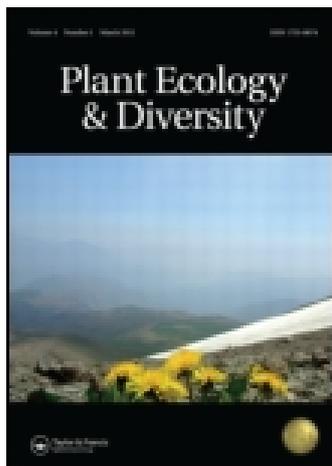


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Changes in forest structure and composition after fire in tropical montane cloud forests near the Andean treeline

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Background: In tropical montane cloud forests (TMCFs) fires can be a frequent source of disturbance near the treeline.

Aims: To identify how forest structure and tree species composition change in response to fire and to identify fire-tolerant species, and determine which traits or characteristics are associated with fire tolerance.

Methods: Shifts in forest structure and diversity were assessed on 15 paired plots in burnt and unburnt (control) forests, along a fire chronosequence. Species were classified as fire-sensitive, fire survivors or fire thrivers, using a fire tolerance index. Regression and tree analyses were used to determine which traits contributed to the fire tolerance of species.

Results: There were more small- and medium-sized trees in the burnt plots independent of time since the last fire. There were shifts in family importance value and in species diversity among the plots. Of the 73 species analysed there were 39 fire-sensitive species, 19 fire survivors and 14 fire thrivers. Sprouting ability and biomass showed a positive relationship with the fire tolerance of species.

Conclusions: There were immediate as well as long-term (up to 15 years) effects of fire on forest structure and species composition, suggesting that TMCFs take more than 15 years to regenerate from a fire. Long-term studies are needed to fully understand regeneration patterns of TMCFs after fires.

Keywords: bark thickness; fire sensitivity; Peruvian Andes; species diversity; sprouting, tree size; wood density

Introduction

Despite their limited global distribution, tropical montane forests harbour exceptionally high levels of biodiversity and endemism (Myers et al. 2000). In Central and South America, they spread over the Andes between about 20° S and 20° N and at elevations above ca. 1000 m (Troll 1956; Stadtmüller 1987). The montane forests of the Andes and the adjoining Amazonian lowlands are the most biodiverse places on Earth, and are thought to host one-sixth of all plant species (Myers et al. 2000).

Tropical montane cloud forests (TMCFs) occur at elevations typically between 2000 and 3000 m asl in the tropical eastern Andes, although they can occasionally be found above 3500 m asl, and are characterised by frequent fog, mist or clouds (Stadtmüller 1987; Ellenberg 1964). TMCFs in the southern tropical Andes sit immediately below the high-elevation *puna* vegetation, with a shrubby transition area between the *puna* and TMCFs. However, this transition vegetation has disappeared in many areas due to frequent fire events and livestock rearing activities (Young and León 2007). This treeline ecotone is a zone of ecological instability (Román-Cuesta et al. 2011). On the one hand, a warming climate with possible rising cloud elevation would favour the forest to migrate in elevation into today's *puna* (Foster 2001; Bruijnzeel et al. 2011). On the other hand, higher flammability of the *puna* due to

the drier climate than in the TMCF, and increased human activities (resulting in an increase in fire frequency and more livestock), may extend the *puna* downslope, resulting in a forest retreat (Román-Cuesta et al. 2011). Feeley and Silman (2010) and Feeley et al. (2011) reported that tree species from TMCFs might migrate upslope in response to increasing temperatures, but they warned that if current patterns of human land-use above the treeline continued, species found above ca. 2400 m asl would no longer be able to migrate and would experience a net decrease in population sizes.

TMCFs have traditionally been considered to be fire-sensitive ecosystems (Shlisky et al. 2007), but paleoecological records in the south-eastern Andes showed that, since 12,000 calendar years BP, a drier climate and an increased fire frequency have caused forests to retreat downslope and virtually eliminate formerly extensive *Polylepis* woodlands (Urrego et al. 2011). In a similar fashion to other montane areas of Central America and the Andes, it is believed that human occupation has changed fire ignition patterns at the treeline, although evidence of this human occupation is geographically varied. For example, in the Cordillera Central (Dominican Republic), Martin et al. (2011) reported that the first human occupation evidence appeared at the end of the nineteenth century, which coincided with an increase in fire frequency in the area.

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In the Peruvian Andes, however, Young and León (2007) recognised that humans have profoundly changed forest habitats in the highlands for millennia, through processes that included the use of grassland/rangeland fires. In the northern Peruvian Andes, Bush et al. (2005) found a sharp increase in charcoal abundance during the last 1200 years that corresponds with archaeological evidence of expanding human presence in the region.

Although there is increasing literature documenting fire disturbance effects on these systems (e.g. Asbjornsen et al. 2005; Hemp 2005; Asbjornsen and Wickel 2009; Román-Cuesta et al. 2011), there is comparatively little quantitative research on the spatial and temporal variability of fires upon Andean ecosystems and how fires interact with other forms of forest degradation across different spatial and temporal scales. Similarly, there is no information about fire behaviour dynamics (rates of spread, flame heights, residence time and intensity). Research on fire behaviour is essential in order to understand the implications of fire, characterise forests' vulnerability to fire and define potential tipping points from which tropical montane forests may no longer recover. Key areas of ecological interest include tree mortality, biodiversity loss, forest regeneration and carbon and nutrient dynamics (Barlow et al. 2011).

Climate and land use changes at the treeline may result in a shift of TMCFs to more fire-dependent plant communities that no longer have sufficient resilience to re-establish the original TMCFs' vegetation (Asbjornsen and Wickel 2009). For example, changes in fire regimes in the TMCFs of Mount Kilimanjaro, Tanzania, lead to a depression of *Erica* shrublands to lower elevations, replacing closed *Erica* and *Hagenia-Podocarpus*-dominated TMCFs (Hemp 2005). TMCFs in Central America, the Caribbean and Mexico are also showing signs of replacement by adjacent fire-dependent pine-oak forests (Ramirez-Marcial et al. 2001; Martin et al. 2007, 2011). Nevertheless, the dynamics

of TMCFs' regeneration remains poorly studied, and comprise a complex interaction between climate change, human land use and disturbance regimes (e.g. Wesche et al. 2000; Cierjacks et al. 2008; Wesche et al. 2008). Further studies in this direction are needed to be able to fully understand the processes underlying TMCFs' regeneration following fire events.

