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Understanding ecological transitions under recurrent wildfire: a case study in the seasonally dry tropical forests of the Chiquitania, Bolivia

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1. Introduction

Wildfires in the southern rim of Amazonia are likely to become more frequent as a result of synergistic disturbances from rapid frontier expansion and extended dry seasons (Cochrane and Barber 2009; Lee *et al.* 2011). Recent droughts, some linked to the El Niño–Southern Oscillation and some to elevated North Atlantic sea-surface temperatures, have affected tropical ecosystem processes (Marengo *et al.* 2008; Malhi *et al.* 2009; Lewis *et al.* 2011; Saatchi *et al.* 2013), contributing to higher susceptibility of forests to wildfire (Lee *et al.* 2011; Brando *et al.* 2014). This is particularly the case in southern Amazonia where forests are exposed to marked seasonality.

Forest fires have become a critical issue in the Chiquitania region of Bolivia, located in the southern edge of Amazonia. This region is characterised by the Chiquitano forest, which links the Amazon rainforests to the north with the Gran Chaco shrublands to the south (Pennington *et al.* 2009; Vides and Justiniano 2011). The Chiquitano forest is one of the largest and best preserved seasonally dry tropical forests in South America (Vides *et al.* 2007). In this region, the use of fire for agriculture and cattle ranching is common practice (Kennard *et al.* 2002; McDaniel 2005) and in the past decades, construction of roads, immigration and development policies have resulted in rapid expansion of the agricultural frontier and an increase in wildfires (Peredo 2011). Recent monitoring studies since 2000 have observed that wildfire peaks in the Chiquitania relate to drought years like in 2007 and 2010 (Rodriguez-Montellano 2012). The 2007 and 2010 forest fires burned 12 and 5% of southern Amazon forests respectively, compared to <1% in non-drought years (Brando *et al.* 2014).

Wildfire events are likely to become more frequent and severe in the future (Barlow *et al.* 2012) with increased moisture stress in southern Amazonia (Christensen *et al.* 2007; Williams *et al.* 2007; Cox *et al.* 2008) and continued land use change (Soares-Filho *et al.* 2006). Increased fire frequency linked to forest fragmentation poses a significant threat to tropical forests. In the Brazilian Amazonia, for example, Cochrane (2001) found that forests up to 2 km from forest edges had fire return intervals that humid tropical forest cannot withstand. Previous studies have analysed the impacts of recurrent wildfire in the Amazon humid and transitional forests (Cochrane *et al.* 1999; Barlow and Peres 2008; Balch *et al.* 2011; Oliveras *et al.* 2014), but less so in seasonally dry tropical forests that occur on more fertile Amazonian landscapes such as the Chiquitano forests (Pennington *et al.* 2006; Quesada *et al.* 2012), which lack an understory of C4 grasses and are more diverse structurally (Pennington *et al.* 2009; Torello-Raventos *et al.* 2013). In general, less attention has been given to the impacts of recurring fire on seasonally dry tropical forests, despite the fact that their rate of conversion has been higher historically (Mooney *et al.* 1995).

Seasonally dry tropical forests may be less vulnerable to wildfire disturbance due to presence of species that can tolerate lower rainfall with drought tolerance traits (Markesteijn and Poorter 2009), species with favourable fire tolerance traits, and a simpler structure with the potential to recover to a mature state more quickly than humid forests (Ewel 1980; Kennard *et al.* 2002; Pinard *et al.* 1999a,b). However, it may be that a disturbance-dominated regime with more frequent wildfires in the future will lead to possible long-term change in vegetation composition and carbon loss (Davidson *et al.* 2012) either through (i) ecosystem collapse with increasing tree mortality (Balch *et al.* 2011; Brando *et al.* 2014), (ii) degradation of forest ecosystems with altered structure and functionality and establishment of light-demanding species (Barlow and Peres 2008), and/or (iii) transition to grass-dominated vegetation facilitated by the invasion of flammable grasses or native bamboos (Veldman 2008; Veldman and Putz 2011).

This study intends to generate insights into how Chiquitano forests may respond to more frequent wildfires expected in the future. To this end, we conducted an observational study to analyse the effects of fire recurrence on these forests. The main focus of this study is on the responses these forests may have to different fire events. Other studies in humid Amazonian forests have found that repeated forest fires can lead to an overall decrease in carbon stocks, an increase in dominance of opportunistic species and a decrease in species richness (Cochrane and Schulze 1999; Barlow and Peres 2008). The specific questions we addressed in this study are:

(i) How do recurrent fires affect the biomass and structure of Chiquitano seasonally dry tropical forests?
(ii) What are the effects of recurrent fire on species composition and diversity?
(iii) What inferences can be made on the response of these forests to increased fire frequency in the future by comparing biomass and species composition under different fire recurrence?

The novelty of this research is in the way it analyses the impacts of recurrent fires by focusing on the dynamics of change in the forest revealed by comparing biomass with tree species diversity and composition. Although effects of recurrent fires have been evaluated in the savanna ecosystems that are intertwined with the Chiquitano dry forest (Veldman and Putz 2011), this study focuses on the tree dynamics within the dry forest system. The observed patterns provide unique and complementary insights into the responses these forests may have to a different disturbance regime. This is particularly important given that wildfires in the region are expected to become more frequent in the future with continuing pressure from deforestation and practices that expand the use of fire into new forest frontiers (Redo *et al.* 2011). New fire management strategies and forest regulations are currently being developed in the Chiquitania to address this issue. This study provides results that can inform such policies and management strategies in the region, and in other frontier landscapes around the world with similar dry tropical forests threatened by an increasing risk of wildfires in the future.

2. Materials and methods

2.1 Study site description

This study was conducted in the Chiquitania region located in the Department of Santa Cruz, Bolivia (Fig. 1). This region is characterised by a marked dry season. Temperature varies little throughout the year with daily means of 24-25 °C. Mean annual precipitation in the central area of the region is 1129 mm with large inter-annual variability ranging between 500 mm and 1710 mm per year (Killeen *et al.* 1998). Based on NASA TRMM data covering the entire region, 6 months a year (starting in April/May) receive <100 mm (2000-2013 average). The driest months are July and August (about 20±3 mm, 2000-2013 average). In the period 2001-2013, the fire peak months of August and September accounted for 83% of the total number of MODIS MCD14ML high-confidence hotspots occurrence (Devisscher *et al. In Review*). Northern winds are predominant throughout the year, with speeds that oscillate between 3.7 and 18.5 km h^{-1}. Southern winds, which are dry and cold and can be more intense, are less frequent and occur during the dry season.

The low mean annual precipitation, high rates of deciduousness during the strong dry season, the presence of more fertile soils and the species composition, characterize the Bolivian Chiquitano forest as seasonally dry tropical forest biome (Pennington *et al.* 2009*).* The Chiquitano forests are semi-deciduous rather than fully deciduous probably because the Chiquitania is more moist than many dry tropical forests in the Neotropics and transitions to humid forest along its northern boundary.

The Chiquitano forest is also intertwined with patches of grassland and shrubbery of the woody savanna *cerrado*, and transitions into the Gran Chaco on its southern boundary (Killeen *et al.* 1998). In the Chiquitania, natural grasslands generally occur on sandy, nutrient-poor soils, whereas forests grow on younger, relatively fertile soils (Killeen *et al.* 1998; Veldman and Putz 2011). Veldman and Putz (2011) found that there are two kinds of savannas in the region, one linked to typical *cerrado* with native grasses and naturalized African forage grass, and the other dominated by the native bamboo *Guadua paniculata*. This native bamboo is dominant in forest-replacing 'derived' savannas, where there is a higher presence of forest tree species and twice the fuel load of natural savannas (Veldman and Putz 2011).

To study the effects of recurrent fire on the Chiquitano dry forest, we focused on a well-conserved study site in the heart of the region, located in the 4,126 ha private reserve of the Research Centre Alta Vista (61°53'W, 16°6'S), Municipality of Concepción (Fig. 1). The site is situated in the south western edge of the Brazilian Shield, in a wide transition zone to the humid forests of the Amazon basin. Mean annual precipitation in this site is 1170 mm (inter-annual variability range 799-1779 mm, 1960-2010 data from the Concepción met station located 15 km from the Alta Vista site, SENAMHI 2012). For comparison we also conducted a more limited study at a site in the 264,757 ha Municipal Reserve of the Tucabaca Valley (59°39'W, 18°17'S), Municipality of Roboré, in the transition zone closer to the Gran Chaco (Fig. 1). Mean annual precipitation in this site is 1088 mm (range 650-1509 mm, 1960-2010 data from the Roboré met station located 17 km from the Tucabaca site and 345 km from the Concepción met station, SENAMHI 2012). We focus our analysis on the Alta Vista site, but occasionally draw on the more limited dataset for the Tucabaca site where appropriate for validation.

