

Limited effects of low-intensity forest management on ant assemblages in southwestern Amazonian forests

Patrícia Nakayama Miranda^{1,2} · Fabricio Beggiato Baccaro³ ·
Elder Ferreira Morato¹ · Marco Antônio Oliveira⁴ ·
Jacques Hubert Charles Delabie^{5,6}

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Abstract One important strategy to conciliate forest conservation and economic development is the use of reduced-impact logging techniques. Here we evaluated the effects of low-intensity forest management on ant assemblages and vegetation structure in a managed area in the southeast of Acre State, Brazil. Ground-dwelling and arboreal ants, and several forest-structure descriptors were sampled in nine paired areas located in control (unlogged) and logged areas in 2005, 2007 and 2009. None of the forest structure predictors were related with either the treatment or the time since logging. However, some ant assemblage descriptors were related with logging activities. Arboreal and ground-dwelling ant species richness was similar between unlogged and logged areas, but more ground-dwelling ant species were found in areas logged in 2005 compared with areas logged in 2009. Ground-

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✉ Patrícia Nakayama Miranda
patricia.miranda@ifac.edu.br

¹ Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, BR 364 – Km 4 – Distrito Industrial, Rio Branco, AC CEP 69920-970, Brazil

² Instituto Federal do Acre, Campus Rio Branco. Avenida Brasil 920, Bairro Xavier Maia, Rio Branco, AC CEP 69903-062, Brazil

³ Departamento de Biologia, Universidade Federal do Amazonas, General Rodrigo Octávio, 62000, Manaus, AM CEP 69077-000, Brazil

⁴ Universidade Federal de Viçosa, Campus Florestal. Rodovia LMG 818, Km 6, Florestal, MG CEP 35690-000, Brazil

⁵ Comissão Executiva do Plano da Lavoura Cacaueira, Centro de Pesquisas do Cacau, Laboratório de Mirmecologia – CEPEC/CEPLAC, Caixa Postal 07, Itabuna, BA CEP 45600-000, Brazil

⁶ Universidade Estadual de Santa Cruz, Ilhéus, BA CEP 45650-000, Brazil

dwelling ant assemblage composition differed between treatments (logged and unlogged) and year of logging, but species composition heterogeneity was similar between areas. Arboreal ant assemblage composition was not related with treatment and year of logging, but assemblage composition was more heterogeneous in managed areas, suggesting that species that forage on the understory vegetation may be more resilient than ground-dwelling species. The general results of functional group approach suggest that changes of species composition between control and managed areas are more related with differences in ant species occurrence than ant species richness. Selective logging had limited effect on both vegetation descriptors and ant assemblage structure, suggesting that the conciliation of impact reduction techniques with low intensity extraction seems a promising alternative for sustainable logging activity in tropical forests.

Keywords Conservation · Reduced impact · Logging · Tropical forest · Formicidae

Introduction

Selective logging is one of the most important economic activities in the Brazilian Amazon (Nepstad et al. 1999; Rist et al. 2012). Forest-conservation programs and reduced-impact logging techniques have been discussed since the creation of the Brazilian Forest Code in 1965 (Barreto et al. 1998). Silvicultural techniques, such as cutting lianas one or two years before logging to prevent damage to interconnected trees (Vidal et al. 1997), directional falling of trees, and preliminary inventories to reduce the density of roads for dragging timber (Felton et al. 2006), have been considered fundamental for sustainable forest management in tropical forest. For example, forest canopies in selectively logged areas that do not use reduced-impact logging techniques are more open than those in managed areas that have applied these techniques (Pereira et al. 2001; Sist et al. 2002). However, how pervasive the impact of selective logging is on vegetation recovery (Darrigo et al. 2016), and on animal species distribution, remains contentious (Azevedo-Ramos et al. 2006).

Several structure facets of selectively logged forests are frequently monitored worldwide, such as vegetation structure (Pereira et al. 2001; Wilson et al. 2013), regeneration (Darrigo et al. 2016), growth (Herault et al. 2010), mortality (Shenkin et al. 2015), phenology (Ogawa-Onishi and Berry 2013), plant species richness (Clark and Covey 2012) and floristic composition (Oliveira et al. 2005). Environmental factors, such as water quality (Kwon et al. 2007), nutrient cycling (Zuquim et al. 2007), soil texture (Clark et al. 1999) and light incidence (Boudreault et al. 2013), are also frequently assessed. In addition to these factors, wildlife is an important element that needs to be monitored, and is present in three of the ten evaluation criteria used for Forest Stewardship Council (FSC Brazil), which evaluates and certifies the forest management actions in Brazil (FSC 2015).

