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Fire threatens the diversity and structure of tropical gallery forests

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Abstract. Gallery forests are widespread in most tropical savanna landscapes creating a mosaic of grass-dominated systems with tree components and forest patches. Interactions among water, nutrient availability, and wildfires have influenced the structure, patterns, and processes of these landscape systems and have shaped today's biodiversity in the savanna–forest transitions of the Orinoco basin in Colombia and Venezuela. However, savanna fires have become larger and more frequent in these areas. In order to investigate the impacts of fire on gallery forests, we established 18 forest plots of 0.1 ha within three different fire exposures: (1) fire affected forests along the edge (<100 m) from open savanna to gallery forest (burned edge), (2) fire affected closed forests (burned interior; >100 m from the edge), and (3) no evidence of fire (unburned). We identified responses of the vegetation to fire (through natural regeneration) by analyzing the compositional and structural changes and quantifying fire-related functional traits for the most abundant tree species. We surveyed 128 species, corresponding to 77 genera and 35 families. Tree height is over 10.70 m (± 2.72) in unburnt forests. Dead tree presence in burnt edges (21.76% ± 24.3) almost doubles that of burnt interior (13.08% ± 15.73). The aboveground biomass (AGB) of unburnt forests (176.9 Mg/ha) was more than double that of the interior burnt forests (74.4 Mg/ha) and four times higher that AGB in the edge burnt sites (41.3 Mg/ha). Of the most abundant species, 62% were classified as fire-sensitive species, 14% were fire survivors and 24% were resistant to fires and mostly present in communities with lower diversity. Although fire-tolerant species in general presented thicker barks, higher wood densities, and higher leaf dry matter content, no clear pattern of fire response was associated only with functional traits. Thus, overall fire is resulting in strong compositional changes, with more fire-resistant species, which are species that establish in disturbed areas and encouraging grasses, resulting in savanna encroachment into gallery forests. Consequences on the long-term should be monitored.

Key words: burn; degradation; disturbance; diversity; forest–savanna transition; functional traits.

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INTRODUCTION

Disturbance is recognized in ecological theory as a spatial process that influences species patterns and abundance (Wimberly and Spies 2002). Globally, there is evidence that most plant communities show idiosyncratic responses to disturbances, with different and specific rates of recovery and timespans before reaching a pre-disturbance state (Cole et al. 2014). Fire is an important disturbance affecting ecosystems globally (Bowman et al. 2013), causing profound changes in ecosystem services and altering the habitat of many species. This is particularly evident in the tropics where many ecosystems are not adapted to this disturbance, and fires can lead to ecosystem degradation and biodiversity loss (Cochrane 2009). Tropical vegetation transitions are widespread in the tropics, spanning over a plethora of grass/savanna/forests vegetation types (Oliveras and Malhi 2016) often separated by sharp boundaries, like the transitions between savannas and tropical gallery forests (Dantas et al. 2016) in which one vegetation type is fire-dependent (grasslands and savannas) and the forests are extremely fire-sensitive. In tropical forests, fire can homogenize the vegetation or facilitate the arrival of open environment species into otherwise closed-canopy forests. These processes might favor herbaceous and grasses to occupy the understory and as such affect the habitat of many species, including different groups of fauna (Henriques et al. 2006, Vasconcelos et al. 2009, Oliveira and Aguiar 2015). Further, the fire driven compositional and structural changes might not only reduce the availability of habitat but also other ecosystem services such as carbon storage or water availability that usually decreases in forests after fire (Hohnen et al. 2015, Bassett et al. 2017).

Tropical savannas are present across the world in Africa, Australia, Asia, and South America and are the result of similar climatic conditions of temperature and rainfall distribution with a vegetation gradient ranging from grassy and shrub savannas in the drier regions to woodland savannas and mosaics of forest savannas in the more wet areas (Oliveras and Malhi 2016). The latter is a vegetation pattern of particular interest since forested areas are gallery forests extending along rivers that border grasslands with either an abrupt or gradual boundary (Oliveras and Malhi 2016). This creates a transitional zone or ecotone between two types of vegetation, forests and savannas, both of them are of key importance for global terrestrial productivity (Oliveras and Malhi 2016). The boundaries between biomes in the tropics go beyond climatic and woody productivity conditions, so that there are complex interactions between disturbance regimes and resource availability (Dantas et al. 2016). Tropical gallery forests represent a critical vegetation state and are vulnerable to changing climate and land use that may contract or shift their distribution. These forest–savanna transitions have been defined by changes in vegetation height, tree crown cover, and grass cover and in many cases have existed for centuries driven by water availability, fire regime, soil properties, and herbivory, among others, that operate at multiple scales (Hoffmann et al. 2012*a*, Oliveras and Malhi 2016). Fire in particular is a well-known natural disturbance in savannas all over the world. It has shaped and maintained the structure and function of fire-prone communities (Bond and Keeley 2005) and is closely associated with tropical forest–savanna vegetation transitions (Oliveras and Malhi 2016). Tree mortality in forests that are adjacent to savannas in Brazil has been found to be relatively low (Hoffmann et al. 2009) particularly if compared with that of humid tropical forests not used to frequent fires (Hoffmann and Moreira 2002). Nevertheless, tree mortality is higher in the forest than in savannas, even with fires of low intensity, fact that is partly explained by their thinner barks (Hoffmann et al. 2009).

In tropical regions where fire has been present for a long time, fires have been showed to spread well in the grasslands and sometimes impact the edge of forests (Cochrane and Laurance 2002, Hébert-Dufresne et al. 2018) but rarely spread within the forests (Hoffmann et al. 2012*b*). This characteristic fire propagation behavior whereby forests in savanna landscapes are only affected by fires in the edges has evolved under the past fire regimes. However, fire regimes are highly sensitive to both climate change and land use (Cochrane and Laurance 2008, Barlow and Peres 2008, Bowman et al. 2009) and are rapidly changing. Thus, in the tropics fires are expected to become even more frequent, severe, and extensive than at present (Krawchuk et al. 2009, Bowman et al. 2013). Under a scenario of changing tropical fire regimes, the characteristic fire propagation behavior in these tropical forest–savanna ecosystems might be altered and cause a shift from particular community stable states to alternative states (Knox and Clarke 2012, Hébert-Dufresne et al. 2018). This is particularly true in the case of these landscape mosaics where the dynamic nature of boundaries is heavily influenced by disturbance regimes that drive savanna and forest as alternative states (Dantas et al. 2016). This would be partly explained by the alternative stable theory where state shifts are triggered by a catastrophic disturbance such as, for instance, a large and intensive fire (Knox and Clarke 2012). A priori, tropical forests, which are naturally less prone to burn and are usually fire-sensitive ecosystems (Oliveras and Malhi 2016), are expected to contain fewer resilient species (Barlow and Peres 2008). Therefore, changes in fire regimes that will affect forests more intensely are expected to produce important shifts in community structure and composition, especially where there are fire-sensitive species that lack fire resistance mechanism or an efficient post-fire regenerative mechanism (Nepstad et al. 1999).

