



RESEARCH ARTICLE - ANTS

Changes in Epigeic Ant Assemblage Structure in the Amazon during Successional Processes after Bauxite Mining

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Article History

Edited by

Evandro N. Silva, UEFS, Brazil

Received 18 January 2020

Initial acceptance 13 April 2020


Final acceptance 15 March 2021

Publication date 26 March 2021

Keywords

Amazonian ants, Trombetas, biomonitoring, biodiversity, ecological indicators, land rehabilitation.

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Abstract

Environmental impact studies often involve monitoring and using bioindicators to evaluate the restoration stage of impacted areas. We aimed to assess ant assemblages' response to the ecological succession of previously disturbed areas in the Brazilian Amazon. We sampled epigeic ant assemblages in five bauxite mining areas, representing different restoration stages, and compared them with two pristine areas. We also compared trends in species richness at the same mine site investigated 14 years earlier. Ten pitfall traps and four Winkler samples of litter were taken along a 100-m transect in each area. We expected that ant species richness would increase with the amelioration in habitat condition (i.e., environmental surrogates of ecological succession, including litter depth, soil penetrability, the circumference of trees, the distance of trees to adjacent trees, and percentage of ground cover). We also compared the efficacy of both sampling methods. Due to more significant sampling effort, pitfall traps captured more ant species than Winkler sacks. However, Winkler samples' addition allowed the collection of more cryptic species than by pitfall traps alone. We sampled a total of 129 ant species, with increases in ant species richness in more mature rehabilitation. Nevertheless, similarity analysis indicated a significant difference between ant assemblages of rehabilitated areas and pristine ones. Assemblages differed mainly by the presence of specialist and rare species, found only in pristine plots. Rehabilitated areas exhibited a significant increase in tree circumference as they reached more ecologically advanced stages, which contributed to increasing ant species richness. These trends and comparison with the earlier study indicate that although there are favorable increases in ant species richness, in terms of species composition, rehabilitated areas were far from achieving an ant assemblage composition or environmental status that closely resembles pristine areas.

Introduction

Brazil has become an important global trader of raw materials in the mineral sector, including bauxite, whose main reserves occur within the Legal Amazon (IBRAM 2010). In light of law enforcement and acquisition of environmental

certificates (Lamb et al. 2005), mining companies have developed ecological restoration programs that aim to restore vegetation that resembles the forest, ecologically and visually (Parrotta & Knowles 1999). Because of high levels of ecosystem impacts during mining operations (Peterson & Heemskerk 2001), restoration needs to develop complex



knowledge associated with the mining process, including restoration with native species and implementing long-term monitoring processes (e.g., Fernandes et al., 2010; Kollman et al., 2016).

Despite law enforcement and efforts by the industries involved, the monitoring of restoration programs in forest ecosystems has mainly been carried out from a dendrological perspective (Kollman et al., 2016). Most environmental components measured relate to the observed changes in factors such as habitat structure and plant biomass (Reis & Kageyama, 2003; but see Fernandes et al., 2010). This simplistic approach underestimates meaningful ecological interactions that can potentially restore biodiversity and ecosystem services through natural succession processes, i.e., interactions necessary to re-establish ecosystem functioning (Stanturf et al., 2001; Harris et al., 2006); for a review, see Kollman et al., 2016. Detailed studies on recolonization of soil biota and distribution of species after mining operations can provide management programs with more robust information on how ecological processes evolve to achieve a sustainable stage (Kollman et al., 2016). In this case, a common approach is the use of bioindicators that can reflect the restored sites' environmental conditions (Ribas et al., 2012; Schmidt et al., 2013, Donoso, 2017).

Some target ant species play specific ecological roles in the soil (Andersen & Sparling, 1997; Bisevac & Majer, 1999; Passos & Oliveira, 2003; 2004; Donoso & Ramon, 2009; Schmidt et al., 2013), and their presence after mining operations can indicate the stage of ecological succession and soil regeneration (Majer, 1983; Underwood & Fisher, 2006; Ottonetti & Tucci, 2006; Ribas et al., 2012). Most of the physical-chemical processes and crucial biological interactions for habitat reestablishment occur in the soil, where most ant species forage (Schmidt et al., 2013). However, colonization and establishment of these species will be dependent on local environmental characteristics, as well as the management practices developed after mining, e.g., by

planting a mix of attractive species that is favorable to the soil biota (Majer, 1983; Andersen & Majer, 2004; dos Santos Alves et al., 2011). A widely used restoration management procedure in Brazil is the return of topsoil after mining activities have ceased (Parrotta & Knowles, 1999). Therefore, monitoring the response of ant assemblages to environmental restoration has to involve sampling sensitive parameters that reflect natural succession and permit evaluation of success and adoption of local management practices (Ribas et al., 2012).

Disturbance in tropical rain forests directly influences ant assemblages' structure (Kaspari, 1996; dos Santos Alves et al., 2011). In contrast, the return of this faunistic group to a disturbed area increases the number of local processes and interactions needed for the ecosystem's sustainability. An earlier 1992 study at the same mine-site considered here (Majer, 1996) sampled ants in three forest reference sites and ten rehabilitation areas, ranging from 0-11 years of age. We built upon this study using some sites between 3-13 years older than those from the earlier study. We aimed to determine how and if ant community structure of restored areas following bauxite mining converges towards the structure level found in pristine adjacent forests with the increased passage of time. We hypothesize that 1) there would be an increase in ant species richness with the improvement of the environmental parameters according to restoration time, and 2) ant species composition would change as a response to ecological succession since some groups of species respond in distinctive ways to environmental parameters (Underwood & Fisher, 2006).

