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Ant recolonization of rehabilitated bauxite mines at Trombetas, Pará, Brazil

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ABSTRACT. Ant species were sampled in three rainforest and 10 rehabilitated bauxite mine plots at Trombetas, in the tropical monsoonal region of Brazil. Rehabilitation ranged from 0 to 11 years in age and was mainly performed by planting mixed native forest tree species. One plot supported single-species blocks of Australian *Eucalyptus* and *Acacia* species. Two hundred and six ant species were recorded, of which 82 were exclusively found in the native vegetation, 54 were confined to the rehabilitation and 70 were found in both situations. In contrast with other studies, ant species richness in the *Eucalyptus/Acacia* plantation was as great as in the areas rehabilitated with native vegetation. The overall rate of return of ant species was considerably greater than in mines situated within subtropical regions of Brazil, Africa and Australia. However, if the greater richness of ants in the native vegetation at Trombetas was accounted for, the proportional return of the original ant fauna was not particularly rapid. The return of ant species slowed as the rehabilitated areas aged. In comparison with forest, the rehabilitation was characterized by proportionately more generalist species and fewer specialists, especially from the soil and litter layers. The full range of habitat requirements for the ant community has not been restored by the eleventh year of rehabilitation and further management may be required to enhance the degree of colonization. It is suggested that the findings for ants may apply to other components of the biota as well.

KEY WORDS: ants, Australia, bauxite mining, Brazil, climate, Formicidae, land rehabilitation, recolonization, restoration.

INTRODUCTION

The clearing of the forests of Amazonia, particularly within Brazil, is a widespread result of extractive logging, mining, peasant holdings and the establishment of vast livestock ranches (Eden 1990). Much of the debate on this issue has focused on the beneficial uses of the forest (Fosberg 1972), the need for sustainable exploitation and protection of Amazonian forest (Goodland 1985, Jordan 1987), the loss of biodiversity when forest is cleared (Myers 1988) and on the effects of forest clearance on atmospheric gas levels and, ultimately, on the global heat balance (Fearnside 1985a,b). Although considerable attention has been given to retaining Amazon forest by such means as 'debt for nature' swaps, research on restoration of degraded areas has been limited. This is evidenced by only 12 title references to restoration, recolonization or recovery occurring among the 850 references cited by Eden (1990). Most work has been in areas which have been affected by ranching or logging (e.g. Nepstad *et al.* 1991).

Mineração Rio do Norte, S.A., is currently mining bauxite near Porto Trombetas, in the state of Pará in eastern Amazonia. The Company's rehabilitation programme provides a good opportunity to elucidate how easily Amazonian forest may be restored. 'Rehabilitation' is here defined as the return of an area to a proper (biological) state such as a pasture, forest or playing field (Langkamp 1979), while 'restoration' is the attainment of the ecosystem's original structure and function (Bradshaw 1984).

Certain invertebrate taxa may act as useful indicators of the degree of success of a rehabilitation programme (Majer 1989a). They include ants which have been used at rehabilitated minesites in differing climatic zones throughout Australia (Majer 1989b) and in subtropical parts of South Africa (Majer & de Kock 1992) and Brazil (Majer 1992). The current study extends this to the equatorial tropics. A comparison is made between tropical and other climatic zones, based on the types of ants which recolonize disturbed sites and on the efficiency of the rehabilitation procedures in facilitating recolonization.

METHODS

Description of mining and rehabilitation

The mine is situated approximately 65 km north-west of the town of Oriximiná and 30 km south of the River Trombetas (1° 45′ S, 56° 30′ W). The climate of this area is Köppen's climatic type A-m (tropical monsoonal – see Eagleman (1976)) and exhibits a distinct dry 'winter' and a wet 'summer'. The average annual rainfall is 2134 mm, exceeding 100 mm in all months except July to October. The mean annual maximum and minimum temperatures are 34.6°C and 19.9°C, respectively.

In general terms, the vegetation is a climax evergreen equatorial moist forest, which extends continuously over the whole region, except for water bodies and the very occasional small, white-sand savannas. Apart from the lake and river margins, which are normally flooded every year during the rainy season, the 'terra firme' lands consist of undulating sandy terrain with occasional flat-topped mountains (mesas) which are capped by clay soils on their plateaus. The natural features of the area, the main forest associations and their associated ant communities have been described by Majer & Delabie (1994). Broadly speaking, the forests of the area are divided into three types: (1) varzea forest – growing on floodplain areas; (2) flanco forest – growing on sandy terrain; and (3) planalto forest – growing on the mesas.

At present, mining only occurs in planalto forest on one mesa near Trombetas (the Saracá mesa). The 2–6 m thick layer of ore occurs under 10 m of yellow clay, 2.5 m of nodular bauxite and 2 m of ferruginous laterite. Following topsoil stripping and storage, the overburden is removed by dragline so that the layer of bauxite may be extracted. The mixed overburden is replaced on the adjacent mined area, the piles of material are then battered flat and, in post-1982 areas, topsoil is replaced. Mining, which commenced in 1971, is continuously moving across the mesa in a west to east direction. So far about one-quarter of the Saracá mesa has been affected by mining.

