



ORIGINAL
ARTICLE

Long-term effects of forest fragmentation on Amazonian ant communities

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ABSTRACT

Aim To analyse the effects of forest fragmentation on ant communities in an Amazonian landscape that has been fragmented for over a century.

Location The region surrounding the village of Alter do Chão in the Brazilian Amazonian state of Pará (2°30' S, 54°57' W).

Methods Collection of ants and measurements of tree density were performed along transects established in eight sites in continuous forest and in 24 forest fragments surrounded by savanna vegetation. Data on size, perimeter, and degree of isolation (distance to continuous forest and distance to nearest area of forest > 5 ha) of each fragment were obtained from a georeferenced Landsat image of the study area.

Results There were significant differences in species richness and composition between fragments and continuous forest, and these differences were not related to intersite variation in vegetation structure (tree density). Fragments supported fewer ant species per plot, and these species tended to represent a nested subset of those found in continuous forests. Fragments had significantly fewer rare species and fewer ant genera. However, fragments and continuous forest had similar numbers of species that also occur in the savanna matrix (i.e. that are not forest specialists). Multiple linear regression analyses indicated that species richness and composition in the fragments are significantly affected by fragment area, but not by fragment shape and degree of isolation. More species were found in larger fragments.

Main conclusions Forest fragmentation influences the organization of ant communities in Amazonian savanna/forest landscapes. Forest fragments harboured, on average, 85% of the species found in continuous forest. That these fragments, despite their long history of isolation, support a relatively large complement of the species found in continuous forest is surprising, especially given that in some recently fragmented landscapes the proportion of species surviving in the fragments is lower. Differences in inter-fragment distance and type of matrix between Alter do Chão and these other landscapes may be involved. The fact that fragments at Alter do Chão are surrounded by a natural (rather than an anthropogenic) habitat, and that most of them are less than 300 m from another forest area, may have helped to ameliorate the adverse effects of forest fragmentation.

Keywords

Amazon forest, ants, area effects, distance effects, habitat fragmentation, shape effects.

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INTRODUCTION

Deforestation and forest fragmentation have been the leading causes of species losses in recent years (Brooks *et al.*, 2002; Wilson, 2002). Forest fragmentation proceeds as intact forest blocks are subdivided and reduced in size. This also subdivides natural populations, often greatly increasing the rate of local species extinction as a result of reduction of population sizes, reduction of immigration rates, forest edge effects, changes in community structure, and invasion of exotic species (Turner, 1996; Laurance & Vasconcelos, 2004). Despite these factors – and contrary to predictions of the Island Biogeography Theory (MacArthur & Wilson, 1967) – small fragments do not always support fewer species per unit of area than do large fragments or areas of continuous forest. In fact, a relatively recent review of habitat fragmentation experiments indicates a ‘remarkable lack of consistency across studies’ (Debinski & Holt, 2000), and this has been attributed at least in part to the relatively short time-span of the experiments. Studies on fragments that have been isolated for a few decades or more are rare. However, as Turner (1996) points out ‘it is information on the long term viability of fragments, and on the nature of the new equilibrium point that they will reach that will be of greatest value in conservation planning’.

Much of global tropical deforestation occurs in the Brazilian Amazon (Skole & Tucker, 1993), a region that covers an area of *c.* 3.5 million km². Such a vast geographic area is highly variable in terms of geomorphology, climate and vegetation cover (Capobianco *et al.*, 2001). In contrast to other parts of Amazonia, the region at the confluence between the Tapajós and Amazon rivers is characterized by a pronounced dry season and elevated incidence of fires (Capobianco *et al.*, 2001). As a result, most of the region is covered by semi-deciduous forest and patches of savanna that are structurally and floristically similar to the *cerrado* vegetation of Central Brazil (Miranda, 1993). Within this savanna are embedded numerous fragments of forest, locally known as ‘ilhas’ (i.e. islands), that vary in size, shape and degree of isolation.

The origin of the savanna and forest fragments is not clear, given that the whole region was covered by forest about 4000 years ago (Sanaiotti *et al.*, 2002; Irion *et al.*, in press), and that there are no obvious differences in topography or in soil characteristics between the fragments and savanna. Some have argued that Amerindian fires have favoured the establishment of savanna on former forested areas of the Amazon (Serena, 1984). Henry Bates visited Santarém and Alter do Chão in the middle of the nineteenth century (Bates, 1892) and described the occurrence of forest islands isolated by savanna, so it is safe to say that the landscape has been fragmented for at least 150 years and probably for much longer. Regardless of the exact mechanisms involved, the occurrence of a relatively large number of fragments and extensive areas of continuous forest in the Santarém region has allowed us to examine the long-term effects of Amazonian forest fragmentation. Most studies on Amazonian forest fragmentation come from the Biological Dynamics of Forest Fragments Project (BDFFP) in Manaus

(Laurance *et al.*, 2002), or from other recently fragmented areas (e.g. Michalski & Peres, 2005).