Numerous studies in different regions of the globe, have been undertaken to evaluate the effects of logging on animal species (Azevedo-Ramos et al. 2006; Hasegawa et al. 2013; Yamada et al. 2014; Bicknell et al. 2015; Costa et al. 2015). For instance, how ants species are affected by logging has been frequently investigated (Vanderwoude et al. 2000; Dunn 2004; Widodo et al. 2004; Azevedo-Ramos et al. 2006; Gunawardene et al. 2010; Schleuning et al. 2011; Fayle et al. 2015). In general, these studies indicate that ants are relatively resilient, and show no changes in species richness due to forest logging (Kalif et al. 2001; Vanderwoude et al. 2000; Vasconcelos et al. 2000). The major effects of forest

management on ant assemblages relate to species composition changes (Kalif et al. 2001; Vasconcelos et al. 2000; Gunawardene et al. 2010; Edwards et al. 2012). However, exception to the mentioned pattern can be verified, probably due to the extraction intensity. Edwards et al. (2012), for example, found significant differences in ant species richness between unlogged and conventional high logging intensity ($113 \text{ m}^3 \text{ ha}^{-1}$) forest.

Most studies involving animal indicators in forest management, including ants, have focused on areas with cutting intensity above $10 \text{ m}^3 \text{ ha}^{-1}$ (Vasconcelos et al. 2000; Kalif et al. 2001; Lima et al. 2001; Pinto et al. 2003; Azevedo-Ramos et al. 2006). This management category is referred to as ‘full sustainable forest management’ (extraction intensity between 10 and $30 \text{ m}^3 \text{ ha}^{-1}$) in accordance with Normative Instruction no. 5 (2006) of the Federal Forest Standard for the Amazon (Brazil 2007). Logged areas with less than $10 \text{ m}^3 \text{ ha}^{-1}$ extraction intensity are labeled as ‘low-intensity forest management’ (Brazil 2007). Rural and indigenous traditional communities normally fall in the low-intensity forest management category, being responsible for the management of 25% of the 350 million hectares of tropical forests destined for timber production (Putz et al. 2008). Although this category of management is quite representative for tropical forests, the effects of low-intensity forest management on animal assemblages are virtually unknown.

This study aimed to evaluate the effects of low-intensity forest management on ant assemblages in southeast of Acre State, Brazilian Amazon. We tested four hypotheses related to the effects of low-intensity forest management on vegetation structure and ant assemblages: (i) forest structure parameters are affected by treatment (managed and control areas) and time after logging (2005, 2007 and 2009); (ii) the forest structure of managed areas is more heterogeneous compared with control areas; (iii) richness and occurrence of ground/litter-dwelling and arboreal ants are similar between treatments (managed and control areas) and time after logging (2005, 2007 and 2009), but the ant composition differs among treatments and years after logging; (iv) ant species heterogeneity is higher in managed than in control areas. To further interpret ecological structure of ant assemblages, we also used a functional-group approach, based on diet, nesting habits, external morphology, and phylogeny (Delabie et al. 2000; Silva and Brandão 2010), which simplifies the assemblage composition providing a useful framework to describe and analyze ant assemblage responses.

Materials and methods

Study area

The study was carried out between August and September of 2010, in logged and unlogged areas at Projeto de Assentamento Agroextrativista (PAE) Chico Mendes ($10^\circ 53' \text{S}$ $68^\circ 21' \text{W}$), Xapuri, southeastern Acre, Brazil. About 90% of PAE consists of upland forests of the following types: (1) open forest dominated by bamboo, (2) open forest with palm trees and (3) dense forest (Acre 2006). The climate is tropical humid with rainfall of 1450 mm per year (Macêdo et al. 2013), with marked seasonality, with most rainfall falling between November and March (Acre 2006). The average annual temperature is 24°C (INMET 2016), with daily variation around 9°C (Acre 2006).

PAE Chico Mendes covers an area of $\sim 25,000$ ha divided between 84 families (Acre 2009), being each family responsible for a particular forest region. The main economic activity is based on forest extractive industries. Approximately 40 families are engaged in

logging activities, characterized as low-intensity forest management (Acre 2009). Initially timber was dragged by animal traction, but since 2005, dragging is done by skidders (Acre 2009). Although there was a production increase associated with the use of skidders, forest management in PAE Chico Mendes is still classified as low intensity ($\sim 5.4 \text{ m}^3 \text{ ha}^{-1}$), under the Normative Instruction n°. 5 (2006) of Federal Forest Standards for Amazonia (Brasil 2007).

Sampling design

Sampling was carried out in nine forest regions within the PAE Chico Mendes, each of them managed by a different family. In each region, the managed area are located next to non-managed areas. Therefore, each managed area was paired with a control area. The distance between paired areas (managed and control) ranged from 300 to 400 m, and the distance between pairs ranged from 1 to 22 km (Fig. 1). We considered 3 years of logging (areas managed in 2005, 2007 and 2009), with three replicates for each logging year studied. This gave us a total of nine managed areas and nine corresponding control areas.

