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A Comparison of the Leaf-Litter Ant Fauna in a Secondary Atlantic Forest with an Adjacent Pine Plantation in Southeastern Brazil

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Comparação da Fauna de Formigas de Serapilheira entre Área de Floresta Atlântica Secundária e Plantação Adjacente de *Pinus* no Sudeste do Brasil

RESUMO - A influência do reflorestamento com *Pinus* na estrutura da fauna de formigas de serapilheira foi investigada, estudando uma floresta Atlântica secundária inalterada há 30 anos e uma área reflorestada com *Pinus elliottii* no Sudeste do Brasil. Em 50 amostras de 1 m^2 tomadas em cada área, foram coletados 12.826 indivíduos, distribuídos em 95 espécies e 32 gêneros de formigas. Foram identificadas 60 espécies na área reflorestada com *Pinus* e 82 espécies na área de floresta secundária; aproximadamente 50% das espécies foram registradas nas duas áreas. A mediana do número de espécies por amostra foi maior na floresta secundária. Táxons com biologia especializada são responsáveis por grande parte das diferenças de composição de fauna, sendo a área de reflorestamento com *Pinus* mais rica em espécies onívoras e dominantes. Predadoras especializadas registradas na área de *Pinus*, como sete espécies de Dacetini, duas *Basiceros*, duas Attini e duas *Discothyrea*, têm ampla distribuição na Floresta Atlântica. A ordenação das amostras com o escalonamento multidimensional não-métrico (NMDS) indicou grande diferença na similaridade entre as amostras das áreas. Adicionalmente, essa análise sugere maior heterogeneidade na composição das amostras da floresta secundária, identificando dois agrupamentos de espécies, enquanto a área de *Pinus* apresenta um agrupamento apenas. Para investigar quais fatores podem explicar a heterogeneidade observada, testes de co-ocorrência e de autocorrelação espacial foram aplicados entre amostras de cada área. Nossa conclusão é que as diferenças observadas devem estar relacionadas com diferenças na qualidade e distribuição da serapilheira entre as áreas.

PALAVRAS-CHAVE: *Pinus elliottii*, modificação do habitat, riqueza de espécies

ABSTRACT - We investigated the influence of *Pinus* afforestation on the structure of leaf-litter ant communities in the southeastern Brazilian Atlantic Forest, studying an old secondary forest and a nearly 30 year-old never managed *Pinus elliottii* reforested area. A total of 12,826 individual ants distributed among 95 species and 32 genera were obtained from 50 1 m^2 samples/ habitat. Of these, 60 species were recorded in the pine plantation and 82 in the area of Atlantic forest; almost 50% of the species found in the secondary forest area were also present in the pine plantation. The number of species per sample was significantly higher in the secondary forest than in the pine plantation. Forest-adapted taxa are the most responsible for ant species richness differences between areas, and the pine plantation is richer in species classified as soil or litter omnivorous-dominants. The specialized ant predators registered in the pine plantation, as seven Dacetini, two *Basiceros*, two Attini and two *Discothyrea*, belong to widely distributed species. The NMDS (non-metric multidimensional scaling) ordination also suggested strong differences in similarity among samples of the two areas. Furthermore, this analysis indicated higher sample heterogeneity in the secondary forest, with two clusters of species, while in the pine plantation the species belong to a single cluster. We applied the ant mosaic hypothesis to explain the distribution of the leaf-litter fauna and spatial autocorrelation tests among samples. We argue that the results are likely related to differences in quality and distribution of the leaf-litter between the pine plantation and the secondary area.

KEY WORDS: *Pinus elliottii*, habitat modification, species richness

The importance of disturbed areas, such as secondary forests, for conservation purposes has been increasingly recognized by their ability to retain a reasonable proportion of species richness and composition of the original biome (Gascon *et al* 1999, Driscoll & Weir 2003, Dunn 2004). Recent scientific, governmental, and public interest in the use and maintenance of the biological diversity globally has stressed the need of comparative inventory efforts of different organisms in native, disturbed and man-made forests around the world to help devise sound sustainable management programs (Bestelmeyer & Wiens 2001, Mittermeier *et al* 2003, Philpott *et al* 2006).

Our previous studies aimed to evaluate patterns of litter-ant diversity along the Brazilian Atlantic Forest, focusing on species richness, composition and guild structure of the leaf-litter ant fauna in pristine Atlantic Forest areas (Brandão *et al* 2005). Now we try to explore what happens with the leaf-litter ant fauna when a secondary Atlantic forest area is replaced by a pine plantation, examining and recording the effects of forest modification on these communities in modified Brazilian Atlantic Forest landscape.