We focused our study on ants, as ants are a key group of insects in Amazonian forests and represent over two-thirds of the insect individuals found in the forest canopy (Adis *et al.*, 1984; Wilson, 1987). We compared ant species richness and composition between isolated fragments and sites in continuous forest, and then evaluated the relative importance of fragment area, isolation, and shape as determinants of ant community structure in fragments. Since apparent effects of habitat fragmentation on animal communities may be the result of pre-existing differences in vegetation between fragmented and non-fragmented landscapes (Mac Nally *et al.*, 2000), measurements of vegetation structure (tree density) were performed at all sites. This allowed us to examine the effects of forest fragmentation on ant species richness independently of the possible effects of tree density.

METHODS

The study site is a 16 × 16 km landscape surrounding the village of Alter do Chão, located on the right (eastern) bank of the Tapajós River, 35 km southwest of the city of Santarém, in the Brazilian Amazon (2°30′ S, 54°57′ W; Fig. 1). The mean annual temperature in Santarém is 27.5 °C, and the mean annual precipitation is 1950 mm (Santarém airport records, 1970–1988). There is a distinct dry season between June and November.

We established parallel transects, 50 m distant from each other, in each of eight randomly selected sites in continuous forest, and in 26 sites in 24 forest fragments (Fig. 1). Transects in fragments were perpendicular to the forest edge, running from the edge towards the interior of the fragment. Fragments ranged in size from 2.4 to 361 ha, although only two were larger than 100 ha. Most sample sites had four 250-m-long transects. However, there was not space for four 250-m transects in the seven smallest fragments. In these, we either increased the length of some transects, or included another transect, to complete 1000 m of transect per sample site. For example, the 3.6-ha fragment had two transects of 350 m and one of 300 m. The two largest fragments were sampled at two locations, but for the purposes of data analysis we pooled data for the two sets of four transects in each fragment and used the resulting mean values.

Ant surveys were performed in November 2001 and again in July 2002. Ants were collected along all transects in each site using three complementary methods of collection: sardine baits, manual collection, and the Winkler method (Bestelmeyer *et al.*, 2000). The Winkler method was employed in both years of the study. Manual collections were performed in 2001, and sardine baits were used in 2002. A single measure of species richness was provided for each study site, and this was based on a total of six ant collections in each site: two with the Winkler method, two with baits (one on the ground and one in the lower vegetation), and two manual collections (one on the ground and one in the lower vegetation).

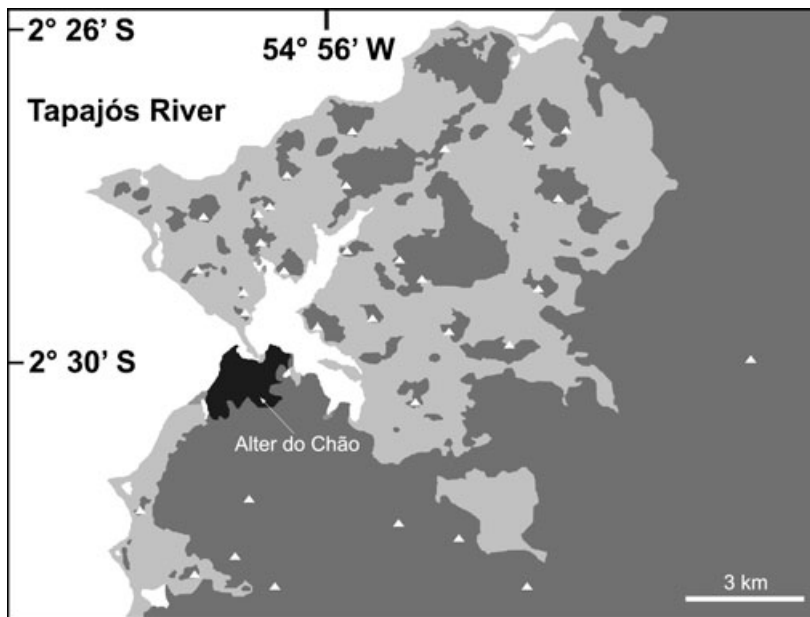


Figure 1 Map of the region surrounding the village of Alter do Chão, in the Brazilian Amazon. Areas in dark grey are covered with forest, while those in light grey are savanna vegetation. White triangles show the locations of sampling sites in continuous forest and in isolated fragments of forest (one site, in continuous forest and located further south, is not shown).

For the Winkler method, small (*c.* 0.25 m² each) leaf-litter samples, spaced 10–20 m from each other, were taken along the whole length of the transects and sieved through a 0.8-cm mesh to make a composite sample of 8 L of sifted litter. Ants were extracted from the sifted litter in a Winkler bag (Bestelmeyer *et al.*, 2000) for 48 h. The manual collection consisted of a visual search and capture of ants foraging on the ground or in the understorey vegetation in each site, for a total of 2 h in each stratum. Two individuals were involved in the manual collections, and each of them spent 1 h searching each stratum along the full 1000 m of transect. For collections using sardine baits, one bait (consisting of a few grams of sardine canned in vegetable oil) was placed every 25 m, alternating between baits on the ground and baits in the vegetation, so that in each sample site there were 20 baits on the ground and 20 in the vegetation. Baits in the vegetation were placed 1–2 m above the soil on a randomly selected branch of the nearest tree or shrub. Baiting was diurnal (sometime between 7:30 and 14:00 h), and all ant species attracted were collected 1 h after setting the baits.