Species response to fires has been associated with functional traits by different mechanisms such as thicker barks or lower wood density that provide structural protection against fire. The bark provides thermal insulation protecting the meristematic tissues (cambium, shoots), the phloem, and the xylem (Romero 2014). Thicker and denser barks are expected to have a higher component of thick-walled cells that provide greater protection, which is why the protection is proportional to their thickness (Rosell et al. 2014). However, even small differences in bark thickness can provide protection and survival benefits to species in ecosystems with low intensity fire regimes (Pausas 2015). In tropical forests, the mortality of trees induced by fire is also modulated by size, with less tree mortality found associated with higher DBH and wood density (Brando et al. 2012). Yet, tolerance of tropical species to fire is far from being understood, for example, in the Brazilian Cerrado, to survive fire some species seem to invest in a higher growth rate and bark density, while others in greater bark thickness and wood density and some species have the strategy of developing a greater outer than inner bark (Corrêa Scalon et al. 2020).

In northern South America, the Orinoco basin holds an extensive savanna system immersed in a complex landscape with gallery forests occupying narrow strips in riparian areas. These seasonally flooded ecosystems are very unique, often have very sharp transitions, and are habitat for many endemic savanna and also freshwater species (Veneklaas et al. 2005), as well as provide valuable ecosystems services and natural resources for humans and domestic animals. Their occurrence is associated with high soil nutrient availability in soils and to a strong annual precipitation seasonality, with several-month long droughts followed by flooding in the wet season. Fire also plays a key role in the maintenance of this type of vegetation systems, particularly in Colombia and Venezuela (Biddulph and Kellman 1998, Medina and Silva 1990, Sarmiento 1992 in Veneklaas et al. 2005). In these areas, most fires tend to occur during the dry season and have a clear interannual variability associated with climatic factors but also to traditional management practices for cattle grazing (Romero-Ruiz et al. 2010, Armenteras et al. 2013).

Despite the importance of these ecosystems and their potential threat in front of climate change, studies on the impacts of global change and disturbances such as fires over these ecosystems are largely missing. The effect of fire on riparian forest systems surrounded by fire-prone vegetation (i.e., savanna or grassland) has been studied in Australia but a major lack of information exists elsewhere (Douglas et al. 2015), and especially in the Orinoco basin. Given the projected increases in climate change and human-related disturbances such as fire, it is a challenge of critical importance to understand the potential shifts and changes of communities that occur in these riparian systems after fire. The objective of our study is to contribute to filling this knowledge gap by investigating how fire shapes the structure, composition, and the regeneration capacity of riparian forests embedded within a savanna landscape. We studied how a single wildfire affected gallery forest structure, composition, and initial regeneration at the edge of the forests (<100 m from the boundary with savanna) and at the core of the forests (more than 100 m from the edge). We hypothesized that:

1. The burned edge (<100 m) of the gallery forest has a lower diversity of surviving adult stems, but higher species richness in the initial regenerating community (of trees, shrubs, and grasses), than the burned interior forest (>100 m) and unburned forest.

2. Fire increases dead trees and reduces total aboveground biomass (compared with the unburned forest).
3. Fire-tolerant species have functional traits that provide them with structural protection to fire (e.g., thicker bark or lower wood density).

Material and Methods

Study area

The study area is located in the Orinoco region, which harbor the main tropical savannas in northern South America (Berrio et al. 2000). The study site is within a private civil society nature reserve of 5460 ha named Bojonawi (Fundación Omacha 2012) in the Department of Vichada, Colombia (between 6°07′ and 6°02′ north latitude and 67°29′ and 67°34′ west latitude; Fig. 1). The climate is seasonal with a dry season that extends from 2 to 5 months (between November and March–April; Armenteras-Pascual et al. 2011). Mean annual temperature of the area is 27°–30°C in the dry months and 23°–26°C in the rainy months and precipitation ranges between 1000 and 3500 mm/yr. The soils present are associations of inceptisols and entisols, which are characterized by a textural class of fine or coarse free sand, and less than 35% of rock fragments. These soils are in saturated water conditions for several months in normal years. The landscapes of this region form a forest and savanna system that holds different vegetation formations such as several savanna formations (i.e., permanently, and seasonally flooded

