	TR	0.00	79.19	3	0.26	0.05
	AREA	0.87	80.05	3	0.17	0.03
	FC	1.48	80.67	3	0.12	0.00
	TD	1.50	80.69	3	0.12	0.07

Table 3 continued

Response variables	Models	ΔAICc	AICc	K	wAICc	R^2
Opportunists	TR	0.00	67.03	3	0.22	0.04
	AREA	0.22	67.26	3	0.20	0.05
	TD	0.90	67.93	3	0.14	0.03
	FC	0.90	67.93	3	0.14	0.05
All Attini	FC	0.00	94.76	3	0.48	0.22

[a] Estimated species richness based on the average of two abundance-based richness estimators, Chao 1 and Jack 1 (Colwell 2009)

[b] Functional diversity based on functional evenness index that measures both the regularity of spacing between species along a functional trait gradient and evenness in the distribution of abundance across species (Villéger et al. 2008)

(1) ant sensitivity to habit fragmentation (correlated with patch/landscape metrics and habitat structure), and (2) the value of ants as bioindicators in the context of human-modified landscapes.

The combination of fragment area and tree density formed the best-fit model predicting ant richness and functional diversity as well as the richness of several functional groups in both classifications. Area effects on ant communities have been detected in other studies in both tropical and temperate zones (e.g. Brühl et al. 2003; Vasconcelos et al. 2006; Debuse et al. 2007). Although area has been considered a key variable for small fragments (Vasconcelos et al. 2006), even very large fragments can be affected. For example, Brühl et al. (2003) reported that fragments of ca. 4,000 ha support less than half the litter-dwelling ant species found in continuous forest of Malaysia. Our largest fragment was only 3,500 ha, but it is the largest patch of Atlantic forest in northeastern Brazil and so it is not possible to know if its species density is substantially lower than previously occurred in continuous forest. However, it does not seem to be the case given that our next-largest fragment, which was only 350 ha, had identical species richness.

Tree density and richness were used as a proxy for habitat structure and proved to be important explanatory variables affecting ant assemblages. This is consistent with the well-documented effects of vegetation structure on ant assemblages (Abensberg-Traun et al. 1996; Lassau and Hochuli 2004), and may provide one mechanism for how fragmentation affects ant species richness. Forest fragmentation promotes a hyper-proliferation of pioneer tree species over other functional groups (Oliveira et al. 2004; Santos et al. 2008; Lopes et al. 2009), thereby simplifying forest structure (Tabarelli et al. 2010). This simplification may reduce the diversity of nesting sites and availability of resources for ants (McGlynn 2006; Campos et al. 2007).

Fragment isolation as measured by percentage of forest cover in the surrounding landscape had a less important influence on ant assemblages as previously documented (Schoereder et al. 2004; Vasconcelos et al. 2006). Schoereder et al. (2004) found that the rate of extinction has a more important influence on ant species richness and composition in forest fragments than does colonization rate. The dispersal abilities of Atlantic forest ants are largely unknown, but a previous study has indicated that the ponerine *Dinoponera lucida* is unable to disperse from one forest fragment to another, even when fragments are close to each other (Vasconcelos et al. 2006). The extent to which the sugar cane matrix is inhospitable to Atlantic forest ants is unknown, but is likely to vary markedly between

