



A Multi-Taxa Assessment of Biodiversity Change After Single and Recurrent Wildfires in a Brazilian Amazon Forest

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ABSTRACT

In the last decades, due to human land management that uses fire as a tool, and due to abnormal droughts, many tropical forests have become more susceptible to recurrent wildfires with negative consequences for biodiversity. Yet, studies are usually focused on few taxa and rarely compare different fire frequencies. We examined if the effects of single and recurrent fires are consistent for leaf litter ants, dung beetles, birds (sampled with point-counts PC and mist net-MN), saplings, and trees. Recurrent fires had a great effect on forest structure, reducing live tree biomass and number of lianas, and increasing canopy openness and numbers of saplings alive. Recurrent fires had consistently stronger effects on species richness and composition across all sample groups than single fires, except ants. Birds and plants were more grouped in the congruence analysis. The average dissimilarities between control and recurrent-burned forest were higher than between control and once-burned forest for all sample groups, furthermore birds and vegetation communities in recurrent-burned forest are almost entirely dissimilar from the unburned forest. While beta diversity of ants, birds (MN), and trees was not affected by the frequency of fire, it changed for dung beetles, birds (PC), and saplings. Effects of fire on faunal community structure were more due to indirect effects, through vegetation, than through the fire itself. These results reinforce the effect of single and recurrent fires on tropical forests, and highlight the mechanisms acting behind them. Policy-makers need to explicitly address protection of tropical forests from wildfires in conservation planning.

Abstract in Portuguese is available with online material.

Key words: beta diversity; community structure; distance-based linear model; multivariate dispersion; Pará state.

MANY TROPICAL FORESTS MAY HAVE BEEN SHAPED BY FIRES THAT OCCURRED ONCE OR TWICE PER MILLENNIUM (Turcq *et al.* 1998, Bush *et al.* 2008, McMichael *et al.* 2012). However, in recent decades, especially in Brazil and Indonesia, fire-return intervals have become decadal or even shorter in some forests (Cochrane 2003, Langner & Siegert 2009). This increase in fire prevalence is primarily caused by an increase in ignition sources from agricultural activities that use fire as a tool for land management (Laurance 2004, Cardoso *et al.* 2008, Morton *et al.* 2013) and an increase in forest flammability from other human activities, such as logging and fragmentation (Cochrane 2001, Siegert *et al.* 2001). In addition, fires are often associated with severe droughts (Chen *et al.* 2011). For example, around 2.6 million hectares and 3.9 million hectares of forest were burned during El Niño Southern Oscillation (ENSO) in Indonesia and Brazilian Amazon (Siegert *et al.*

2001, Alencar *et al.* 2006, respectively). Most of the predictions of fires associated to climate changes and human land uses in general, state that such events may occur more often in the coming years (*e.g.*, Cochrane & Barber 2009, Fu *et al.* 2013), affecting not only Amazon forest, but also the hyper-fragmented Brazilian Atlantic Forest. Thus, the interactions between human economic activities, climate change, and fire pose a serious threat for tropical forests.

One of the consequences of this increase in fire-return intervals is an increase in the area of forests being subjected to repeated burns, which can alter forest structure and composition when compared to single burns (Barlow & Peres 2008). For example, when tropical forests are burned for the first time (or when fire-return intervals are millennial), it is a surface fire that usually burns just a thin layer of available fuels, such as the leaf litter and small fallen branches, as well as some small trees and saplings (Cochrane *et al.* 1999). Although these fires are relatively small, they kill a large proportion of trees and aboveground bio-

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mass (Cochrane *et al.* 1999), and have long-term impacts on forest biodiversity (Mestre *et al.* 2013, Silveira *et al.* 2013). Yet, these changes are relatively minor when compared to fire impacts when fire return intervals are in decades: in these cases, the changes in forest structure and composition resulting from the first fire tend to produce a much more severe fire (Cochrane *et al.* 1999) as the fuel available for a second burn is higher, and the forest is drier due to increased canopy openness made by the fall of some large trees (*e.g.*, Ray *et al.* 2005). Recurrent fires may reach into the forest canopy, killing many mid-sized, and large trees and most of the remaining aboveground biomass (Kinnaird & O'Brien 1998, Cochrane *et al.* 1999, Peres 1999, Cochrane 2003).

While the effects of single fires on tropical forests are relatively well described, much less is known about recurrent fires. For example, single fires change the plant, bird and leaf litter ant species composition (Barlow *et al.* 2002, Barlow & Peres 2008, Silveira *et al.* 2013, respectively), reduce sapling, seedling and tree densities (Clearly *et al.* 2006), and cause substantial reptile mortality (Kinnaird & O'Brien 1998). Existing studies on the impacts of recurrent fires are primarily focused on plants (*e.g.*, Cochrane & Schulze 1999, Barlow *et al.* 2003a,b, Haugaasen *et al.* 2003a, Slik & Eichhorn 2003, Toma *et al.* 2005, Barlow & Peres 2008, Slik *et al.* 2008) and secondly on birds (*e.g.*, Barlow & Peres 2004, Adeney *et al.* 2006, Mestre *et al.* 2013). It is known that, compared to single fires, recurrent fires are more severe, reducing fruit production and large frugivorous vertebrate abundance (Barlow & Peres 2006), reducing biomass (Kinnaird & O'Brien 1998, Cochrane & Schulze 1999), drastically changing plant species composition (Cochrane & Schulze 1999, Barlow & Peres 2008, Slik *et al.* 2008) and changing bird species composition (Haugaasen *et al.* 2003b, Barlow & Peres 2004, Slik & Van Balen 2006). However, each of those studies only included a single taxon. Comparisons between effects of single and recurrent fires on multiple taxa within the same study sites are currently lacking, yet are beneficial as different groups often provide complementary insights into intensity of anthropogenic impacts (*e.g.*, Barlow *et al.* 2007).

