LUCAS NAVARRO PAOLUCCI

FIRE IN THE AMAZON: IMPACTS OF FUEL LOADS AND FREQUENCY ON ANTS AND THEIR INTERACTIONS WITH SEEDS

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Ecologia, para obtenção do título de *Doctor Scientiae*.

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APROVADA: 15 de fevereiro de 2016.

Tathiana Guerra Sobrinho
(Coorientadora)

Inara Roberta Leal

Júlio Neil Cassa Louzada

Ricardo Ribeiro de Castro Solar

José Henrique Schoereder
(Orientador)

Dedico novamente aos meus pais, Helenice
e Ricardo, por quem tenho eterna admiração,
respeito e amor.

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ÍNDICE

RESUMO

PAOLUCCI, Lucas Navarro, D.Sc., Universidade Federal de Viçosa, Fevereiro de 2016. **Fogo na Amazônia: impactos da quantidade de combustível e frequência sobre as formigas e suas interações com sementes.** Orientador: José Henrique Schoereder. Coorientadores: Tathiana Guerra Sobrinho e Ricardo Ildefonso de Campos.

O fogo é um importante distúrbio que influencia a distribuição e diversidade de espécies em vários biomas. As florestas tropicais raramente queimam naturalmente, mas atividades humanas como a exploração madeireira e a agricultura fragmentam o hábitat original, aumentando a carga de combustível e, consequentemente, a inflamabilidade e frequência de incêndios em seu sub-bosque. Atualmente as florestas do sul da Amazônia enfrentam mudanças extremas no uso da terra, e encontram-se sob um estado de incêndios recorrentes. Incêndios de sub-bosque degradam severamente a estrutura destas florestas, mas o papel da quantidade de combustível ou da frequência do fogo em suas comunidades faunísticas ainda é pouco conhecido. Nós abordamos experimentalmente como incêndios de sub-bosque afetam comunidades de formigas associadas às florestas do sul amazônico. No primeiro capítulo, investigamos a influência do fogo e da quantidade de combustível (serapilheira) sobre as comunidades de formigas e suas interações com sementes mirmecocóricas. Incêndios únicos e combustível foram aplicadas em parcelas contidas em seis blocos, e as formigas foram amostradas em quatro estratos: subterrâneo, serapilheira, epigéico, e arbóreo. Nós encontramos que táxons altamente especializados são os mais sensíveis a incêndios, mas a composição de espécies permaneceu pouco alterada. O fogo reduziu as taxas de localização e transporte de sementes, o que atribuímos a um maior estresse térmico, mas maiores cargas de combustível não diminuem a diversidade de formigas ou seus serviços ecossistêmicos por um aumento na severidade do fogo. No segundo capítulo nós investigamos o papel de incêndios recorrentes sobre as comunidades de formigas, e avaliamos a medida em que as suas respostas são consistentes com as de árvores. Duas parcelas foram submetidos a incêndios anuais e trienais ao longo de um período de seis anos, enquanto uma parcela permaneceu intacta. A diversidade e a composição de espécies variaram de modo semelhante para árvores e formigas, com efeitos mínimos sobre a riqueza, aumento na equidade e diferente composição de espécies devido ao fogo. Entretanto, o fogo teve um impacto muito mais severo na abundância e biomassa de árvores do que de formigas, refletindo os efeitos diretos do fogo nas primeiras e indireto nas últimas. Concluindo, nós sugerimos atenção particular à prevenção de incêndios recorrentes, afim de se manter a biodiversidade dessas florestas, especialmente considerando-se que as formigas têm um papel bem estabelecido como indicadores de distúrbios em outros grupos da fauna, de modo que esses efeitos negativos provavelmente também ocorrem em outros táxons destas florestas.

ABSTRACT

PAOLUCCI, Lucas Navarro, D.Sc., Universidade Federal de Viçosa, February, 2016. **Fire in the Amazon: impacts of fuel loads and frequency on ants and their interactions with seeds.** Adviser: José Henrique Schoereder. Co-advisers: Tathiana Guerra Sobrinho and Ricardo Ildefonso de Campos.

Fire is a major disturbance shaping the distribution and diversity of species across several biomes. Tropical forests rarely burn naturally, but human activities such as logging and agriculture fragment the original habitat, increasing fuel loads and consequently the flammability and frequency of understory fires. Southern Amazonian forests are currently facing extremely land-use change, and are under a state of high recurrent burning. Understory fires severely degrade the structure of these forests, but the role of fuel loads or fire frequency on their faunal communities has been little studied. Here we experimentally addressed how understory fires affect shade-adapted ant communities from southern Amazonian forests. In the first chapter we investigated the influence of fire and fuel loads on ant communities and their interactions with myrmecochorous seeds. Single fires and fuel addition were applied to plots in six replicated blocks, and ants were sampled in four strata: subterranean, litter, epigaeic and arboreal. We found that highly specialized taxa are the most sensitive, but species composition remained little altered. Fire reduced rates of seed location and transport, which we attribute to increased thermal stress, although enhanced fuel loads will not decrease ant diversity and ecosystem services through increased fire severity. In the second chapter we investigated the role of recurrent fires on ant communities, and assessed the extent to which their responses are consistent with those of trees. Two plots were subjected to annual and triennial fires over a six-year period, while one plot remained unburnt. Species diversity and composition varied similarly for trees and ants, with minor effects on richness, increased evenness and different species composition due to fire. However, fire had a much more severe impact on abundance and biomass of trees than of ants, reflecting the direct effects of fire on the former and indirect on the latter. In conclusion, we suggest that the prevention of recurrent fires should be of special concern for the maintenance of biodiversity of these forests, particularly considering that ants have a well-established role on indicating disturbances on other faunal groups, so such negative effects likely occur for other taxa from these forests as well.

GENERAL INTRODUCTION

Fire is a major agent of disturbance across different biomes, shaping the patterns of diversity, distribution and composition of several taxa (Bond et al. 2005). Many biomes as tropical savannas, Mediterranean scrubs, grass fields, boreal forests and eucalypt woodlands burn naturally (Bond and Keeley 2005), and the biotas of such fire-prone biomes are usually highly resilient to fire, because of their association with it over the evolutionary time. However, fire currently represents an important disturbance also for tropical forests, which rarely burn naturally due to their humid microclimate and high rates of litter decomposition (Uhl and Kauffman 1990). These habitats are facing high anthropogenic pressures that increase the risk of fire occurrence and its intensity (Nepstad et al. 1999; Ray et al. 2005).

The rainforest-savanna transitional region of the southern Amazon is known as “The Arch of Deforestation”, and it is particularly threatened by human disturbances, mainly due to the expansion of its agricultural frontier. These forests are now experiencing high rates of deforestation and consequently understory fires (Morton et al. 2013). Such human activities causes lower tree cover, drier microclimate, and higher and drier fuel loads of forest edges, increasing the risk of fire occurrence. Once burned, a positive fire feedback may be established (Cochrane et al. 1999), and natural fire return intervals can dramatically decrease (Cochrane 2001; Pivello 2011).

Despite the current state of extremely high recurrent burning that the southern Amazon region is facing (Alencar et al. 2015), and the well-established detrimental effects that understory fires have on its vegetation (e.g. Balch et al. 2015; Balch et al. 2013; Brando et al. 2014; Brando et al. 2012), the role of fire, its fuel loads and frequency remains little understood for the shade-adapted fauna from southern

Amazonian forests, and also for the ecosystem services they provide.

Here we experimentally assessed how fire affects the shade-adapted ant fauna from southern Amazonian forests. Specifically, in the first chapter we investigated the impacts of fire and fuel loads on ant communities from four strata and on their interactions with seeds. In the second chapter, we addressed how extremely high fire frequencies impact ant communities from three strata, by comparing variation among experimental plots with that shown by trees.

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CHAPTER ONE

FIRE IN THE AMAZON: IMPACT OF EXPERIMENTAL FUEL ADDITION ON RESPONSES OF ANTS AND THEIR INTERACTIONS WITH MYRMECOCHOROUS SEEDS

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Fire in the Amazon: impact of experimental fuel addition on responses of ants and their interactions with myrmecochorous seeds

Authors: Lucas N. Paolucci[1*]; Maria L. B. Maia[1]; Ricardo R. C. Solar[1]; Ricardo I. Campos[2]; José H. Schoereder[2] and Alan N. Andersen[3].

[1] Programa de Pós-Graduação em Ecologia; [2] Departamento de Biologia Geral, Universidade Federal de Viçosa, Av. P.H. Rolfs, s/n, *Campus Universitário*, CEP 36570-000, Viçosa, MG, Brasil. [3] CSIRO Land and Water, Tropical Ecosystems Research Centre PMB 44, Winnellie, NT, 0822, Australia.

*Corresponding author. E-mail: lucaspaolucci@gmail.com

Abstract

The widespread clearing of tropical forests causes lower tree cover, drier microclimate, and higher and drier fuel loads of forest edges, increasing the risk of fire occurrence and its intensity. We used a manipulative field experiment to investigate the influence of fire and fuel loads on ant communities and their interactions with myrmecochorous seeds in the southern Amazon, a region currently undergoing extreme land-use. Experimental fire and fuel addition was applied to 50 x 50 m plots in six replicated blocks, and ants were sampled between 15-30 days after fires in four habitat strata: subterranean, litter, epigaeic, and arboreal. Understory fire had extensive negative effects on ant communities. Highly specialized taxa such as cryptobiotic species of the litter layer and epigaeic specialist predators were the most sensitive, but we did not find evidence of overall biotic homogenization following fire. Fire reduced rates of seed location and transport, and therefore the effectiveness of a key ecosystem service provided by ants, which we attribute to increased thermal stress. Experimental fuel addition had only minor effects on attributes of fire severity, and had limited effects on ant responses to fire. Our findings indicate that enhanced fuel loads will not decrease ant diversity and ecosystem services through increased fire severity, at least in wetter years. However, higher fuel loads can still have an important effect on ant diversity in Amazonian rainforests because it increases the risk of fire occurrence, which has a detrimental impact on ant communities and a key ecosystem service they provide.

Key words: Ecosystem services, fuel loads, seed removal, tropical forest, understory fires.

Introduction

Fire is a dominant agent of disturbance worldwide, shaping global patterns of vegetation structure and biodiversity (Bond et al. 2005; Bowman et al. 2009). The biotas of fire-prone biomes are usually highly resilient to fire as a consequence of their association with it over evolutionary time (Bond and van Wilgen 1996; Whelan 1995). However, fire-prone biomes often occur in close juxtaposition with less-flammable habitats whose biotas do not have an evolutionary association with frequent fire. Fire can penetrate such habitats if unusual fuel conditions allow it, thus posing a risk to their fire-sensitive biotas.

Throughout high rainfall regions of the seasonal tropics, highly fire-prone savannas often occur in close juxtaposition with rainforest, with the boundary between these biomes being determined largely by fire (Bowman 2000; Hoffmann et al. 2009; Hopkins 1992). A lack of grassy fuels, moist litter and humid microclimate in rainforest combine to form a fire barrier, such that the forest-savanna boundary is often extremely abrupt (Bowman 2000). However, if fire penetrates rainforest it can cause substantial top kill of trees (Hoffmann et al. 2009; Uhl and Kauffman 1990), and such degradation of forest structure has severe consequences for its shade-adapted fauna (Barlow and Silveira 2009). For example, fire in central Amazonian forests negatively affects specialist vertebrate species (Barlow et al. 2002; Barlow and Peres 2006; Mestre et al. 2013; Peres et al. 2003), and has marked impacts on the composition of litter-dwelling insects (Silveira et al. 2015).

The rainforest-savanna transitional region of the southern Amazon has recently undergone extreme land-use change (Hansen et al. 2008), and the forests are now highly fragmented. The expansion of agriculture (Macedo et al. 2012), livestock grazing (Soares-Filho et al. 2006) and selective logging (Nepstad et al. 1999) in this region has increased the flammability of forest edges, due to lower tree cover, drier microclimate, and invasion by exotic grasses (Balch et al. 2015; Cochrane 2001; Cochrane and Schulze 1999; Silvério et al. 2013). The resultant higher and drier fuel loads not only increase fire occurrence, but can also lead to increased fire intensity due to higher flame heights and faster rates of spread (Balch et al. 2015; Balch et al. 2008; Ray et al. 2005). The increased fire-proneness of such transitional regions has resulted in substantial mortality of trees and lianas (Balch et al. 2011; Brando et al. 2014), declines in carbon storage (Balch et al. 2015), disruption of plant regeneration process (Balch et al. 2013; Massad et al. 2013), and the further establishment of exotic grasses (Silvério et al. 2013). However, the consequences of increased fire intensity due to enhanced fuel loads for the fauna are poorly known.

Ants are a dominant faunal group throughout the tropics, contributing a large proportion of total faunal biomass and playing a wide range of key ecological roles (Del Toro et al. 2012; Folgarait 1998). They are highly sensitive to anthropogenic disturbances (Hoffmann and Andersen 2003; Philpott et al. 2010), and are widely used as indicators of broader ecological change (Andersen and Majer 2004; Majer et al. 2007). Disturbance leads to predictable change in the functional composition of ant communities, and such functional change can help provide a mechanistic understanding of ecosystem change (Hoffmann and Andersen 2003; Leal et al. 2012).

The effects of fire on ant communities can be through direct mortality (Kimuyu et al. 2014), but are primarily indirect, through alterations in habitat structure and food resources (Andersen et al. 2007). Fire typically has a negative impact on specialist forest-adapted ant species, which tend to be patchily distributed and especially sensitive to disturbance, and favors generalists along with thermophilic species characteristic of open habitats (Andersen et al. 2014; Andersen et al. 2012;

Frizzo et al. 2012). Fire-mediated changes in forest structure have a marked impact on litter-dwelling ant communities in the Amazon (Silveira et al. 2013; Silveira et al. 2012; Silveira et al. 2015), and this can have important implications for ecological services provided by ants. For example, ants are key seed dispersers, and rates of seed removal can increase following fire because habitat simplification leads to increased foraging ranges of ant species (Andersen 1988; Beaumont et al. 2011; Parr et al. 2007).

Here we use a manipulative field experiment to investigate the influence of fire and enhanced fuel loads on rainforest ants and their interactions with myrmecochorous seeds in the Amazonian-Cerrado transitional region in the southern Amazon. We test four hypotheses.

First, we hypothesize that fire will have an overall negative effect on ant abundance and species richness, but such effects will vary according to the functional characteristics of ant species and the habitat stratum in which they occur. We expect that litter-dwelling species will be most affected, because their habitat is directly consumed by fire, and that subterranean and arboreal species will remain largely unaffected, because their habitat strata are not burnt. We expect epigaeic species to be differentially affected according to their functional characteristics, with highly specialized taxa most sensitive (Hoffmann and Andersen 2003; Leal et al. 2012).