Materials and Methods

Study site

The study area is in the district of Porto Trombetas, 65 km from Oriximiná (western region of Pará State, Brazil, eastern Amazon) (Fig 1), and 100 km west of the Trombetas river confluence with the Amazon River, northern Brazil.

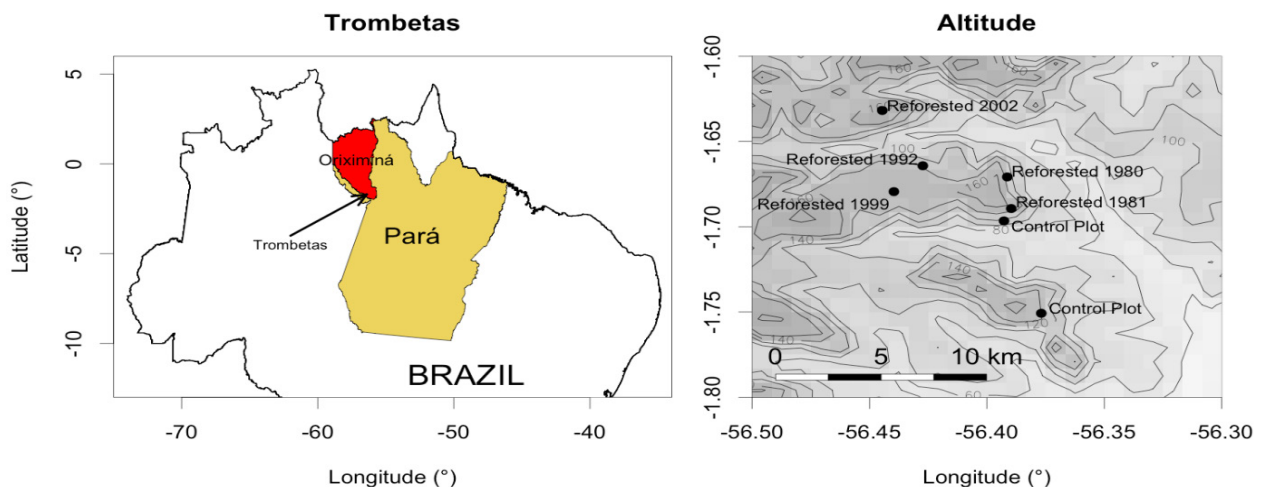


Fig 1. Left: Geographical localization of Porto Trombetas, north of Brazil, Pará State. Right: study areas inserted in a hypsometric map.

We carried out the study restoration areas of Trombetas bauxite mines, operated by Mineração Rio do Norte S.A. (hereafter, MRN) and situated in areas of tropical, pristine forest. Since the 1980s, the restoration program used by MRN has involved topsoil replacement, application of litter and triturated wood, and planting mixed stands of native forest species, aiming to restore approximately 100 ha/year (Parrotta & Knowles 1999).

The vegetation is characteristic equatorial evergreen rainforest. According to Köppen, the local climate is Am (tropical monsoonal), with well-established dry (winter) and wet (summer) seasons (see Parrotta & Knowles 1999). Mean annual rainfall at Porto Trombetas in past years (1970–1993) was 2185.64 mm, whereas the mean maximum and minimum temperatures were 34.6 and 19.9 °C (see Parrotta & Knowles 1999). During our study period (undertaken between May 20 and June 20, 2006), the maximum and minimum temperatures in Porto Trombetas were respectively 32.5°C and 22.0°C; 476.5 mm of rainfall fell in May 2006, and 133.0 mm of rain fell in June 2006 (CPTEC / INPE).

Sampling design

We selected two areas of undisturbed forest as controls (a plateau and a flank) and five areas with different ages since restoration (4 to 26-year-old rehabilitation areas) (Table 1). Within each area, a 100 m-long transect was arbitrarily set for sampling ants and measuring habitat structure. The latter included tree spacing and circumference at breast height, percentage soil cover and depth, litter depth and dry weight of litter, all commonly used as surrogate explanatory variables for ecological succession.

We considered epigeic ants as all those ants foraging or nesting on the soil surface or in the litter. We used Pitfall traps and Winkler extractors to survey the ant fauna. Combining these two methods yields a good sample, and they are the two most efficient techniques recommended for studying epigeic ants (Bestelmeyer et al., 2000; Delabie et al., 2000; Brown & Mathews, 2016). We installed ten pitfall traps, consisting of cups of 7 cm diameter, 200 ml volume, containing 30 ml of 70% ethanol, in the ground every 10 m along the 100 m transect. Traps remained for seven consecutive days in each area.

Along the same transect, we sift 1 m² litter samples taken every 25 m, producing a total of four samples per plot.

The litter was sieved and placed in Winkler sacks that we left in Winkler extractors for 72 hours outside the laboratory. This process allows sieved litter material to dry and ants to migrate in search of other habitats, falling into the vial of ethanol attached to the bottom of the extractor. After the sampling procedure, we sorted all material, identified it, and deposited voucher specimens at CEPLAC (Comissão Executiva do Plano da Lavoura Cacaueira), Bahia, Brazil.

