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Fire effects and ecological recovery pathways of tropical montane cloud forests along a time chronosequence

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Abstract

Tropical montane cloud forests (TMCFs) harbour high levels of biodiversity and large carbon stocks. Their location at high elevations make them especially sensitive to climate change, because a warming climate is enhancing upslope species migration, but human disturbance (especially fire) may in many cases be pushing the treeline downslope. TMCFs are increasingly being affected by fire, and the long-term effects of fire are still unknown. Here, we present a 28-year chronosequence to assess the effects of fire and recovery pathways of burned TMCFs, with a detailed analysis of carbon stocks, forest structure and diversity. We assessed rates of change of carbon (C) stock pools, forest structure and tree-size distribution pathways and tested several hypotheses regarding metabolic scaling theory (MST), C recovery and biodiversity. We found four different C stock recovery pathways depending on the selected C pool and time since last fire, with a recovery of total C stocks but not of aboveground C stocks. In terms of forest structure, there was an increase in the number of small stems in the burned forests up to 5–9 years after fire because of regeneration patterns, but no differences on larger trees between burned and unburned plots in the long term. In support of MST, after fire, forest structure appears to approximate steady-state size distribution in less than 30 years. However, our results also provide new evidence that the species recovery of TMCF after fire is idiosyncratic and follows multiple pathways. While fire increased species richness, it also enhanced species dissimilarity with geographical distance. This is the first study to report a long-term chronosequence of recovery pathways to fire suggesting faster recovery rates than previously reported, but at the expense of biodiversity and aboveground C stocks.

KEYWORDS
carbon allocation, forest structure, metabolic scaling theory, regeneration, species diversity

1 | INTRODUCTION

Tropical montane cloud forests (TMCFs) represent around 14% of all tropical forests, with an estimated area of 2.2 Mkm^2 between 23.5°N and 35°S (Mulligan, 2010). They are characterized by a unique set of biological features including being one of the world's most diverse ecosystems with high levels of endemism and many critically endangered species (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). They are also carbon rich and store high amounts of carbon in their forest biomass and soils (Girardin et al.,

2010, 2013; Zimmermann et al., 2010). In the tropical Andes, many TMCFs sit on organic soils (ca. 360,000 km^2) (Román-Cuesta et al., 2014) with carbon stocks over the range of 137–285 MgC ha^{-1} (Oliveras, Girardin, et al., 2014; Zimmermann et al., 2009). The upper limit of the Andean TMCFs forms a treeline with high-altitude grasslands (*puna* or *páramo* ecosystems) that is a zone of ecological tension where climate and fires play opposite roles. While there is evidence of TMCF species migrating upslope (Feeley et al., 2011) due to increases in mean annual temperature (0.11°C per decade since 1950s, (Urrutia & Vuille, 2009), the treeline has abundant presence of fires (Oliveras, Anderson, & Malhi, 2014; Sarmiento, 2006; Young & León, 2007). Treeline fires are increasingly penetrating into the Andean TMCFs as they tend to burn downslope from the grassland ecosystems through the treeline (Oliveras, Girardin, et al., 2014; Román-Cuesta et al., 2011).

Forest fires are one of the most important drivers of tropical forest degradation (Aragão & Shimabukuro, 2010; van Marle et al., 2016), and are currently one of the main sources of carbon emissions in many tropical regions (de Andrade et al., 2017; Van Der Werf et al., 2010). Fire-driven tropical forest degradation causes major alterations to ecosystems composition, structure and function (Barlow & Peres, 2008; Malhi, Gardner, Goldsmith, Silman, & Zelazowski, 2014) and represents a major threat to global biodiversity (e.g. Peres et al., 2010) and to ecosystem services, such carbon storage and climate regulation (Berenguer et al., 2014; Malhi et al., 2014).

Currently, most forest degradation studies combine several drivers (e.g. logging and fire (Berenguer et al., 2014; Ewers et al., 2016; de Andrade et al., 2017), implying that the responses of forests to disturbance will be idiosyncratic (de Andrade et al., 2017; Chazdon et al., 2016; Connell & Slatyer, 1977). Therefore, there is a pressing need to better understand the mechanism and processes that lead to fire-driven ecosystem degradation, as well as the recovery pathways after fire.

In the lowland Amazon, repeated burning causes irreversible shifts in forest tree-size distribution (Balch et al., 2008; Barlow & Peres, 2008; Barlow, Peres, Lagan, & Haugaasen, 2003), and a reduction in carbon stocks (Zarin et al., 2005). Fires are also a recognized driver of forest degradation and emissions in TMCFs (Asbjornsen, Velázquez-Rosas, García-Soriano, & Gallardo-Hernández, 2005; Asbjornsen & Wickel, 2009; Crausbay et al., 2014; Oliveras, Girardin, et al., 2014; Román-Cuesta et al., 2011). Palaeological records suggest that fires may have caused profound changes in the species diversity of forests in the past, increasing the abundance of generalists (Bush et al., 2015). More recently, in a study in the southern tropical Andes, Oliveras, Malhi, et al., (2014) reported that around 45% of the species in burned TMCFs were fire tolerant or fire thrivers (thrivers being species that improve in performance after fire). However, there is still very little information on the processes and mechanisms that lead to shifts or differences in species composition, forest structure and carbon dynamics after fires in TMCFs. Most importantly, the long-term ecological pathways of TMCF recovery after fire are still, to the best of our knowledge, still largely undocumented.

This study provides an analysis of the short-, mid- and long-term ecological pathways of TMCF recovery after fire in the southern Peruvian Andes. We present a 28-year chronosequence on changes in diversity, carbon dynamics and forest structure after fire. Our objective is to quantify how TMCFS tree biodiversity, carbon stocks and forest structure recover from fire and if they return to pre-burn conditions. We address three specific questions and present several hypotheses:

1. What are the short- and long-term effects of fire on carbon stocks in TMCFs? We hypothesize that fire has a long-term effect on C stocks, and that, on a thirty-year timescale, old-burned forests do not recover C stocks to prefire conditions in the aboveground biomass and soil (Barlow & Peres, 2008; Barlow et al., 2003).

2. Do fire-affected TMCFs recover the forest structure of unburned forests? We hypothesize significant changes over forest structure after fire, with mortality of big stems shortly after fire, and an increase on small stems in medium-term burned forests (Barlow et al., 2003; Berenguer et al., 2014). We expect, however, that old-burned forests will not have reached a mature forest tree-size distribution within the time chronology of this study (28 years) and therefore will deviate from predicted scaling exponents by the Metabolic Scaling Theory (Enquist, West, & Brown, 2009).

3. What are the effects of fire over tree species alpha and beta-diversity, and species turnover? Our working hypothesis is that alpha diversity will be reduced immediately after fire, but diversity will increase with time since last fire, with old-burned forests being more diverse than unburnt forests (Oliveras, Malhi, et al., 2014). However, beta-diversity will not be affected by fire, as species turnover because of fire will override fire effects on species.

2 | MATERIALS AND METHODS

The study area was located in the Cusco Department of Peru (13°53′S, 70°8′W). A total number of 48 plots (30 × 30 m) were sampled at altitudes ranging from 2,180 m to 3,552 m a.s.l. (Table S1). Plots were located near the forest-grassland treeline, and distributed inside or across the buffer area of several parks: the Manu National Park and the Historical Sanctuary of Machu Picchu (Figure 1). We explicitly searched for areas with low human impact to avoid mixed and frequent disturbances (e.g. grazing, fire, logging). Plots were therefore established in remote locations (e.g. up to 2 days' walk). The plots encompassed undisturbed primary forests, and a gradient of primary forests that have been exposed to different levels of fire. Fieldwork was conducted during 2010, 2011 and 2012.

