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Implications of fires on carbon budgets in Andean cloud montane forest: The importance of peat soils and tree resprouting

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ABSTRACT

Fire in tropical montane cloud forests (TMCFs) is not as rare as once believed. Andean TMCFs sit immediately below highly flammable, high-altitude grasslands (Puna/Páramo) that suffer from recurrent anthropogenic fire. This treeline is a zone of climatic tension where substantial future warming is likely to force upward tree migrations, while increased fire presence and fire impacts are likely to force it downwards. TMCFs contain large carbon stocks in their peat soils and their loss through fire is a currently unaccounted for regional source of CO_2. This study, conducted in the southern Peruvian Andes (>2800 m), documents differences in live tree biomass, fine root biomass, fallen and standing dead wood, and soil organic carbon in 4 paired-sample plots (burned versus control) following the severe ground fires that occurred during the 2005 Andean drought. Peat soils contributed the most to biomass burning emissions, with lower values corresponding to an 89% mean stock difference compared to the controls (mean ± SE) (54.1 ± 22.3 vs. 5.8 ± 5.3 MgC ha^{-1}). Contrastingly, carbon stocks from live standing trees differed by a non-significant 37% lower value in the burned plots compared to the controls, largely compensated by vigorous resprouting (45.5 ± 17.4 vs. 69.2 ± 13.4 MgC ha^{-1}). Both standing dead trees and fallen dead wood were significantly higher in the burned plots with a three-fold difference from the controls: dead Trees 45.2 ± 9.4 vs. 16.4 ± 4.4 MgC ha^{-1}, and ca. a 2 fold difference for the fallen dead wood: 11.2 ± 5 vs. 6.7 ± 3.2 MgC ha^{-1} for the burned plots versus their controls. A preliminary estimate of the regional contribution of biomass burning emissions from Andean TMCFs for the period 2000–2008, resulted in mean carbon emission rates of 1.3 TgC yr^{-1} (max-min: 1.8–0.8 TgC yr^{-1}). This value is in the same order of magnitude than South American annual fire emissions (300 TgC yr^{-1}) suggesting the need for further research on Andean forest fires. On-going projects on the region are working on the promotion of landowner participation in TMCFs conservation through REDD+ mechanism. The heart of the proposed initiative is reforestation of degraded lands with green fire breaks enriched with economically valuable Andean plant species. The cultivation of these species may contribute to reduce deforestation pressure on the Amazonian cloud forest by providing an alternative income to local communities, at the same time that they prevent the spread of fire into Manu National Park and adjacent community-held forests, protecting forest and reducing CO_2 emissions.

1. Introduction

Though much attention has lately been paid to the dynamics and impacts of fires in tropical lowlands ecosystems (Barlow et al., 2003; Cochrane et al., 1999; Uhl et al., 1988), fire has frequently been neglected in tropical montane cloud forests (TMCFs). Fire is, however, not as rare in cloud forest ecosystems as once believed (Asbjornsen and Wilcke, 2008; DiPasquale et al., 2008). In the Andes, humid TMCFs sit immediately below highly flammable, high-altitude grasslands (Puna or Páramo) that suffer from recurrent anthropogenic fires (Sarmiento and Frolich, 2002; Young and León, 2007). The resulting human-influenced treeline is a zone

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Fig. 1. Puna fire moving down towards the surrounding cloud forests in the buffering area of the Manu National Park, Peru. Nearby slopes display an anthropogenic mosaic of TMCFs and Puna, where fire has resulted in a retreat of the treeline.
Photo: J. Rapp. (2006).