Second, we hypothesize that fire will lead to biotic homogenization (Solar et al. 2015; Tabarelli et al. 2012) through the elimination of specialized species (McKinney and Lockwood 1999; Olden and Poff 2003), which tend to be patchily distributed and especially sensitive to disturbance, and the favoring of widespread, disturbance-tolerant generalists. We expect that fire will result in a convergence of ant communities dominated by disturbance-tolerant opportunistic species.

Third, we hypothesize that the magnitude of the effects of fire on ant communities will be related to fire attributes associated with intensity and severity, and that fuel addition will exacerbate the effects of fire on ant communities because it will promote these attributes.

Finally, since seed-dispersing ants are typically unspecialized epigaeic species (Andersen 1997), we expect their populations to be little affected by fire. We hypothesize that seeds will be found faster in burned treatments because of increased foraging efficiency due to fire-induced simplification of ground-layer habitat structure (Parr et al. 2007).

Materials and Methods

Study site

This study was conducted in a privately-owned property located 75 km north of Canarana, Mato Grosso state, Brazil, in the southern Amazon basin (12º49’70”S, 52º21’65”W). The vegetation is tropical evergreen forest, typical of the transitional region between the *Cerrado* (savanna) and central Amazon rainforest, and shows no signs of previous disturbance by fire or logging. The area has lower tree and liana diversity in comparison with central Amazon forests, as well as a high dominance of nine tree species, mainly from Lauraceae and Burseraceae, which represent 50% of the Importance Value Index (Balch et al. 2008). The climate is tropical humid, with average annual rainfall of 1,770 mm and a marked dry season (<10 mm/month) between May and September (Rocha et al. 2014). Rainfall was unusually high in the study year (2,309 mm), especially when compared with the average of the four years prior to the experiment (1,563 mm; data collected at a meteorological station located 21 km from the study site).

Fire experiment

The experiment had a fully-replicated block design with six blocks, each composed of three 50 x 50 m plots, separated by trails approximately 2-m in width. Each block included three treatments: Control – unburned; B0 – burned without fuel manipulation; and B+ – burned with an average of 50% addition (~3.2 Mg ha^{-1}) of fine fuel (dead leaves and twigs). The added fuel was obtained from nearby areas, and transferred to the treated plots two days prior to burning. Burning occurred on 27–29 August 2013, at the end of dry season. Two blocks were burned per day, and the fires lasted for approximately one hour in each plot. The burns were carried out in the driest period of the day (early afternoon, between 12:30 and 13:30 pm), using kerosene drip torches. Wind speed was low (0.77 m s^{-1}) in the understory, and had no effect on fire behavior. The experimental site has < 2% of slope and was surrounded by undisturbed forest for at least 1 km in all directions. Average daytime air temperature during the four months prior the experiment was lower than the long-term averages, while precipitation and relative humidity were higher, which led to below-average fire danger (Brando et al. 2016). All litter was removed from the outer 5 m of each plot to act as a fire break, such that areas of 40 x 40 m were actually burned.

Details of the effects of fuel addition on fire rate of spread (m min^{-1}), flame height (cm), proportion of burned area (%), total fuel consumption (MgC ha^{-1}), frontal fire intensity (kW m^{-1}), and leaf area index (LAI; used as an estimate for canopy cover) are provided by Brando et al. (2016). In summary, fine fuel addition was associated with a 20% increase in the proportion of burned area (B0 = 0.68 ± 0.03, B+ = 0.88 ± 0.01; mean ± SE, $P < 0.01$), an increase of 10 cm in flame height (B0 = 23.87 ± 2.22; B+ = 33.81 ± 7.32; $P < 0.05$), and of 3 MgC ha^{-1} in fine fuel consumption (B0 = 9.62 ± 0.62; B+ = 12.25 ± 2.35; $P < 0.05$). Fuel addition did not influence fire rate of spread or fire intensity. LAI did not differ among treatments prior to the experiment, but following the fires it decreased by 25% in B+ and by 10% in B0 treatments (from 4.6 m^2 m^{-2} to 3.5 m^2 m^{-2} and from 4.6 m^2 m^{-2} to 4.1 m^2 m^{-2} respectively), while remaining unchanged in the Control.

Ant sampling

Ant sampling commenced 15 days after the last fires, and continued for two weeks. In each plot we established a 5 x 2 grid of sampling stations with 10 m spacing. Each sampling station consisted of three unbaited pitfall traps – one subterranean, one epigaeic and one arboreal, as well as a 1 m^2 litter sample. All pitfall traps were 5 cm in diameter, partly filled with a salt solution and detergent, and left open for 48 hours. We buried the subterranean pitfalls 15 cm deep; they had lids to avoid filling with soil, and four 1 cm-diam holes in their sides to allow ant entry. We buried the epigaeic traps with their rims flush to the soil surface, and tied arboreal traps at a height of 2 m to the trunk of the nearest tree with DBH >10 cm. We sifted litter samples and placed in mini-Winkler extractors for 48 hours at ambient temperature.

Seed removal

We established a 5 x 5 grid of seed depots with 2 m spacing in the centre of each plot to quantify rates of seed removal, as the basis of successful seed dispersal

(Leal et al. 2015; Leal et al. 2007). We also measured rates of cheating, whereby ants feed on the elaiosome *in situ*, without seed removal (Andersen and Morrison 1998; Leal et al. 2014b). A single seed of *Mabea fistulifera* (Euphorbiaceae), a myrmecochorous shrub that occurs naturally in the region, was placed on a white piece of paper (10 x 15 cm) at each depot. Seeds were collected one month prior to the experiment, and refrigerated during this period. After setting the 25 depots in a plot, we walked around the area for one hour, noting the time that each removal event (defined as moving a distance >5 cm) occurred, and, where observed, the identity of the ant responsible. If the ant was not observed, we replaced the seed to make further observations on the ant species responsible for removal (but any subsequent removal was not included in analysis of rates of removal). We also noted "cheating" events, defined as ants remaining for at least 15 minutes feeding on the elaiosome. In order to cover different ant activity periods, we conducted these trials twice in each plot, once in the morning (between 9:00-11:00 am) and again in the afternoon (between 3:00-5:00 pm).

Ant functional groups

We classified ants into functional groups following Leal et al. (2012), who adapted the global scheme of Andersen (1995) to be more specific to Neotropical rainforest (see also Delabie et al. 2000). There was one exception: we considered all species from the genus *Camponotus* as a separate group, Subordinate Camponotini. The other groups were: Cryptic Predators; Cryptic Omnivores; Epigaeic Predators; Epigaeic Omnivores; Arboreal Dominants; Arboreal Subordinates; Opportunists; Army Ants; Leaf-cutting fungus-growing ants; and Non leaf-cutting fungus-growing ants (Electronic supplementary material, Table S1).

Data analysis

In all cases, our unit of analysis was plot, with data combined across sampling stations, and considering each stratum separately. We fitted generalized linear mixed models (GLMMs) with total ant species richness, abundance, and the abundance of common functional groups as response variables. We calculated species and functional group abundances as the sum of frequencies of any species and component species of each group, respectively. Only those functional groups with abundance ≥15 in the analyzed stratum were considered. In all GLMM analyses we set block as a random factor to account for the hierarchical spatial nature of the sampling design, and used Poisson distribution as response variables were count-data. We performed pairwise contrast analyses (Crawley 2012) to evaluate differences among treatments.

We evaluated if ant species and functional group composition differed among treatments by performing a permutational multivariate analysis of variance based on Jaccard's dissimilarity (which is more suitable for presence/absence data) and with 5,000 permutations (PERMANOVA; Anderson 2001). We accounted for the hierarchical spatial nature of the sampling design by allowing randomizations to occur only within each block (Oksanen et al. 2015).

We tested the hypothesis that fire leads to biotic homogenization by evaluating whether β diversity differed among plots across treatments through a test for homogeneity of multivariate dispersions (PERMDISP; Anderson 2006; Anderson et al. 2006). This test computes a *F*-statistic to compare the average distance of each plot to their treatment median, which is defined in space by the dissimilarity index used (Sørensen pairwise dissimilarity in this case, which includes both turnover and nestedness components of β diversity). To test if the dispersions are different among treatments we used a permutation test (999 permutations). As the same β diversity value can be generated by different mechanisms, replacement and nestedness (Baselga 2010; Baselga 2012), we tested if the contribution of the nestedness component is higher for the B+ treatment by conducting the same procedures described above, but using the nestedness-fraction of Sørensen pairwise dissimilarity.

We performed hierarchical partitioning to estimate the independent contribution of fire attributes and LAI to both ant species richness and abundance, and evaluated if each factor accounted for a greater unique variation than expected by chance by using a randomization test with 5,000 randomizations, based on an upper confidence limit of 0.95% ($Z \geq 1.65$) (Mac Nally 2002). For this analysis, only data from burnt plots (B0 and B+) were used, as fire attributes do not apply to Control plots. There was no significant effect of blocks in any variables, and therefore no spatial autocorrelation. All models were built with a Poisson distribution. The direction of significant relationships was assessed with Pearson correlation analysis.

We compared the time for the seeds to be discovered in each treatment through a survival analysis. We built a model using the Weibull distribution, with fire treatments as explanatory variables and time for occurrence of each event (either removal or cheating) as the response variable. In order to account for the hierarchical spatial nature of our sampling design, we set blocks as a frailty random effect in the model, with gamma distribution. We also analyzed if the proportion of seed removal and cheating events varied among treatments by fitting GLMMs with block as a random factor and binomial distribution. Events for each plot were summed across the two sampling periods, giving a maximum of 50 possible events per plot.

We conducted all analysis in the software R (R Core Team 2015), and analyzed the residuals to check for distribution suitability and homoscedasticity in all models. For all GLMM models we calculated the conditional coefficient of determination $R^2_{(c)}$ following (Nakagawa and Schielzeth 2013), which represents the proportion of variance explained by the fixed and random effects combined. We checked for overdispersion in all GLM and GLMM models. When detected, we asserted a Quasi-poisson correction in the former, and fitted a Poisson-lognormal model in the latter, which is a simple and robust method to account for overdispersion in mixed models with count data (Harrison 2014). We used the *lme4 v1.1-7* package (Bates et al. 2014) to build GLMMs models, *betapart v1.3* package (Baselga et al. 2013) to calculate the pairwise dissimilarities, and the package *vegan* v2.3 (Oksanen et al. 2015) to PERMANOVA and PERMDISP tests. Diversity partitioning analyses were conducted using the *hier.part v1.0-4* (Walsh et al. 2013), and survival analyses with the *survival v2.38-1* package (Therneau and Grambsch 2015).

Results

We recorded 201 ant species, from 44 genera and 7 subfamilies, with 46, 118, 63, and 83 species occurring in the subterranean, epigaeic and arboreal traps and litter samples respectively (Table S2). There were no treatment differences in ant abundance in the epigaeic stratum, whereas B+ plots had the lowest mean ant abundance for the subterranean ($R^2_{(c)} = 0.53$, $P = 0.03$), litter ($R^2_{(c)} = 0.70$, $P = 0.02$) and arboreal strata ($R^2_{(c)} = 0.35$, $P = 0.01$) (Fig. 1). There were no treatment differences in ant richness in the arboreal stratum, but mean species richness was highest in Control plots for the subterranean ($R^2_{(c)} = 0.39$, $P = 0.05$), litter ($R^2_{(c)} = 0.67$, $P = 0.01$) and epigaeic strata ($R^2_{(c)} = 0.21$, $P = 0.03$) (Fig. 2). In each case there was no difference in mean richness between the two burning treatments. Reductions in total abundance and species richness in burnt plots were highest (75% and 38% respectively) in the litter stratum, where the abundances of Arboreal Dominants ($R^2_{(c)} = 0.36$, $P = 0.02$), Cryptic Omnivores ($R^2_{(c)} = 0.55$, $P = 0.03$) and Epigaeic Predators ($R^2_{(c)} = 0.5$, $P < 0.01$) were highest in Control plots (Fig. 3). The abundance of Cryptic Predators ($R^2_{(c)} = 0.73$, $P < 0.01$) and Subordinate Camponotini ($R^2_{(c)} = 0.67$, $P < 0.01$) in the litter stratum was lowest in B+ plots. In the epigaeic stratum, Epigaeic Predators were most abundant in Control plots ($R^2_{(c)} = 0.29$, $P = 0.01$) (Fig. 3). Other groups and strata either showed no significant variation, or did not have enough occurrences (abundance ≤ 15) for analysis.

There were no significant differences in ant species composition among treatments in any strata: subterranean (PERMANOVA $F_{2,15} = 0.68$; $P = 0.88$), litter ($F_{2,15} = 0.90$; $P = 0.21$), epigaeic ($F_{2,15} = 0.86$; $P = 0.71$), and arboreal ($F_{2,15} = 1.08$; $P = 0.36$). Likewise, the composition of functional groups did not differ among treatments in either subterranean (PERMANOVA $F_{2,15} = 0.24$; $P = 0.98$), litter ($F_{2,15} = 1.06$; $P = 0.06$), epigaeic ($F_{2,15} = 0.39$; $P = 0.79$) or arboreal ($F_{2,15} = 0.43$; $P = 0.87$) strata. We also found no evidence of faunal convergence among burnt plots, as total β diversity did not differ among treatments in any strata: subterranean (PERMDISP $F_{2,15} = 0.1$; $P = 0.9$), epigaeic ($F_{2,15} = 0.23$; $P = 0.78$), litter ($F_{2,15} = 0.69$; $P = 0.51$) or arboreal ($F_{2,15} = 0.1$; $P = 0.90$). The nestedness component did not differentially explain total β diversity among treatments in either the subterranean (PERMDISP $F_{2,15} = 0.47$; $P = 0.63$), epigaeic ($F_{2,15} = 2.33$; $P = 0.12$), litter ($F_{2,15} = 1.35$; $P = 0.29$) or arboreal stratum ($F_{2,15} = 1.01$; $P = 0.38$).

With just one exception, variation in neither ant abundance nor species richness in any stratum was related to either LAI or any of the fire variables. The single exception was that epigaeic ant abundance was negatively related to Proportion of Burned Area (z-score = 1.74), which explained 26.7% of total deviance.

