Oecologia (2016) 182:335–346
DOI 10.1007/s00442-016-3638-x

HIGHLIGHTED STUDENT RESEARCH

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

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Received: 11 January 2016 / Accepted: 19 April 2016 / Published online: 20 May 2016

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 intensification. Experimental fires and fuel addition were applied to 40 × 40-m plots in six replicated blocks, and ants were sampled between 15 and 30 days after fires in four strata: subterranean, litter, epigaeic, and arboreal. Fire had extensive negative effects on ant communities. Highly specialized cryptobiotic and predator species of the litter layer and epigaeic specialist predators were among the most sensitive, but we did not find evidence of overall biotic homogenization following fire. Fire reduced rates of location and transport of myrmecochorous seeds, and therefore the effectiveness of a key ecosystem service provided by ants, which we attribute to lower ant abundance and increased thermal stress. Experimental fuel addition had only minor effects on attributes of fire severity, and 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 a significant effect on ants from Amazonian rainforests because they increase the risk of fire occurrence, which has a detrimental impact on ant communities and a key ecosystem service they provide.

Keywords 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

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Communicated by Raphael Didham.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3638-x) contains supplementary material, which is available to authorized users.

This study used a manipulative experiment to assess the impacts of fire on ant communities and ecosystem services that they provide in tropical forests. Although fire had variable effects, specialized taxa were particularly affected by fire. Changes in abundance, richness and foraging efficiency of the ant fauna reduced the rates of seed location and the transport of seed by ants, an important ecosystem service provided by these social insects. The widespread clearing and fragmentation of tropical forests increases the risk of fires and this study provides a framework to understand the effects of such disturbances for biodiversity and ecosystem services.

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(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 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 to, thus posing a risk to their fire-sensitive biotas.

Highly fire-prone savannas often border rainforest throughout high-rainfall regions of the seasonal tropics, 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 the 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 and Schulze 1999; Cochrane 2001; 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. 2008, 2015; 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 processes (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 to 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. 2012, 2014; 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. 2012, 2013, 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 in open habitats 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 to fire (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, we hypothesize that this shade-adapted ant fauna will take more time to discover seeds, and remove them in lower rates in burnt treatments due to fire-induced negative effects on ant abundances and foraging efficiency.

Materials and methods

Study site

This study was conducted on privately owned property located 75 km north of Querência, Mato Grosso, Brazil, in the southern Amazon basin (12°49′S, 52°21′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 the 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 1770 mm and a marked dry season (<10 mm month^{-1}) between May and September (Rocha et al. 2014). Rainfall was unusually high in the study year (2309 mm), especially when compared with the average of the 4 years prior to the experiment (1563 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 40 × 40-m plots, separated by trails approximately 2 m in width. Each block included three treatments: unburned (control), burned under natural conditions (B0), and burned with an average of 50 % addition (~3.2 Mg ha^{-1}) of fine fuel (B+) (see Fig. 1 in Brando et al. 2016). The added fuel was obtained from nearby forested areas, and transferred to the treated plots 2 days prior to burning. We acknowledge that some litter-dwelling ant species might have been inadvertently introduced along with the fuel addition, but as we expected a decrease in species richness due to fire, the possibility of such an outcome makes our experimental results conservative. Burning occurred on 27–29 August 2013, at the end of dry season. Two blocks were simultaneously burned per day in the driest period of the day (between 12:30 and 13:30 p.m.) 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 a slope of <2 % and was surrounded by undisturbed forest for at least 1 km in all directions. Average daytime air temperature during the 4 months prior to the experiment was lower than the long-term averages, whereas precipitation and relative humidity were higher, which led to below-average fire danger (Brando et al. 2016).

Details of the effects of fuel addition on fire rate of spread (meters per minute), flame height (centimeters), proportion of burned area (percentage), total fuel consumption (megagrams carbon per hectare), frontal fire intensity (kilowatts per meter), and leaf area index (LAI; squared meters per square meter; 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 Mg ha^{-1} in 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 to 3.5 m^2 m^{-2} and from 4.6 to 4.1 m^2 m^{-2}, respectively; $P < 0.01$), while remaining constant in the control. Despite the small area of our plots, all fire variables considered here were similar to those from larger burnt plots in the southern Amazon (Balch et al. 2008, 2011). Also, the observed minor effects of fuel addition on fire intensity were similar to previous observations in larger fires within these forests during non-drought years, as well as canopy losses and mortality of small trees (Balch et al. 2008, 2011, 2012, 2016).