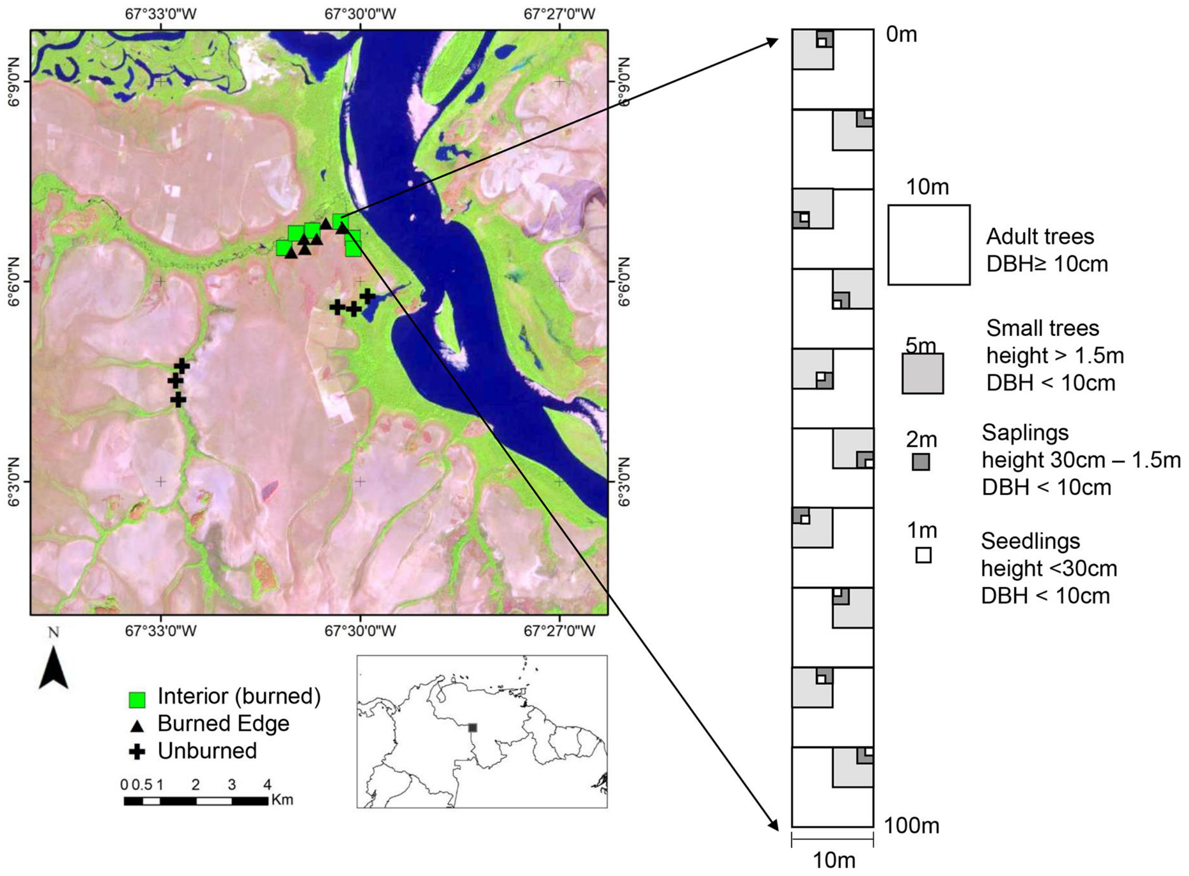

Fig. 1. Location of the study area and plot nested sampling design. Sites were stratified by the time of the last fire (unburnt and burnt) and the location in relation to the edge of the forest (edge or interior if >100 m from edge).

savannas, high plain savannas), riparian or gallery forests, palm forests, and swamp vegetation. The predominant savanna vegetation is composed of C4 grasses, especially from the Poaceae and Cyperaceae families, in association with some dispersed woody plants. Most of the gallery forests are very narrow wooded strips along creeks and rivers and are relatively species-rich ecosystems (Veneklaas et al. 2005). In December 2015, in the Bojonawi reserve a severe fire occurred that spread into the closed-canopy gallery forests in the northern part of the reserve.

Study design

Eighteen 0.1 ha vegetation plots (100 × 10 m) were established in early 2017 in three different post-uncontrolled fire conditions (last land use fire reported that escaped into adjacent gallery forest was in 2015) that we call sites (Fig. 1): six plots located in unburned (no evidence of recent 2015 fire in areas of 100–120 m forest width along the creek) forests, 6 plots in burned edges (forest edge with evidence of the 2015 fire), and 6 in burned interiors (forest interior more than 100 m from the edge and evidence of the 2015 fire). We considered as evidence of fire the burning scars visually identified in the tree trunks. Given the fact that we were using uncontrolled fire conditions and this is not ideal as a sampling design but unavoidable in Colombia where controlled fire or fire experiments are not allowed, we controlled the possible aggregation in the data by separating the plots by a minimum of 400 m.

Data collection

Tree sampling.—In each plot, we identified all live and dead (i.e., stem killed and no resprout) mature trees with a diameter at breast height (DBH) ≥ 10 cm. Most individuals (76%) were identified to the level of species. When this was not possible, we identified the individuals to the level of genus (6.2%) or family (3.9 %), while 14% were only catalogued at the morphospecies level. Standing dead trees were counted to determine the percentage of dead trees. We annotated any visible fire scars in the alive trees to determine the percentage of burned trees. For each alive tree, we measured its total tree height with a hypsometer (TruPulse 200 L Laser Rangefinder Hypsometer) and its DBH with a diametric tape. We calculated also basal area of all trees in the plot.

Natural regeneration sampling.—We include in this category:

1. Small trees (DBH < 10 cm, tree height >1.5 m) were sampled in 10 nested subplots of 5 × 5 m (Fig. 1).
2. Saplings (DBH < 10 cm, total height between 0.3 and 1.5 m) were sampled in 10 nested subplots of 2 × 2 m (Fig. 1).
3. Seedlings (DBH < 10 cm, total height < 0.3 m) were sampled in 10 nested 1 × 1 m subplots (Fig. 1).

In all cases, we measured diameter and total height and determined, when possible, the species of each individual. It was possible to determine 61.7% of individuals in these size classes at the species level, 23.1% at the genus level, 8.4% at the family level, and 6.9% at the morphospecies level.

Biomass.—The estimation of biomass of each living tree was based on the allometric equation $(\mathrm{AGLB} = 0.0673 \times (\rho D^2 H)^{0.976})$ of where AGLB is aboveground live biomass, ρ (g/cm^3)is the wood density of each species, D (cm) is the diameter at breast height, and H (m) is the total tree height. Biomass was estimated only for trees, individuals with other growth habits such as lianas and palms were excluded.

Fire tolerance and functional traits.—We determined the fire tolerance of species adapting the empirical fire tolerance index (FTI) developed by (Oliveras et al. 2014). We computed FTI as.

$$\mathrm{FTI} = (\text{no. ind burned plots} - \text{no. ind unburnt plots} \times 2)/\text{no. ind unburnt plots} \times 2$$

where no. ind is the number of individuals for a given species in the burnt (both burned edge and burned interior) or unburnt plots. According to their FTI, we classified species as fire-sensitive (FTI ≤ −0.5); fire survivors (FTI > −0.5 and ≤0.5), and fire thrivers (FTI > 0.5). Species with FTI > 0 were considered fire-tolerant. We only considered tree species with more than five individuals.

For the four most abundant species per fire tolerance category, we measured three functional traits: bark thickness, wood density (WD; two fire protection traits), and the leaf dry matter content (LDMC; a trait related to flammability).

1. For bark thickness measurements, we selected five individuals per species to which a section of bark at 1.3 m height was extracted. We undertook five random measurements of the maximum (outside the fissure) and five measurements of the minimum (inside the fissure) using a digital REXBETI micrometer. We corrected it by tree size and calculated the relative bark thickness (inner, outer, total), as the ratio between bark thickness and the stem radius × 100 (Lawes et al. 2013) although the vegetation structure in the area is very homogeneous with no relevant individual variation in size.
2. For wood density measurements, we selected per individual a branch exposed to the sun, with a length of 8 cm and a diameter greater than 1 cm. These branches were collected between 6:00 a.m. and 9:00 a.m. and were kept in plastic containers submerged in water to keep them rehydrated. In the laboratory, the bark of the branches was removed and its volume was determined by means of the method of water displacement, in which the wood core was immersed in a beaker with water on a semi-analytical balance, 0.001 g, and was consider the measured weight of displaced water as the volume of the sample. Subsequently, each wood sample was dried in an oven at 70°C for 72 h to determine its dry weight. Wood density was determined by dividing the volume (cm^3) per the dry mass (g) of each sample.
3. For leaf dry matter content (LDMC) measurements, we collected 10 young leaves per individual sampled without visual evidence of herbivory, pathogens, or presence of epiphytes. The leaves were collected in the morning, maximum three hours after sunrise, or in the afternoon, three hours before sunset. The samples were stored in sealed bags to prevent dehydration. For transportation, they were kept in a refrigerator. We measured leaf mass (g) with a precision balance. The leaves were then oven dry at a temperature of 60°C for 72 h to obtain the oven dry leaf mass (g). LDMC of each leaf was then calculated by dividing the oven dry leaf mass by its fresh mass.