2.1 | Experimental design and fire chronology

We assessed the fire impacts on TMCFs' (1) carbon recovery pathways, (2) structural recovery and (3) biodiversity. We selected a chronology of representative fire-affected, fire-unaffected and
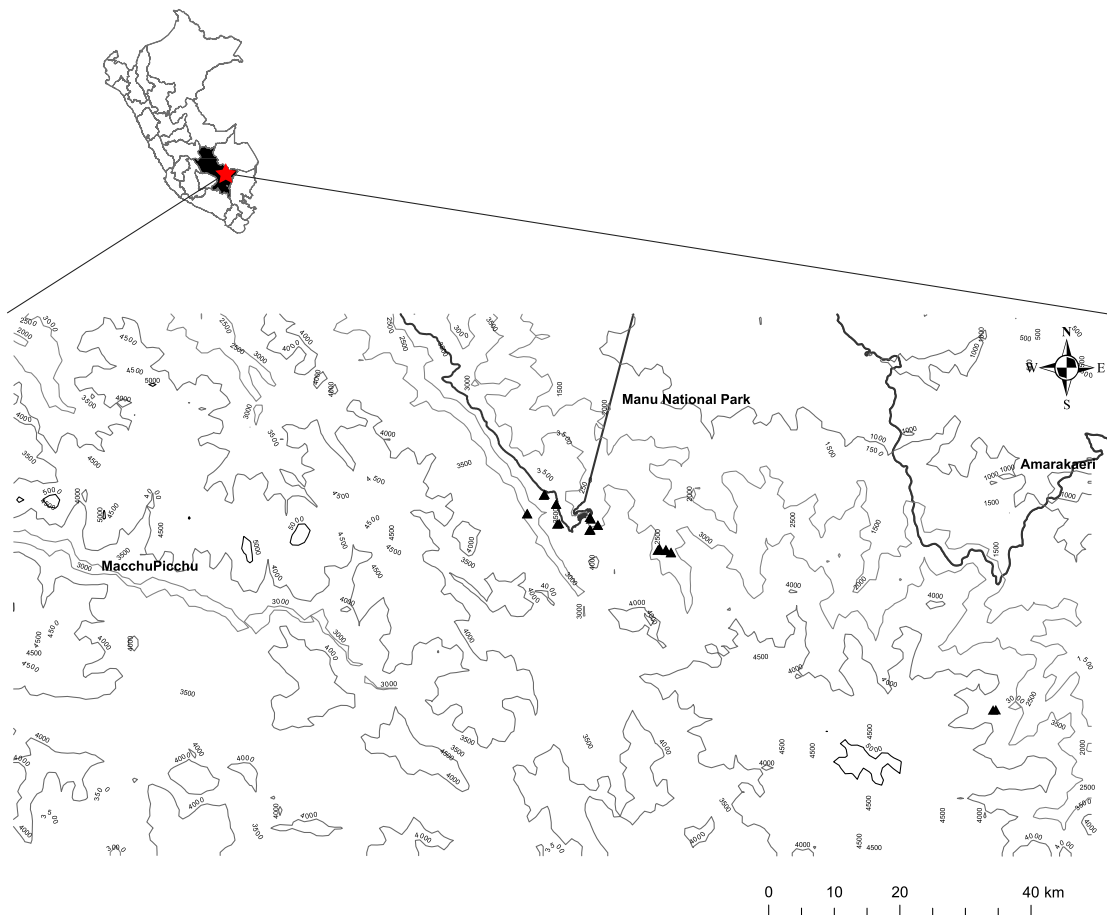
FIGURE 1 Map of the study area in south-eastern Peru (Cusco district) Triangles represent the sampled paired-plot locations selected for the study

carbon-similar forests ecosystems, in what is a classical space-for-time substitution as an alternative to long-term studies (Benscoter & Vitt, 2008; Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013; Dunne, Harte, & Taylor, 2003; Pickett, 1989). We followed the temporal recovery responses through a chronology of burned forests that presented different times since last fire (TLF) subdivided into Recent Burns (RB: 1–4 years since last fire, $n = 9$), Middle-term Burns (MB: 5–9 years since last fire, $n = 8$) and Old Burns (OB: 10–28 years since last fire, $n = 7$).

We obtained the last burning date of the burned forests through local information (local forest rangers, land owners), previous efforts (Román-Cuesta et al., 2011) and satellite records (Oliveras, Anderson, et al., 2014) (Table S1). We selected areas that had suffered crown fires with flame lengths equalling at least the trees' heights (e.g. up to 15 m) and intensities and residence times that allowed organic soil removal (e.g. Oliveras, Anderson, et al., 2014; Román-Cuesta et al., 2011).

To assess fire-specific responses, we followed a matched, or paired-plot design, appropriate for after-only studies that controls for spatial heterogeneity (Van Butsic, Lewis, Radeloff, Baumann, & Kuemmerle, 2017). For every burnt plot, an adjacent unburnt plot was sampled (paired). A total number of 24 paired burned-unburned plots (48 plots), each of 30 × 30 m, were included in the study. We

identified unburnt plots in nearby forests (but at least 50 m from the burned forests) that showed little fire disturbances, were in the same slope (or at least the same aspect and elevation), and were structurally similar.

Due to a myriad of factors (soil, endemism, human influences, climate, land use legacy, etc.), Andean forests show high heterogeneity in forest structure and composition. In spite of it, we expected to see emerging trends from our chronology due to wildfire and explicitly assumed that both unburnt plots and burnt plots in the three chronological groups were structurally similar (similar tree-size distributions) and showed similar carbon allocations among pools (i.e. similar carbon stocks in the aboveground biomass, CWD, soils, etc.) before the fire. The unburnt plots were explicitly selected to maximize homogeneity among these factors, and we further tested this assumption for each carbon pool, with Kruskal–Wallis tests, using the three chronologies (RB, MB, OB) as the grouping factor. The burned plots, because of the strict selection criteria and matched experimental design, were also assumed to be very similar before the fire (Van Butsic et al., 2017).

2.2 | Carbon pools and forest inventories

In each plot, we measured different pools of forest carbon: aboveground biomass (live standing trees), coarse woody debris (dead

standing trees and fallen wood material >2 mm in diameter), litter and belowground biomass (fine <2 mm and coarse roots >2 mm in diameter) and soil organic carbon.

2.2.1 | Standing live and dead trees

We recorded all live and dead standing trees ≥10 cm in diameter at breast height (DBH = 1.3 m). Tree height was estimated as the average value of five independent visual estimates using a clinometer. We recorded all small live and dead stems with DBH ≥2–10 cm in a subplot of 300 m^2 (30 × 10 m). Biomass for each tree was estimated by applying Chave's allometric equation for wet forest stands that includes DBH and height (Chave et al., 2005). Lianas were sampled but were not included in the study as their abundance was very low even in burned forests (Table S1). Trees were identified to species level, but 28% could not be identified to the species level and were identified to genus or family level. We extracted wood samples with a wood corer of 2.5 mm diameter for each tree ≥10 cm DBH and measured its wood density in the laboratory through water displacement methods (Table S2). We used a carbon ratio of 0.5 g C/g biomass.

2.2.2 | Litter

Litter was collected at nine fixed points in each plot, in 25 × 25 cm^2 squares. Material was taken to the laboratory and oven dried at 72°C until constant weight. Components of litterfall included leaves; reproductive organs (fruits and flowers); twigs; epiphytes and bromeliads (all parts combined) and fine debris (unidentifiable particles that pass through 2 mm mesh). We used a carbon ratio of 0.45 g C/g biomass (Girardin et al., 2010).