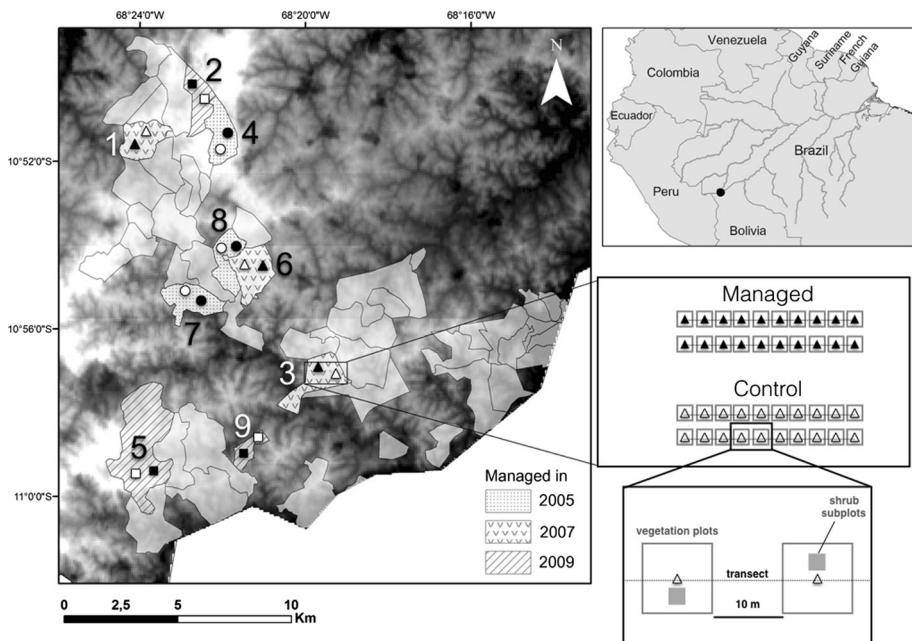


Fig. 1 Map of the study area showing all managed areas of PAE Chico Mendes. The studied managed areas are indicated by different texture. The *numbers* represents the name of the forests region in PAE Chico Mendes managed by a family: (1) Arlete, (2) Fazendinha, (3) Igarapé Grande, (4) Lago, (5) Porto Alegre, (6) Retiro I, (7) Retiro II, (8) São Luiz and (9) São Raimundo. The remaining *shaded areas* represent the areas logged at different years and areas that will be logged in the future. *Circles* represent control and managed areas in 2005, *triangles* represent control and managed areas in 2007, and *squares* represent control and managed areas in 2009. *Darker areas* represent the stream network. The detailed figure illustrates the arrangement of one of the two parallel 190 m-long transects established in paired samples (managed and control areas) in each site, and the pitfall and beating samples (*triangles*) placed in the middle of 10 × 10 m plots used for vegetation structure measurements. *Shaded squares* represents the 2 × 2 m plots where the shrubs density were estimated. In PAE Chico Mendes each managed area is always surrounded by unmanaged forest where the control sampling units were established

Two parallel 190 m-long transects, 50 m distant from each other were established in the center of each managed and control areas. Plots of 100 m² (10 × 10 m) were established along the two 190 m-long transects (Fig. 1). The interval between plots was 10 m, totaling 10 plots per transect and 20 per sampling unit (360 plots in total). These transects and plots were used for sampling ground-dwelling and arboreal ants and also for forest-structure descriptors.

Forest structure

Seven forest-structure descriptors (tree density, basal area of living trees, shrub density, fallen-tree density, basal area of fallen trees, canopy cover and litter depth) were sampled in each plot. The diameter of all trees at breast height ≥ 10 cm was measured at 1.3 m above the ground (DBH). Tree diameter (2r) values were then used to calculate the living-tree basal area, by using the formula for the area of a circle (πr^2). Tree-density calculation per plot was based on division of the total number of individuals by the total plot area (2000 m²). All fallen trees with DBH ≥ 10 cm were measured. We measured canopy cover using a spherical convex densiometer. The measurements were taken at the center and at the four edges of the plots, and the mean for each plot was used to describe the canopy cover per sampling unit. Litter depth was measured at 10 points spaced 1 m apart from each other. At each point, a metal ruler was gently pressed through the litter until it reached the soil and the height of the litter (in cm) was measured based on the highest litter contacting the ruler. The mean for each plot was used to describe the litter depth per sampling unit.

One sub-plot of 4 m² (2 × 2 m) was established inside each 100 m² plots to quantify the shrub density. Given that the 190 m-long transects crosses the plots in the middle, this subplots was established on one side of the plot (left or right), two meters away from the 190 m-long transect, to avoid the transect effects. The side for the first subplot establishment was randomly chosen and the sequential sub-plots were established on alternate sides of the main 190 m-long transect. In these sub-plots, all plants between 0.5 and 2 m tall were counted. In each area, the shrub density was quantified by dividing the total number of plants in the 20 sub-plots, by the total area (80 m²).