Ants were sorted to morphospecies or species (whenever possible). Voucher specimens were deposited at the Entomological Collection of the National Institute for Amazonian Research (INPA) in Brazil. We classified as rare species those found in less than 10% of the sampling sites (*i.e.* in three or fewer sites). Based on a previous survey of ants in the savanna matrix using sardine baits (Vasconcelos & Vilhena, 2006) and manual collections (H.L. Vasconcelos & J.M.S. Vilhena, unpubl. data), we were able to distinguish between species that were recorded only in forest habitats and those that were found in both forest and savanna.

Data on tree density in each site were collected by counting all trees (diameter at breast height > 1.6 cm) located within

1 m of the transects (total area sampled = 0.2 ha). Data on size, perimeter, and degree of isolation of each fragment were obtained from a georeferenced Landsat TM5 image of the study area. Fragment isolation was calculated both as distance to the nearest portion of forest > 5 ha (hereafter distance to NF) and as distance to continuous forest (hereafter distance to CF). Measurements were made with the Arc-View 3.2 program (ESRI, 1996). Fragment shape was calculated using the formula provided by Ochoa-Gaona *et al.* (2004), which uses data on fragment area and perimeter.

Statistical analyses

We calculated the degree of nestedness of ant assemblages from different sampling sites with the Nestedness Temperature Calculator Program (Atmar & Patterson, 1995). This method estimates the maximum nestedness in a given matrix (of species by sites) by re-arranging ant species and sites in such a way as to minimize unexpected species occurrences (Atmar & Patterson, 1993). The degree of nestedness is calculated by the temperature index (T°) of the matrix, which ranges from 0° for a perfectly nested matrix, to 100° for a random matrix. The significance of the observed temperature index value was determined through a randomization procedure with 1000 iterations (Atmar & Patterson, 1995).

The numbers of species found in the fragments and continuous forest (all sites combined) were compared using sample-based rarefaction curves (Gotelli & Colwell, 2000). These curves were built using the program EstimateS (Colwell, 2000). Differences in the total number of species, in the number of rare species, in the number of species that also occurred in the savanna matrix, and in the number of ant genera between fragments and continuous forest were

compared using *t*-tests. Analysis of covariance was used to determine the effects of tree density and habitat (fragments vs. continuous forest) on ant species richness.

A study in Colombia (Armbrecht & Ulloa-Chacón, 2003) indicated that *Wasmannia auropunctata*, an opportunistic and highly aggressive species of ant, has a negative influence on overall ant species richness in isolated fragments of forest. To test this hypothesis we analysed the correlation between *W. auropunctata* abundance (expressed as the total number of baits explored by this species) and the total number of species recorded in each site.

To evaluate the influence of fragment area, distance to NF, distance to CF, and fragment shape on ant species richness, we used multiple linear regression. Multiple linear regression rather than stepwise or other data mining procedures was chosen because only this method gives valid probability values (Magnusson & Mourão, 2005). The partial regressions resulting from the multiple linear regression procedure are based on residual values after the other independent variables have been taken into account.

Multidimensional scaling (MDS) was employed to ordinate sites by their similarity in ant species composition (Sørensen index). We used MDS (an indirect gradient analysis) because we were interested in determining the major gradient in species composition. MDS has been shown to be one of the most robust methods of summarizing data on ecological communities (Minchin, 1987). Two ordinations were run. The first, with a two-dimensional solution, employed data from all sites, and the resulting ordination scores were used in a multivariate analysis of variance (MANOVA) to evaluate the difference in ant species composition (expressed as ordination scores) between fragments and continuous forest. The second ordination, with a one-dimensional solution, employed data from fragments only. The use of a single ordination axis allowed us to examine the partial effects of fragment area, distance to NF, distance to CF, and fragment shape on ant species composition, by means of multiple linear regression as described above. Data on fragment area and distance to NF were \log_{10} -transformed prior to analysis in order to meet the assumptions of data normality. Ordinations and inferential statistical tests were performed using Systat 10 (SPSS, 2000).

RESULTS

In total, we recorded 268 species/morphospecies of ants from 58 genera (see Appendix S1 in Supplementary Material for a complete list of species), and all of these were native species. Sixty-seven species (25.0% of the total) were recorded in only one site, 27 (10.1%) in two, and 22 (8.2%) in three sites. Only eight species were found in all 34 sampling sites, which include eight sites in continuous forest and 26 sites in 24 forest fragments. These were *Ectatomma tuberculatum*, *Odontomachus haematodus*, *Pheidole fracticeps*, *Pseudomyrmex tenuis*, *Solenopsis (Diphloprotrum)* sp. HLV 6, *Strumigenys denticulata*, *Strumigenys perpava*, and *Wasmannia auropunctata* (Appendix S1). Of the 268 species/morphospecies recorded in the

fragments and continuous forest sites, 48 (17.9% of the total) are also known to inhabit the surrounding savanna patches.