Six ant species (of *Pheidole*, *Trachymyrmex* and *Crematogaster*) were observed removing seeds, and 25 were observed cheating by feeding on elaiosomes without removal (Table S2). The mean time for ants to discover a seed (independent of it leading to removal or cheating) was lower in the Control (43.8 min ± 1.22; mean ± SE) than in B0 (45.77 min ± 1.19; $P = 0.05$), which in turn was lower than in B+ plots (49.18 min ± 1.10; $P = 0.02$; Fig. 4). The mean total abundance of species interacting with seeds was lower in B+ plots (35.66 ± 4.97; mean ± SE; $R^2_{(c)} = 0.45$, $P = 0.02$) than in the Control (48.66 ± 4.19) and B0 (45.16 ± 6.09), which did not differ from each other. The averaged proportion of seed removal (over 1 hr) was higher in the Control ($R^2_{(c)} = 0.12$, $P < 0.01$) than in B0 and B+ (Fig. 5), which did not differ from each other. The abundances of remover species did not differ across treatments ($P = 0.23$). Rates of cheating did not differ across treatments ($P = 0.23$) (Fig. 5), but the abundances of cheater species were lower in B+ plots ($R^2_{(c)} = 0.67$, $P < 0.01$) than in Control and B0 plots, which did not differ from each other.

Discussion

Our study experimentally addressed how fire affects shade-adapted Amazonian ant communities from all four habitat strata and an important service they provide to plants, as well as the extent to which such effects are exacerbated by fuel addition. We first hypothesized that fire will have an overall negative effect on ant abundance and species richness, but such effects will vary according to the functional characteristics of ant species and the habitat stratum in which they occur. As we expected, litter-dwelling ants were the most affected by fires, with highest reductions in both abundance and species richness. Most litter-dwelling species nest in litter rather than within soil (Byrne 1994), and so would suffer substantial mortality during fire either through direct consumption or through radiant heat (Swengel 2001). Indirect effects due to the removal of litter also cause declines in litter-dwelling ants after fire through loss of habitat (Vasconcelos et al. 2009), including loss of nest sites (such ants are nest-site limited; Jiménez-Soto and Philpott 2015).

As also predicted, the ants most sensitive to fire in the epigaeic stratum were highly specialized species – fire caused a decrease in the abundance of Specialist Predators, but did not affect the abundance of any other functional group. Epigaeic predators are large bodied and occupy the highest trophic position among ants; both these traits make insects especially sensitive to disturbance (e.g. Andrade et al. 2014; Filgueiras et al. 2011; Leal et al. 2014a).

As we predicted, arboreal species remained relatively unaffected by our experimental burning, because the arboreal stratum is mostly removed from direct effects of understory fire. However, contrary to our prediction, fire had a marked effect on the abundance and species richness of subterranean ants, reducing both by about 30%. This is the first study investigating the effects of fire on a subterranean ant fauna, and its sensitivity to fire contrasts with the resilience of below-ground arthropods shown in previous studies (reviewed by Swengel 2001). The heating effects of fire are usually negligible below the top 5 cm of soil (DeBano 2000), and so the majority of arthropods in the soil are not affected. However, most ant species collected in subterranean traps also occur in the soil-litter interface (Andersen and Brault 2010), and so the marked reductions in subterranean catches that we observed in burnt plots likely reflect the effects of fire on the litter fauna.

Our second hypothesis was that fire would lead to biotic homogenization by eliminating patchily distributed specialists and favoring widespread generalists. Fire did reduce species richness and had a particular effect on highly specialized species (Specialist Predators). However, we found no evidence of overall biotic homogenization, as shown by a lack of treatment variation in either total β diversity or its nestedness component. There was also little evidence for biotic homogenization of litter-dwelling ant communities after fire in the central Amazon (Silveira et al. 2015). This can be explained by the highly patchy nature of understory fires in the Amazon due to low fuel loads and variation in fuel moisture (Balch et al. 2008), which produces a fine-scale mosaic of burned and unburned areas. Such a mosaic would enable even highly sensitive species to persist in unburnt refuges, although at lower overall levels of abundance.

Biotic homogenization is not only a product of differential extinction, but can also be a result of post-disturbance invasion by similar species (Olden and Poff 2003). However, there was not enough time for this to be a major factor in our study, given that we sampled within a month after experimental fires and it is unlikely that ants could re-colonize the area in such a short period. Ant composition did not change after eight months or 10 years following fire at a nearby site (Silveira et al. 2013), which suggests that for this level of post-fire impact, invasion by disturbance-promoted species is not an issue in such forests even in the longer term. The lack of biotic homogenization of ant communities following fire in the Amazon is in striking contrast to the high biotic homogenization that follows the conversion of forests to agricultural landscapes (Solar et al. 2015).

Our third hypothesis was that the magnitude of the effects of fire will be directly related to fire attributes associated with intensity and severity. We found only very weak support for this. There was a negative correlation between the proportion of burned area and the abundance of epigaeic ants, but we found no relationship between flame height, total fuel consumption, fire rate of spread or frontal fire intensity and any measure of ant abundance or richness. Fuel addition reduced overall ant abundance in the subterranean, litter and arboreal strata, but fuel loads had only minor effects on fire attributes. This appears to be typical for non-drought years across the southern Amazon (Balch et al. 2011). Fires are far more intense during drought years (Brando et al. 2014) and our experiment was conducted during an unusually wet year; the relationship between fuel loads and fire attributes, and the effects of fuel addition on ant communities, might be stronger during drier years.

Our final hypothesis was that seeds will be found faster in burned treatments because of increased foraging efficiency. We actually found the reverse: seeds were located fastest, and rates of removal were highest, in Control plots. The abundances of species interacting with seeds did not differ between Control and B0 plots, and the abundances of remover species did not differ across treatments. We therefore attribute the treatment differences in the rates at which seeds were located and removed to the reductions in canopy cover (as measured by LAI) caused by fire, with the warmer and drier microclimate (Uhl and Kauffman 1990) limiting the activity of rainforest ant species due to thermal stress (Levings 1983). This contrasts with the situation in open habitats dominated by thermophilic species, where fire promotes an increase in ant activity (Andersen 1988; Parr et al. 2007). The slower removal of myrmecochorous seeds that we observed following fire makes them more vulnerable to seed predators (Turnbull and Culver 1983).

In conclusion, low intensity understory fire had extensive negative effects on southern Amazonian ant communities, with highly specialized taxa (cryptobiotic species of the litter layer, and epigaeic specialist predators) being most sensitive. Fire reduced the effectiveness of a key ecosystem service provided by ants, which we attribute to reductions in foraging activity due to increased thermal stress. Our findings indicate that enhanced fuel loads at rainforest margins will not directly decrease ant biodiversity and ecosystem services through increased fire severity, at least in wet years. However, higher fuel loads can still have an important negative effect on ant diversity in Amazonian rainforests by increasing the risk of fire occurrence (Balch et al. 2015), which has a detrimental impact on ant communities and a key ecosystem service they provide.

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Figure legends

Fig. 1 Variation in ant abundance among treatments (C = Control; B0 = No fuel addition; B+ = Fuel addition) in each habitat stratum. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Fig. 2 Variation in ant species richness among treatments (C = Control; B0 = No fuel addition; B+ = Fuel addition) in each habitat stratum. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Fig. 3 Abundances of ant functional groups that showed statistically significant variation among treatments (C = Control; B0 = No fuel addition; B+ = Fuel addition) in a habitat stratum. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Fig. 4 Variation in seed discovery time among treatments (C = Control; B0 = No fuel addition; B+ = Fuel addition). Seeds were discovered fastest in the Control, and slowest in the B+ treatment

Fig. 5 Variation in the proportion of (a) seed removal and (b) cheating among treatments (C = Control; B0 = No fuel addition; B+ = Fuel addition) after 1 hr. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Figures

Figure 1

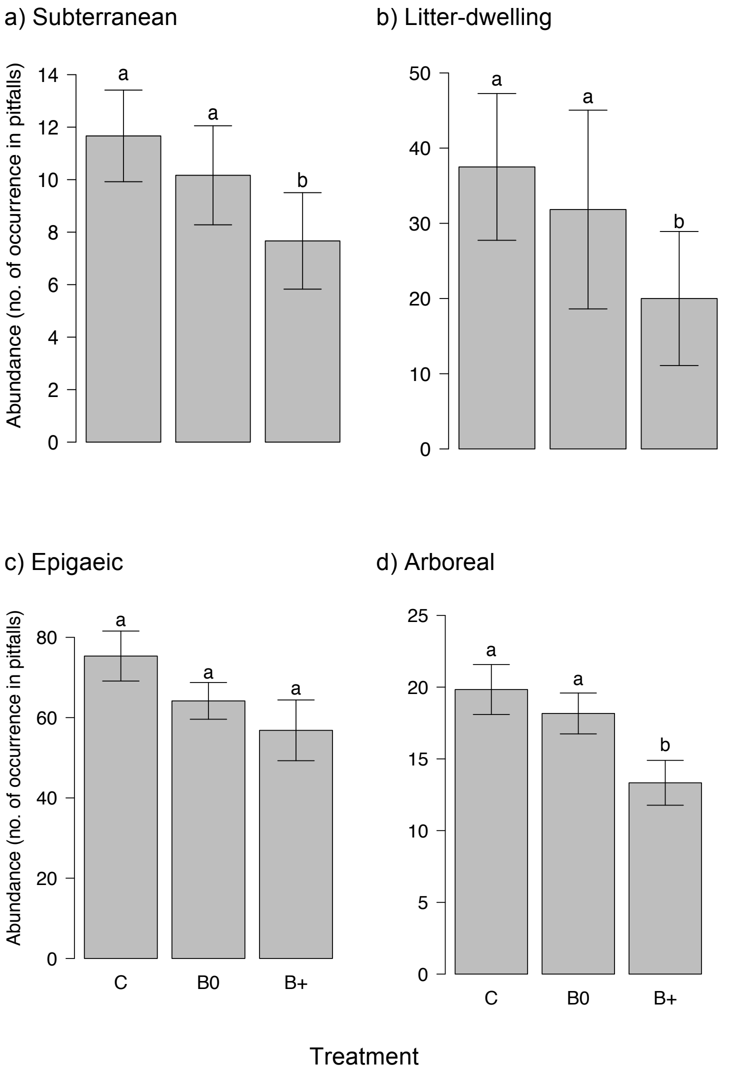
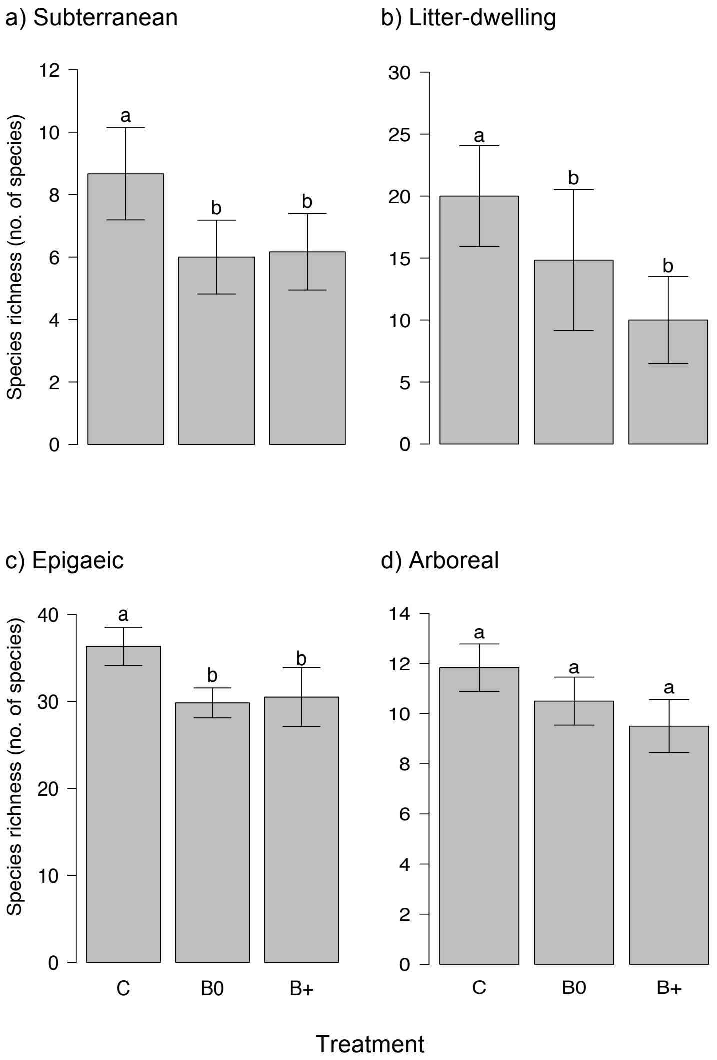


Figure 2



a) Subterranean
b) Litter-dwelling
c) Epigaeic
d) Arboreal
Species richness (no. of species)
0
2
4
6
8
10
12
a
b
b
0
5
10
15
20
25
30
a
b
b
0
10
20
30
40
a
b
b
0
2
4
6
8
10
12
14
a
a
a
C
B0
B+
C
B0
B+
Treatment

Figure 3

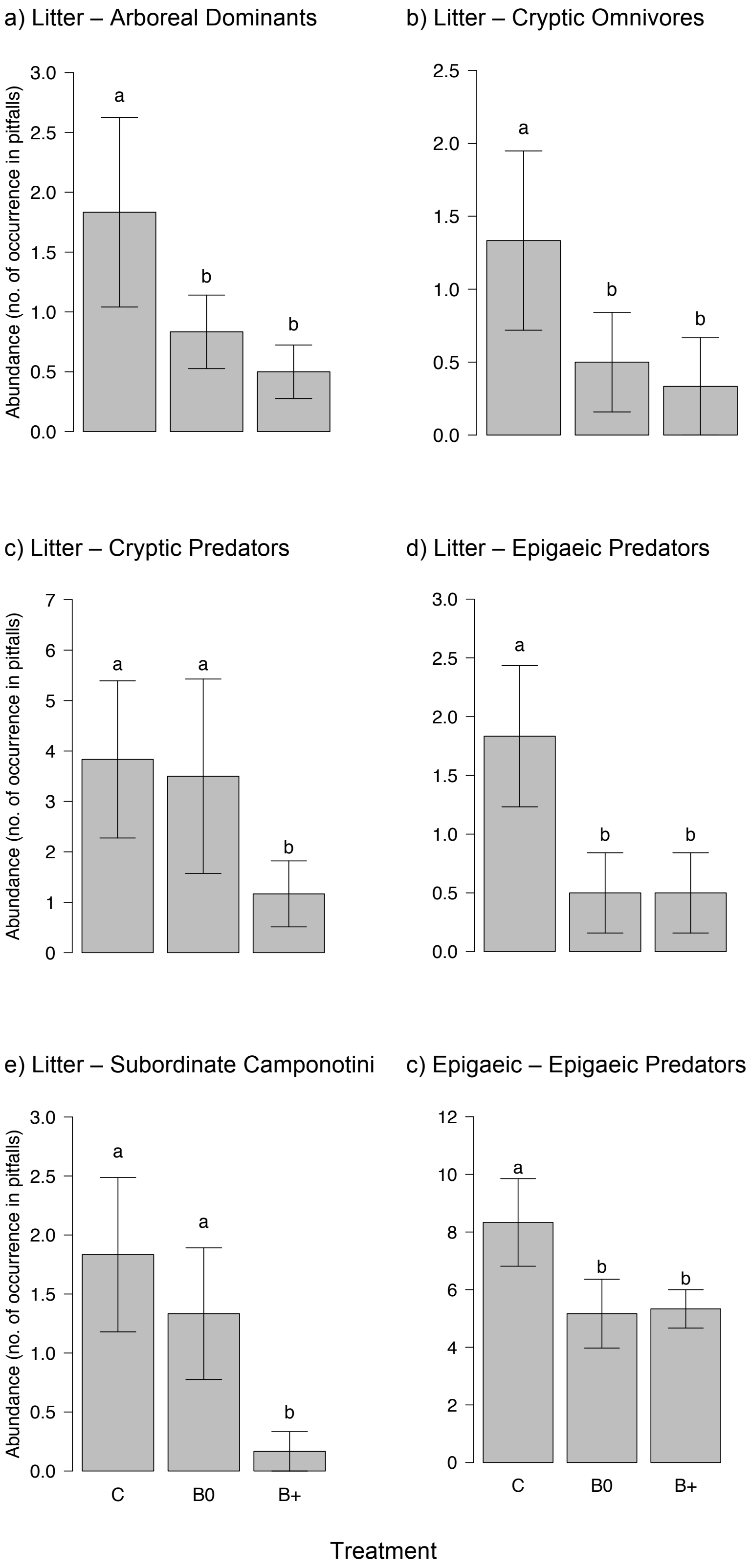

a) Litter – Arboreal Dominants
b) Litter – Cryptic Omnivores
c) Litter – Cryptic Predators
d) Litter – Epigaeic Predators
e) Litter – Subordinate Camponotini
c) Epigaeic – Epigaeic Predators
Abundance (no. of occurrence in pitfalls)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
1
2
3
4
5
6
7
2
4
6
8
10
12
a
b
C
B0
B+
Treatment