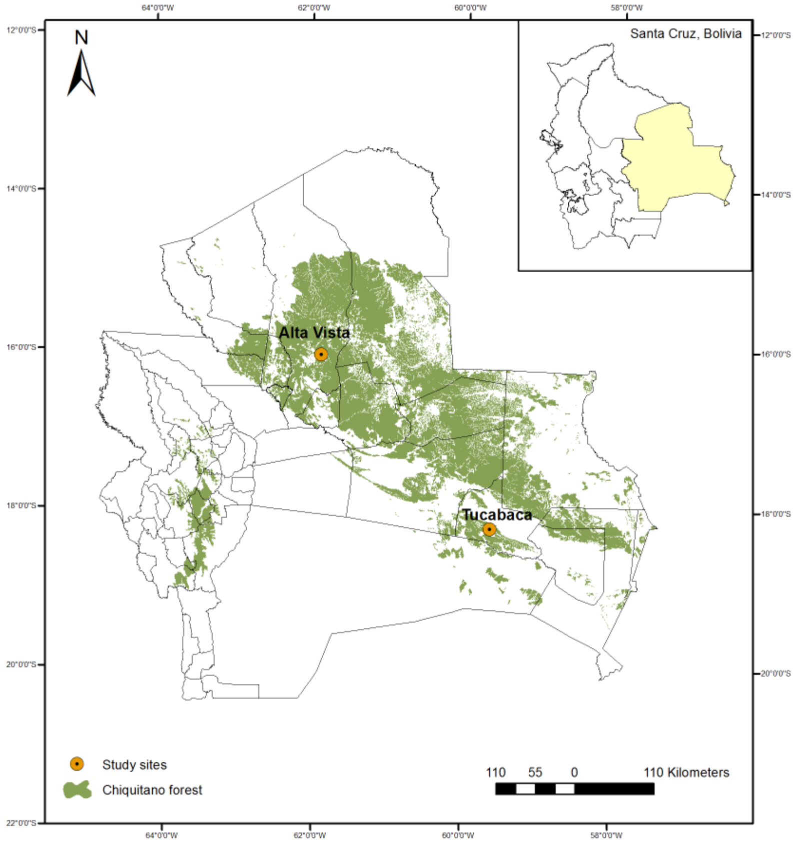

Fig. 1. The semi-deciduous forest of the Chiquitania in the Department of Santa Cruz, Bolivia, as defined by Navarro and Ferreira (2005). Location of the Alta Vista Research Centre (study site) and the Tucabaca Valley Municipal Reserve (validation site).

2.2 Study design and data collection

In the Alta Vista site, a set of four plots of 2000 m^2 area (100 x 20 m) each was located in distinct forest patches affected by a different number of fire events since 2000: unburnt forests, forests burned once (B1), forests burned twice (B2), and forests burned thrice (B3). The time since last fire varied for each case, where B1 forests burned in 2007, B2 forests burned in 2007 and again in 2010, and B3 forests burned first in 2002, then in 2007 and 2010. The total area sampled per forest type (i.e. forest burned different times) was equivalent to 0.8

ha. Plot coordinates, their distances to roads and distances between plots are provided in Table A.1 and Table A.3. In the Tucabaca site plots were established in unburnt forests and forests burned twice (B2) in 2007 and 2012 (more details in Table A.2, A.3).

Post-burn observational studies assessing the impacts of wildfires on forests are generally spatially constrained. To assess the effects of recurrent fires it was necessary to locate the sampling plots in forest patches that were burnt by the same wildfires, making sure that all the plots sampled in one treatment would have been affected by the forest fires of that particular treatment. The sampling size of forests types does not differ much from other studies conducted to assess fire impact on forests in Brazilian Amazonia (Cochrane *et al.* 1999; Barlow *et al.* 2003; Barlow and Peres 2008), where forest structure is even more complex and floristic diversity higher. In addition, even if plots were located in single burnt forest patches, the burnt sample plots can be considered independent because fire does not burn a forest patch uniformly, resulting in heterogeneity within the patch (Barlow *et al.* 2003a,b; Oliveras *et al.* 2014). The 100 m long rectangular plots used in this study also capture more variability than small square plots and reduce the risk of ‘majestic forest bias’ (Marthews *et al*. 2012).

In both sites, forest plot location was aided by support from a team of fire fighters and park rangers who assisted fire fighting in the locations, and had around 10 years experience working or living in the sites. In Alta Vista, control forest has been under conservation for the past 20 years, while in Tucabaca control forests were more difficult to find and park rangers indicated that they might have burned 10-15 years ago. However, given the background ecology of this site, a never burnt control may not be realistic or desirable. Instead, control forests represent a type of longer fire-return interval. There were signs of past logging in the forest burned thrice in Alta Vista (one logged tree in one sample plot) and in the control forest of Tucabaca (one logged tree). In Alta Vista there was limited presence of grasses in B1, B2 and B3 forests, and we observed *Guadua* bamboo invasion particularly in forests burned twice. However, grasses and native bamboo were not measured in this study.

While there is no detailed record of the fire history or baseline prior to 2000 for this frontier region, forest fires have become a serious regional problem in recent years with increasing expansion of the agricultural frontier and severe droughts (Peredo 2011, see Fig. B.1). Wildfires in the region are mainly anthropogenic, with about 70% of forest fires since 2000 occurring within 1 km distance from deforested areas (Rodriguez-Montellano 2014). For these reasons, it is reasonable to assume that the contemporary fire regime in the Chiquitania presents shorter fire return intervals than the historic range of variability, and hence the impacts of recent recurrent wildfires can serve as a proxy to analyse the effects of an expected regime of more frequent fires in the future. Wildfires are likely to become more frequent due to current policies promoting immigration and a rapid expansion of the agricultural frontier spreading the use of fire (Redo *et al*. 2011), combined with drier climatic conditions (Malhi *et al.* 2009).

Tree inventories were collected between July and September 2013. In each sample plot, all living and dead (standing and fallen) trees >10 cm in diameter at breast height (dbh, 1.3 m) were tagged and identified to species level, their diameter measured at dbh, total height estimated visually and for a sub-set of each dbh size class with a TruePulse 200 rangefinder and hypsometer (LASER Technology, Centennial, USA) for height calibration, and tree condition noted. In addition, lianas >10 cm in diameter were measured. All procedures followed the RAINFOR-GEM protocol v 2.2 (Marthews *et al.* 2012). Notation and visual recording of plot characteristics followed the Fire Monitoring Handbook (USDI 2003) guidelines.

In terms of morphological traits, visible char height of fires was recorded and categorized in three classes 0=no visible marks; 1= burnt at base to 30 cm; 2= burnt from 30 cm to breast height; 3=burnt above breast height (Barlow *et al.* 2003b). Bark texture was also recorded and graded as either rough (strongly fissured or very flaky), medium (lightly fissured or flaky) or smooth (Barlow *et al.* 2003b). Bark thickness was measured for all living trees >10 cm dbh in at least two sample plots per treatment using a bark thickness gauge (Haglöf Company Group, Långsele, Sweden) in three different points around the circumference of a tree at 0.5-1.3 m height (Pinard *et al.* 1999b) avoiding ridges, furrows and wounds, and then average was calculated.

Within each sample plot, two sub-plots 10 x 10 m were randomly located in the first two and last two quadrats (Fig. 2). In these sub-plots, trees between 2.5 and 10 cm dbh were identified to species level, measured dbh, total height estimated visually, and tree condition noted. In the central quadrat, 4 line transects 20 m long and 2 transects 1 x 20 m each were established randomly (Fig. 2) to measure combustible fuel load with the planar intersect method (Brown 1974) and coarse woody debris with the RAINFOR-GEM protocol (Marthews *et al.* 2012). Fuel load measurements following the planar intersect technique included 1 hour, 10 hours, 100 hours, and 1000 hours standard moisture time-lag size classes (Brown 1974), corresponding to diameters 0-0.62 cm, 0.62-2.54 cm, 2.54-7.62 cm, and >7.62 cm respectively. Coarse woody debris (CWD) were classified in 3 diameter classes 2.54-7.62 cm, 7.62-10 cm, and >10 cm (tree branches), which were further separated into five decomposition categories. For CWD, each piece within transect was cut at the intersection, then length and average diameter measured. To avoid double counting, this study reports only 1-hour and 10-hour fuel load and total coarse woody debris – excluding standing and fallen dead trees as these were accounted for in the tree inventories.

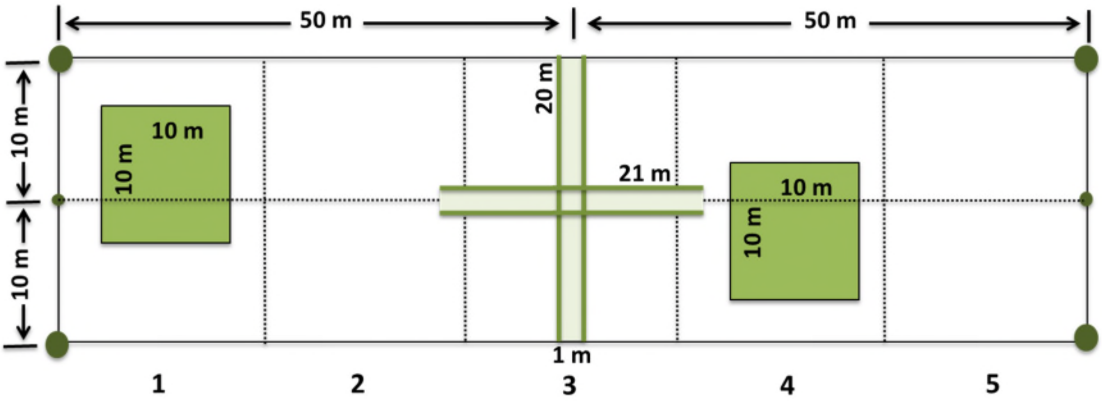

Fig. 2. Layout of sample plot with 5 quadrats, 2 sub-plots, 4 Brown transects, and 2 coarse woody debris transects. Design adapted from Brown 1974, the USDI Fire Monitoring Handbook 2003, and the RAINFOR- GEM protocol 2012.

2.3 Aboveground biomass measurement

Live aboveground biomass (AGB) was estimated for large trees (LT) >10 cm dbh, small trees (ST) 2.5-10 cm dbh, palm trees (PT) >10 cm dbh and large lianas (LL)

>10 cm dbh. Biomass for large and small trees was calculated using the Chave *et al.* (2005) allometric biomass equation for dry forest (i.e. corresponding to <1500 mm year^{-1} in rainfall). Wood density specific to each identified species (if no data at species level, then genus) was used in the calculation. Biomass for lianas was estimated using the Schnitzer *et al.* (2006) allometric biomass equation for lianas, which is based on data from five different geographic locations, and suitable for samples between 1 and 23 cm in diameter. Biomass for palm trees used the Nascimiento and Laurence (2002) allometric biomass equation for palms.