Site-to-site variation in ant species richness was large. The number of species in the richest site (100 species in one site in continuous forest) was 67% larger than in the poorest site (60 species in a fragment of 8.9 ha). The distribution of species among sites was significantly nested ($T^{\circ}_{\text{observed}} = 39.08^{\circ}$, $T^{\circ}_{\text{random}} = 73.22^{\circ}$, $SD = 1.53^{\circ}$, $P < 0.001$), indicating that species present in the poorest sites tend to represent a subset of the species found in the richest sites. Variations in ant species richness were not related to variations in tree density ($F_{1,28} = 1.49$, $P = 0.233$), nor was there a significant interaction between the effects of habitat type (fragments vs. continuous forest) and tree density on ant species richness ($F_{1,28} = 2.74$, $P = 0.109$). Similarly, variations in ant species richness were not related to variations in the abundance of *W. auropunctata* ($r = -0.029$, $P = 0.871$, $n = 34$), but *W. auropunctata* was not very abundant in any site (maximum percentage of baits with *W. auropunctata* in a given site = 17.5%).

On average, there were significantly fewer species in the fragments than in the continuous forest sites ($t = 4.09$, $d.f. = 30$, $P < 0.001$; Fig. 2a). The mean number of species in the fragments (71.4, $SD = 7.4$) was c. 15% less than that found in continuous forest (84.1, $SD = 8.3$). In addition, fragments had significantly fewer rare species ($t = 3.26$, $d.f. = 30$, $P = 0.003$; Fig. 2b) and fewer ant genera ($t = 4.39$, $d.f. = 30$, $P < 0.001$; Fig. 2c) than continuous forest. However, fragments and continuous forest had similar numbers of species that are known to also occur in the savanna matrix ($t = 0.02$, $d.f. = 30$, $P = 0.985$; Fig. 2d).

Differences in species richness between fragments and continuous forest were also detected when combining data from all sites. Sample-based rarefaction curves (Fig. 3) indicate that the total number of species found in continuous forest (195 species) is significantly greater than the number expected to be found in the fragments with the same sampling effort (170.3 ± 5.2 species in 48 samples).

Multiple linear regression ($r^2 = 0.39$, $F_{4,19} = 3.04$, $P = 0.043$) indicated that species richness in the fragments was significantly affected by fragment area (Table 1), with more species being found in larger than in smaller fragments (Fig. 4). The second most important predictor of species richness in the fragments was distance to the nearest forest area (continuous or not). There was a trend, although not statistically significant ($P = 0.145$), towards finding fewer species in the more isolated fragments (standardized regression coefficient = -0.281). Distance to continuous forest and fragment shape contributed very little to the overall regression model (Table 1). Similar results were obtained when data were analysed excluding all species also found in the savanna matrix (48 species). Here again, species richness was significantly affected by fragment area (standardized regression coefficient = 0.537 , $t = 2.78$, $P = 0.012$), but not by distance to NF (regression coefficient = -0.234 , $t = 1.31$, $P = 0.205$), distance to CF (regression coefficient = -0.029 , $t = 0.17$,

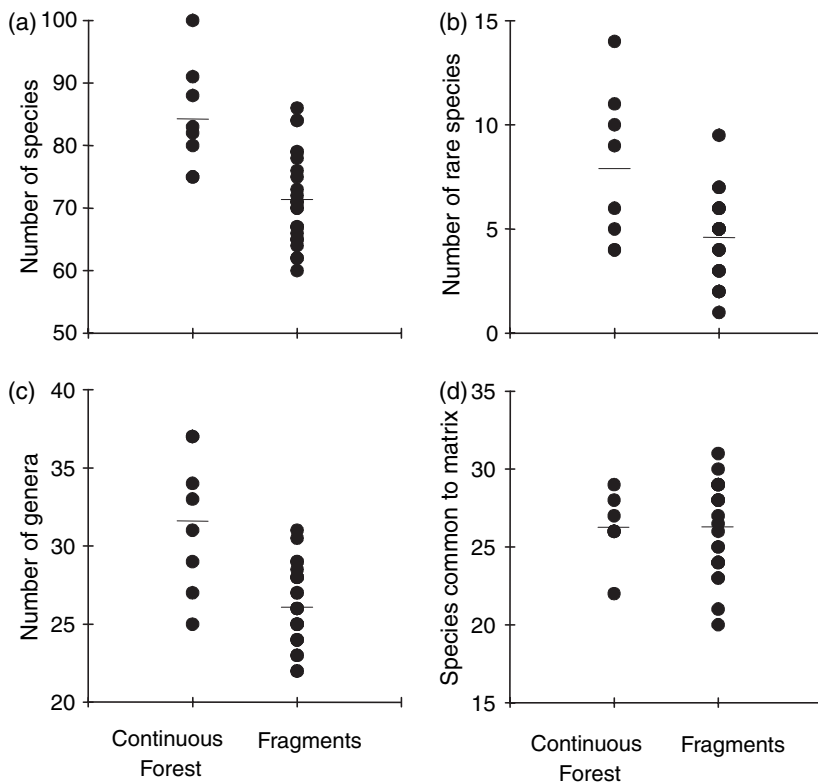


Figure 2 Differences between continuous forest and forest fragments in (a) total number of species, (b) number of rare species (i.e. species recorded in fewer than four forest sites), (c) number of genera, and (d) number of species common to the savanna matrix. Each point represents a different site, while horizontal lines represent mean values.

