

Bird functional diversity and wildfires in the Amazon: the role of forest structure

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Abstract

Fire is becoming a common phenomenon in Amazonian forest, modifying the structure and composition of natural assemblages. In particular, fire is known to affect patterns of bird diversity in tropical forests, but we have little understanding of the consequences of this for the functional diversity of bird assemblages. For example, frequent fires could act as an environmental filter selecting species with similar traits and, thus, producing a functional clustering pattern. Here, we used body mass, and dietary and foraging traits to calculate the functional structure of understorey bird assemblages in Amazonian forests analysed 3 years after they had passed under three disturbance levels within the 1997–1998 El-Niño period: unburned, burned once and burned twice. First, we tested whether observed levels of functional diversity were different among these forests and also from what one would expect by chance. Then, we investigated if habitat structure was able to predict changes in the functional structure of the studied bird assemblages. In general, there was no evidence of fire reducing functional diversity nor selecting species functionally more similar than expected by chance. Therefore, bird functional diversity was not different from random in unburned and burned forests. This provides some evidence in favour of high functional redundancy of bird species in the tropics, but also indicates that neutral theories of biodiversity, where processes such as dispersal and survival are more important than biological traits to community assembly, may apply to the assemblages studied. Also, we showed that bird assemblages from forests disturbed by wildfires have the tendency to be functionally overdispersed whereas assemblages from pristine forests tend to be functionally clustered. Thus, environmental structure, in part driven by forest responses to fire, is more important than simple categorical definitions of burn frequency for explaining trait-based assembly rules of understorey birds in the Amazon forest.

Introduction

Tropical forest biodiversity is under constant threat because of selective logging (Nepstad *et al.*, 1999; Asner *et al.*, 2005), fragmentation (Stoke & Tucker, 1993; Broadbent *et al.*, 2008), deforestation and the synergy between deforestation and fire (Aragão & Shimabukuro, 2010). Even if fire is not a natural factor in humid tropical forests (Cochrane, 2003) it is becoming a common phenomenon. Within the Amazon, forests are burning as a consequence of extensive droughts related to the El Niño Southern Oscillation (ENSO) (Cochrane, 2003) and changes in Atlantic sea surface temperatures (Lewis *et al.*, 2011), as well as the human expansion in the region (Nepstad *et al.*, 2001; Vieira *et al.*, 2008). In the Brazilian Amazon forest, fire occurrence has increased in more than half of the total area that have

experienced reduced deforestation rates in the last decade (Aragão & Shimabukuro, 2010). Fires are a major threat for tropical forests because they modify the vegetation structure and composition (Haugaasen, Barlow & Peres, 2003; Blair, 2005), and impoverish native fauna (Peres, Barlow & Haugaasen, 2003). Fires also simplify the guild structure of mammal and bird assemblages (Peres *et al.*, 2003; Barlow & Peres, 2004a; Adeney *et al.*, 2006) and favour colonization by animal species commonly found in disturbed habitats (Lovejoy *et al.*, 1986).

Consequences of fire may vary for birds inhabiting tropical forests. Usually, fire has negative effects on birds, decreasing nesting success (Cahill & Walker, 2000), diminishing species abundance (Kinnaird & O'Brien, 1998) and changing species composition (Barlow & Peres, 2004a; Adeney *et al.*, 2006). Some foraging and dietary guilds show

predictable responses: in the Central Brazilian Amazon, arboreal omnivore and terrestrial gleaning insectivore birds were not affected by fire; arboreal granivores, frugivores and nectarivores showed unimodal responses to fire severity, and all other insectivores were negatively affected after fires (Barlow & Peres, 2004a). Also, habitat structure variables such as canopy openness and understorey vegetation are important for determining bird diversity and abundance in burned forests (Barlow & Peres, 2004a), and severe recurrent fires lead to a dramatic loss of habitat specialists, which are replaced by generalists. Therefore, fire may act as a filter, simplifying the phenotypic structure of bird assemblages in tropical forests. Nevertheless, up to now, there is a lack of information on the effects of fire on the phenotypic structure of these assemblages.