We addressed this by sampling leaf litter ants, dung beetles, birds (sampled with point-counts PC and mist nets-MN), trees and saplings in once and thrice-burned forests, to assess whether: (1) recurrent fires are consistently worse for biodiversity across all sample groups than single fires; (2) responses to wildfires are consistent across sample groups; and (3) wildfires have an indirect and consistent effect on faunal communities through changes in local vegetation structure among the studied sample groups. We selected birds and dung beetles based on Gardner *et al.* (2008), where they were identified as cost-effective indicators of disturbance in Amazon forests. We included plants as they are the most commonly studied response taxa examined after fires (*e.g.*, Cochrane & Schulze 1999, Barlow & Peres 2008), and leaf litter ants as they are widely used as biological indicators in other studies on disturbed forests (Kalif *et al.* 2001, Andersen *et al.* 2006, Bihn *et al.* 2008, Vasconcelos *et al.* 2008, Silveira *et al.* 2013).

METHODS

STUDY SITE.—Fieldwork was carried out at Tapajós-Arapiúns Extractive Reserve (55°20'43"W, 3°23'30"S), in an upland, non-flooded forest (*terra firme*), located in Santarém municipality, Pará state. The reserve is located in the Arapiúns river basin and it has an area of 647,610 ha. The vegetation is classified as dense closed-canopy vegetation, with small enclaves of edaphic savannahs (*campinarana*) on white sand soils and narrow portions of seasonally flooded forest (*igapó*) (Barlow & Peres 2008). The climate is warm-tropical, type Am according to Köppen's classification (Alvarez *et al.* 2014) and the average annual rainfall at the nearest meteorological station (Santarém) is 2041 mm/yr. The region has a strong dry season lasting three to 5 mo (see Barlow & Peres 2006). Data were collected in the late-dry season (December 2007–January 2008). The area was previously researched for effects of fires on birds, frugivorous vertebrates, and plants (Barlow *et al.* 2002, 2003a,b, Barlow & Peres 2004, 2006, 2008, Mestre *et al.* 2013). We expand these previous investigations by including other previously unstudied groups (leaf litter ants and dung beetles) and by providing long-term information on the responses of birds and large trees to single and recurrent wildfires.

SAMPLING METHODS.—We selected 12 transects to survey: four in once-burned forest, burned in 1997 during ENSO (therefore, sampled 10 yr after a single fire), four in thrice-burned forest, burned in 1982, in 1997, and 2002, ENSOs (therefore sampled six yr after the last fire event), and four nearby unburned transects used as control. Each transect was marked at four sampling points 150 m apart (at 50 m, 200 m, 350 m, and 500 m) and all the data were collected at these four sampling points.

We registered six forest structure variables that can influence biodiversity: percentage of canopy openness, live biomass, number of live lianas, number of dead standing trees, volume of leaf litter, and number of live saplings. To register the percentage of canopy openness we took hemispherical photographs at each sampling point, therefore, four photographs per transect. To estimate the live biomass, we measured the diameter of all trees ≥ 10 cm (diameter at breast height, dbh) and all lianas ≥ 5 cm dbh in a 10 m \times 500 m (0.5-ha) vegetation plot of each transect. Trees were also identified to species level, thereby providing us with tree species diversity. Standing dead trees were also recorded with trees, classified as dead if none of the bark at breast height was living (implying that the entire aboveground biomass associated with that stem was dead). Dead stems could potentially resprout from living roots, therefore, all observations of stems resprouting from tree bases were recorded.

We treated sapling as a different sample group from the larger stems, as they respond much faster to disturbance than larger stems (where there is an obvious recruitment lag). We sampled these within four 5 m \times 5 m subplots placed in pairs at the four sampling points (150 m apart) in each transect, with plots located on either side and one metre from the transect. We counted the

number of live saplings ≥ 1 m height and ≤ 10 cm dbh and identified them to species level, thus registering sapling diversity. Finally, we registered the leaf litter volume by estimating the percentage that a 0.25 m^2 quadrat of collected leaf litter occupied in a $26 \text{ cm} \times 28 \text{ cm}$ cylinder. This cylinder was the litter sifter in which we measured the amount of leaf litter before sieving the fine material to extract the ants (see leaf litter ants method in the following section). Two quadrats were placed inside each subplot, therefore collecting 1 m^2 of leaf litter. All leaf litter estimates were made by the same person to avoid any observer bias.

We collected the leaf litter ants using the Winkler sack method (Agosti *et al.* 2000). At each one of the four sampling points of each transect, we placed four 0.25 m^2 quadrats, 2 m aside from each other and collected all the leaf litter inside. This material was placed in a $26 \text{ cm} \times 28 \text{ cm}$ cylinder, sieved to remove larger debris and leaves (mesh = 1 cm^2), and combined into one litter sample per point, totaling four 1 m^2 samples per transect. The resulting sieved material was kept in Winkler funnels in a shaded place for 3 d (72 h). Ants were identified to species level or morphospecies, and voucher specimens are stored at the Universidade Estadual do Sudoeste da Bahia-UESB, Itapetinga, Bahia, Brazil.