of ecological tension where both climate and humans play roles that affect TMCFs in opposite directions. On the one hand, Andean montane forests are currently suffering from on-going warming which has been reported as up to 0.11 °C per decade since 1950s (Vuille and Bradley, 2000; Vuille et al., 2008; Garreaud et al., 2009). Climatic simulations for the tropical Andes predict a substantial warming in the order of 4.5–5 °C by the end of the 21st century (Still et al., 1999; Foster, 2001; Vuille et al., 2008) with unknown effects on cloud dynamics (Lawton et al., 2001). Taking a measured lapse rate with elevation of 5.5 °C per 1000 m (Bush et al., 2004), TMCFs will need to migrate ~800 m altitudinally into the Puna/Páramo within a single generation to remain in equilibrium with temperature (Foster, 2001; Vuille et al., 2003; Bush et al., 2005). On the other hand we have fire. Human-induced fires start in the Puna and move downwards towards the treeline (Fig. 1). Therefore, even if TMCFs were able to quickly respond to climatic pressures and effectively migrate upwards, this process would be – and it currently is – jeopardized by downward fires (Cavelier et al., 1998; Young and León, 2000). There is clear evidence that fires are widespread in TMCFs: Mexico (Asbjornsen et al., 2005), Africa (Hemp, 2005), South America (Bush et al., 2005), the Caribbean (Horn et al., 2001; Martin et al., 2007), Costa Rica (Islebe and Hooghiemstra, 1997), and Indonesia (Hope, 2001).

TMCFs contain large carbon stocks in the form of peat soils, and their loss through fire is a currently unaccounted for source of greenhouse gases. Research done in TMCFs in southern Mexico reported standing live tree biomass losses of above 80% (86–123 MgC ha^{-1}) and a reduction of soil organic carbon up to 89% in burned TMCFs compared to unburned controls (Asbjornsen et al., 2005). Unlike tropical lowland forests where aboveground biomass contributes the most to carbon emissions (Goldammer, 1999; Cochrane, 2003; Barlow and Peres, 2008), peat soils in TMCFs contain carbon stocks that frequently more than double the aboveground stocks (i.e. Delaney et al. (1997) reported mean carbon stocks of 257 MgC ha^{-1} for Venezuelan montane wet forests soils versus aboveground carbon stocks of 157 MgC ha^{-1}. Schrumpf et al. (2001) reported a mean carbon stock of 152 MgC ha^{-1} for the soil organic layers, versus aboveground carbon stocks of 56 MgC ha^{-1} for the same site in the Ecuadorian Andes (Leuschner and Moser, 2008).

Since a significant fraction of the total amount of atmospheric emissions is driven by biomass burning (Page et al., 2002; Achard et al., 2004; Van der Werf et al., 2004), it could be regionally important to include the emissions associated to carbon-rich TMCFs fires. A better understanding of fire dynamics and biomass burning emissions of TMCFs is, therefore, needed. This study was conducted in 2008 in the southern Peruvian Andes and documents differences in live tree biomass, live fine-root biomass, fallen and standing dead wood, and soil carbon following deep ground fires of 2005. We pose the following questions: (i) how are TMCFs carbon stocks affected by intense fires? and (ii) what would that represent for regional emission balances if we considered fires in the period 2000–2008 in the entire tropical high Andes?. For this research the tropical high Andes is defined as the territory above 2000 m, from Venezuela to Bolivia.

1.1. Study area

Our research was embedded in the frame of an international multi-partner project focused on the impacts of climate change on Andean montane forests. This on-going project evaluates forest dynamics, composition, and structure on an elevation gradient that ranges from 200 m down in the Peruvian Amazon up to 3800 m in the Puna region in the Manu National Park, Peru.

In our study we exclusively selected TMCFs that fulfilled the following conditions: (i) TMCFs had been affected by intense and severely damaging fires (i.e. deep ground fires with clear torching episodes). These fires resulted in more than 50% of the plot trees being leafless, clear evidence of trunk charring and clear evidence of organic soil losses; and (ii) the affected forests were mature cloud montane stands before the fire episode. Currently, an on-going three-year project is expanding this research into other successional stages and into other fire intensities, which will result in a gradient of carbon stock impacts. Besides time and logistic constraints, we opted for this approach since severely affected mature stands are easier to identify and also represent the largest contribution to biomass burning emissions. Mature forests were visually selected as forests above 2800 m, mean tree heights ≥8 m, mean Diameter at Breast Height (DBH) ≥20 cm. Table 1 summarizes the structure of our selected cloud forests.