2.2.3 | Coarse woody debris

Coarse woody debris was assessed using a modification of the linear intercept method (Brown, 1974) along a 30 m transect in the middle of the plot. Fallen dead wood was separated into five diameter classes: (I) <0.6 cm, (II) 0.61–2.54 cm, (III) 2.55–7.5 cm, (IV) 7.51–12 cm and (V) >12 cm. Pieces of fallen dead wood on categories I and II were tallied for the first 10 m along each transect in all plots. Pieces of fallen dead wood in categories III, IV and V were tallied along the entire 30-m transect in all plots. Decomposition class was noted for each piece of fallen wood and was classified into five states, from solid to fully decomposed (Baker et al., 2007). Wood samples were oven dried at 72°C until constant weight and their values divided by water-displaced volumes to obtain wood densities. (Table S3). We used a carbon ratio of 0.5 g C/g biomass.

2.2.4 | Roots

Roots were divided into fine (<2 mm diameter) and coarse (>2 mm). We extracted the fine roots for the first 20 cm of soil at four fixed points per plot, using a soil corer. We measured coarse roots by digging a 1 × 1 m pit at the centre of the plot and extracting all roots at 10 cm-depth intervals until 50 cm, and then 50–100 cm-depth. Coarse roots could not be sampled in all plots, and therefore they are reported for C pools but not accounted for total C stocks. All samples were taken to the laboratory, rinsed and oven dried at 70°C until constant weight. We used a carbon ratio of 0.475 g C/g biomass. Coarse roots were only measured for $n = 8$ ($n = 3$ for RB, MB, and $n = 2$ for OB).

2.2.5 | Soils

Soil samples were extracted at four fixed points per plot using horizon depths Oi, Oe and Oa (Zimmermann et al., 2010). The Oi horizon was characterized by entire recognizable leaves at early stages of decomposition. The Oe horizon was a laminated mixing of leaf fragments and small twigs at a further stage of decomposition, also containing large amounts of small roots. Oa was a compacted dark coloured organo-mineral material, with fewer small roots and frequent presence of charcoal. At each point, we measured the depth of the horizon and we extracted a soil sample of known volume of 20 cm^3. Soil carbon content was analysed for one composite soil sample per horizon and per plot, with a Carlo Erba Elemental Analyser (Milano, Italy) at the University of Saint Andrews (UK). Soil bulk densities were determined from undisturbed samples collected with stainless steel rings of 166 cm^3. Bulk density was calculated as the soil dry weight after subtracting the stone and fine root dry weights (Table S4). Final carbon stock values per horizon were obtained by multiplying the horizon depths by the carbon contents and by the bulk densities, and appropriately transformed to MgC ha^{-1}.

Total carbon stocks were calculated as the sum of all the forest pools. To assess carbon allocation per chronology and fire category (burned/unburned), we first estimated the medians for the different chronologies, for the burned and unburned plots separately. We then estimated the contribution of each pool, for each chronology, as the percentage of their stocks in relation to the median. We ran a statistical test to assess carbon recovery pathways and resilience (i.e. restoring the original conditions): (1) Kruskal–Wallis tests to check for carbon stock differences along time in the burned and unburned plots separately, and (2) Wilcoxon Signed-Rank paired tests to assess carbon responses between the control and the burned plots, along time. We used IBM SPSS statistics version 23. Significance levels were assessed at the 0.05 (significant) and 0.1 (marginally significant) levels.

2.3 | Forest structure

Changes in forest structure were assessed through variations in diametrical tree-size density and relative frequency distributions binned at 1 cm DBH size among plots. We explored the difference in the proportion of grouped tree-size categories in burnt and control plots. In each plot, based on the tree-size frequency distributions, we grouped trees in DBH bins: 2–5, 5–10, 10–20, 20–40 cm, and bigger than 40 cm and calculated the proportion of number of trees within each bin.

We tested differences between burned and mature forest plot structure, by assessing predictions from metabolic scaling theory or MST (Enquist & Niklas, 2001). Metabolic scaling theory predicts that the structure of a forest, as measured by the sizes and numbers of plants in a community will tend to follow an inverse power function (e.g. self-thinning, Yoda, Kira, Ogawa, & Hozumi, 1963; Weller, 1987) with characteristic scaling exponents. Enquist and Niklas (2001), Enquist et al. (2009) proposed a model to explain how the inverse size density relationship could emerge from shared individual plant allometries. They assumed, first, that all individuals share a common allometry of resource use, which is proportional to metabolic rate (B), and B is proportional to M, mass raised to the 3/4 power ($M^{3/4}$); and, second, that all individuals in the community compete for limiting resources such that, in steady state, the rate of resource use approximates that of resource supply (R). Thus, the maximum number of individuals per size class, N_{max}, that can be supported per unit area is related to the average size of an individual as $N_{max} \propto R(M^{-3/4})$. As plant biomass is generally proportional to the 8/3 power of diameter (West, Brown, & Enquist, 1999), the size distribution under approximate resource use steady state, in terms of stem diameter, is predicted to follow an inverse square rule where $N \propto D^{-2}$.

Metabolic scaling theory predicts that under approximate resource use steady state, the $N \propto D^{-2}$ relationship also indicates the forest is in approximate demographic steady state where recruitment and growth are offset by mortality. Thus, many ecological dynamics that influence demography (such as competitive size hierarchies, episodic recruitment and disturbance) will produce systematic deviations away from the MST predicted −2 size distribution (e.g. Coomes, Duncan, Allen, & Truscott, 2003; Kerkhoff & Enquist, 2006, 2007). Deviations away from the −2 exponent then are diagnostic of community reorganization and are useful for understanding (and managing for) ecosystem resilience (Enquist et al., 2009; Kerkhoff & Enquist, 2007). If correct, the MST predictions offer a baseline by which to quantify the relative magnitude of how differing drivers and time size last burn influence forest structure and ecosystem dynamics within and across TMCFs. To test these predictions in our burned plots, we fitted their tree-size frequency distributions using the package powerRlaw (Gillespie, 2015), and compared on whether their scaling exponents differed across time since last fire. As maximum tree size appears to reach a limit, we fit a truncated Pareto distribution to the data, setting a maximum tree size of 300 cm DBH. Exponents were estimated using the Maximum Likelihood Estimate (MLE, White, Enquist, & On, 2008).

2.4 | Diversity: Species richness and turnover

We compared three gradients of dissimilarity to predict shift in species richness and composition: (1) fire chronosequence, (2) burned/unburned status and (3) geographical distance. We estimated alpha diversity using the Fisher's alpha metric based on a species abundance matrix per burned/unburned forests and fire chronosequence, using the function *fisher.alpha()* of the R package vegan (Oksanen et al., 2017). We explored turnover and beta-diversity using the