We used various habitat variables as evidence of forest structural changes along the restoration chronosequence (a surrogate of forest succession). We considered these variables influential on ant community richness and composition (Andersen, 2000; Yanoviak & Kaspari, 2000; Ribas & Schoederer, 2007; Schmidt et al., 2013; Solar et al., 2016a, see also Paolucci et al., 2016). We obtained an average of tree spacing (distance) and tree circumference at breast height from the four nearest trees at each sampling point. We took other measures inside a 1 m² frame placed around each trap before installation. We visually estimated soil cover percentage within each quadrat. We measured litter depth in each corner of the quadrat, with the mean providing an average litter depth per quadrat. At each corner, we measured soil penetrability by using a metal stick with standard pressure, obtaining the average of these four penetration measures.

Statistical analyses

Aiming to test sampling efficiency and using two distinct sampling methods and different sampling efforts between them, we built a species accumulation curve that calculated the expected richness for random samples of data. We used the Chao 2 index as recommended by Colwell and Coddington (1994) as the best estimate for incidence-based richness.

To test the influence of environmental parameters on ant species richness, we built a complete model. We used the mean values of tree spacing, tree circumference at breast height, percentage of soil cover, percentage of litter, and soil compression (using data for ten pitfall traps combined). Winkler samples do not appear in the model as they were randomly taken in each area, not following the same statistical design as the pitfall trap samples. After evaluating the variables' contribution, we simplified the model by removing non-significant variables until reaching the minimum suitable

Table 1. Location and rehabilitation time for five mined areas and two pristine areas surveyed for epigeic ants in 2006 in the district of Porto Trombetas, Pará State, Brazil. The species richness of ants found in these areas is also shown.

Areas	Latitude	Longitude	Restoration time (years)	Total richness
Plateau Forest	1°45' 044'' S	56°22' 611'' W	pristine	34
Flank Forest	1°41' 795'' S	56°23' 564'' W	pristine	53
Rehabilitated 2002	1°37' 911'' S	56°26' 675'' W	4	32
Rehabilitated 1999	1°40' 765'' S	56°26' 378'' W	7	40
Rehabilitated 1992	1°39' 855'' S	56°25' 639'' W	14	39
Rehabilitated 1981	1°41' 360'' S	56°23' 379'' W	25	39
Rehabilitated 1980	1°40' 248'' S	56°23' 481'' W	26	47

model. We fitted multiple regression models and tested them using Poisson errors. We performed all analyses using the R Development Core Team software.

We compared the differences in species composition in ant assemblages between rehabilitated and native plots using non-Metric Multidimensional Scale (nMDS) multivariate analysis. We prepared a binary matrix (ant species absence or presence in each area) and calculated the dissimilarities between these areas by the Jaccard index. The second step was a one-way Analysis of Similarity (one-way ANOSIM) that established whether there were significant differences in species composition between plots (R-value and $p < 0.01$) (Clarke & Green 1988). A posteriori, we built a table for ant species relative abundance. We considered all 14 samples in each area (10 pitfall traps and four Winkler samples). We calculated the number of records (maximum 14 in each area) to represent each species' relative abundance.

Results

We recorded 129 ant species, representing 40 genera and eight subfamilies (Table 1). Myrmicinae was the richest subfamily, while *Pheidole* was the richest genus, with 15 species, followed by *Solenopsis* (10 spp.), *Crematogaster* (7 spp.), *Strumigenys* and *Pseudomyrmex* (7 spp. each). *Solenopsis* sp.1 presented the highest relative abundance (number of species occurrences among all samples) in rehabilitated and

pristine areas. *Strumigenys denticulata* was also widespread, both in rehabilitated and pristine plots. *Crematogaster tenuicola*, *Nylanderia steinheili*, *Crematogaster brasiliensis* and *Ectatomma brunneum* were the most common species. They were only found in rehabilitated areas, not found in any plateau or flank samples. *Mayaponera constricta* and *Pachycondyla harpax* were also widely distributed in the rehabilitated plots but were also found less frequently in pristine areas. We found 26 species exclusively in pristine areas, including species of the genera *Apterostigma*, *Cyphomyrmex*, *Discothyrea*, *Thaumatomyrmex*, *Eciton*, *Gnamptogenys*, *Basicrosus*, *Blepharidatta* and *Strumigenys* (Table 2).

We observed a tendency for an asymptote in the accumulation curve of total species sampled in the study. After combining all samples, the Chao 2 index indicated a sampling efficiency of 74% (129 species observed), giving an expected number of 173 species (Fig 2). Pitfall traps captured 111 ant species, while Winkler extractors collected 69 ant species, of which 17 we sampled exclusively by this method. In total, pitfall trap and Winkler extractor samples differed by 37.7 % in terms of ant species composition (Jaccard; $p = 0.006$). Winkler extraction captured four species of the genus *Hypoponera* (including the species *H. foreli*), *Strumigenys denticulata* and *S. tridifera*. *Gnamptogenys horni* was found three times more frequently in pitfall traps than by Winkler extraction, while *Pheidole* sp.3 and *Acromyrmex* sp.2 were only captured by pitfall trapping.