Ant sampling

Ant sampling commenced 15 days after the last fires and continued for 2 weeks. In each plot we established a 5 × 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 water, salt and detergent, and left open for 48 h. We buried the subterranean pitfalls 15 cm deep; they had lids to avoid them filling with soil, and four 1-cm-diameter 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 diameter at breast height >10 cm. We sifted litter samples and placed them in mini-Winkler extractors for 48 h at ambient temperature. Voucher specimens of all species are held at the Laboratório de Ecologia de Comunidades, from the Universidade Federal de Viçosa, Brazil.

Seed removal

We established a 5 × 5 grid of seed depots with 2-m spacing in the center of each plot to quantify rates of seed removal, as the basis of successful seed dispersal (Leal et al. 2007, 2015). 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* (globular 0.8 × 0.5 mm; Euphorbiaceae), a myrmecochorous shrub that occurs naturally in the region, was placed on a white piece of paper (10 × 15 cm) at each depot. Seeds were collected 1 month prior to the experiment, and refrigerated during this period. After setting the 25 depots in a plot, we walked around the area for 1 h, 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 the analysis of rates of removal). We also noted cheating events, defined as ants remaining for at least 15 min 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 and 11:00 a.m.) and again in the afternoon (between 3:00 and 5:00 p.m.).

Ant functional groups

We classified ants into functional groups following Leal et al. (2012) with some minor adjustments (Electronic supplementary material, Table S1), 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), due to its high number of species, likely with variable nesting and foraging habits. By taking this approach we do not erroneously inflate other groups that they would fit, and can distinguish fire effects on this group separately. The other groups were: Cryptic Predators, Cryptic Omnivores [which comprise all cryptobiotic species that do not specialize on live prey, and include species of *Acropyga* that are heavily dependent on subterranean honeydew (Delabie et al. 2000)], Epigaeic Predators, Epigaeic Omnivores, Arboreal Dominants, Arboreal Predators, Arboreal Subordinates, Opportunists, Army Ants, Leaf-cutting Fungus-growing Ants, and Non-leaf-cutting Fungus-growing Ants.

Data analysis

In all cases our unit of analysis was plot, with data combined across sampling stations, and each stratum considered separately. We fitted generalized linear mixed models (GLMMs) using Poisson error distribution structure with total ant species richness, abundance, and the abundance of 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 frequency ≥ 15 in the analyzed stratum were considered. We performed pairwise contrast analyses to evaluate differences among treatments (Crawley 2012).

We evaluated if ant species and functional group composition differed among treatments by performing a permutational multivariate ANOVA (PERMANOVA) based on Jaccard's dissimilarity (which is more suitable for presence/absence data) with 5000 permutations (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 homogeneity of dispersion PERMDISP test (Anderson et al. 2006), with the Sørensen index (which includes both turnover and nestedness components of β-diversity). To test if the dispersions were different among treatments we used a permutation test (999 permutations).

We performed hierarchical partitioning to estimate the independent contribution of fire attributes and LAI to both ant species richness and frequency by using a randomization test with 5000 randomizations, based on an upper confidence limit of 0.95 % ($Z \geq 1.65$) (Mac Nally 2002). There was no significant effect of blocks in any variables, and therefore no spatial autocorrelation. These models were built with a Poisson error distribution, and 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. We set blocks as a frailty random effect in the model, with γ-distribution. We analyzed if the proportion of seed removal and cheating events varied among treatments by fitting GLMMs with binomial error 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 2016), and analyzed the residuals to check for distribution suitability and homoscedasticity in all models. For all GLMM models we set block as a random factor, and calculated the conditional coefficient of determination $[R^2_{(c)}]$ (Nakagawa and Schielzeth 2013). We checked for overdispersion in all GLM and GLMM models. When detected, we asserted a quasi-Poisson correction in the former, and