In a three-month period, March–August 2008, we identified and measured four burned sites that fulfilled the above-mentioned conditions in the Andean range of the Manu National Park (>2800 m) in the southern Peruvian Andes (12° 79′–13° 20′South, 71° 91′–71° 58′ West) (Figs. 2 and 3).

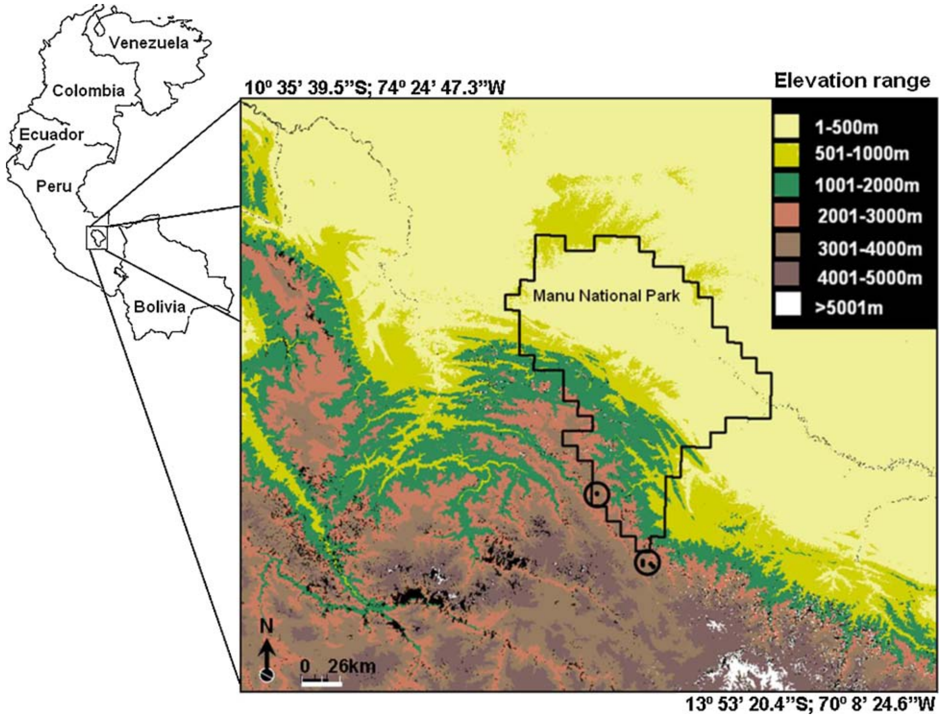

Fig. 2. Altitudinal gradient in the study area based on data from the Shuttle Radar Topography Mission. Encircled black dots represent our research sites, at the southern Andean regions of the Manu National Park.

Fig. 3. Burned Montane Cloud Forest resprouting after the severe 2005 fire season. Plots were established in 2008 at the buffer zone and protected area of the Manu National Park, in the southern Peruvian Andes.

Table 1
Plot descriptions and forest structural variables of the pair-sampled plots: control-unburned (C) versus their burned (B) pairs. The last column includes the mean ±SE of each variable.