Dead AGB included coarse woody debris and dead (standing and fallen) trees and palms >10 cm dbh. For coarse woody debris, samples for each diameter and decomposition category were weighted and oven-dried in laboratory to estimate an average density for each combined category. This category-specific density was then used to estimate biomass of coarse woody debris by multiplying by the volume of each piece measured during fieldwork. For dead trees, a biomass-weighted density average was calculated, which was used to estimate biomass using the Chave *et al.* (2005) allometric equation if dead trees were standing or had fallen but had not started decomposition yet, and using tree volume if dead trees had fallen and were decomposing. Dead palm biomass was estimated using the Nascimiento and Laurence (2002) allometric equation for palms. In addition, fuel load was calculated using the Van Wagner (1982) equation.

2.4 Data analysis

Changes in forest structure, aboveground biomass and morphological traits for different fire recurrence were statistically analysed and compared using ANOVA (after testing homoscedasticity with Bartlett test and Fligner test), and Welch two-sample t-test where relevant. Detrended correspondence analysis (DCA, Hill and Gauch 1980) was used to analyse changes in species abundance composition and fitted environmental gradients for different burnt forest types. To test differences between species in the sites, the Bray-Curtis method was used to measure distances between samples, homogeneity of multivariate dispersion was tested, and group means were compared using ANOVA. Species diversity was assessed using the Menhinick's index and rarefaction curves (Magurran 2004). Statistical analyses were implemented in R 3.0.2 (The R Foundation 2013), ordination and diversity analyses were conducted using the vegan package (Oksanen *et al.* 2013).

To further explore shifts in species composition between treatments, identified species were categorized into three types from low to high capacity to tolerate fire disturbance. This categorisation was based on four characteristics. The first two are bark thickness and bark texture from field inventories. These are traits associated with species' capacity to tolerate fire (Pinard *et al.* 1999a; Barlow *et al.* 2003b; Shenkin 2014). The other two are based on classification by Pinard *et al.* (1999b) for shade tolerance of regeneration and capacity for propagule dispersal. These are ecological characteristics used to determine species' vulnerability to disturbance. Species were scored based on these four characteristics following Pinard *et al.* (1999b) and Kennard *et al.* (2002), and then categorised into "*fire-tolerant species*", "*intermediate species*", or "*fire-intolerant species*". Distribution of abundance (i.e. by number of individuals) and dominance (i.e. by AGB) of these three species types was then assessed for each fire recurrence.

3. Results

3.1 Forest structure and aboveground biomass

As expected unburnt forests showed higher live AGB than burnt forests (Fig. 3). The AGB difference between unburnt forests and forests burned at different times was significant when all components measured to estimate AGB were accounted for (Pr(>F) 0.038; ANOVA). Live biomass in burnt forests declined to 90%, 63%, and 84% relative that found in the unburnt forest for B1, B2, and B3 respectively. Pairwise comparisons showed that AGB of live trees >10 cm dbh in unburnt forests was statistically different from B2 forests (P = 0.004) and B3 forests (P = 0.049) forests, but not from B1 forests (P = 0.445; Welch Two Sample t-test). Surprisingly, forests burned twice exhibited the lowest live AGB (128.5±12.9 Mg ha^{-1}), even when compared to B3 forests (171.7±11.3 Mg ha^{-1}) (Table 1). In the Tucabaca site, live biomass in B2 forests (151.4±10.8 Mg ha^{-1}) was higher and equivalent to 85% of that in unburnt forests (Fig. C.1, Table C.1).

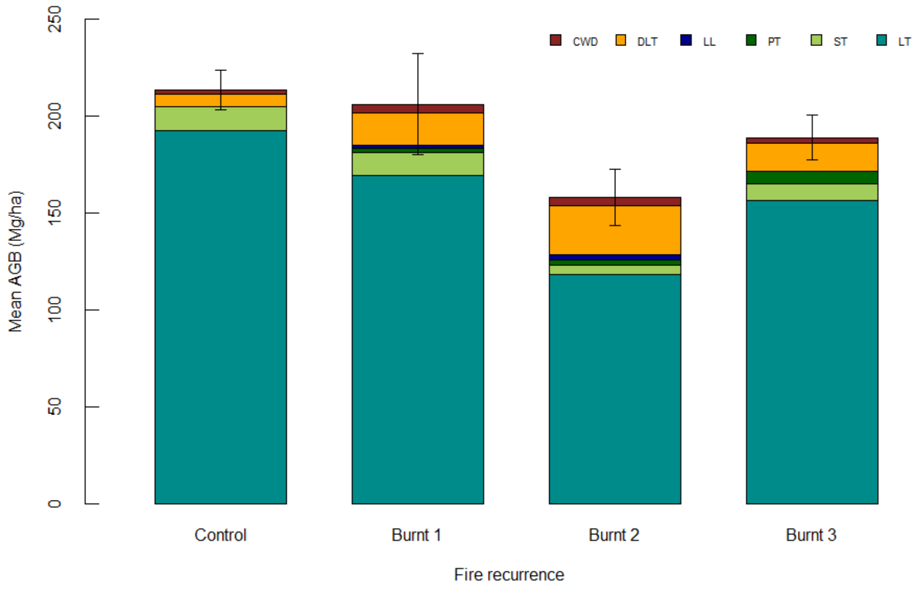

Fig. 3. Mean (±SE) of live and dead AGB of unburnt forests and forests burned once, twice and thrice in Alta Vista. LT (large trees >10 cm dbh), ST (small trees 2.5-10 cm dbh), PT (palm trees>10 cm dbh), LL (large lianas >10 cm dbh), DLT (dead large trees >10 cm dbh), CWD (coarse woody debris).

Fire also affected the distribution of different tree sizes (i.e. forest structure). In forests burned once, tree density and biomass in trees <10 cm and >30 cm dbh size were particularly affected. Recurrent fires further impacted small <10 cm (i.e. regeneration and new recruits) and large >30 cm dbh sizes (i.e. trees surviving after first fire) (Fig. 4).

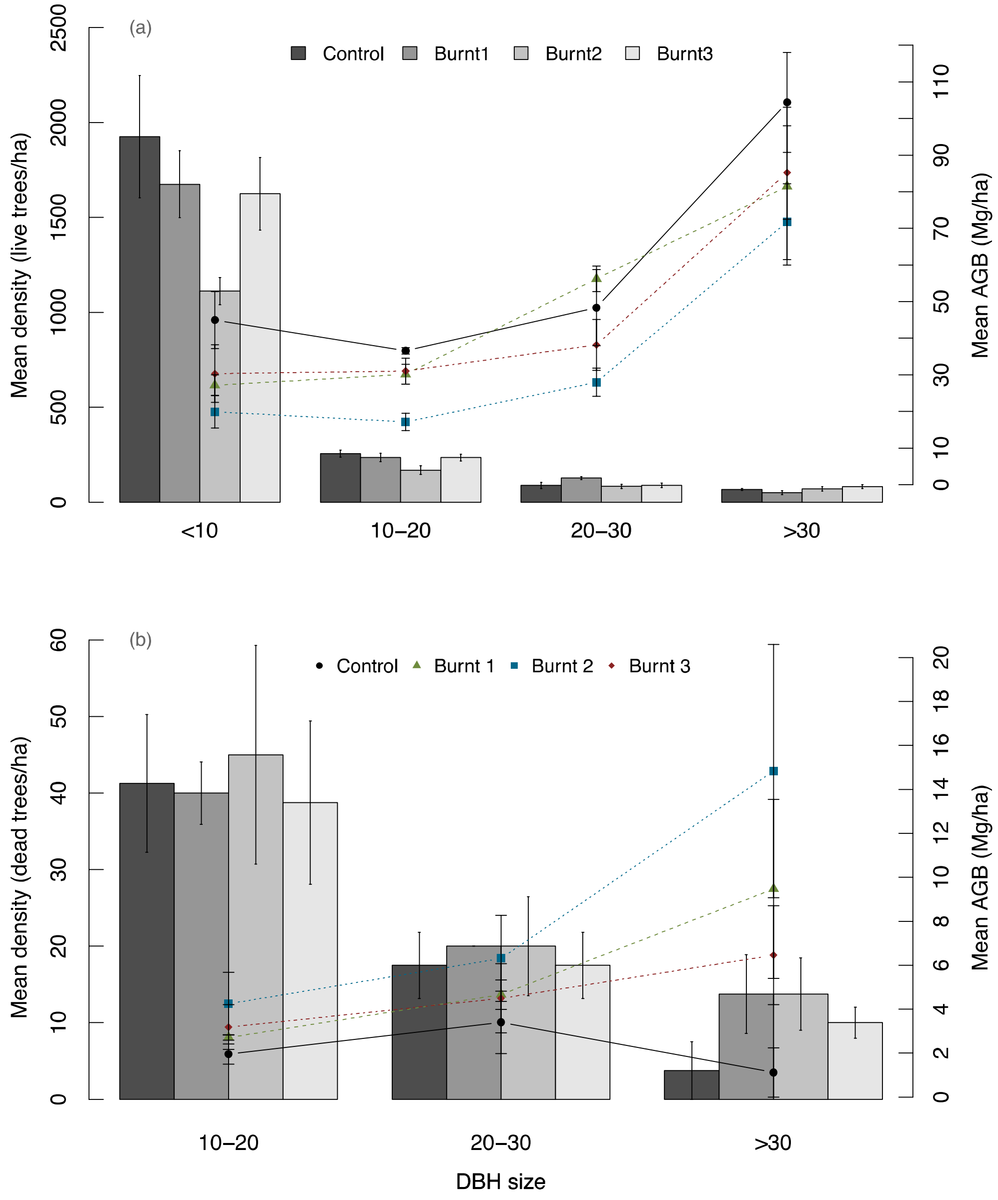

Fig. 4. Bars show mean tree density (±SE) of (a) living and (b) dead trees in each dbh size for forests burned different times in Alta Vista. Lines show the mean AGB (±SE) for (a) live and (b) dead tree sizes.