Brazil has introduced massive plantations of exotic and fast-growing tree species, such as *Eucalyptus* spp. and *Pinus* spp., in order to supply wood for industry and energy production, holding one of the largest planted area in the world (Majer & Recher 1999). In the state of São Paulo, pine and eucalyptus afforestation (158,500 and 611,500 hectares, respectively) cover approximately 3.27% of the land area (Kronka 2005).

Pine was first introduced in southern Brazil during the 1950s as a forestry experiment; from 1966 on with the promulgation of fiscal incentive laws, large areas of pine afforestation were established for the production of paper and cellulose. *Pinus elliottii* has great invasive capacity, and has been introduced even in conservation areas (Bechara 2003), causing environmental problems.

Afforestation does not require annual or constant tillage and cultivation, and it is normally considered as a system of conservation land use. Nevertheless, the alterations imposed on invertebrate communities through afforestation with fast-growing trees have not been fully described yet (Gunther & New 2003, Sinclair & New 2004, Corley *et al* 2006). This is especially true for areas covered by Atlantic rain forest, one of the most threatened tropical ecosystems in the world. The Atlantic Forest originally covered an area of 1.1 million km^2 and is now reduced to only 7.6 percent of its original cover, with most remnants and fragments being small, disturbed in various degrees, and still under severe anthropogenic pressure (Morellato & Haddad 2000, Oliveira-Filho & Fontes 2000). In the state of São Paulo, the natural vegetation cover was estimated in 13.9% of the state area, of which 8.4% is formed by Atlantic rain forests remnants (ombrophylous dense forest) (Kronka 2005).

Ants are commonly used as a focal group of insect biodiversity studies (Wolters *et al*. 2006) and environmental monitoring work (Andersen *et al* 2004, Hoffmann & Andersen 2003, Yves *et al* 2004), because they are ubiquitous, diverse and abundant (Wilson & Hölldobler 2005), sensitive to habitat changes (Andersen *et al* 2002), have a straightforward taxonomy (Agosti *et al* 2000), and because of the general ease with which they can be studied (Agosti *et al* 2000, Philpott & Armbrecht 2006).

This study describes the results of an analysis of the leaf-litter ant fauna found in an area reforested with *Pinus elliottii* in relation to an adjacent relatively old undisturbed secondary Atlantic Forest, both localized in southeastern Brazil. Our main goal was to assess how much of ant diversity is lost with habitat modification and to describe which guilds are more susceptible to man-made disturbance and their relative importance in maintaining biodiversity.

Material and Methods

Study site. Research was carried out during the rainy season in Salesópolis county, in the Serra do Mar, state of São Paulo, Brazil, representative of the southern section of Brazilian Atlantic rainforest. The mean annual rainfall in Salesópolis is *circa* 2000 mm. Ants were collected in two adjacent areas of comparable size, of approximately 30 ha: an old secondary forest (23°36’04” S; 45°58’10” W, 812 m above sea level), and an area logged from 1972 to 1973 (23°35’57” S; 45°58’07” W, 783 m above sea level) and now covered by *P. elliottii* (henceforth pine plantation). In the latter, the ground is permanently shaded and lacks shrub layers, and the litter is composed of a dense coverage of pine needles, with homogeneous distribution and approximately 30 cm of deep along the transect sampled.

The old secondary forest is located about 1 km away from the pine plantation, and is characterized by a canopy between 15 m to 20 m in height, a dense cover of young shrubs and trees in the understorey, and a well-developed leaf litter. The secondary forest has the same age of the pine plantation and was formed after timber extraction. Tree species richness in secondary forest is higher than in the pine plantation.

We took measures of litter depth for 50 leaf-litter samples collected in a near placed transect in this same secondary area, at the center of 1m^2 plots. Because the transects (the one from where we took litter samples for ant extraction and the one we measured litter depth) established in the secondary area are roughly visually similar in terms of litter distribution, the depth of litter information was used as surrogate for secondary forest litter characteristic. The average litter depth was 3.94 cm (SD = 1.96; median = 4.0; range = 1.0-9.0). We ranked the litter quantity in the secondary area according to four arbitrary classes of amplitude: very shallow (0-2 cm), shallow (2-4 cm), deep (4-6 cm) and very deep (> 6 cm). The most frequent class of litter quantity was deep (40% of samples), followed by very shallow (32%), and shallow (22%); only 6% of samples have litter depth greater than 6 cm.

Ant sampling. At each area, a 1200 m long line transect with 25 points apart 50 m from each other was selected for the ant survey, beginning 200 m from the forest edge. At each point, two samples were collected, 25 m to the left and 25 m to the right of the point. At each of the 50 sample points a 1 m^2 plot was established on the ground. All leaf-litter inside the plot was collected, sifted and put in a bag. The sifted material was brought back to the field-laboratory and its fauna extracted in mini-Winklers for 48h (Fisher 1999, Agosti & Alonso 2000, Bestelmeyer *et al* 2000).