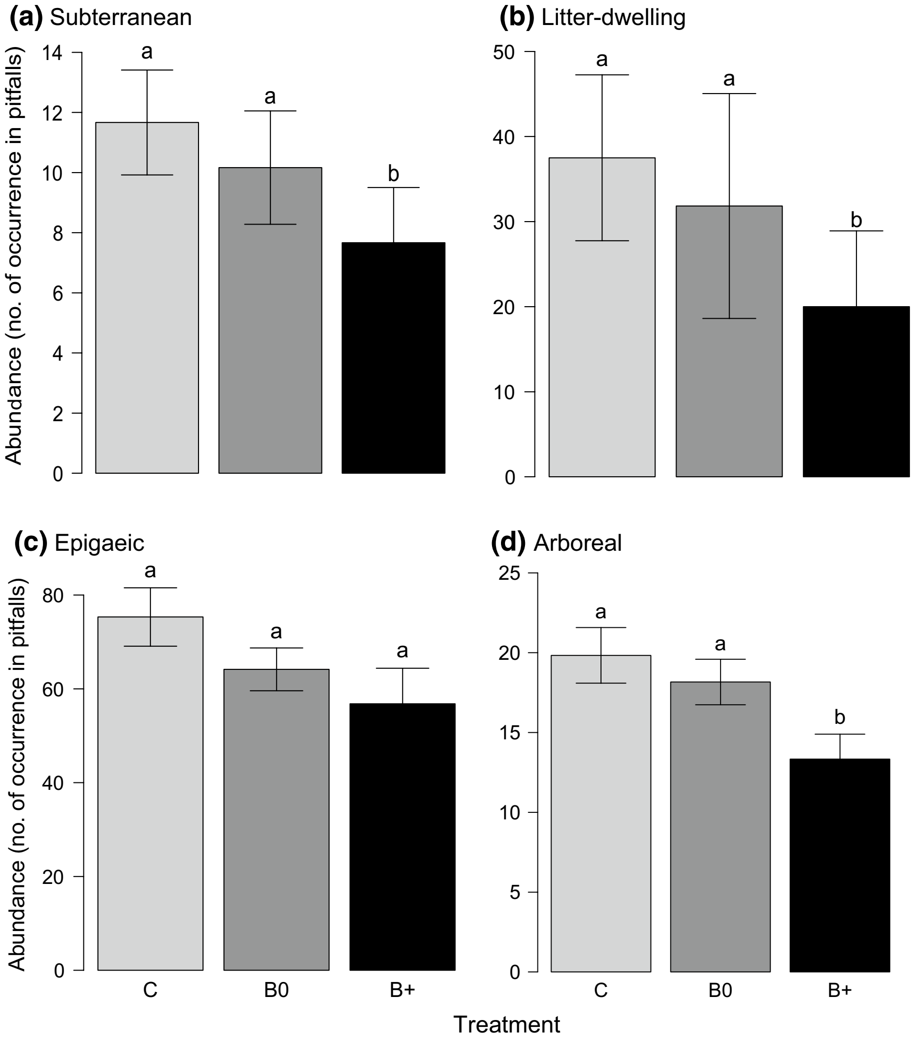


Fig. 1a–d Variation in ant abundance among fire treatments [control (*C*), no fuel addition (*B0*), fuel addition (*B+*)] in each habitat stratum of the southern Amazon. *Bars* represent SE. *Different letters* indicate significant differences among treatments, according to ANOVA

fitted a Poisson-lognormal model in the latter (Harrison 2014). We used lme4 version 1.1-7 (Bates et al. 2014) to build GLMM models, betapart version 1.3 (Baselga et al. 2013) to calculate the pairwise dissimilarities, and vegan version 2.3 (Oksanen et al. 2015) for PERMANOVA and PERMDISP tests. Diversity partitioning analyses were conducted using hier.part version 1.0-4 (Walsh et al. 2013), and survival analyses using the survival package version 2.38-1 (Therneau and Grambsch 2015).