Sampling ants

Ants were sampled using 9 cm diameter pitfall traps and by manually beating the vegetation (Coddington et al. 1991; Höffer and Brescovit 2001; Souza et al. 2012). One pitfall trap was established in the center of each plot. Overall, ten pitfalls distributed at 20 m intervals were placed along each transect. Each pitfall trap contained a solution of 70% ethanol and remained active for 4 days. Manual beating the vegetation were undertaken in ten sub-plots of 25 m² (5 × 5 m) in the center of the 100 m² plots. During 5 min all small trees and shrubs within the sampling area were beaten. During beating a square white canvas measuring 70 × 70 cm supported by a wooden structure was placed bellow the trees and shrubs. All ants specimens that fell in the canvas were collected. Thus, there were ten pitfall traps and ten manual collections per transect, 20 per area and 360 considering all areas (nine logged and nine unlogged areas). The pitfall and beating vegetation data per area were combined and used as sampling unit. For all analyses, we ran separate tests for samples performed by pitfall traps and manually beating the vegetation.

Ants were identified to species or morphospecies using identification keys (Wilson 2003; Fernández 2003; Bolton et al. 2006) and by comparison with specimens deposited at

Entomological Collection of Instituto Nacional de Pesquisas da Amazônia (INPA), Regional Museum of the Universidade Federal de Viçosa and the Laboratório de Mirmecologia do Centro de Pesquisas do Cacau (CPDC Collection). Voucher specimens were deposited on the Entomological collections described above.

Data analysis

Forest structure predictors

We considered each forest-structure predictor as a response variable and the treatment (managed and control areas) and the year of logging (2005, 2007 and 2009) as explanatory variables. A generalized linear mixed model (GLMM) (Bolker et al. 2009) was constructed for each forest-structure variable. We adopted Gaussian error distribution and included ‘site’ (each pair of managed and control area) as random effects in the model. To validate the model fit, we compared the Akaike’s Information Criterion (AIC) of each GLMM with the respective AIC of the null model (intercept and random effect only). Full GLMM models were selected when the delta AIC (difference between full and null models) were >2 (Akaike 1982). We calculated the marginal and the conditional R^2 for each GLMM to measure the importance of the random variable (site) in our results. Marginal R^2 provide the variation explained only by the fixed effects, while the conditional R^2 gives the variation explained by fixed and random effects in the model (Nakagawa and Schielzeth 2013). We also performed residual analysis to verify the adequacy of the model predictions. GLMM models were created with *lme4* package (Bates et al. 2015) and residual analysis was done using the DHARMA package (Florian Hartig 2016) in R 3.2.3 (R Core Team 2016).

We used a permutational multivariate analysis of variance (np-MANOVA), based on Euclidean distances of standardized environmental data, to evaluate the effects of treatment and year of logging on all forest-structure predictors. This analysis allows simultaneous testing of multiple factors and covariates based on permutation tests (Anderson 2001). We also tested whether the overall forest structure heterogeneity differed between treatments, using analysis of homogeneity of multivariate dispersions (hereafter PERMDISP). PERMDISP is a multivariate analyses analogue of Levene’s test for homogeneity of variances, and the statistic (average distance of group members to the PCoA group centroid) is tested by permutation (Anderson 2006). Euclidean distances of standardized environmental data were used. The statistical probabilities of np-MANOVA and PERMDISP were based in 999 permutations for each test.

Ant species richness

We used a similar analytic scheme for ant species richness. The ground and arboreal ant species richness were the response variables, and treatment (managed or control areas) and year of logging (2005, 2007 or 2009) were the explanatory variables in GLMM models. In each model, ‘site’ (each pair of managed and control area) was also set as random-effect variable and the Poisson error distribution were adopted. We also validate each model comparing with a simpler model (intercept + random effect variable), calculate the marginal and conditional R^2 and performed residual analysis to verify the adequacy of the model predictions.

Ant assemblage composition

We used ant species occurrence (presence/absence) accumulated among transects in each area as our ant metric. Therefore, each ant species occurrence varied between 0 (no species in the area) to 20 (the species were sampled in all subsamples of a given method) per area. We ran separate tests for assemblage composition sampled by pitfall traps and by beating the vegetation. We used a permutational multivariate analysis of variance (np-MANOVA), based on Bray-Curtis distances, to evaluate the effects of treatment and year of logging on ant assemblage composition. In this design, we used ‘site’ as strata, so that randomizations occur only within each site and not across all sites. Similar to forest structure, PERMDISP analysis based on Bray-Curtis distance was used to test whether heterogeneity in ant species composition differed between treatments. The statistical probabilities were based on 999 permutations for each test. To investigate the contribution of ‘rare’ species to the main results, a comparison of the composition of most common ants (species present in at least five plots) was also carried out, using the same procedures described above.

Functional group

We placed the species into functional groups based on the classifications for Neotropical ants (Silvestre et al. 2003; Silva and Brandão 2010) to further interpret and analyze ant assemblage structure. This functional group scheme is based on microhabitat distribution, trophic position, natural-history information, body size, and phylogeny; grouping species with potentially similar life styles. We followed the nomenclature proposed by Silva and Brandão (2010). The functional groups adopted were: Arboreal omnivores; Arboreal predators; Generalized dolichoderinaes, formicinaes and myrmicinaes (Generalists); Ground-dwelling specialist predators (Dacetini predators); Hypogaic generalist predators; Epigaic generalist predators; Leaf-cutters; Litter-nesting fungus-growers and Raid-hunting predators. Some functional groups were combined because they represent species from the same trophic position (Silva and Brandão 2010). The Subterranean mealybug-dependent species group was not included because the species in this group were not adequately sampled by our methods. A complete list of species membership for each functional group can be found in Supplementary Material (Online Resource 1).