The material was initially identified to genera and then into morphospecies. Identification to species level was carried out by comparison with the Formicidae collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), and the pertinent literature. Classification follows Bolton (2003) and Baroni-Urbani & Andrade (2007). Vouchers were deposited at the Universidade de Mogi das Cruzes (SP) and MZUSP.

Data analysis. In all analyses we treated each sample as a statistical replicate. All samples come from points at least 50 m apart across transects; as the home range of most leaf-litter ant species covers less than few meters, the samples were considered independent unities. Species richness was defined as the number of ant species occurring in each litter sample. The total number of occurrences of each species, in 50 samples, was recorded as absence and presence data.

Species richness and ordination analysis. To estimate the total ant species richness, EstimateS 7.5 (Colwell 2005) was used to compute cumulative species curves of the pooled samples, and the extrapolated incidence was based on Chao 2 calculations, which have performed well for low sample sizes and in moderate degree of patchiness (Chazdon *et al* 1998, Brose 2002). Chao and jackknife estimators usually perform better than other methods (Walther & Moore 2005). All calculations were randomized 100 times.

Free distribution statistical tests were applied to test for significant differences between species richness in the samples (Mann-Whitney test). We used species rank-abundance plots (or Whittaker plots) to compare relative species abundance distributions between the ant communities and non-metric multidimensional scaling (NMDS) to graphically evaluate the similarity between the samples taken from the secondary forest area and the pine plantation.

Dissimilarities among samples were based on the Jaccard index of association, an index widely employed in multivariate analysis of assemblage data based on sound biological reasons (Anderson *et al* 2006, Clarke *et al* 2006). Dissimilarities matrices were calculated with the “vegdist” function, and NMDS with “metaMDS” function from the vegan library version 1.15-1 (Oksanen *et al* 2008), using the statistical software R 2.7.1 (R Development Core Team 2008).

Testing for the ant mosaic of leaf-litter. In order to test whether species clusters revealed with NMDS ordination in the secondary forest leaf-litter resulted from an “ant mosaic”, we applied species co-occurrence analyses using the software EcoSim (Gotelli & Entsminger 2004), which tests for non-random patterns of species co-occurrences from a presence/absence matrix (Gotelli 2000). The analyses were performed separately for each cluster, using the whole matrix of species occurrence or using only the most common species (characterized here as those with more than four occurrences in each cluster). We used the default settings of the program for analyses (C-Score index, fixed columns and rows, and 1000 random matrices; see Ribas & Schoereder 2002).

Testing for spatial autocorrelation. To determine whether the homogeneity of conditions of the understorey leads to higher spatial autocorrelation in pine plantation samples, we conducted tests for spatial autocorrelation within the transects of the pine plantation and secondary forest area. The distance matrices were compared for (a) Bray-Curtis dissimilarities (presence/absence data), and (b) a matrix of the geographic distance (Euclidean, in meters) between pairs of leaf-litter samples. The dissimilarities matrices for each area (pine or secondary forest) were converted to a single vector. The “cor” function from the Base package of R 2.7.1 (R Development Core Team 2008) was used to correlate vectors of the species and distance dissimilarity values. The “boot” function from the Boot library was used to conduct a permutation test for whether the correlation coefficient is different than expected by chance with 999 different permutations of randomized reallocations of distances in the Euclidean distance vector. The Spearman Rank Correlation coefficient provided an estimate of the degree of spatial autocorrelation. Visual interpretation of the standard normal quantile plot and a plot of the distribution of correlation coefficients assessed the assumption of normality of the permuted correlation distribution (see Baker & Barmutta 2006).

Results

Species richness. We collected a total of 12,826 individuals in the summed hundred 1 m^2 of leaf litter samples in both studied communities, which were assigned to 95 species representing 32 genera. Of these, 60 species were found in the pine plantation and 82 in the area of secondary Atlantic Forest. Forty-seven ant species (49.5%) are shared by these two forest types, 13 species (13.5%) were found exclusively in the pine plantation, and 35 species (36.8%) exclusively in the secondary Atlantic Forest (Table 1).

Myrmicinae was the richest subfamily in the two forests, with 50 species in the secondary forest area and 35 in the pine plantation, followed by the Ponerinae, with 15 and 13 species, respectively. In the pine plantation, species with the highest number of occurrences in the 50 samples were *Solenopsis* (*Diplorhoptrum*) sp.1 (43 occurrences), *Basiceros rugiferum* (Mayr) (36), *Hypoponera* sp.1 (35), *Strumigenys crassicornis* Mayr (31) and *Cyphomyrmex* sp.1 (27); whereas in the area of secondary forest, *Strumigenys denticulata* Mayr (47), *Solenopsis* (*Diplorhoptrum*) sp.1 (45), *Pheidole* sp.7 (41), *Solenopsis* sp.4 (37) and *Hypoponera* sp.1 (35) were the most common species. The genera with the greatest richness were *Pheidole*, with 19 species in the secondary forest and 13 in the reforested area, and *Hypoponera*, with 10 and 9, respectively (Table 1).