Results

We recorded 199 ant species from 44 genera and seven 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 [$\chi^2_{16} = 4.48$, $P = 0.03$; $R^2_{(c)} = 0.53$], litter [$\chi^2_{16} = 5.08$, $P = 0.02$; $R^2_{(c)} = 0.70$] and arboreal strata [$\chi^2_{16} = 7.83$, $P < 0.01$; $R^2_{(c)} = 0.34$; 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 [$\chi^2_{16} = 3.71$, $P = 0.05$; $R^2_{(c)} = 0.39$], litter [$\chi^2_{16} = 6.32$, $P = 0.01$; $R^2_{(c)} = 0.67$] and epigaeic strata [$\chi^2_{16} = 4.62$, $P = 0.03$; $R^2_{(c)} = 0.21$; 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 [$\chi^2_{16} = 5.78$, $P = 0.01$; $R^2_{(c)} = 0.4$] and epigaeic predators [$\chi^2_{16} = 4.98$, $P = 0.02$; $R^2_{(c)} = 0.4$] were highest in control plots. The abundances of cryptic predators [$\chi^2_{16} = 14.22$, $P < 0.01$; $R^2_{(c)} = 0.78$] and Subordinate Camponotini [$\chi^2_{16} = 9.66$, $P < 0.01$; $R^2_{(c)} = 0.67$] in the litter stratum were lowest in B+ plots. In the epigaeic stratum, epigaeic predators were most abundant in control plots [$\chi^2_{16} = 7.62$, $P < 0.01$; $R^2_{(c)} = 0.34$], whereas the abundances of epigaeic omnivores in the arboreal stratum

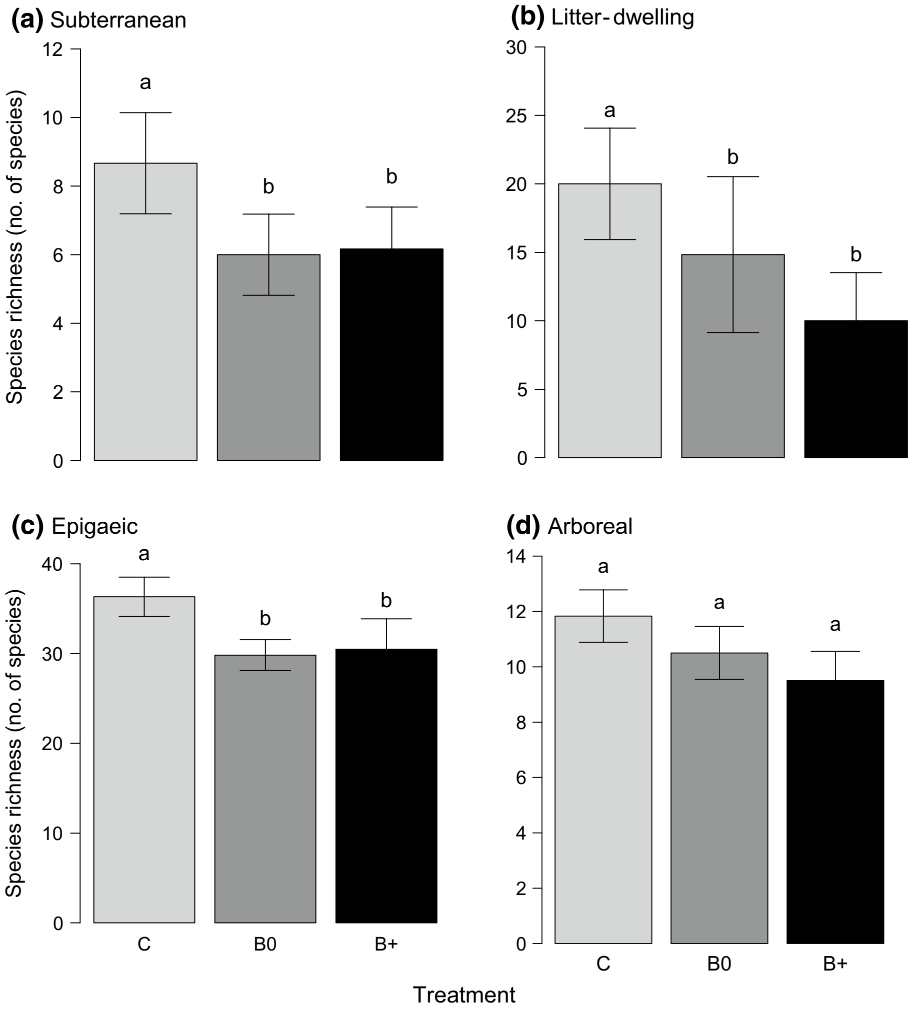


Fig. 2a–d Variation in ant species richness among fire treatments in each habitat stratum of the southern Amazon. *Bars* represent SE. *Different letters* indicate significant differences among treatments, according to ANOVA. For abbreviations, see Fig. 1