Plots	Challabamba	Laguna-Acjanaco	Pahititi	Sondor	
Elevation	3100 m	3400 m	2920 m	2850 m	
Aspect	250° SW	230° SW	40° NE	290° NW	
Slope	65%	45%	75%	30%	
Control	Ccha	Clag	Cpa	Cson	Control (mean ±SE)
Tree density DBH≥10 (num tree ha^{-1})	833	731	1133	690	847 ± 100
DBH of mean BA (cm)	26.3	26.4	16.5	27.2	24.1 ± 2.5
Basal area (m^2 ha^{-1})	45.1 ± 0.8	40 ± 0.8	24.4 ± 0.2	40.1 ± 0.8	37.4 ± 4.5
Stem height (m)	7.6 ± 0.3	7.3 ± 0.3	8.5 ± 0.3	10.4 ± 0.5	8.5 ± 0.7
Dead trees (% of stems)	21.3%	21.1%	14.7%	18.8%	19 ± 1.5%
Number sprouting trees (% of stems)	12%	9%	3%	19%	9.8 ± 2.7%
Liana density (% of stems)	3%	16%	6%	4%	7.3 ± 3
Burned	Bcha	Blag	Bpa	Bson	Burned (mean ± SE)
Tree density DBH≥10 (num tree ha^{-1})	990	857	1633	959	1110 ± 177
DBH of mean BA (cm)	26.6	25.9	15.5	23.3	22.8 ± 2.5
Basal area (m^2 ha^{-1})	55.1 ± 0.7	45 ± 0.8	30.8 ± 0.1	40.9 ± 0.7	43.5 ± 0.6
Stem height (m)	7.6 ± 0.3	7.7 ± 0.3	8.2 ± 0.2	7.2 ± 0.4	7.7 ± 0.2
Maximum flame height (m)	13	15	12	15	14
Dead trees (% of stems)	50%	31%	60%	78%	54.8 ± 9.8%
Number sprouting trees (% of stems)	50%	69%	40%	13%	43 ± 11.7%
Liana density (% of stems)	0%	4%	5%	0%	2.2 ± 1.2%

Total burned areas differed in size at different locations but none of them were smaller than 15 forested hectares and the largest ones: Laguna-Acjanaco and Pahititi easily burned more than 50 forested hectares each. We are unsure of the burning period of our sites but an analysis of regional fires in the Andes concluded that most cloud montane forest fires occur at the very end of the dry period (September– November), especially on years of delayed rains. Personal communication with Park Guards confirmed that all fires had burned for several days. The Andean section of the park is suffering from increased fire pressures, resulting from both climate (e.g. 2005 severe drought) and human influence (e.g. poor cattle management and abundant fires for Puna regeneration purposes) (Suárez and Medina, 2001; Bustamante-Becerra and Bitencourt, 2007)

The Puna/Páramo ecosystems are mainly formed by herbaceous and shrub species and even trees in areas protected from night frosts and fire (i.e. *Baccharis, Berberis, Brachyotum, Chuquiraga, Clethra, Escallonia, Gynoxys, Miconia, Myrsine, Weinmannia, Alnus* and *Polylepsis* (Keating, 2008)). These ecosystems are located between 2500 and 4500 masl, occupying the upper montane sections of the eastern Andean slopes, adjacent and intertwined with TMCFs. Precipitation is inversely related to elevation with total annual rainfall varying from 3800 mm at 2500 masl to 1500 mm at 3400 masl. Mean annual temperatures also decrease with elevation: from 15 to 10 °C for the same elevation range.

The Puna/Páramo region (>2000 masl) has long been populated leaving a strong human footprint in the current configuration of the landscape, both through agriculture and fire, particularly affecting the distribution of the treeline (Sarmiento and Frolich, 2002; Keating, 1997; Young and León, 2007). Although land use activities in TMCFs vary greatly depending on socio-economic and environmental drivers, a predominant pattern common to most TMCFs is the conversion to pasture (Young and León, 2007). Once established, pastures are generally burned annually to promote new growth of grasses and to prevent invasion by shrubs and trees (Asbjornsen and Wilcke, 2008). Both climate fluctuations and human activities play interlinked roles in determining fire regimes in TMCFs, with severe drought years such as 2005, leading to generalized fire in the tropical high Andes (>2000 masl) (Román-Cuesta et al., Personal observation) and montane ecosystems in Central America (Sherman et al., 2008). Under these drought spells, fires from adjacent more fire-prone regions (Puna/Páramo), which usually get extinguished when reaching the wet and foggy TMCFs, are able to extent into the forest with severe crown fire episodes being not rare.

2. Methods

2.1. Experimental design

We selected a paired-plot design which is appropriate for after-only studies where no pre-disturbance data are available. We carefully matched pairs of 30 m× 30 m treatment (burned) and control plots, where pre-treatment conditions are assumed to have been similar, with a minimum of 30 m between plots (Asbjornsen et al., 2005). Our selected sites were all surrounded by Puna grasslands, where fire was initiated. The paired plots have similar elevation (>2800 m), aspect and slope. We assumed that forest structures were similar in the control and the burned plots.