The consequences of disturbances to biodiversity are often investigated using measures of diversity (e.g. species richness, Shannon or Simpson diversity indices), which are unable to take into account the fact that some species are more similar than others in their life history traits (Chalcraft & Reseritis, 2003; Chown, Gaston & Robinson, 2004), or in other words, in their ecological niches. In fact, there are studies indicating that 'traditional measures of diversity' are unsuitable indicators of ecological features and changes in community structure following forest disturbance and may thus obscure the actual extent of biodiversity loss (e.g. Nummelin & Kaitala, 2004; Ernst, Linsenmair & Rödel, 2006). One solution is to use measures of functional diversity, which incorporate species ecological similarities and can be defined as the value and range of the functional differences (i.e. trait differences) among species in a community (Tilman *et al.*, 1997). Thus, functional diversity measures can be seen as a manner to represent the diversity of different phenotypes in a given community (Gómez *et al.*, 2010). In doing so, this approach aims to bridge the gap between two components of biodiversity: species diversity and species composition.

Measures of functional diversity can be used to understand how local communities are assembled from the regional species pool (Weiher & Keddy, 1999; Petchey *et al.*, 2007; Gómez *et al.*, 2010). Such assembly is usually understood as the outcome of two opposing mechanisms: (1) environmental filtering, where coexisting species tend to be ecologically more similar to one another than would be expected by chance (i.e. functional clustering), because environmental conditions act as a filter allowing only a narrow spectrum of traits to persist (Keddy, 1992; Mouchet *et al.*, 2010); (2) limiting similarity, where coexisting species are prevented from being too similar (i.e. functional overdispersion) assuming the stable coexistence of less ecologically similar species (MacArthur & Levins, 1967; Mouchet *et al.*, 2010). Niche theory considers that species composition is influenced by species ecological traits and, therefore, interspecific competition, habitat selection and resource diversity are determinants to species co-occurrence (Weiher & Keddy, 1999; Gómez *et al.*, 2010). Values of functional diversity different from those expected by chance after perturbations would support niche theory. However, neutral

theory of biodiversity (Hubbel, 2001) advocates that species coexist in assemblages independently of their traits, because individuals and species are equivalent. In this case, species composition in a given place should be the result of dispersal, reproduction and death of individuals (Ostling, 2005). Values of functional diversity equal to those expected by chance (i.e. random phenotypic structure) would support one of the principal premises of neutral theory.

Functional diversity of assemblages could also be related to habitat structure and several forest features can be used as structural indicators, including tree size, vertical foliage distribution, canopy cover and density and abundance of deadwood (Noss, 1990; Spies, 1998; Smith *et al.*, 2008). Moreover, it is known that habitat heterogeneity is positively related to species richness (Bell, McCoy & Mushinsky, 1991) and that the forest structure is associated to changes in the composition of bird assemblages (Mason, 1996; Barlow & Peres, 2004a). A mechanism that explains this is niche diversification: more heterogeneous habitats offer better opportunities for resource partitioning and, consequently, should harbour species with different ecological features (Schoener, 1974; Bradford & Kastendick, 2010). Also, organisms vary in how they are affected by habitat structure (Whittingham & Evans, 2004). Therefore, it is important to analyse the relation between environmental variables and functional diversity, because disturbances (e.g. wildfires) can indirectly affect the functional diversity of bird assemblages through modifications of vegetation structure.

Here we examined the effects of wildfires on the functional diversity of Amazonian understorey bird assemblages 3 years after the 1997–1998 ENSO. Specifically, we ask the following questions: Do wildfires reduce the observed functional diversity in the burned forests? Do wildfires act as an environmental filter and, thus, species from burned forests would be more functionally similar than expected by chance? Does forest structure explain the observed functional diversity and the functional structure of the studied bird assemblages?