Rehabilitation on a wide scale commenced in 1980 and, although not changing appreciably in approach, has gradually been refined in the light of past experience. A diverse mixture of native trees, grown from propagules collected in the local flanco and planalto forest, is planted out in an attempt to achieve a cover as rapidly as possible. Some trial plantations of *Eucalyptus* spp. and *Acacia* spp. have also been grown. No understorey is planted or seeded, although considerable self-sown understorey has grown up in some of the areas.

Description of study plots

Three control plots, representing the three broad forest types in the area, were surveyed and are described in detail in Majer & Delabie (1994). Planalto forest, which was situated immediately in front of the mining path, was selected because it represents the original ecosystem where mining took place. Two other forest types were surveyed because they might contain a source of colonizing ant species. These were the flanco plot, situated at the base of the mesa and 5 km from the mine plus the varzea plot which was adjacent to the Trombetas River, 30 km from the mine. In addition to the forests, areas of rehabilitation ranging from 0 to 11 years old were also selected. The plots do not represent an even distribution of ages since there were no sizeable examples of 1–4-year-old rehabilitated areas at the minesite. The rehabilitated plots are described in Table 1. With the exception of the 7-year-old plantation of exotics, all plots were randomly planted with mixed native trees. The plantation consisted of a series of single-species blocks of *Eucalyptus* and *Acacia* spp., through which the transect passed.

A 100 m ant sampling transect was marked out in a representative area of each plot in such a way as to minimize edge-effects. Markers were placed at

Table 1. Description of the 10 rehabilitated plots used in the ant recolonization study.

Age (y)	Trees planted[1]	Comments[2]
0	none	TS + L
0.3	MN	TS + L
5	MN	TS
6	MN	TS
7	MN	TS
7	S	TS
8	MN	TS
9	MN	TS
10	MN	No TS
11	MN	No TS

[1] MN = mixed native species; S = single species plots of *Eucalyptus* and *Acacia* spp.
[2] TS = topsoil applied; L = logs applied.

10 m intervals along the transect in order to facilitate ant sampling and also to serve as sites for characterizing the environment.

Soil penetrability was measured at each marker by recording the depth to which a spike penetrated the soil when exposed to a constant force. Then, 1 m^2 quadrats were installed at each marker in order to assess visually the percentage litter cover, percentage grass cover and percentage herb cover. The percentage shrub and tree cover were visually assessed in the vicinity of each quadrat. The depth of litter was also recorded in each quadrat and an index of litter load was calculated by multiplying percentage litter cover by litter depth. The number of understorey plant species within each quadrat was then recorded and the number of logs greater than 10 cm diameter was counted along a 2 m strip adjoining the entire 100 m transect. Finally, the mean tree height on the plot was measured.

Ant sampling

A series of complementary sampling methods was used to survey the ant fauna. Ten pitfall traps, consisting of 2 cm internal diameter test tubes containing ethanol, were installed along each transect. Traps were left open for seven days. Hand collections were performed during mid-morning for two person-hours and repeated during the night for a further one person-hour. These were augmented by sampling trees and large shrubs, respectively, with a beating tray and sweep net, both of which were used for two person-hours during day-time. In addition to this 'standard' set of sampling procedures, the ants in the 5- and 11-year-old plots and in the three forest controls were also sampled by additional methods. Ten tuna fish/honey/crumbed biscuit baits were placed out in the early morning and the ants which attended were collected after a 2-hour period. Secondly, ants were extracted from a series of litter samples by means of Winkler sacks (see Besuchet *et al.* 1987), which are devices that act like Tullgren funnels but which use sunlight to heat and dry the litter. The total sampling regime in these five plots is referred to as the 'extended' set of samples. All samples were taken between 24 July and 4 August 1992, during which time the total rainfall was 46.1 mm and the mean maximum and minimum temperatures were 35.2°C and 21.8°C, respectively.

Ants were sorted to species level and assigned species code numbers within each genus. Generic names generally conform to those in Hölldobler & Wilson (1990) in order to ensure comparability of generic counts with those which are being prepared by other workers in the Amazon (J. Tobin & M. Verhaagh, pers. comm.). It should be noted, however, that the genera *Dolichoderus*, *Hypoclinea* and *Monacis* have recently all been grouped together within the first-mentioned genus (Shattuck 1992). Full collections of voucher specimens are deposited in the Zoological Museum of the University of São Paulo and in the Myrmecology Laboratory of the Centre for Cocoa Research (CEPLAC), Itabuna, Bahia.