Here we report a study that examined the effects of forest fires at the Andean treeline on forest biomass, structure and tree species composition, based on an inventory of paired burnt and unburnt forests in the Andes of south-eastern Peru. We asked three specific questions: (1) how does forest structure (i.e. stem and tree density, tree-size distribution) change in response to fire? We hypothesised that fire would cause shifts in forest structure by killing the above-ground biomass of a large proportion of trees, some of which will regenerate by sprouting; (2) how is forest species composition affected by fire? We hypothesised that burnt forests would shift in composition towards a less diverse tree community; (3) can we identify fire-tolerant species, and determine which traits or characteristics are associated with fire tolerance? We hypothesised that bark thickness, resprouting ability and tree size would be predictors of fire tolerance of species.

Materials and methods

Study area

The study area was located in the Cusco Department of Peru ($13^{\circ} 53' S$, $70^{\circ} 8' W$), in the Santa Teresa and Paucartambo Districts. We selected 15 sites in TMCFs: six sites in the Santa Teresa District and nine sites in Paucartambo, at altitudes ranging from 2180 m to 3552 m asl. Several plots were located in the buffer area of Manu National Park and the Historical Sanctuary of Machu Picchu (Figure 1).

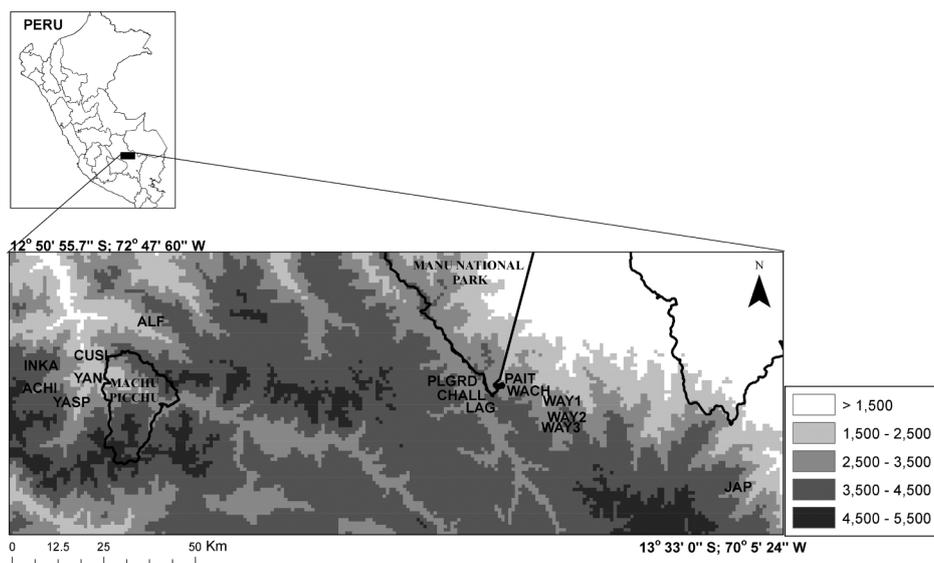


Figure 1. Location of the sample plots in tropical montane cloud forest stand near the treeline, eastern Andes, Peru. Each point represents a site where paired plots were sampled (one burnt and one unburnt plot). Site codes: ACHI, Achirayoc; ALF, Alfamayo; CHALL, Challabamba; CUSI, Cusihualpa; INKA, Incahuasi; Jap, Japu; PAIT, Paititi; PLGRD, Pilco Grande; WACH, Wayqecha; WAY1, WAY2, WAY3, Wayzampilla; YAN, Yanatile; YASP, Yaspay.

The study area has marked seasonality in precipitation but low seasonality in temperature (Lieth et al. 1999). Mean precipitation tends to decline with elevation (Girardin et al. 2010). Drier and cooler weather prevails in the area from April to October, with July being the coolest and driest month. In the Santa Teresa District, mean annual rainfall was 2015 mm and mean annual temperature 12.4°C for the period 1999–2010 (Huayllabamba meteorological station, 3000 m asl in elevation, Servicio Nacional de Areas Naturales Protegidas por el Estado, Peru (SERNAMP)). In the Paucartambo District mean annual rainfall was 1980 mm and mean annual temperature 9.0°C for the period 2004–2010 (Acjanaco meteorological station, 3487 m asl elevation, Servicio Nacional de Meteorología e Hidrología del Perú (SENAMHI)). However, there is likely to be high spatial variability in rainfall according to aspect, position and topography within the study site. Both valleys showed similar annual cloud frequency (K. Halladay, unpublished data).

Sampling sites

We chose a paired-plot design, carefully matching paired control (unburnt) and burnt plots of 900 m² in area (30 m × 30 m). We assumed that forest structures before the fire were similar in the control and burnt plots. All the unburnt plots were mature TMCFs that had no known history of recent disturbance (grazing, logging, fire), although they might have been affected by either landslides or fire at some stage in the past due to the area being a highly dynamic environment. We were able to identify burnt forests up to 15 years after the fire event. Burnt and control plots were separated by at least 50 m and were comparable in terms of elevation, slope and orientation (Table 1). Burnt plots were placed at least 10 m inside the boundary of the burnt zone to

avoid heterogeneity at the border. This limited the available site selection as we observed that many fires had heterogeneous penetration in the forest, with long and narrow fire fingers. Ease of access was another limiting factor in site selection because all sites had to be located less than two days walking distance from the nearest road, and within two hours distance walking from a water source. Field work was conducted between April and October 2010.

It was not possible to obtain any information about past fire history in the area so we do not have any information on fire recurrence, but all selected unburnt sites had similar forest structure (mature montane forest, no signs of disturbance). We obtained the latest burning date (year) by consolidating several independent opinions (local people, forest managers, land owners). According to these dates, sites were classified according to time since last fire (TLF) in the burnt plot: recent burn (1–5 years since last fire, RB), mid-term burn (6–10 years since last fire, MB) and old burn (11–15 years since last fire, OB).

Inventories

In each plot, we described forest structure by recording all live and dead trees ≥10 cm in diameter at breast height (DBH) (DBH = 1.3 m). Tree height was estimated as the average value of five independent visual estimates. We recorded all live and dead stems with a DBH ≥2.5 cm in a subplot of 300 m² (30 m × 10 m). Biomass for each tree was estimated by applying the Chave et al. (2005) allometric equation for wet forest stands that includes DBH and height. Lianas were not included in the study. Where possible, trees were identified to species level, otherwise they were classified to genus or family level (28% of total individuals sampled could not be identified to the species level). We excluded from the analysis 69 individuals that could

Table 1. Plot description and spatial variables of the paired unburnt and burnt plots, eastern Andes, Peru.