Materials and methods

The Amazon forest is thought to harbour one of the highest biological diversity on Earth (Myers & Myers, 1992) being the largest and relatively intact tropical forest in the world. We used the data about species composition previously published in Barlow & Peres (2004a), in which understorey bird species were sampled in forests with different wildfire histories. Sampling was carried out in the central Brazilian Amazon forest in the Arapiuns and Maró River catchments, located in the west of the state of Pará (2°44' S, 55°41' W). To examine the fire effects over the bird functional diversity, we used the information from 28 forest sites sampled 3 years after the fires that occurred during the 1997–1998 ENSO years. Ten sites did not burn, 12 sites burned once and six sites burned twice. Data was collected from July 2000 to May 2001, completing 20 160 mist-net hours (see Barlow & Peres, 2004a). Plots were separated by a minimum of 500 m to ensure their independence, and < 1% of colour-banded

birds were subsequently recaptured in other netlines (Barlow & Peres, 2004a). Plots were also spaced across the widest area that was logistically possible, ensuring we captured a wide range of different burn intensities within each treatment (see maps and figures in Barlow & Peres, 2004b). An analysis of tree family composition in unburned and once burned forests suggests the forests were similar before the fires (Barlow *et al.*, 2003).

For each of the understorey bird species occurring in the study sites, we collated information on 21 traits (Del Hoyo, Elliot & Sargatal, 1992–1997; Sick, 1997; Ramirez, Diniz-Filho & Hawkins, 2008; Batalha, Cianciaruso & Motta-Junior, 2010). We selected traits associated with the amount and type of resources used, feeding behaviour, and body size. In total, we used resource and dietary traits (vertebrates, invertebrates, leaves, fruits, grains and nectar; presence/absence); behavioural traits based on foraging methods (pursuit, gleaning, pouncing, grazing, digging, scavenging and probing; presence/absence) and foraging substrate (water, mud, ground, vegetation and air; presence/absence); and body mass (in grams). These traits were also used on previous studies involving bird functional diversity (e.g. Petchey *et al.*, 2007; Batalha *et al.*, 2010) and are likely to capture well how these species use and compete for resources (Sekercioglu, 2006).

We produced a functional dendrogram based on the data matrix, with species in rows and species traits in columns. Then we used a modification of Gower distance (Pavoine *et al.*, 2009), because we used qualitative and quantitative traits, and the unweighted pair-group method using arithmetic averages (UPGMA) clustering method to construct the dendrogram. To test whether fire modifies the functional diversity of the Amazonian understorey bird communities, we calculated the following metrics: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). We used these two indexes that were originally proposed to analyse the phylogenetic structure of communities (Webb, 2000) because functional dendrograms have the same structure of a phylogenetic tree and, therefore, any measure of phylogenetic community structure can be used with a functional dendrogram (Pavoine & Bonsall, 2010). In that sense, here MPD is a measure of the functional distance among species within a community. It is considered a basal measure (i.e. which is more sensitive to distant taxa) because it calculates the pairwise distance between each species in the community (Webb, 2000). MNTD is a measure that quantifies the distance between each species and its nearest neighbour on the dendrogram which co-occurs in the same community. Therefore, it is considered a terminal relatedness measure, and it is more sensitive to variations towards the tips of the dendrogram (Webb, 2000).

First, to test whether bird functional diversity values were different in burned and unburned forests, we compared MPD and MNTD values among unburned, once burned and twice burned forests using one-way analysis of variance (Zar, 2009). To examine whether coexisting species in communities were more or less similar than expected by chance, we used null models to compare observed MPD and MNTD

values in each forest wildfire treatment (unburned, once burned and twice burned) with a mean value obtained from 1000 randomly generated communities using an independent swap algorithm, maintaining the observed species richness and occurrence frequency in the null communities (Gotelli & Entsminger, 2001). We defined our species pool as all species found in the 28 forest sites. For both metrics we calculated a standardized effect size as

$$\text{standardized effect} = -(\text{obsMetric} - \text{rndMetric})/\text{sd.rndMetric}$$

where obsMetric is the observed value of MPD or MNTD, rndMetric is the metric corresponding mean value of randomized communities, and sd.rnd is the respective standard deviation of the 1000 randomized values.