Figure 4

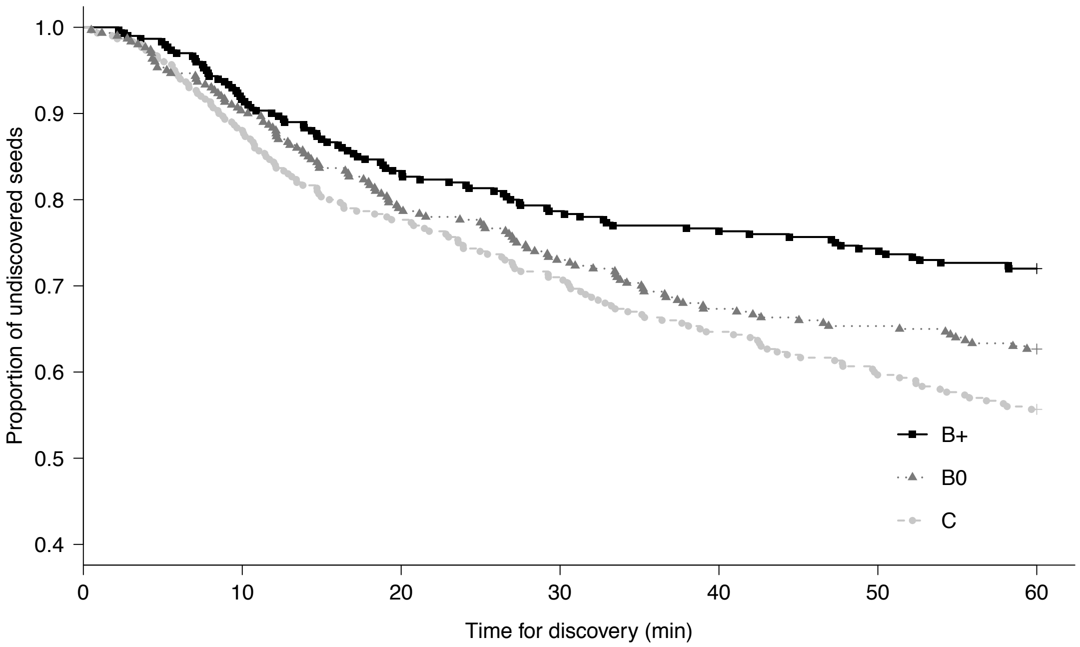
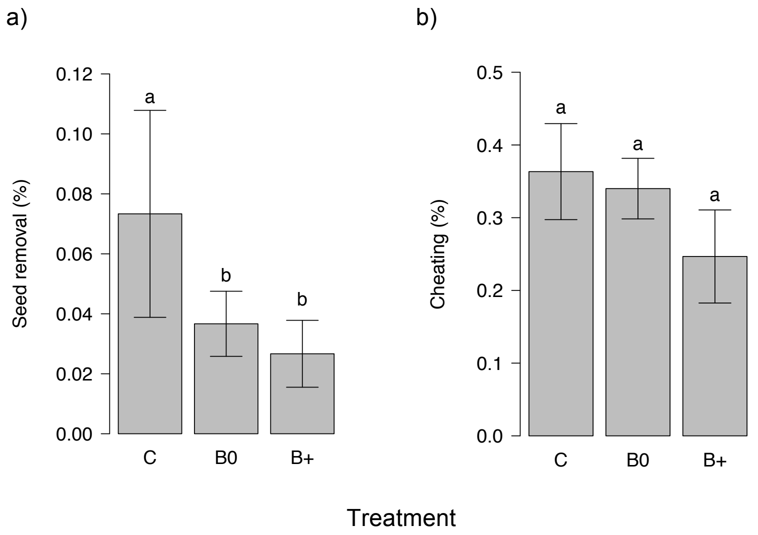

1.0
0.9
0.8
0.7
0.6
0.5
0.4
Proportion of undiscovered seeds
0
10
20
30
40
50
60
Time for discovery (min)
B+
B0
C

Figure 5


a)
b)
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Seed removal (%)
a
b
b
C
B0
B+
0.5
0.4
0.3
0.2
0.1
0.0
Cheating (%)
a
a
a
C
B0
B+
Treatment

Electronic supplementary material

Table S1. Classification of ant genera into functional groups, adapted from Andersen (1995) and Leal et al. (2012).

Genus	**Functional group**
Acropyga	Cryptic Omnivores
Anochetus	Epigaeic Predators
Apterostigma	Non leaf-cutting fungus-growing ants
Atta	Leaf-cutting fungus-growing ants
Azteca	Arboreal Dominants
Basiceros	Cryptic Predators
Brachymyrmex	Opportunists
Camponotus	Subordinate Camponotini
Carebara	Cryptic Omnivores
Cephalotes	Arboreal Subordinates
Crematogaster	Arboreal Dominants
Cyphomyrmex	Non leaf-cutting fungus-growing ants
Daceton	Epigaeic Predators
Dolichoderus	Arboreal Dominants
Ectatomma	Opportunists
Gigantiops	Epigaeic Omnivores
Gnamptogenys	Epigaeic Omnivores
Hylomyrma	Epigaeic Omnivores
Hypoponera	Cryptic Omnivores
Labidus	Army Ants
Linepithema	Epigaeic Omnivores
Megalomyrmex	Epigaeic Omnivores
Monomorium	Epigaeic Omnivores
Myrmelachista	Cryptic Omnivores
Myrmicocrypta	Non leaf-cutting fungus-growing ants
Neivamyrmex	Army Ants

Neoponera	Epigaeic Predators
Nesomyrmex	Epigaeic Omnivores
Nylanderia	Opportunists
Ochetomyrmex	Epigaeic Omnivores
Odontomachus	Epigaeic Predators
Pachycondyla	Epigaeic Predators
Pheidole	Epigaeic Omnivores
Pseudomyrmex	Arboreal Subordinates
Rasopone	Epigaeic Predators
Rogeria	Cryptic Omnivores
Sericomyrmex	Non leaf-cutting fungus-growing ants
Solenopsis	Epigaeic Omnivores
Strumigenys	Cryptic Predators
Tapinoma	Opportunists
Trachymyrmex	Non leaf-cutting fungus-growing ants
Tranopelta	Cryptic Omnivores
Xenomyrmex	Arboreal Subordinates
Wasmannia	Epigaeic Omnivores

Table S2. List of ant species sampled in each strata and treatment (C = Control; B0 = No fuel addition; B+ = Fuel addition), and removing seeds or cheating. Numbers indicate the frequency of occurrence of each species in correspondent stratum and treatment.

Stratum/Treatment	Subterranean			Litter			Epigaeic			Arboreal			Removed			Cheated		
Subfamily/Species	C	B0	B+	C	B0	B+	C	B0	B+	C	B0	B+	C	B0	B+	C	B0	B+
Dolichoderinae																		
Azteca sp.1		1		1			5	2	2	3	3	2				1	1	
Azteca sp.2											1							
Azteca sp.3										1		1						
Azteca sp.4									1		1							
Azteca sp.5									1			1						
Azteca sp.6												1						
Dolichoderus ghilianii							1					1						
Dolichoderus imitator					1		1	2		3		1						
Dolichoderus attelaboides																1		
Linepithema sp.2																	1	
Linepithema aztecoides								1										
Tapinoma sp.2												1						
Dorylinae																		
Labidus mars		1																

Labidus praedator				1									
Neivamyrmex sp.1	1	1	1										
Ectatomminae													
Ectatomma edentatum						1	4	1					
Ectatomma lugens				1			3	1	1				
Ectatomma tuberculatum				1			1		1		1		
Gnamptogenys striatula					2			1	1				
Formicinae													
Acropyga sp.1	3												
Acropyga sp.2			2										
Acropyga sp.3			1										
Brachymyrmex sp.1			1	14	11	8	1	3	5			3	
Brachymyrmex sp.2	1						5	6	3	3	2		1
Brachymyrmex sp.4				1					1	1		1	
Brachymyrmex sp.5										3	1		
Camponotus atriceps			1				21	15	14	14	18	16	
Camponotus crassus				4	5		28	26	15	13	11	8	
Camponotus sericeiventris							1						

Camponotus sp.1							7	1	3	1		1
Camponotus sp.2							1			1		
Camponotus sp.5								2	1			
Camponotus sp.7							1	2	1			
Camponotus sp.8	1						4	2	1			
Camponotus sp.11							7	9	6	3	4	
Camponotus sp.13				2			2			1	1	
Camponotus sp.15												1
Camponotus sp.19										1		
Camponotus sp.21							2	1	1			1
Camponotus sp.22				3			3	7	6		2	1
Camponotus sp.28		1		5	3	1	8	5	4	2	3	1
Camponotus sp.34								1				
Camponotus sp.37												1
Camponotus sp.39							1					
Camponotus sp.42											1	
Gigantiops destructor							16	9	11	3	7	
Myrmelachista nodigera											1	1
Nylanderia sp.1	1	1					8	2	2			

Nylanderia sp.2					5	6	3		5	8	6	1	1	
Nylanderia sp.4										1	1			
Nylanderia sp.5									1		1			
Myrmicinae														
Apterostigma carinatum									1	2	2			
Apterostigma megacephala									1					1
Apterostigma sp.1					1		1		8	4	2			
Apterostigma sp.3					1	1	1			1				
Apterostigma sp.4										1				
Atta laevigata					1				5	3	4	1		
Atta sp.6										1				
Atta sp.8									3			1		
Basiceros militaris					1	1								
Carebara sp.1							1							
Carebara sp.2									1					
Carebara sp.3					1									
Carebara sp.4	9	11	6					1						
Carebara sp.6				1										

Cephalotes atratus								1							
Cephalotes oculatus									1						
Cephalotes patellaris			1	1					1						
Cephalotes sp.2										1					
Cephalotes sp.9										1					
Crematogaster crassinoda								1							
Crematogaster flavosensitiva			1												
Crematogaster sp.1	2	1	4			12	14	5	9	9	4	1			1
Crematogaster sp.2			3	3	3	2			1						
Crematogaster sp.9														1	
Crematogaster sp.10						1	1	3					1		
Crematogaster sp.12			2	1		1	1								
Crematogaster sp.13										1					
Cyphomyrmex laevigatus			2	4			2	3							
Cyphomyrmex sp.1				2	2		1	1							
Cyphomyrmex sp.2						1									
Cyphomyrmex sp.3			2												

Cyphomyrmex sp.4							2	1										
Cyphomyrmex sp.5								1										
Daceton armigerum							1		1									
Hylomyrma immanis					1													
Megalomyrmex sp.1								1										
Megalomyrmex sp.2	1																	
Megalomyrmex sp.3							1											
Monomorium floricola	1		1			1											1	
Myrmicocrypta foreli				1														
Nesomyrmex sp.1							1					1						
Nesomyrmex sp.3												1						
Ochetomyrmex neopolitus				1		1	1											
Ochetomyrmex semipolitus				1	2		1	2	1	4	2	3						1
Pheidole fimbriata	2	1	2						1									
Pheidole sp.1				2	4		6	9	6									
Pheidole sp.2	8	11	10	12	15	10	39	40	44	2	1		1		1	5	4	9
Pheidole sp.3	1					1	10	10	14									

Pheidole sp.4									2	2	5	4						
Pheidole sp.5								1										
Pheidole sp.6	2	1	1	1	1		9	7	6					1		1		1
Pheidole sp.7	3	1		3	10	7	14	14	14	3						5	8	5
Pheidole sp.9							3	7	11									
Pheidole sp.10				9	8	3	11	8	9							1		
Pheidole sp.11					3		7	6	5								1	
Pheidole sp.14				3			1		1		1							
Pheidole sp.15						1	2											
Pheidole sp.17	1	1		3		1	12	23	15							1		
Pheidole sp.18				2	1	2												
Pheidole sp.20																	2	4
Pheidole sp.21					1													
Pheidole sp.26				1	2	3												
Pheidole sp.28				1			1		1									
Pheidole sp.31							1	3										
Pheidole sp.32																	1	
Pheidole sp.33										1	4	2						
Pheidole sp.34				2	1		1	3										

Pheidole sp.37							3	1										
Pheidole sp.38							1	1	1						1			
Pheidole sp.41									1									
Pheidole sp.42			1				1	1	3									
Pheidole sp.43	1			2	5	8	1	1										
Pheidole sp.44							1											
Pheidole sp.46							1											
Pheidole sp.49					1		1		1									
Pheidole sp.52							4		2	1								1
Pheidole sp.54							1											
Pheidole sp.60									1									
Pheidole sp.61	1	1		1	1		2	3	4								1	
Rogeria sp.1				1														
Sericomyrmex sp.1		2			1		3	4	3									
Sericomyrmex sp.2									1									
Sericomyrmex sp.5							1											
Solenopsis saevissima																1	2	
Solenopsis sp.1	3	2	1	29	20	15	21	11	9	19	15	10				3	5	2
Solenopsis sp.2	4	9	3	8		3	6	11	5									