Site code	Unburnt					TLF	Burnt				
	Elevation (m a.s.l.)	Slope (%)	X	Y	ASP		Elevation (m a.s.l.)	Slope (%)	X	Y	ASP
ACHI	2680	56	-13.16512	-72.68154	W	OB	2660	49	-13.16651	-72.68364	NW
ALF	2203	35	-13.04932	-72.45880	S	RB	2180	41	-13.04884	-72.45923	S
CHALL	3457	65	-13.19417	-71.63016	SW	MB	3311	67	-13.19499	-71.63280	SW
CUSI	2663	25	-13.15187	-72.64133	NW	RB	2551	33.5	-13.15187	-72.64421	NW
INCA	2673	32	-13.16429	-72.69268	NW	OB	2791	44	-13.16566	-72.68921	NW
JAP	3121	32	-13.44911	-71.03111	NE	MB	3120	31	-13.44951	-71.03488	NE
LAG	3394	45	-13.16756	-71.63428	SW	MB	3423	47	-13.16768	-71.63427	SW
PAIT	2906	73	-13.19619	-71.57711	NE	MB	2923	77	-13.19657	-71.57696	NE
PLGRD	3552	68	-13.15541	-71.65118	SE	MB	3534	78	-13.15408	-71.65000	SE
WACH	2962	42	-13.18577	-71.58815	SE	MB	3021	44	-13.18796	-71.58654	SE
WAY1	2408	57.8	-13.23092	-71.48378	W	RB	2428	60.2	-13.22975	-71.48374	W
WAY2	2802	43.3	-13.22987	-71.49347	E	MB	2775	40	-13.22806	-71.49254	E
WAY3	2667	46	-13.23418	-71.47693	N	RB	2659	47.8	-13.23345	-71.47666	NW
YAN	2456	54	-13.17690	-72.65100	NW	OB	2652	46	-13.17912	-72.65351	NW
YASP	2926	30.5	-13.11980	-72.63377	NW	MB	2933	28	-13.11889	-72.63328	NW

TLF, time since last fire; RB, recently burnt plot, burned 1–5 years before sampling; MT, plot burned 6–10 years before sampling; OB, plot burned more than 10 years before sampling. X, longitude; Y, latitude; ASP, aspect. Site code names are specified in Figure 1.

not be identified to at least the family level. Sprouting ability (i.e. presence of sprouts) from the canopy, stem buds or through root suckers was recorded. We recorded all the sprouting stems in both burnt and unburnt plots to account for natural sprouting. From each tree >10 cm DBH we extracted a wood sample with a wood corer of 2.5 mm diameter. We measured the sample's length, placed it in a bag immediately after extraction and weighed it. In the laboratory, we air-dried the samples until constant weight and then calculated wood density by wrapping the wood in plastic film and following the water displacement method.

Bark thickness was measured in a set of 20 randomly selected live individuals in each plot, sampling 25 different species in the whole area. From each individual we took five small samples (ca. 4 cm²) at 1 m height on the north-facing side of the tree. Following Pinard and Huffman (1997) and Barlow, Lagan, et al. (2003), the maximum thickness was measured whenever variation was detected. We did not measure bark thickness in standing dead trees because they could not be identified, and often the stems were starting to decompose. We developed predictive models of bark thickness by using species-specific linear relationships between bark thickness and DBH to estimate a value of bark thickness for each surveyed individual of the target species ($n = 1050$). When there was no relationship for a given species, predicted bark thickness was based on the intercept of the model, following Brando et al. (2012).

We determined the percentage of standing dead trees (with no sprouts) in each plot. Fallen trees were not considered as they were often at an advanced stage of decomposition and covered by mosses and lichens, making them difficult to identify.

Fire tolerance index

We determined the fire tolerance of species by developing an empirical fire tolerance index (FTI):

$$FTI = \frac{No.Ind_{burnt\ plot} - No.Ind_{unburnt\ plot}}{No.Ind_{unburnt\ plot}} \quad (1)$$

where *No. Ind* is the number of individuals for a given species in the burnt or unburnt plots.

In order to avoid rare species, we excluded species with less than five individuals in the unburnt plots from the analysis. According to their FTI, we classified species as: fire-sensitive ($FTI \leq -0.5$, i.e. species that showed a decline in numbers in the burnt plots relative to the unburnt plots); fire survivors ($FTI > -0.5$ and ≤ 0.5 , i.e. species that showed little change or a moderate increase in numbers in the burn) and fire thrivers ($FTI > 0.5$, i.e. species that were much more common in the burnt plots). We generally refer to fire-tolerant species as those with a FTI value >0 .

Data analysis

We focused the analyses exclusively on specific comparisons between paired burnt and unburnt plots,

and species-specific responses to fire at each fire history category. Site pairs were grouped according to time since last fire within the burnt plot. Differences in forest structure (tree-size distribution, stem and tree density) between burnt and unburnt forest stands were tested with paired *t*-tests, or Wilcoxon paired tests when data were not normally distributed. We refer to tree density as the number of live stems per ha. In addition to overall differences, we also analysed differences between burnt and unburnt plots for proportion of small trees (<10 cm DBH), medium-sized trees (>10 cm DBH <30 cm) and large trees (>30 cm DBH), which is referred as tree-size distribution.

We calculated the relative abundances, frequencies and dominances (on a basal area basis) for main families and species. The family importance value (FIV) for each family was derived according to Mori et al. (1983):

$$FIV_i = [Div_i + Dens_i + Dom_i] \times 100 \quad (2)$$

where Div_i is relative diversity (number of species in the family *i* divided by total number of species), $Dens_i$ is relative density (number of stems in the family *i* divided by the total number of stems) and Dom_i is relative dominance (basal area of the family *i* divided by total basal area).

Variability in family richness among plots, i.e. the compositional distance of the different plots, was explored with a detrended correspondence analysis (DCA) (Hill and Gauch 1980), using FIV as input variable. We opted for a DCA after computing a principal component analysis and observing a strong arch effect (data not shown). DCA performs detrending to counteract the arch effect and rescaling of ordination axes, so that the spacing of plots and family scores are scaled in units of β -diversity (Hill and Gauch 1980). To test if the sample size was representative, we produced rarefaction curves on the basis of 1000 random iterations, using data pooled from burned and unburnt plots with different time since the last fire. We calculated the species accumulation curves, using bootstrapping (Sokal and Rohlf 1995) for burnt and unburnt forests and TLF separately. All analyses were carried out by using the vegetation analysis package 'vegan' for R (Oksanen et al. 2011).

We visually inspected for potential correlations between traits (sprouting, biomass, wood density and bark thickness) and the FTI through scatterplots. We applied a tree classification model (Breiman et al. 1984) to determine which traits contributed to FTI. Bark thickness was excluded from the tree classification model as the number of species for which there was information available was very low and inclusion of bark thickness would have biased results. Analyses were carried out with the 'tree' package for R (Ripley 2011).