Visually, the species accumulation individual-based curves for observed and estimated species richness suggest that in both old secondary forest and pine plantation they approximate the level of an asymptote (Fig 1), indicating that the sample size was sufficiently large for richness estimation. The Chao 2 estimator calculates an extrapolated maximum of 93 species for the secondary forest and 77 species for the pine plantation. Therefore, the Chao 2 algorithm hypothetically estimates 12 (13%) more ant species than recorded in the

Table 1 Number of occurrences of each ant species collected in 50 1m^2 samples of leaf-litter in the studied areas.

Subfamily/species	Sec. forest area	Pine plantation
Amblyoponinae		
Prionopelta antillana Forel	1	0
Dolichoderinae		
Linepithema humile (Mayr)	2	4
Linepithema sp.2	2	0
Tapinoma melanocephalum (Fabricius)	0	1
Ectatomminae		
Gnamptogenys continua (Mayr)	2	0
G. striatula Mayr	33	23
Formicinae		
Brachymyrmex heeri Forel	18	14
B.incisus Forel	5	10
B. luederwaldti Santschi	1	0
B. pictus Mayr	4	3
Camponotus crassus Mayr	0	1
C. rufipes (Fabricius)	0	5
C. sericeiventris Guérin-Méneville	1	0
Myrmelachista sp.2	1	0
Paratrechina fulva (Mayr)	27	10
Heteroponerinae		
Heteroponera dentinodis (Mayr)	2	0
H. dolo (Roger)	1	0
H. mayri Kempf	5	0
Myrmicinae		
Acanthognathus ocellatus Mayr	4	1
Acromyrmex niger (Smith F.)	2	0
Apterostigma sp.1	0	9
Apterostigma sp.2	11	0
Atta cephalotes (L.)	2	0
Basiceros rugiferum (Mayr)	11	36
B. spectabile (Kempf)	2	0
B. stenognathum (Brown & Kempf)	20	1
Carebara sp.1	10	3
Crematogaster (*Arthocrema*) sp.1	3	1
Crematogaster (*Arthocrema*) sp.2	1	0
Crematogaster (*Neocrema*) *magnifica* Santschi	2	0
Crematogaster sp.3	3	3
Crematogaster sp.5	1	0
Cyphomyrmex sp.1	29	27
Hylomyrma balzani (Emery)	0	2
H. reitteri (Mayr)	19	15
Megalomyrmex iheringi Forel	20	3
Mycetarotes senticosus Kempf	2	0
Oxyepoecus rastratus (Mayr)	1	0
O. myops Albuquerque & Brandão *in litt*	11	0
Pheidole sp.2	1	0
Pheidole sp.4	0	3
Pheidole sp.6	1	0
Pheidole sp.7	41	9
Pheidole sp.9	2	10
Pheidole sp.10	4	0
Pheidole sp.12	4	0
Pheidole sp.13	5	3
Pheidole sp.14	1	0
Pheidole sp.15	9	0
Pheidole sp.16	4	21
Pheidole sp.18	0	1
Pheidole sp.20	3	0
Pheidole sp.22	3	0
Pheidole sp.23	7	0
Pheidole sp.26	2	2
Pheidole sp.28	8	0

Continue

Table 1 Continuation.

Subfamily/species	Sec. forest area	Pine plantation
Pheidole sp.30	1	22
Pheidole sp.31	6	5
Pheidole sp.36	1	4
Pheidole sp.37	0	3
Pheidole sp.38	0	2
Pheidole sp.39	3	1
Procryptocerus pr. *schmalzi*	1	0
Solenopsis saevissima (Smith)	0	5
S. wasmannii Emery	15	4
Solenopsis (*Diplorhoptrum*) sp.1	45	43
Solenopsis sp.4	37	22
Strumigenys crassicornis Mayr	20	31
S. denticulata Mayr	47	24
S. eggersi Emery	1	5
S. elongata Roger	11	5
S. louisianae Roger	1	22
S. schmalzi Emery	9	1
Strumigenys sp.13	1	0
Wasmannia sp.3	18	9
Ponerinae		
Anochetus altisquamis Mayr	1	0
A. neglectus Emery	1	4
Hypoponera sp.1	35	35
Hypoponera sp.2	13	15
Hypoponera sp.3	6	0
Hypoponera sp.4	6	9
Hypoponera sp.5	3	0
Hypoponera sp.6	2	11
Hypoponera sp.7	5	3
Hypoponera sp.8	17	17
Hypoponera sp.9	6	2
Hypoponera sp.11	2	1
Hypoponera sp.15	0	2
Odontomachus affinis Guérin-Méneville	3	1
O. chelifer (Latreille)	0	1
O. meinerti Forel	1	0
Pachycondyla striata Smith	3	1
Proceratiinae		
Discothyrea neotropica Bruch	2	1
D. sexarticulata Borgmeier	14	11
Pseudomyrmecinae		
Pseudomyrmex gracilis (Fabricius)	0	1
Number of occurrences	691	544
Number of species	82	60

secondary forest area, and 17 (28%) for the *Pinus* area. Overall, we captured between 72% and 87% of the estimated species richness for the studied sites, which can be taken as an indication of the completeness of our sampling protocol.