MPD and MNTD standardized effect size values are also known, respectively, as nearest relative index (NRI) and nearest taxon index (NTI), and indicate functional clustering when greater than zero or functional overdispersion when values are lower than zero (see Gómez *et al.*, 2010). We used a one-sample *t*-test to test whether NRI and NTI were significantly different from what one would expect by chance (mean = 0). These analysis were carried out in R (R Development Core Team, 2011), using the 'ses.mpd' and 'ses.mntd' functions from the picante package (Kembel *et al.*, 2010).

Finally, for each forest site, we gathered data on vegetation structure (see Barlow & Peres, 2004a, for details on how this data was collected) to evaluate whether this can predict the standardized effect size of bird functional diversity. We used two model selections with Akaike's information criterion (AIC) approach (Johnson & Omland, 2004). Our response variables were respectively MPD, MNTD, NRI and NTI, while predictor variables used the following environmental characteristics: number of dead trees, number of live trees, understorey vegetation density (measured based on visual assessment of a 2.5 m striped pole, see Barlow & Peres, 2004a), number of woody stems < 10 cm DBH, log-transformed number of non-woody stems < 10 cm DBH, basal area of live trees ≥ 10 cm DBH ($\text{m}^2 \text{ha}^{-1}$), basal area of dead trees ≥ 10 cm DBH ($\text{m}^2 \text{ha}^{-1}$), arcsin square root of canopy cover (%) and arcsin square root of ground cover (%). We used the log and arcsin square root transformations because they stabilize the variance for the binomial distribution (Zar, 2009). For model selection, we retained the environmental models which best explained the variation of bird functional structure among the studied forests (those with $\Delta\text{AICc} < 2$). We then used a model averaging approach, using the relative importance of each environmental characteristic to predict changes in bird functional structure across all possible models. We did this because models with lower ΔAICc might have similar explanatory potential but different predictor variables. By using the model averaging, we could better understand which were the best predictor variables across our models, and also the relative importance of each one across all possible models. Model selection analyses were carried out in the Spatial Analysis in Macroecology (SAM; Rangel, Diniz-Filho & Bini, 2006) software, available for free at <http://www.ecoevol.ufg.br/sam>.

Results

We listed 152 species from the 28 studied sites: 92 from unburned forests, 118 from once burned and 71 from twice burned forests. On average, there were 42.9 ± 4.01 species

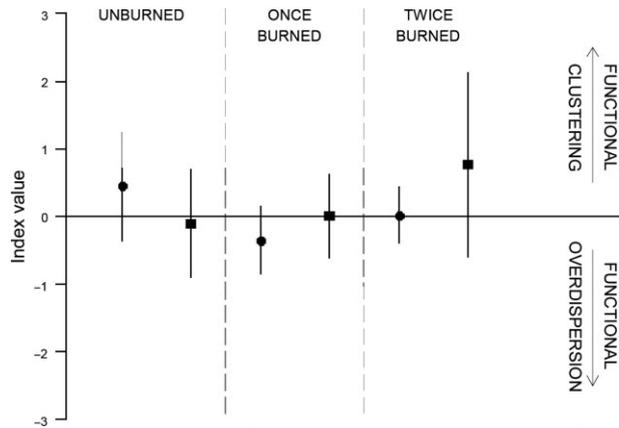


Figure 1 Standardized effect sizes of functional diversity (nearest relative index confidence intervals and mean values are represented by circles and nearest taxon index by squares) in Amazon understorey bird assemblages and their 95% confidence intervals for each wildfire frequency in the studied forests. All values were equal to what one would expect by chance (see Supporting Information Table S1 for details on the significance of the results).

per site in unburned forests, 46.5 ± 7.22 species in once burned sites and 28.7 ± 7.78 in twice burned sites; with a total mean of 41.4 ± 9.29 species per site.

We did not observe differences among MPD ($F = 2.54$; $P = 0.098$) and MNTD ($F = 0.285$; $P = 0.754$) in forests with different wildfires frequencies. Therefore, wildfires did not reduce the functional diversity of the studied bird communities. Functional diversity of bird assemblages in unburned and burned forests was equal to what one would expect by chance (both NRI and NTI average values were not different from zero; Fig. 1). Thus, we did not find evidence of functional clustering or functional overdispersion, which would provide evidence of environmental filtering and limiting similarity in the studied bird assemblages, respectively. This indicates that species were randomly assembled in respect of their traits in all forests independently of fire frequency.