Statistical analysis

Forest composition and diversity.—The measure of absolute abundance was taken as the number of individuals for each species registered within each plot. The relative abundance was calculated as the percentage of individuals of each species.

1. Adult trees.—We estimated the family importance value index (FIV) of each site with the following variables: relative abundance (number of species in the family i divided by the total number of species), relative density (number of individuals with DBH > 10 cm in family i divided by the total number of individuals), and relative dominance (basal area of family i divided by the total basal area).

We also determined significant differences in composition between sites with a non-metric multidimensional scaling analysis (NMDS) using the Bray-Curtis dissimilarity coefficient and ANOSIM analysis (analysis of similarity of the abundance matrix) with P value of 0.05. Only tree species with an abundance of more than 5 individuals were used for the analyses. For the NMDS and ANOSIM analysis, the Vegan 2.3-5 library of the R software (*version* 1.1.463) was used.

2. Natural regeneration.—We used NMDS using the Bray-Curtis dissimilarity coefficient and ANOSIM analysis to determine significant differences in composition between sites. Only species with an abundance in natural regeneration of more than 20 individuals were used for the analyses.

3. Diversity.—To determine the alpha diversity values in each site, we used Shannon diversity indices that were calculated for adult trees (individuals with DBH > 10 cm) and natural regeneration separately. To analyze the differences among sites, we constructed several models depending on the distribution of the variable. For adult trees, we used a generalized linear mixed-effects model (GLMM) with a Poisson distribution, and for natural regeneration, we used a linear mixed-effects model (LMM via restricted maximum likelihood REML). The calculations were performed with the software INFOSTAT 2017.

3. *Forest structure.*—To analyze differences in forest structure among sites, we used multivariate analyses with the following variables: DBH, basal area, biomass, dead trees (%), burned trees, species richness (individuals with a DBH > 10 cm and in natural regeneration), and the Shannon index. We constructed several models depending on the distribution of the response variable using the software INFOSTAT. Candidate models were compared and chosen according to the Akaike information criterion (AIC), taking as the best model the one with the lowest AIC.

For tree height and DBH, we used the values per tree. The models included type of site as fixed effect and plot as random effect. Tree height had a normal distribution, and we carried a general lineal model (GLM). DBH did not have a normal distribution, and we carried out a generalized linear mixed-effects model (GLMM) with a gamma distribution (Log) of the response variable.

For biomass, basal area, and mortality, we use the total values per plot. These models only included type of site as fixed effect. As the data did not comply with normality, we carried out a generalized linear model (GLZ), checked the dispersion of the data and chose a Poisson distribution.

We did a principal component analysis (PCA) to represent the variability of the data of diversity and structure between plots and types of site (unburnt, burned interior, and burned edge). For this analysis, we used the software INFOSTAT 2017. Finally, we selected a linear mixed model (LMER) for determining significant differences in bark thickness, wood density, and dry matter leaf content (LDMC) between fire tolerance categories.

RESULTS

Forest composition and diversity

Adult trees.—In the unburnt sites, we registered 78 species and 59 genera out of the total of 128 species and 77 genera for the whole study area. Fabaceae was the most common of the 31 families present in unburnt forests with a FIV of 36.69% (Appendix S1: Fig. S1), followed by Euphorbiaceae (34.63%), Chrysobalanaceae (24.5%), Calophyllaceae (24.7%), and Sapotaceae (20.5%). Fabaceae was the family with most species and greatest density of individuals (Table 1).

In burned interior sites, we found 61 species in 37 genera. Of all 21 families present in burned interior sites, Fabaceae was the most representative family with a FIV of 53.6%. This family is followed by Lecythidaceae (35.4%), Chrysobalanaceae (FIV 31.6%), and Myrtaceae (24.5%).

In the burned edges, we found 14 species in 7 genera. Of the 6 families present, the two families with the highest FIV (Appendix S1: Fig. S1) were Calophyllaceae (111.2%) and Vochysiaceae (47.6%), due to the high density and dominance of the species *Caraipa llanorum* and *Vochysia venezuelana*. The family Chrysobalanaceae, with a FIV value of 51.2% and four species, was also important in these sites.

In relation of the species composition, significant differences among burned edge, burned interior, and unburnt sites were evidenced in the NMDS (Fig. 2A) and ANOSIM ($R = 0.23$; $p < 0.05$, $p = 0.035$). Each one of the ellipses represents a site, and we can observe the distribution of the species. Those that are in the overlapped portion of the ellipses are shared between sites. The three sites only share three species that are the palm *Astrocaryum jauari* and the trees *C. llanorum* and *Licania heteromorpha* var.*glabra*. The following are the species that were recorded exclusively in each site and that are not shared between areas: In the burned edge site, six species were registered only in this area, of which they stand out *Couepia paraensis subs. glaucescens* and *Licania* cf. *tomentosa*. On the burned interior, 41 species were registered, the most representative were *Piranhea* cf. *trifoliata*, *Myrcia* aff. *calycampa*, *Cynometra bauhiniifolia,* and *Trichilia* aff. *rubra*. In the unburned site, 60 species were registered, the most representative were *Richeria grandis*, *Protium* cf. *llanorum*, *Virola carinata,* and *Amanoa oblongifolia*.

Regarding the diversity index for adult trees (Fig. 3a, F = 321,21, $P < 0.01$), the burned edge forest had significantly lower Shannon index than the burned interior and unburnt forests.

Natural regeneration.—In the unburnt sites, we registered a total of 171 species as natural regeneration (Appendix S1: Table S1). The most abundant species were the palms *L. pulchra*

Table 1. Number of adults per species in each site of each fire tolerance category determined from its Fire Tolerance Index (FTI).