Data treatment

The transect means for all physical and vegetation recordings were calculated. A checklist of ants for each transect was obtained by combining the collection data from the four standard sampling methods. The total number of species obtained for each transect is referred to as ant species richness. The quantitative data from the pitfall traps were then used to calculate the equitability index (J′; Shannon 1948). The formula for this index is:

$$J' = [(N \log N - \Sigma\, n_i \log n_i)/N]/\log S,$$

where N is the total number of individuals, n_i is the importance value of the *i*th species and S equals species richness.

In order to assess the plots in terms of the ant species which were present, the plots were compared using principal components analysis of the correlation matrix derived from ant presence/absence data. Species occurring in two or less plots were excluded from the analysis since these could lead to over-definition of samples. The resulting ordination of the plots summarizes the variation present within the data matrix in a few dimensions, with the first principal component representing the combination of plots with maximum variance and subsequent components representing ones with smaller variances. In addition to this, the ordination provides an indication of the degree of relatedness of plots in terms of the species which were present within them. Only the first three components of the ordination were considered since subsequent components accounted for relatively small variance in the data.

RESULTS

The mean plot values of physical and biological measurements are shown in Table 2. With the exception of the 0.3- and 9-year-old plots, which had exceptionally friable soil, the soil in the rehabilitated plots was less penetrable than that of the forest. This was probably associated with the passage of heavy machinery, with the bringing of clay up to the surface and also with the fact that the soil in the newly rehabilitated areas tended to harden up on exposure to rain and sunlight. The percentage bare ground rapidly declined with increasing age of rehabilitation and, by nine years, had attained values similar to those of the adjacent planalto forest. Associated with this was a build-up of leaf litter, which also attained forest cover values by the ninth year of rehabilitation. However, the litter depth, and consequently the litter mass index, was generally considerably lower in the rehabilitated areas than in the forest. The only exception was the 6-year-old plot, where the ground was covered in leaves of pioneer trees such as *Cecropia* spp. The number of logs was generally lower in the rehabilitated areas, although there was a slight increase in the 7- and 8-year-old

Table 2. Mean (N = 10) values for physical and biological measurements recorded along 100 m transects in the 10 rehabilitated and three control plots.

Plot type	Rehabilitation										Forest		
Age of rehabilitation (y)	0	0.3	5	6	7	7*	8	9	10	11	Planalto	Flanco	Varzea
Soil penetrability (cm)	13.6	22.0	13.1	15.9	14.0	13.3	13.0	81.2	10.6	14.0	17.9	18.3	20.0
% bare ground	100.0	100.0	5.5	12.0	17.0	0.9	17.0	3.2	3.2	1.4	3.9	0.0	0.0
% litter cover	0.0	0.0	87.3	84.0	69.5	77.0	76.0	96.0	96.8	95.0	95.0	100.0	100.0
Litter depth (cm)	0.0	0.0	0.9	6.2	1.8	2.2	0.9	0.9	1.3	1.2	4.6	3.5	3.7
Litter index (cover × depth)	0.0	0.0	78.6	520.8	125.1	169.9	68.4	86.4	125.8	114.0	437.0	350.0	370.0
No. of logs	82	81	6	9	19	1	14	4	9	0	42	26	9
% grass cover	0.0	0.0	35.2	0.1	23.4	14.5	6.4	5.3	0.1	32.6	0.0	0.0	0.0
% herb and shrub cover	0.0	1.9	13.3	5.2	4.4	2.0	7.2	4.7	11.1	2.2	21.3	9.3	12.5
No. of understorey species (m^{-2})	0.0	1.9	3.1	2.8	3.0	1.2	3.0	2.8	3.0	2.1	7.3	4.5	4.4
% tree cover	0.0	0.0	41.5	52.0	27.0	19.5	30.5	38.0	44.0	26.5	77.0	81.5	88.9
Height range of trees (m)	0.0	0.0	1–6	1–12	2–12	6–24	2–14	2–9	2–16	4–8	5–45	18–45	22–40

* *Eucalyptus/Acacia* plantation.

plots when many of the pioneer trees were senescing. The high number of logs in the 0- and 0.3-year-old plots resulted from the recently introduced practice of adding logs at the time of topsoil emplacement (Table 1).

Although absent in the forested areas, much of the rehabilitated areas bore some grass cover. Shrub and herb cover increased to low or moderate levels in these areas and did not reach the level of the adjacent planalto forest. This trend was also reflected in the richness of understorey species which, on a number of species per m^2 basis, only reached about half the level of the planalto forest (Table 2). Tree cover rapidly built up by the sixth year of rehabilitation but, with the death of pioneer trees, rapidly declined before increasing again as some of the long-lived trees grew up. Neither tree cover nor tree height reached forest levels by the eleventh year of rehabilitation.

The numbers of ant species within each genus from the rehabilitated and control plots are shown in Table 3. A copy of the full species count by plot matrix may be obtained by writing to the author and a list of those species found in the forest controls is given in Majer & Delabie (1994). A total of 206 ant species was recorded in the plots. In terms of number of species, *Pheidole* (28 species), *Camponotus* (20) and, to a lesser extent, *Pseudomyrmex* (12), *Solenopsis* (12), *Crematogaster* (11) and *Pachycondyla* (8) were the most species-rich genera in both the rehabilitated areas and the forest.