Sorensen's index (bSOR), Simpson's dissimilarity index (bSIM) and species nestedness (bSNE) using the R package betapart (Baselga, 2010; Baselga & Orme, 2012). We calculated multisite SOR, SIM and SNE with the function *beta.multi()*, pairwised SOR, SIM and SNE along spatial (geographic location) and disturbance gradient (burned/unburned, fire chronosequence) with the function *beta.pair()*, and the SOR, SIM SNE between matched paired control-burned plots using the function *beta.temp()*. We used distance matrices for all pairwise analysis of beta-diversity. The resulting dissimilarity matrices which we then compared with a distance matrix of the main quantifiable parameters (fire chronosequence, geographical distance) using a Mantel permutation test, based on 9,999 permutations. Regressions parameter statistics and 95% confidence intervals were obtained using bootstrap resampling with the *boot()* function from the boot R package (Canty & Ripley, 2017). We transformed the latitude/longitude coordinates of the plots into geographical distances using the *spDists()* function (package sp, Pebesma & Bivand, 2005; Bivand & Pebesma, 2013).
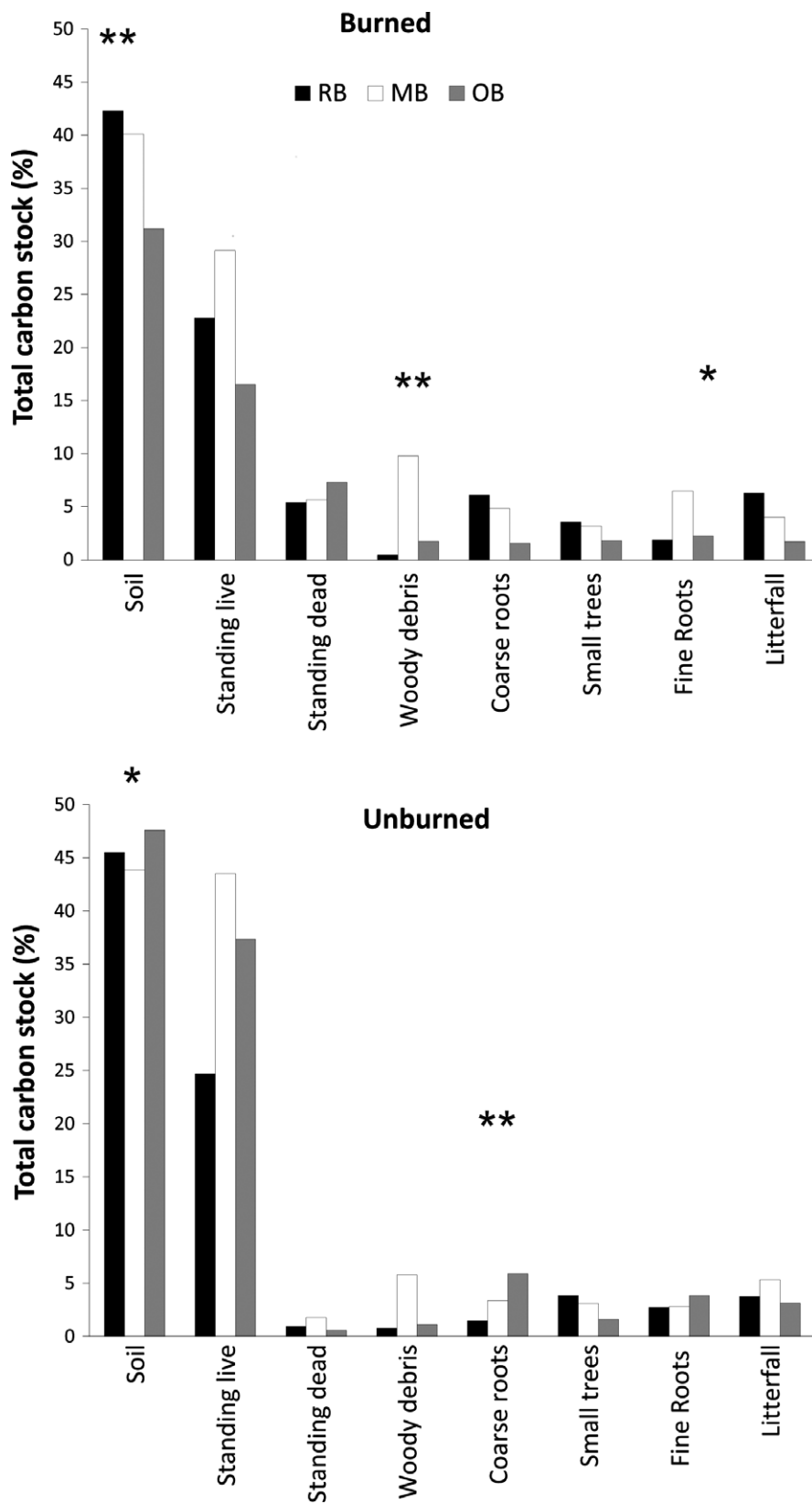
3 | RESULTS

3.1 | Effects of fire on TMCF carbon dynamics

3.1.1 | Responses of carbon stocks along time in burned and control plots

The carbon stocks of unburned plots along time were not significantly different for most of the pools, therefore confirming our assumption that all sampled plots were similar (Figure 2).

The exception was coarse roots C stock, which was significantly different along time in these unburned (Table 1): 19.6 MgC ha^{-1} in the unburned plot from RB category vs. 3.4 MgC ha^{-1} in the unburned plot from OB category. Soils were marginally significantly different (96.7 vs. 158.2 MgC ha^{-1}). Contrarily to the unburned TMCFs, we expected significant differences along time among the carbon stocks of several pools in the burned TMCFs, as an indication of postfire carbon stocks recovery. However, only three pools (CWD, soils and fine roots) showed significant responses (Figure 2, Table 1). Soil was the most dynamic carbon variable in the burned TMCFs, with a ca. twofold increase in soil carbon, in the time-span of 28 years: RB: 48.5, MB: 59.4, OB: 90.3 MgC ha^{-1} (Table 1, Figure 3). Coarse woody debris and fine roots significantly increased too (×3 and ×3.5 respectively), but had accumulation peaks in the middle of the chronology: RB 1.5, MB: 14.5, OB: 5 MgC ha^{-1}, and RB: 1.8, MB: 9.6, and OB: 6.3 MgC ha^{-1} for CWD and fine roots respectively). Contrary to these carbon accumulations, the aboveground biomass (standing live trees) and the standing dead trees of burned TMCFs showed nonsignificant differences with time, although dead standing trees increased their carbon stocks (Table 1). The total carbon stocks of burned plots showed remarkable carbon accumulation: RB: 116.6, MB: 161.1, OB: 295.3 MgC ha^{-1}. As it was the case for the unburned plots, soils also led the increases in total carbon stocks along time (Table 1, Figure 3).

FIGURE 2 Carbon allocation expressed as the percent of total carbon stock in each pool, for the burned (upper panel) and unburned (lower panel) TMCFs. Stars express significant results from Kruskal–Wallis test on the effects on C stocks (over medians) for the burned and unburned TMCFs at *$p < .1$, **$p < .05$

TABLE 1 Carbon stocks (median [min–max]) for all the pools: aboveground (standing live trees, standing dead trees), belowground (fine and coarse roots), coarse woody debris (CWD), litter, soil organic carbon, and derived total carbon, for the burned and unburned plots for the Recent Burns (1–4 years since last fire) (n = 9); Mid-term Burns (5–9 years since last fire) (n = 7); and Old Burns (10–28 years since last fire) (n = 7). p values (columns p) indicate significance of paired burned-control Wilcoxon Signed-Rank tests. Type of carbon response column indicates overall carbon response based on the paired burned-unburned analysis along the chronosequence