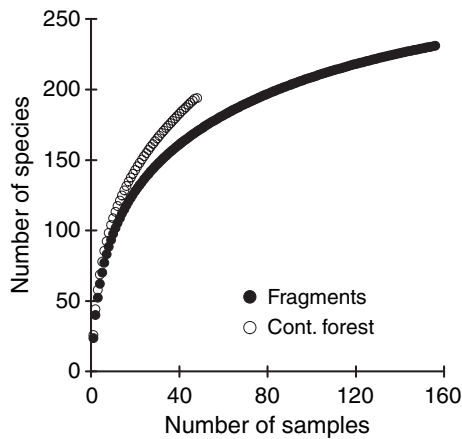


Figure 3 Sample-based rarefaction curves of the numbers of ant species in continuous forest and forest fragments.

$P = 0.869$) or fragment shape (regression coefficient = 0.053, $t = 0.28$, $P = 0.783$).

Ordination of sites according to ant species composition (species presence/absence data) showed a clear separation between fragments and continuous forest sites (MANOVA, Pillai trace = 0.271, $F_{2,29} = 5.38$, $P = 0.010$; Fig. 5). Multiple linear regression analysis revealed that ant species composition in the fragments was significantly influenced by the area of the fragment, whereas fragment shape and distance (to the nearest forest or to continuous forest) had no detectable effect (Table 1). The full regression model explained about 41% of the variance in the ordination scores ($F_{4,19} = 3.24$, $P = 0.035$).

DISCUSSION

Our results strongly suggest that forest fragmentation influences the organization of ant communities in

Dependent variable	Explanatory variable	Regression coefficient	Standardized coefficient	<i>t</i>	<i>P</i>
Species richness	Area	6.506	0.459	2.302	0.033
	Distance to NF	-5.200	-0.281	1.521	0.145
	Distance to CF	-0.001	-0.092	0.513	0.614
	Shape	2.059	0.072	0.371	0.714
Species composition	Area	0.876	0.448	2.275	0.035
	Distance to NF	-0.517	-0.202	1.110	0.281
	Distance to CF	0.000	0.188	1.060	0.303
	Shape	0.574	0.146	0.760	0.457

Table 1 Results of multiple linear regression analysis for the effects of fragment area (log-transformed), distance to nearest forest patch (NF) (log-transformed), distance to continuous forest (CF), and fragment shape on ant species richness and composition (multidimensional scaling scores). $n = 24$ fragments

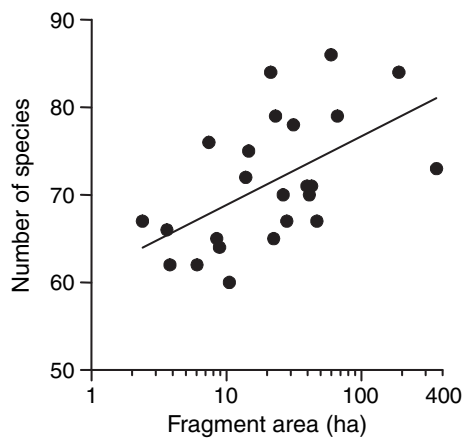


Figure 4 Scatterplot of the relationship between fragment area and ant species richness (species per plot).

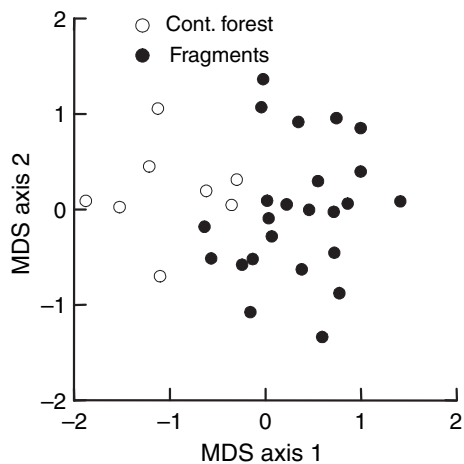


Figure 5 Multidimensional scaling (MDS) ordination in two dimensions of the ant community inhabiting forest fragments or continuous forest sites. Ordination was based on species presence/absence data.

Amazonian savanna/forest landscapes. Fragments supported fewer ant species per unit area, and the species present in the fragments tended to represent a nested subset of those found in sites in continuous forest. Differences in species richness between fragmented and non-fragmented forests were not related to variation in tree density, suggesting that the observed pattern in species richness is a result of the effects of fragmentation *per se* rather than of pre-existing differences in vegetation structure between these sites (cf. Mac Nally *et al.*, 2000). Most of the species that were often found in continuous forest but not in the fragments were rare species, supporting the idea that populations of these species are more likely to decline in fragments than those of abundant species (Davies *et al.*, 2000).