The number of species within each genus which were only found in the rehabilitated areas, in the forest or in both is shown in Table 3. Some species were only found in the rehabilitated areas (54 species) and, although represented by 23 genera from all subfamilies except the Ecitoninae, are mainly generalist, pioneer species. A further 70 species were found in both forest and rehabilitated areas and a further 82 species were only found in the forest. Some of the latter groups are probably flanco or varzea forest species which would not necessarily occur in association with the soils or vegetation of the mesas where mining is taking place; others may be species whose requirements have not yet been provided for in the rehabilitated areas. This is probably the case with *Anochetus horridus*, *A. neglectus*, *Crematogaster* sp. 221, *Dolichoderus attelaboides*, *Gnamptogenys teffensis*, *Odontomachus hastatus*, *Trachymyrmex* sp. 216 and various *Pheidole* spp., which were common in the planalto forest but which were totally absent in the rehabilitated areas.

The number of ant species increased to 46 prior to the fifth year of rehabilitation, although it is not possible to say precisely when this level was reached as no examples of 1–4-year-old rehabilitated areas were available (Figure 1a). Thereafter, the species richness value oscillated, with a subsequent decline followed by an increase to a high of 55 by the ninth year, followed by a second decline. It is not known whether this pattern is a true oscillation, with some underlying cause, or whether it is a consequence of differences in rehabilitation success between years. Species richness in the 7-year-old area, which was planted with a patchwork of *Eucalyptus* spp. and *Acacia* spp. monocultures, was similar to that of the 7-year-old plot which had been planted with mixed native

Table 3. Numbers of species within each ant genus and summary statistics for the ant communities sampled in the 10 rehabilitated and three forest control plots. The first section of the table shows the numbers of species sampled by the standard survey procedure, the second section the number of species sampled by the extended survey procedure and the third section shows the number of species which were only found in the rehabilitated area, in the forest, or in both situations.

		Rehabilitation										Forest			Rehabilitation		Forest			Summary of data			
												P.	F.	V.			P.	F.	V.				
Type of revegetation		N.	N.	N.	N.	N.	*E.*	N.	N.	N.	N.	–	–	–	N.	N.	–	–	–	Confined to rehabilitation	Present in both	Confined to forest	Total species
Age of rehabilitation (y)		0	0.3	5	6	7	7	8	9	10	11	–	–	–	5	11	–	–	–				
Sampling intensity*		st	st	st	st	st	st	st	st	st	st	st	st	st	all	all	all	all	all				
Ponerinae	*Amblyopone*																	1				1	1
	Anochetus						2		1			2				2	2	3		2	2	1	5
	Discothyrea																	1				1	1
	Ectatomma			1	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1		2
	Gnamptogenys						1	1				3	2	2			4	2	2	2		4	6
	Hypoponera		2		1		1	3	2	2	1	3	1	1	2	1	7	3	1	2	1	2	5
	Leptogenys								1								1				3		3
	Odontomachus			3	2	1	1	1	2	2	1	4	4	2	3	1	5	4	2		5	2	7
	Pachycondyla			3	3	2	2	3	4	3	3	6	4	3	3	3	8	5	3	2	1	5	8
	Paraponera								1				1					1				1	1
	Platythrea													1					1			1	1
	Thaumatomyrmex													1					1			1	1
Myrmicinae	*Acanthognathus*														1	1				1			1
	Apterostigma											2	1		1	1	2	2				3	3
	Atta			1		1		1		1			1		1		1	1			1		1
	Blepharidatta											1					1	1				1	1
	Carabara																1					1	1
	Carabarella			1					1			1	1	1	1		1	1	1		1		1
	Cephalotes								1				1	1				1	1		1		1
	Crematogaster			3	4	3	4	4	4	4	3	4	3	4	4	3	4	3	4	4	3	4	11
	Cyphomyrmex				1	1			2	1	2	3	1	1		3	3	2	3	1	3	2	6
	Erebomyrma						1										2				1	1	2
	Eurhopalothrix																1					1	1
	Hylomyrma													1					1			1	1
	Lachnomyrmex																1					1	1

