

# Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants

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**Abstract** The savannas of South America support a relatively diverse ant fauna, but little is known about the factors that influence the structure and dynamics of these assemblages. In 1998 and 2002, we surveyed the ground-dwelling ant fauna and the fauna associated with the woody vegetation (using baits and direct sampling) from an Amazonian savanna. The aim was to evaluate the influence of vegetation structure, disturbance by fire and dominant ants on patterns of ant species richness and composition. Variations in the incidence of fires among our 39 survey plots had no or only limited influence on these patterns. In contrast, spatial variations in tree cover and cover by tall grasses (mostly *Trachypogon plumosus*), significantly affected ant species composition. Part of the variation in species richness among the study plots correlated with variations in the incidence of a dominant species (*Solenopsis substituta*) at baits. Ant species richness and composition also varied through time, possibly as an indirect effect of changes in vegetation cover. In many plots, and independently of disturbance by fire, there was a major increase in cover by tall grasses, which occupied areas formerly devoid of vegetation. Temporal changes in vegetation did not directly explain the observed increase in the number of ant species per plot. However, the incidence of *S. substituta* at baits declined sharply in 2002, especially in plots where changes in vegetation cover were more dramatic, and that decline was correlated with an increase in the number of ground-dwelling species, a greater turnover of bait-recruiting species and the appearance of the little fire ant *Wasmannia auropunctata*. The extent to which these changes in fact resulted from the relaxation of dominance by *S. substituta* is not clear. However, our results strongly suggest that the ant fauna of Amazonian savannas is affected directly and indirectly by the structure of the vegetation.

**Key words:** ant communities, competition, fire ants, fire, vegetation cover.

## INTRODUCTION

The savannas of South America, including those which occur as isolated patches within the Amazon basin, support a relatively diverse ant fauna, with several unique species (Verhaagh & Rosciszewski 1994; Silva *et al.* 2004; Vasconcelos & Vilhena 2006). However, relatively little is known about the factors influencing the structure and dynamics of these insect communities. Vegetation structure is often an important factor affecting ant populations in both temperate and tropical habitats (Perfecto & Snelling 1995; Retana & Cerdá 2000; Ribas *et al.* 2003; Lassau & Hochuli 2004). This is because vegetation is a major regulator of microclimatic conditions which influence ant activity. Furthermore, vegetation can directly and indirectly affect the

availability of food and nesting sites for ants, as well as the competitive interaction between species (Morrison 1988; Perfecto & Snelling 1995; Retana & Cerdá 2000; Gotelli & Ellison 2002; Ribas *et al.* 2003; Lassau & Hochuli 2004). In particular, changes in the abundance of dominant ant species, mediated by changes in vegetation structure, can have major impacts on ant assemblages (e.g. Perfecto & Vandermeer 1996; Puntilla *et al.* 1996). Dominant species can interfere with the foraging of other ant species (Savolainen & Vepsäläinen 1988; Andersen & Patel 1994) and often regulate ant community structure (e.g. Savolainen & Vepsäläinen 1988; Porter & Savignano 1990; Andersen 1992). Therefore, spatial and temporal changes in the abundance of dominant species may lead to concomitant changes in species richness and composition of ant assemblages (Andersen 1992).

Studies with Amazonian savannas indicate that extensive variation in the cover of trees, shrubs and

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grasses can be found within relatively short distances (Magnusson *et al.* 2002). However, the extent to which such variations affect the associated ant fauna is not clear. Furthermore, the increased utilization of these savannas for pasture and crops has resulted in an elevated incidence of fires in recent years (Sanaiotti & Magnusson 1995), but information about ant responses to fire disturbance is lacking. Fire can have a direct effect on ants by destroying their nests (Morais & Benson 1988; Parr *et al.* 2004). However, most commonly, the effect is indirect through the effect of fire on vegetation structure. Therefore, the effect of fire on ants may depend on the magnitude of changes in the structure of the vegetation that was burned (Farji-Brener *et al.* 2002; Parr *et al.* 2004).

The aim of this study was to assess the spatial and temporal variability in ant species richness and composition in an Amazonian savanna and how it is influenced by vegetation structure and disturbance by fire. Furthermore, we evaluated the possible role of a dominant species in structuring the ant assemblages of this savanna.

## METHODS

### Study area

The study site (Fig. 1) is a 16 × 16 km landscape surrounding the village of Alter do Chão. The village is located on the eastern bank of the Tapajós River, 35 km south-west of the city of Santarém, in the Brazilian Amazon (2°30'S, 54°57'W). The mean annual temperature in Santarém is about 27.5°C, with mean annual precipitation of 2215 mm (Santarém airport records, 1984–2002). There is a pronounced dry season between June and November, when monthly