As expected small trees <10 cm and 10-20 cm dbh in unburnt forests showed higher AGB than in burnt forests (Fig. 4a). Unburnt forests also presented higher AGB and density of large trees >30 cm dbh than burnt forests. Unexpectedly however, B3 forests exhibited higher density of trees 30-40 cm dbh than B1 and B2 forests (Fig. 4a).

Dead AGB in burnt forests was significantly higher than in unburnt forests (Fig. 4b) when all components measured for dead AGB were considered ($P = 0.023$; ANOVA). Comparing each burnt forest type to the control forest, only B2 forests ($P = 0.034$) and B3 forests ($P = 0.042$) showed significantly higher dead AGB, but not B1 forests ($P = 0.069$; Welch Two Sample t-test). Dead AGB in unburnt forests (8.7±1.5 Mg ha^{-1}) was lower across all dbh sizes (Fig. 4b). Large trees >30 cm dbh represented a large part of the dead biomass pool in burnt forests, and dead tree fraction was the highest for B2 forests (Table 1). B2 forests showed higher levels of dead AGB (29.6±6.2 Mg ha^{-1}) than B1 forests and B3 forests. This represented a loss of ≈15% (B2), 10% (B1), and 8% (B3) of the initial AGB estimated at 204.8±10 Mg ha^{-1} for unburnt forests (Table 1). This was similar to the validation site where dead AGB in B2 forests was equivalent to ≈12% of the live biomass in unburnt forests estimated at 178.7±31.5 Mg ha^{-1} (Table C.1). Assuming dry biomass is 47.4% carbon (Martin and Thomas 2011), combustion reduced onsite carbon (i.e. live and dead AGB stocks) in Alta Vista by 3.7±13.9 Mg C ha^{-1}, 27.7±8.8 Mg C ha^{-1} and 12.3±7.7Mg C ha^{-1} in first, second and recurrent burns respectively.

Table 1. Data summary for forest structure and biomass in unburnt (4) and burnt (12) plots in Alta Vista, Chiquitania

Characteristics	Unburnt		Burnt 1		Burnt 2		Burnt 3	
	Mean	(±SE)	Mean	(±SE)	Mean	(±SE)	Mean	(±SE)
Large tree density (LT ha^{-1})	470.00	26.06	452.50	19.31	355.00	48.56	453.75	4.73
Standing dead tree density (DT ha^{-1})	55.00	7.91	31.25	4.73	36.25	9.44	36.25	7.47
BA of large trees (m^2 ha^{-1})	18.57	0.96	18.88	2.21	16.33	1.93	18.91	1.53
BA of standing dead tree (m^2 ha^{-1})	1.60	0.23	1.13	0.28	1.26	0.27	1.78	0.42
Mean dbh (Large living trees, cm)	19.72	0.13	20.62	0.98	21.69	1.24	20.89	0.74
Mean BT (Large living trees, cm)§*	0.73	0.03	1.11	0.03	1.46	0.19	1.48	0.12
Live AGB (Mg ha^{-1})*	204.85	9.99	184.99	25.68	128.53	12.95	171.75	11.31
Dead AGB (Mg ha^{-1})*	8.74	1.45	21.11	4.36	29.58	6.22	17.18	2.85
Fine fuel load								
1 hour (Mg ha^{-1})	2.18	0.27	2.99	0.12	1.19	0.20	0.91	0.12
10 hours (Mg ha^{-1})	3.60	0.50	4.84	0.53	2.19	0.34	2.74	0.25
Dead tree fraction (All dead trees live trees^{-1})	0.14	0.02	0.16	0.01	0.25	0.09	0.15	0.02

LT: large trees >10 cm dbh; BA: basal area; dbh: diameter at breast height 1.3 m, BT: bark thickness; AGB: aboveground biomass

Live AGB includes biomass estimated for small trees 2.5-10 cm dbh, and large trees, lianas and palm trees >10 cm dbh

Dead AGB includes biomass estimated for dead trees and palms >10 cm dbh and coarse woody debris

§ BT was measured in at least 2 plots per fire recurrence; palm trees were not included

* significant difference Pr(>F) <0.05; ANOVA

3.2 Species composition and diversity

Detrended correspondence analysis (DCA) showed a significant shift in species abundance in forests affected by multiple fire events ($R^2 = 0.67$ for all trees >10 cm dbh, $R^2 = 0.62$ for small trees 10-20 cm dbh, Pr(>F)<0.001; ANOVA 999 permutations). Assessing species abundance of trees >10 cm dbh, the DCA resulted in clustering of unburnt forest plots with B1 forest plots (Fig. 5a). Separated by >2 σ in the DCA1-axis (eigenvalue 0.572) we found a more dispersed cluster of B3 and B2 forest plots with different composition of species abundance. B2 forest plots were also separated by the DCA2-axis (eigenvalue 0.334) denoting higher variability within the treatment. In the DCA for species of small trees 10-20 cm dbh (DCA1-axis eigenvalue 0.626, DCA2-axis 0.419), we observed that B2 forest plots were dispersed in the central area between a cluster of unburnt-B1 forest plots and a cluster of B3 forest plots (Fig. 5b).

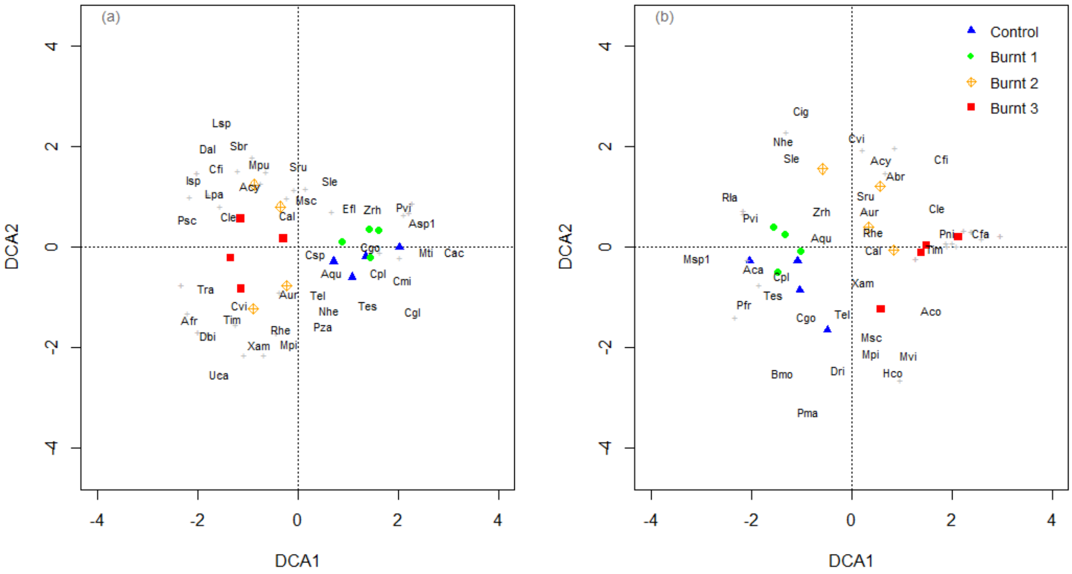

Fig. 5. Detrended correspondence analysis for (a) species abundance of trees >10 cm and (b) species abundance of small trees 10-20 cm in four 2000 m^2 plots in unburnt forests and forests burned once, twice and thrice in Alta Vista. Abbreviated names correspond only to most abundant species (See list of all species full names in Table D.1).

Similar patterns were recognised in DCA plots for species of trees <10 cm and 20-30 cm dbh, showing clustering of unburnt forest with B1 forest plots, separated from a more dispersed cluster of B3 forest plots by the DCA1-axis (Fig. 6). B2 forest plots were spread in-between these two clusters. Forest plots were less dispersed in the ordination for species of trees >30 cm dbh, but uncertainty in the data was higher due to a smaller sample size.

Fitting variables to the DCA plots pointed to different directions and strengths of gradients that complement the ordination results. Some of these variables are traits known to enhance protection to fire-induced damage, such as bark thickness and wood density (Pinard *et al.* 1999b; Shenkin 2014). In Alta Vista, average bark thickness of trees >10 cm dbh increased with number of fires from 0.7±0.03 cm in unburnt forests to 1.5±0.1 cm in forests burned thrice ($P < 0.01$, Table 1). Average bark thickness was calculated for each dbh category to account for co-variance. This variable showed a gradient and significant correlation ($P < 0.05$) with B2 and B3 forests across all dbh sizes except 20-30 cm (Fig. 6).