Results

Forest structure

The field inventory over the total of 2.7 ha surveyed yielded a total of 1947 live and 412 standing dead trees ≥ 10 cm

Table 2. Inventoried area, number of individuals per hectare, basal area of live trees, number of families, number of species and percentage of mortality at the paired plots in different time since last fire sites, eastern Andes, Peru.

TLF		Inventoried area (m ²)	Live individuals (n ha ⁻¹)	BA (cm ² ha ⁻¹)	Families (n)	Species (n)	Mortality (%)
RB	U	4500	1664	467 ± 120	41	132	7.0 ± 1.6
	B	4500	1791	380 ± 60	41	123	26.3 ± 9.9
MB	U	6300	1506	338 ± 47.6	31	83	13.5 ± 2.6
	B	6300	1174	248 ± 42.9	25	62	25.2 ± 8.9
OB	U	2700	892.6	1860 ± 304	27	47	6.7 ± 2.4
	B	2700	1541	1567 ± 256	35	81	12.3 ± 4.1

TLF, time since last fire; RB, 1–5 years; MB, 6–10 years; OB, >10 years; BA, basal area; U, unburnt; B, burnt.

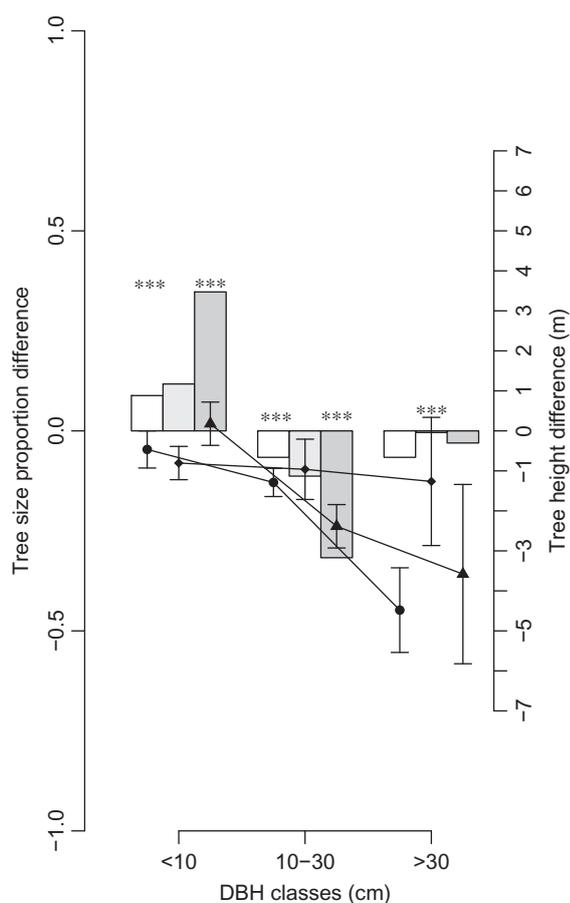


Figure 2. Differences in the proportion of tree sizes (burnt–unburnt) and differences in tree height (for each tree size category, average tree height in the burnt plots – average tree height in the unburnt plots) for different lengths of time since the last fire in the surveyed plots, in tropical montane cloud forest stands near the treeline, eastern Andes, Peru. Bars represent tree size proportion difference and refer to the left y-axis, and lines represent tree height difference and refer to the right y-axis. White bars denote short-term paired plots (time since last fire 1–5 years), light grey bars denote medium-term paired plots (time since last fire 6–10 years), and dark grey bars indicate long-term paired plots (times since last fire >10 years). Error bars indicate standard error. ***, significant differences in tree size proportions (burnt vs. unburnt) at $P < 0.001$. All differences in tree height were statistically significant at $P < 0.05$.

DBH (Table 2). Overall, trees had a higher basal area ($t = -2.77$, $df = 14$, $P = 0.015$) and were taller ($t = -4.35$, $df = 14$, $P < 0.001$, see Figure 2) in the unburnt plots. The

overall percentage of standing dead trees was higher in the burnt plots ($t = 2.29$, $df = 14$, $P = 0.038$). The percentage of standing dead trees was also significantly higher in the RB burnt plots ($t = 3.21$, $df = 4$, $P = 0.033$) and MB burnt plots ($t = 2.88$, $df = 6$, $P = 0.028$) but no significant differences were found for the OB sites (Table 2).

Mean (\pm SE) tree density was similar in unburnt and burnt plots (1470 ± 55 trees ha⁻¹ and 1462 ± 66 trees ha⁻¹ respectively). There were no significant differences of tree densities for any of the three tree-size categories. In the RB and OB sites, the proportion of small trees was significantly higher in burnt plots, whereas the proportion of medium-sized trees was significantly higher in the unburnt plots (Figure 2). There was a significantly lower proportion of large trees in the burnt plots of the RB sites. No differences between burnt and unburnt plots in stand tree-size distribution were detected for MB sites, despite there being a greater difference than for the RB sites (Figure 2).

Bark thickness ranged between 1.7 and 23.8 mm with higher values found in bigger trees (Figure S1, see online supplemental material). Average bark thickness was slightly lower in the burnt plots but not significantly different (5.7 ± 0.19 mm vs. 6.1 ± 0.16 mm in the unburnt plots). A total of 44.9% of the trees, representing 23.8% of the total basal area (BA), had bark thickness of <5 mm, whereas only 9.5% of the sampled individuals, accounting for 26.5% of the total measured BA, had bark thicker than 10 mm. There was a significant correlation between bark thickness and tree diameter for 17 of the 25 species analysed. Several species had too-small a sample size for detection of a significant relationship.

Total sprouting (the percentage of total stems that were sprouting) was 14.2% higher in the unburnt plots of RB sites (compared to the matched burnt plots), but it was 13.6% and 18.2% higher in the burnt plots of the MB and OB sites (compared to matched unburnt plots), respectively. Canopy sprouting was higher in the unburnt plots regardless of TLF, although the difference with regard to burnt plots was not significant (Figure 3). RB burnt plots had a significantly higher root resprouting percentage than the matched unburnt plots (12.2% vs. 4.8%, $t = 4.027$, $df = 4$, $P = 0.016$). MB sites showed higher percentages of stem bud resprouting and root bud resprouting in the burnt plots compared to the matched unburnt plots (stem sprouting: 24.7% vs. 10.4%, $t = 2.51$, $df = 6$, $P = 0.042$; root sprouting: 18.3% vs. 6.2%, $t = 2.89$, $df = 6$, $P = 0.028$).