2.2. Statistical analysis

All above- and belowground biomass values were converted to a per hectare basis. Paired sample Student's *t*-tests were used to examine differences between measured parameters within burned and control sites (SPSS Inc. 1989–2006). We ran statistical analyses to guarantee similar forest structures between the control and burned plots. This was an important requirement to support that the differences in carbon emissions between paired plots were related to fire impacts and not to heterogeneous forest structures. Most data were normally distributed and ln-transformations were applied, when necessary.

2.3. Carbon stocks and fluxes: aboveground and belowground components

2.3.1. Aboveground carbon stocks

We measured trees with a minimum Diameter at Breast Height (DBH) of 10 cm, as it is commonly done in tropical forests (Richards, 1936). We estimated the total height of all trees, and identified them taxonomically to genus level. Burned plots frequently had unidentifiable trees. We used the plot mean tree density when that occurred. We also reported the regenerative strategy of each burned tree: resprouting, germination or no response. Trees that showed regenerating responses were considered to be alive. To estimate the aboveground biomass (AGB) for both live and dead trees we selected three different allometric equations:

- Tanner (1980) for montane cloud forests in Jamaica: Ln $T = -1.71 + 1.16 \ln(BA)$ where T is total dry-weight tree biomass in kg and BA is basal area in cm^2.
- Chave et al. (2005), based on 2410 trees: $AGB = \exp(-2.557 + 0.940 \ln(\rho D^2 H))$ where the AGB is in kg per tree, ρ is the specific wood density ($g.cm^{-3}$); D is DBH (cm); and H: tree height (m). We selected Chave et al. (2005) *wet* allometric equation due to its humidity thresholding: "Forests where evapotranspiration exceeds rainfall during less than one month".
- Nenninger (2006) is an empirically derived biomass equation ($n = 56$, $R^2_{adjusted} = 0.9$) based on typical cloud montane tree species from southern Ecuador: $AGB = 0.07 DBH^{2.417}$ where M is the AGB per tree in kg, and DBH is in cm.

Results offered in this research rely on Nenninger's equation since it is specific to Andean montane forests. Total tree biomass per plot was calculated as the sum of individual trees DBH>10 cm separated in live and dead standing trees. We assumed a 50% carbon content in biomass (Brown and Lugo, 1992).

Re-sprouting trees complicated the estimations of carbon due to biomass burning. We finally assumed 90% stability in their carbon stocks with 10% of immediate loss due to canopy leaves and small twigs and branches, which has been a normal approach in other carbon balances (Brown and Lugo, 1982; Delaney et al., 1998). There were two reasons behind this decision: (1) to not overestimate the biomass burning emissions at the regional level. Any emission coming from the re-sprouting trees would have been part of the Mb value, and (2) from our experience in the region we could see that other re-sprouting trees were successful in retaining their vigour and in recovering a "normal" canopy aspect with no trunk decomposition. Current on-going re-measurements of our burned plots have proven this assumption right.

We estimated the biomass of fallen dead wood using a modification of the linear intercept method (Brown, 1974). We conducted assessments along a 30-m transect established within each plot. Fallen dead wood was separated into four diameter classes (Burgan and Rothermel, 1984): (I) < 0.6 cm, (II) >0.6 and < 2.6 cm, (III) >2.6 cm and < 12 cm, and (IV) >12 cm. Pieces of fallen dead wood less than 2.6 cm in diameter were tallied for the first 10 m along each transect in both the burned and control plots. Pieces of fallen dead wood greater than 2.6 cm diameter were tallied along the entire 30-m transect for both treatment and control plots. Decomposition state (solid, partially decomposed, fully decomposed) was noted for each piece of fallen dead wood. Wood samples were oven dried (103 °C) and their values divided by water-displaced volumes to obtain wood densities.