Species†	Family	Burned Edge	Burned Interior	Unburned	Total	FTI
Fire-sensitive						
Xylopia cf. *emarginata* Mart.	Annonaceae			6	6	−1.00
Parahancornia oblonga (Benth. ex Müll.Arg.) Monach.	Apocynaceae			8	8	−1.00
Mauritia flexuosa L.f.	Arecaceae			7	7	−1.00
Protium cf. *llanorum* Cuatrec.	Burseraceae			19	19	−1.00
Licania mollis Benth.	Chrysobalanaceae			11	11	−1.00
Licania hypoleuca Benth.	Chrysobalanaceae			8	8	−1.00
Licania longistyla (Hook.f.) Fritsch	Chrysobalanaceae			6	6	−1.00
Richeria grandis Vahl	Euphorbiaceae			24	24	−1.00
Amanoa oblongifolia Müll.Arg.	Euphorbiaceae			13	13	−1.00
Virola carinata (Spruce ex Benth.) Warb.	Myristicaceae			14	14	−1.00
Eugenia cf. *lambertiana* DC.	Myrtaceae			7	7	−1.00
Elaeoluma glabrescens (Mart. & Eichler ex Miq.) Aubrév.	Sapotaceae			11	11	−1.00
Pouteria elegans (A.DC.) Baehni	Sapotaceae			8	8	−1.00
Handroanthus barbatus (E.Mey.) Mattos	Bignoniaceae		2	8	10	−0.88
Macrolobium angustifolium (Benth.) Cowan	Fabaceae	5		16	21	−0.84
Campsiandra comosa Benth.	Fabaceae		13	20	33	−0.68
Astrocaryum jauari Mart.	Arecaceae	7	6	19	32	−0.66
Fire survivors						
Mabea nitida Spruce ex Benth.	Euphorbiaceae		5	5	10	−0.50
Eschweilera cf. *parvifolia* Mart. ex DC.	Lecythidaceae		17	15	32	−0.43
Duroia micrantha Zarucchi & J.H.Kirkbr.	Rubiaceae		24	19	43	−0.37
Licania heteromorpha var. *glabra* (Mart. ex Hook.f.) Prance	Chrysobalanaceae	2	7	7	16	−0.36
Caraipa llanorum Cuatrec.	Calophyllaceae	37	8	32	77	−0.30
Swartzia leptopetala Benth.	Fabaceae		13	4	17	0.63
Fire-tolerant						
Heisteria cf. *acuminata* (Humb. & Bonpl.) Engl.	Olacaceae		5	1	6	1.50
Gustavia augusta L.	Lecythidaceae		14	1	15	6.00
Couepia cf. paraensis (*Mart. & Zucc.) Benth.*	Chrysobalanaceae	7	6		13	10.00
Piranhea cf.*trifoliata* Baill.	Euphorbiaceae		6		6	10.00
Myrcia aff.*calycampa* Amshoff	Myrtaceae		6		6	10.00
Vochysia venezuelana Stafleu	Vochysiaceae	16	8		24	10

† Reported only species with total abundance >5 individuals.

(9.2%) and *A. jauari* (8.8%), the shrub *M. aplostachya* (5.9%), and the tree *A. jupunba* (5.3%). In the burned interior, 116 species were recorded (Appendix S1: Table S1). The most abundant species were the palm *A. jauari* (5.3%), an undetermined Myrtaceae species (5.0%), the shrubs *S. jamaicense* (4.7%), and *Chelonanthus sp.* (4.4%; Appendix S1: Table S1). In the burned edge, we registered 47 species (Appendix S1: Table S1). The most abundant species were the palm *A. jauari* (29.0%), *O.* cf. *sanariapensis* (15.0%), *H. semilunatus* (13.3%), *C. ramosa* (8.4%), *V. lehmannii* (7.4%), and *M. aplostachya* (6.2%).

Significant differences in the composition of species with DBH < 10 cm between the three types of sites are evidenced in the NMDS (Fig. 2 b) and ANOSIM ($R = 0.45$, $P < 0.05$, $P = 0.001$). In the same way than with adult trees, the species present in the overlapped portion of the ellipses were species shared between sites. In this

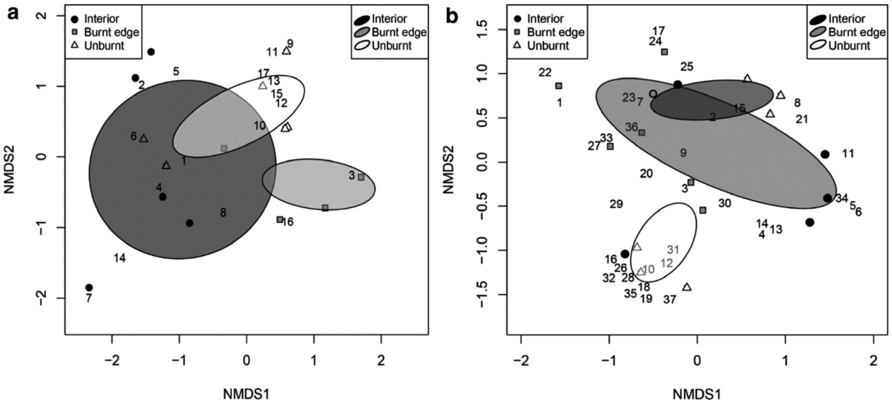

Fig. 2. Multidimensional scaling ordination of floristic plots (NMDS) both for (a) most abundant adult trees (stems of DBH > 10 cm) and for regeneration (b) with 95% confidence ellipses for the three study sites. Species in (a): 1. *A. jauari*. 2. *C. comosa*. 3. *C. llanorum*. 4. *D. micrantha*. 5. *E.* cf. *Parvifolia*. 6. *E. lambertiana*. 7. *G. augusta*. 8. *L. heteromorpha* var *glabra*. 8. *L. heteromorpha*. 9. *L. mollis*. 10. *M. angustifolium*. 11. *P. elegans*. 12. *P.* cf. *lanorum*. 13. *R. grandis*. 14. *S. leptopetala*. 15. *V. carinata*. 16. *V. venezuelana*. 17. *X.* cf. *emarginata*. Species in (b): 1. *A. nitens*. 2. *A. jauari*. 3. *C. cf guildingii*. 4. cf *Eugenia* sp. 1. 5. *Chelonanthus* sp. 6. *C. spinosa*. 7. *C. ramosa*. 8. *D. laurifolia*. 9. *D. micrantha*. 10. *E.* cf *parvifolia*. 11. *E.* cf *pedicellata*. 12. *E. chrysophyllum* 13. *Eugenia* sp. 2. 14. *Eugenia* sp 3. 15. *H. semilunatus*. 16. *I. rosea*. 17. *Lacmellea* sp 2. 18. *L. pulchra*. 19. *M. lexuosa*. 20. *M. aplostachya*. 21. *Ind. 1*. 22. *Myrtaceae* sp. 6. 23. *Ind. 2*. 24. *Ocotea* sp. 1. 25. *O. cf sanariapensis Lasser*. 26. *P. croceoides*. 27. *Pouteria* sp. 1. 28. *P. cf calanense*. 29. *P. capitate*. 30. *Q. cf rhytidopus*. 31. *Q. longifolia*. 32. *S. taxifolia*. 33. *S. subinerme*. 34. *S.jamaicense*. 35. *Virola* sp. 36. *V. lehmannii*. 37. *X. cf amazonica*.

case, the three sites had only in common the following species: the palm *A. jauari*, the tree *H. barbatus*, the shrub *M. aplostachya* shrub, and the undergrowth species *P. capitata*. The diversity index for natural regeneration showed a significantly higher value ($F = 321{,}21$, $P < 0.01$) in the unburnt forests and in the burned interior than the burned edge (Fig. 3b).