More species were found in larger than in smaller fragments, suggesting that at least part of the difference in species richness between isolated fragments and continuous forest is the result

of area effects. Area effects on ant species richness have been detected in other studies in both tropical and temperate zones (Dean & Bond, 1990; Terayma & Murata, 1990; Brühl *et al.*, 2003). There seems, however, to be a large variation in the magnitude of the effect. For instance, in South Africa, area effects were only apparent for fragments smaller than 20 ha (Dean & Bond, 1990). Similarly, at Alter do Chão, area effects were more pronounced for fragments with less than 15 ha. Only one of the 10 fragments with less than 15 ha had more than 75 ant species, which is the number of species found in the least species-rich site in continuous forest. In contrast, 43% of the remaining 14 fragments (all with > 15 ha) had more than 75 ant species. Brühl *et al.* (2003) have reported that, in Malaysia, even fragments of c. 4000 ha support less than half of the litter-dwelling ant species found in continuous forest. Further studies are needed to elucidate which mechanisms are causing these large discrepancies in the magnitude of area effects on ant communities.

Distance to continuous forest did not have a significant influence on species richness in the fragments. However, there was a trend towards finding more species in fragments near to than far from other forested areas (i.e. near to than far from *any* area of forest > 5 ha, regardless of whether it was a fragment or continuous forest). This suggests that not only continuous forest is a source of potential colonists of the fragments, as expected from the theory of island biogeography (MacArthur & Wilson, 1967), but is also in agreement with a model of metapopulation dynamics, involving nearby fragments. The lack of a significant distance effect for the ant communities inhabiting the fragments at Alter do Chão may reflect the fact that many fragments were relatively close to other areas of forest and that there was little variation in the distances that separate these fragments from other areas of forest (continuous or not). Most (66.7%) of the fragments we studied were less than 300 m from another area of forest and none was more than 1100 m from another area of forest. These distances are probably not large enough to prevent the immigration of most ant species. However, it is possible that even small areas of open savanna represent a barrier to species that reproduce by colony budding and/or that show a strong association with the forest habitat. For these species, recolonization of a given fragment may be difficult, regardless of whether the fragment is close to or distant from another forest area. The dispersal abilities of Amazonian ants are largely unknown, but a study in the Brazilian Atlantic Forest has indicated that one ponerine ant, *Dinoponera lucida*, is unable to disperse from one forest fragment to another, even when fragments are close to each other (J.H.C. Delabie, pers. comm.). Similarly, studies with Amazonian understorey birds have shown that some species typical of the forest interior do not cross forest clearings as small as 30–40 m wide (Laurance *et al.*, 2002).

The shape index we used reflects in part edge effects, as the greater the value of the index, the greater the extent of edges relative to the area of the fragment (McGarigal & Marks, 1994). However, the shape index was not related to ant species richness or composition in the fragments. In contrast, in an

experimentally fragmented landscape near Manaus, ant species composition was more affected by distance to edge than by fragment area (Carvalho & Vasconcelos, 1999). Many edge effects, including effects on forest microclimate (Camargo & Kapos, 1995), on leaf-litter decomposition (Rubinstein & Vasconcelos, 2005), and on communities of dung beetles (Quintero & Roslin, 2005) have been found to be transitory in nature, and this may also apply for ant communities. The study in Manaus was conducted in relatively young forest edges less than 12 years old (Carvalho & Vasconcelos, 1999), while studies in 'old' edges (i.e. sharp edges between grassland and natural forest fragments) in South Africa did not find an edge effect on forest ant assemblages (Kotze & Samways, 1999).

Fragments of Alter do Chão are not only much older than those from Manaus, but are also different in other characteristics such as tree size and architecture. Trees in Alter do Chão are smaller and have much deeper roots, which are necessary to maintain their leaves during the pronounced dry season (Nepstad *et al.*, 1994), than those in Manaus. Therefore, trees in Alter do Chão are likely to be much less susceptible to windthrow, which is the major cause of tree mortality in fragment edges near Manaus (Laurance *et al.*, 1998). The elevated rate of tree mortality near the edges of the Manaus fragments (Laurance *et al.*, 1998) has many cascading effects that are known or are presumed to affect the associated ant communities (Carvalho & Vasconcelos, 1999).

Several studies have indicated that habitat fragments may support fewer ant species because they are more prone to invasion by exotic ant species and/or because fragmentation favours populations of some native, numerically and behaviourally dominant species (Dean & Bond, 1990; Terayma & Murata, 1990; Suarez *et al.*, 1998; Brühl *et al.*, 2003; Schoereder *et al.*, 2004). However, we did not find evidence for this in our study. None of the species we recorded is exotic. Furthermore, there was no significant relationship between the number of ant species and the abundance of *W. auropunctata* (as indexed by its frequency in sardine baits) in the fragments. Native to the Neotropics, *W. auropunctata* is an aggressive species that thrives in disturbed areas throughout the world (McGlynn, 1999). In Colombia, many fragments of dry forest have a depauperated ant fauna because they became dominated by *W. auropunctata* (Armbrecht & Ulloa-Chacón, 2003). *Wasmannia auropunctata* was present in up to 90% of the baits placed in the Colombian fragments (Armbrecht & Ulloa-Chacón, 2003), whereas in Alter do Chão this was a relatively uncommon species. The landscape we studied is still relatively undisturbed, in the sense that fragments are surrounded by natural habitats rather than by agroecosystems, and this may have contributed to the fact that these fragments of forest have not been invaded by exotic species or dominated by opportunistic ant species. It was even the case that many of the species from the savanna matrix were rarely found in the fragments. For example, *Solenopsis substituta*, a numerically dominant species in the savanna (Vasconcelos & Vilhena, 2006), was recorded in only five of the 24 fragments.