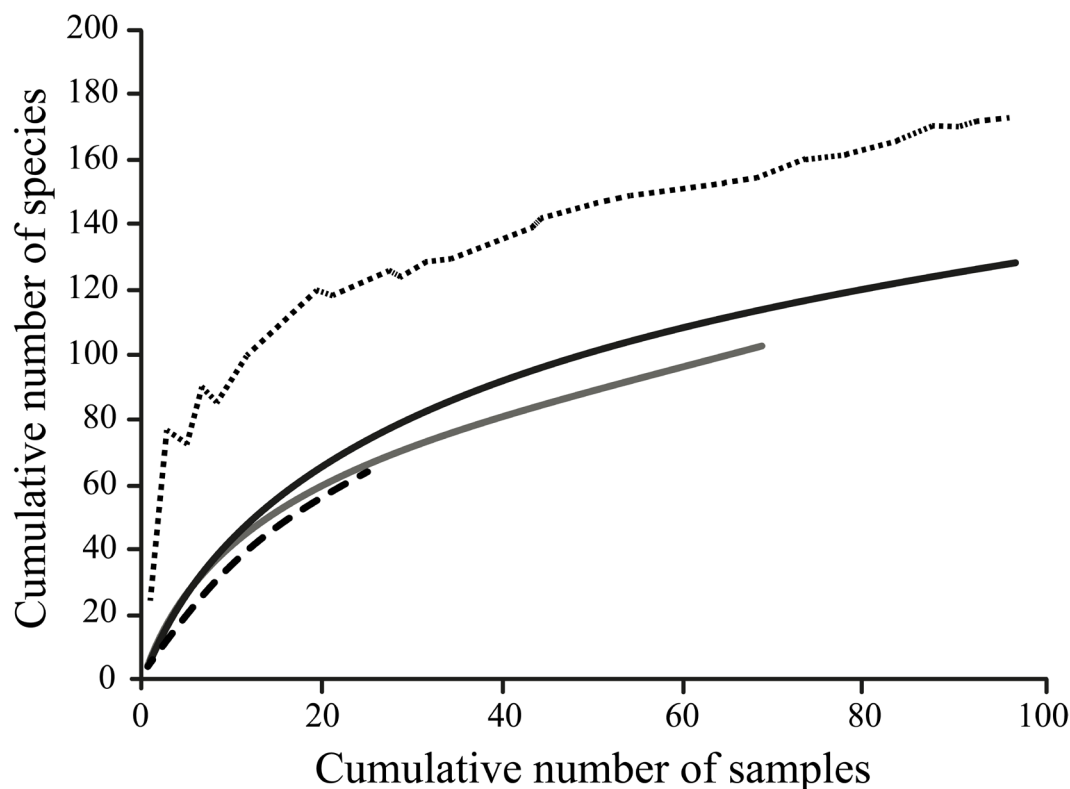


Fig 2. Cumulative species number by accumulation curve and cumulative sampling effort. The dotted line represents the estimated species richness by Chao 2 index. The continuous black line is the effort of all samples – Coleman curve. The continuous gray line shows the sum of species collected in rehabilitated areas, whereas the black dashed line shows collected species in pristine plots (Control).

Means for the environmental parameters are shown in Table 3. None of these parameters explained ant species richness. Rehabilitated plot means showed increased tree circumference toward a higher advanced stage close to values in pristine areas. This trend was positively correlated with increasing distance (spatial distribution) between trees

($R=0.93$, $p=0.003$). Litter depth was significantly thicker in pristine areas and showed a high value in some of the younger rehabilitated plots (Table 3). Soil penetrability varied between rehabilitated areas, and pristine ones exhibited higher values. Regarding soil litter cover, all plots except the seven yr-old plot exhibited complete coverage of soil (Table 3)

Table 3. Environmental characteristics (mean + SD) of rehabilitated and pristine areas. Numbers with similar letters indicate no significant differences between means (see Materials and Methods).

Years since rehabilitation	2002 4	1999 7	1992 14	1981 20	1980 21	Plateau pristine	Flank pristine
Soil cover (%)	85.1+0.11a	69.5+0.23b	92.3+0.09a	94.7+0.08a	96.8+0.04a	89.5+0.12a	93.0+0.10a
Litter thickness (cm)	11.7+4.94a	5.4+2.61c	8.2+1.41b	7.9+2.12b	7.3+1.28b	12.0+2.51a	11.3+3.43a
Soil penetrability (cm)	10.2+4.86a	9.8+2.42a	10.8+2.51a	11.9+1.99a	7.1+2.01b	16.97+2.16 c	16.2+4.79 c
Distance to nearest trees (cm)	166.0+41.96a	175.8+44.12a	206.6+56.46b	196.5+45.35b	200.9+53.00b	315.2+85.29c	299.5+121.55c
Circumference at breast height Tree circumference (cm)	18.9+3.14a	20.1+4.63a	30.4+6.74b	41.1+11.33c	31.03+9.24b	63.9+45.91e	53.6+22.65 d

Discussion

The high richness of ant genera and morphospecies found in this study confirms previous studies showing that the Amazon forest exhibits a very rich ant community (Majer, 1996; Majer & Delabie, 1994). Compared to inventory studies in tropical rainforests, our combined sampling effort of both methods was sufficient for a satisfactory survey of the community (129 spp, 74% of efficiency) (see Solar et al., 2016b). We expected an increase of ant species richness in older successional stages associated with increases in environmental parameters (Ribas et al., 2003; Donoso et al., 2013). However, unlike in other studies in disturbed areas (Ottonetti & Tucci, 2006; Vasconcelos et al., 2000; Schmidt et al., 2013), this was not the case. However, the ant community structure was significantly distinct between areas (see Solar et al., 2016a), mainly due to the presence of specific and sensitive species. The natural history and function of these ant species can tell us much about the ecological state and health of the areas where they occur (see Bihn et al., 2010; Leal et al., 2012; Schmidt et al., 2013; Solar et al., 2016b; Donoso 2017). That could be the case of ant species exclusively found in pristine areas, such as *Basicerros balzani* and *Blepharidata brasiliensis*, associated with undisturbed forest (Vasconcelos et al., 2000). Also of relevance are *Gnamptogenys horni* and *Strumigenys tridifera*, endemic from the Brazilian Amazon (Kempf & Brown, 1969), *Discothyrea*, with a low tolerance to disturbance (Brown, 1957), and *Thaumatomyrmex*, all of which are exclusive of tropical native areas (Cerdá & Dejean, 2011). Moreover, the two species of army ants, *Eciton burchellii* and *Neivamyrmex swainsonii*, which prefer wetter and more pristine areas (Levings, 1983), were only found in native areas. In this case, humidity, lower temperature oscillation, higher litter thickness, among other environmental conditions in the forest, probably favor their biological requirements over conditions in rehabilitated plots.