Carbon pools MgC ha^{-1}	RB			MB			OB			Type of carbon response ($p_{RB} + p_{MB} + p_{OB}$)
	Burned	Unburned	p_{RB}	Burned	Unburned	p_{MB}	Burned	Unburned	p_{OB}	
Small stems <10 cm	4.1 (0.9–6.5)	8.2 (2.2–24.1)	ns	4.7 (2.5–10.4)	4.4 (1–13.4)	ns	5.2 (0.1–7)	5.4 (0.8–15.4)	ns	No response
Standing live trees >10 cm	26.1 (7.1–88.3)	52.4 (8.5–163.3)	ns	43.2 (10.3–55.5)	61.9 (37.4–123.5)	**	36.6 (5.7–132.3)	113.4 (35.6–192.1)	**	Time lagged
Standing dead trees	6.2 (1–64.6)	2 (0.6–11.8)	*	8.4 (0.7–41.4)	2.5 (1.3–7.9)	*	21.1 (1.1–140.8)	1.9 (0.9–5.6)	ns	Medium term
CWD	1.5 (0–4.4)	1.6 (0–17.7)	ns	14.5 (0.1–56.7)	8.3 (0–30.2)	*	5 (0.3–52.8)	3.7 (0.8–15.5)	ns	Time lagged
Litter	7.2 (2.7–8.0)	8 (1.7–14.3)	ns	6.0 (5.2–11.0)	7.6 (3.5–9.6)	ns	5.0 (5.0–5.0)	10.4 (8.0–12.7)	ns	No response
Soil	48.5 (8.8–150)	96.7 (66.9–315.7)	**	59.4 (26.4–109.6)	62.4 (44.7–116.2)	*	90.3 (66.1–303.7)	158.2 (60.3–360.4)	ns	Medium term
Fine roots	1.8 (0–6.1)	4.1 (1.3–15.6)	**	9.6 (0.8–19.8)	4 (0.5–6.4)	ns	6.3 (0.4–10.2)	10.1 (1.7–18.5)	ns	Short term
Coarse roots[a]	7 (0.5–9.8)	3.1 (1.1–4.0)	ns	7.2 (3.2–11.2)	4.8 (1.8–5.8)	ns	4.6 (3.6–5.5)	19.6 (5.4–20.4)	ns	No response
Total C	116.6 (51.7–79.8)	236.5 (111.2–441.2)	**	161.1 (94.4–214.0)	154.3 (136.7–254.8)	ns	295.3 (238.2–408.5)	341.5 (136.9–494.9)	ns	Short term

[a]For coarse roots n = 8 (n = 3 for RB, n = 3 for MB, and n = 2 for OB).
*p ≤ .1, **p ≤ .05.

3.1.2 | Responses of carbon stocks along time: Burned vs. unburned plots

Fire in TMCFs had a different effect in the carbon stock for the different carbon pools (Table 1, Figure 3), and therefore we identified four possible carbon recovery pathways along the fire chronosequence (Table 1, Figure 3):

1. Short-term carbon responses (significant differences in RB only). This response was found for fine roots and total carbon stocks.
2. Time-lagged carbon responses (no significant difference on carbon stocks immediately after fire, but it becomes significant 5–9 years after fire, that is, RB not significant and MB and OB significant). These responses were found for standing live trees and CWD.
3. Medium-term carbon responses (significant effects up to 9 years after fire, that is, RB and MB significant but OB not significant): this was the case for standing dead trees and soils.
4. No carbon responses (no significant differences on carbon stocks along the 28 years of this chronology): seedlings, large trees (DBH ≥ 40 cm), coarse roots and litter.

Therefore, our results showed that the fire effects in TMCFs C stocks were surprisingly short-lived. At the end of the chronology, all carbon variables showed nonsignificant differences against their unburned paired plots except for standing live trees, whose lack of carbon recovery persisted after 28 years, mainly affecting small-medium trees (DBH 10–40 cm) (Figures 3 and 4). There were no significant differences on soil carbon and on total carbon (sum of all carbon pools) stocks between unburnt-burnt plots at the MB and OB categories (Figure 3).

3.1.3 | Responses in carbon allocation

Relative to their total carbon stocks, both the burned and unburned TMCFs consistently held the most carbon in the soil and aboveground biomass (standing live trees) along time (Figure 2). However, in the unburned plots soils and standing live stocks consistently represented ≥70% of the total carbon, while in the burned plots the contribution to total carbon was lower and more time-dependent (ca. 60% for RB and MB, and 45% for OB). The pool with least carbon allocation varied between the burned and unburned forests: standing dead trees in the case of the unburned plots (≤2.5% in all the chronologies), while the burned plots showed that CWD was the lowest for the RB and OB plots. The burned forests showed standing dead trees as the third highest allocation along the chronology (5%–7.5%), followed by litterfall (5%–2.5%), whose contribution decreased with time and peaked in the RB plots (Figure 2).

3.2 | Effects of fire on TMCFs forest structure

The tree-size distributions were similar for all plot types and fire chronosequences. We observed a bimodal distribution of tree sizes

with a higher relative frequency of small stems (smaller than 10 cm DBH) and of trees between 10 and 15 cm DBH (Fig. S1). However, the burned plots had consistently a higher relative frequency of the smallest stems (2–5 cm DBH) than the unburned plots (Fig. S1), suggesting regeneration through either recruitment or resprouting after fire. Indeed, in the RB and MD fire categories, the proportion of smallest stems (2–5 cm DBH) was significantly higher in the burned plots compared to their paired unburned plots (Figure 4). Compared to the proportion of trees in the unburned TMCFs, the proportion of 5–10 cm diameter trees was significantly lower in burned plots in RB (probably due postfire mortality), nonsignificantly different in the MB category, and significantly higher in the burned plots in the OB category—suggesting postfire recovery. Interestingly, there were no significant differences in the proportion of larger trees between recently burned plots and their paired unburned plots, while there was a significantly less proportion of trees 10–40 cm in the burned plots in the MB category, suggesting medium-term responses after fire in these tree-size categories (Figure 4).

The MLE exponents of plot-specific tree-size frequency power-law distributions increased with time since last disturbance, converging to the exponent of −2 in old burned plots, confirming that these forests experienced a directed succession towards primary forests (Figure 5). Our results suggested a wide variation of disturbance state within the first 10 years after disturbance and a convergence towards a size distribution consistent with a steady-state mature forest at about 15 years after fire.

3.3 | Effects of fire over TMCFs species richness and turnover

The unburned TMCFs in the RB (seven out of nine sites) and MB (six out of eight) fire chronosequences usually presented a higher number of species than the burned plots (Table S1), but the difference was not significant when expressed as a diversity measure (Fisher's alpha, RB: $F = 0.77$, $p = .390$; MB: $F = 2.00$, $p = .109$, Figure 6). For the OB sites, however, four of seven burned plots had more species than their paired unburned plots, with a significantly higher Fisher's alpha coefficient than the control plots ($F = 3.62$, $p = .041$, Figure 6).

Total species dissimilarity among plots showed a high species turnover between plots (bSOR = 0.973, bSIM = 0.965), which was similarly partitioned between control and burned plots (Table S5). When looking at dissimilarity within fire chronosequences (Table S5), the bSOR values between burned and unburned plots were usually slightly higher in the burned plots, showing higher nestedness in the burned plots, especially in the RB and OB chronosequences (Table S5).

Paired-plot dissimilarity (i.e. that of matched paired burned-unburned plots) ranged from site to site from bSOR = 0.95 (WAY2 site) to bSOR = 0.51 (PLGD site) (Table 2). For all sites but ALF, bSIM was higher than bSNE, revealing that changes in species were more associated to species turnover than to nestedness. Dissimilarity partitioning also revealed that usually those sites with higher paired bSOR had a very small contribution of bSNE, i.e. that most of the differences in species composition were associated to species turnover and little to nestedness, and that sites with more shared species (i.e. lower values of bSOR) showed also more nestedness (Table 2). However, this was not always the case (e.g. PAIT and PLGRD showed bSOR, 0.6 and bSNE < 0.10).

When species dissimilarity was explored in terms of geographical distance, Mantel permutation tests revealed no increases in species dissimilarity with distance for the unburned plots in any of the three time categories (RB: $r = .170$, $p = .12$; MB: $r = −.145$, $p = .838$; OB: $r = .432$, $p = .060$, Figure 6), but the species dissimilarity was significant for burned plots on the RB and OB categories (RB: $r = .336$, $p = .021$, MB: $r = .148$, $p = .232$; OB: $r = .660$, $p = .003$, Figure 7).