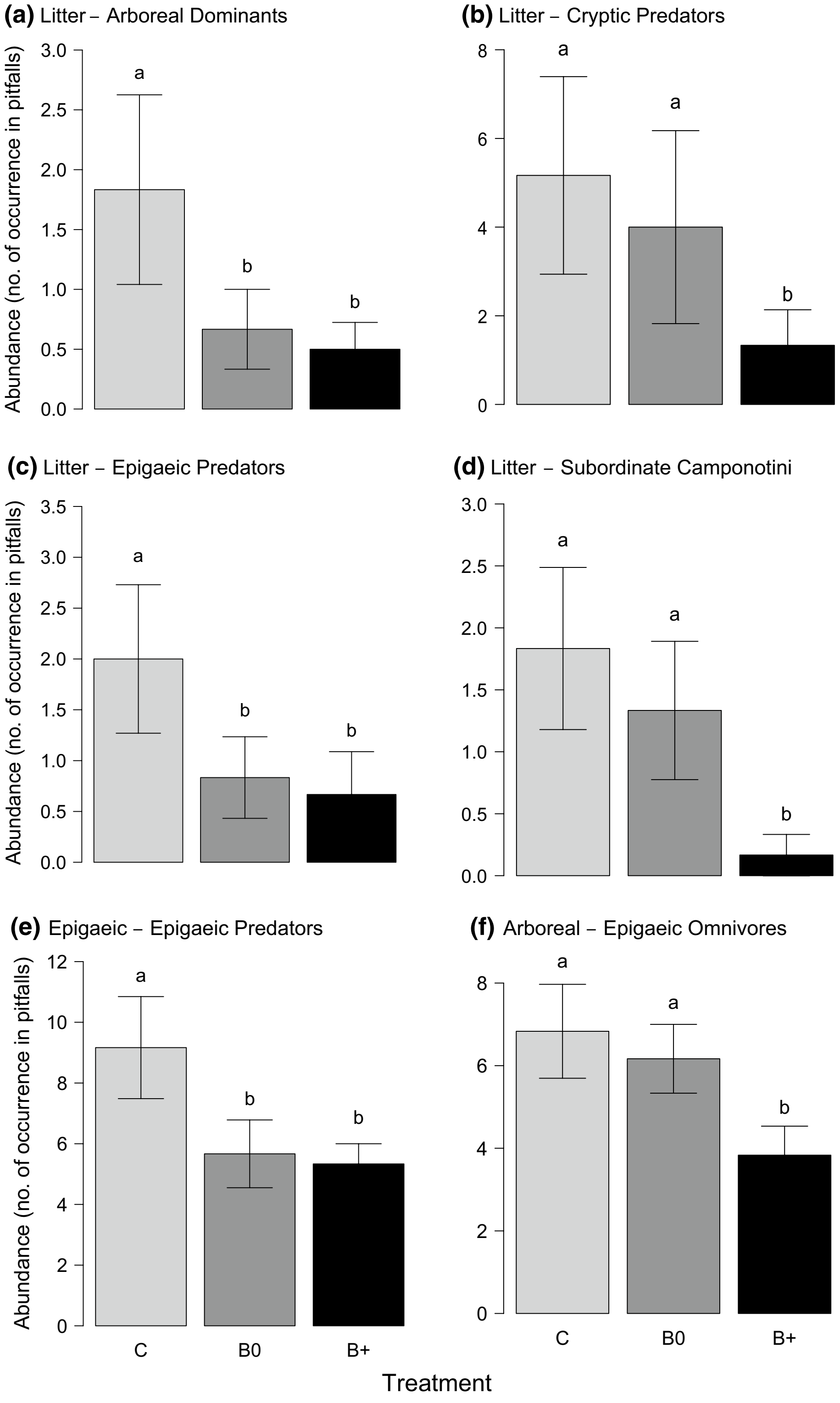
were lowest in B+ plots [$\chi^2_{16} = 5.41$, $P = 0.02$, $R^2_{(c)} = 0.28$; Fig. 3]. Other groups and strata either showed no significant variation, or did not occur sufficiently (abundance ≤15) for analysis.