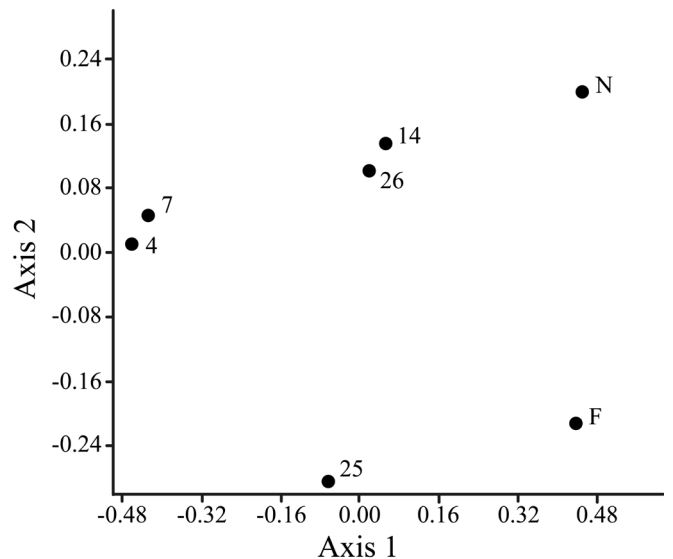


Fig 3. Diagram of multivariate analysis of NMDS (Non-Metric Multidimensional Scale). Pristine areas are represented by N = plateau and F = flank, whereas rehabilitated areas are represented by the number of years since restoration (Jaccard index, Stress = 0.13).

The increase in circumference and spacing of trees in rehabilitated plots towards or near values in pristine areas indicates a positive trend in ecological succession (Ruiz-Jaen & Aide, 2005). In the early 1980s, MRN started a restoration program with a mix of native species of trees. This process favors the establishment of early growth trees. Still, due to the short life-span of pioneer species (10-20 years), there would be no certainty about whether succession will proceed towards the mature forest for many years. In our study, a more sustainable succession is expected to be occurring because of the presence of climax species in rehabilitated areas, including *Bertholletia excelsa* (Lecythidaceae), *Stryphnodendron guianensis* (Fabaceae), *Sclerolobium paniculata* (Fabaceae),

Tapirira guianensis (Anacardiaceae), and *Bowdichia virgilioides* (Fabaceae) (GWF. pers. obs). Also, these rehabilitated areas may be enriched with propagules coming from nearby native vegetation. Secondary forests can support their characteristic ant fauna, probably containing pioneer and/or generalist ant species and rare and more specific ones. Furthermore, the presence of well-developed and established plants of rapid-growth, like *Cecropia* (e.g., in the four-year-old area), resulting in a thicker litter layer formed by fallen leaves, which is as thick as in the two native plots. These facts mean that even the young rehabilitated plots can support a rich epigeic ant community.

Despite a higher number of pitfall trap units than Winkler samples, the latter method allowed us to sample smaller and cryptic species of the genera *Carebara*, *Cyphomyrmex*, *Discothyrea*, *Hypoconera* and *Strumigenys*. Pitfall traps collected exclusive species and, as expected, more active and larger ones (Olson, 1991; Orsolon-Souza, 2011), including all species of the genus *Pseudomyrmex* which mainly forage on plants. In our study, Winkler extractors could have their efficacy impeded due to the atypical rainfall, with rainfall rates being much higher than 17 years ago (MRN data). Lassau and Hochuli (2004), using only pitfall traps, argued that a range of possible biases might accompany pitfall trapping as a sampling technique in structurally complex areas. In our study, pitfall traps and Winkler extractors were complementary in sampling epigeic ants in structurally more complex native areas. Despite the lower effort devoted to Winkler samples, the number of ant species sampled by the two methods was sufficient. Since the effectiveness of methods differs, we suggest future brief surveys must consider a combination of both methodologies, allowing a more accurate census of ant species in structurally complex areas of Amazonia.

Table 4 compares the ant species richness values in rehabilitation between the earlier (Majer, 1996) and the current study. The comparison focuses on species richness since the morphospecies code numbers are not standardized across the two studies. Also, the earlier study data include arboreal ants, so values in sites where the tree stratum is well developed will tend to be relatively higher in Majer's (1996) study. With these limitations in mind, the values seem reasonably comparable in the younger sites, with similar values for the youngest two areas being obtained in both studies (Table 4). Although richness in the oldest three sites was lower, or in the range of Majer's (1996) 9-14-year-old sites, we remember that the earlier study included arboreal species, thus making richness in the pristine sites 62 to 75% higher. By analogy, the 14-26-year-old sites in the current study might be performing well in terms of species richness, supporting ant richness close to that of pristine sites. As in the earlier study, the multivariate analysis indicates that there is still a significant difference between rehabilitated and pristine sites in terms of species composition. Unfortunately, it is impossible to compare this degree of difference between the earlier and the current study due to different analytical procedures.