	Leptothorax			1	1				2						1					2			2
	Myrmicocrypta											1					1					1	1
	Neostruma																1					1	1
	Ochetomyrmex								1			1	1				1	1			1		1
	Pheidole	3	1	5	5	6	4	4	5	3	6	10	12	5	7	7	12	13	7	6	8	14	28
	Quadristruma																1	1				1	1
	Rogeria			1	1		1	1	2	2					2	1	3			1	3		4
	Sericomyrmex											1	1				1	1				1	.1
	Solenopsis	1	2	4	3	2	2	3	2	3	1	2			5	2	5	3	1	6	4	2	12
	Strumigenys		1	1				2	1		1	1	2		1	2	3	5	2	2	2	4	8
	Trachymyrmex			1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	1	1	1	2	4
	Wasmannia		1	1	1	1	1	1	1	1	1		1	1	2	1		1	1	1	1		2
	Zacryptocerus			2	2	2	1	2	3	4	2		1	2	2	2		1	2	3	2		5
Ecitoninae	*Eciton*											1					1					1	1
	Labidus											1					1					1	1
	Neivamyrmex												1					1			1		1
Pseudomyrmecinae	*Pseudomyrmex*			6	3	7	4	5	4	4	5	1	4	5	6	5	1	4	5	6	5	1	12
Formicinae	*Acropyga*																1					1	1
	Brachymyrmex		1		1		2	1	2	2	2		2	1	1	2	1	2	1		2		2
	Camponotus			9	9	9	8	6	8	7	10	5	11	6	10	10	5	11	7	5	9	6	20
	Dendromyrmex											2					2					2	2
	Gigantiops									1	1	1	1			1	1	1			1		1
	Paratrechina			1	1		3	2		2	1	4	3	2	2	2	5	4	2	1	3	3	7
Dolichoderinae	*Azteca*			1		1		1		1		2	4	2	1		2	4	2		3	2	5
	Dorymyrmex										1					1				1			1
	Dolichoderus (Dolichoderus)				1							2		2			2		2		1	2	3
	Dolichoderus (Hypoclinea)					1		1				1	1				1	1		1		1	2
	Dolichoderus (Monacis)					1			1					1					1	2		1	3
	Tapinoma			1	1			1			1		1		1	1		1		1		1	2
Mean ants per pitfall trap		0.2	4.7	43	12.8	14.3	15.1	8.8	13.6	8.7	42.3	11	5.3	6.7									
Total species		4	8	46	43	41	41	46	55	46	44	68	68	47	59	54	98	88	55	54	70	82	206
Total genera		2	6	19	19	16	18	21	24	19	19	28	28	23	23	23	39	34	25				
Ant species evenness (J')		0.99	0.53	0.64	0.64	0.8	0.71	8.89	0.64	0.77	0.61	0.6	0.86	0.72									

P. = Planalto; F. = Flanco; V. = Varzea.
N. = Native; *E.* = *Eucalyptus*.
* st = pitfall traps, vegetation sweeps, tree beats and hand collections; all = the preceding plus baits and litter samples.