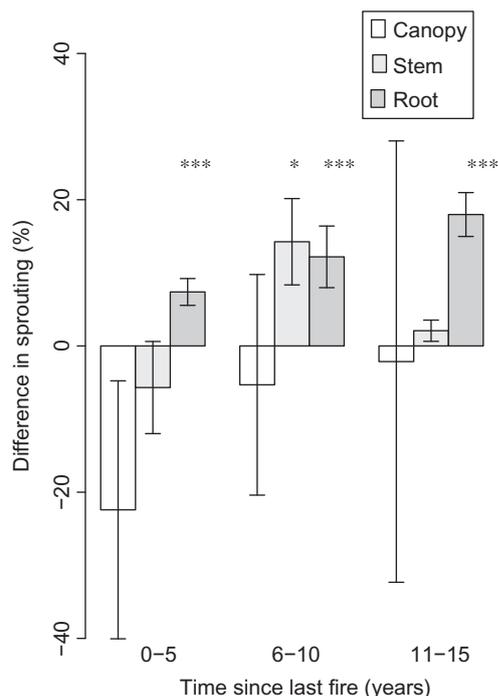


Figure 3. Differences in tree sprouting (burnt vs. unburnt) from bole (canopy), stem buds (stem) or root suckers (root) in tropical montane cloud forest stands near the treeline, eastern Andes, Peru. *, $P < 0.05$; ***, $P < 0.001$; RB, 1–5 years since fire; MB, 6–10 years since fire; OB, >10 years since fire.

OB sites showed a significantly higher percentage of root suckers resprouting in the burnt plots compared to the matched unburnt plots (24.4% vs. 6.4%; $t = 5.99$, $df = 2$, $P = 0.027$).

Diversity

A total of 333 species or morphotaxa were identified, belonging to 124 genera and 43 families (Table 2). There was a very large number of rare species, with only 73 species (out of 333 identified species) having more than five individuals in the unburnt plots.

The relative frequency, abundance and dominance of families reflected the high diversity of the sites (Table 3). Moreover, DCA results attested the high FIV variability among plots (Figure 4). In the RB sites, DCA1 and DCA2 explained 53.0% and 39.9% of variance, respectively. The DCA1 axis segregated the ALF, CUSI paired plots, burnt in 2009, with a distance of 2.9σ between burnt and unburnt sites for ALF, a distance of 1.4σ between burnt and unburnt sites in CUSI (Figure 4(a)). The second axis separated the site WAY3 from the rest of the sites (Figure 4(a)). In the MB sites, DCA1 and DCA2 explained 59.3% and 34.4% of the variance, respectively (Figure 4(b)). Interestingly, DCA1 tended to separate sites burnt in 2005 on the left side of the axis and sites burnt in 2003 in the right side of the axis, excepting WACH-B, which burnt in 2003 and was placed on the left side of the axis. Plot WAY2-U was placed at the end of the DCA1 axis and clearly segregated from other plots. DCA2 segregated plots WACH-B and WACH-U with a distance of 2.8σ .

In the OB sites, DCA1 and DCA2 explained 55.7% and 23.7% of the variance, respectively (Figure 4(c)). Two unburnt sites were placed at each of the extremes of the DCA1 axis, reflecting the different FIV in the forests. Two of the sites, INCA and YAN, had distances between burnt and unburnt plots greater than 2σ (Figure 4(c)).

The main families were similar in all sites (Table 3) but sites and burnt/unburnt plots showed differences in the relative abundance (rA) and relative dominance (rD) of families and FIV (Table 3). In the RB sites, Lauraceae was the most important family (highest FIV) in the unburnt plots, and Rubiaceae was the most important family in the burnt plots (Table 3). Rosaceae, Clethraceae, Araliaceae and Clusiaceae showed higher FIV values in the burnt plots, while Lauraceae, Melastomataceae, Euphorbiaceae and Primulaceae showed a lower FIV in the burnt plots. In unburnt MB plots, Cunoniaceae, Melastomataceae, Clusiaceae, Clethraceae and Rosaceae were the dominant families. In the burnt MB plots, the dominant families were Cunoniaceae, Clethraceae, Melastomataceae and Ericaceae. In the OB sites, Lauraceae was again the most important family in both burnt and unburnt plots (Table 3).

The species accumulation curves showed that sample size was large enough to account for diversity in the MB sites alone (Figure 5). Species accumulation curves suggested a shift in species diversity with time since the last fire (Figure 5). In RB sites there was a similar cumulative number of species in burnt and unburnt plots (Figure 5). The burnt plots of the MB sites showed a decrease in the number of species with respect to the unburnt plots (Figure 5). OB burnt sites appeared to have a larger number of species than the unburnt sites (Figure 5).

Fire tolerance index (FTI)

FTI was derived for 73 species (Table S1). There were 39 fire-sensitive species, of which 21 species had the most negative value ($FTI = -1$), showing strong intolerance to fire. There were 19 fire survivor species and 14 fire-thrivers species. The strongest fire-thrivers species was *Alnus acuminata* ($FTI = 9.4$). Other fire-thrivers species were *Miconia alpina*, *Myrsine* sp., *Clethra revoluta*, *Miconia setulosa*, *Clusia* sp., *Clethra cuneata*, *Myrsine* sp1, *Weinmannia fagaroides*, *Symplocos* sp1, *Myrcianthes* sp1, *Miconia barbeyana*, *Gynoxys pillahuatensis* and *Piper acutifolium* (Table S1). *Polylepis* species, the most characteristic tree genus of the high elevation Andes, appeared to be highly fire-sensitive (*Polylepis sericea* had $FTI = -0.92$ and *Polylepis* sp. had $FTI = -1.00$). Some other typical genera from TMCFC (*Clusia* spp., *Weinmannia* spp., *Miconia* spp., *Myrsine* spp.) had mostly fire-sensitive species and few fire survivors, or fire thrivers.

Most traits investigated showed a positive relationship with FTI. Species with <40% of canopy sprouting capacity were not among the fire thrivers (Figure S2, see online supplemental material). All fire thrivers had wood density values $>0.48 \text{ g}\cdot\text{cm}^{-3}$ (with the exception of *Piper acutifolium*, $\rho = 0.39 \text{ g}\cdot\text{cm}^{-3}$) and bark thickness $>3.8 \text{ mm}$.

Table 3. Relative abundance, relative dominance and family importance value for the 15 most common families in the paired-plot (burnt, unburnt) inventoried sites, eastern Andes, Peru.