Table 4. Comparison of ant species richness values in rehabilitation from the earlier 1992 study (Majer 1996) with values obtained in the current study.

Age of rehabilitation (yr)	1992 Study	Current study
0	4	
0.3	8	
4		32
5	46	
6	43	
7	41	40
7	41	
8	46	
9	55	
10	46	
11	44	
14		39
25		39
26		47
Plateau	54	34
Flank	70	53

Some studies have evaluated ant's efficacy as bioindicators, but mining areas are poorly represented (Ribas et al., 2012; Schmidt et al., 2013). Despite changes in the ant fauna composition between rehabilitation stages (Schmidt et al., 2013), and even though 26 years is considered a relatively long time for restoration, these areas still have a valuable conservation value (e.g., Rozendaal et al., 2019). Thus, despite aiming to develop restoration of a forest characteristic of the area, succession still needs more time to achieve a full recovery in these previously impacted areas (see Fernandes et al., 2010, also see Rozendaal et al., 2019). These areas lack some species that indicate a healthy, stable, and advanced ecological stage found in native areas. The adjacent pristine areas play a fundamental role as the source of rare species' propagules for the colonization of areas under the ecological successional process. Hence, for reliable information on species diversity and ecosystem function, long-lasting monitoring is needed in rehabilitated and native areas (see Bihn et al., 2010).

Acknowledgments

We thank two anonymous reviewers for their valuable comments on earlier versions of this ms. We also thank Kevin Cazelles for his support in map design. Financial aid was provided by the Programa de Pós-Graduação em Entomologia (UFV), CNPq, Planta Ltda, and Fapemig, while MRN provided field logistics.

Table 2. Ant species found within each sample area and total species richness. The last column represents the relative percentage of occurrence of each species among all 98 traps. In this column, asterisks represent ant species sampled exclusively by Winkler extractors.

Species	4 yrs	7 yrs	14 yrs	25 yrs	26 yrs	Flank	Plateau	Occurrence
Subfamily Dolichoderinae								
<i>Dorymyrmex</i> sp. 1	0	1	0	0	0	0	0	1.02
Subfamily Dorylinae								
<i>Acanthostichus brevicornis</i> (Emery)	0	0	1	0	0	1	0	2.04
<i>Eciton burchelli</i> (Westwood)	0	0	0	0	0	2	0	2.04
<i>Labidus spininodis</i> (Emery)	1	0	0	0	0	1	1	3.06
<i>Neivamyrmex</i> sp. 1	0	0	0	1	0	1	0	2.04
<i>Neivamyrmex swainsonii</i> (=fallax) Shuckard	0	0	0	0	0	1	0	1.02
<i>Nomamyrmex esenbeckii</i> (Santschi)	0	0	1	0	0	0	0	1.02
Subfamily Ectatomminae								
<i>Ectatomma brunneum</i> (Smith)	3	8	0	3	2	0	0	16.33
<i>Ectatomma suzanae</i> (Almeida)	0	0	0	2	0	2	0	4.08
<i>Ectatomma tuberculatum</i> (Olivier)	0	0	0	0	2	0	0	2.04
<i>Gnamptogenys horni</i> (Santschi)	0	0	0	0	1	2	6	9.18
<i>Gnamptogenys moelleri</i> (Forel)	0	0	1	1	0	1	0	3.06
<i>Gnamptogenys striatula</i> (Mayr)	0	0	0	0	0	1	0	1.02
<i>Gnamptogenys sulcata</i> (Smith)	0	0	0	1	0	1	0	2.04
Subfamily Formicinae								
<i>Brachymyrmex</i> sp. 1	0	8	0	0	0	0	0	8.16
<i>Brachymyrmex</i> sp. 2	0	0	0	0	1	0	0	1.02
<i>Camponotus atriceps</i> (Smith)	1	0	0	0	0	0	0	1.02
<i>Camponotus fastigatus</i> (Roger)	0	2	0	1	0	0	0	3.06
<i>Camponotus leydigi</i> (Forel)	0	1	0	0	0	0	0	1.02
<i>Camponotus melanoticus</i> (Emery)	0	5	0	0	0	0	0	5.10
<i>Camponotus novogranadensis</i> (Mayr)	0	8	2	0	1	0	0	11.22
<i>Camponotus rufipes</i> (Fabricius)	0	8	0	0	1	0	0	9.18
<i>Gigantiops destructor</i> (Fabricius)	0	0	1	0	1	0	0	2.04
<i>Nylanderia fulva</i> (Mayr)	1	3	0	0	0	0	0	4.08
<i>Nylanderia guatemalensis</i> (Forel)	0	1	2	0	1	0	0	4.08
<i>Nylanderia</i> sp. 1	2	5	1	2	0	1	0	11.22
<i>Nylanderia</i> sp. 2	2	6	3	0	2	0	0	13.27
<i>Nylanderia</i> sp. 3	0	3	4	2	2	1	0	12.24
<i>Nylanderia steinheili</i> (Forel)	2	1	4	2	1	0	0	10.20
Subfamily Myrmicinae								
<i>Acromyrmex</i> sp. 1	0	0	1	0	0	1	0	2.04
<i>Acromyrmex</i> sp. 2	0	0	0	0	0	1	4	5.10
<i>Apterostigma</i> sp. 1	0	0	0	0	0	0	1	1.02
<i>Apterostigma</i> sp. 2	0	0	0	0	0	1	0	1.02
<i>Atta sexdens</i> (Forel)	1	2	0	0	0	0	0	3.06
<i>Basiceros balzani</i> (Emery)	0	0	0	0	0	3	0	3.06
<i>Blepharidatta brasiliensis</i> (Wheeler)	0	0	0	0	0	1	2	3.06
<i>Carebara</i> sp. 1	0	0	0	0	1	0	0	1.02*
<i>Centromyrmex gigas</i> (Forel)	0	0	0	0	1	0	0	1.02
<i>Cephalotes</i> sp. 1	0	0	1	0	0	0	0	1.02
<i>Cephalotes</i> sp. 2	0	2	1	0	0	0	0	3.06
<i>Cephalotes</i> sp. 3	0	0	0	0	0	1	0	1.02
<i>Crematogaster brasiliensis</i> (Mayr)	5	0	0	4	8	0	0	17.35