Solenopsis sp.4			1			1	8	7	4			
Solenopsis sp.6				12	15	6						
Solenopsis sp.7			1					1				
Solenopsis sp.9	1		2									
Solenopsis sp.10							1					
Solenopsis sp.11											1	1
Solenopsis sp.12	1											
Solenopsis sp.13	1			10	12	9	4	3	1			
Solenopsis sp.14				15	6	8	5		1			
Solenopsis sp.16	1	1	1									
Solenopsis sp.17	2		1					1				
Solenopsis sp.18												1
Solenopsis sp.19					1							
Solenopsis sp.20							1					
Solenopsis sp.21										2	1	
Solenopsis sp.22										1		
Solenopsis sp.23					1							
Solenopsis sp.25	1	1	1		3							
Solenopsis sp.26				1								

Solenopsis sp.29												1						
Solenopsis sp.35				1			1											
Strumigenys aff. *crassicornis*				1														
Strumigenys denticulata	1			13	12	7												
Strumigenys elongata				1	1													
Strumigenys perpava				5	5													
Strumigenys trudifera					1													
Strumigenys zeteki				2	1													
Trachymyrmex sp.1				2	7	8	15	14	15							2	2	
Trachymyrmex sp.2					1	1	1	2										
Trachymyrmex sp.3															1	2		2
Trachymyrmex sp.4															1		3	
Trachymyrmex sp.6	1						17	16	15									
Trachymyrmex sp.9							1											
Tranopelta sp.1	11	12	6				2	1										
Xenomyrmex sp.1									1									
Wasmannia sp.1							1											
Wasmannia auropunctata				1														

Ponerinae												
Anochetus diegensis				1		2						
Anochetus mayri				3	1							
Anochetus targionii				3			1					
Hypoponera sp.1	1											
Hypoponera sp.2	1											
Hypoponera sp.3		1										
Hypoponera sp.4	1			1		1						
Hypoponera sp.5				5	3							
Hypoponera sp.6				2								
Neoponera apicalis							3				1	
Neoponera carinulata										1		1
Neoponera commutata							3		4			
Neoponera verenae							24	12	7			
Neoponera villosa							1		1	1	1	
Odontomachus meinerti				1	1							
Odontomachus sp.2			1									
Pachycondyla crassinoda							17	18	18			

Pachycondyla harpax		3		1		1	1			
Rasopone aff. *lunaris*	1									
Rasopone arhuaca			1							
Pseudomyrmecinae										
Pseudomyrmex sp.1					1				1	
Pseudomyrmex sp.2		1			1					
Pseudomyrmex sp.3								6	2	1
Pseudomyrmex sp.4								7	2	2
Pseudomyrmex sp.5								1		4
Pseudomyrmex sp.6									2	
Pseudomyrmex sp.9										1

CHAPTER TWO

RESPONSES OF RAINFOREST ANTS TO HIGH FIRE FREQUENCY: CONGRUENCE WITH VEGETATION CHANGE IN THE SOUTHERN AMAZON

Artigo a ser submetido à revista Conservation Biology

Responses of rainforest ants to high fire frequency: congruence with vegetation change in the southern Amazon

Running Head: Fire frequency and rainforest ants

Authors: Lucas N. Paolucci[1*]; José H. Schoereder[2] and Alan N. Andersen[3].

[1] Programa de Pós-Graduação em Ecologia; [2] Departamento de Biologia Geral, Universidade Federal de Viçosa, Av. P.H. Rolfs, s/n, *Campus Universitário*, CEP 36570-000, Viçosa, MG, Brasil. [3] CSIRO Land & Water, Tropical Ecosystems Research Centre PMB 44, Winnellie, NT, 0822, Australia.

*Corresponding author. E-mail: lucaspaolucci@gmail.com

Abstract

Human activities on tropical forests fragment the original habitat, and increase the flammability of its edges. Once burned, a positive fire feedback may be established and fire return intervals can drastically decrease. Here we assess the effects of repeated fires on forest ant communities in the southern Amazon using a manipulative experiment where treatment plots were subject to annual and triennial fires over a six-year period. We ask the question: Do ant communities show comparable plot differences in abundance, biomass, species diversity and species composition to that shown by trees? Experimental fires were applied to adjacent forest plots (0.5 X 1.0 km): one plot was burnt annually, another was burnt triennially, and a third was left unburnt. Trees from three size-classes (small, 10-19.9; medium, 20-39.9 and large, ≥ 40 cm diameter at breast height) were surveyed in each 50-ha treatment prior to the first experimental fires, and again two years after the last fires. Ants were sampled three years after the last fires in three strata: subterranean, epigaeic and arboreal. Ant responses to burning were highly consistent with those of trees. Epigaeic ant species were the most sensitive, and particularly affected by annual fires. Fire had a much more severe impact on abundance and biomass of trees than of ants, as the effects on ants are primarily indirect rather than through direct mortality. Changes in ant biomass in burnt plots were disconnected from changes in ant abundance, which has important implications for using changes in abundance as proxies for changes in ecological function. Species diversity and composition varied similarly for ants and trees. Recurrent fires in southern Amazonian forests have dramatic effects not only on trees, but also on ants, one of the most abundant and ecologically important faunal groups. Preventing such disturbance should be a priority for conservation management.

Key words: Biomass, evenness, recurrent fires, tropical forest, understory fires.

Introduction

Tropical forests rarely burn naturally, due to their humid microclimate and high rates of litter decomposition (Bond and van Wilgen 1996; Mueller-Dombois 1981; Uhl and Kauffman 1990). However, fire risk is increased by logging and agricultural development, which create fire-prone agricultural habitats, fragment the original forest, and increase the flammability of forest edges (Alencar et al. 2004; Nepstad et al. 1999). Once burned, a positive fire feedback may be established due to higher canopy openness, and higher and drier fuel loads (Cochrane et al. 1999; Nepstad et al. 2001). Such factors can drastically alter fire return intervals in tropical forests, from an historical 500-1000 years (Pivello 2011) to as little as 5-10 years (Cochrane 2001).

Recurrent fires in tropical forests influence both fire intensity and ecological responses. Compared with a single fire, recurrent fires are usually more intense due to higher flame heights and faster spread rates (Ray et al. 2005). Trees with thick bark and larger diameter are less susceptible to fire (Brando et al. 2012), but sufficient fire-free intervals are required to allow recruitment into fire-resistant size classes (Hoffmann et al. 2009). Recurrent fires increase the vulnerability of resprounting stems, extirpate more pioneer species than do single fires, and lead to higher turnover in tree species composition (Barlow and Peres 2008). It also leads to a greater impact on faunal communities (Barlow and Peres 2006; Silveira et al. 2015).

The rainforest-savanna transitional region of the southern Amazon is undergoing extreme land-use change that is increasing the fire risk of remaining forest (Morton et al. 2013). These forests are already more fire-prone than those in the central Amazon because they experience more frequent and intense droughts (Coe et al. 2013) and occur in close juxtaposition with the highly fire-prone *Cerrado* biome

(Brazilian savanna), with the boundary between these two biomes largely determined by fire (Bowman 2000; Hoffmann et al. 2009; Hopkins 1992). Under suitable conditions, fire can penetrate the forest edges, reducing canopy cover, increasing fuel loads and therefore making them more fire-prone (Silvério et al. 2013).

Forests of the southern Amazon are relatively resistant to single fires, but can be dramatically impacted by repeated burning, especially under extreme climatic conditions (Balch et al. 2015; Brando et al. 2014; Brando et al. 2012). Repeated fires cause high tree mortality and severely degrade forest structure (Balch et al. 2011; Brando et al. 2014), promote the invasion of native and pasture grasses (Silvério et al. 2013), and markedly change patterns of plant regeneration and succession (Balch et al. 2013). However, the extent to which repeated fires have comparable impacts on faunal assemblages has been little studied.

Ants are a globally dominant faunal group that are widely used as environmental and biodiversity indicators of the effects of habitat disturbance (Andersen and Majer 2004; Majer et al. 2007). They are especially abundant and ecologically important in tropical forests (Agosti et al. 2000; Hölldobler and Wilson 1990). Single fires in southern Amazonian forests decrease ant species richness, alter functional group composition, and reduce the effectiveness of ecosystem services they provide (Paolucci et al. 2016; Silveira et al. 2012). However, there has been only one study of the effects of repeated fires on ant communities of southern Amazon forests, where the abundance of epigaeic ants was found to be promoted by burning on three occasions over a three-year period, due at least in part to an increased occurrence of leaf-cutting ants (Silveira et al. 2010).

Here we assess the effects of repeated fires on forest ant communities in the southern Amazon using a manipulative experiment where treatment plots were subject to annual and triennial fires over a six-year period. The treatment plots were not replicated and no pre-treatment ant data are available; it is therefore not possible to conduct a formal analysis of treatment effects. Instead, we focus on differences between plots (Davies and Gray 2015), and strengthen our inference of treatment effects by comparing plot differences in ant communities with those of trees, where treatment effects have been previously demonstrated through BACI analysis. We ask the question: Do ant communities show comparable plot differences in abundance, biomass, species diversity and species composition to that shown by trees? Previous analysis has shown that tree responses to fire vary with size class, with those in the smallest size class most affected. We predict that plot variation in ant communities will similarly vary with habitat stratum because of differential fire effects, with epigaeic ants showing greater differences between burned and unburned plots than those in the subterranean and arboreal strata. We also predict that plot variation in richness and composition will be similar for ants and trees, but that trees will show far greater variation in abundance and biomass because these variables are directly impacted by fire, whereas the effects of fire on ants are primarily indirect through changes in habitat structure (Andersen et al. 2012).

Materials and methods

Study site

The study was conducted at “Fazenda Tanguro”, a privately-owned property located 75 km north of Canarana, Mato Grosso, southern Amazon basin (13°04’35”S, 52°23’08”W). The climate is tropical humid, with average annual rainfall of 1,770 mm and a marked dry season (<10 mm/month) between May and September (Rocha et al. 2014). Local vegetation is characterized by tropical evergreen forest, typical of the transitional area between the Cerrado and the Amazon rainforest. The area was not previously disturbed by fire or logging, has <2% slope and contains >1000 m of forest extending around experimental plots. Plant species richness and canopy leaf area index are lower compared with central Amazon forests, and there is a high dominance of nine tree species, mainly from Lauraceae and Burseraceae, which represent 50% of the Importance Value Index (Balch et al. 2008).

Fire experiment

Experimental fires were applied to adjacent forest plots (0.5 X 1.0 km) along a soybean field edge (Fig. 1). One plot (AB) was burnt annually from 2004 to 2010 (except for 2008), and another plot (TB) was burnt triennially (in 2004, 2007 and 2010). All burning was conducted at the end of the dry season (August or September). Fires were set with kerosene drip torches during 3–4 consecutive days between 9:00 and 16:00 hours. A third adjacent plot (C) was left unburnt as a control. A full description of experimental burns and fire behavior can be found in Balch et al. (2008).

Vegetation measurements

Vegetation assessments were conducted using a BACI design. Floristic surveys were conducted in each 50-ha treatment plot in July 2004, prior to the first experimental fires (see Balch et al. 2008; 2011 for a full description). There were no significant pre-treatment differences among plots in vegetation variables such as species richness, relative abundance of the five most common species, Importance

Value Index (IVI) for species inventoried, adult composition, woody stem density and composition, and stem regeneration density, nor microclimate variables such as vapor pressure deficit near the soil surface (~ 10 cm height) and litter moisture content (Balch et al. 2013; Balch et al. 2008).

Vegetation was assessed two years after the last burning (end of the 2012 dry season), focusing on trees with diameter at breast height (dbh) ≥10 cm. Within each plot, small (10-19.9 cm dbh) trees were surveyed in six transects of 500 m x 10 m, while medium (20-39.9 cm dbh) and large-sized (≥ 40 cm dbh) trees were sampled in six transects of 500 m x 20 m. The transects were at 0, 30, 100, 250, 500, and 750 m from the edge (see Fig. 1 in Balch et al. 2011). Height (m) and dbh (at 1.3 m) measurements were taken for each tree. Leaf Area Index (LAI) as a proxy for canopy cover was also documented. LAI was measured in October 2013 (N = 92 for Control; N = 69 for TB and N = 68 for AB). Two LiCor-2000 Plant Canopy Analyzers were used in differential mode (LI-COR 1992; Welles 1990), with one placed in an adjacent open field to obtain radiation without canopy influence, and the other taking simultaneous understory measurements. The instruments were inter-calibrated before each set of measurements. All measurements were taken before 8:00 am, under diffuse light conditions. Balch et al. (2015) provided an overall summary of fire effects on trees in our site: in general, fire intensities and burned areas were greater with a triennial rather than annual fire return interval. The annually fire frequency caused a negative fire feedback, due to reduced litterfall rates and high consumption of fuel, while the triennially enabled higher fuel accumulation, usually leading to more severe fires.

Ant sampling

Ant sampling was conducted on a single occasion in June 2013, three years after the last experimental fires. We set six transects at each plot spaced by 220 m, and with 10 sampling stations with 10 m spacing in each transect. Each sampling station consisted of three unbaited pitfall traps, one subterranean, one epigaeic and one arboreal. All pitfall traps were 5 cm in diameter, were partly filled with a salt solution and detergent, and left open for 48 hours. The subterranean pitfalls were buried 15 cm deep, with lids to avoid filling with soil, and four radial holes – 1 cm diameter – to allow ant entry; the epigaeic traps were buried with their rims flush to the soil surface; and arboreal traps were tied at a height of 2 m to the trunk of the nearest tree with dbh ≥10 cm.

Data analysis

In all cases our unit of analysis was transect. We analyzed trees separately by dbh size-class, and for ants considered each stratum separately.

Abundance and biomass

We fitted generalized linear models (GLMs) with Poisson distribution with tree and ant abundance as response variables, and fire treatment as a predictor. We used two separate measures of tree abundance, the number of individual trees and LAI. Ant abundance was calculated as the sum of frequencies of occurrence of species in traps.

We estimated aboveground tree biomass (Mg ha^{-1}) for each individual by using the allometric equation for tropical forests proposed by Chave et al. (2014):

$$AGB_{est} = 0.0673 \text{ X } (\rho D^2 H)^{0.976}$$

Where ρ is wood specific gravity, which was estimated by Balch et al. (2008) as 0.59 g cm^{-3} for this region; D is dbh (cm) and H is height (m). We summed all values from each individual to obtain the biomass for each transect.

We estimated ant biomass (mg) for each ant species by using the equation proposed by Kaspari and Weiser (1999):

$$M = (4.7297 \text{ X } 10^{-4})HL^{3.179}$$

Where HL is head length (mm), which was measured as the maximum length from the apex of the head to the anterior-most portion of the clypeus. We measured up to three individuals of each species, and averaged the values to obtain HL estimation for each species. To obtain ant biomass for each transect, we multiplied the estimated biomass for each species by their abundances, and then summed throughout.