The dung beetles were sampled using human feces baited pitfall traps (one per sampling point), modified from Halfpeter and Favila (1993). Each pitfall consisted of a 1 L, 15 cm wide, 9.5 cm deep plastic container buried at ground level and half-filled with salted water and detergent. A small bag made of cotton gauze, containing 20–30 g of human feces, was suspended above the pitfall with a wooden stick. The lid of the plastic container was placed 10 cm aboveground level with three wooden sticks, helping protect both the bait and the pitfall from the rain. All traps were collected after 2 d, rebaited, and collected again after two more days. All dung beetles were pinned and dried. Beetle sorting was carried out at the Universidade Federal de Lavras with identifications confirmed by Dr. Fernando Vaz de Mello at Universidade Federal de Mato Grosso. Voucher specimens are deposited in both institutions.

The birds were sampled using both mist nets (MN) and point-counts (PC) along transects. As in previous studies (Barlow *et al.* 2007), we treated mist net and point-count data separately. Both techniques are useful, but they often provide complementary information with very different relative abundances which reduce the interpretability of pooling the two samples—for example, mist net samples register many of the understory species, including cryptic birds that rarely vocalize, while point-counts provide information on the whole bird community including canopy specialists but may underestimate more cryptic species (*e.g.*, Blake & Loiselle 2001). Twenty-eight mist nets ($12 \text{ m} \times 2.5 \text{ m}$; mesh size 36 mm) were erected in four groups of seven nets along each sampling point of transects. Each group created a netline of $7 \text{ m} \times 12 \text{ m}$ extending for 90–100 m. Groups were separated by an open space of 50 m. We opened the 28 nets for 2 d, from sunset (0630 h) to about 1330 h accruing 392 mist net hours per transect and 4704 mist net hours in total. We checked the nets hourly and closed them during periods of heavy rain. All birds captured were identified to species level, weighed, and measured (standard measurements included

wing, tail, bill, and total length) and, whenever possible, were aged, sexed and photographed. The captured birds were banded with a numbered metal ring obtained from Centro Nacional de Pesquisa para Conservação de Aves Silvestres (CEMAVE)—Instituto Chico Mendes de Conservação e Biodiversidade (ICMBio). All recaptures from the same sampling period and from the same net line were excluded from the analysis to avoid double counting.

Point-counts were conducted for a period of 10 min at the four sampling points of each transect, spaced 150 m from each other (at 50 m, 200 m, 350 m, and 500 m along the transect). We carried out observations twice at each sampling point, over two different days, avoiding transects where mist-netting was taking place. The first sample was between 0600 h and 0730 h and second between 0730 h and 0900 h. Most of the bird registrations were recorded during point-counts (using a digital recorder and a directional microphone) and confirmed (if possible) visually (with binoculars). Unknown vocalizations were subsequently checked against known calls and, if necessary, confirmed by consulting other ornithologists. The distance from the observer and height were also noted. To maintain independence between point counts (and to avoid any potential double counting), we excluded from the analysis all the birds over flying or registered outside the range of 50 m radius of each point-count. To avoid double counting during the second visit, we excluded any observations of species that had already been recorded at the subsequent point. We analysed separately the two methods used (mist nets and point-counts).

Each sample group was sampled by different authors during the same field trip. Caution was taken to survey transects at least 2 d after any previous work has been carried out.

DATA ANALYSES.—Spatial autocorrelation within transects was assessed using Mantel-type RELATE tests in Primer 56.0. Similarity matrices were constructed based on normalized Euclidean distance between the locations of the sampling sites. These were correlated with community composition matrices based on the Bray–Curtis similarity index.

We analysed the patterns of species richness between different burn treatments by comparing individual-based rarefaction curves calculated using the analytical formulae from EstimateS v.7 (Colwell 2004). Comparisons between treatments were standardized by of the number of individuals and ant occurrences, as we were interested in patterns of species richness and not species density (Gotelli & Colwell 2001). We also analysed patterns of species richness at the transect level and test using a General Linear Model (GLM).

We analysed the community composition at transect level using multidimensional scaling (MDS) to ordinate samples based on the Bray–Curtis dissimilarity index for all groups. We used the Bray–Curtis index to analyse the ants by counting the incidence of ants per transect into a measure of abundance (0–4). An analysis of similarity (ANOSIM) was used to test for significant differences in community composition between burned and control forests. The ANOSIM provides a way to test statistically whether there is a significant difference between two or more groups of sampling units (control and burned forests in this case), operating directly on a

dissimilarity matrix. The ANOSIM R is based on the difference of mean ranks between groups and measures the degree of separation between treatments. To evaluate congruence of responses across the taxonomic groups, we conducted a second-stage community analysis, which uses MDS ordination to plot the pairwise similarities between MDS plots (Clarke *et al.* 2006).

To calculate average dissimilarity between control and burned forests, we conducted a SIMPER analysis which decomposes average Bray–Curtis dissimilarities between all pairs of samples, one from each group, into percentage contributions from each species, which are used to calculate the average dissimilarity between groups. These were undertaken in Primer v6.

To test if there were significant differences between results from ANOSIM from control versus once-burned forest and control versus recurrent-burned forest, we performed a Wilcoxon test with the R from ANOSIM. To test if there were differences in average dissimilarity between the same pairs of treatments from SIMPER, we also performed a Wilcoxon test. These were undertaken in SPSS v20 (SPSS Statistics for Windows, Version 20. Armonk, NY: IBM Corporation).