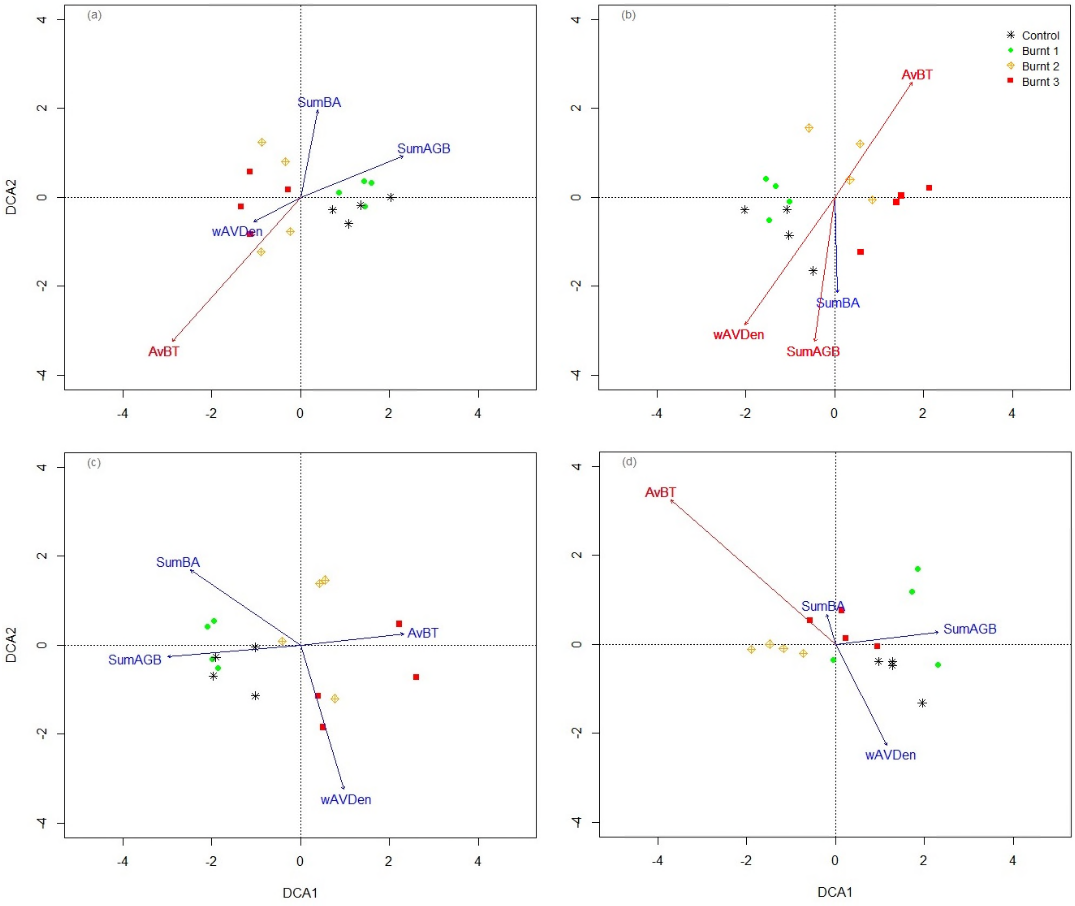

Fig. 6. Average bark thickness (AvBT), biomass weighted average wood density (wAVDen), total basal area (SumBA) and total aboveground biomass (SumAGB) estimates fitted to the detrended correspondence analysis of species abundance for (a) all trees >10 cm dbh, (b) trees 10-20 cm dbh, (c) trees 20-30 cm dbh and (d) trees >30 cm dbh in unburnt forests and forests burned once, twice and thrice in Alta Vista. Arrows in bold/red represent significant correlation (P<0.05).

For all tree size classes there was a clear distinction between control/B1 forests and B2/B3 forests. For the tree community as a whole, the control and B1 plots were characterised by high biomass ($P < 0.05$ for AGB). For small trees (10-20 cm dbh) the community shifted from high biomass to low biomass but high bark thickness (Fig. 6). Biomass weighted average wood density did not show a clear trend. Oliveras *et al*. (2014) did not find wood density to be a trait associated with ‘fire-thriver’ species selected with a fire tolerance index.

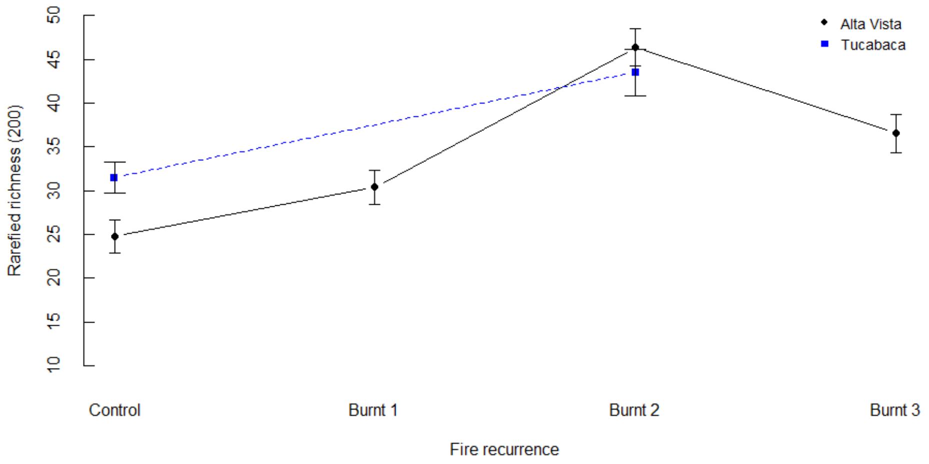

Fig. 7. Rarefied species richness (±SE) using a sub-sample of 200 individuals for unburnt forests and forests burned twice in Tucabaca, and unburnt forests, forests burned once, twice and thrice in Alta Vista.

Diversity measurements using species rarefaction and Menhinick's index revealed higher diversity in B2 forests (M index 3.14) compared to unburnt forests, B1 forests and B3 forests (Fig. 7, Table 2, Fig. E.1). Higher tree species diversity in B2 forests was also observed in the Tucabaca site (Fig. 7, Fig. E.2).

Table 2. Tree bark texture, char height and species diversity in unburnt and burnt forests

Characteristics	Unburnt		Burnt 1		Burnt 2		Burnt 3	
Alta Vista	No	%	No	%	No	%	No	%
Bark texture class								
Smooth bark	46	12%	24	7%	35	12%	59	16%
Regular bark	258	69%	243	67%	178	63%	124	34%
Rough/ fissured bark	69	18%	95	26%	71	25%	180	50%
Char height class								
No scar	376	100%	288	80%	146	51%	162	45%
< 30cm	0		46	13%	71	25%	133	37%
30-130cm	0		21	6%	45	16%	40	11%
>130cm	0		7	2%	22	8%	28	8%
Alta Vista								
LT species	31		37		53		45	
Menhinick's index (S richness LT)	1.60		1.94		3.14		2.36	
Tucabaca								
LT species	37				58			
Menhinick's index (S richness LT)	1.86				2.80			

Sampled area per forest affected by a different number of fire events is 0.8 ha, LT: large trees > 10 cm dbh, No: number of trees, or number of LT species

3.3 Comparing biomass with species composition and diversity

Contrary to what was expected, we found that the biomass level in B3 forests was higher than in B2 forests. The shift in species composition revealed by the DCA analysis and rarefaction curves provided a first insight into the possible explanation for these results, denoting an ecological transition in response to recurrent forest fires. B2 forests seemed to show signs of being in the transition between an initial state (cluster of unburnt and B1 forest plots in the DCA) and a changed state (cluster of B3 forest plots). Also, B2 forests showed an increase in number of species and species richness despite the loss in biomass. Categorizing the species by their tolerance to fire based on specific traits (see section 2.4) and using these species types to compare AGB with species abundance and composition helped to further explain the findings and elucidate, at least for this case, a possible response these forests may have to more frequent fires.

In Alta Vista, distributions of species abundance and dominance showed a higher number of individuals of “*fire-intolerant species*” in unburnt forests (relative abundance 0.39) and B1 forests (0.55) than in B2 forests (0.15) and B3 forests (0.08). On the contrary, “*fire-tolerant species*” were more abundant in B2 forests (0.28) and particularly B3 forests (0.56) (Fig. 8a). A similar pattern was observed with species dominance in terms of biomass associated to each species type (Fig. 8b). Biomass of “*fire-intolerant species*” was higher in unburnt forests (AGB fraction 0.25) and B1 forests (0.60), while biomass of “*fire-tolerant species*” was higher in B2 forests (0.50) and particularly in B3 forests (0.78). Abundance and dominance of “*intermediate species*” remained relatively constant across all forests affected by a different number of fire events in Alta Vista.

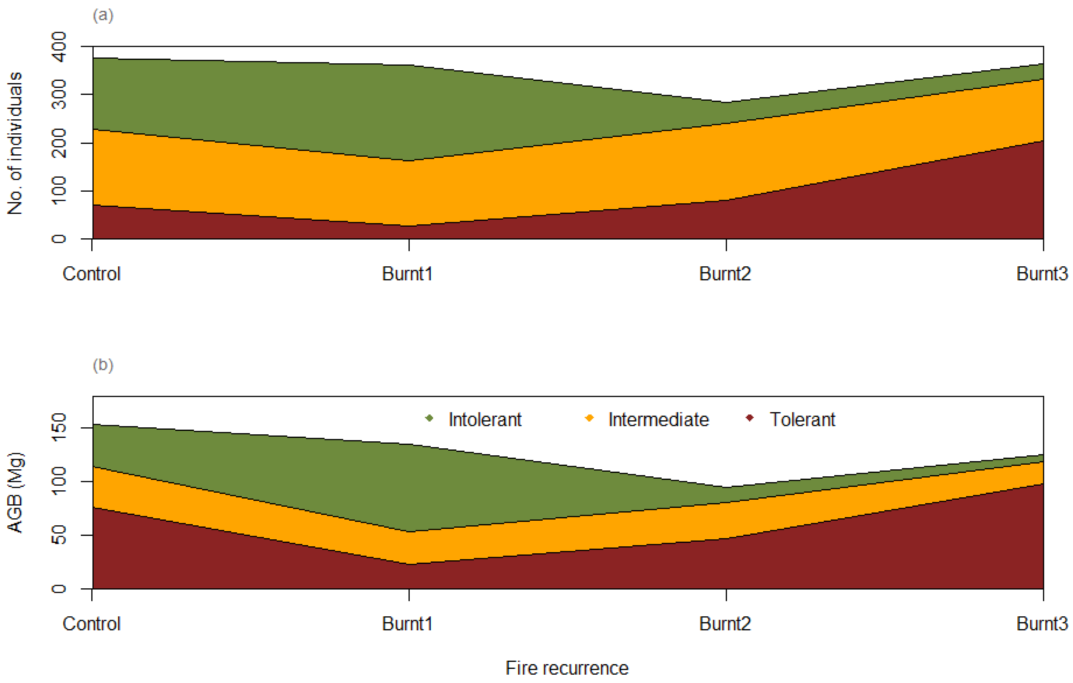

Fig. 8. Distribution of (a) species abundance (i.e. by number of individuals) and (b) dominance (i.e. by biomass) in total sampled area of unburnt forests, and forests burned once, twice and thrice in Alta Vista.