Species diversity and composition

We analyzed species richness and evenness separately. We fitted GLMs with tree and ant species richness as response variables, and fire treatment as a predictor. Tree richness was calculated as the number of species from each dbh class occurring within a transect. Ant richness was calculated as the number of species occurrence in all traps from a transect in each stratum. Similarly, we fitted GLMs with tree and ant evenness as response variables, and fire treatment as a predictor. We used the E_{var} index to calculate evenness, as it is independent of species richness and symmetric with regards to rare or dominant species (Crowder et al. 2012). We analyzed *a posteriori* if any changes in evenness were due to decreases in abundances of common species or increases in abundances of rare species. For that, we also fitted GLMs with the combined abundances of the 10 most and 10 least common species in the control plot as response variables, and fire treatments as a predictor. We used Poisson distribution in all these models.

We evaluated the extent to which tree and ant species composition differed among plots by performing permutational multivariate analyses of variance with 5,000 permutations (PERMANOVA; Anderson 2001) on presence/absence data, using Jaccard's dissimilarity index. When the result was significant, we assessed if dispersion within-group was homogeneous, which otherwise could lead to bias (Anderson 2001; Warton et al. 2012). We assessed differences between treatments by pairwise comparisons with Bonferroni correction. We evaluated whether β diversity differed among transects across plots, in order to assess if fire leads to biotic homogenization. For trees, we conducted this analysis for pre-treatment as well as 2012 data, because β diversity analysis of pre-treatment data had not been previously conducted. We first tested for homogeneity of multivariate dispersions (PERMDISP; Anderson 2006; Anderson et al. 2006), which computes a *F*-statistic to compare the average distance of each transect to their treatment median, defined in space by the dissimilarity index used (Sørensen pair-wise dissimilarity in this case, which includes both turnover and nestedness components of β diversity). To test if the dispersions are different among treatments we used a permutation test (5,000 randomizations).

We conducted all analyses in the software R (R Core Team 2015), and analyzed the residuals to check for distribution suitability and homoscedasticity in all models. We evaluated differences among plot treatments by performing pairwise contrast analyses, lumping together the most similar treatments and comparing models (Crawley 2012). We asserted a "quasi" correction for Poisson models with overdispersion. We calculated Nagelkerke's pseudo R^2 for all models. We used the *betapart v1.3* package (Baselga et al. 2013) to calculate the pairwise dissimilarities, and *vegan* v2.3 (Oksanen et al. 2015) to PERMANOVA and PERMDISP tests.

Results

We recorded 107 tree species, from at least 61 genera and 35 families. We recorded 189 ant species, from 44 genera and 8 subfamilies, with 47, 138, and 93 species occurring in the subterranean, epigaeic and arboreal traps respectively (Table S1).

Abundance and biomass

Total tree abundance in burnt plots was only about half that in the control for all dbh classes (small: $R^2 = 1$, $P < 0.01$; medium: $R^2 = 0.99$, $P < 0.01$ and large: $R^2 = 0.89$, $P = 0.01$), and the two burnt plots did not differ from each other (Fig. 2a-c). LAI yielded similar results (C = 4.32 $m^2\ m^{-2} \pm 0.12$; TB = 2.09 ± 0.15; AB = 2.30 ± 0.16; mean ± SE, $R^2 = 0.71$; $P < 0.01$). Mean abundance of ants in subterranean traps was also highest in the control plot ($R^2 = 0.33$, $P = 0.03$; Fig. 2d) and did not differ between the two burning treatments; however, the difference between control and burnt plots was not as marked as for trees. Mean ant abundance for the epigaeic stratum was lower in the annually burnt plot compared with triennially burned and control plots, which were not significantly different from each other ($R^2 = 0.69$, $P = 0.01$; Fig. 2e). There were no plot differences for ant abundance in the arboreal stratum (Fig. 2f).

The biomass of trees in burnt plots was about half that in the control for all dbh classes (small: $R^2 = 0.99$, $P < 0.01$; medium: $R^2 = 1$, $P = 0.04$; large: $R^2 = 1$, $P = 0.05$; Fig. 3a-c). The biomass of subterranean ants did not differ among plots ($R^2 = 1$, *P* = 0.52; Fig. 3d), was lower in the annually burned plot for epigaeic ants ($R^2 = 1$, *P* = 0.01; Fig. 3e) and about two-fold time higher in the triennially burned for arboreal ants ($R^2 = 1$, *P* = 0.01; Fig. 3f).

Species diversity and composition

The species richness of small trees was far lower in burnt than in control plots ($R^2 = 0.99$, $P < 0.01$; Fig. 4a), but there were no plot differences for larger trees (Fig. 4b,c). Ant species richness in epigaeic traps was lower in burnt plots compared with the control, and this was significant for the annually burnt plot ($R^2 = 0.60$, $P < 0.01$; Fig. 4e). Ant species richness in subterranean and arboreal traps did not differ among plots (Fig. 4d,f).

Species evenness was highest in the triennially burned plot for small ($R^2 = 0.24$, *P* = 0.05; Fig. 5a) and medium-sized ($R^2 = 0.23$, *P* = 0.04; Fig. 5b) trees, and both burnt plots had higher evenness than in the control plot for large trees ($R^2 = 0.32$, *P* = 0.01; Fig. 5c). Both burnt plots had slightly higher ant species evenness than in the control plot for both subterranean ($R^2 = 0.26$, *P* = 0.02; Fig. 5d) and arboreal ($R^2 = 0.21$, *P* = 0.05; Fig. 5f) traps, but there were no differences among plots for epigaeic ants (Fig 6e). The most abundant subterranean ($R^2 = 0.54$, $P < 0.01$; Fig. S1a) and arboreal ($R^2 = 0.52$, $P < 0.01$; Fig. S1b) species in the control plot were collectively only about half as abundant in burned plots. Such decreases in their abundances were much higher than those for all subterranean (about 30%) and arboreal (no significant) ants taken together. The least abundant subterranean species in the control did not vary across plots ($R^2 = 0.02$, *P* = 0.64; Fig. S2a), but decreased in burned plots for arboreal ants ($R^2 = 0.25$, $P < 0.01$; Fig. S2b). We did not conduct this analysis for epigaeic ants as their evenness was not different among plots.

Species composition of small trees was different in the control plot compared with both the triennially burned (PERMANOVA $F_{1,9} = 2.62$, $R^2 = 0.22$; $P < 0.01$) and annually burned ($F_{1,9} = 2.75$, $R^2 = 0.23$; $P = 0.01$) plots, which were not different from each other. The composition of medium trees differed between the control and triennially burned plots ($F_{1,10} = 2.14$, $R^2 = 0.17$; $P = 0.02$), but did not vary between the control and annually burned plots, or between burnt plots. There was no difference among plots in species composition for large tress.

There was significant overall variation among plots in species composition of subterranean ants (PERMANOVA $F_{2,15} = 1.52$, $R^2 = 0.16$; $P < 0.01$), but none of the pairwise comparisons were significant following Bonferroni correction. For epigaeic ants, species composition in the control plot differed from that in the triennially burnt ($F_{1,10} = 3.06$, $R^2 = 0.23$; $P < 0.01$) and annually burnt ($F_{1,10} = 3.87$, $R^2 = 0.27$; $P < 0.01$) plots, but did not differ between burnt plots. We found the same pattern for arboreal ants (C and TB comparison: $F_{1,10} = 3.01$, $R^2 = 0.23$; $P < 0.01$; C and AB comparison: $F_{1,10} = 2.35$, $R^2 = 0.19$; $P < 0.01$).

We found no evidence of biotic convergence within burnt plots. For trees, β diversity did not vary among plots in any tree class: small (PERMDISP $F_{2,13} = 2.39$; $P = 0.12$), medium ($F_{2,15} = 3.62$; $P = 0.06$) and large ($F_{2,14} = 1.19$; $P = 0.17$). Tree β diversity also did not vary among plots before burning in any class: small ($F_{2,15} = 0.95$; $P = 0.42$), medium ($F_{2,15} < 0.01$; $P = 0.99$) and large ($F_{2,15} = 0.39$; $P = 0.68$). Similarly, for ants β diversity did not vary among plots for any stratum: subterranean (PERMDISP $F_{2,15} = 0.04$; $P = 0.95$), epigaeic ($F_{2,15} = 2.39$; $P = 0.12$), or arboreal ($F_{2,15} = 0.9$; $P = 0.42$).

Discussion

Our study experimentally addressed how repeated fires affect ant communities from a southern Amazonian rainforest, by comparing variation among experimental plots with that shown by trees. Variation in ant communities among plots in relation to that shown by trees was consistent with our predictions, reflecting the differential effects of fire according to vertical stratum, and the relative importance of direct versus indirect impacts.

Abundance and biomass

Repeated fire dramatically reduced the abundance of trees in all size classes, and subsequently overall tree biomass, reflecting the high fire-induced mortality that has previously been documented (Balch et al. 2011; Brando et al. 2014). As predicted, there was less marked variation in ant abundance among plots, although it was still lower in burnt than control plots in the subterranean stratum, and in the epigaeic stratum it was lower in the annually burned plot than in the control, while it did not vary for arboreal ants. Unlike the study of Silveira et al. (2010), there was not a proliferation of leaf-cutting ants at our burnt sites.

Variation in ant biomass among plots matched that for ant abundance in the epigaeic stratum, but not for the other strata - the biomass of subterranean ants was not affected despite the variation in abundance, and the biomass of arboreal ants increased in the triennially burned plot despite no variation in abundance. The increase in arboreal ant biomass in the triennially burned plot was directly related to a higher number of the giant tropical ant *Paraponera clavata* workers sampled (19, Vs. eight in the arboreal stratum at Control and Annually burned plots; Table S1). These eleven extra individuals accounted for 32% of estimated ant biomass in the triennially burned plot, and when removing them from the analysis we did not obtain significant differences among plots. *Paraponera clavata* nests preferentially in drier habitats

(Elahi 2005), and therefore may be expected to be more abundant in fire-simplified habitat. Additionally, this species forages extensively on extrafloral nectaries (Fewell et al. 1996), that may secrete a better quality nectar in resprounting plants after fire (Alves-Silva and Del-Claro 2013) or under higher light availability conditions (Radhika et al. 2010). However, it is not clear why *P. clavata* abundance was higher in the triennially burned but not annually burned plot. The disconnect that we have shown between responses of subterranean and arboreal ant abundance and biomass is noteworthy because biomass rather than abundance is directly related to energy and nutrient flow, and therefore ecological function (Brown et al. 2004; Saint-Germain et al. 2007). Most studies of ant responses to disturbance do not measure biomass, and assume that changes in abundance reflect changes in ecosystem function.

Species diversity and composition

For trees, species richness was far less affected by fire than was abundance and biomass. Only small trees had their number of species reduced, and these trees are expected to be the most sensitive to fire: small stems were killed even after initial fires in this area, largely due to their thinner bark (Brando et al. 2012). Similarly, the only stratum where ant richness was lower in burnt than control plots was the epigaeic, and this is the stratum most affected by fire. Recurrent fires led to increased species evenness for all tree size classes, and this also occurred for ants from the subterranean and arboreal strata. Many studies have shown increased species evenness following disturbance due to increased abundance of rare species (reviewed by Crowder et al. 2012). However, we found no such responses of rare species, and our increased ant evenness was due to reductions in the abundance of common species.

Recurrent fires altered the composition of tree species, except for those in the large-size class, which are least sensitive to the effects of fire (Brando et al. 2012). Similarly, fire altered the composition of ant species, particularly in the epigaeic stratum, which is most directly affected. However, this variation in composition did not result in biotic homogenization within burned plots. These results are consistent with those for fires in the central Amazon, where the composition of trees ($\geq$ 10 cm dbh) and leaf litter ants differed strikingly between unburned and thrice-burned forests, but beta diversity was not altered (Silveira et al. 2015).

Conclusion

Ant responses to burning were highly consistent with those of trees, strengthening our inference that observed plot differences in ant communities were due to fire treatments. We confirmed that the impact of fire on ants varies among habitat strata, with epigaeic species being the most sensitive. Epigaeic ants were particularly affected by annual fires, with lowest abundance, biomass and richness in the annually burnt plot, whereas subterranean and arboreal ants showed no variation between the annual and triennial plots. Subterranean ants were affected by frequent fire despite the strong buffering qualities of soil; this can be explained by the fact that much of the subterranean ant fauna forages in the litter layer, which is strongly impacted by fire (Paolucci et al. 2016). We also confirmed that richness and composition similarly varied for ants and trees, and that fire has a much more severe impact on abundance and biomass for trees than for ants, as the effects on ants are primarily indirect rather than through direct mortality.

Our ant results are consistent with the conclusion from studies of plants that the effects of repeated fires are much more pervasive than those from single fires in the southern Amazon (Brando et al. 2012). Previous studies have shown that neither ant abundance nor species composition during the dry season are affected by single fires (Paolucci et al. 2016; Silveira et al. 2013; Silveira et al. 2012), although the composition of wet-season samples was affected (Silveira et al. 2012). Taken together these results indicate a very well marked effect of recurrent fires on species identity of southern Amazonian ant communities, while a weak and context-dependent effect of single fires. Our results also strongly differ from those in fire-prone savannas, where recurrent fires increase (Andersen 1991; Andersen et al. 2014) or do not change (Parr et al. 2004) ant abundance, and often have minor effects on ant composition (Andersen et al. 2014; Parr et al. 2004).

Southern Amazonian forests are currently experiencing a high rate of recurrent burning (Alencar et al. 2015). We have shown that recurrent fires in these forests have dramatic effects not only on trees, but also on ants, one of most abundant and ecologically important faunal groups. These effects were demonstrated three years after the last fires, indicating low resilience to recurrent fires. The prevention of recurrent fires should be a priority for conservation management.