We considered ant species richness and ant species occurrence (presence accumulated among transects in each area) of each functional group as response variables, and the treatment (managed and control areas) and the year of logging (2005, 2007 and 2009) as explanatory variables. We applied the same analysis protocol described above, creating a GLMM (Bolker et al. 2009) for each functional group. We adopted Gaussian error distribution for richness and Poisson error distribution for occurrence models. In both cases, ‘site’ (each pair of managed and control area) was declared as random effects in the models. GLMM models were created with lme4 package (Bates et al. 2015) and residual analysis was done using the DHARMa package (Florian Hartig 2016) in R 3.2.3 (R Core Team 2016).

Results

Forest structure between managed and control areas

None of the forest structure predictors were related to either treatment (managed and control) or time since logging (2005, 2007 and 2009), when individually evaluated by

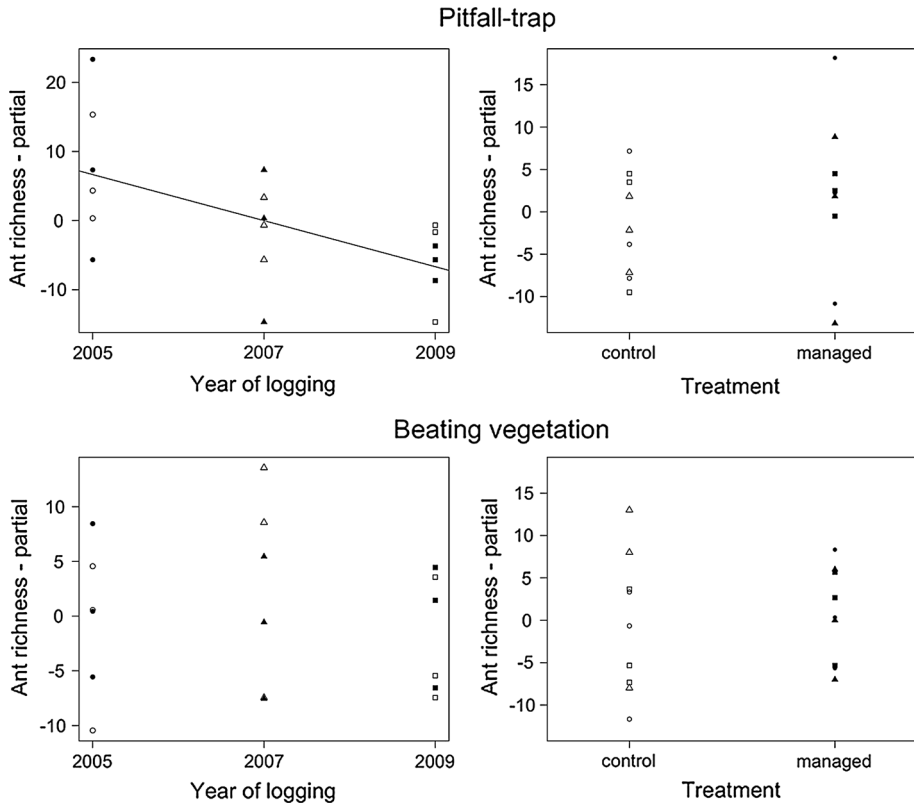


Fig. 2 Partial residual plots of the effects of year of logging and treatment on ground-dwelling ant species richness sampled by pitfall traps and beating the vegetation at PAE Chico Mendes, Acre, Brazil. *Open symbols* represent control and *closed symbols* represent managed areas. *Circles* represent control and managed areas in 2005, *triangles* represent control and managed areas in 2007, and *squares* represent control and managed areas in 2009

GLMM: shrub density (treatment: $b = 0.388$, $P = 0.470$; year of logging: $b = -0.372$, $P = 0.458$), dead-tree density (treatment: $b = 0.022$, $P = 0.923$; year of logging: $b = -0.012$, $P = 0.944$), basal area of dead trees (treatment: $b = 0.014$, $P = 0.215$; year of logging: $b = 0.001$, $P = 0.954$), tree density (treatment: $b = -0.822$, $P = 0.242$; year of logging: $b = -0.166$, $P = 0.432$), basal area of living trees (treatment: $b = -0.017$, $P = 0.684$; year of logging: $b = -0.009$, $P = 0.550$), canopy cover (treatment: $b = -0.711$, $P = 0.340$; year of logging: $b = -0.281$, $P = 0.540$) and litter depth (treatment: $b = 0.147$, $P = 0.755$; year of logging: $b = 0.017$, $P = 0.941$). The null models had a better or equivalent fit (Delta AIC < 2) in all comparisons performed, therefore the calculation of marginal R^2 is meaningless.