To test the multivariate dispersion of sampling points between each group formed by MDS, we performed a Permutational Analysis of Multivariate Dispersions (PERMDISP). It calculates the centroid of each treatment (Control, Single Fire, and Recurrent Fires) in multivariate space based on the chosen similarity measure (in this case, Bray–Curtis), and then calculates the distance of each transect within the treatment from the treatment centroid. To compare average dispersion values between treatments PERMDISP performs a permutational ANOVA and calculates a pseudo F -statistic and P -value. A large pseudo F -ratio indicates that one treatment presents more dispersed points in the multivariate space than another, or, in other words, that the spatial variability in species composition between transects is higher in one treatment than in the other one. Thus, PERMDISP can be used as a direct test to evaluate differences in beta diversity between treatments (Bunn *et al.* 2010).

For the forest structure variables, first we analysed the canopy hemispherical photographs using the program Gap Light Analyzer. To check if the forest structure variable had changed after fire, we conducted an ANOVA with a Tukey's post-hoc test. These were undertaken with SPSS v20.

We performed a distance-based linear model (DistLM) to investigate the relationship between the fauna community structure, described by a resemblance matrix, and the forest structure variables (Anderson 2004). DistLM is a routine for analysing and modeling the relationships between a multivariate data cloud, described by a resemblance matrix, and one or more predictable variables. The resemblance matrix described dissimilarities among a set of samples on the basis of multivariate species abundance data, and interests lie in determining the relationships between this data cloud and the environmental variables that were measure for the same set of samples. We used Bray–Curtis resemblance measure for all taxonomic group matrices and standardized square-root transformed predictors. The selection criterion and selection procedure used were ALL and Adjusted

R^2 (9999 permutations), respectively. The most parsimonious model was used to express the proportion of explained variation for each isolated factor (vegetation structure and fire frequency) for partitioning the pure vegetation and fire effects from the join vegetation + fire effect. We carried out DistLM with PERMANOVA+ for PRIMER v6 (Clarke & Gorley 2006).

RESULTS

Our analysis of forest structure confirmed a strong influence of recurrent fires across all sample groups: compared to the once-burned forest, thrice-burned forests had a more open canopy, less aboveground biomass, fewer lianas, less dead standing trees, and fewer live saplings. The volume of leaf litter was not significantly different between control, once-burned and thrice-burned forests (Fig. 1).

There was no correlation between spatial location within treatments (P -values ranged between 0.11 and 0.99 for the 18 RELATE tests conducted for all groups; R values were very low, especially for control forest [Table S2]).

Species accumulation curves indicate two patterns of responses to the frequency of fire: (1) no effect at all (ants and birds-MN); and (2) reduction in species richness only in thrice-burned forest (dung beetles, birds-PC, saplings, and trees) (Fig. 2). Mean species richness at transect level corroborated patterns of species accumulation curves, excepted for dung beetles, where there was no difference between treatments (Fig. 2).

Community composition was also changed after fire in general (Fig. 3). Birds (MN, PC) and sapling communities were very different in burned plots, while ants and dung beetles were less affected (Global R of Table S1). The pairwise comparisons between control versus once-burned forest and control versus thrice-burned forest revealed that once-burned forest and thrice-burned forest were different from control forest for all groups (Statistical R of Table S1). The average dissimilarities between control and thrice-burned forest were higher than that between control and once-burned forest for all groups (Wilcoxon test $P = 0.03$), except for ants. However, the dissimilarities for birds (MN, PC), saplings and trees were much greater (Fig. 4). The second-stage community analysis revealed some additional differences in congruence across sample groups. Independently of sampling method, plants lay close to the center of the MDS plots resulting from the second-stage community analysis, indicating their responses are close to being an average of the faunal groups. Irrespective of sampling approach, birds were similar to plants on Axis 1, while ants and dung beetles were dispersed in the different directions. However, both ants and dung beetles were considerable more dispersed in the MDS plots resulting from the second-stage community analysis (Fig. 3), suggesting they each had more unique patterns of community turnover across sites.

Multivariate dispersion of each group across treatments (Fig. 5) showed that frequency of fire had no effect on beta diversity of ants, birds (MN) and trees. For dung beetles, the beta diversity was highest in the once-burned forest, intermedi-