Table 2. Ant species found within each sample area and total species richness. The last column represents the relative percentage of occurrence of each species among all 98 traps. In this column, asterisks represent ant species sampled exclusively by Winkler extractors. (Continuation)

Species	4 yrs	7 yrs	14 yrs	25 yrs	26 yrs	Flank	Plateau	Occurrence
Subfamily Myrmicinae								
<i>Crematogaster curvispinosa</i> (Mayr)	1	0	0	0	0	0	0	1.02*
<i>Crematogaster evallans</i> (Forel)	0	0	0	2	0	0	0	2.04
<i>Crematogaster flavosensitiva</i> (Longino)	0	0	2	0	0	0	1	3.06
<i>Crematogaster limata</i> (Smith)	0	0	3	2	3	0	0	8.16
<i>Crematogaster stollii</i> (Longino)	0	0	0	0	0	0	1	1.02
<i>Crematogaster tenuicula</i> (Forel)	2	3	5	12	6	0	0	28.57
<i>Cyphomyrmex costatus</i> (Mann)	0	0	0	0	0	0	1	1.02*
<i>Cyphomyrmex rimosus</i> (Mayr)	2	3	0	0	0	0	0	5.10
<i>Cyphomyrmex</i> sp. 1	0	1	0	0	1	0	2	4.08
<i>Cyphomyrmex</i> sp. 2	1	0	0	0	0	0	0	1.02
<i>Cyphomyrmex</i> sp. 3	0	0	0	1	1	0	0	2.04*
<i>Cyphomyrmex</i> sp. 4	0	0	0	2	1	0	0	3.06
<i>Myrmicocrypta</i> sp. 1	0	0	0	0	1	0	0	1.02
<i>Ochetomyrmex</i> sp. 1	0	0	3	1	2	1	1	8.16
<i>Pheidole jeannei</i> (Wilson)	0	0	1	0	0	3	0	4.08
<i>Pheidole midas</i> (Wilson)	0	0	1	0	1	1	1	4.08
<i>Pheidole</i> sp. 1 gp fallax	0	0	1	3	0	0	0	4.08
<i>Pheidole</i> sp. 2 gp fallax	2	0	0	0	0	0	0	2.04
<i>Pheidole</i> sp. 3 gp diligens	0	0	2	0	1	1	4	8.16*
<i>Pheidole</i> sp. 4 gp diligens	0	0	0	0	0	1	0	1.02
<i>Pheidole</i> sp. 5 gp fallax	0	0	0	0	0	1	0	1.02
<i>Pheidole</i> sp. 6 gp gertrudae	1	1	0	0	0	2	0	4.08
<i>Pheidole</i> sp. 14	0	0	0	0	0	1	0	1.02
<i>Pheidole</i> sp. 16	0	1	0	0	0	0	0	1.02
<i>Pheidole</i> sp. 17	2	0	0	0	0	2	0	4.08
<i>Pheidole</i> sp. 19	0	0	0	0	1	0	1	2.04
<i>Pheidole</i> sp. 24	0	0	0	0	0	1	0	1.02*
<i>Pheidole</i> sp. 25	0	0	0	0	1	0	0	1.02
<i>Pheidole</i> sp. 29 gp gertrudae	0	0	1	0	0	1	1	3.06*
<i>Rogeria</i> sp. 1	0	4	0	4	2	1	1	12.24
<i>Sericomyrmex</i> sp. 1	0	0	3	7	0	0	1	11.22
<i>Sericomyrmex</i> sp. 2	0	0	1	0	1	0	1	3.06
<i>Solenopsis geminata</i> (Fabricius)	1	0	0	0	0	0	0	1.02
<i>Solenopsis</i> sp. 1	2	7	11	3	3	1	4	31.63
<i>Solenopsis</i> sp. 2	0	0	4	1	3	1	0	9.18
<i>Solenopsis</i> sp. 3	0	0	0	0	0	1	0	1.02
<i>Solenopsis</i> sp. 4	1	0	0	0	0	0	0	1.02
<i>Solenopsis</i> sp. 5	0	0	2	0	0	0	0	2.04
<i>Solenopsis</i> sp. 6	0	0	1	0	0	0	0	1.02
<i>Solenopsis</i> sp. 7	1	0	0	0	1	0	0	2.04
<i>Solenopsis</i> sp. 8	0	0	0	1	0	1	1	3.06*
<i>Solenopsis</i> sp. 9	1	0	0	0	0	0	0	1.02
<i>Strumigenys</i> sp.2	0	0	0	1	0	0	0	1.02
<i>Strumigenys cordovensis</i> (Mayr)	0	0	0	1	0	0	0	1.02*
<i>Strumigenys denticulata</i> (Mayr)	2	2	3	1	4	2	3	17.35
<i>Strumigenys elongata</i> (Roger)	0	0	0	0	0	1	0	1.02*