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Figure legends

Fig. 1 Satellite image (2-m resolution) of the experimental treatments in 2011. From left to right: burnt annually (burned in 2004, 2005, 2006, 2007, 2009, and 2010), burnt triennially (burned in 2004, 2007, and 2010), and the control (unburned). Reproduced with authorization from Balch et al. (2015). Satellite image: © 2011, DigitalGlobe; NextView License

Fig. 2 Variation in tree and ant abundance among treatments (C = Control; TB = Triennially burned; AB = Annually burned) in each habitat stratum and dbh class. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Fig. 3 Variation in tree and ant biomass among treatments (C = Control; TB = Triennially burned; AB = Annually burned) in each habitat stratum and dbh class. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

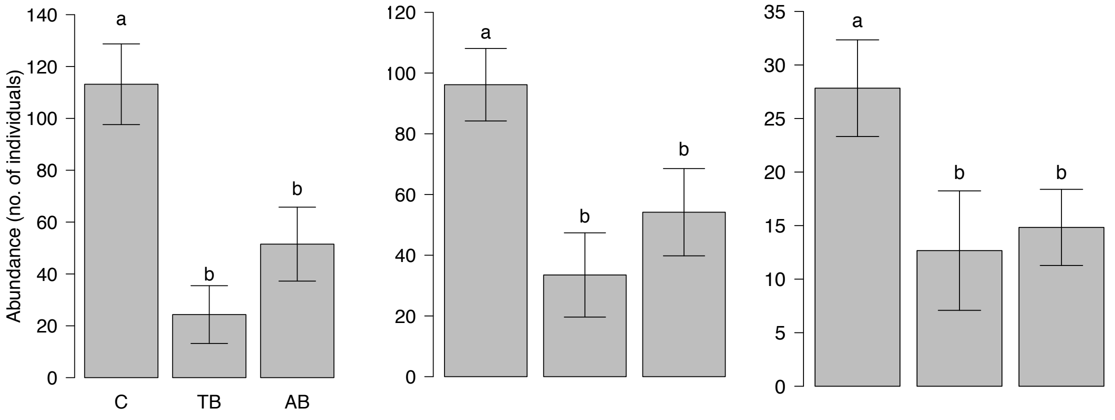
Fig. 4 Variation in tree and ant species richness among treatments (C = Control; TB = Triennially burned; AB = Annually burned) in each habitat stratum and dbh class. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Fig. 5 Variation in tree and ant evenness among treatments (C = Control; TB = Triennially burned; AB = Annually burned) in each habitat stratum and dbh class. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

Figures

Figure 1

Figure 2



a) 10-19.9 cm dbh trees

b) 20-39.9 cm dbh trees

c) ≥ 40 cm dbh trees

d) Subterranean ants

e) Epigaeic ants

f) Arboreal ants

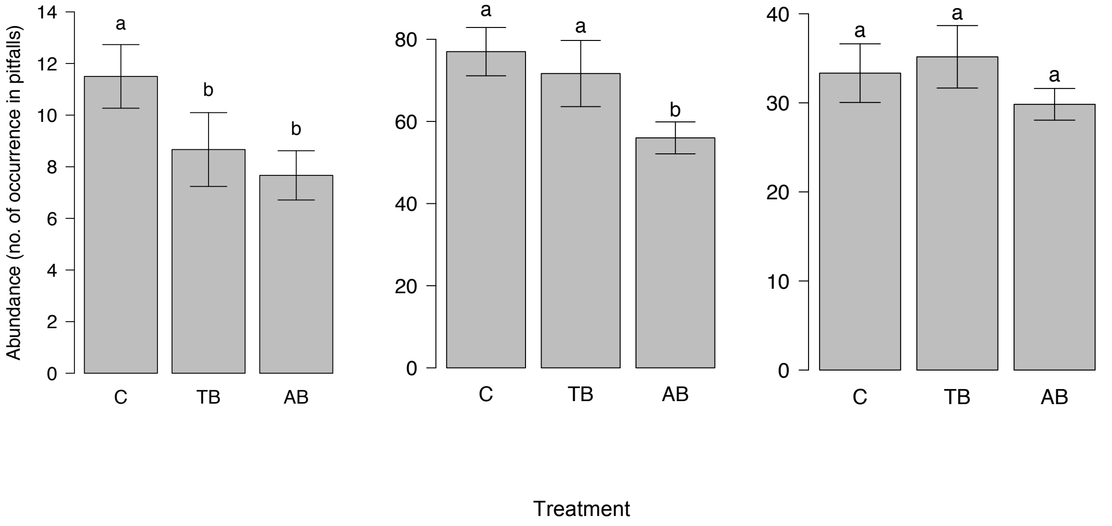


Figure 3

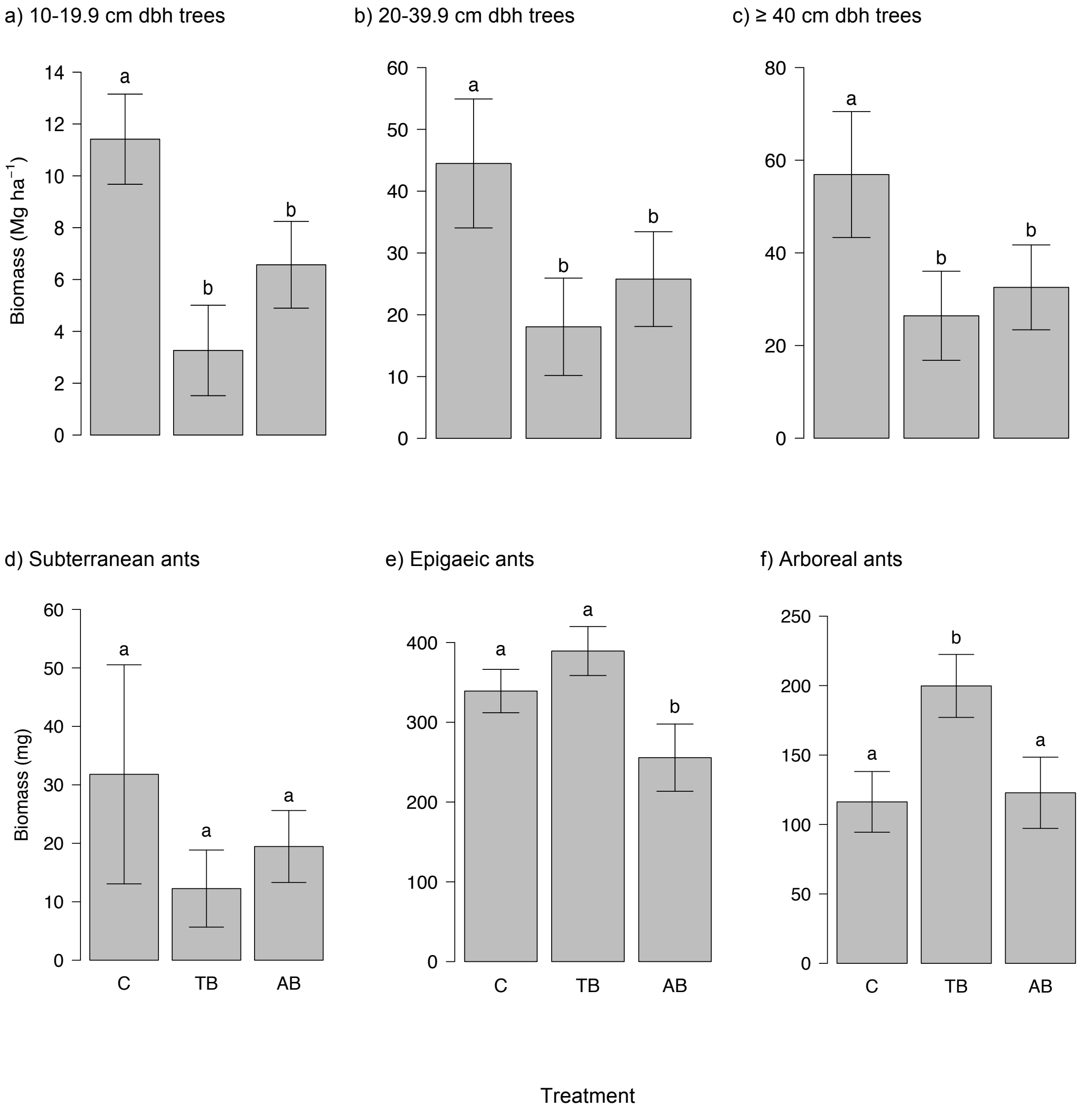
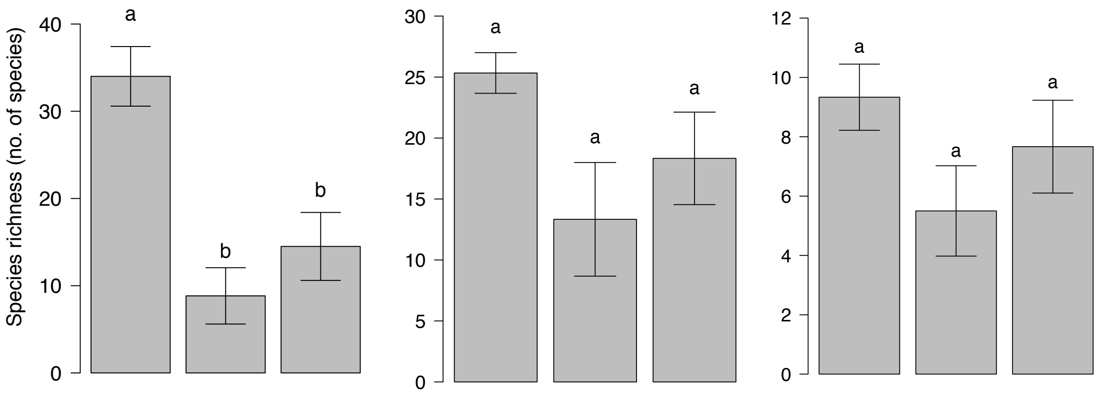

a) 10-19.9 cm dbh trees
b) 20-39.9 cm dbh trees
c) ≥ 40 cm dbh trees
Biomass (Mg ha^{-1})
0
2
4
6
8
10
12
14
a
b
b
0
10
20
30
40
50
60
a
b
b
0
20
40
60
80
a
b
b
d) Subterranean ants
e) Epigaeic ants
f) Arboreal ants
Biomass (mg)
0
10
20
30
40
50
60
a
a
a
0
100
200
300
400
a
a
b
0
50
100
150
200
250
a
b
a
C
TB
AB
C
TB
AB
C
TB
AB
Treatment

Figure 4

a) 10-19.9 cm dbh trees b) 20-39.9 cm dbh trees c) ≥ 40 cm dbh trees



d) Subterranean ants e) Epigaeic ants f) Arboreal ants

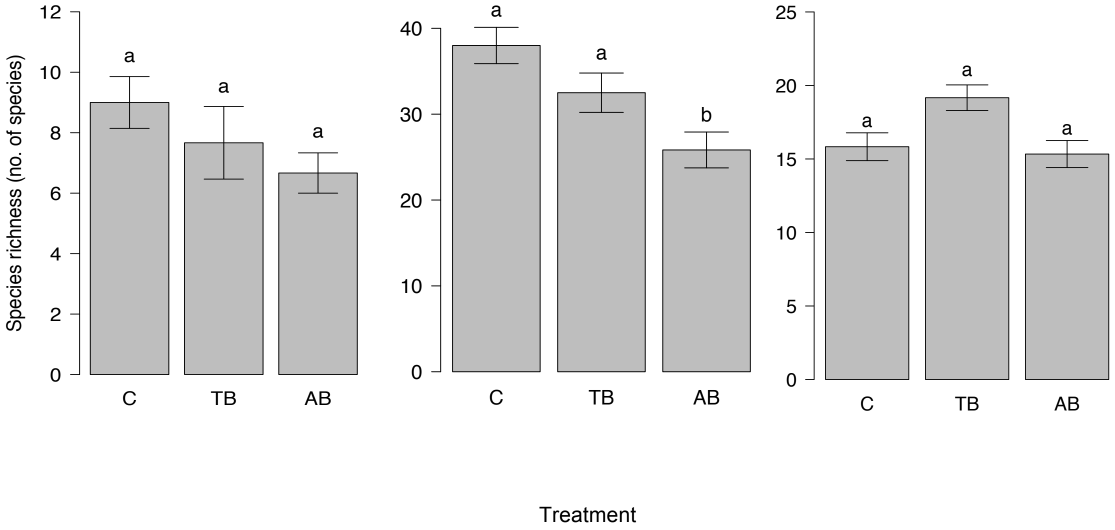
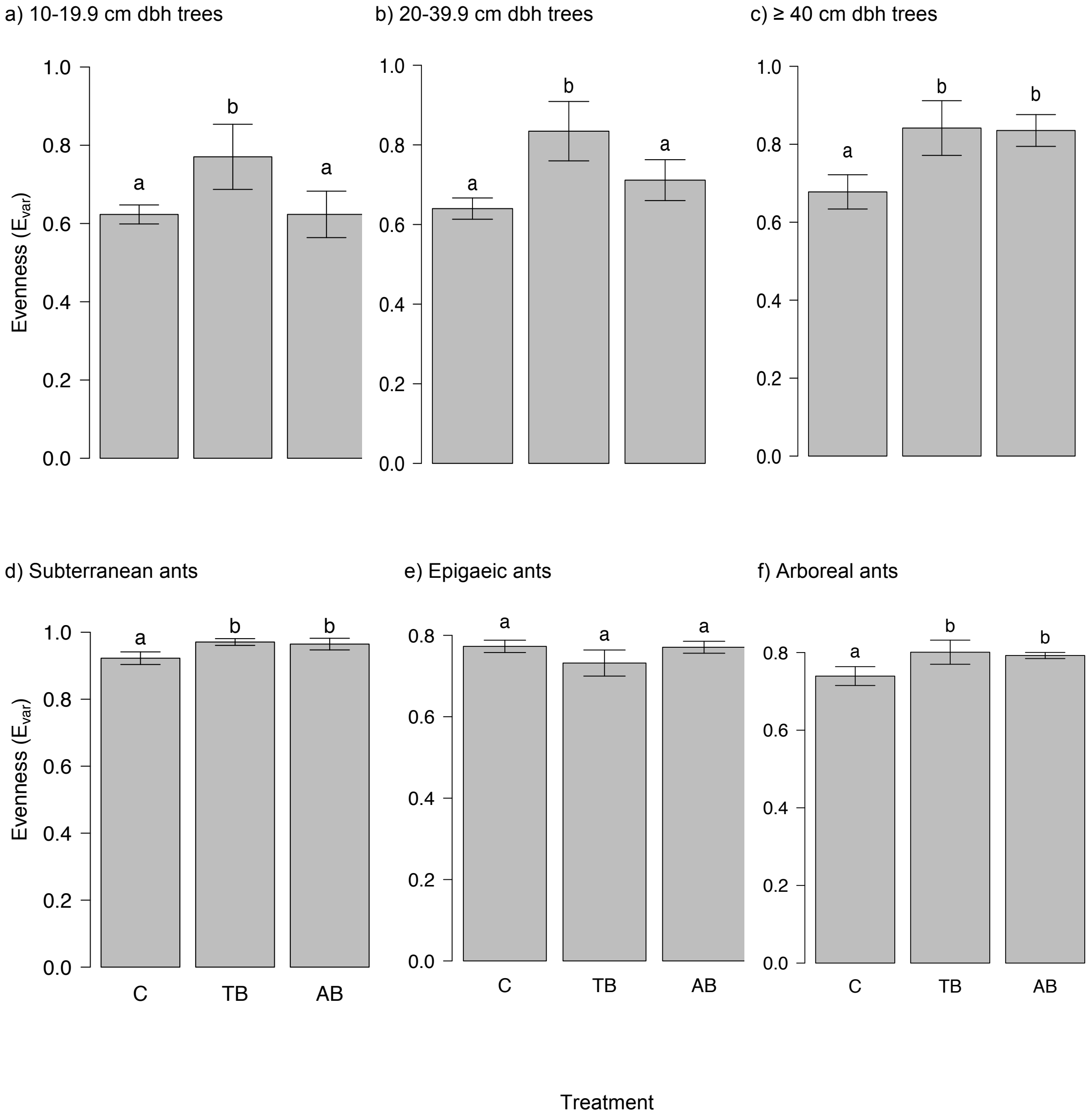


Figure 5


a) 10-19.9 cm dbh trees
b) 20-39.9 cm dbh trees
c) ≥ 40 cm dbh trees
d) Subterranean ants
e) Epigaeic ants
f) Arboreal ants
Evenness (E_{var})
Evenness (E_{var})
0.0
0.2
0.4
0.6
0.8
1.0
a
b
a
a
b
a
a
b
b
a
b
b
a
a
a
a
b
b
C
TB
AB
C
TB
AB
C
TB
AB
Treatment

Appendix

Table S1. List of ant species sampled in each stratum and treatment (C = Control; TB = Triennially burned; AB = Annually burned). Numbers indicate the frequency of occurrence of each species in correspondent stratum and treatment.