Concluding remarks

The fragments of Alter do Chão harbour, on average, 85% of the species found in continuous forest. Given that these fragments have been isolated for a century or more, we suppose that this represents a new equilibrium in species numbers. All but the rarest species were generally found in the fragments. These rare species may have special habitat requirements (e.g. Zimmerman & Bierregaard, 1986) or a patchy distribution, and thus may be absent from the fragments simply as a result of sampling effects (Laurance & Vasconcelos, 2004). Increased demographic stochasticity or the disruption of metapopulation dynamics (Harrison & Bruna, 1999; Schoereder *et al.*, 2004) may also be involved. That the fragments of Alter do Chão, despite their long history of isolation, support a relatively large complement of the species found in continuous forest is surprising, especially given that in some recently fragmented landscapes (e.g. Dean & Bond, 1990; Brühl *et al.*, 2003) the proportion of species surviving in the fragments is less. Differences in inter-fragment distance and type of matrix between Alter do Chão and these other landscapes may be involved. The facts that fragments at Alter do Chão are surrounded by a natural (rather than an anthropogenic) habitat and that most of them are less than 300 m from another forest area may have helped to ameliorate the adverse effects of forest fragmentation. Future studies should analyse the influence of different matrix types on the ant assemblages of forest remnants (cf. Ricketts, 2001). Comparative studies between young and old forest edges may also help to determine how edges of different ages affect ant assemblages.

ACKNOWLEDGEMENTS

We thank Emilio Bruna, Jacques Delabie, Albertina Lima, Dov Sax and three anonymous referees for their helpful comments on earlier versions of this manuscript. J. Delabie is also acknowledged for his continuous help with the identification of Amazonian ants. Ernane H. M. Vieira-Neto helped with the preparation of Fig. 1. Financial support was provided by the Brazilian Council of Research and Scientific Development (CNPq) and by FINEP (PPD no. 64.00.0021.00).

REFERENCES

- Adis, J., Lubin, Y.D. & Montgomery, G.G. (1984) Arthropods from the canopy of inundated and terra-firme forests near Manaus, Brazil, with critical considerations on the pyrethrum-fogging technique. *Studies on Neotropical Fauna and Environment*, **19**, 223–236.
- Armbrecht, I. & Ulloa-Chacón, P. (2003) The little fire ant *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) as a diversity indicator of ants in tropical dry forest fragments of Colombia. *Environmental Ecology*, **32**, 542–547.
- Atmar, W. & Patterson, B.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitats. *Oecologia*, **96**, 373–382.