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 $F_{2,15} = 0.76$; $P = 0.64$), litter ($F_{2,15} = 0.97$; $P = 0.24$), epigaeic ($F_{2,15} = 1.6$; $P = 0.17$) or arboreal ($F_{2,15} = 0.21$; $P = 0.95$) 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 ($F_{2,15} = 0.1$; $P = 0.90$).

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 the total deviance.

Five ant species (of *Pheidole*, *Trachymyrmex* and *Crematogaster*) were observed removing seeds, and 23 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 different among all treatments plots [$\chi^2_{15} = 19.4$, $P < 0.01$; control, 43.8 min ± 1.22 (mean ± SE); B0, 45.77 min ± 1.19; B+, 49.18 min ± 1.10; Fig. 4]. The mean total abundance of species interacting with seeds was lower in B+ plots [35.66 ± 4.97, mean ± SE; $\chi^2_{16} = 4.77$, $P = 0.02$; $R^2_{(c)} = 0.45$] 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 h) was higher in the control [$\chi^2_{16} = 7.6$, $P < 0.01$; $R^2_{(c)} = 0.12$] than in B0 and B+ (Fig. 5), which did not differ from each other. The abundances of seed-removal species did not differ across treatments [$\chi^2_{15} = 2.9$, $P = 0.23$]. Rates

Fig. 3a–f Abundances of ant functional groups that showed statistically significant variation among fire treatments in each habitat stratum of the southern Amazon. *Bars* represent SE. *Different letters* indicate significant differences among treatments, according to ANOVA. For abbreviations, see Fig. 1



of cheating did not differ across treatments [$\chi^2_{15} = 2.89$, $P = 0.23$; Fig. 5], but the abundances of cheater species were lower in B+ plots [$\chi^2_{16} = 12.16$, $P < 0.01$; $R^2_{(c)} = 0.67$] 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, i.e.,

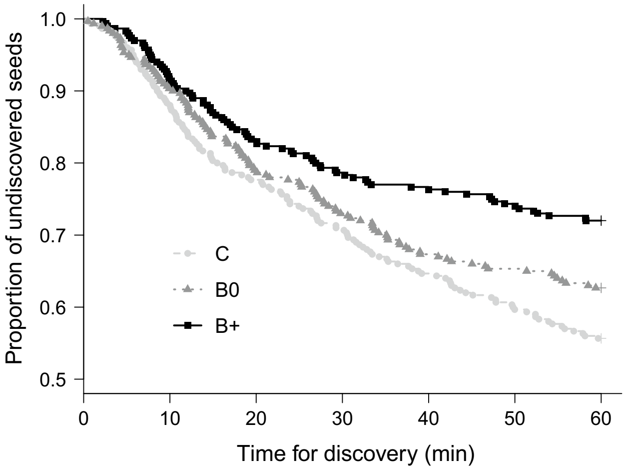


Fig. 4 Variation in seed discovery time among fire treatments in southern Amazon. Seeds were discovered faster in the control than in the B0 and B+ treatments, according to survival analysis. For abbreviations, see Fig. 1