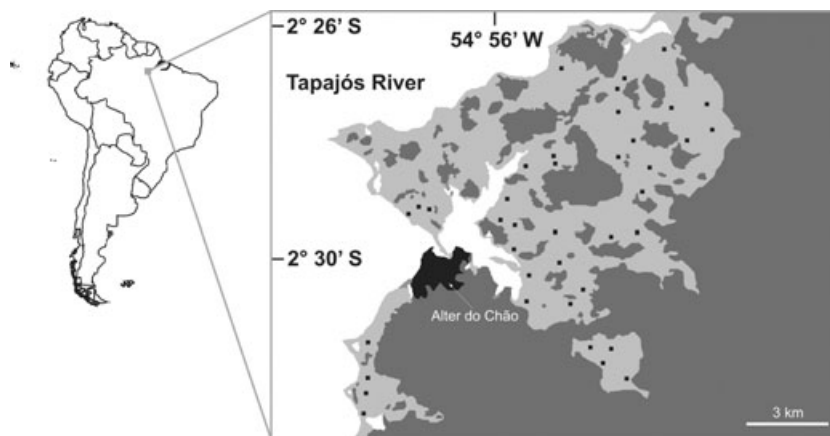
precipitation is less than 65 mm on average (Santarém airport records, 1984–2002). The incidence of fires is high during the dry season, particularly towards the end of the season.

Most of the region is covered by semideciduous forest or by patches of savanna. The latter are floristically similar to the *cerrado* vegetation of Central Brazil, and harbour an assemblage of trees and bushes that form islands in the grassland (Magnusson *et al.* 1999). The savannas in the region were described by the first European naturalists to visit the area more than 150 years ago. These savannas may represent a disclimax in that they may have been created by Amerindian fires (Serena 1984); however, they predate modern land uses.

### Ant sampling

We randomly established 39 permanent plots over the existing savanna patches (Fig. 1). Each plot encompassed an area of 3.75 ha, and each of them had four parallel line transects, 250 m long and separated by 50 m. Ant surveys were undertaken in all plots during the dry season of 1998 (between June and August) and again during the dry season of 2002 (in July and August). The rainfall regime was similar in both years of the study: precipitation totalled 80.6 mm in July and August 1998, and 83.3 mm during the same months in 2002.

Ants were collected along all transects in each plot using two methods: sardine baits and direct hand sampling (Bestelmeyer *et al.* 2000). Baits have been commonly used in studies of ant community structure (Bestelmeyer *et al.* 2000). However, this is a selective method which samples mainly omnivorous species that recruit to protein-rich food sources. Similarly, as



**Fig. 1.** Map of the region surrounding the village of Alter do Chão, in the Brazilian Amazon, showing the location of the 39 sampling plots (represented by black squares). Areas filled with dark grey were covered with forest, while those in light grey have savanna vegetation.

both baiting and direct sampling were performed during day-time, results presented here do not apply for strictly nocturnal species. Time and logistical constraints prevented us from collecting with other, complementary methods. Nevertheless, ant surveys relying on baits and direct search have been shown to produce estimates of species richness which correlate relatively well with those produced by various other methods combined (King & Porter 2005).

We placed one bait (consisting of a few grams of sardine canned in vegetable oil) every 25 m, alternating between baits on the ground and baits in the woody vegetation, so that in each plot there was a total of 20 baits on the ground and 20 in the vegetation. Baits in the vegetation were placed 1–2 m above the soil on an arbitrarily selected branch of the nearest tree or shrub. Baiting was diurnal between 7.30 and 14.00 hours, and all ant species attracted were collected 1 h after setting the baits. Before we removed ants from baits, we estimated visually the abundance of individuals from each species exploiting that bait. Ant abundance on baits was determined in 1998 only and using the following abundance scores (Andersen 1992): 1 = 1 ant; 2 = 2–5 ants; 3 = 6–20 ants; 4 = 21–100 ants; 5 = more than 100 ants. Ant abundance at baits, number of baits exploited and number of baits monopolized were used as criteria to define which species in our study sites were potentially dominants (*cf.* Andersen 1992).

Direct sampling consisted of a visual search and capture of ants foraging on the ground or in the woody vegetation, for a total of 2 h in each stratum in each plot. Two individuals were involved in these collections, and each spent 1 h searching each stratum along the full 1000 m of transect. Ants collected through direct search or on baits were sorted to species or morphospecies. Voucher specimens are deposited at the Entomological Collections of Brazil's National Institute for Amazonian Research and the Federal University of Uberlândia.

### Vegetation cover and incidence of fires

We used the number and extent of burns as a measure of the fire regime in each plot used to survey ants. Estimates of the extent of fire in each plot were made in 1997, after the dry-season fire of that year, and again in 1999, 2000 and 2001. Within each study plot, we noted the presence or absence of recently burned vegetation at 2-m intervals along the same transects in which we undertook the ant surveys. The percentage of the plot area affected by fire in each year was determined by dividing the number of sampling points with burned vegetation by the total number of points checked (500).

Estimates of vegetation cover, made within the same plots and transects as above, were first conducted in the

wet season of 1998. We used the point quadrat method (Bullock 1996) to measure the cover by each of the following vegetation strata: large (>2 m in height) trees, small trees and shrubs (<2 m tall), tall grasses (mostly *Trachypogon plumosus*), short grasses (mostly *Paspalum carinatum*) and bare ground. Points were spaced at 2-m intervals along the transects, giving 500 points per plot. At each point we recorded cover by noting the first type of plant in contact with a 2-mm diameter rod held vertically (for further details on vegetation measurements see Magnusson *et al.* 1999). Vegetation was measured again in 2002, but as differences with the initial measurement were minimal, except for tall grasses and bare ground, only data for these two strata were used in the analyses presented here.