Forest structure

In terms of tree mortality, the overall percentage of standing dead trees was significantly different between sites (GLMM, $F = 17.23$, $P < 0.001$), higher in the burned sites than in the unburnt sites (Fig. 4a).

Concerning tree height (Fig. 4b), there were significant differences (GLM, $F = 409.6$, $P < 0.01$) between the unburned forests, much taller than the burned edge and burned interior sites. For DBH, there were also significant differences among sites (GLMM, $F = 16.04$, $P < 0.01$), with higher DBH in the burned edge than in the unburnt site and the burned interior (Fig. 4c). The scatterplot of these two variables can be seen in the Appendix S1: Fig. S2.

There were also significant differences in biomass among the three types of sites (GLMM, $F = 26976.5$, $p < 0.001$), with higher biomass values in the unburned forest than in the burned interior and the burned edge sites (Fig. 4d). Total tree basal area was also significantly different among the three sites (GLMM, $F = 9.5$, $P < 0.01$) with higher basal area in the burned edge than in the burned interior and unburnt sites (Fig. 4e).

The PCA conducted to explore composition and structural patterns of the three different types of sites showed that that first two components explained almost 84% of the variance (Appendix S1: Fig. S3). According to Axis I (72.8%), we separated unburnt forest sites in the right corner of the graphic from the burned interior sites to the center and burned edge sites on the left. The right side of Axis I was characterized by high values of basal area, biomass, and diversity, while the left side was characterized by high values of burned and dead trees. Axis II (10.9%) separated the edge burnt sites and was characterized by high values of DBH on the top left corner of the graphic.

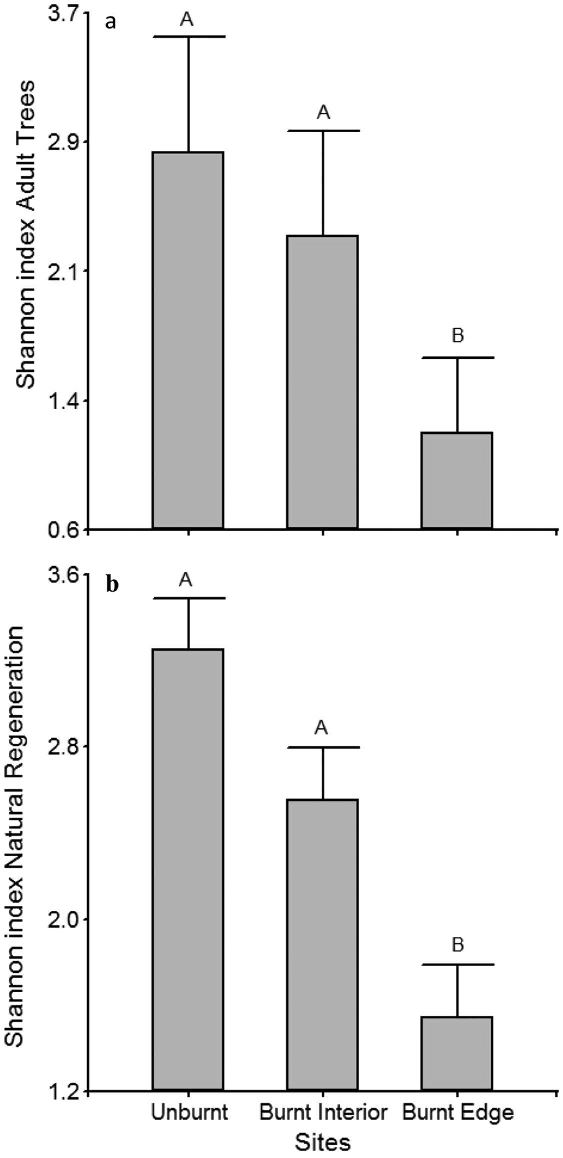

Fig. 3. Mean ± SE values of (a) Shannon index for adult trees, (b) Shannon index for natural regeneration.

Fire tolerance

FTI was computed for the 29 species with more than 5 individuals in the study area (Table 1). Of those, 18 species were fire-sensitive species, 4 were fire survivors and 7 were fire thrivers. Of the 12 most dominant tree species, 4 were fire-sensitive species belonging to the Fabaceae (*C. comosa, M. angustifolium)*, Burseraceae (*P.* cf. *llanorum*), and Euphorbiaceae (*R. grandis)* families. Of the four fire survivor species, two belonged to the Calophyllaceae (*C. llanorum, L. heteromorpha*), one to Lecythidaceae (*E.* cf. *parvifolia),* and one to Rubiaceae *(D. micrantha*) families. Finally, the 4 fire thrivers belonged to the families Fabaceae (*S. leptopetala*), Crysobalanaceae (*C. paraenesis*), Lecythidaceae (*G. augusta*), and Vochysiaceae *(V. venezuelana*).

Bark thickness ranged between 0.1 and 33.9 mm with higher average values found in two fire survivors species (Fig. 5a. *L. heteromorpha* and *C. llanorum*), one fire-sensitive species (*R. grandis*), and three fire thrivers (C. *paraensis, G. augusta* and *V. venezuelana*). Overall the fire survivors have significantly different ($F = 0{,}83$, $P < 0.05$) thicker bark thickness (Mean bark thickness = 8.76 ± 3.91 SE) than fire thrivers (Mean bark thickness = 3.20 ± 3.89 SE) and fire-sensitive species (Mean bark thickness = 2.16 ± 2.16 SE).

Wood density of the studied species ranged between 0.36 and 0.85 g/cm^3 (Fig. 5b). A fire-sensitive (*M. angustifolium*) and a fire survivor (*C. llanorum*) had the highest wood density values. LDMC ranged between 122.17 and 706.1 mg/g (Fig. 5c) with again a fire survivor (*L. heteromorpha*) and a fire-sensitive species (*M. angustifolium*) with the highest average values of 381.94 and 367.04 mg/g, respectively. The mixed linear model determined there were also significant differences in the wood basic density (WD, $F = 218{,}2$, $P < 0.05$) and the dry matter leaf content (LDMC, $F = 217.54$, $P < 0.05$) between the category of fire survivors that have higher densities (mean WD = 0.64 ± 0.07 SE) and more dry matter leaf content (mean LDMC = 292,8 ± 33.75 SE) with respect to the categories of fire thrivers (mean WD = 0.55 ± 0.07 SE, mean LDMC = 286.3 ± 33.73 SE) and fire-sensitive (mean WD = 0.54 ± 0.07, mean LDMC = 282.31 ± 33.69 SE).