The shape of species rank-abundance curves for the two areas is relatively similar and indicates that they are different in terms of rare species. The number of unique and duplicate species was respectively 1.4 and 2.8 higher in the forest area (Fig 2). Between 5 and 25 (median = 13.5) ant species were found per sample in the secondary forest, and between 3 and 24 (median = 10) in the reforested area. The median number of species per sample (alpha diversity) was significantly different for the two habitats (Mann-Whitney U test = 762; N = 50; $P < 0.05$).

Community composition. The two-dimensional non-metric multidimensional scaling (NMDS) suggests clear differences in similarity between the samples taken in the secondary and the pine plantation forests. Furthermore, two distinct clusters of samples were identified in the secondary forest, which suggests greater heterogeneity of the fauna in the secondary forest when compared to the reforested area (Fig 3). The 25 samples in the cluster 1 have negative values in axis 1 and positive values in axis 2, and include 55 species, while the 23 samples in the cluster 2 have negative values in axis 1 and 2, and include 56 species. There are great differences in species composition and frequency of most abundant species between the two clusters: cluster 1 has thirty-three species with more than four occurrences, while cluster 2 has only ten dominant

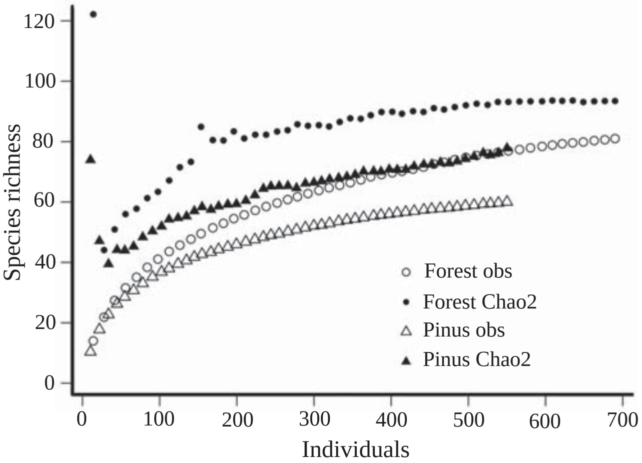

Fig 1 Ant species accumulation curves in two sites (pine plantation and old secondary Atlantic forest area) for observed richness, and for species richness estimator (Chao2) created with EstimateS. Richness was assessed with 50 1m^2 leaf-litter samples. For clarity, standard deviation curves are omitted.

species (Table 2). On average, the dissimilarities values among samples is higher in the pine plantation (average = 0.622; SD = 0.176) than those of the secondary forest area (average = 0.566; SD = 0.112).

Ant mosaic hypothesis of leaf-litter test results. In the analyses of species co-occurrences performed for each species cluster observed in the secondary forest, using either the whole matrix or only the dominant species matrix, clusters could not be distinguished from randomly assembled ones. The observed index of species co-occurrence did not differ from the random pattern (Cluster 1: whole matrix C-score = 11.129, P = 0.585; dominant species matrix C-score = 24,153, P = 0.219; Cluster 2: whole matrix C-score = 5.706, P = 0.403; dominant species matrix C-score = 16.952, P = 0.586). Therefore, there is no evidence that interspecific competition is a factor that may explain the faunistic composition of these clusters.

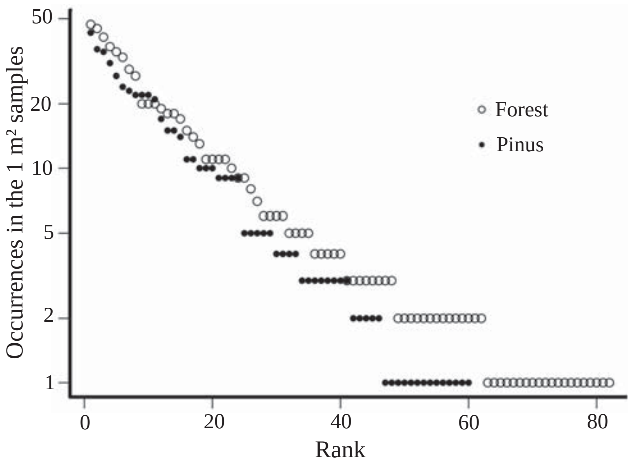

Fig 2 Species rank-abundance relations for the leaf-litter ant species in the two sites studied.