Table 2. Ant species found within each sample area and total species richness. The last column represents the relative percentage of occurrence of each species among all 98 traps. In this column, asterisks represent ant species sampled exclusively by Winkler extractors. (Continuation)

Species	4 yrs	7 yrs	14 yrs	25 yrs	26 yrs	Flank	Plateau	Occurrence
Subfamily Myrmicinae								
<i>Mycetomoellerius farinosus</i> (Emery)	0	0	0	4	1	0	0	5.10
<i>Mycetomoellerius</i> sp. 1	0	0	0	0	0	2	0	2.04
<i>Strumigenys trudifera</i> (Smith)	0	0	0	0	0	1	2	3.06*
<i>Strumigenys</i> sp. 1	2	1	0	0	1	3	1	8.16*
<i>Strumigenys</i> sp. 6	0	0	0	0	0	1	0	1.02
<i>Wasmannia auropunctata</i> (Roger)	1	13	3	0	0	0	1	18.37
<i>Wasmannia</i> sp. 2	0	1	2	0	0	0	0	3.06
<i>Wasmannia</i> sp. 3	0	1	0	0	0	0	0	1.02
Subfamily Ponerinae								
<i>Anochetus diegensis</i> (Forel)	0	0	0	1	0	0	1	2.04
<i>Anochetus horridus</i> (Kempf)	0	0	0	2	0	2	0	4.08
<i>Anochetus mayri</i> (Emery)	0	5	0	2	1	0	0	8.16
<i>Anochetus</i> sp. prox. <i>bispinosus</i> (Smith)	0	0	0	1	1	0	0	2.04*
<i>Anochetus</i> sp. 1	0	0	0	0	1	0	1	2.04
<i>Anochetus</i> sp. 2	0	0	0	1	0	0	0	1.02*
<i>Hypoponera foreli</i> (Mayr)	0	2	6	5	2	3	1	19.39
<i>Hypoponera</i> sp. 1	0	1	0	0	1	3	3	8.16*
<i>Hypoponera</i> sp. 2	2	5	1	2	2	3	2	17.35
<i>Hypoponera</i> sp. 3	1	1	0	5	0	0	0	7.14
<i>Hypoponera</i> sp. 4	0	0	0	0	1	2	2	5.10*
<i>Hypoponera</i> sp. 5	3	0	2	0	1	1	1	8.16
<i>Leptogenys</i> sp. 1	0	0	2	0	0	1	1	4.08
<i>Mayaponera arhuaca</i> (Forel)	1	2	0	1	0	0	0	4.08
<i>Mayaponera constricta</i> (Mayr)	6	1	1	6	5	0	1	20.41
<i>Neoponera apicalis</i> (Latreille)	2	0	0	0	3	0	0	5.10
<i>Neoponera verena</i> (Forel)	0	0	7	0	0	0	0	7.14
<i>Odontomachus allolabis</i> (Kempf)	0	0	0	1	0	0	0	1.02
<i>Odontomachus bauri</i> (Emery)	0	8	0	0	0	0	0	8.16
<i>Odontomachus caelatus</i> (Brown)	0	0	0	0	0	2	0	2.04
<i>Odontomachus haematodus</i> (Linnaeus)	3	0	0	1	2	1	0	7.14
<i>Odontomachus meinerti</i> (Forel)	0	0	0	0	0	0	1	1.02
<i>Pachycondyla crassinoda</i> (Latreille)	0	0	1	0	5	0	0	6.12
<i>Pachycondyla harpax</i> (Fabricius)	1	2	4	5	0	1	0	13.27
<i>Thaumatomyrmex</i> sp. 1	0	0	0	0	0	0	1	1.02
Subfamily Proceratiinae								
<i>Discothyrea</i> sp. 1	0	0	0	0	0	2	0	2.04*
Subfamily Pseudomyrmecinae								
<i>Pseudomyrmex boopis</i> (Roger)	0	0	0	0	1	0	0	1.02
<i>Pseudomyrmex filiformis</i> (Fabricius)	0	0	0	0	0	1	0	1.02
<i>Pseudomyrmex gracilis</i> (Fabricius)	0	0	0	0	1	0	0	1.02
<i>Pseudomyrmex oculatus</i> (Smith)	0	1	0	0	0	0	0	1.02
<i>Pseudomyrmex termitarius</i> (Smith)	0	2	0	0	0	0	0	2.04
<i>Pseudomyrmex</i> sp. 1 gp <i>pallidus</i> (Smith)	0	0	0	0	0	1	0	1.02
<i>Pseudomyrmex</i> sp. 2 gp <i>pallidus</i> (Smith)	0	1	0	0	0	0	0	1.02
Total species richness	32	40	39	39	47	53	34	

Authors' contributions

GWF: conceptualization, methodology, resources, data curation, writing & reviewing

TCL: conceptualization, formal analysis, investigation, data curation, writing & reviewing

JDM: conceptualization, methodology, formal analysis, investigation, data curation, writing & reviewing

EFV: conceptualization, methodology, formal analysis, resources, writing & reviewing

CRC: formal analysis, writing & reviewing

RS: formal analysis, writing & reviewing

EGC: formal analysis

JHS: formal analysis

JHCD: data curation, writing & reviewing

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