### Data analysis

We evaluated the extensiveness of our sampling protocol by constructing sample-based accumulation curves. For this analysis, plot was our sample unit. The observed number of species was then compared with the expected number of species, as calculated by the first-order Jackknife richness estimator, a non-parametric estimator of species richness that performs relatively well under a wide range of sample sizes (Colwell & Coddington 1994). Sample accumulation curves and estimates of species richness were computed using EstimateS (Colwell 2000).

Differences in the total number of ant species collected per plot between surveys in 1998 and 2002 were evaluated using paired *t*-tests. In addition, we evaluated if eventual temporal differences in plot species richness were related to foraging strata (i.e. ground or vegetation) using repeated measures ANOVA, where number of species per sampling year was the repeated measure and strata the between-subject factor.

To evaluate the possible influence of vegetation cover on spatial and temporal variation in ant species richness we performed Pearson correlation analyses. The number of species per plot in each sampling year was used here as a measure of spatial variability in species richness. As a measure of temporal variability in species richness we calculated, for each plot, the difference in the number of species collected in 2002 and the number collected in 1998. Similarly, differences in plant cover between the final and initial plant surveys were used as a measure of change in vegetation cover through time.

We used correlation analysis instead of multiple regression analysis because many of the vegetation variables measured were strongly correlated to each other. Pearson correlation analysis was also used to evaluate the relationship between fire extent and ant species richness, as well between the incidence of

dominant ants at baits (i.e. number of baits exploited) and ant species richness. Whenever necessary data were arcsine transformed.

A two-dimensional ordination of plots in relation to ant species composition, was carried out with multidimensional scaling using the Bray–Curtis index of dissimilarity. Ordination was undertaken using species presence/absence data (in which case the Bray–Curtis index is equivalent to  $1 -$  the Sørensen similarity index) and also using data on species frequencies at baits. The resulting ordination scores were used in multivariate analysis of covariance (MANCOVA) to test the influence of spatial variation in plant cover, fire disturbance and dominant ants on species composition. A separate test was carried out with each of the independent variables. To evaluate the influence of temporal changes in plant cover on changes in species composition, correlation analyses were undertaken between the difference in plant cover (between final and initial survey) and the difference in species composition (i.e. dissimilarity) in each plot over time. A similar procedure was used to evaluate the influence of fire and dominant ants. Ordination and inferential statistical tests were carried out using Systat 10 (SPSS 2000).

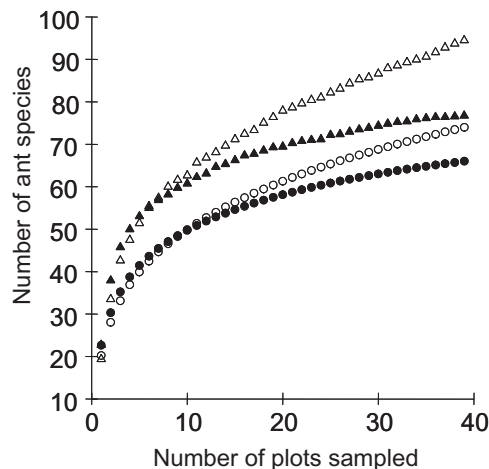
## RESULTS

### Species richness and composition at the landscape level

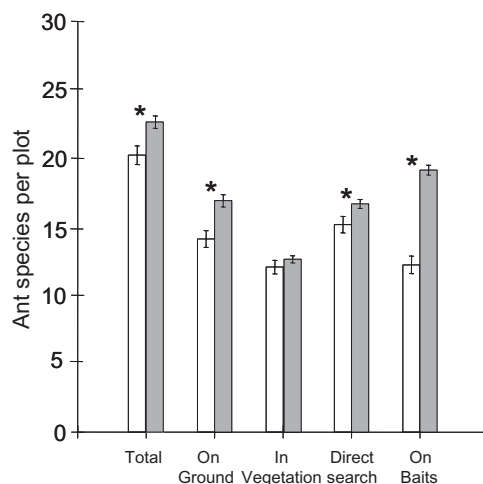
We collected a total of 84 ant species, representing 26 genera (the species list is available at <http://www.ecolosc.org.au/What%20we%20do/Publications/Austral%20Ecology/AE.html>). The total number of species collected in 1998 (74 species) represented 78.3% of the number of species expected to be detected in that year ( $94.5 \pm 6.1$  species; mean  $\pm$  SD based on calculation of the Jackknife first-order richness estimator), while the number collected in 2002 (66 species) represented 86.0% of the number of species expected to be detected ( $76.7 \pm 3.1$  species) (Fig. 2).

The majority of the species found in one sampling year were also found in the other (dissimilarity between sampling years, based on species presence/absence data = 0.20). The exclusive species tended to be relatively rare. Of the 18 species found only in the 1998 survey, 17 were collected in no more than three plots (7.7% of the total), and usually at no more than one bait per plot. The one exception was the fungus-growing ant *Cyphomyrmex rimosus* which was hand collected in 23% of the study plots. Of the 10 species found only in 2002, eight were rare species. However, the other two species, *Wasmannia auropunctata* and *Dolichoderus bispinosus*, were present in 56.4% and 12.8% of the plots surveyed in 2002, respectively.