TLF	Family	Burnt			Unburnt			
		rA	rD	FIV	Family	rA	rD	FIV
1–5 years after fire								
	Rubiaceae	0.16	0.11	35.53	Lauraceae	0.09	0.22	45.00
	Lauraceae	0.05	0.16	27.71	Melastomataceae	0.18	0.03	31.77
	Melastomataceae	0.13	0.03	27.28	Euphorbiaceae	0.06	0.11	22.51
	Rosaceae	0.05	0.13	22.88	Myricaceae	0.08	0.07	15.53
	Clethraceae	0.07	0.09	17.25	Primulaceae	0.06	0.04	15.33
	Araliaceae	0.04	0.05	16.73	Asteraceae	0.04	0.01	15.33
	Clusiaceae	0.04	0.08	15.18	Rosaceae	0.06	0.06	13.87
	Euphorbiaceae	0.02	0.06	11.28	Rubiaceae	0.05	0.03	13.62
	Primulaceae	0.04	0.02	9.88	Araliaceae	0.03	0.03	12.56
	Symplocaceae	0.02	0.02	8.25	Clethraceae	0.04	0.06	12.43
	Myrtaceae	0.03	0.02	8.15	Clusiaceae	0.06	0.03	12.04
	Piperaceae	0.04	0.00	8.03	Urticaceae	0.03	0.04	10.46
	Urticaceae	0.02	0.03	7.64	Betulaceae	0.01	0.07	8.95
	Chloranthaceae	0.04	0.01	7.40	Monimiaceae	0.05	0.01	7.77
	Sabiaceae	0.02	0.03	7.04	Cyatheaceae	0.02	0.04	6.99
	Other families (16–41)	0.22	0.18	69.79	Other families	0.14	0.14	55.86
	Total	1.00	1.00	300.00	Total	1.00	1.00	300.00
6–10 years after fire								
	Cunoniaceae	0.17	0.25	45.30	Cunoniaceae	0.14	0.16	33.88
	Clethraceae	0.19	0.22	43.36	Melastomataceae	0.10	0.06	32.57
	Melastomataceae	0.09	0.03	23.64	Clusiaceae	0.11	0.13	28.89
	Ericaceae	0.08	0.04	23.32	Clethraceae	0.10	0.14	27.19
	Primulaceae	0.10	0.05	19.74	Rosaceae	0.06	0.11	25.76
	Betulaceae	0.04	0.12	17.32	Symplocaceae	0.04	0.09	15.49
	Clusiaceae	0.04	0.06	16.41	Araliaceae	0.03	0.04	14.72
	Symplocaceae	0.06	0.05	16.08	Primulaceae	0.06	0.03	14.55
	Asteraceae	0.03	0.01	14.14	Asteraceae	0.06	0.02	13.62
	Rosaceae	0.02	0.06	11.36	Lauraceae	0.03	0.03	13.37
	Araliaceae	0.02	0.01	8.57	Solanaceae	0.03	0.00	8.68
	Lauraceae	0.02	0.01	7.33	Pentaphragmalaceae	0.01	0.04	7.72
	Chloranthaceae	0.02	0.02	5.76	Ericaceae	0.02	0.02	6.40
	Solanaceae	0.01	0.00	4.35	Sabiaceae	0.02	0.02	6.38
	Piperaceae	0.01	0.00	4.24	Papaveraceae	0.05	0.00	5.14
	Other families (16–25)	0.10	0.06	39.08	Other families (16–31)	0.15	0.11	45.63
	Total	1.00	1.00	300.00	Total	1.00	1.00	300.00
>10 years after fire								
	Lauraceae	0.06	0.30	49.32	Lauraceae	0.10	0.22	49.30
	Myrtaceae	0.04	0.24	30.48	Melastomataceae	0.06	0.20	34.68
	Melastomataceae	0.12	0.01	22.74	Moraceae	0.05	0.22	33.62
	Asteraceae	0.14	0.01	22.72	Begoniaceae	0.25	0.00	27.60
	Ericaceae	0.01	0.14	16.41	Myrtaceae	0.03	0.08	17.55
	Chloranthaceae	0.11	0.01	13.73	Symplocaceae	0.06	0.03	13.16
	Solanaceae	0.04	0.03	13.12	Cornaceae	0.01	0.09	12.98
	Symplocaceae	0.06	0.02	12.04	Rubiaceae	0.05	0.00	11.29
	Primulaceae	0.05	0.02	9.42	Solanaceae	0.03	0.01	10.04
	Clusiaceae	0.03	0.04	9.36	Arecaceae	0.07	0.01	10.01
	Euphorbiaceae	0.02	0.07	9.32	Cannabaceae	0.04	0.04	9.36
	Rosaceae	0.03	0.03	8.44	Urticaceae	0.04	0.01	9.17
	Sabiaceae	0.03	0.01	7.75	Cyatheaceae	0.04	0.02	8.24
	Rubiaceae	0.02	0.00	7.04	Sapindaceae	0.03	0.01	5.48
	Siparunaceae	0.03	0.00	6.99	Rosaceae	0.02	0.01	5.22
	Other families (16–35)	0.24	0.05	68.12	Other families (16–27)	0.15	0.05	47.51
	Total	1.00	1.00	300.00	Total	1.00	1.00	300.00

rA, relative abundance; rD, relative dominance; FIV, family importance value.

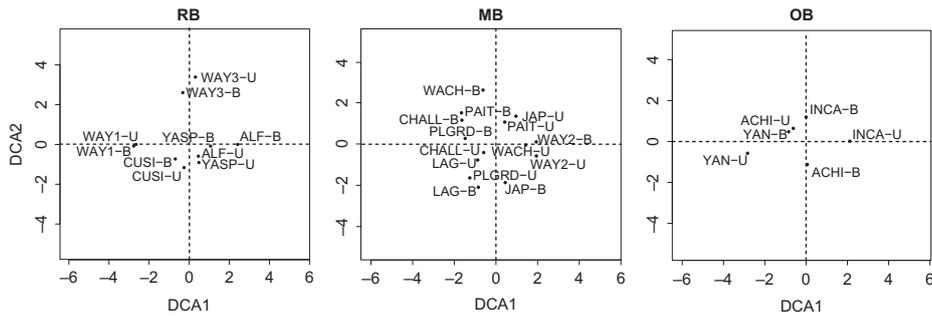


Figure 4. DCA with the family importance value (FIV) index for the 30 sampled plots (15 unburnt, 15 burnt) near the treeline, eastern Andes, Peru. DCA1, DCA first axis scores (x -axis). DCA2, DCA second axis scores (y -axis).