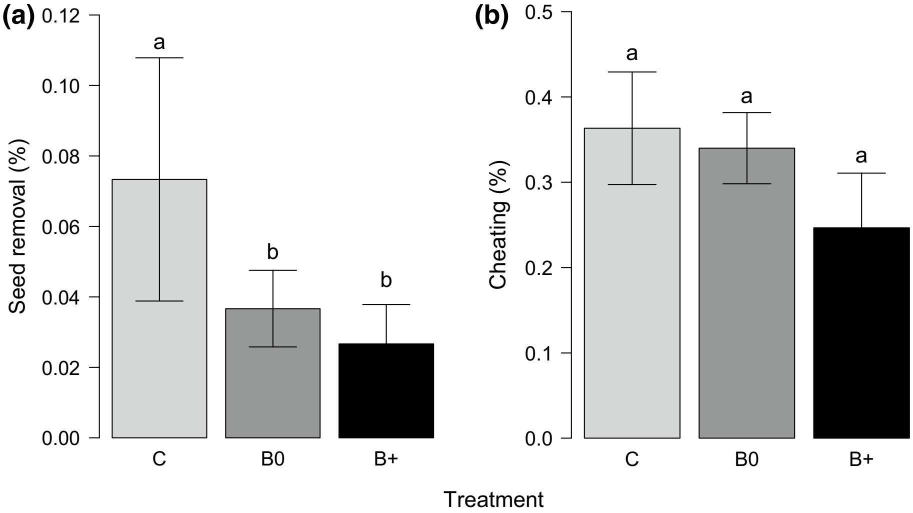
seed dispersion, as well as the extent to which such effects are exacerbated by fuel loads. We first hypothesized that fire will have an overall negative effect on ant abundance and species richness, but such effects will vary according to the functional characteristics of ant species and the habitat 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 predators, but did not affect the abundance of any other functional group. Epigaeic predators tend to be 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 other belowground 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, and so the marked reductions in subterranean catches that we observed in burnt plots likely reflect the effects of fire on the litter fauna, including some of their prey.

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 (cryptobiotic and predator species). However, this did not result in overall biotic homogenization, as shown by a lack of treatment variation in β-diversity. There was also little evidence for biotic homogenization

Fig. 5 Variation in the proportion of **a** seed removal and **b** cheating among fire treatments during 1 h in southern Amazon. *Bars* represent SE. *Different letters* indicate significant differences among treatments, according to ANOVA. For abbreviations, see Fig. 1



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 1 month after experimental fires and it is unlikely that ants could recolonize the area in such a short period. Ant composition did not change after 8 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 production areas (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 did reduce 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; Brando et al. 2016). 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 under drier conditions.

We confirmed our final hypothesis that ants will take more time to discover seeds, and remove them in lower rates in burnt treatments because of decreased abundance and foraging efficiency of ants. The abundances of species interacting with seeds were lower in B+ plots, while they did not differ between control and B0 plots. We therefore attribute the treatment differences in the rates at which seeds were located and removed to both the reductions in ant abundance and in canopy cover 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 and predator species of the litter layer and epigaeic specialist predators) being most sensitive. Fire reduced the effectiveness of a key ecosystem service provided by ants, i.e., seed dispersion, which we attribute to reductions in ant abundance and 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) and decreasing ant abundance, which has a detrimental impact on ant communities and a key ecosystem service they provide.

Acknowledgments We thank M. Padilha for his field assistance, T. Reis and F. Nery for helping with ant sorting, and R. Jesus and J. Chaul for assisting with ant identification. I. Leal, J. Louzada, T. Sobrinho and two anonymous referees provided valuable comments. The fire experiment was conducted by the Instituto de Pesquisa Ambiental da Amazônia, and its staff provided field support. P. Brando and C. Oliveira-Santos provided fire data and information about the site. A. Maggi provided access to the field site and logistical support. This study was supported by the Gordon and Betty Moore Foundation, the National Science Foundation (Division of Environmental Biology grant 1146206), and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG). L. N. P. and R. R. C. S. are supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior grants, M. L. B. M. is supported by FAPEMIG grants, and J. H. S. and L. N. P. (process 205659/2014-4) are supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico grants.

Author contribution statement L. N. P., M. L. B. M., R. R. C. S., R. I. C. and J. H. S. conceived and designed the experiments. L. N. P. and M. L. B. M. performed the experiments. L. N. P. and R. R. C. S. analyzed the data. L. N. P. and A. N. A. discussed the data and wrote the manuscript with input from all authors.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Statement of human and animal rights All applicable institutional and/or national guidelines for the care and use of animals were followed. This article does not contain any studies on human participants performed by any of the authors.

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