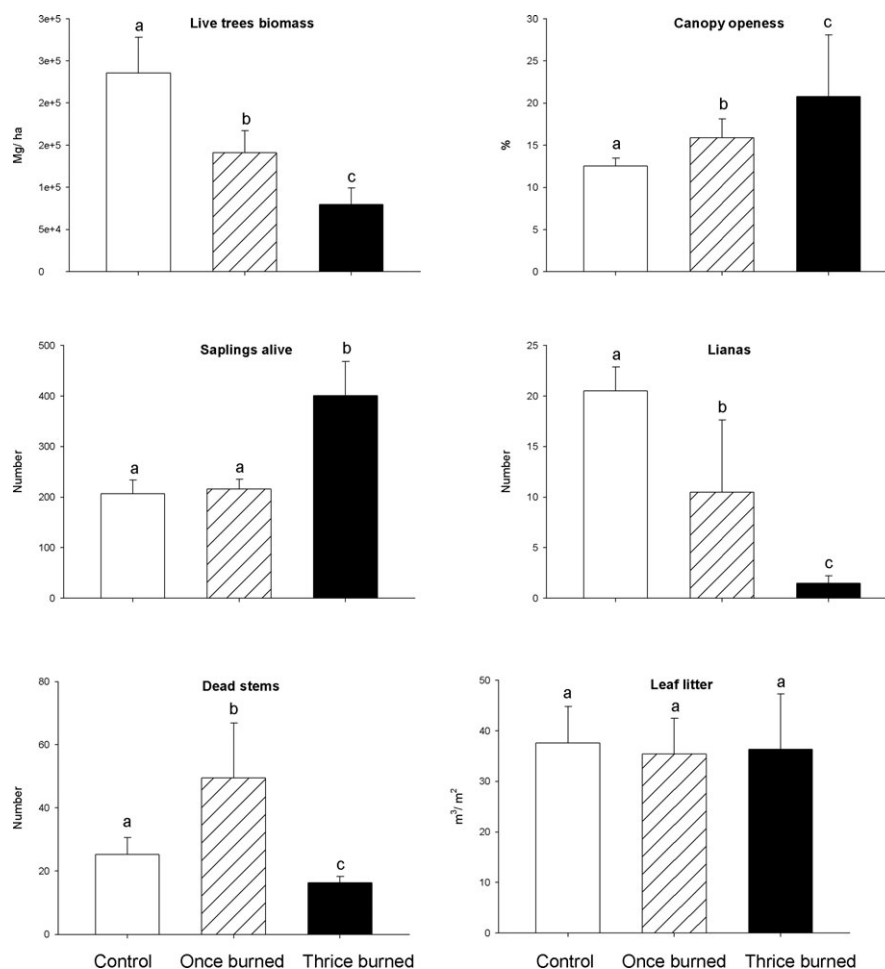


FIGURE 1. Forest structure in control (white bars), once-burned (striped bars) and thrice-burned forests (black bars). The letters above each bar indicate significant subsets after an ANOVA and Tukey's *post-hoc* test at 95%.

ate in control forest and lowest in the thrice-burned forest, and all of them were significantly different from each other. For birds (PC), beta diversity was similar between control and once-burned forests, which was significantly higher than that found in thrice-burned forests. For saplings, beta diversity was similar in both fire treatments, which were lower than the control forest.

The DistLM confirmed the importance of changes in forest structure for faunal community structure, as many of the effects of fire were indirect, acting via changes in the vegetation (Fig. 6).

DISCUSSION

This is the first multi-taxa study comparing the effects of single and recurrent fires in humid tropical forests. Although it is difficult to isolate the effect of time since last fire (c. 10 yr after fire in once-burned forest and 6 yr after fire in thrice-burned forest) with fire frequency, our results do provide important insights into the general influence of wildfires on biodiversity in Amazonian forests. Summarizing, we found that species richness was lower

in thrice-burned forest than in controls or once-burned forests for all groups except the leaf litter ants and birds-MN, and recurrent fires had consistently severe effects on species composition across all sample groups. The community structure of the faunal sample groups was most strongly influenced by the indirect effects of fire (*i.e.*, the forest structure) than by fire frequency itself, while our analysis of congruence of responses showed that vegetation samples best reflected the average responses of all groups while invertebrate taxa were least similar to each other in their responses.

These results confirm the negative consequences of recurrent forest fires in humid tropical forests (Kinnaid & O'Brien 1998, Cochrane & Schulze 1999, Haugaasen *et al.* 2003b, Barlow & Peres 2004, 2006, 2008, Slik & Van Balen 2006, Slik *et al.* 2008). By analysing species turnover (pairwise dissimilarity), we show that forests that have undergone recurrent fires contain bird and vegetation communities that are almost entirely dissimilar from nearby undisturbed forests. However, there were some important differences in responses between sample groups, which we outline below.