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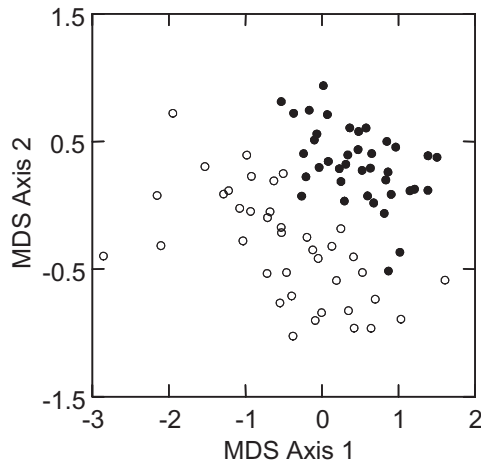
**Fig. 2.** Sample-based accumulation curves of the observed (circles) and estimated ant species richness (triangles) during surveys in 1998 (filled symbols) and 2002 (open symbols).



**Fig. 3.** Total number of species found during surveys in 1998 (open bars) and 2002 (grey bars), the number of species on ground or in the vegetation, and the number of species recorded with each method of collection. Bars represent mean  $\pm$  1 SE per plot ( $n = 39$ ). An asterisk denotes a significant difference between years in mean number of species.

### Species richness and composition at the level of individual plots

The total number of species recorded per plot varied from 11 to 29 in 1998 and from 18 to 29 in 2002. On average, we recorded a higher number of species per plot in 2002 than in 1998 ( $t = 3.07$ , d.f. = 38,  $P = 0.004$ ; Fig. 3). This difference was also detected when we analysed data for each collection method separately. More species were hand collected ( $t = 1.51$ , d.f. = 38,  $P = 0.043$ ), and more species were found on baits ( $t = 10.23$ , d.f. = 38,  $P < 0.001$ ) in 2002 than in



**Fig. 4.** Multidimensional scaling (MDS) ordination of the study plots sampled in 1998 (open symbols) and in 2002 (filled symbols) according to ant species composition. Ordination was based on species presence/absence data.

1998. Inter-survey differences in species numbers, however, were dependent upon strata. There was a significant interaction between the effects of sampling year and stratum on the number of species collected per plot (Repeated measures ANOVA, sampling year  $\times$  stratum,  $F_{1,76} = 6.50$ ,  $P = 0.013$ ). While the number of ant species found in vegetation was similar in both years of this study ( $t = 1.00$ , d.f. = 38,  $P = 0.32$ ), the number of species on ground was significantly greater in 2002 ( $t = 4.17$ , d.f. = 38,  $P < 0.001$ ; Fig. 3).

The composition of ant species varied not only between different study plots (i.e. spatially) but also within the same plot in different sampling years (i.e. temporally). Multidimensional scaling ordination indicated almost complete separation in species composition of plots sampled in 1998 and 2002 (Fig. 4). Dissimilarity values for the same plot in different years ranged from 0.127 to 0.439 (Bray–Curtis Index, mean =  $0.261 \pm 0.067$ ,  $n = 39$ ), when analysis were carried out using species presence/absence data, and from 0.345 to 0.650 (mean =  $0.470 \pm 0.085$ ,  $n = 39$ ) when using data on the frequency of individual species at baits. These results indicate that temporal changes in species composition were variable among our study plots, being greater in some plots than in others. Also, temporal changes in species composition were comparatively greater for data on incidence at baits than for presence/absence data, indicating that species turnover at baits was stronger than overall species turnover.

### Effects of vegetation cover

Plant cover was highly variable among our study plots. During our initial survey, tree cover ranged from 8.4%

to 42.8%, cover by small shrubs and trees from 4.4% to 60.8%, cover by large grasses from 0.4% to 41.4%, cover by small grasses from 2.2% to 41.2%, and the amount of bare ground from 19.9% to 71.6%. However, spatial variation in plant cover explained poorly the observed variation in ant species richness (Table 1). The only exception was tree cover which had a small but significant positive correlation with the number of species per plot in 1998 (Table 1). Similar results were obtained when we analysed ant samples from ground and vegetation separately. In both cases, none of the correlations between species richness and the vegetation variables measured were significant (Pearson correlation;  $P > 0.05$  in all analyses). In contrast, spatial variation in plant cover, particularly in tree cover and cover by tall grasses, significantly affected ant species composition in the study plots, and this pattern was detected in the two sampling years (MANCOVA: tall grass cover in 1998  $F_{2,36} = 5.244$ ,  $P = 0.010$ , tree cover in 1998  $F_{2,36} = 7.79$ ,  $P = 0.002$ ; tall grass cover in 2002  $F_{2,36} = 5.242$ ,  $P = 0.010$ , tree cover in 2002  $F_{2,36} = 6.59$ ,  $P = 0.004$ ) (Table 1).