- Atmar, W. & Patterson, B.D. (1995) *The nestedness temperature calculator*. AICS Res. Inc., New Mexico (<http://aics-research.com/nestedness/tempcalc.html>).
- Bates, H.W. (1892) *A naturalist on the river Amazon*. Murray, London.
- Bestelmeyer, B.T., Agosti, D., Alonso, L.E., Brandão, C.R.F., Brown, W.L., Delabie, J.H.C. & Silvestre, R. (2000) Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. *Standard methods for measuring and monitoring biodiversity* (ed. by D. Agosti, J.D. Majer, L.E. Alonso and T.R. Schultz), pp. 122–144. Smithsonian Institution Press, Washington, DC.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, **16**, 909–923.
- Brühl, C.A., Eltz, T. & Linsenmair, K.E. (2003) Size does matter – effects of tropical rain forest fragmentation on the leaf litter ant community in Sabah, Malaysia. *Biodiversity and Conservation*, **12**, 1371–1389.
- Camargo, J.L.C. & Kapos, V. (1995) Complex edge effects on soil moisture and microclimate in Central Amazonian forest. *Journal of Tropical Ecology*, **11**, 205–221.
- Capobianco, J.P.R., Veríssimo, A., Moreira, A., Sawyer, D., Santos, I. & Pinto, L.P. (eds) (2001) *Biodiversidade na Amazônia Brasileira: avaliação e ações prioritárias para conservação*. Editora Estação Liberdade/Instituto Socioambiental, São Paulo.
- Carvalho, K.S. & Vasconcelos, H.L. (1999) Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. *Biological Conservation*, **91**, 151–158.
- Colwell, R.K. (2000) *EstimateS: Statistical estimation of species richness and shared species from samples*, Version 6. User's guide and application published at: <http://vice-roy.eeb.uconn.edu/estimates>.
- Davies, K.F., Margules, C.R. & Lawrence, J.F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**, 1450–1461.
- Dean, W.R.J. & Bond, W.J. (1990) Evidence for rapid faunal changes on islands in a man-made lake. *Oecologia*, **83**, 388–391.
- Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.
- ESRI (1996) *ArcView GIS*. Environmental Systems Research Institute, Redlands, CA.
- Gotelli, N. & Colwell, R.K. (2000) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Harrison, S. & Bruna, E. (1999) Habitat fragmentation and large-scale conservation: what do we know for sure. *Ecography*, **22**, 225–232.
- Irion, G., Bush, M.B., Nunes de Mello, J.A., Stüben, D., Neumann, T.M.G., de Morais, J.O. & Junk, J.W. (in press) A multiproxy palaeoecological record of Holocene lake sediments from the Rio Tapajós, eastern Amazonia. *Palaeogeography, Palaeoclimatology, Palaeoecology*.
- Kotze, D.J. & Samways, M.J. (1999) Invertebrate conservation at the interface between the grassland matrix and natural forest fragments. *Biodiversity and Conservation*, **8**, 1339–1363.
- Laurance, W.F. & Vasconcelos, H.L. (2004) Ecological effects of habitat fragmentation in the tropics. *Agroforestry and biodiversity conservation in tropical landscapes* (ed. by G. Schroth, G.A.B. Fonseca, C. Harvey, C. Gascon, H.L. Vasconcelos and A.M. Izac), pp. 33–49. Island Press, Washington, DC.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M. & Laurance, S.G. (1998) Rainforest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, **79**, 2032–2040.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments, a 22-year investigation. *Conservation Biology*, **16**, 605–618.
- Mac Nally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation: evaluation of species-specific predictions of the impact of forest fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7–29.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Magnusson, W.E. & Mourão, G. (2005) *Statistics without math*. Sinauer Associates, Inc., Sunderland, MA.
- McGarigal, K. & Marks, B.J. (1994) *FRAGSTATS 2.0, Spatial pattern analysis program for quantifying landscape structure*. Oregon State University, Corvallis, OR.
- McGlynn, T.P. (1999) The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography*, **26**, 535–548.
- Michalski, F. & Peres, C.A. (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, **124**, 383–396.
- Minchin, P.R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, **69**, 89–107.
- Miranda, I.S. (1993) Estrutura do estrato arbóreo do cerrado Amazônico em Alter-do-Chão, Pará. *Revista Brasileira de Botânica*, **16**, 143–150.
- Nepstad, D., Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., Silva, E.D., Stone, T.A., Trumbore, S.E. & Vieira, S. (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, **372**, 666–669.
- Ochoa-Gaona, S., González-Espinosa, M., Meave, J. & Sorani-Dal Bon, V. (2004) Effects of forest fragmentation on the woody flora of the highlands of Chiapas, Mexico. *Biodiversity and Conservation*, **13**, 867–884.
- Quintero, I. & Roslin, T. (2005) Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. *Ecology*, **86**, 3303–3311.

- Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, **158**, 87–99.
- Rubinstein, A. & Vasconcelos, H.L. (2005) Leaf-litter decomposition in Amazonian forest fragments. *Journal of Tropical Ecology*, **21**, 699–702.
- Sanaiotti, T.M., Martinelli, L.A., Victoria, R.L., Trumbore, S.E. & Camargo, P.B. (2002) Past vegetation changes in Amazon savannas determined using carbon isotopes of soil organic matter. *Biotropica*, **34**, 2–16.
- Schoereder, J.H., Sobrinho, T.G., Ribas, C.R. & Campos, R.B.F. (2004) Colonization and extinction of ant communities in a fragmented landscape. *Austral Ecology*, **29**, 391–398.
- Serena, M. (1984) Distribution and habitats of parthenogenetic and sexual *Cnemidophorus lemniscatus* (Sauria: Teiidae) in Surinam. *Copeia*, **1984**, 713–719.
- Skole, D. & Tucker, C. (1993) Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science*, **260**, 1905–1910.
- SPSS (2000) *Systat version 10*. SPSS Inc., San Francisco, CA.
- Suarez, A.V., Bolger, D.T. & Case, J.T. (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology*, **79**, 2041–2056.
- Terayma, M. & Murata, K. (1990) Effects of area and fragmentation of forests for nature conservation: analysis by ant communities. *Bulletin of the Biogeographical Society of Japan*, **45**, 11–18.
- Turner, I.M. (1996) Species loss in fragments of tropical forest: a review of the evidence. *Journal of Applied Ecology*, **33**, 200–209.
- Vasconcelos, H.L. & Vilhena, J.M.S. (2006) Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas. *Biotropica*, **38**, 100–106.
- Wilson, E.O. (1987) The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica*, **19**, 245–251.
- Wilson, E.O. (2002) *The future of life*. Alfred A. Knopf, New York.

- Zimmerman, B.L. & Bierregaard, R.O., (1986) Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. *Journal of Biogeography*, **13**, 133–143.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from <http://www.Blackwell-Synergy.com>:

Appendix S1. List of the ant species collected.

BIOSKETCHES

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Editor: Dov Sax