DISCUSSION

This study shows that fire can have important ecological effects on gallery forests. The pattern observed in the presented results, with a clear separation of the three forest types in the PCA (Fig. 4), suggests that fire indeed induces substantial shifts in forest composition and structure, as well as results show a significant change

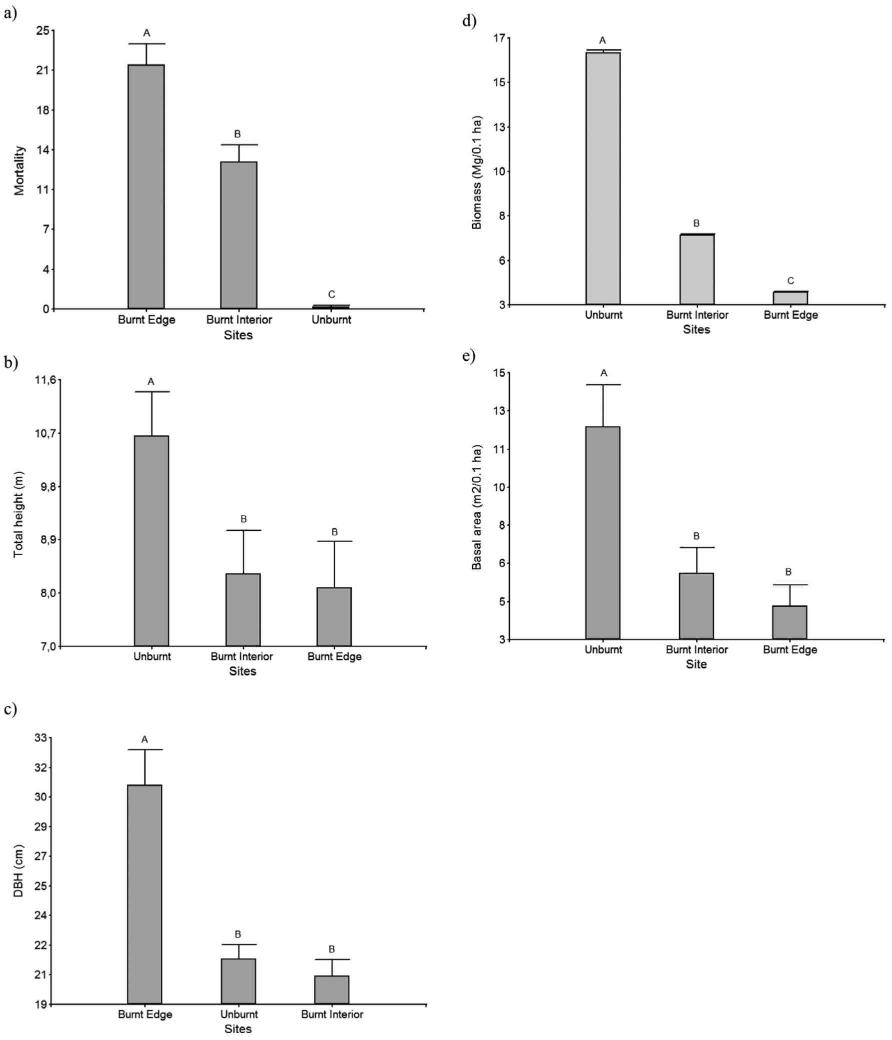

Fig. 4. (a) Percentage of dead individuals, (b) tree height, (c) diameter at breast height (DBH), (d) biomass, and (e) basal area among types of sites (burnt edge, burned interior, unburnt). Different letters indicate significant differences among types of sites according to the DGC test.

in forest structure, in terms of canopy cover, tree height, and aboveground biomass in burnt areas. The unburnt forests were distinctly different from both burned interior and edge sites which had a lower canopy cover. The percentage of standing dead trees was much higher in the burnt areas, reflecting some mortality of adult trees due to fire. The impact of fire in forest structure was also detected in terms of reduced tree height in burnt plots and a significant biomass reduction of up to 58% in the burned interior forests and up to 76.6% in the edge burnt forests in comparison with the biomass in unburnt forests plots. This indeed could be caused by mortality due to fire and the fact that trees surviving fires generally are bigger trees and have larger diameters (Balch et al. 2011). Bark thickness, which reduces heat flux to the cambium (Brando et al. 2012), tends to increase with size and thus might favor the survival rate of large trees. Another potential explanation may be that fire intensity at the edge might have been higher than at the forest interior, which could have led to greater mortality of the small- and medium-sized trees—this has been documented in other tropical forest edges (Balch et al. 2015) and might help