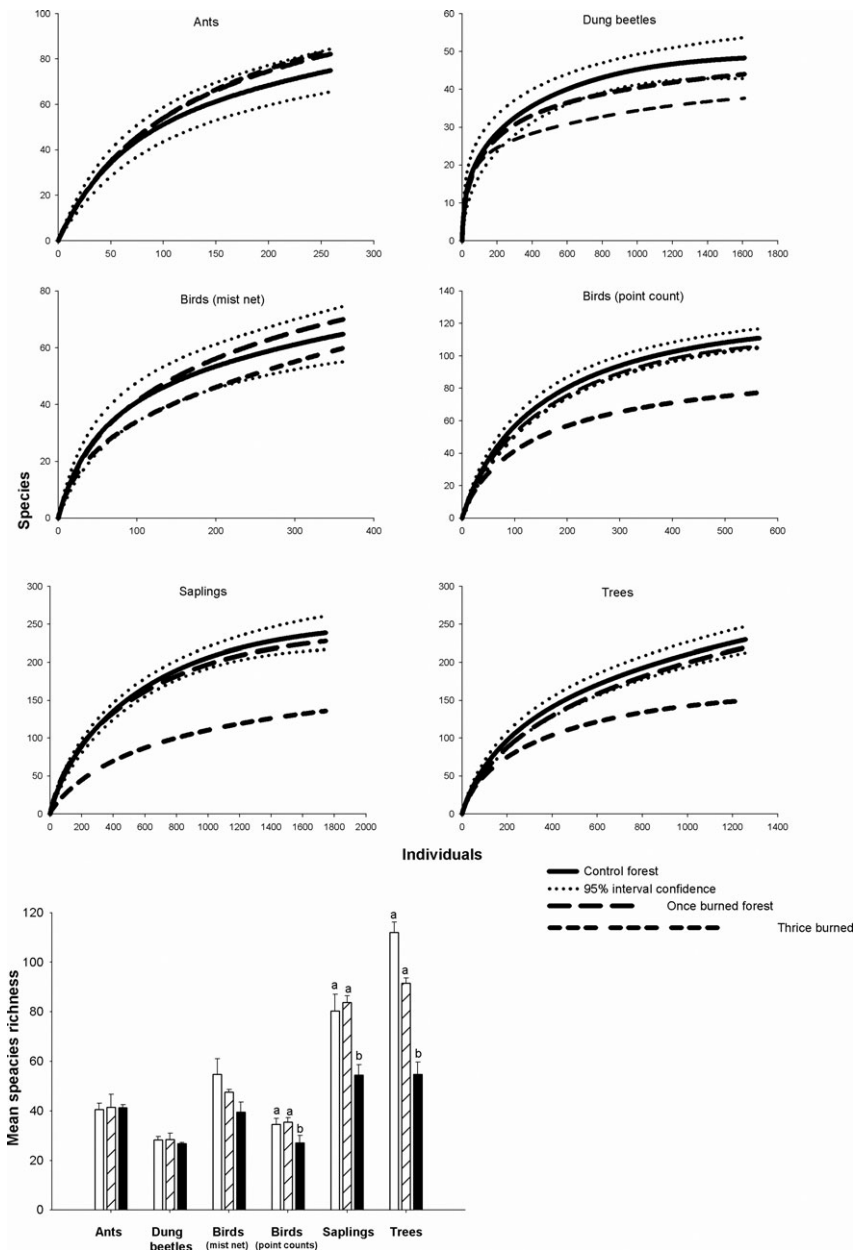


FIGURE 2. Randomized individual-based species accumulation curves for leaf litter ants, dung beetles, birds (mist net and point-count), trees and saplings in control forest, single-burned forest, and thrice-burned forest.

When focusing on species richness as the response metric, neither leaf litter ants and birds-MN showed significant differences across treatments. These results help confirm the problem of relying on species richness, which is known to be an unreliable indicator of the impacts of disturbance (*e.g.*, Su *et al.* 2004, Barlow *et al.* 2007). This may be particularly so for ants, as many of them are generalists and the loss of some sensitive species to disturbance is compensated by the invasion of other opportunist species and generalists (Hoffmann 2010, Ribas *et al.* 2012). For birds sampled with mist nets, the lack of clear responses could be attributed to the increased capture of canopy species that

forage lower down in disturbed forests, as well as the colonization of edge-loving species often found in flooded forests and scrubby vegetation (Barlow & Peres 2004).

There were also important differences in community turnover across sample groups. If you take a broad-scale (*i.e.*, between treatment) assessment, then the additional impact of multiple fires was noticeable for most sample groups. However, the additional change in community dissimilarity was lower for dung beetles than for the plants and birds, while for ants the thrice-burned forests were marginally more similar to the unburned controls than once-burned forests (Fig. 4). Moreover, both invertebrate