For the 511 possible models using habitat structure to predict MPD and NRI, five and six, respectively, presented $\Delta AICc$ values lower than 2.0. From these models, five environmental structures best explained changes in functional structure: basal area of live trees, canopy cover, dead standing basal area, non-woody stems and understorey vegetation density. The best model consisted of only dead standing basal area for MPD and non-woody stems for NRI. Based on the average model approach, three variables best predicted the functional structure of understorey bird assemblages in the studied forests: dead standing basal area, non-woody stems and canopy cover (Tables 1 and 2). Both

Table 1 Mean model results of parameter estimates for mean pairwise distance as response variable, using Akaike weights

Variable	Importance	Coefficient	<i>t</i>	95% Lower	95% Upper
Non-woody stems	0.596	0.010	2.772	0.003	0.017
Dead standing basal area	0.488	0.011	3.388	0.005	0.017
Canopy cover	0.467	-0.100	-3.261	-0.160	-0.040
Woody stems	0.374	0.013	3.352	0.005	0.020
Understorey vegetation density	0.286	-0.031	-2.096	-0.061	-0.002
Dead trees	0.273	0.006	2.754	0.002	0.010
Basal area of live trees	0.229	-0.005	-1.282	-0.013	0.003
Ground cover	0.203	<0.001	-0.254	-0.006	0.004
Live trees	0.199	-0.004	-1.250	-0.009	0.002

Most important environmental variables have their values in bold (average model $R^2 = 0.30$).

Table 2 Mean model results of parameter estimates for nearest relative index as response variable, using Akaike weights

Variable	Importance	Coefficient	<i>t</i>	95% Lower	95% Upper
Non-woody stems	0.637	-1.126	-2.670	-1.953	-0.299
Dead standing basal area	0.541	-1.331	-3.270	-2.129	-0.533
Canopy cover	0.395	2.970	3.349	1.804	5.136
Dead trees	0.315	-0.899	-3.136	-1.461	-0.337
Understorey vegetation density	0.313	4.401	1.818	0.839	7.964
Woody stems	0.271	-0.986	-2.873	-1.659	-0.313
Basal area of live trees	0.239	0.609	1.223	-0.367	1.584
Ground cover	0.214	0.502	1.634	-0.100	1.104
Live trees	0.203	0.439	1.330	-0.208	1.085

Most important environmental variables have their values in bold (average model $R^2 = 0.33$).

Table 3 Mean model results of parameter estimates for mean nearest taxon distance as response variable, using Akaike weights

Variable	Importance	Coefficient	<i>t</i>	95% Lower	95% Upper
Non-woody stems	0.512	0.025	2.934	0.008	0.042
Canopy cover	0.388	-0.283	-3.124	-0.460	-0.040
Dead trees	0.301	-0.024	-3.144	-0.040	0.009
Understorey vegetation density	0.264	0.058	1.564	-0.015	0.130
Basal area of live trees	0.255	0.034	2.523	0.008	0.060
Woody stems	0.228	-0.014	-1.966	-0.029	<0.001
Dead standing basal area	0.222	0.001	0.176	-0.011	0.013
Ground cover	0.215	-0.019	-1.943	-0.038	<0.001
Live trees	0.214	0.010	0.973	-0.011	0.032

Most important environmental variables have their values in bold (average model $R^2 = 0.11$).

Table 4 Mean model results of parameter estimates for nearest taxon index as response variable, using Akaike weights

Variable	Importance	Coefficient	<i>t</i>	95% Lower	95% Upper
Canopy cover	0.568	5.954	3.002	5.537	6.370
Non-woody stems	0.440	-0.948	-3.171	-1.533	-0.362
Basal area of live trees	0.377	2.434	3.315	0.992	3.870
Understorey vegetation density	0.265	-3.350	-2.404	-6.081	-0.619
Live trees	0.247	-1.011	-1.937	-2.033	0.012
Ground cover	0.219	0.657	1.675	-0.112	1.427
Dead standing basal area	0.209	-0.271	-1.220	-0.707	0.164
Woody stems	0.206	-0.574	-2.090	-1.111	-0.036
Dead trees	0.196	0.248	1.045	-0.163	0.659