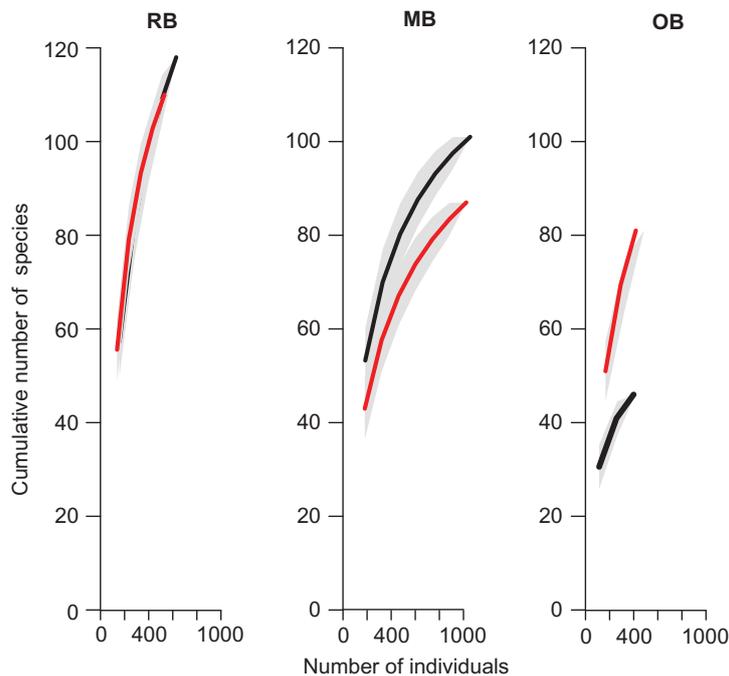


Figure 5. Species accumulation curves using rarefaction (x -axes, number of individuals per plot), in tropical montane cloud forest stands near the treeline, eastern Andes, Peru.

While there was not a direct relationship between FTI and stem or bud sprouting capacity (Figure S2), the tree classification model (Figure 6) showed that percentage of stem sprouting was the first trait separating the most fire-sensitive species. Amongst species with high amounts of stem sprouting ($>20.5\%$, see Figure 6), biomass was the most important feature related to fire tolerance: species with more than 115 kg-tree^{-1} were more fire-resistant. When biomass was smaller than 115 kg-tree^{-1} , root sprouting separated the third node of the classification tree (Figure 6). However, according to the classification, species with stem sprouting between 9.4% and 20.5% were slightly more fire-sensitive than species with stem sprouting $<9.4\%$. This may be related to four species, *Miconia barbeyana*, *Clethra revoluta*, *Myrsine* sp1 and *Symplocos* sp1 (species numbers 12, 4, 8 and 10 in Figure S2), that had stem-sprouting values $<9.4\%$ but were fire thrivers (Figure S2). Other traits may explain their tolerance (for example, *Clethra revoluta* and *Symplocos* sp1 had high

percentages of root sprouting, while *Myrsine* sp1 had an average biomass of 150 kg-tree^{-1}). The tree classification analysis did not select wood density, despite only one fire-thriver species having wood density $<0.48 \text{ g-cm}^{-3}$, as there were many fire-sensitive species with wood densities over this value. *Miconia barbeyana* did not show, in our analysis, any relevant trait (apart from wood density of 0.6 g-cm^{-3}) that could explain its fire tolerance. Tree classification analysis did not include bark thickness because these data were only available for a subset of species.

Discussion

Time since last fire and fire frequency

All unburnt plots were carefully selected in mature montane forest with no evident signs of disturbance. We were able to identify burn scars up to 15 years after the fire, therefore we are confident that our ‘unburnt’ forests had not burnt for at least 15 years, and that the last fire in the oldest burn sites

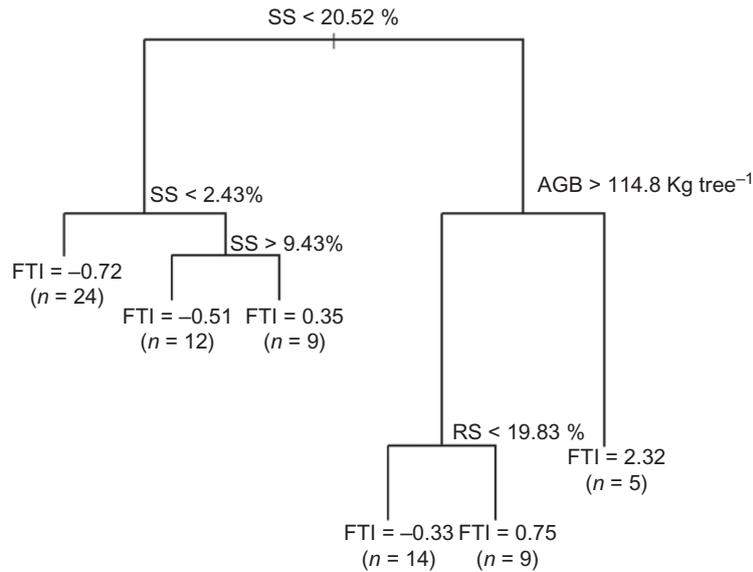


Figure 6. Tree classification of fire tolerance index (FTI) vs. plant traits in 15 burnt plots of 900 m² in size in tropical montane cloud forest stands near the treeline, eastern Andes, Peru. SS, stem bud sprouting; AGB, above-ground biomass; RS, root suckers sprouting.

was between 10 and 15 years prior to sampling. However, we recognise that longer-term fire recurrence regimes can be important in affecting forest structure and composition (e.g. Cochrane et al. 1999; Barlow, Peres, et al. 2003). The study lacks information on fire frequency and recurrence (i.e. how many times the study sites had been burnt, and the time interval between fires), which may have important effects on different regeneration patterns of forests. In addition to the effects of fire, some of the study sites are located on very steep slopes that may have been affected by landslides in the past, or by undetected previous livestock grazing.

Forest structure and composition

We found that fire had significant lasting effects on forest structure, although our time frame of 10–15 years since the last fire is not a long-term period in the life of a forest. In the recently burnt sites, there was a significantly higher number of small (<10 cm DBH) trees and a smaller number of medium (10–30 cm DBH) and large (>30 cm DBH) trees in the burnt plots (Figure 2), probably because of the effects of fire in killing trees and enhancing sprouting and gap opening to benefit new recruits. Barlow, Peres, et al. (2003) also reported a decrease in the number of trees between 10 and 20 cm DBH following fire in eastern Amazonian lowland forests. Old burnt sites showed a low number of medium-sized trees and more small stems, which may be related to an indirect effect of fire intensity. Fires in moist forests of the Andes are usually deep ground fires with some torching episodes (Román-Cuesta et al. 2011), slow back-slope burning (hence long fire residence times), low rates of spread and substantial water vapour release due to high fuel moisture (I. Oliveras, pers. obs.). Torching episodes usually cause tree top kill, but the damage from ground

fires to the tree depends on several variables, such as fire residence time, tree insulation (e.g. bark traits, see Pinard and Huffman 1997; Barlow, Lagan, et al. 2003; Brando et al. 2012) and tree size (e.g. Pinard and Huffman 1997; Cochrane et al. 1999; Peres 1999; Barlow, Peres, et al. 2003; Barlow, Lagan, et al. 2003). Although we do not have any fire behaviour information for the sampled study sites, we observed burning heterogeneity within the plots (reflected by some charred trees surrounded by trees without burning scars) and also among plots, with evidence of some places burning at higher intensities than others. Forests burnt in dry years (e.g. 2005, 2009) usually showed more charred canopies than forests burnt in wetter years, which is an indicator of high burn severity. Trees with charred canopies may have been damaged by fire, but not killed, thereby becoming more vulnerable to other disturbances or diseases, as has been reported from other neotropical studies (Cornwell et al. 2009). Such an indirect effect of fire may have caused a longer-term increased mortality in trees in the burnt plots, as well as a canopy gap opening that would have favoured new recruits and sprouts.