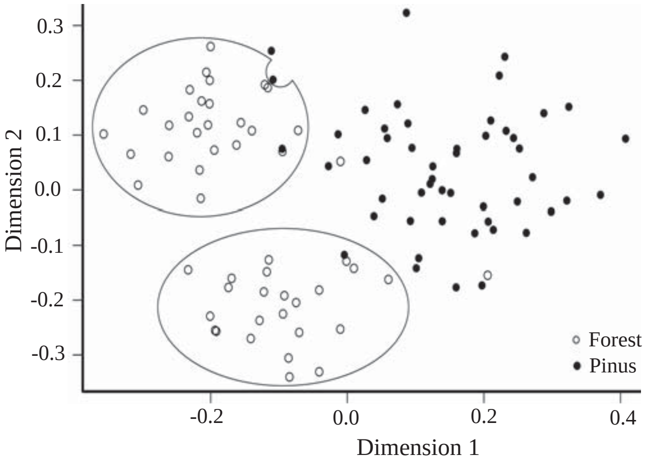

Fig 3 Non-metric Multidimensional Scaling (NMDS) ordination in two dimensions of the leaf-litter ant community inhabiting a secondary forest area and a pine plantation in the southeast Atlantic Forest. Ordination was based on species presence/absence data (Jaccard dissimilarity index). Two samples cluster in the secondary forest were labelled and component samples linked by black lines. Stress in ordination: 6.80%.

Autocorrelation test results. Although weak, there is evidence of spatial correlation within the 1200 m transects for secondary forest area (Bootstraped correlation coefficient *r* = 0.078; P = 0.008) and pine plantation (Bootstraped correlation coefficient *r* = 0.059; P = 0.021). Thus there is evidence of a slightly more similar community composition when plots are in closer proximity than between relatively distant plots.

Discussion

We are aware that the absence of replication areas in this study limits us from drawing strong conclusions about ant species loss and habitat modification in the Brazilian Atlantic Forest. Although factors not evaluated in this study could have been responsible for our results (as for instance, surrounding matrix composition, topography and soil type), we selected two contrasting vegetations that had approximately the same size and the same age since habitat modification. Our descriptive results show some important differences between the leaf-litter ant fauna of the pine plantation and the secondary forest. We describe some factors that could explain the observed differences at the transect scale.

Ant fauna in the secondary forest is more diverse and heterogeneous than in the pine afforestation area. The ant community we found in the secondary forest presents higher species richness and three fold as many exclusive ant species than in the *Pinus* afforestation area; the alpha diversity found in 1 m^2 samples was also significantly higher in the secondary forest than in the reforested area. Furthermore, the secondary forest shows unique and duplicate numbers approximately 1.5 and three orders of magnitude higher (species represented by one or two samples) than the pine plantation.

Table 2 A list of the most common ant species and number of occurrences in each cluster identified by NMDS analysis from secondary Atlantic forest area (see Fig 3).

Species	Cluster	
	1	2
Apterostigma sp.2	10	-
Basiceros rugiferum	8	-
B. stenognathum	13	7
Brachymyrmex heeri	13	5
B. incisus	5	-
Carebara sp.1	6	-
Cyphomyrmex sp.1	13	15
Discothyrea sexarticulata	10	-
Gnamptogenys striatula	15	17
Hylomyrma reitteri	15	-
Hypoponera sp.1	21	14
Hypoponera sp2	13	-
Hypoponera sp.3	5	-
Hypoponera sp.7	5	-
Hypoponera sp.8	13	-
Hypoponera sp.9	5	-
Megalomyrmex iheringi	20	-
Oxyepoecus sp.2	8	-
Paratrechina fulva	23	-
Pheidole sp.7	19	22
Pheidole sp.13	5	-
Pheidole sp.15	9	-
Pheidole sp.23	7	-
Pheidole sp.28	8	-
Pheidole sp.31	6	-
Strumigenys crassicornis	5	14
S. denticulata	26	21
S. elongata	9	-
S. schmalzi	8	-
Solenopsis sp.2	24	20
Solenopsis sp.3	15	-
Solenopsis sp.4	19	18
Wasmannia sp.3	16	-
Number of species	33	10

cluster 1: n = 25 samples; cluster 2: n = 23 samples

The question of why the secondary forest area is richer than the pine plantation in our study could be answered by the fact that the secondary area has higher tree species richness, and possibly greater availability and better quality of nesting sites, food, and favorable abiotic and microclimatic conditions, which may support higher numbers of ant species in litter samples taken in this area. Sites with greater resources heterogeneity could shelter more species (Lassau & Hochuli 2004, Lassau *et al*. 2005) because of a higher number of partitionable niche dimensions (the "microhabitat specialization hypothesis"; Brose 2003, Cramer & Willig 2005). These resources are less accessible in monocultures, especially in areas covered by *Pinus*, by virtue of the allelopathic effects caused by the pine needles that form exclusively the understorey, composed of fatty acids, terpenes and a variety of phenols, preventing the regeneration of native plants. As a result of these allelopathic effects, pine plantations tend to have extremely simplified understorey (Corley *et al* 2006), reduced microhabitat diversity and relatively high environmental uniformity (Sinclair & New 2004).