4. Discussion

The post-fire biomass loss and putative effects on large and small trees observed in this study are similar to other studies in tropical forests (Cochrane *et al.* 1999; Pinard *et al.* 1999a; Barlow *et al.* 2003a,b). Smaller trees < 10 cm dbh are expected to be more at risk because of their thinner bark and higher probability of being affected by the fire flame and suffering cambial damage (Pinard and Huffman 1997). The large contribution of large trees > 30 cm dbh to the dead biomass pool after a forest fire was also reported by Barlow *et al.* (2003a), who noted a decline in density and biomass of large trees 3 years after a fire event in the Brazilian Amazonia. Recurrent fires seemed to further affect large trees, suggesting that repeated fire occurrence could lead to a rapid collapse in the abundance of mature trees in a tropical forest (Barlow and Peres 2008; Brando *et al.* 2014). We acknowledge that large tree loss may not only relate to fire, but also to other disturbances like the severe droughts that affected the region in 2007 and 2010 (Fig. B.1). Impacts of fire-drought interactions have been reported in other Amazonian forests (Brando *et al.* 2014).

Our observed fire-mediated dead tree fraction (15-25%) falls in the tree mortality range recorded by Barlow and Peres (2006) in forests affected by fire at the edge of the Amazon basin (8-23%). This study also found comparable initial live AGB to Balch *et al.* (2011), although lower biomass loss in burnt forests relative to initial AGB in control forests. In an annual fire experiment in Mato Grosso Brazil, Balch *et al.* (2011) found that fire-induced stem mortality in evergreen transition forests contributed to a biomass loss of 32% (first fire) and 21% (third fire) of the initial AGB estimated at 192±2.5 Mg ha^{-1}. Difference in results may relate to differences in fire history, fire-return intervals, and burning conditions in the sites.

The dead tree fraction in our control forest indicates this forest is likely to have undergone a past disturbance (Araujo-Murakami *et al.* 2014). This current state of the control forest means that impacts of fire measured in this study may be underestimated. It also points to the difficulty of finding control forests in a region where logging and wildfires are widespread (Kennard 2002; Redo *et al.* 2011). However, the similar patterns we observed in Alta Vista and Tucabaca showed that the effects and response to multiple fires may be generalizable to the wider Chiquitano seasonally dry tropical forest.

In the study, B2 forests showed particularly large reductions in biomass, but at the same time an unexpected increase in species richness. Also, biomass in B3 forests was higher than in B2 forests. These observations may be explained by a combination of the following factors: (i) combustion of dead trees and coarse woody debris in the second fire; (ii) a different suite of pioneer species dominating the vegetation composition after the first fire, which themselves are more susceptible to subsequent fires, increasing overall mortality rate (Barlow and Peres 2008); (iii) fire-induced mortality among species that are unable to tolerate thermal stress and dominance of more fire-tolerant species with traits that enable them long-term survival post-fire (Pinard *et al.* 1999a; Barlow and Peres 2008; Balch *et al.* 2011); (iv) insufficient time for post-burn saplings and juveniles to grow into a size class that enables survival in a recurrent burn when fire-return intervals are short (Barlow *et al.* 2003b); (v) difficulty of juvenile light-demanding pioneer species to survive dry conditions (Markesteijn et al. 2010); (vi) invasion of grasses and particularly invasion of native bamboo *Guadua* in B2 forests able to convert tree-dominated forests to bamboo stands through positive feedbacks with fire (Veldman 2008; Veldman and Putz 2011); (vii) a decline of fine 1-hour fuel load after recurrent burning limiting fire intensity and spread of the third fire (Balch *et al.* 2008); and (viii) a stochastic anomaly like more large trees in B3 forest plots or anomalously low AGB levels in B2 forests before fires. In relation to this last point, we acknowledge that the size of sample plots in our study may represent a limitation for tree biomass estimates. We face a trade-off between plots being large enough to be insensitive to stochastic effects, yet small enough to be homogenous in fire exposure which is critical for the study.

The observed patterns in this study, in terms of both biomass and species composition, point at a response that the Chiquitano seasonally dry tropical forest may have to a regime of more frequent forest fires in the future. The response we observed is based largely on a shift in species after each fire event associated with the capacity of some species to survive, regenerate or grow in post-fire microclimatic conditions. The data suggest that this species differentiation becomes greater with increased number of fire events, shifting towards a new more fire-adapted tree community. The intermediate stage shows high tree species diversity, probably due to a mix of original large tree individuals able to survive the fires, some light-demanding short-lived pioneering species growing after fires, some species that are able to survive in drier sites, and increasingly dominant fire-tolerant species. This result is different from other post-fire evaluation studies that show tropical understory fires tend to decrease species richness (Cochrane and Schulze 1999) or do not observe substantial change in species diversity (Balch *et al.* 2011). One reason for this difference may be the higher fertility in the Chiquitano seasonally dry tropical forest and spatial heterogeneity in soil water availability, which facilitates more rapid growth and community turnover, and provides greater potential for niche partitioning among species at various levels if species adapt to exploit variation (Markesteijn et al. 2010).

If fire acts as an extinction and selection filter (Pinard et al. 1999a; Barlow and Peres 2008; Oliveras *et al*. 2014), its recurrence could also create the amplifying feedbacks (Cochrane *et al.* 1999; Nepstad *et al.* 2001) that push a forest into a new state (Scheffer *et al.* 2001; Gunderson and Holling 2002), with different species composition and modified structure and functionality. In Alta Vista, unburnt and B1 forest plots seem to relate to an initial state, while the change in biomass, species composition and diversity with dominance of fire-tolerant species in B3 forest plots may be indicating the transition to a different state more adapted to recurrent fires. The already existing presence of fire-adapted species in the plots may have facilitated this transition. In other instances, the fire-induced transition could be even more extreme from tree-dominated vegetation to an alternative stable state of grass-dominated vegetation as reported in other areas of the Chiquitania (Veldman 2008).

Recently Balch *et al.* (2011) questioned whether there is a threshold in fire frequency beyond which the majority of trees will collapse from direct or indirect fire damage. Although this is a small-scale study, our findings seem to show that recurrent fires may not necessarily lead to the collapse of tropical dry forests, but instead that these forests may respond and adapt in different ways. Certainly, this shift is also partly facilitated by a long fire history in the region.

Yet the effects of more recurrent fires – and a potential disturbance regime of more frequent fires in the future – would involve important losses. Some of these were observable in this study, such as the significant loss of aboveground carbon stocks and fire-intolerant tree species. Some of these tree species have high economic value for the wood market (Pinard *et al.* 1999a). Stem damage caused by fires (Schoonenberg *et al.* 2003) can also decrease their economic value. There are other ecosystem losses associated to recurrent forest fires that are not specifically addressed in this study. For instance, recurrent fires may cause changes to the local hydrological regime due to loss of water infiltration and retention capacity affecting local water sources and reservoirs (*Pers obs in Robor*é). Loss of habitat and maintenance capacity of forest fauna can also be expected (Barlow and Silveira 2009).

Results in this study may vary with shorter interval times between fire, higher fire intensities or higher number of fire events. There are also a series of fire tolerance traits that have not being measured in this study, such as rate of wound closure (Balch *et al.* 2011) and resprouting capacity (Pinard *et al*. 1999a; Kennard *et al*. 2002). These seem important for dry tropical forests due to the susceptibility of seedlings to drought and the greater proportion of biomass invested in root systems (Ewel 1980). In addition, there are studies on grass-fire interactions in the Chiquitania that complement this study (Veldman 2008; Veldman *et al.* 2009; Veldman and Putz 2011). Species composition of forests, logging, forest fragmentation, and proximity to seed sources of invasive grasses, become highly relevant when assessing the different responses that forests can have to recurrent wildfires (Brando *et al.* 2014).

Our findings provide evidence of a fire-response in semi-deciduous seasonally dry tropical forests worth studying further. Conducting longitudinal studies in more sites of the Chiquitania and large-scale fire experiments could contribute to gain more detailed understanding of how the effects of recurrent fire may change across different spatial and temporal scales and interact with other ongoing climatic and anthropogenic drivers. Developing a better understanding of the consequences of recurrent forest fires is essential for the implementation of forest management strategies that can reduce increased risk of wildfires in the future.