Fig. 2 Biplot of the first and
second axes of the CCA of
Atlantic forest fragments
(*n* = 19) based on ant species
composition (**a**), global
functional groups (**b**) and
Atlantic forest functional groups
(**c**). *Numbers* (*1–19*) and Coimbra
forest are fragments. *Black
circles* represent the species
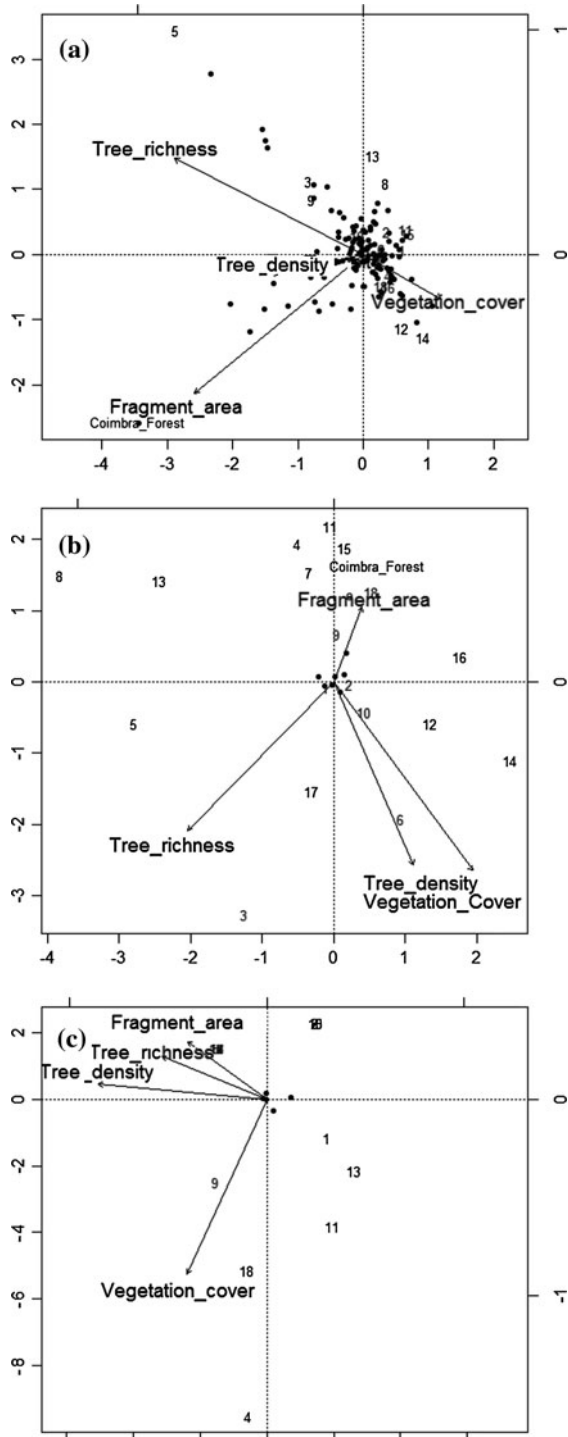
species. In general, ant generalist species have higher colonization rate of smaller fragments than do specialists (Schoereder et al. 2004).

We found that ants with more specialised habits (cryptic species, specialist predators and climate specialists) tended to be most sensitive to forest fragmentation, decreasing in abundance in small fragments. This contrasts with opportunist ants, which were less influenced by explanatory variables. For a wide range of taxa, forest fragmentation often favours common, generalist species over rare and specialised species (Tabarelli et al. 2010; Filgueiras et al. 2011). Such a pattern is true for the response of ant communities to disturbance more generally (Hoffmann and Andersen 2003; Andersen and Majer 2004; Philpott et al. 2010). Highly specialised species are sensitive to disturbance-induced loss of key resources, whereas unspecialised species are buffered by their wide habitat tolerances, flexible nesting requirements and generalised diets (Andersen 1995). Unspecialised ants can also re-colonise disturbed habitat more quickly than specialists (Philpott and Foster 2005; Campos et al. 2007), which can also help them persist in small fragments (Schoereder et al. 2004).

It is possible that we were unable to detect significant effects of fragmentation in some functional groups because of mixed responses within those groups. For example, we considered all attine ants together, but a positive response by leaf-cutting *Atta* (Wirth et al. 2007; Dohm et al. 2011) may have masked negative responses of other more disturbance-sensitive lower attines (Leal and Oliveira 2000). Similarly, Tropical-climate Specialists include taxa that vary widely both taxonomically and ecologically (Andersen 1995), and different taxa might show contrasting responses to fragmentation.

Ants represent a dominant faunal group with an extremely diverse range of life histories in the neotropics, but ant responses to habitat loss and fragmentation, and their persistence in human-modified landscapes, remain poorly understood. By simultaneously examining taxonomic and functional attributes of ant assemblages in an aging and hyper-fragmented landscape, our study was able to extend current knowledge of ant responses to forest fragmentation by demonstrating that ants respond to several fragmentation metrics in addition to habitat structure. This reinforces the notion that ants represent a very useful bioindicator of human disturbance in these landscapes. Moreover, specialised ant species (e.g. cryptic species, specialist predators and climate specialists) emerged as functional groups that are particularly sensitive to forest fragmentation, and therefore might be considered as especially useful bioindicators for monitoring biodiversity persistence in tropical human-modified landscapes.

Appendix

See Table 4.

Table 4 Pearson correlation coefficients (R^2) for fragment and landscape metrics and habitat structure in 19 fragments of the Atlantic forest pertaining to Usina Serra Grande, Alagoas, northeastern Brazil

	Fragment area ($\log_{10}$ ha)	Forest cover	Tree density
Forest cover	-0.07^{ns}	–	
Tree density	-0.02^{ns}	0.11^{ns}	–
Tree richness	0.04^{ns}	-0.06^{ns}	0.16^{ns}

NS no significant

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