4 | DISCUSSION

The long-term effects of fire on tropical forests are still largely unknown, and to the best of our knowledge this is the first study that utilizes a long-term chronosequence to assess the effects of fire and recovery pathways of TMCFs to fires, with a detailed analysis on carbon stocks, forest structure and diversity recovery pathways.
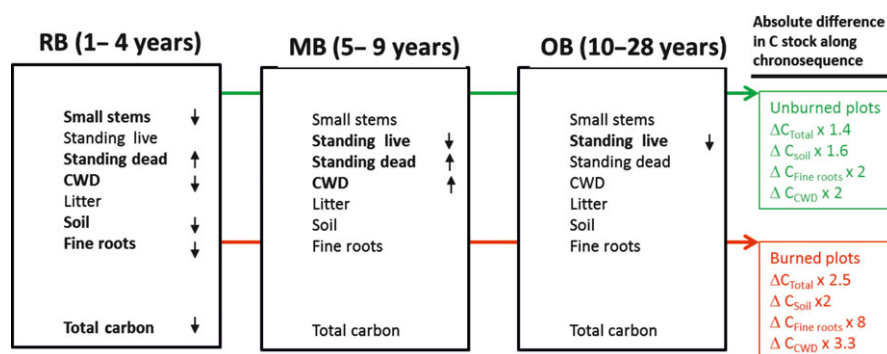
FIGURE 3 Panels show relative differences in C stocks for each C pool compared to the paired unburned plots. Significant differences are highlighted in bold, and arrows indicate significantly higher (upper arrow) or lower (lower arrow) C stocks in the burned plots compared to the unburned. On the right side, absolute difference in carbon stocks along the chronosequence for burned plots (red) and unburned plots (green). For absolute values, refer to Table1
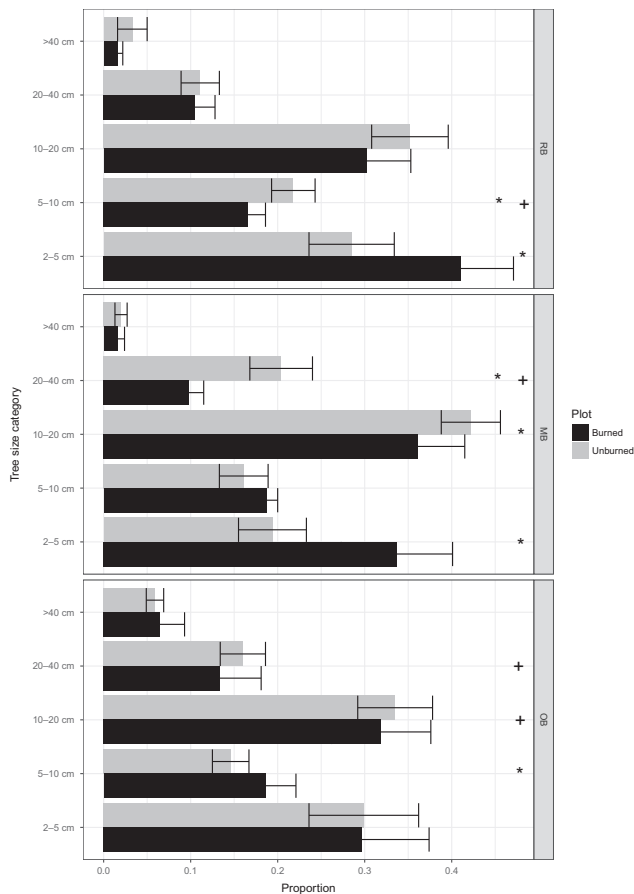
FIGURE 4 Relative proportions (with regard to total number of stems) of trees per tree-size diameter classes in burnt (B) and unburnt (U) forests along the fire chronosequence. RB, Recent Burns (1–4 years since last fire); MB, Mid-term Burns (5–10 years since last fire); and OB, Old Burns (10–28 years since last fire). Error bars represent standard deviations. Star symbols (*) indicate significant differences in the proportion of trees, and sum symbols (+) indicate significant differences in C stocks between U and B plots for that tree-size category at $p < .05$ (Wilcoxon-rank tests)

4.1 | Effects of fire on forest carbon stocks

Our study shows that carbon stocks recovery depends on the selected pools (i.e. total carbon vs. aboveground carbon), and on the time-allowed to recover. Our results showed four possible recovery pathways (short-term, middle-term, no response and time-lagged, Table 1). Thus, if we look at the total carbon stocks, TMCFs are highly carbon resilient as there was a surprisingly short-lived significant effect on carbon stocks for all forest pools and for total carbon, with the exception of the standing live tree pool. However, if we only looked at aboveground biomass (standing live trees), then we could conclude that TMCFs are highly carbon nonresilient with time-lagged carbon responses (appearing after 5–9 years) leading to significantly reduced carbon stocks after 28 years. These results are supported by the time-lagged effects on CWD and standing dead tree biomass, suggesting that fire-associated mortality shows a medium-term response—some trees die charred from the fire, but a
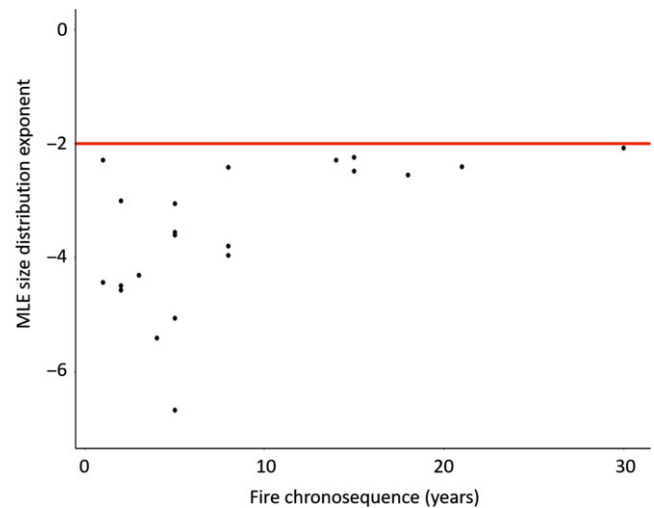
FIGURE 5 Maximum likelihood estimate (MLE) for the power-law fit of the tree-size distributions of each burned plot through time since last fire

number of them might not immediately die from fire, but result highly damaged and be unable to recover or be more prone to herbivore or pathogen attacks.