Forest structure, considering all predictors together, was also not related to treatment (np-MANOVA: $F = 0.386$, $r^2 = 0.024$, $P = 0.799$) or year of logging (np-MANOVA: $F = 0.749$, $r^2 = 0.046$, $P = 0.526$) (Fig. 2). Forest-structure heterogeneity was also similar among control and managed areas at the site scale (PERMDISP, $F_{2,16} = 0.009$, $P = 0.925$) (Fig. 2).

Ant diversity

We collected 263 ant species distributed in 48 genera. Pitfall traps collected 222 ant species distributed in 44 genera and manually beating the vegetation sampled 115 species belonging to 29 genera. The number of species sampled was similar between treatments. We sampled 200 species distributed in 46 genera in the control areas and 212 species distributed in 41 genera in managed areas. The most common genera collected with pitfall traps samples were *Pheidole*, *Camponotus*, *Pachycondyla*, *Crematogaster* and *Ectatomma*, and the most common genera collected by manually beating the vegetation were *Crematogaster*, *Camponotus*, *Brachymyrmex*, *Pseudomyrmex* and *Azteca*. Some genera were uncommon in both methods, such as *Octostruma* and *Myrmelachista*, which were only collected in managed and control areas respectively.

Ant species richness

Ground-dwelling ant species richness was negatively related to year of logging (GLMM: $b = -5.601$; $P = 0.027$), but no differences were detected between treatments (GLMM: $b = 3.000$; $P = 0.451$). The areas logged in 2005 and their respective controls showed higher ant species richness, than areas recently managed and their respective controls (Fig. 2). The marginal (0.33) and conditional R^2 (0.35) were similar. No relation was detected between arboreal ant species richness and date of logging (2005, 2007 and 2009) (GLMM: $b = -0.560$; $P = 0.7000$) or the treatment (GLMM: $b = 1.111$; $P = 0.795$) (Fig. 2). However, the importance of the site-to-site variation for arboreal ant richness was higher, given that the marginal R^2 (0.01) was much lower than the conditional R^2 (0.36). In all comparisons, the full model had a lower AIC than null model (Delta AIC >2).

Assemblage composition

The ground-dwelling ant assemblage composition differed between treatments (np-MANOVA: $F = 2.391$, $r^2 = 0.125$, $P = 0.001$) and year of logging (np-MANOVA: $F = 1.680$, $r^2 = 0.089$, $P = 0.010$), but species composition heterogeneity was similar between control and managed areas (PERMDISP: $F_{2,16} = 1.549$, $P = 0.231$). A different picture emerged from arboreal samples. The arboreal ant assemblage composition was similar between control and managed areas (np-MANOVA: $F = 0.914$, $r^2 = 0.053$, $P = 0.605$) and date of logging (np-MANOVA: $F = 1.288$, $r^2 = 0.075$, $P = 0.164$), but species heterogeneity was higher in managed areas (PERMDISP: $F_{2,16} = 5.043$, $P = 0.039$, Fig. 3). A similar pattern held when rare species were excluded.

Functional group responses

Overall the functional group approach showed limited effects of low intense selective logging. Only ant species richness and ant species occurrence of Arboreal predators differed between treatments (Table 1). In this case, the managed areas presented more species of this group than the control areas. In addition, the null model had a better fit compared with the full model for Arboreal omnivores, Dacetini predators, Leaf-cutters, Hypogeic predators and Raid-hunting predators ant species richness (Table 1). However, occurrence data showed contrasting responses. In most cases, the full model had a better fit than the

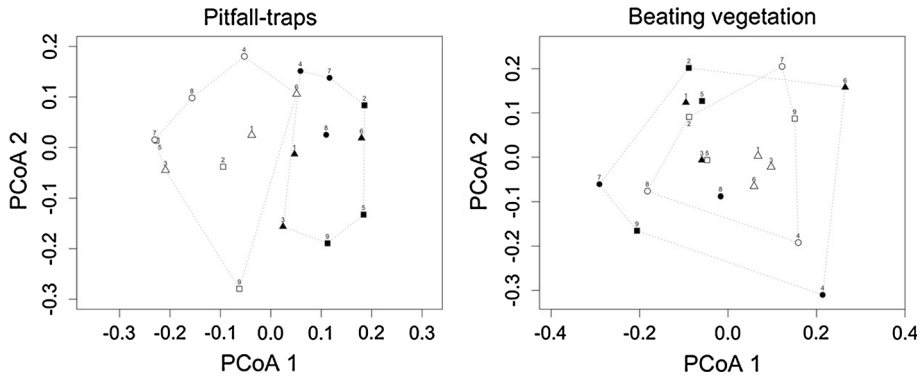


Fig. 3 Principal coordinates analysis (PCoA), of ground-dwelling ants and ants sampled in vegetation in managed (*closed symbols*) and control areas (*open symbols*). *Circles* represent control and managed areas in 2005, *triangles* represent control and managed areas in 2007, and *squares* represent control and managed areas in 2009

Table 1 Summary of the generalized-linear mixed models of ant species richness for each functional group related to treatment (control and managed areas) and year of logging (2005, 2007 and 2009)