During the period of this study, tree cover, cover by small trees and shrubs and cover by small grasses, remained virtually unchanged. However, in many plots, and independently of the fire regime, there was a major increase (of up to 50%) in cover by tall grasses, which occupied areas formerly devoid of vegetation. However, neither changes in cover by tall grasses, nor changes in the amount of bare ground between surveys in 1998 and 2002, were significantly correlated with the observed changes in the number of ant species per plot (tall grasses:  $r = 0.131$ ,  $n = 39$ ,  $P = 0.43$ ; bare ground:  $r = -0.002$ ,  $n = 39$ ,  $P = 0.90$ ). The same was true when ant samples from ground and vegetation were analysed separately (Pearson correlation;  $P > 0.05$  in all analyses). Temporal differences in plant cover also did not explain the differences in ant species composition in our survey plots. This was the case both for the analysis using presence/absence data (tall grasses:  $r = 0.078$ ,  $n = 39$ ,  $P = 0.64$ ; bare ground:  $r = -0.118$ ,  $n = 39$ ,  $P = 0.48$ ) as well for the one using data on species frequencies at baits (tall grasses:  $r = -0.039$ ,  $n = 39$ ,  $P = 0.81$ ; bare ground:  $r = -0.031$ ,  $n = 39$ ,  $P = 0.85$ ).

### Disturbance by fire

Neither in 1998 nor in 2002 did we find a significant relationship between the per cent of the plot area burned and the number of ant species per plot (Table 1), and analyses using samples from ground and vegetation separately produced the same qualitative results (Pearson correlation;  $P > 0.05$  in all analyses). Fire had some influence on the observed spatial variation in ant species composition (Table 1), but the overall effect was only significant for the 1998

**Table 1.** Influence of vegetation cover and extent of fires on the spatial variation in ant species richness and composition (multidimensional scaling ordination scores) in an Amazonian savanna. Values represent Pearson correlation coefficients ( $n = 39$  in all cases)

	1998 Survey			2002 Survey		
	Ant species	Ordination axis 1	Ordination axis 2	Ant species	Ordination axis 1	Ordination axis 2
Cover by tall (>2 m) trees	0.319*	-0.526***	0.164	0.172	0.441**	0.271
Cover by small trees and shrubs	0.244	-0.038	-0.193	0.140	0.149	0.185
Cover by tall grasses	-0.228	0.334*	-0.340*	-0.224	0.422**	0.218
Cover by small grasses	0.083	-0.274	-0.063	0.132	0.323*	0.155
Amount of bare ground	-0.107	0.126	0.306	-0.084	0.257	0.162
Extent of fire (previous season)	0.017	0.009	0.392*	-0.158	0.333*	0.029
Extent of fire (previous 3 seasons)	n.d.	n.d.	n.d.	-0.247	0.254	0.015

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . n.d., not determined.

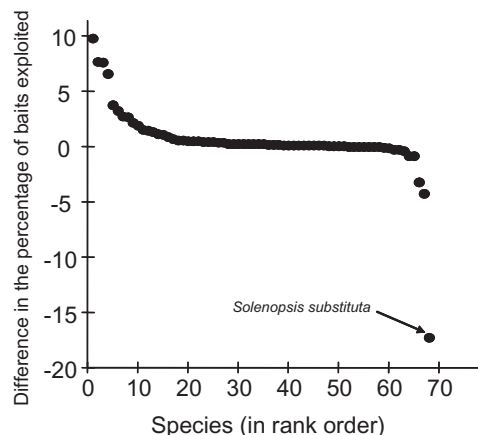
data (MANCOVA: 1998 data  $F_{2,36} = 3.27$ ,  $P = 0.049$ ; 2002 data  $F_{2,36} = 2.27$ ,  $P = 0.118$ ).

Differences in the number of species encountered per plot between surveys in 1998 and 2002 were not significantly related to differences in the fire regime (mean per cent plot area burned between 1999 and 2001;  $r = -0.082$ ,  $n = 39$ ,  $P = 0.62$ ). Finally, fire did not explain the observed temporal differences in species composition in our survey plots (presence/absence data:  $r = -0.107$ ,  $n = 39$ ,  $P = 0.52$ ; data on frequency at baits:  $r = -0.136$ ,  $n = 39$ ,  $P = 0.41$ ).

### Dominance at baits

We recorded 68 ant species on baits. Of these, 73.5% were present at a greater number of baits in 2002 than in 1998, while only 20.5% declined in frequency at baits. However, for most species, the difference in the total number of baits exploited between the two years of this study was minor (Fig. 5). The most notable exception was *Solenopsis substituta* whose frequency at baits declined sharply in 2002; it was found in 41.4% of the 1560 available baits in 2002 but in only 24.1% of the 1560 baits in 1998 (Fig. 5). *Solenopsis substituta* was much more common on baits placed on the ground (88.75% of the total) than in the vegetation (11.25%), and baits with *S. substituta* had more ants per bait than baits with other ant species. The average abundance score for *S. substituta* was 4.4, while for the remaining four most common species at baits in 1998 (*Crematogaster erecta*, *Crematogaster* sp. 19, *Ectatomma brunneum* and *Pheidole* sp. 6) this score ranged from 2 to 3.6 (<http://www.ecolsoc.org.au/What%20we%20do/Publications/Austral%20Ecology/AE.html>).