Soil carbon stocks showed an unexpected and remarkable medium-term recovery at 5–9 years after fire, which was confirmed by the significant positive increase of soil carbon stocks along time for both the burned and the unburned plots, separately (Table 1). Similar to boreal peatlands (Turetsky & Wieder, 2001; Turetsky et al., 2015) and several tropical soils (e.g. "terra-preta" in the Amazon, Glaser, Balashov, Haumaier, Guggenberger, & Zech, 2000), Andean montane cloud forests have high soil carbon densities (Gibbon et al., 2010; Oliveras, Girardin, et al., 2014; Zimmermann et al., 2010) which relate to low decomposition rates due to low temperatures that allow the slow incorporation of labile carbon pools. In TMCFs, fine roots and CWD and litter- are labile carbon pools that are behind the temporal increases in soil carbon, and should result in a reasonably closed carbon balance. However, the observed rapid increase of soil carbon stocks in the burned plots ($\Delta C_{soil} = 42$ MgC ha^{-1} in 28 years), can only be partly explained by the contribution of these labile carbon variables ($\Delta C_{CWD} = 11.5$ MgC ha^{-1} and $\Delta C_{fineroots} = 3$–6 MgC ha^{-1} and $\Delta C_{litter} = 0$–1.1 MgC ha^{-1}) (Table 1), suggesting some external entrance of carbon material into the soil pool. A component that may have influenced on the recovery of soil C stocks is the *Sphagnum* moss. The genus *Sphagnum* is one of the most important groups of plant species sequestrating carbon in temperate and northern bog ecosystems (Berendse et al., 2001), and an important genera for TMCFs, because of the low decomposability of the dead material it produces (Berendse et al., 2001). The genus-specific p-hydroxy-b-carboxymethyl-cinnamic-acid strongly retards the decay of litter of both *Sphagnum* and other neighbouring plants (Clymo & Hayward, 1982). Moreover, by creating anoxic and acid conditions, *Sphagnum* strongly reduces microbial degradation of the litter of co-occurring plant species. Therefore, carbon sequestration in peatlands
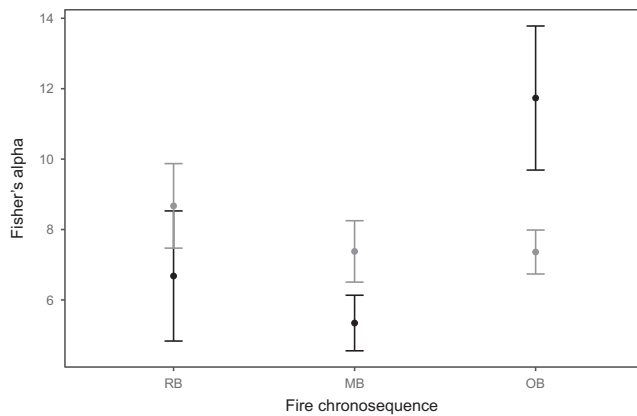
FIGURE 6 Fisher's alpha index for burnt (black) and unburnt (grey) TMCFs forest along the fire chronosequence. RB, Recent Burns (1–4 years since last fire, $n = 9$); MB, Mid-term Burns (5–10 years since last fire, $n = 8$); and OB, Old Burns (10–28 years since last fire, $n = 5$)

strongly depends on *Sphagnum* mass growth (Berendse et al., 2001). *Sphagnum* has also been recognized as a keystone genus for habitat restoration of bogs and peatlands (Gorham & Rochefort, 2003; Rochefort, 2000). Unfortunately, this study did not directly quantify *Sphagnum* moss and therefore we cannot prove that *Sphagnum* was the ultimate responsible for the reported soil C recovery, but our results clearly point out for a future research priority in this matter.

4.2 | Forest succession pathways

There were medium-term responses (5–9 years) on the proportion of small stems, with an increase of stems <5 cm in the burnt plots and a decrease of proportion of stems between 5 and 10 DBH in the recently burned plots. This was reflected in lower C stocks on the 5–10 cm DBH category, but not in the 2–5 cm DBH category. The increase on the smallest size stems proportion is likely to be due to regeneration patterns via recruitment or resprouting (Oliveras, Malhi, et al., 2014), and the decrease of stems 5–10 cm is likely to be caused by a high mortality of these stems after fire. Small stems contribute little to total C and therefore the variation of tree sizes within this smallest DBH category (e.g. more 4 cm trees in the unburnt plots and more 2.5 cm trees in the burnt plots) may override absolute differences in C between paired plots. However, mortality of 5–10 cm stems after fire was high and led to a thinning process of trees within this category, reflected in lower proportion of trees and C stocks.

In the mid-term (5–9 years), the lower proportion of 10–40 cm trees in burned TMCF provides further support to the time-lagged mortality and woody decomposition dynamics on these forests. However, recovery is clearly reflected in the much larger proportion of small stems (2–5 cm) in the burned TMCFs 5–9 years after fire, which results in a larger proportion of 5–10 cm in the long term (>10 years after fire). The lack of significant difference in the proportion of trees, but significant difference in long-term C stocks

TABLE 2 Pairwise dissimilarity indices (bSOR, Sorensen's; bSIM, Simpson species turnover; bSNE, nestedness) between paired burned-unburned plots. TLF, fire chronosequence category (see text for details). Site: site code where a paired pair burned-unburned plots were sampled (Table S1)

TLF	Site	bSIM	bSNE	bSOR
RB	AHO	0.571	0.189	0.760
	ALF	0.167	0.511	0.677
	CUSI	0.731	0.028	0.759
	QORI	0.333	0.238	0.571
	SAC	0.462	0.170	0.632
	SUNCH	0.875	0.014	0.889
	WAY1	0.560	0.032	0.593
	WAY2	0.905	0.004	0.909
	WAY3	0.613	0.018	0.631
MB	CHALL	0.615	0.128	0.743
	JAP	0.706	0.031	0.737
	LAG	0.333	0.187	0.520
	PAIT	0.500	0.088	0.588
	PLGRD	0.471	0.043	0.513
	WACH	0.765	0.061	0.826
	WAY2a	0.944	0.004	0.949
	YASP	0.667	0.054	0.721
OB	ACHI	0.867	0.025	0.892
	INKA	0.545	0.029	0.574
	QUIPE	0.429	0.275	0.704
	ROMPE	0.538	0.128	0.667
	WINAY	0.538	0.048	0.586
	YAN	0.708	0.066	0.774
	YAN2	0.647	0.134	0.782

in 10–40 cm DBH trees may be attributed to different dynamics in succession patterns—our fire chronosequence includes a range of years, and therefore variability in the responses. This is also reflected in the large range of scaling exponent when fitting power-law tree size scaling laws to the tree-size distribution of the burned plots (Figure 3). Successional trajectories are known to be largely uncertain (Chazdon et al., 2016)—in a recent study of forest succession, it was identified that plot identity explained over 60% of the total variance on stem density, overriding stand age (Norden et al., 2015).