Most important environmental variables have their values in bold (average model $R^2 = 0.16$).

dead standing basal area and non-woody stems were positively correlated with MPD and negatively correlated with NRI. Therefore, as their values increased, bird functional diversity also increased and assemblages tended to be functionally overdispersed (i.e. coexisting species tend to be less similar in their ecological traits). On the other hand, canopy cover was negatively correlated with MPD and positively correlated with NRI, that is, there was a tendency to observe lower functional diversity and functional clustering in forests with high canopy cover.

For the 511 possible models for predicting MNTD and NTI, six and five, respectively, presented $\Delta AICc$ values lower than 2.0. Their environmental variables were: canopy cover, non-woody stems, basal area of live trees, understorey vegetation density, number of dead trees, number of live trees and woody stems (the last three only for MNTD). Moreover, the best model both for MNTD and NTI was a combination of non-woody stems and canopy cover. Based on the average model approach, two and three variables best predicted the MNTD and NTI values, respectively. Canopy cover was negatively correlated with MNTD and positively correlated with NTI (Tables 3 and 4). On the other hand, non-woody stems was positively related to MNTD (Table 3) but negatively to NTI (Table 4) and basal area of live trees was positively related to NTI (Table 4). Such results were quite similar to what we found in the MPD and NRI analysis: they indicate that more disturbed

forests tend to present high functional diversity and functionally overdispersed bird assemblages.

Discussion

We found that wildfires did not reduce the bird functional diversity in once or twice burned forests. This could have happened because the persistence of these assemblages is more influenced by traits related to dispersal and colonization. Our results indicate that decreasing bird species richness in twice burned forests does not reduce the functional diversity. These results contrast with a study on tropical anuran communities, which did not present differences on richness but a significant reduction of functional diversity in disturbed forests (Ernst *et al.*, 2006). Therefore, understorey bird assemblages in the Amazon seem to be more resistant, in functional terms, to perturbations even if such perturbations decreased species richness in twice burned forests (Barlow & Peres, 2004a). Moreover, we observed that all bird assemblages in the studied forests, independently of their wildfire history, had functional diversity equal to what one would expect by chance. Thus, single and recurrent wildfires were not a strong enough filter to promote the coexistence of understorey bird species that are more similar in their ecological traits. Also, there was no evidence that bird assemblages from unburned forests were assembled through competition because of limiting similarity based on

the traits that we included, as we would expect in such cases. This supports one of the main premises of neutral theory, which postulates that species traits are not important to explain species coexistence patterns. In this case, dispersion, reproduction and death are thought to be more important to species assembly and diversity and should explain the high species diversity in tropical areas (Hubbel, 2001, 2006).

Using a phenotypic evolution model, De Mazancourt, Johnson & Barraclough (2008) argued that very speciose regional faunas could restrict the range of new adaptations to changing environments because of the prevalence of niche conservatism. Given that observed bird functional diversity in the studied forests was not different from what one would expect by chance, the high bird species diversity in the Amazon forest might have stabilized the selection of novel life history traits, resulting in low trait diversity among birds in the regional pool. Such high functional similarity in tropical assemblages was recently reported for mammal species pools that are more redundant in their ecological traits in the tropics than in temperate regions (Safi *et al.*, 2011). However, we cannot exclude the possibility that trait convergence among distant related lineages is also producing this pattern on the functional structure of our assemblages. Finally, Barlow & Peres (2004a) showed that bird assemblage composition in the studied forests became increasingly dissimilar in burned forests. This is an interesting finding because it shows that assemblages with dissimilar compositions may have similar functional structure. This gives consistency to the idea of high redundancy among the studied understorey tropical birds, and shows that high levels of species turnover do not necessarily lead to high levels of functional turnover.