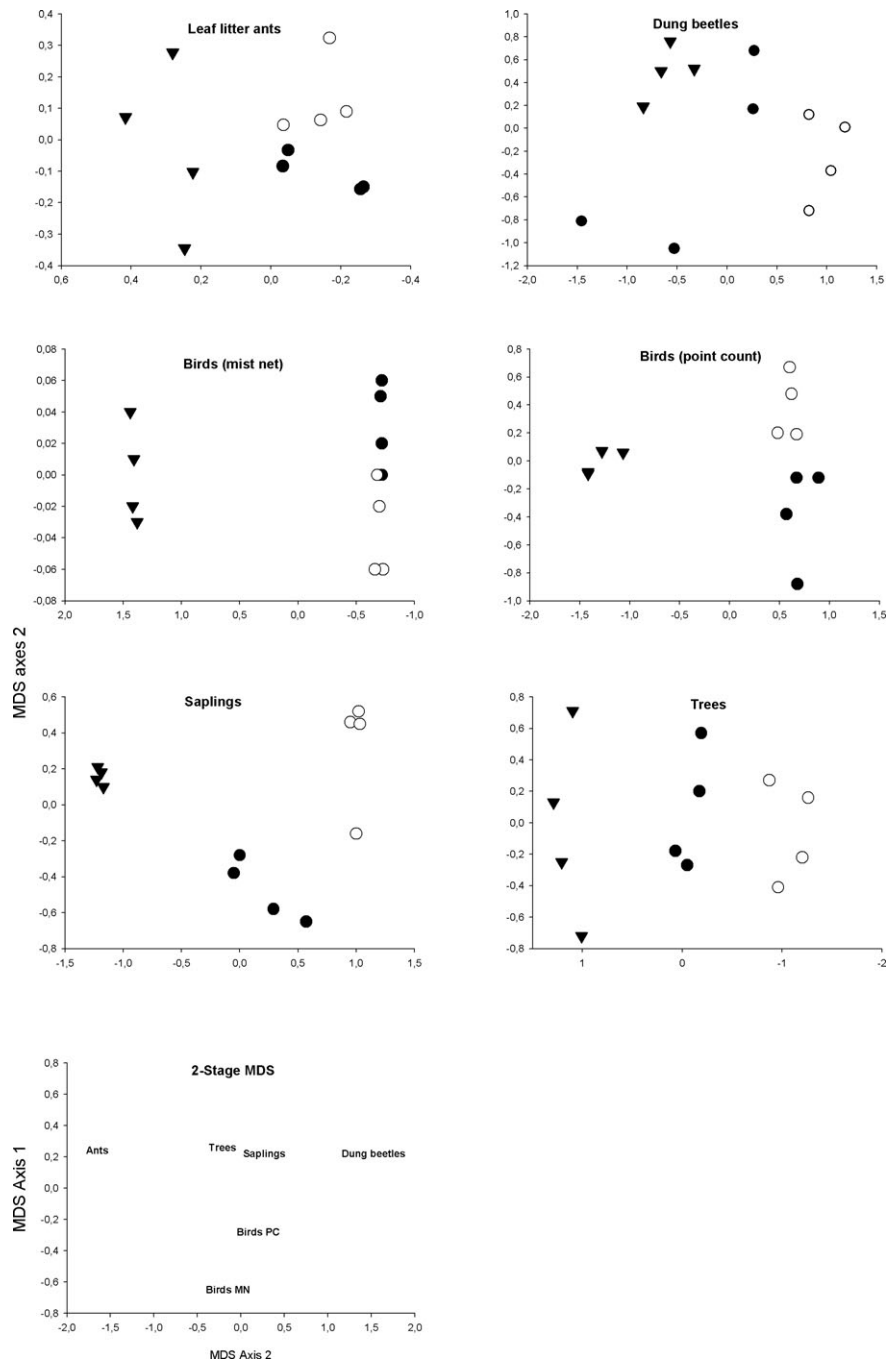


FIGURE 3. Multi dimensional Scaling ordinations for leaf litter ants, dung beetles, birds (mist net and point-count), trees and saplings in control forest (open circles), single-burned forest (closed circles), and thrice-burned forest (triangle). The final panel shows the ordination resulting from a two-stage MDS, revealing the congruence in responses to fire disturbance across the six groups.

taxa (dung beetles and ants) had distinct responses when considering the similarity of community turnover across all sites along Axis 1 of the second-stage MDS plot (Fig. 3), suggesting there is no reason to expect similarity of responses between different groups of invertebrates. These results also suggest that while previous studies carried out assessing the impacts of recurrent fires

on trees (*e.g.*, Cochrane & Schulze 1999, Barlow & Peres 2008, Slik *et al.* 2008) are likely to be good indicators of the responses of birds (*cf.* Andrade *et al.* 2014), they may be much less reliable indicators of responses of invertebrate taxa.

There were also important differences in multivariate dispersion across sample groups across burn treatments. Some sample

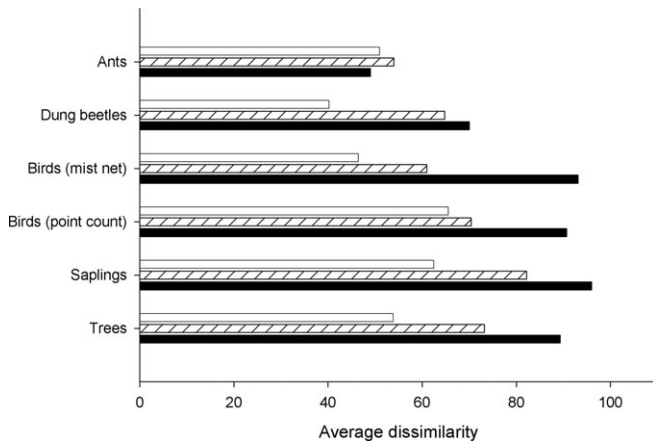


FIGURE 4. Average dissimilarity after a SIMPER test for ants, dung beetles, birds mist net and point-count, saplings and trees. White bars: average dissimilarity inside control forest (between transects); dashed bars: average dissimilarity between unburned controls and once-burned forest; black bars: average dissimilarity between unburned control and thrice-burned forest. Dissimilarity scores for the control to thrice-burned forest comparison were significantly higher than the control to once-burned forest comparison (Wilcoxon test, $P = 0.03$).

groups were significantly less dissimilar between sites in thrice-burned forests than in unburned forests (dung beetles, birds-PC and small stemmed vegetation), providing some evidence that recurrent fires causes biotic homogenization, leading to a reduction in species turnover across the landscape, with consequent reduction in beta diversity. However, other sample groups (ants, birds- MN, and large trees) did not change. The rather limited number of sites within each burn treatment ($n = 4$) and the varied responses across the same taxa sampled by different methods (*i.e.*, birds and vegetation) suggest that our results should be taken with caution, and that further research is necessary on this important phenomenon (*c.f.* Olden & Rooney 2006).

Finally, we focused exclusively on the faunal sample groups to examine the extent to which fire influences community composition through changes in local vegetation structure. Overall, and across all groups, local forest structure has more explanatory power than the fire treatment itself. These results are consistent with previous studies that found strong associations between forest structure and community structure for birds (see Barlow *et al.* 2002, Haugaasen *et al.* 2003b), ants (*e.g.*, Silveira *et al.* 2013), and dung beetles (Andrade *et al.* 2011). However, they also suggest that predicting faunal responses to large-scale