Our results support the metabolic scaling theory that predicts a scaling relationship associated to disturbance (Enquist et al., 2009). The MST predicts that the parameters of tree-size distribution scaling laws (their coefficients and exponents) are significantly correlated with the stem density, and that the shape of the size distributions (i.e. its exponents) is indicative of time since disturbance (Kerkhoff & Enquist, 2007). According to this, we may predict that burned TMCFs have recovered their ecosystem function and are structurally similar to primary undisturbed forests from 14 years after fire, when they asymptotically converge to a scaling exponent of −2 (Figure 3, Kerkhoff & Enquist, 2007).
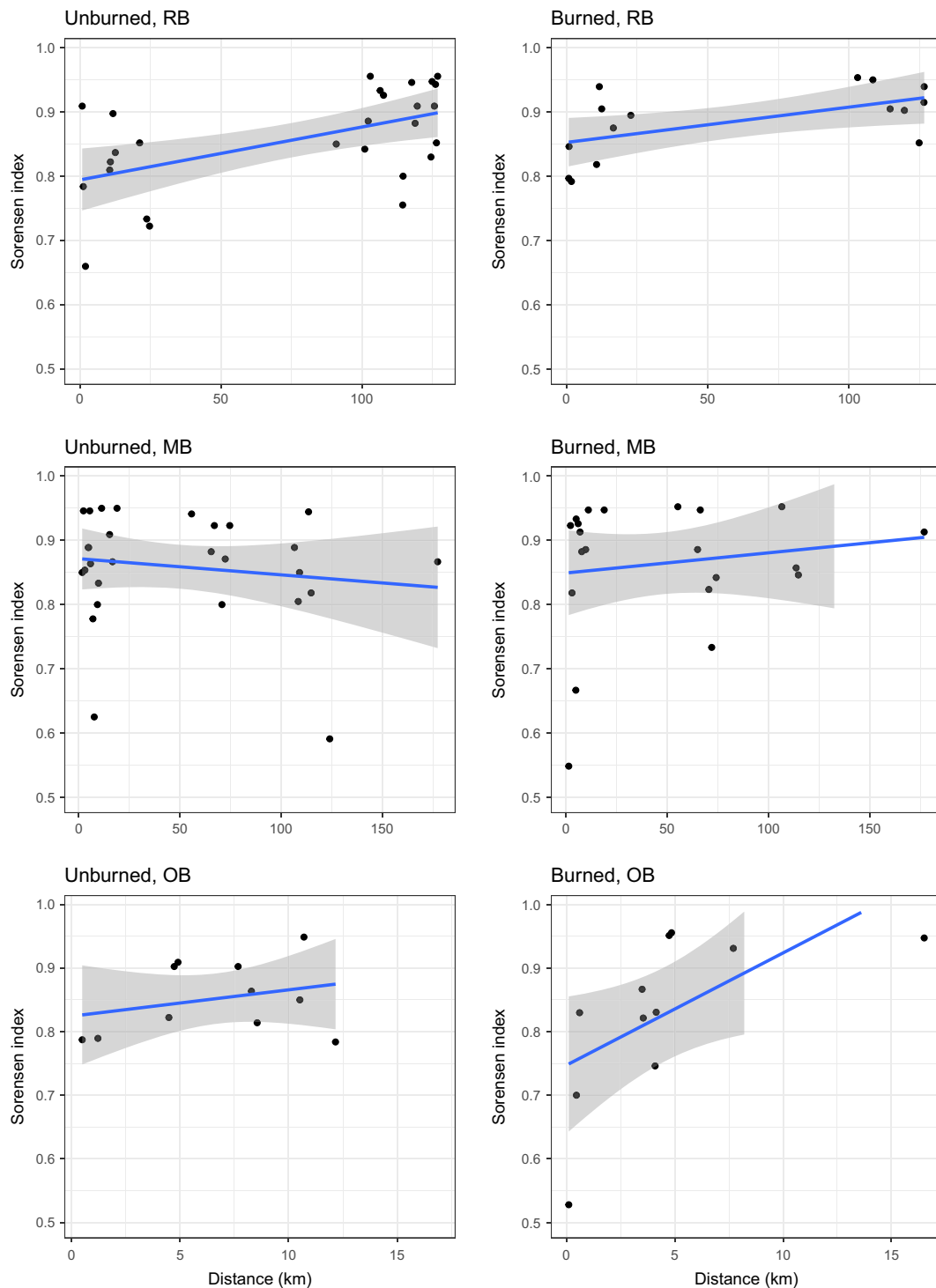
FIGURE 7 Relationship between Sorensen's similarity index and geographical distance between the studied plots, grouped by the fire (burned, unburned) and time since last fire chronosequence (RB, recent burn; MB, mid-term burn; OB, old burn)

4.3 | Effects of fire over diversity

All sites showed high levels of species richness, regardless of disturbance. Our results support the observations that fire enhances diversity in the long term (>10 years), as previously reported by other studies in the area (Oliveras, Malhi, et al., 2014) as well as in other Neotropical lowland forests (Balch et al., 2011; Devisscher, Malhi, Rojas Landiar, & Oliveras, 2016). Palaeoecological studies provide evidence that fire has been present in TMCFs since the beginning of the Holocene (e.g. approx. 11,500 years) (Urrego, Silman, Correa-

Metrio, & Bush, 2011; Urrego et al., 2013), which may have already induced a species-composition shift with the disappearance of fire-sensitive species (Bush et al., 2015).

Nevertheless, our study shows how fire enhances species dissimilarity with geographical distance in recently burned and old burned plots. In the mid-term burned plots, species succession and turnover may override overall effects in species dissimilarity. Our beta-diversity analyses highlight the high species turnover in the region, due to the high biodiversity values that make TMCFs one of the biodiversity hotspots of the world (Myers et al., 2000).

4.4 | Overall ecological responses

Time-lagged responses have been identified in tropical lowland forests as an ecological response of trees that are not adapted to fire, with a preferential mortality from large trees (Barlow et al., 2003; Berenguer et al., 2014). Interestingly, high-elevation TMCFs show time-lagged responses after 5–9 years that persist along the rest of the chronosequence, but these carbon reductions were led by the mortality of small and medium tree sizes (i.e. DBH 10–20 cm and 20–40 cm). Thus, while time-lagged responses in TMCFs may suggest nonfire adaptation, the lack of fire effects on large trees suggests some fire tolerance. However, time-lagged responses may not only relate to fire susceptibility but rather to slow forest dynamics in these cold and cloudy ecosystems, with particularly slow stem productivities as suggested by Malhi et al. (2017) in their comparative estimates of forest NPP along an elevational gradient that cover our study area (i.e. NPPstems of ca. 1.1 ± 0.11 MgC ha^{-1} yr^{-1} in $\geq$3,020 m a.s.l., compared to NPPstems of ca. 2.7 ± 0.33 MgC ha^{-1} yr^{-1} in $\leq$210 m a.s.l.). Fire tolerance has long been described in TMCFs through resprouting mechanisms which promotes the survival and generalized expansion of fire-resistant TMCFs tree genera (e.g. *Clethra*, *Oreopanax*, *Weinmannia*) with the detriment of fire-sensitive species that only thrive in isolated fire protected patches (i.e. *Polylepis*, *Clusia*) (Oliveras, Malhi, et al., 2014; Román-Cuesta et al., 2011).

4.5 | Challenges in monitoring fire disturbance

Assessing changes in forest structure, diversity and carbon stocks following fire disturbance is a major challenge that includes the challenge of monitoring before natural burning events, and having to rely on experimental approaches with obvious caveats and limitations. The natural high forest heterogeneity of TMCFs ecosystems, together with noncontrolled treatment conditions and the statistically low number of plots in our research, can lead to underestimations in the significance tests (Type II errors). In practice, this means that nonsignificant responses as those observed in Table 1 may be the result of large data variability. Nonetheless, the strict sampling design and careful data analysis allows to infer processes such as successional pathways, supported with new ecological theory, ensures the validity of the presented results, and this study still responds to the largest and more ambitious field work done on recovery pathways of TMCFs.

4.6 | Implications for conservation

This study provides a detailed description of the pathways to recovery of TMCF after fire disturbance, which has important implications for their conservation. Our results show the immediate losses in carbon, and forest structure after fire, and a gradual recovery over time of about 15 years. The good news is that our results show a relative rapid recovery on soil carbon–in comparison, forest recovery of tropical lowland forests is around100 years. However, this comes at a price, and our results indicate that the highest price might biodiversity and aboveground C stocks: the most fire-sensitive species may disappear, and other more fire-tolerant species may replace them. Therefore, burned TMCFS may recover total C stocks (although not standing live carbon stocks) and tend towards a forest structure of a primary forest within three decades after fires, but their species composition will be different from undisturbed forests. Therefore, investments in avoiding further disturbance can ensure the recovery and high carbon storage large carbon in TMCFs, hence constituting a great conservation opportunity.

In this century, the Andean region and most montane areas are experiencing rises in temperature, elevation of the lower cloud level (Malhi et al., 2010), and increasing droughts (Román-Cuesta et al., 2014). Severe droughts in the region enhance the occurrence of fires and with this the chance of recurrent burning (Oliveras, Girardin, et al., 2014; Román-Cuesta et al., 2014). The tropical Andes host the largest fraction of the world's TMCFs, and given the climatic, edaphic and biological similarities among TMCFs, we anticipate that any results of this study will probably apply for many other fire-threatened TMCFs in the world. Therefore, if we are to protect these hugely important systems in terms of ecosystem services, and climate change mitigation strategies, postburn protection of these forests is imperative.

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