In general, the plant composition of monoculture understorey is poor and a more homogeneous litter may support fewer species than a heterogeneous one, since homogeneity offers a lower variety of opportunities with respect to resources and microclimatic conditions which affect ant colony survival (Kaspari 1996, Campos *et al* 2003). In addition, the understorey in the studied pine plantation has little shade cover, and species richness of ants generally decreases with decreasing shade (Perfecto *et al* 2003, Philpott & Armbrecht 2006).

Our results are consistent with other studies on the effects of habitat modification on ant communities. Previous studies have described how afforestation methods using a single tree species can have a marked negative effect on ant species richness and composition (Majer & Recher 1999 Watt *et al* 2002); the reduction in ant diversity that occurs when original forests are replaced by monocultures has also been verified in Brazil (Oliveira *et al* 1995, Tavares *et al* 2001, Marinho *et al* 2002). In the pine tree forests of the Patagonian steppe

(Corley *et al* 2006) or south eastern Australia (Sinclair & New 2004), ant abundance within pine plantations is lower and species composition significantly impoverished when compared to more pristine habitats. Ant diversity in tropical forest declines strongly with structural simplification of the vegetation because the regional ant fauna consists largely of forest-habitat specialists (Brühl *et al* 2003).

The distinction between the species composition in the secondary Atlantic Forest area and the reforested area was indicated by two-dimensional NMDS. In addition, the analysis also suggests higher spatial heterogeneity in the species distribution in the leaf-litter of the secondary forest. The present study did not address which variables led to higher heterogeneity in the ant distribution in the Atlantic Forest area in comparison to the pine plantations, but it may suggest interspecific competition or clumped distribution of the leaf-litter ant fauna as the possible causal mechanisms.

The hypothesis of interspecific interaction as a structuring factor for the spatial distribution of species in the secondary forest involves the mosaic concept, defined as the distribution of dominant arboreal ant species in patches, so that their territories do not overlap (Ribas & Schoereder 2002). Also, distribution in mosaics has been described for leaf-litter ant communities resulting from the interactions of two groups of ants, one formed by ground-dwelling species with cryptic behavior and which generally interact with each other, and the second group, consisting of a few arboreal species that forage on the floor and interact with the ground ant fauna (Delabie *et al* 2000).

We have tested the application of the mosaic hypothesis in the secondary forest by means of an analysis of species co-occurrence (Ribas & Schoereder 2002). We applied the analyses for each cluster identified in the secondary forest, using the whole matrix of species occurrence and using only the most common species (those with more than four occurrences). In both analyzed clusters and matrix of species occurrence (the entire set of species or only the dominant species), the observed species co-occurrence laid within the 95% limit of frequency distribution of the randomized matrices, suggesting the mosaic hypothesis is not the determinant of ant spatial distribution observed in the leaf-litter of the secondary forest. Therefore, the mosaic hypothesis was rejected by the species co-occurrence analysis.

We can also hypothesize that the cluster observed in the secondary forest can be explained by a clumped distribution of species along the sampled transect. The leaf-litter ant communities in tropical rain forests are characterized by a patchy distribution of colonies, due to both biotic (nest availability, food abundance, food distribution, frequent colony fission, small home ranges) and abiotic constraints (microclimate and disturbance). All these factors may lead to nest aggregations in suitable zones (Soares & Schoereder 2001, Theunis *et al* 2005, McGlynn 2006).

Because there are more litter patches within the forest, we expected a higher heterogeneity in the spatial structure of the leaf-litter ant fauna in secondary forest in comparison to pine plantation. In contrast, the conditions of the understorey in pine plantations could have a homogenization effect on the leaf-litter ant fauna, resulting thus in increased taxonomic similarity among samples across the pine plantation (Olden 2006). However, on average, the dissimilarities values among samples in the secondary forest are higher than the pine plantation values. Further, the autocorrelation analysis showed that there is a very weak spatial correlation at the scale of our 1200 m transects and that it is unlikely to bias the interpretation of dissimilarities between the pine plantation and the secondary forest area.

Ultimately, whilst we can not confirm what determined the species clusters in the secondary forest, we can not exclude that stochastic processes, such as the random placement of individuals, could produce the observed patterns of species distributions (Higgins *et al* 2006).