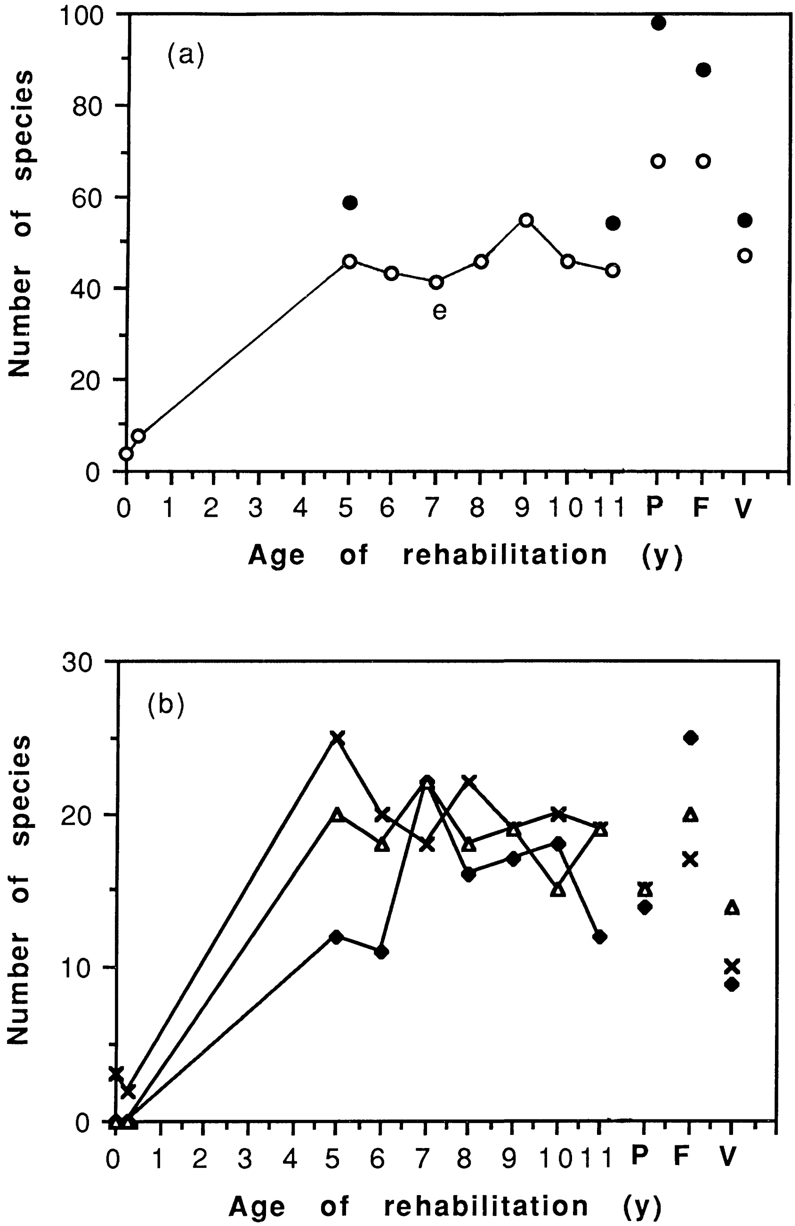

Figure 1. Relationship between (a) the total number of ant species (○) with rehabilitation age and also (b) the number of species sampled from the ground (×), the shrubs (◆) and the trees (△). The (e) in the upper graph indicates that the 7-year-old plot which was rehabilitated with exotics overlapped the data point for the plot which was planted with mixed natives. P, F and V, respectively, stand for planalto, flanco and varzea forest. Points depicted by (●) represent the total species obtained when the results of baiting and litter extraction are included.

vegetation (Table 3). Ant species richness in the rehabilitated areas was always lower than in the forest, especially when compared with the near-by planalto forest. Similar time-trends were shown when the data from the litter samples and baits were included, although the extended survey techniques revealed a further 13 and 10 ant species in the 5- and 11-year-old rehabilitated areas, respectively (Table 3 and Figure 1a). The discrepancy between the rehabilitated area and forest values was further increased by the addition of species from these two sampling methods, with an extra 30 species being encountered in the planalto and an extra 20 in the flanco forest. The lower value of eight extra species in the varzea was probably associated with the less rich litter fauna in this annually flooded ecosystem.

The time-trends in ant species richness were largely mirrored by the number of ant genera within each plot. The number of genera increased to 19 prior to the fifth year of rehabilitation and thereafter oscillated, with a peak of 24 genera in the ninth year of rehabilitation. The generic count never attained the value of 28 in the planalto forest and the discrepancy between rehabilitated area and planalto forest values was exacerbated when ants from the extended samplings were included (Table 3).

The rise, and apparent oscillation, in ant species richness was mirrored by the ground (pitfall trap samples), the shrub (vegetation sweep samples) and the tree (tree beat samples) fauna (Figure 1b). However, the rise in the ground fauna preceded that of the vegetation-associated species and the rise in tree-associated species was more rapid than that associated with the shrubs. The richness of ants within each stratum was comparable with the near-by forest by the later ages of rehabilitation. However, this does not mean that species richness values were similar in the rehabilitated areas and forest, since the species turnover between strata was much greater in the forest than in the rehabilitated areas.

The evenness index values exhibited few trends, either between rehabilitation and controls, or through age of rehabilitation (Table 3). Evenness was high (0.99) in the 0-year-old rehabilitated areas as none of the ants had yet become abundant. It subsequently dropped to 0.16 in the 0.3-year-old area because *Solenopsis* sp. 25 had already attained densities which far exceeded those of the other seven species. In the 5–11-year-old plots the evenness values fell within, or close to, the range of the forest controls.

The first three axes of the principal components analysis accounted for 32.4, 11.8 and 8.6% of the variance, respectively. Figure 2 shows the position of the plots on the first two axes of the ordination and clearly indicates three groupings of plots: the controls, the youngest two rehabilitated plots and the 5–11-year-old plots. No time-trends were evident within the 5–11-year grouping and the 7-year-old plots which were rehabilitated with native vegetation or plantations were situated close together. The implications of the groupings shown in Figure 2 are that, although there is a considerable change in the ant community in the first five years of rehabilitation, the changes between five and 11 years are relatively small and

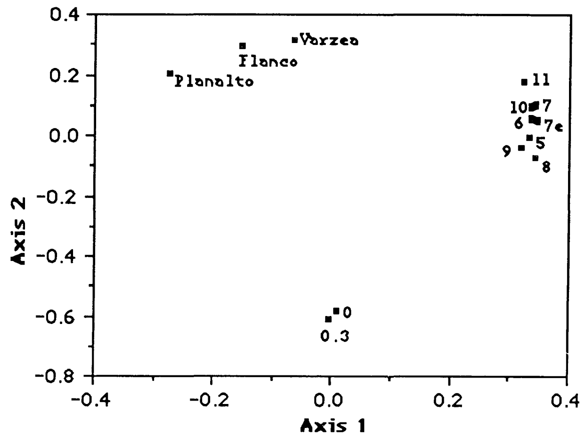

Figure 2. Ordination of forest and rehabilitated plots by the use of principal components analysis of the correlation matrix derived from the ant species presence/absence data. Numbers refer to the age of the rehabilitated areas in years and all such plots were rehabilitated with native vegetation, except for 7e, which was planted with *Eucalyptus* and *Acacia* spp.

result in a community which is still appreciably different from that of the three forest controls. Inspection of the positions of plots on axis 3 indicates that, as on axis 2, the species composition of ants in the 5–11-year-old plots is most similar to that of the planalto than to that of the other two forest plots.