2.4. Belowground biomass

Root biomass was based on multiple soil core extractions taken in the same cloud montane forests by Girardin et al. (2010). Only roots below 2 mm were measured by this method.

2.5. Soil carbon

We measured the depths of the organic soil layers (Oi + Oe + Oa) at 10 randomly located sampling points within each plot as it has been done in other studies (Asbjornsen et al., 2005). These measures were a way to evaluate organic soil carbon losses, and could be used as an indicator of fire severity. The Oi horizon was characterised by entire recognisable 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. We derived soil bulk densities and carbon contents for the organic soil layers by applying Zimmermann et al's (Zimmermann et al., 2009) data (Table 2), which had been obtained in the same region, as part of the multi-partner project mentioned before. Zimmermann's soil sampling methods included repeated soil samples ($n = 3$) in thin-walled metal tubes with an inner diameter of 35 mm and stratified according to the different soil horizons. All samples were dried to constant mass weight at 60 °C, and sieved to 2 mm. Stones and roots >2 mm were removed and the fine earth densities calculated. Total carbon concentrations of ground fine earth samples were then quantified with a Carlo Erba NA 2500 Elemental Analyser (Carlo Erba, Milano, Italy). We used these values to transform our soil depths into final biomass contents (Eq. (1)).

$$\begin{aligned}&\text{Organic soil carbon stocks } (\mathrm{MgC\,ha^{-1}})\\&= \text{depth organic soil layer (cm)} \times \text{bulk density } (\mathrm{g\,cm^{-3}})\\&\times \text{carbon content} \times 10^{-6}\,\mathrm{Mg\ g^{-1}} \times 10^{4}\,\mathrm{cm^2\,m^{-2}}\\&\times 10^{4}\,\mathrm{m^2\,ha^{-1}}\end{aligned} \quad (1)$$

Table 2
Organic soil carbon depths, stocks, and mean densities in our study area in Peru (Zimmermann et al., 2009). We relied on these variables to estimate the soil carbon contents in our burned and unburned plots using Eq. (1) in the text. n.a. indicates non available data to display variability.

(A) Zimmermann et al. (2009)					
Layer	Depth (cm)	Mean density ($g\,cm^{-3}$)	Mean C (%)	C/N	C ± SE ($MgC\,ha^{-1}$)
Litter (L)			45.52	27.3	5.8 ± n.a.
Organic layer (O)	5	0.048	44.48	21.8	14.4 ± 7.0
Organic layer (O)	10	0.070	38.07	20.7	26.2 ± 4.8
(B) Our study					
Organic soil Carbon depths (cm)	Challabamba	Laguna-Acjanaco	Pahititi	Sondor	Mean ± SE
Control	5 ± 1.1	41.5 ± 9.8	28.3 ± 6.2	10.4 ± 1.8	21.3 ± 11.8
Burned	0 ± 0	9.2 ± 0.7	0 ± 0	0.7 ± 0.4	2.5 ± 0.8
Organic soil					
Carbon stock ($MgC\,ha^{-1}$)					
Control	10.7	108	72.6	25.1	54.1 ± 22.3
Burned	0	21.7	0	1.4	5.8 ± 5.3
Difference burned control	10.7	86.3	72.6	23.7	48.3

Table 3
Variables from Seiler and Crutzen (1980) "bottom up" approach to estimate biomass burning emissions. "*A*" values derive from MODIS hotspot with a conservative 20% of the total area retained. "Mb" values correspond to the carbon stock *differences* between burned and control plots in TMCFs in the Andes (Table 4). The combustion factor estimates (Cf) are derived from our field experience in the burned plots, and correspond to severe intense ground fires with large torching episodes. "Gef" Emission factors for tropical forests ($g\,Kg^{-1}$ dry matter burned) for various types of burning.