5. Conclusions

The findings generated in this study have considerable relevance for forest ecology and management in the Chiquitania, particularly given the risk of more frequent wildfires in the future. This study generated insights into the effects of recurrent fires in Chiquitano seasonally dry tropical forests, showing significant losses in on-site carbon and changes in species composition and diversity. Most importantly, the patterns that emerged from analysing and comparing shifts in biomass and species composition provided insights into a response that forests, which host a community of fire-tolerant species, may have to more frequent wildfires. These insights contribute to advance ecological knowledge about the region, as well as fire and forest management strategies, providing a basis to further study possible ecosystem transitions induced by increasing feedbacks between wildfire, climate and rapid land use change.

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Appendix A. Plot characteristics

Table A.1. Plot location in the Alta Vista site, Chiquitania

Forest type	Plot ID	Latitude	Longitude	Altitude
Burnt 1	Z1F1	-16.113042	-61.888855	447
	Z1F2	-16.113265	-61.888799	446
	Z1F3	-16.113340	-61.889694	457
	Z1F4	-16.113227	-61.888053	436
Burnt 2	Z2F1	-16.104677	-61.842389	425
	Z2F2	-16.104728	-61.842159	436
	Z2F3	-16.105201	-61.841832	438
	Z2F4	-16.105323	-61.841656	437
Burnt 3	Z3F1	-16.084060	-61.829316	427
	Z3F2	-16.084193	-61.829433	428
	Z3F3	-16.082389	-61.829782	406
	Z3F4	-16.082538	-61.829669	404
Control§	ZC	-16.109929	-61.886703	425

§ Control plots were located within a 1 ha square Rainfor plot (ppm1) see http://www.rainfor.org/en/map

Table A.2. Plot location in the Tucabaca site, Chiquitania

Forest type	Plot ID	Latitude	Longitude	Altitude
Burnt 2	2F1	-18.291193	-59.658398	752
	2F2	-18.291202	-59.658759	752
	2F3	-18.291491	-59.656771	736
	2F4	-18.291511	-59.657011	749
Control	C1	-18.289976	-59.654269	726
	C2	-18.289828	-59.654365	724
	C3	-18.308223	-59.63743	693
	C4	-18.308095	-59.637499	699

Table A.3. Distance characteristics for plots in different forest types

Forest type	Site	D to road§	D between plots	
			min	max
Burnt 1	Alta Vista	355	15	170
Burnt 2	Alta Vista	1550	25	60
Burnt 3	Alta Vista	140	20	170
Control	Alta Vista	60		
Burnt 2	Tucabaca	250	40	150
Control	Tucabaca	100	25	2700

D: distance in metres

§ Tertiary road, i.e. dirt road not always accessible during the wet season

Appendix B. Estimated maximum climatological water deficit and burned area of forests in the Chiquitania region

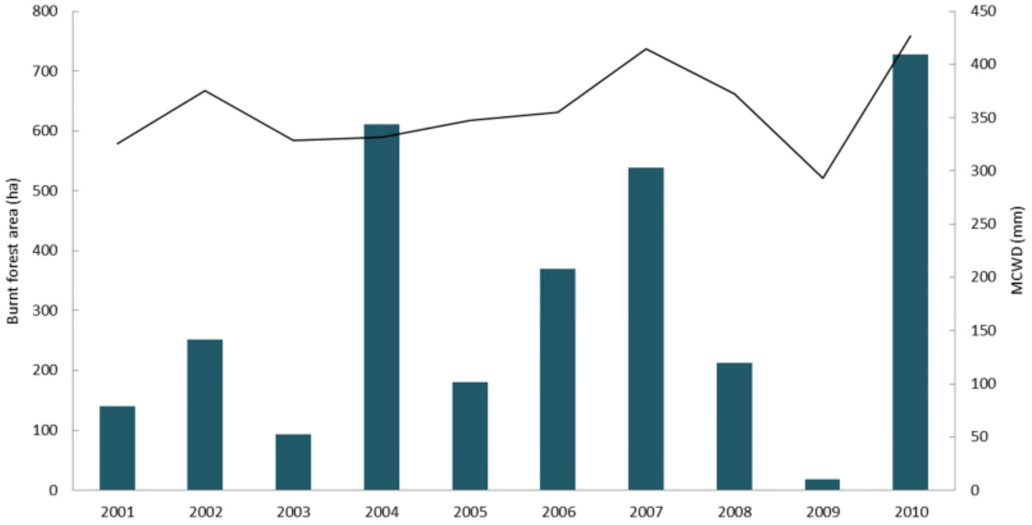

Fig. B.1. Bars show burnt forest area estimated based on data from the MODIS sensor MCD45A1 product. Burnt forest area is calculated for the Department of Santa Cruz, Bolivia (Rodriguez-Montellano 2012). Lines show maximum climatological water deficit (MCWD) where higher values represent higher deficit for the Chiquitania, estimated from total monthly precipitation (averaged for the region) for the period 2001 to 2010 obtained from the Tropical Rainfall Measuring Mission (TRMM, http://trmm.gsfc.nasa.gov/).

Appendix C. Aboveground biomass and forest structure for the Tucabaca site

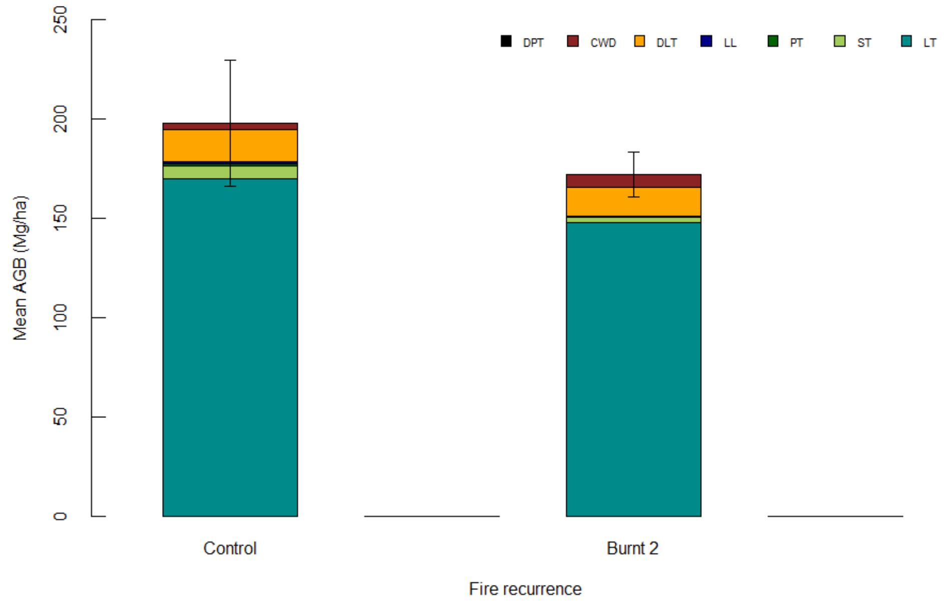

Fig. C.1. Mean (±SE) of live and dead AGB of unburnt forests and forests burned twice in Tucabaca. LT (large trees >10 cm dbh), ST (small trees 2.5-10 cm dbh), PT (palm trees>10 cm dbh), LL (large lianas >10 cm dbh), DLT (dead large trees >10 cm dbh), CWD (coarse woody debris), DPT (dead palm trees > 10 cm dbh).

Table C.1. Data summary for forest structure and biomass in unburnt (4) and burnt (4) plots in the Tucabaca site

Characteristics	Unburnt		Burnt 2	
	Mean	(±SE)	Mean	(±SE)
Large tree density (LT ha^{-1})	492.50	70.55	535.00	24.41
Standing dead tree density (DT ha^{-1})	43.75	14.77	43.75	8.75
BA of large trees (m^2 ha^{-1})	13.86	1.06	19.81	1.56
BA of standing dead tree (m^2 ha^{-1})	1.92	0.88	1.58	0.41
Mean DBH (Large living trees, cm)	22.51	1.35	21.62	0.69
Mean BT (Large living trees, cm)§	0.79	0.06	0.96	0.03
Live AGB (Mg ha^{-1})	178.70	31.47	151.39	10.81
Dead AGB (Mg ha^{-1})	19.33	3.43	20.56	3.33
Fine fuel load				
1 hour (Mg ha^{-1})	1.02	0.15	1.18	0.17
10 hours (Mg ha^{-1})	2.84	0.32	1.72	0.31
Dead tree fraction (All dead trees live trees^{-1})	0.19	0.03	0.13	0.02

LT: large trees >10 cm dbh; BA: basal area; dbh: diameter at breast height 1.3 m, BT: bark thickness; AGB: aboveground biomass

Live AGB includes biomass estimated for small trees 2.5-10 cm dbh, and large trees, lianas and palm trees >10 cm dbh

Dead AGB includes biomass estimated for dead trees and palms >10 cm dbh and coarse woody debris

§ BT was measured in at least 2 plots per fire recurrence; palm trees not included

Appendix D. Full names of species identified in unburnt and burnt forest plots, Alta Vista site

Table D.1. Species full names and abbreviations for all trees >10 cm dbh and trees 10-20 cm dbh in unburnt (4) and burnt (12) forest plots in Alta Vista, Chiquitania