DISCUSSION

The results confirmed the findings of both Cover *et al.* (1990) and Verhaagh (1990) that Amazonian forest supports a very rich ant community. Additional baiting and litter sampling indicated that the plots were undersampled by other sampling techniques which did not locate rare or cryptic species. Total species counts compared with standard sampling procedures (Table 3) indicate that sampling efficiency was about 80% in the rehabilitated areas and 69% in the planalto forest, indicating that more ant species are missed in the more complex natural ecosystem.

The species richness of the forest controls (47–68 species) is out of the range which has been observed by identical standard sampling procedures in Australia, southern Brazil and southern Africa (25–35 species) (see references in Majer (1992) and Majer & de Kock (1992)). Thus, although it has previously been possible to make direct comparisons between rehabilitated areas without the confounding influence of differences in ant species richness within the native vegetation, the exceptionally high ant species richness in Amazonia poses problems when making comparisons with other areas.

The lack of examples of rehabilitation in the 1–4-year range also presents a problem as it is unclear whether the recruitment of species in this time-span is linear or curvilinear. Experience gained in other rehabilitation studies suggests that the pattern is almost certainly curvilinear (e.g. see Majer 1985). Majer (1989b, 1992) has used the ant species richness value in 3-year-old rehabilitation as a measure which may be compared between different minesites. The prevailing trend has been for the ant succession to be more rapid in areas of higher, or more favourable, rainfall distribution. If the linear graph is used to derive this 3-year value at Trombetas (Figure 1), it would be approximately 30 species; if the curvilinear pattern was followed it would be closer to 35 species. Whichever value is accepted, the initial colonization by ants is considerably more rapid than in subtropical areas such as Poços de Caldas in the south of Brazil (14.5 species; Majer 1992), Richards Bay, South Africa (18–22 species; Majer & de Kock 1992), and northern Australia (22 species; Majer 1983a). Thus, using this yardstick, the rate of ant succession, or the elasticity of the succession (Westman 1986) is greater at Trombetas than in the higher latitudes. In order to correct for the high ant species richness in Amazonia it is also possible to express the 3-year value as a proportion of the species richness in the planalto forest. Using values from the standard sampling procedure, this figure is between 44 and 51%, which compares with 50% in southern Brazil (Majer 1992), about 50% in southern Africa (Majer & de Kock 1992) and 62% in northern Australia (Majer 1983a). In these terms, the rate of recolonization at Trombetas is not exceptionally rapid.

An additional aspect of the pattern of succession is that after an initial rapid rise, the increase in richness slows down and shows no overall increase in the oldest rehabilitated plot in relation to the 5-year-old plot. Indeed, the results of the ordination suggest that there is little or no tendency for ant community composition in the 5–11-year age range to converge towards any of the forest controls (Figure 2).

What is the obstacle to the restoration of the ant community? Firstly, it is common for the rate of increase in animal species to slow down in the later stages of succession (e.g. thrips (Stannard 1967), reptiles and amphibians (Nichols & Bamford 1985) and birds (Nichols & Watkins 1984)). Secondly, it is also known that species richness can exhibit oscillations during the succession (e.g. birds; Crawford *et al.* (1978)) and the degree of this oscillation is referred to as the dampening property of an ecosystem's resilience (Fox & Fox 1986). By drawing on an analogy with a stretched spring, Fox & Fox (1986) suggested that an ecosystem which appears to recover rapidly but which exhibits large oscillations in some feature, such as species richness, is underdampened while one which slowly returns to the pre-disturbance level with little or no oscillation is overdampened. Thus, an underdampened ecosystem may take a considerable time to stabilize out at its pre-disturbance level, even though it at first exhibits a rapid rate of recovery. If the oscillation in ant species richness at Trombetas is a true feature of the succession rather than an artefact resulting from rehabilitation processes, it may well be that the pattern conforms to the underdampened situation. If so, it should be noted that the oscillations have commenced well before the pre-disturbance level of species richness has been attained.