Functional group richness	R ² marginal	R ² conditional	Fixed factor	B	P-value
Arboreal omnivores	—	0.15	—	—	—
Arboreal predators	0.20	0.69	Year of logging	0.292	0.441
			Treatment	1.667	0.020
Generalists	0.14	0.14	Year of logging	−0.542	0.364
			Treatment	2.556	0.196
Dacetini predators	—	0.38	—	—	—
Epigeic predators	0.22	0.22	Year of logging	−0.833	0.052
			Treatment	0.667	0.612
Leaf-cutters	—	0.56	—	—	—
Litter-nesting fungus-growers	0.43	0.61	Year of logging	−1.458	0.016
			Treatment	0.777	0.501
Hypogeic predators	—	0.13	—	—	—
Raid-hunting predators	—	<0.01	—	—	—

Marginal R² values and model parameters of Arboreal omnivores, Dacetini predators, Leaf-cutter, Hypogeic predators and Raid-hunting predator ant species functional groups were omitted because the null model had a better fit compared with the full model. For these groups the conditional R² values represent the variance explained by the random factor only. A list of species membership for each functional group can be found in Supplementary Material (Online Resource 1)

null models suggesting a more important effect of the fixed treatment compared with site-to-site natural variation. The ant species occurrence of Arboreal predators, Generalists and Raid-Hunting predators were higher in managed areas, while the ant species occurrence of Fungus-grower and Litter-nesting fungus grower species were related with time since last logging (Table 2). The frequency of ant species occurrence of the other functional groups did not show clear patterns.

Table 2 Summary of the generalized-linear mixed models of ant species occurrence for each functional group related to treatment (control and managed areas) and year of logging (2005, 2007 and 2009)

Functional group occurrence	R ² marginal	R ² conditional	Fixed factor	B	P-value
Arboreal omnivores	0.03	0.03	Year of logging	0.033	0.599
			Treatment	0.052	0.480
Arboreal predators	0.28	0.45	Year of logging	−0.086	0.556
			Treatment	0.625	<0.001
Generalists	0.16	0.16	Year of logging	−0.037	0.227
			Treatment	0.109	0.009
Dacetini predators	–	0.31	–	–	–
Epigeic predators	–	0.22	–	–	–
Leaf-cutters	0.47	0.47	Year of logging	−1.032	0.002
			Treatment	0.441	0.298
Litter-nesting fungus-growers	0.44	0.75	Year of logging	−0.339	0.004
			Treatment	−0.155	0.171
Hypogeic predators	–	0.08	–	–	–
Raid-hunting predators	0.29	0.36	Year of logging	0.006	0.369
			Treatment	1.029	<0.001

Marginal R² values and model parameters of Dacetini predators, Epigeic predators, and Hypogeic predators functional groups were omitted because the null model had a better fit compared with the full model. For these groups the conditional R² values represent the variance explained by the random factor only. A list of species membership for each functional group can be found in Supplementary Material (Online Resource 1)

Discussion

Overall, our results suggest a limited effect of low-intensity selective logging on either vegetation and ant assemblage structure. Selective logging usually modifies vegetation structure, even when reduced-impact techniques are used. Generally, more canopy openness and more shrubs are found in logged areas, compared to areas without exploitation (Pereira et al. 2001; Vasconcelos et al. 2000; Darrigo et al. 2016). In our study, however, the forest structure descriptors evaluated and forest-structure heterogeneity were similar between managed and control areas. In fact, null model comparisons suggest that site-to-site variation is more relevant than the effects of selective logging for the vegetation descriptors investigated here. This lack of differences between logged and control areas may be related to the lower extraction intensity ($5.4 \text{ m}^3 \text{ ha}^{-1}$) used at PAE. All previous studies investigated the effect of selective logging intensity of $>17 \text{ m}^3 \text{ ha}^{-1}$ (Darrigo et al. 2016). Therefore low-intensity selective logging seems a promising alternative to conciliate environmental health and local economical development.

Species richness of ground-dwelling ants was positively associated with time since logging. However, it is important to note that the differences in ant species richness between logged areas in different years probably is not a result of time after logging, since treatment had no effect. The areas logged in 2005 and their respective unlogged pairs had more species than areas managed in 2009 and their respective unlogged pairs. In addition, this pattern is the opposite of that found in other studies. Forests with high structural diversity and shading (in most cases, unlogged areas or areas managed long before), tend to have less ant abundance and richness (Azevedo-Ramos et al. 2006). The ant species richness variation detected among our paired plots may be related to other factors, such as

soil characteristics or water drainage, which was not assessed in this study. Soil granulometry and water-table level, for instance, are related with ant species distribution in other Amazonian forests (Oliveira et al. 2009; Baccaro et al. 2013), and may be more relevant for ant assemblage composition, than the disturbance caused by low-intensity logging.