Sprouting from below-ground organs was significantly higher in burnt forests and it increased with time across the fire chronosequence. Kammesheidt (1999) also reported that regeneration by root suckers was more abundant in disturbed lowland neotropical forests and, similarly, Kauffman (1991) found more species with sprouting emerging from subterranean shoots than from stumps or boles. Our results showed that stem bud sprouting was only significantly high in forests burned more than six years before sampling. Fire kills most above-ground meristematic tissue and it might stimulate the growth of resting buds below-ground shortly after fire, but meristematic tissue of stumps or boles may need more than five years to regenerate.

The percentage of standing dead trees was much higher in the burnt than in the unburnt plots and decreased with time since the last fire, probably because dead trees fell over with time. The post-fire percentage of standing dead trees was low compared to those found by Román-Cuesta et al. (2011) for the same forest type. The difference between the two studies may be due to the passage of time between the fire and the time of sampling (three years for Román-Cuesta et al. (2011) and one to 15 years in this study).

Diversity

The sites showed high levels of diversity, with a total of 333 tree species identified. The results suggested that changes in diversity were more characterised by shifts in FIV, abundance and dominance than by changes in occurrence of specific families, similar to that observed by Balch et al. (2011) in a lowland Amazon forest. At the species level, our results suggested that there was a shift in species richness and species composition with time since the last fire. The latter was reinforced by the species accumulation curves that, contrary to our hypothesis, showed a strong pattern of higher diversity in the old burn plots with respect to their paired unburnt plots.

The high β -diversity, at the family level, of the sites was attested to by the DCA results and, although it masks to a large extent the effects of fire on FIV, some interesting trends were observed. There was greater compositional distance between paired plots than between sites for six of the 15 sites studied. Moreover, paired plots from two of the three studied LB sites were segregated by the DCA results, suggesting long-term effects of fire on diversity and composition. While bearing in mind that there were only three LB burnt sites, the strong patterns observed suggest that the effects of fire in forest composition would have long-term effects, and would favour the establishment of new species that would not be able to establish in undisturbed forests. Nevertheless, further research on the long-term effects of fires on tree diversity would be needed to decipher whether the patterns observed in this study are supported.

Fire tolerance index (FTI)

We derived the FTI for 73 out of a total of 333 species because of the high number of rare species. The species with the highest FTI, *Alnus acuminata*, is an early successional and nitrogen-fixing species (Asbjornsen and Wickel 2009) and results indicated that it was strongly favoured by fire. Interestingly, for some of the most common TMCF genera, such as *Clethra*, *Clusia*, *Miconia*, *Myrsine* and *Weinmannia*, there were some fire-tolerant species (either fire thrivers or fire survivors), as well as fire-sensitive species, suggesting the importance of addressing species-specific response in disturbance studies, especially in such diverse environments. *Miconia alpina*, which scored the second highest FTI, is a species endemic to the Peruvian

Andes, and is usually found in disturbed forests (Leon 2006). Our study found two *Myrsine* morpho-species to be fire-tolerant. A study about species composition changes in burnt forest in montane forests of Bolivia (Araujo-Murakami et al., 2005) found *Myrsine dependens* to be very common in burnt forests. Although it may not be the same species as in our study, these results show how some *Myrsine* species have traits that provide them with the ability to thrive under fire and post-fire conditions. Similarly, the Bolivian study also found a high abundance of *Clethra cuneata*, *Miconia setulosa* and *Weinmannia fagaroides*, which were found to be fire-thrivers in our study.

The tree classification model showed that the combination of some traits, specifically stem sprouting, tree size and root sprouting, could largely explain species tolerance to fire. Interestingly, whereas a simple bivariate plot of FTI and stem sprouting showed no pattern (Figure S2), the tree model selected stem sprouting as the first variable in determining fire tolerance (with species having less than 21% stem sprouting being fire-sensitive). The role of sprouting ability in survival has previously been reported by Román-Cuesta et al. (2011) for TMCFs. Tree size has been broadly reported to be a key morphological feature that determines survival after fire events in lowland Amazonian forests. For example, Barlow, Peres, et al. (2003) found that DBH was a predictor of mortality in burnt forests. Balch et al. (2011) also reported that the biggest trees in the Tanguro, Mato Grosso burnt sites were the most fire-resistant.

Brando et al. (2012) has reported the role of wood density in post-fire tree survival for Amazonian forests but, to our knowledge, it has not yet been reported for tropical montane forests. Although the tree analysis did not select wood density as a significant trait in determining fire tolerance, all fire thrivers (excepting *Piper acutifolium*) had wood density values $>0.48 \text{ g}\cdot\text{cm}^{-3}$, suggesting that species with denser wood may be more resistant to fire.

The role of bark thickness could not be evaluated with the tree classification model, because bark thickness data were not available for all species. Nonetheless, our results suggest that this was not a key trait for determining species tolerance to fire, contrary to what has been reported for lowland neotropical forests (Barlow, Peres, et al 2003; Barlow, Lagan, et al. 2003; Brando et al 2012). Bark thickness values of 1.7–23.8 mm in this study were relatively low compared to other studies in lowland neotropical ecosystems (2–45 mm reported by Pinard and Huffman 1997, and maximum thickness of 37.6 mm reported by Barlow, Lagan, et al. (2003)), perhaps because trees in TMCFs tend to be smaller than in the lowlands. However, further investigation is needed to evaluate in more detail the role of bark thickness upon tolerance to fire in TMCF ecosystems.

Conclusions

Our study showed how TMCFs' regeneration after fire is a long process, with changes in forest structure and species composition noticeable in forests burned more than 10 years prior to the time of sampling. Higher sprouting

was recorded six years after burning compared to their matched unburnt control plots, suggesting that tissue regeneration may take several years for some TMCF tree species. Sprouting and tree size largely determined species' tolerance to fire. Effects on tree diversity were more marked at the species level than at the family level, and 45% of the species were shown to be fire survivors or fire thrivers. However, long-term studies are needed in order to fully decipher the regeneration patterns of TMCFs after fire, as well as to understand the underlying mechanisms of species composition shifts and forest succession after disturbance in these highly diverse forests.

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