A second reason may be that an inadequate period of time may have passed for the ecosystem to recover. Evidence for this is provided by the physical and biological measurements recorded in the rehabilitated areas (Table 2). In comparison with the forest, most rehabilitated plots are characterized by changed soil structure, lower litter and dead wood, lower plant species richness, lower understorey and tree cover and smaller trees. Although the ecological requirements of the numerous Amazonian ant species are not well known, it is possible to make a tentative description of the broad nesting and feeding habits of individual genera by consulting the literature on South American ants. Figure 3 shows the relative proportion of ant species within broad nesting habits and feeding categories in the confined-to-forest, confined-to-rehabilitated-areas and present-in-both categories (see Table 3). In comparison with the forest ants, the species which have colonized the mines are represented by proportionally more generalist feeders, fewer specialist feeders and fungus cultivators, fewer soil and litter nesters, and proportionally more tree nesters. The high proportion of tree nesters in the rehabilitated areas is in part an artefact caused by the low

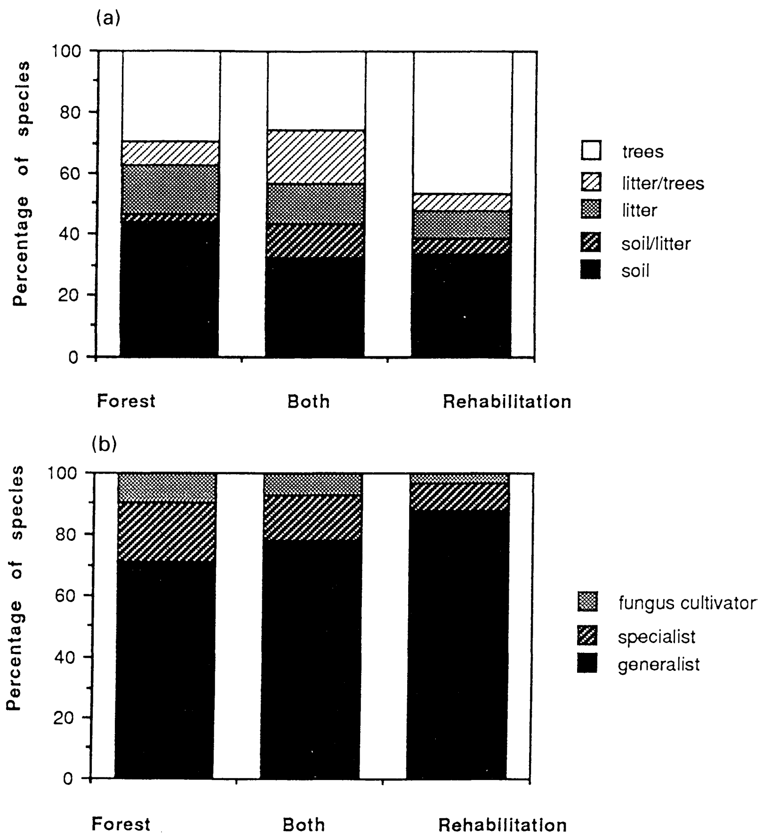

Figure 3. Percentage composition of ant species by (a) nesting site and (b) feeding specialization for those species which were only found in the forest, in the rehabilitated areas or in both situations.

trees being easier to sample than the tall trees of the forest. However, the data sugggest that although the tree stratum in the rehabilitated areas is well developed and able to cater for the requirements of a wide range of ant species, the structure or chemical nature of the soil and litter may still be inadequate to provide for appropriate nesting and feeding sites. The paucity of fungus cultivators and species which specialize in feeding on particular soil or litter invertebrates also tends to support this suggestion.

A third possibility is that the whole restoration process has stalled after five years. This could be associated with the failure of the rehabilitated areas to provide adequate floristic and structural diversity. There are many examples from around the world of vertebrate and invertebrate diversity being positively associated with floristic or structural characteristics of rehabilitation (see Table 6.3 in Majer 1989b). In terms of tree and understorey species richness, epiphyte loads, forest stratification, quantity of litter and logs and soil composition, the rehabilitated areas still lack many of the features of the original forest and it may be necessary for further management practices to be applied before succession will continue. The full habitat diversity and the dependent ant community cannot develop within 11 years; how long this will take or whether further management is required will depend on later surveys.

The similar ant species richness in the *Eucalyptus*/*Acacia* plantation and in the rehabilitated areas with mixed native vegetation contrasts with what was observed in southern Brazil (Majer 1992) where there were fewer species in *Eucalyptus* than in areas rehabilitated with native vegetation. This does not seem to be related to the existence of more than one tree species at Trombetas because the plantation was arranged in single-species blocks and the turnover in ant species between blocks was minimal. In part, it may be related to the absence of some species of *Atta*, *Cyphomyrmex*, *Azteca* and *Dolichoderus* in the Trombetas plantation being offset by an increase in generalists such as *Crematogaster* and *Paratrechina* spp. (Table 3). Additionally, the plantations support a high litter load and, in areas where trees have died, a moderate density of understorey shrubs, so the habitat requirements of a range of species would be present.

The data presented in this paper concern the ant community. It is likely that the composition of the ant community reflects the variation in many other components of the invertebrate fauna (Andersen 1990, Majer 1983b). Therefore, the general comments on the nature and rate of return of the ant fauna at Trombetas may have some applicability to the biota as a whole. However, it should be recognized that only after recolonization by a wider range of taxa over an extended period of time has been studied, will a complete understanding of the rehabilitation process at Trombetas be obtained.

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