Despite the fact that 71% of ant species sampled at vegetation were also collected in pitfall traps, our results suggest contrasting responses to low-intensity selective logging between each stratum. Ground-dwelling ant species composition differed between treatments and year of logging. Managed and control areas had distinct species compositions even when the rare species were excluded. However, differences in composition were not observed among ants sampled in the vegetation, even when rare species were excluded. Changes in ground-dwelling ant assemblage composition related to selective logging intensity of $>17 \text{ m}^3 \text{ ha}^{-1}$ in tropical forests is often reported (Vasconcelos et al. 2000; Kalif et al. 2001; Widodo et al. 2004; Gunawardene et al. 2010), even where reduced-impact logging techniques are applied (Edwards et al. 2012). Our results complement previous studies suggesting that ground-dwelling ants may be also good indicators for low intensity selective logging (up to $5.4 \text{ m}^3 \text{ ha}^{-1}$). The differences in ground-dwelling ant species composition between managed and control areas reported here were spatially consistent, as the distance between logged and unlogged sampled areas was always less than 400 m. Therefore, the differences in species composition related with natural environmental variation (Bestelmeyer and Wiens 2001) or ant dispersal abilities (Peeters and Ito 2001) were controlled.

Although our extensive vegetation evaluation has not detected environmental differences between logged and unlogged areas, changes in ant species assemblage may be reflecting possible subtle environmental changes caused by low-intensity reduced-impact logging. It is possible that direct impacts on soil caused by skidder tracks accounted for differences in ant composition between treatments. Normally, the soil below the tracks becomes more compacted than in other areas, which may delay forest recovery (Guariguata and Dupuy 1997) and change ant assemblage composition (Vasconcelos et al. 2000). Given that skidders have been used in PAE Chico Mendes since 2005, we cannot exclude the possibility that the ground-dwelling ant-composition differences between managed and control areas may be related to soil disturbances. The network of skidder tracks within sites may also increase the soil heterogeneity, which is an important driver for shrub vegetation diversity and structure (Wagenbrenner et al. 2015). Therefore, the higher heterogeneity of arboreal-ant composition in managed areas may be also reflecting the impacts caused by skidder tracks.

The general results of functional group approach suggest that changes of species composition between control and managed areas are more related with ant species occurrence than ant species richness differences. Only arboreal predators showed a consistent pattern, with higher ant species richness and ant species occurrence in managed areas. Arboreal predators group was mostly composed by *Pseudomyrmex* species that usually nest on the branches or live inside the domatia of *Tachigalia* tree species (Fowler et al. 1991; Fowler 1993; Bruna et al. 2005). Some *Tachigalia* species are protected against herbivores by their ant partners (Izzo and Petini-Benelli 2011), and this relationship is more important to plant fitness at early ontogenetic stages (Del Val and Dirzo 2003). Therefore, the frequency and abundance of *Pseudomyrmex* ant species in a site is dependent of the associated plant abundance, and vice versa. Given that *Tachigalia* trees have no commercial use in PAE and are pioneer species, the selective logging techniques may indirectly favor these trees species and consequently the higher occurrence and richness of *Pseudomyrmex* species in managed areas.

The other functional groups showed less consistent results, showing differences only in ant species occurrence between treatments. Generalists and Raid hunting predators species were more common in managed compared with control areas. Generalists species may show wide habitat tolerances (Hoffmann and Andersen 2003) with occurrence increase in anthropogenic environments (Silvestre et al. 2003). Raid-hunting species are top predators of many forest litter arthropods (LaPolla et al. 2002; Kaspari and O'Donnell 2003), which may be more abundant in logged areas (Azevedo-Ramos et al. 2006). These ants have narrow humidity variation requirements, decreasing in abundance in areas with intense environmental disturbances (Terborgh et al. 1997; Boswell et al. 1998; Peters et al. 2009). Therefore, the low disturbance levels associated with the maintenance of vegetation standards parameters in logged areas may favor the occurrence of both functional groups.

The ant species occurrence of Leaf-cutters and Litter-nesting fungus growers species were only related with time since logging. In both cases they were more abundant in areas managed longer time ago, but since the treatment had no effect, this pattern are more related with site-to-site environmental variation. The higher conditional R^2 for ant species richness and ant species occurrence of Litter-nesting fungus grower's models suggests that natural variation among sites were very important for these group. In fact, about half of the richness and occurrence models showed higher explained variance when site was included as random factor.

The results found here provided some important insights about ant assemblage structure response to selective logging. The general effect of selective logging on ant assemblages previous reported was also detected even for low-intensity selective logging management (up to $5.4 \text{ m}^3 \text{ ha}^{-1}$). The reduced-impact logging techniques combined with low intensity extraction promoted only subtle changes in forest structure, but the ground-dwelling ant species composition was different between control and managed areas. The ant assemblages that live and forages on understory plants, rarely investigated in previous studies, seems to be much more resilient or favored by selective logging than ground-dwelling species. Logging activities in tropical forests are increasing (Asner et al. 2005; Vidal et al. 2014), and some studies suggest that this activity is unsustainable in the long term (Macpherson et al. 2010). Therefore, the conciliation of impact reduction techniques with low intensity extraction seems to be a promising alternative for sustainable logging activity in tropical forests.

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