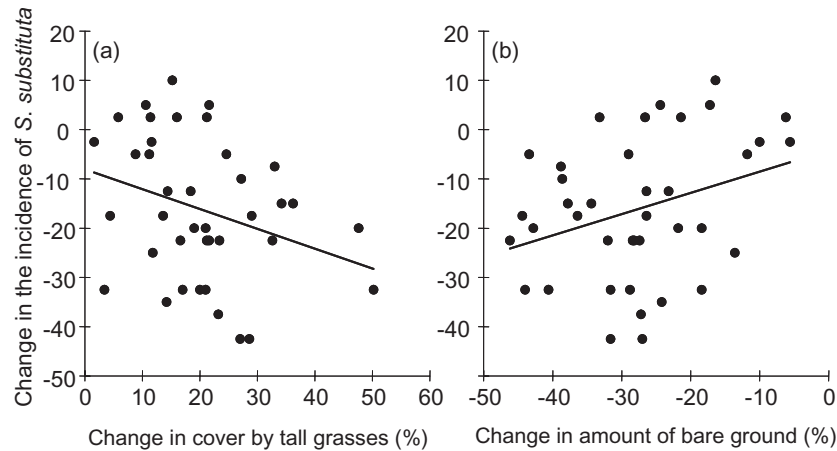
We found a small but significant correlation between the temporal change in the incidence of *S. substituta* at baits and the temporal change in cover of tall grasses ( $r = -0.315$ ,  $n = 39$ ,  $P = 0.05$ ) and in



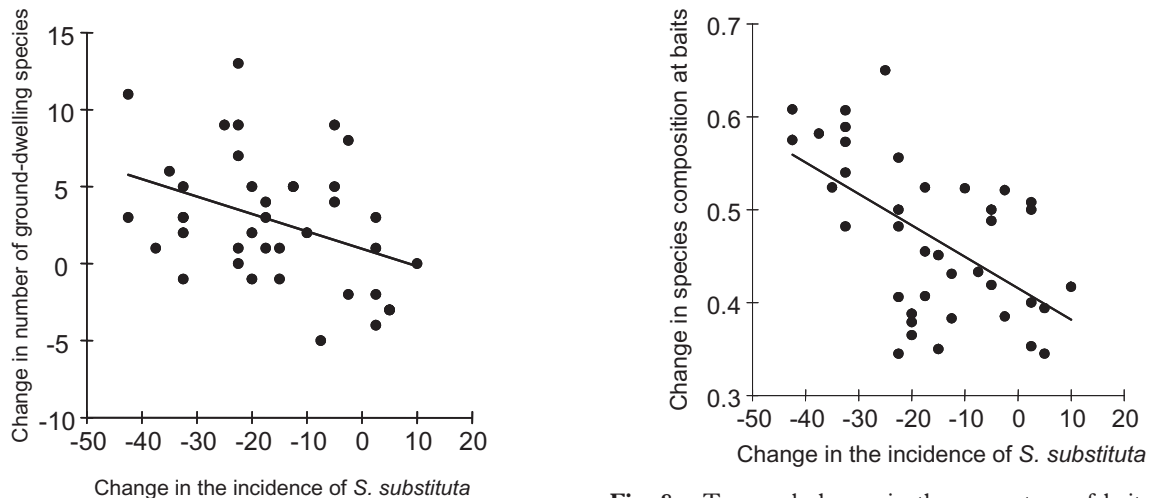
**Fig. 5.** Temporal differences in the number of baits exploited by 68 bait-recruiting ant species. Values represent the difference in the percentage of baits exploited between surveys in 2002 and in 1998. Each point represents a different ant species.

the amount of bare ground ( $r = 0.323$ ,  $n = 39$ ,  $P = 0.045$ ) (Fig. 6). These data suggest that at least part of the difference in the number of baits exploited by *S. substituta* in 1998 and 2002 was due to changes in plant cover. Inter-survey differences in the incidence of *S. substituta* at baits were independent of the variations in the fire regime (mean plot area burned during the previous 3 years;  $r = 0.115$ ,  $n = 39$ ,  $P = 0.49$ ).

In both 1998 and 2002, we found a negative correlation between the total number of baits with *S. substituta* and the total number of ant species per plot (1998:  $r = -0.428$ ,  $n = 39$ ,  $P = 0.007$ ; 2002:  $r = -0.331$ ,  $n = 39$ ,  $P = 0.04$ ). In addition, we found that in plots where the incidence of *S. substituta* declined (relative to the 1998 survey) the number of ground-dwelling species tended to increase ( $r = -0.384$ ,  $n = 39$ ,  $P = 0.016$ ; Fig. 7). The temporal change in the



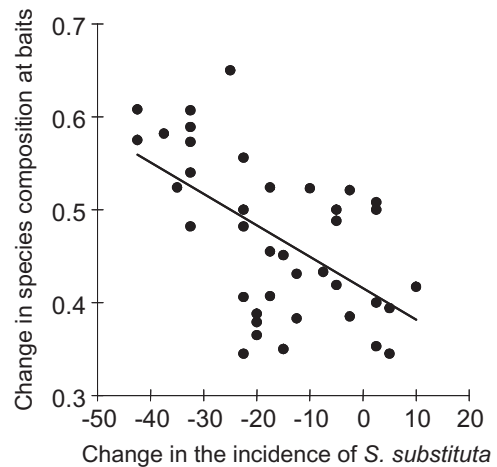
**Fig. 6.** Influence of temporal changes in vegetation structure on the incidence of a dominant ant, *Solenopsis substituta*, at baits. The change in per cent cover by tall grasses (a) and in bare ground (b) in each plot over a 4-year period (1998–2002) in relation to the change in the percentage of baits with *S. substituta* during the same period. Each point represents a different plot.