Which leaf-litter ant species are excluded with pine afforestation? A common effect of habitat modification on the ant fauna is a change in abundance and species richness across functional groups (Bestelmeyer & Wiens 1996). The pine plantation is richer in species classified as soil or litter omnivorous-dominants that also forage in the vegetation (Delabie *et al* 2000), such as *Brachymyrmex*, *Camponotus* and *Solenopsis*. These species are in general opportunist taxa that indicate lower-quality or disturbed environments for ants (Andersen 1997). The Atlantic forest area, on the other hand, is richer in litter species that are classified as omnivores and scavengers (*Pheidole*) and litter generalist predators (*Heteroponera*, *Hypoponera* and *Gnamptogenys*).

Some cryptic foraging species were also found in the leaf-litter of the pine plantation, including two species of Basicerotini (*B. rugiferum* and *B. stenognathum*) and seven species of Dacetini (*A. ocellatus* and *Strumigenys* spp.), generally considered to be specialized predators (Delabie *et al* 2000), and two egg-predators of spiders (*D. neotropica* and *D. sexarticulata*) (Brown 2000). However, most of these species have broad distribution ranges and are frequently found elsewhere. We termed them as “resilient specialized predators”.

Seemingly, species of *Heteroponera* and many species of *Pheidole* were excluded by *Pinus* afforestation. *Heteroponera* nests in small trunks and fallen branches (Brown 1958), not found in areas planted with *Pinus*; therefore, *Heteroponera* species have been excluded from *Pinus* afforestation by relatively low availability of nest sites. Limitation of nesting resources for leaf-litter and twig-nesting ants has been show as a diversity loss mechanism in agroecosystems (Armbrecht *et al* 2004, 2006, Philpott & Foster 2005). *Pheidole* are primarily generalist scavengers, but include also predator and granivore species. It is the dominant ant taxon of the New World ground assemblages and has been highlighted as an ideal focal group for the assessment of local ant biodiversity (Wilson 2003). The strong negative responses of *Pheidole* species to forest modification indicates that the genus should be also evaluated as a surrogate for assessment of ant community responses to habitat modification, in the context of simplifying the protocol in studies on ecological change associated with human land-use (Andersen *et al* 2002).

Some rare forest species (probably species with low densities at the forest site), as *A. altisquamis*, *B. spectabile*, *P. antillana*, two species of *Hypoponera*, one species of *Gnamptogenys*, and some Attini (fungus-growers) were not registered in the *Pinus* afforestation. These species can represent forest-adapted species that do not tolerate altered microclimate resulting from habitat modification. Therefore, many of the ecologically more specialized ants are eliminated locally by the processes of forest clearing and plantation establishment, leaving a more generalist set which is sufficiently tolerant to persist in the altered plantation conditions (Sinclair & New 2004).

The ant community of pine plantation is not a subset of the one collected in adjacent old secondary Atlantic forest. There are thirteen ant species in pine plantation not present in nearby secondary Atlantic forest. However, most of the taxa exclusively found in the pine plantation are omnivorous, opportunist (such as those of *Camponotus*, *Pheidole*, *Solenopsis* and *Tapinoma*) and present in relatively low frequencies in samples (mainly uniques and duplicates). It is possible that these species belong to a set of ant species characteristic of more open areas that invaded the pine plantation. We termed them as "opportunist edge species".

Although we still have not compared the ant litter-diversity between primary and secondary areas of Atlantic forest, studies in other regions (e.g., Amazonia) suggest that the major changes occur in species richness, composition and population density, rather than in guild losses (Vasconcelos 1999, Vasconcelos *et al* 2000, Azevedo-Ramos *et al* 2006). In this case, the secondary forest is likely to conserve many ecological processes as well as species (Dunn 2004) of the pristine situation. In contrast, the monoculture nature of the pine plantations reduces microhabitat diversity and increase environmental uniformity, altering the ant assemblages with the elimination of many guilds characteristic of mature forests.

The consequences of *Pinus* afforestation in the Atlantic Forest leaf-litter ant fauna, examined in two adjacent areas in different stages of modification, were profound, and correspond well to results found in previous studies on the effects of the conversion of native forests to more simplified vegetation structures. Our results suggest a loss of ant biodiversity in the leaf-litter following *Pinus* afforestation in areas originally covered by the Atlantic Forest.

The more pristine studied forested area, despite being secondary, yielded a larger number of species and a spatially more heterogeneous fauna than in the reforested area. Differences in ant species richness between samples taken in the two study areas were significant, with the reforested area being the poorer. Furthermore, the secondary forest showed a higher number of exclusive ant species. It is clear that many specialized ants were not able to colonize the pine plantation (or, at least, have not become established there) over periods of more than 30 years from planting, so that changes in ant assemblages appear to be relatively long-lasting.

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