Overall, the same environmental variables predicted the amount of functional diversity on the assemblages as well as the functional structure (i.e. clustered or overdispersed). Although we observed that the number of times a forest burns does not directly impact functional diversity of birds, burn intensity may be important as it acts on the vegetation structure. For example, canopy cover, basal area of live trees, dead standing basal area and non-woody stems were the best environmental variables to predict changes in the functional structure of the examined bird assemblages, and all of these are strongly influenced by burn intensity (Barlow & Peres, 2004b), as well as other disturbances that tropical forests are usually submitted to, for example, selective logging or fragmentation). Forest management strategies clearly need to focus on reducing human impact on forest structure as much as possible, as well as considering landscape scale issues relating to connectivity and species area relationships.

In particular, more open canopies, high number of non-woody stems in the understorey vegetation and high values of dead standing basal area were related to higher functional diversity values and to the functional overdispersion of the studied bird assemblages, selecting species with different ecological traits (limiting similarity). Wildfires are related to higher values of these variables, as woody plants are likely to be more affected by fire (Moreira, 2000; Otterstrom &

Schwartz, 2006), increasing dead standing basal area and creating new habitats for feeding, nesting or roosting (Zarnowitz & Manuwal, 1985; Lohr, Gauthreaux & Kilgo, 2002; Mestre *et al.*, 2009). Such modifications on vegetation structure because of wildfires are also likely to increase the probability that bird species more adapted to open areas or disturbed habitats (consequently presenting more complementary traits) colonize these forests. In fact, lightly disturbed forests can harbour bird species that are typical of both extremes of the disturbance gradient (Barlow & Peres, 2004a). Thus, it is reasonable to expect an increase in the functional diversity and the functional overdispersion of bird assemblages in such forests, at least in the short term. However, data not constrained to the understorey and from mist nets would improve our ability to understand the mechanisms behind the relationship between bird assembly rules and environmental variables. Moreover, the tendency of functional clustering in forests with a more closed canopy cover and few non-woody stems in the understorey vegetation (indicating less disturbed forests) could be explained by the fact that the trait variables we used were not detailed enough to detect bird specializations (e.g. more specific dietary traits or foraging strata). For example, two species would have quite similar values of the traits we analysed (e.g. frugivory) but be specialized in different food items (e.g. different types of fruits) or feed on specific species. This single non-overlap in their niches would be enough to promote their coexistence, avoiding limiting similarity to operate. In fact, a high degree of specialization is usually expected and found in tropical forests (Rosenberg, 1990) but datasets with that level of detail for tropical bird species are still to be gathered. Even though birds are one of the best known tropical taxa, we are still constrained by the lack of refined information for many tropical bird species (Ricklefs, 2000).

In summary, we provide important new information about the effects of wildfires on tropical understorey birds. Contrary to our expectations, wildfires did not simplify the functional structure of understorey bird assemblages in Amazonian forests, as they did not select species that were more similar in their traits than expected by chance. In fact, we showed that different aspects of vegetation structure can predict bird assembly rules (i.e. whether it is likely to find functional clustering or overdispersion) in the studied forests, indicating that fire affects the assembly of understorey birds through its impact on vegetation structure.

Trait-based mechanisms are important in ecology (Ernst *et al.*, 2006), and conserving the largest possible number of functional traits increases the likelihood of maintaining ecosystem processes and functioning (Ernst *et al.*, 2006; Laliberté *et al.*, 2010). Also, there is evidence that communities with higher functional diversity are more resistant to invasion by exotic species (Symstad, 2000); and that functional traits of particular species could influence the success of invasion (Xu *et al.*, 2004). Our findings demonstrate that results from studies using traditional ecological metrics such as species richness, abundance and composition, can differ markedly from those that include bird species traits or their

functional ecology (Loyola *et al.*, 2008; Carvalho *et al.*, 2010; Vandewalle *et al.*, 2010). The two approaches capture different aspects of biodiversity, and provide complementary mechanisms for understanding the human impacts on the world's ecosystems.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Summary of the one sample *t*-tests which we used to test the significance deviations of our indices (NRI and NTI) from a null expectation (mean = 0). CI.min is the lower confidence interval (2.5%), and CI.max is the higher confidence interval (97.5%).

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