**Fig. 7.** Temporal change in the percentage of the total number of baits with *Solenopsis substituta* in relationship to the temporal change in the total number of ant species foraging on the ground.

incidence of *S. substituta* at baits was also significantly correlated with the observed temporal difference in the composition of species exploiting baits ( $r = -0.567$ ,  $n = 39$ ,  $P < 0.001$ ; Fig. 8), but not with overall species composition (i.e. presence/absence data;  $r = -0.085$ ,  $n = 39$ ,  $P = 0.61$ ).

Plots in which we recorded the appearance of *W. auropunctata* in 2002 tended to present a greater decline in the incidence of *S. substituta* than those in which *W. auropunctata* was not found, but the difference was not significant (Mann–Whitney  $U$ -test comparing the relative change in the frequency of *S. substituta* at baits between plots with *W. auropunctata* and without *W. auropunctata*:  $P = 0.062$ ).



**Fig. 8.** Temporal change in the percentage of baits with *Solenopsis substituta* in relationship to temporal change in species composition of ants recruiting to baits. Change in species composition is expressed as the dissimilarity between the two surveys.

## DISCUSSION

### Effects of vegetation cover

Variations in plant cover among our study plots explained poorly the observed variation in ant species richness. Of all vegetation variables measured, only tree cover was associated with ant species richness and even so only in 1998. However, it is important to note that our results apply only to a subset of the savanna ant species. Here, we only sampled species that have diurnal foraging habits, and mostly those that are attracted to baits. As these species in many cases have generalized foraging and nesting habits (Bestelmeyer

*et al.* 2000), it is possible that further studies, directed at searching for the more cryptic and specialized species, may detect a different pattern. Nevertheless, despite these methodological limitations, we found evidence for an effect of plant cover on ant species composition, with the latter being significantly influenced by tree cover and cover by tall grasses in both years of the study. In the savannas of Alter do Chão there is a strong vertical partitioning of the ant community, with many species foraging and/or nesting primarily on the ground, and others in the woody vegetation (Vasconcelos & Vilhena 2006). Changes in plant cover may therefore benefit one group of species at the expense of the other, and consequently affect community composition. Species which only nest on open ground are likely to perform poorly in sites with a relatively dense tree cover, as observed for instance in an Australian woodland (Lassau & Hochuli 2004). On the other hand, arboreal species are likely to benefit from an increased availability of nesting and foraging sites (e.g. Ribas *et al.* 2003). Similarly, species which nest on twigs on ground are likely to benefit by the increased amount of shade and litter provided by trees. In both cases changes in species composition can result not only from changed foraging and nesting conditions, but also from altered species interactions (e.g. Perfecto & Vandermeer 1996).

Our data suggest that at Alter do Chão both mechanisms may be operating, given that temporal changes in plant cover affected the abundance of a dominant species and this, ultimately, may have resulted in altered richness and composition of the community over time. *Solenopsis substituta* met all the criteria established by Andersen (1992) to define a dominant species, with the exception of the fifth criterion – representation in baits relative to pitfall traps – for which data are not available. *Solenopsis substituta* occurred in a large (>20%) proportion of baits, it dominated and monopolized most of the baits at which it occurred at, and recruited more ants to baits than other species. Of all species that were attracted to baits, *S. substituta* showed the greatest absolute change in the number of baits exploited between 1998 and 2002, especially in plots where cover by *Trachypogon* grasses increased most extensively and, consequently, where the amount of bare ground decreased. Habitat structure can affect ant movement and foraging success, and a similar phenomenon may have occurred with *S. substituta* in plots with increased cover of tall grasses. The changed habitat structure at these plots may have interfered with the foraging of *S. substituta*, decreasing its success at finding and dominating sardine baits, as seen with other similar species (Carroll & Risch 1983; Lassau & Hochuli 2004; Gibb 2005). In addition, it is likely that nest densities of *S. substituta* decreased in these plots, thus allowing other ant species to exploit the baits (see Gibbons & Simberloff 2005 for a similar case). Nests

of *S. substituta* are usually located in open areas with bare ground (H. L. Vasconcelos, pers. obs. 1998), and by reducing the amount of bare ground, tall grasses may have reduced the availability of nesting sites for *S. substituta*. Similarly, nests of *Solenopsis geminata*, a close relative of *S. substituta* (Pitts *et al.* 2005), are also commonly found in sunny locations (Perfecto & Vandermeer 1996). Moreover, if a nest of *S. geminata* is artificially shaded, the colony moves within 24 h (Perfecto & Vandermeer 1996).

Therefore, the altered species composition and elevated number of species per plot detected in 2002 was possibly an indirect consequence of changes in cover by tall grasses. By affecting the nest density and/or foraging efficiency of *S. substituta*, tall grasses may have alleviated the intensity of competition between *S. substituta* and other ants. However, given the correlative nature of our findings, we cannot excluded the possibility that competition is not involved, and that whatever factors regulate overall species richness and composition in our sites also regulate *S. substituta* populations (cf. Ribas & Schoereder 2002; Morrison & Porter 2003).