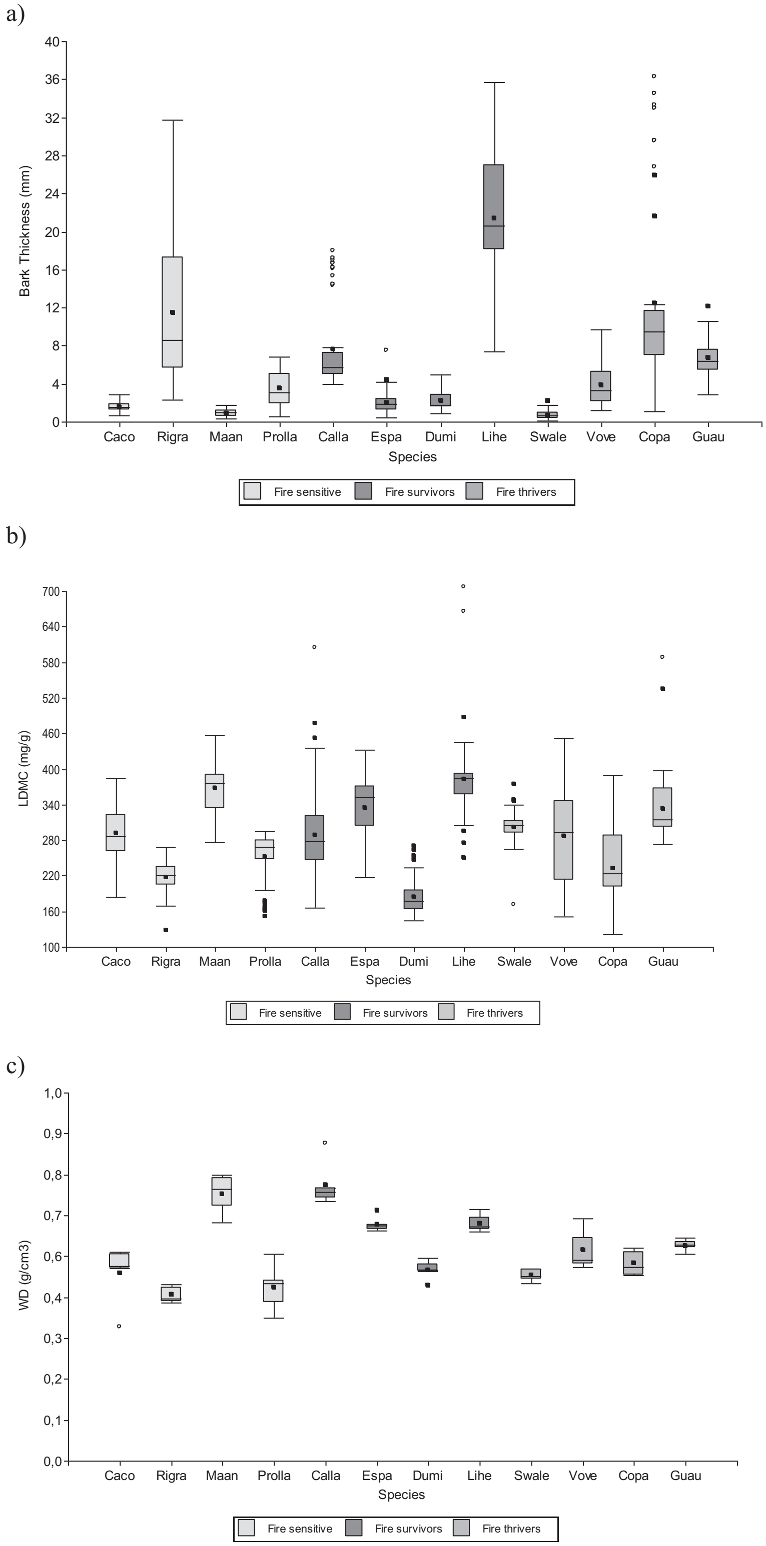

Fig. 5. Boxplot of (a) bark thickness, (b) leaf dry matter content (LDMC), and (c) wood density.

explaining the higher DBH of individual tress in the edge, despite the overall lower density and lower tree height of the edge burnt forests.

In terms of diversity, there was a much lower alpha diversity for adult trees in forests with the evidence of the recent fire than in unburnt forests. This is in agreement with the initial proposed hypothesis where we expected fewer adult species in edge burnt forests and it might be associated with thinner bark species that require longer fire-free intervals to reach a size that gives them greater fire resistance (Hoffmann et al. 2009). This agrees with similar reports in flood forests of Venezuela (Godoy et al. 1999) and also with reports of fire resistance of palms of the *Astrocaryum* genus in the Brazilian Amazonia explained by their spiny texture and trunk, which allows them to form monodominant associations as a result of fire (Walker Nelson and Nascimiento Irmao 1998). Nevertheless, the edge burnt sites were the poorest in terms of species diversity not only for adult trees but also for regeneration and a great number of species of unburnt forest are totally absent in the natural regeneration as the *Leopoldinia pulchra Mart.*, *Abarema jupunba (Willd.) Britton & Killip*, *Eschweilera* cf. *parvifolia Mart. ex DC.*, *Montrichardia arborescens* (L.) Schott, *Protium* cf. *calanense Cuatrec.* and *Eugenia chrysophyllum Poir.* We initially expected a natural higher regeneration richness, but the fact that edge might have a longer history of fire exposure might mean that there could have been a fire induced selection of species able to regenerate. Further, competition with grasses might affect the capacity of forest species to regrow (Barlow and Peres 2008). As such, the absence of many forest species and the dominance of species such as the palm *A. jauari* Mart. in the natural regeneration might indicate that these ecosystems are not necessarily bouncing back to pre-fire state but rather changing to an alternative state with fire-tolerant species and more open canopies structures that support higher grass cover. Despite that the evidence provided in this study is not sufficient to conclude that fire contributes to an alternative stable state, it provides support that it causes a significant change in the structure and composition in these forests. Further research and specifically long-term studies are needed to decipher whether this change is irreversible or not.

Some species were exclusively found in unburned sites such as the palms species *Leopoldinia pulchra* and *Abarema jupunba*, as these palms do not have traits that facilitate fire resistance. *Abarema jupunba* is a species of wide distribution in N South America, but *L. pulchra* is listed in the IUCN red list with the Least Concern category. All sites showed high levels of diversity, but differences observed are due to shifts in the changes of abundance and dominance of certain species of the Fabaceae and Euforbiacea families. Our results suggest that fire occurrence influences changes in forest composition, for example, the communities of the edge burnt sites are distinctly different with more presence of *C. llanorum* and *V. venezuelana.*; this was supported by the diversity differences between the sites, consistent with other studies on post-fire plant regeneration. This kind of effects of fire on vegetation has been observed elsewhere with a shift in species composition and richness post-fire (Balch et al. 2008, Oliveras et al. 2014), even in a short time period after the last fire is noticeable.

Fire-tolerant species (either fire survivors or fire thrivers) presented the thickest barks, highest wood densities, and highest leaf dry matter content. Bark thickness (Barlow et al. 2003) and wood density have been previously reported as key mechanisms for post-fire survival (Brando et al. 2012). Nonetheless, the species with the higher FTI (fire thrivers) were not the species with higher values in these three functional traits (bark thickness WD, LDMC). Species classified as fire survivors such as *C. llanorum*. with both high values of bark thickness and WD or *L. heteromorpha* with thicker barks and high LDMC might be favored by fire. However, the fact that some sensitive species are also presented high values of bark thickness (*R. grandis*), and high WD and LDMC (*M. angustifolium*) suggests the importance of starting to address specific responses to fire and further explore the combination of some traits in offering species the ability to survive fire and post-fire conditions. These fire-sensitive examples are species with a high capacity for sprouting. As such the combination of traits needs to be further explored to better understand species tolerance to fire.

Neotropical studies of how post-fire alterations in the vegetation structure and composition alter the habitat are scarce and most of the research has been conducted in Brazil (Litt and Steidl 2011, Mowat et al. 2015). In this case and in association with the post-fire vegetation dynamics that is occurring, we expect changes in faunal communities in terms of composition, richness, and abundance but there is a need to monitor these aspects to better understand the short- and long-term trends.

We acknowledge the limitations associated with space-for-time approaches such as the presented in this study, and the fact that this is the best way to approach fire impacts given the impossibility of having before–after approaches even through conditions previous to fire have a role into driving forest complexity (van Mantgem and Schwilk 2009). Nonetheless, our results provide robust evidence and we are confident of the patterns reported.

Our results also highlight the importance of effective fire suppression practices during the temporal window when traditional burning is undertaken to reduce the risk of savanna fires spreading further into forests. Fire might result in forests more like young secondary forests regeneration on degrading lands (Barlow and Peres 2008). The changes in forest structure and species composition might have many more ecological consequences of the ones describe here. Long-term studies are needed to decipher the consequences for habitat, ecosystems functioning, and the feedback with increased edge effects that could lead to even more fire-prone risk for these highly diverse and important gallery forests. There is a clear need for detailed studies to quantify the extent of these gallery forests and certainly to monitor whether they are contracting or shifting to another state. Studies for better managing fire practices under extreme drought conditions are also essential to preserve these narrow strips of forests under climate change fire regime shifts.

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