Species of trees >10 cm dbh		Species of trees 10-20 cm dbh	
Acacia.polyphylla	Apo	*Acosmium.cardenasii*	Aca
Acosmium.cardenasii	Aca	*Agonandra.brasiliensis*	Abr
Agonandra.brasiliensis	Abr	*Anadenanthera.colubrina*	Aco
Amburana.cearensis	Ace	*Aspidosperma.cylindrocarpon*	Acy
Anadenanthera.colubrina	Aco	*Aspidosperma.quirandy*	Aqu
Aspidosperma.cylindrocarpon	Acy	*Astronium.urundeuva*	Aur
Aspidosperma.quirandy	Aqu	*Ateleia.guaraya*	Agu
Astronium.fraxinifolium	Afr	*Bauhinia.rufa*	Bru
Astronium.urundeuva	Aur	*Bougainvillea.modesta*	Bmo
Ateleia.guaraya	Agu	*Caesalpinia.pluviosa*	Cpl
Bauhinia.rufa	Bru	*Callisthene.fasciculata*	Cfa
Bougainvillea.modesta	Bmo	*Casearia.aculeata*	Cac
Caesalpinia.pluviosa	Cpl	*Casearia.gossypiosperma*	Cgo
Callisthene.fasciculata	Cfa	*Casearia.rupestris*	Cru
Casearia.aculeata	Cac	*Cedrela.fissilis*	Cfi
Casearia.gossypiosperma	Cgo	*Ceiba.speciosa*	Csp
Casearia.rupestris	Cru	*Celtis.iguanea*	Cig
Cecropia.concolor	Cco	*Centrolobium.microchaete*	Cmi
Cedrela.fissilis	Cfi	*Cochlospermum.vitifolium*	Cvi
Ceiba.speciosa	Csp	*Combretum.leprosum*	Cle
Celtis.iguanea	Cig	*Cordia.alliodora*	Cal
Centrolobium.microchaete	Cmi	*Cordia.glabrata*	Cgl
Cereus.tacuaralensis	Cta	*Dalbergia.riparia*	Dri
Cochlospermum.vitifolium	Cvi	*Dilodendron.bipinnatum*	Dbi
Combretum.leprosum	Cle	*Dipteryx.alata*	Dal
Cordia.alliodora	Cal	*Eriotheca.roseorum*	Ero
Cordia.glabrata	Cgl	*Eugenia.florida*	Efl
Dalbergia.riparia	Dri	*Genipa.americana*	Gam
Dilodendron.bipinnatum	Dbi	*Guazuma.ulmifolia*	Gul
Dipteryx.alata	Dal	*Heliocarpus.americano*	Ham
Eriotheca.roseorum	Ero	*Hymenaea.courbaril*	Hco
Erythrina.poeppigiana	Epo	*Luehea.paniculata*	Lpa
Eugenia.florida	Efl	*Machaerium.seemanni*	Mse
Ficus.obtusifolia	Fob	*Machaerium.pilosum*	Mpi
Genipa.americana	Gam	*Machaerium.scleroxylon*	Msc
Guazuma.ulmifolia	Gul	*Machaerium.villosum*	Mvi
Guibourtia.chodatiana	Gch	*Maclura.tinctoria*	Mti
Heliocarpus.americano	Ham	*Magonia.pubescens*	Mpu

Hymenaea.courbaril	Hco
Luehea.paniculata	Lpa
Machaerium.pilosum	Mpi
Machaerium.scleroxylon	Msc
Machaerium.seemanni	Mse
Machaerium.villosum	Mvi
Maclura.tinctoria	Mti
Magonia.pubescens	Mpu
Neea.hermaphrodita	Nhe
Physocalymma.scaberrimum	Psc
Piptadenia.viridiflora	Pvi
Pisonia.zapallo	Pza
Platymiscium.fragrans	Pfr
Platypodium.elegans	Pel
Pseudobombax.marginatum	Pma
Psidium.sartorianum	Psa
Pterogyne.nitens	Pni
Rhamnidium.eleocarpum	Rel
Rollinia.herzogii	Rhe
Ruprechtia.laxiflora	Rla
Sapium.glandulosum	Sgl
Schinopsis.brasiliensis	Sbr
Senna.spectabilis	Ssp
Simira.rubescens	Sru
Spondias.mombin	Smo
Steinbachiella.leptoclada	Sle
Sweetia.fruticosa	Sfr
Tabebuia.impetiginosa	Tim
Tabebuia.ochraceae	Toc
Tabebuia.rosea.alba	Tra
Talisia.esculenta	Tes
Trichilia.elegans	Tel
Urera.caracasana	Uca
Ximenia.americana	Xam
Zanthoxylum.rhoifolium	Zrh
Acacia.spp	Asp1
Andira.spp	Asp2
Erythrina.spp	Esp
Inga.spp	Isp
Lonchocarpus.spp	Lsp
Myrcia.spp	Msp1
Myrciaria.spp	Msp2

Neea.hermaphrodita	Nhe
Physocalymma.scaberrimum	Psc
Piptadenia.viridiflora	Pvi
Pisonia.zapallo	Pza
Platymiscium.fragrans	Pfr
Platypodium.elegans	Pel
Pseudobombax.marginatum	Pma
Pterogyne.nitens	Pni
Rhamnidium.eleocarpum	Rel
Rollinia.herzogii	Rhe
Ruprechtia.laxiflora	Rla
Sapium.glandulosum	Sgl
Senna.spectabilis	Ssp
Simira.rubescens	Sru
Spondias.mombin	Smo
Steinbachiella.leptoclada	Sle
Sweetia.fruticosa	Sfr
Tabebuia.impetiginosa	Tim
Tabebuia.ochraceae	Toc
Tabebuia.rosea.alba	Tra
Talisia.esculenta	Tes
Trichilia.elegans	Tel
Urera.caracasana	Uca
Ximenia.americana	Xam
Zanthoxylum.rhoifolium	Zrh
Acacia.spp	Asp1
Andira.spp	Asp2
Erythrina.spp	Esp
Inga.spp	Isp
Myrcia.spp	Msp1

Appendix E. Rarefaction curves, Alta Vista and Tucabaca sites

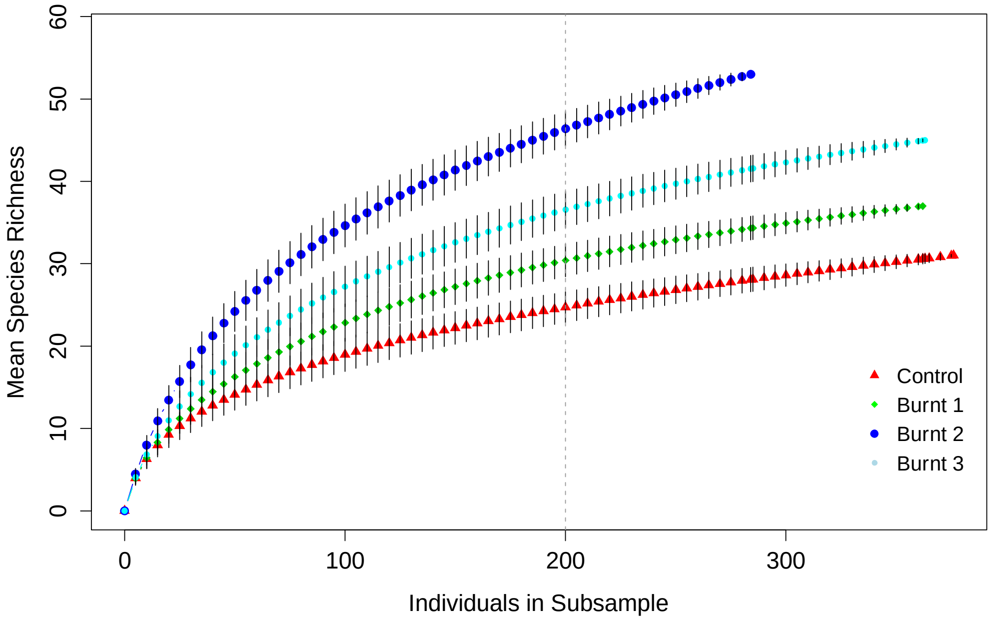

Fig. E.1. Mean rarefied species richness (±SE) for unburnt forests, forests burned once, twice and thrice in the Alta Vista site. Error bars represent the SE of the iterations, not true SE of the means.

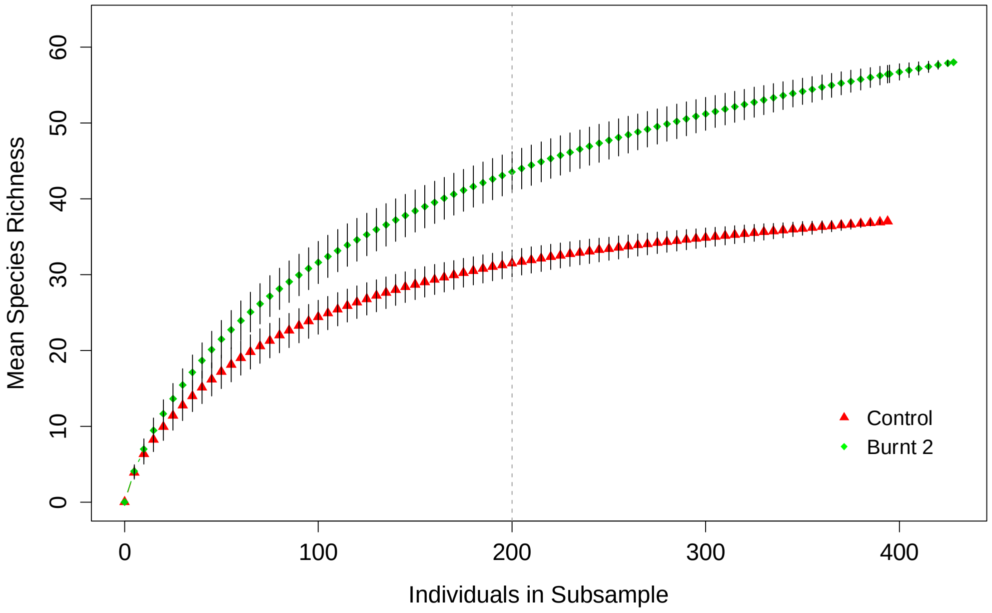

Fig. E.2. Mean rarefied species richness (±SE) for unburnt forests and forests burned twice in the Tucabaca site. Error bars represent the SE of the iterations, not true SE of the means.