### Disturbance by fire

Fire is a frequent source of disturbance in the savannas of Alter do Chão (Sanaiotti & Magnusson 1995), but differences in the incidence and extent of fires between our survey plots did not significantly influence ant species richness, while the effect on composition was minor and only significant in one sampling year. However, these negative results may simply reflect the fact that savanna ant assemblages are resilient to the effect of fires (Parr *et al.* 2004), and that our study was not appropriately designed to evaluate possible short-term effects of fire. We sampled ants 8–10 months after burning, but studies in African savannas indicate that ant assemblages show full recovery within a period of only 8 months (Parr *et al.* 2004). Therefore, at the time of our sampling the ant fauna may have completely recovered from fire disturbance.

Previous studies on the long-term effects of fire on ant assemblages indicate that fire can have strong positive (Andersen 1991; York 1994; Andersen *et al.* 2006) or negative (Morais & Benson 1988; Farji-Brener *et al.* 2002) effects, only minor effects (Parr *et al.* 2002; Rodrigo & Retana 2006), or have no detectable effect on species richness (Farji-Brener *et al.* 2002; Hoffmann 2003; Parr *et al.* 2004). However, most of the studies that showed an effect compared burned plots with plots protected from fire for many years (>10 years) (Andersen 1991; York 1994; Andersen *et al.* 2006). In contrast, all of our sampling sites were burned at least once over the 5-year period of data collection (1997–2001). Consequently, it is possible that the time since last



disturbance by fire in all of these sites was too short for a distinct ant assemblage to develop. If fire is intense, nests of arboreal nesting species are destroyed (Morais & Benson 1988). However, at Alter do Chão, where fire occurs on an annual or semi-annual basis (and consequently the amount of plant fuel to burn each year is low) flames rarely go higher than 1.5 m (Sanaiotti & Magnusson 1995), and therefore may have just a minor impact on arboreal ant nests. Soil-nesting species, in contrast, appear not to suffer any direct effects from fires, as soil temperatures during a fire are not dramatically altered, even at relative shallow depths (Coutinho 1978). However, fire directly affects the litter-nesting species (which are relatively common in forested areas in the region; Vasconcelos & Vilhena 2006), and therefore the establishment of these species in savannas may only occur after long-term fire exclusion (Andersen *et al.* 2006).

### Community dynamics

There is little evidence that any ant species became extinct within the savanna landscape over the course of this study. Most of the species found in 1998 but not in 2002 were rare species, so the fact that these species were recorded in one survey but not in the other is more likely due to the vagaries of surveying than local extinctions. Similarly, as *Cyphomyrmex rimosus* was only recorded through direct searching, and as it was not possible to have all the same collectors in different years, we cannot discard the possibility that the absence of this relatively cryptic species in the 2002 survey represents a sampling bias rather than a biological phenomenon.

In contrast, the appearance of *W. auropunctata* in 2002 is likely to represent a true colonization event. *Wasmannia auropunctata* is an easily recognizable species which forms large colonies that are active during day and night, both on ground and in the vegetation (Clark *et al.* 1982; Delabie 1988). In spite of this, not a single worker of this species was found in over 150 h of search in 1998. *Wasmannia auropunctata* was also not recorded on any of the >1500-baits set in 1998, in spite of the fact that it actively recruits to baits and often displaces competing species (Clark *et al.* 1982; Delabie 1988). Therefore, it seems unlikely that *W. auropunctata* was present but overlooked in the 1998 survey. Although evidence is limited, the same may apply to *D. bispinosus*, another species only recorded in the 2002 survey. Even though *D. bispinosus* nests in trees, where it builds polydomous colonies in the foliage (Delabie *et al.* 1991), it forages actively on the ground where it often monopolizes rich food resources such as sardine baits (H. L. Vasconcelos, pers. obs. 2000). Therefore, this is another species unlikely to have been overlooked in 1998.

The extent to which colonization by *W. auropunctata* was a response to changes in vegetation cover or to the relaxation of dominance by *S. substituta* deserves further investigation. Plots colonized by *W. auropunctata* tended to be those in which *S. substituta* declined more strongly, but these were the same plots in which vegetation cover changed most. Both species have similar nesting and feeding requirements and therefore are likely to compete with each other. For instance, *W. auropunctata* relies heavily on honeydew-producing Hemiptera living on plant roots (Delabie 1988) and the same is true for a close relative of *S. substituta* (Perfecto & Vandermeer 1996). Although we cannot discard the possibility that *W. auropunctata* affected *S. substituta* and not the opposite, this seems unlikely given that the number of baits with *W. auropunctata* was nearly an order of magnitude smaller than the number with *S. substituta*, suggesting that the former had only recently established in our savanna plots.

### Concluding remarks

The results of this study suggest that ant assemblages from Amazonian savannas near Alter do Chão show variation in species richness and composition over relatively short spatial (<20 km) and temporal (<5 year) scales. Fire had no or only limited influence on these patterns, which apparently resulted from variation in plant cover. Plant cover explained part of the observed spatial variation in species composition. In addition, there is evidence that temporal changes in plant cover affected *S. substituta*, which may be a keystone species in our study area. One possibility is that changes in its population, caused by altered vegetation cover, influenced other ecologically similar species. We hope that this study will stimulate further experimental work to rigorously evaluate this hypothesis.

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