Stratum/Treatment	**Subterranean**			**Epigaeic**			**Arboreal**		
Subfamily/Species	C	TB	AB	C	TB	AB	C	TB	AB
Dolichoderinae									
Azteca sp.1						1			
Dolichoderus ghilianii								1	1
Dolichoderus imitator				5			4	2	
Dolichoderus varians							1		
Dorymyrmex sp.1					2	4			1
Dorymyrmex sp.2					16	17		5	2
Dorymyrmex sp.4					3	1			
Forelius sp.1					2				
Forelius sp.2					5				
Linepithema aztecoides				3			1		
Nylanderia sp.2					1				
Tapinoma sp.2								3	3
Dorylinae									
Acanthostichus sp.1	1								
Acanthostichus sp.2			1						
Asphinctanilloides anae						1			
Labidus praedator					1	2			
Neivamyrmex sp.1	1	3	6	1		2			
Neivamyrmex sp.2					1				
Nomamyrmex esenbeckii				1	1				
Ectatomminae									
Ectatomma edentatum				4	1	3			

Ectatomma lugens				4					
Ectatomma opaciventre					4				
Ectatomma tuberculatum				1	1	1	2	1	
Gnamptogenys haenschi	1								
Gnamptogenys striatula				1					
Gnamptogenys sulcata								1	
Formicinae									
Brachymyrmex sp.1	1	5	4	5	17	8	1	4	4
Brachymyrmex sp.2		1		10	1	1	1		3
Brachymyrmex sp.3		1						1	
Brachymyrmex sp.4				1					
Brachymyrmex sp.6					1				
Brachymyrmex sp.10		1						2	
Brachymyrmex sp.19					1				
Camponotus atriceps				13	3	1	21	9	9
Camponotus crassus		1		33	32	20	25	30	29
Camponotus renggeri						2		1	5
Camponotus sericeiventris					2			4	3
Camponotus sp.1				11	1		1		
Camponotus sp.2				1	9	13	3	11	14
Camponotus sp.3				3	19	22		11	18
Camponotus sp.5					1		1		1
Camponotus sp.6				4	8	8		5	4
Camponotus sp.7				6	7	3		4	4
Camponotus sp.8				7	1		3	1	1
Camponotus sp.9							2	4	2
Camponotus sp.10				1					
Camponotus sp.11				5	2		1		
Camponotus sp.13				2			1		

Camponotus sp.16							1		
Camponotus sp.18						1			1
Camponotus sp.19									1
Camponotus sp.21				4	6	8		4	1
Camponotus sp.22				4	4	1	4	2	
Camponotus sp.24									1
Camponotus sp.26								1	
Camponotus sp.28				6	1		8		
Camponotus sp.29					1			1	
Camponotus sp.31									3
Camponotus sp.32					1	1		1	
Camponotus sp.35							1		
Camponotus sp.36					1			1	
Camponotus sp.38					1				
Camponotus sp.39				1				1	
Gigantiops destructor				10	5	5	4	1	3
Myrmelachista sp.3							1		
Nylanderia sp.1				3	1	1	1		
Nylanderia sp.2	2	3		8	7	10		1	1
Nylanderia sp.6				1					
Myrmicinae									
Acromyrmex sp.1									1
Acromyrmex sp.2				1					
Apterostigma megacephala				2					
Apterostigma sp.1				1					
Atta laevigata			2	2	20	12		2	2
Atta sp.1	1	1	2	17	11	13		2	2
Atta sp.6				1					
Atta sp.10						1			
Carebara brevipilosa		1			1				
Carebara sp.4	3	1	6						

Carebara sp.5		2	1						
Carebara sp.6	1								
Cephalotes grandinosus								1	
Cephalotes oculatus								1	
Cephalotes pusillus					2	1		6	
Cephalotes sp.2					1			3	
Cephalotes sp.8								1	
Crematogaster sp.1	8	4		18	14	4	23	22	14
Crematogaster sp.2				1	3	1	2	3	2
Crematogaster sp.3				1					
Crematogaster sp.7								1	
Crematogaster sp.8				4			1		
Crematogaster sp.10		1					2	1	1
Crematogaster sp.11				1					
Crematogaster sp.12				1					
Crematogaster sp.14					1				
Crematogaster sp.16					1				
Crematogaster sp.17									1
Cyphomyrmex sp.2						1			
Daceton armigerum								1	
Monomorium floricola	1		2			1	1	1	
Nesomyrmex sp.1								1	
Nesomyrmex sp.2									1
Ochetomyrmex semipolitus			1	2			2		
Octostruma iheringi	1			1					
Pheidole sp.1				3	2				
Pheidole sp.2	7	1	3	27	19	27	2		2
Pheidole sp.3	1			2	2	2			
Pheidole sp.4							6		
Pheidole sp.5		2		3	26	24			

Pheidole sp.6	4	2	1	5	3	2			
Pheidole sp.7	1		2	19	22	11	2		
Pheidole sp.9		1		9	3	1			
Pheidole sp.10		1		3	2	1			
Pheidole sp.11				6	3	3			
Pheidole sp.12	1	5	3		22	30		4	3
Pheidole sp.14				4					
Pheidole sp.15				3					
Pheidole sp.16				2	1	1			
Pheidole sp.17	1			3	2	3			
Pheidole sp.26				2	2				
Pheidole sp.28				1					
Pheidole sp.30							1		
Pheidole sp.31					2				
Pheidole sp.33								1	
Pheidole sp.36						3			
Pheidole sp.37					1				
Pheidole sp.38				1					
Pheidole sp.39						1			
Pheidole sp.40					3	1			1
Pheidole sp.41				1					
Pheidole sp.43				2					
Pheidole sp.44				1					
Pheidole sp.48						1			
Pheidole sp.50					1				
Pheidole sp.51					1				
Pheidole sp.52				1	1				
Pheidole sp.55					1				
Pheidole sp.57							1		
Pheidole sp.58						1			
Pheidole sp.61					1				
Pheidole sp.62					1				

Sericomyrmex sp.1			1	3	2	3			
Sericomyrmex sp.2				1					
Sericomyrmex sp.3					1				
Solenopsis sp.1	8		1	26	5	4	33	3	11
Solenopsis sp.2	6	2		7	3	3			
Solenopsis sp.4	2		2	13	3				1
Solenopsis sp.9	2			1					
Solenopsis sp.10							1		
Solenopsis sp.12	1		2						
Solenopsis sp.13				4	2		1		
Solenopsis sp.14		2		3	2				
Solenopsis sp.15					3	3			
Solenopsis sp.16				1					
Solenopsis sp.17	1	3	1		5	7			
Solenopsis sp.20	2	4	3	1	3				
Solenopsis sp.21				4			3	2	1
Solenopsis sp.22							1		
Solenopsis sp.25		1							
Solenopsis sp.34						1		1	
Strumigenys denticulata						1			
Trachymyrmex sp.1				5					
Trachymyrmex sp.2				2		1			
Trachymyrmex sp.3									
Trachymyrmex sp.6	1			7	2	1			
Trachymyrmex sp.9				2					
Tranopelta sp.1	6	1	1						
Wasmannia sp.2					1				3
Paraponerinae									
Paraponera clavata					2	1	8	19	8
Ponerinae									
Hypoponera sp.3	1								

Neoponera apicalis				7	1				
Neoponera striatinodis							1		
Neoponera verenae				35	19	12			
Neoponera villosa				2	1		11	7	2
Odontomachus meinerti				1	1	1			
Pachycondyla crassinoda	2	1		24	23	12			
Pachycondyla harpax	1			1	2	1			
Pseudoponera gilberti			1						
Pseudomyrmecinae									
Pseudomyrmex sp.1		1					1		
Pseudomyrmex sp.2				2	1				
Pseudomyrmex sp.3							6		
Pseudomyrmex sp.4							3	6	2
Pseudomyrmex sp.5									2
Pseudomyrmex sp.6						1		1	1
Pseudomyrmex kuenckeli								1	
Pseudomyrmex sp.8									1
Pseudomyrmex sp.9						1		2	1
Pseudomyrmex sp.10								3	1
Pseudomyrmex sp.11								2	
Pseudomyrmex sp.12					1				

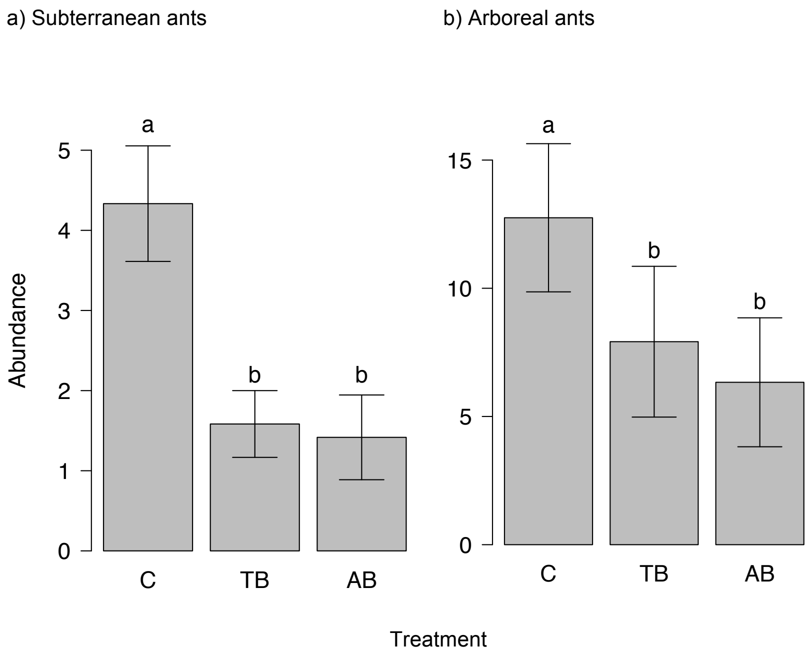


Figure S1. Comparison among treatments (C = Control; TB = Triennially burned; AB = Annually burned) of the abundances of the 10 most common (a) subterranean and (b) arboreal ant species in the Control plot. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

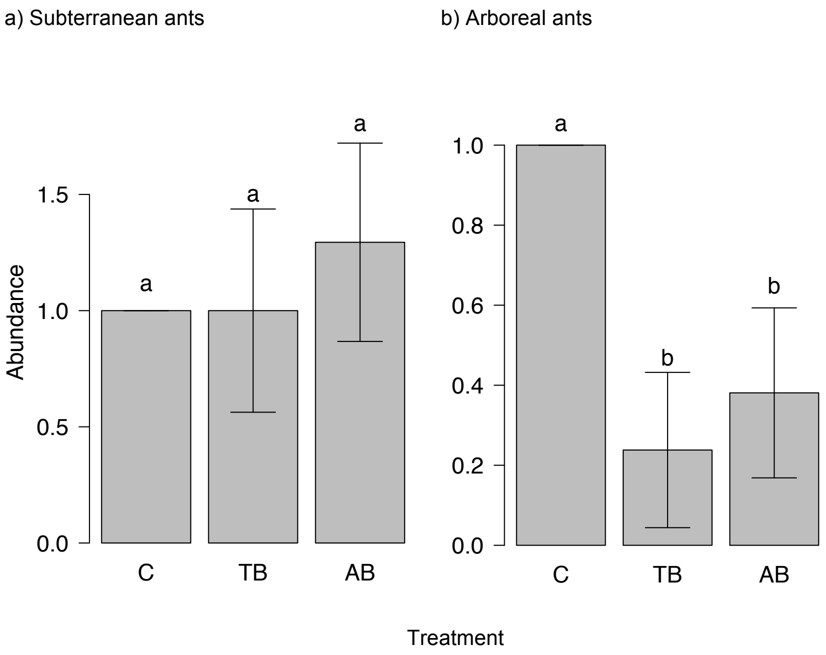


Figure S2. Comparison among treatments (C = Control; TB = Triennially burned; AB = Annually burned) of the abundances of the 10 least common (a) subterranean and (b) arboreal ant species in the Control plot. Bars represent standard error. Different letters indicate significant differences among treatments, according to ANOVA

GENERAL CONCLUSIONS

In this thesis we outline the overall effects of understory fires on shade-adapted ant communities from southern Amazonian forests. We showed that this disturbance is highly detrimental for ants, as reflects of their lack of association with it over evolutionary time. Moreover, we demonstrate for the first time the negative effects of fire on a subterranean ant fauna, and also on the effectiveness of a key ecosystem service provided by rainforest ants, which likely have negative effects on plant communities structure in the long-term.

Despite overall negative effects of fire on ant communities, there were some context-dependent responses: i) more specialized ants and those from more exposed habitats are more sensitive to fire; ii) fuel loads exert minor influence on ant responses, but can still have an important role by increasing the risk of fire occurrence; iii) recurrent fires are more pervasive than single fires, and may even trigger negative effects of at least three years. We also found that ant abundance and biomass responses to disturbance are not necessarily convergent, and we suggest that future studies should consider biomass more often, and preferably than abundance, as a proxy for changes in ecological function. Given the current regime of extreme land-use and high recurrent burning state faced by southern Amazonian forests, we conclude that the prevention of recurrent fires should be of special concern for the maintenance of biodiversity and proper ecosystem functioning of these forests. Since ants have a well-established role on indicating disturbances on other faunal groups, these results call for attention in a broader conservational context, as such effects likely occur for other taxa from these forests as well.