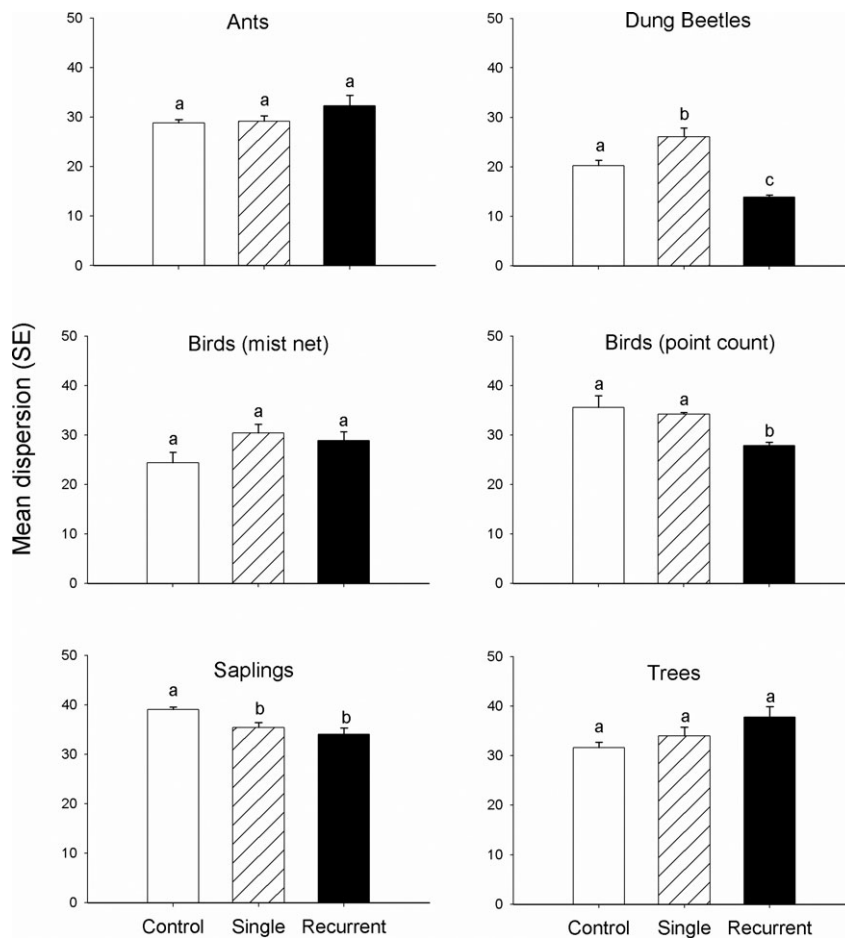


FIGURE 5. Permutational Analysis of Multivariate dispersion (PERMDISP) of faunal groups across each treatment. Different letters mean significant differences.

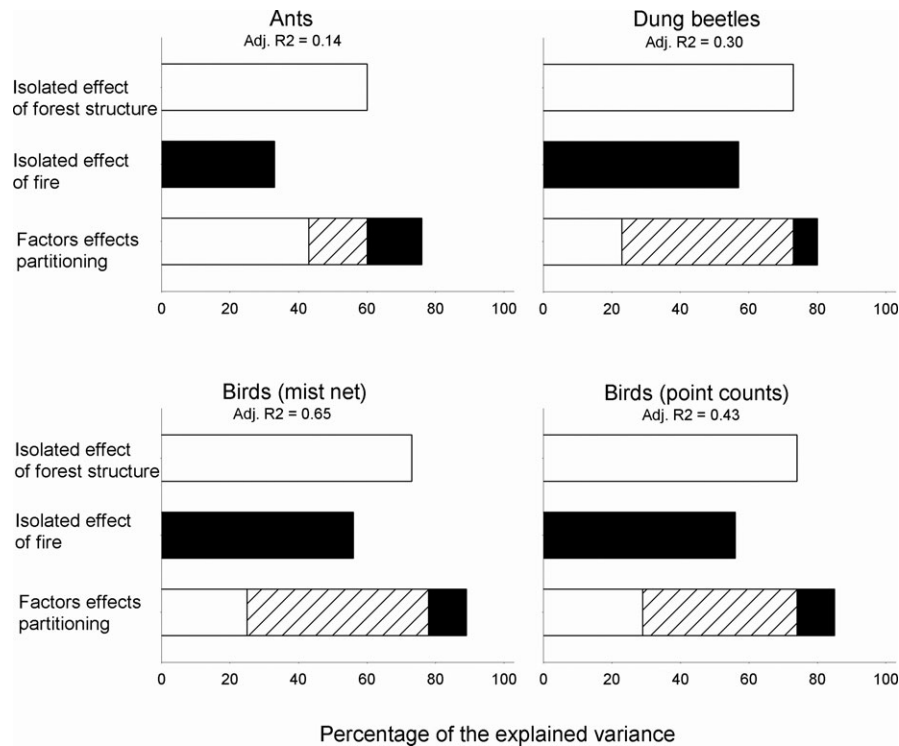


FIGURE 6. Distance-based linear model (DistLM) for the fauna groups with a Bray–Curtis resemblance measure and standardized square-root transformed predictors. Gray: isolated effect of forest structure, black: isolated effect of fire, hatching: shared explanatory power.

disturbance events such as fire may require finer scale information, highlighting the importance of taking accurate measurements of forest structure to understand turnover of faunal taxa. Such measurements presumably add to categorical classes of fire treatments by capturing some of the pre-existing variation in forest condition and structure and some of the local variation in fire intensity.

CONCLUSION

By comparing the impacts of single and recurrent fires on different sample groups, we make the first assessment of their important influence for forest invertebrates, while reaffirming their impacts on other tropical forest biota such as birds and vegetation. We show that invertebrates share many responses with plants and birds, they may have distinct patterns of turnover, and may be less affected by recurrent wildfires. Our results also suggest that we may need a finer scale assessment of vegetation structure to accurately assess fire impacts. Given the difficulty of quantitating this across large-scale using field surveys, they therefore provide support for more detailed assessments of forest structure that are attainable using remote sensing methods such as LiDAR (Asner *et al.* 2012). Finally, although the objectives of his study were to quantitate impact of fires, rather than develop applied solutions to the fire problem, our results for plants and birds clearly demonstrate the importance of preventing recurrent forest fires from taking places in regions already affected by

single burns. However, there is little doubt that reducing degradation from both single and recurrent fires should be an important component of efforts to reduce forest degradation and biodiversity loss in the humid tropics.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. R-values from Anosim for each sample groups.

TABLE S1. *ANOSIM results based on a Bray–Curtis dissimilarity matrix.*

TABLE S2. *R and P values for spatial autocorrelation among treatments control, once-burned and thrice-burned forests.*

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