Variables				Total	
A	6251 km^2 (hotspots)		20%	125,020 ha	
		Mean (max–min)	Cf ($g\,g^{-1}$)	$MgC\,ha^{-1}$	
Mb	Standing live which has lost leaves and little twigs and branches due to fire	23.7 (45.7–1.7)	0.1	2.4	
	Dead standing wood that will decompose	28.8 (39.2–14.4)	0.8	23	
	Fallen dead wood that will decompose	4.5 (10.5–0)	0.8	3.6	
	Fine root biomass that burns	14.8 (15.6–14)	1	14.8	
	Soil organic carbon that burns	48.3 (71.2–25.4)	1	48.3	
	Total carbon stock losses due to fire		92 (126–58) $MgC\,ha^{-1}$		
	Total regional C emissions in the Andes		11.5 TgC (15.8–7.3)		
Gef ($g\,Kg^{-1}$)[a]	CO_2	CO	CH_4	N_2O	NO_x
Tropical forest	1580 ± 90	104 ± 20	6.8 ± 2	0.2	1.6 ± 0.7
L	36.4Tg	2.4Tg	156.6Gg	4.6Gg	36.8Gg

Source of data: Table 25 IPCC 2006. AFOLU. The total biomass emissions.
[a] Values are mean ± SD and are based on a comprehensive review by Andreae and Merlet (2001).

2.6. Fire data

In a preliminary attempt to offer regional estimates of TMCFs biomass burning in the Andes we selected the "bottom up" approach by Seiler and Crutzen (1980) (Eq. (2)):

$$L = A \times Mb \times Cf \times Gef, \tag{2}$$

where the quantity of emitted gas or particulate *L* [g] is the product of the area affected by fire *A* [m^2], the fuel loading per unit area Mb [$g\,m^{-2}$], the combustion factor Cf, i.e. the proportion of biomass consumed as a result of fire [$g\,g^{-1}$], and the emission factor or emission ratio Gef, i.e. the amount of gas released for each gaseous specie per unit of biomass load consumed by the fire [$g\,g^{-1}$]. Rather than attempting to measure directly the emission *L*, this method estimates pre-fire biomass [$A \times$ Mb], then estimate what portion of it is burned (Cf) and finally converts the total biomass burned [$A \times$ Mb $\times$ Cf] into emissions by means of a coefficient Gef (emission factors), which have been fairly precisely estimated from laboratory measurements (GOFC-GOLD, 2009). It is however uncertain how these translate into non-laboratory ecosystem conditions. The IPCC 2006 guidelines offer Cf and Gef factors for various types of burning and ecosystems. We used tropical forest Gef for this research (Table 3). Fuel loading (Mb) relied on carbon stock losses due to fire, as estimated in our Andean plots. To estimate the total biomass burning emissions we assumed: (i) only immediate emissions were considered, not committed carbon (Houghton et al., 1983), (ii) all the extra dead wood material resulting from the fire will decompose and it is accounted as a one-time emission at the time of fire. This simplification will result in an overestimation of actual emissions in the year of the fire but on an underestimation of emissions in the years following the fire.

Besides calculating the value *L* for different Greenhouse Gases we also estimated the total amount of C emitted through fire ($A \times$ differences in carbon stocks: burned control). Estimates of *A* (burned area in m^2) for the region relied on satellite fire data to compensate for the unavailability of local, regional and national fire datasets, as it has been done by other researchers (Bradley and Millington, 2006). We downloaded MODIS thermal anomalies (2000–2008) (MOD14, Justice et al., 2002) that capture active fires or hotspots from the LP DAAC dataset (https://lpdaac.usgs.gov/lpdaac/get_data/wist). While MODIS burned area products have recently been liberated, Roy et al. (2008) report a better performance of hotspots over burned areas for forested areas. Since the real total burned area for each pixel is unknown in these databases, we selected a conservative pixel fraction of 0.2 for the total burned area for the MODIS-1 km^2 fire active area (2000–2008) (Table 3).These fire data were then masked by vegetation and elevation to exclusively select burned areas on TMCFs in the tropical Andes.

2.7. Vegetation database

TREES (Achard et al., 2002): Initiated In the early 1990s the TREES project was designed to help develop forest cover assessment throughout the tropics, using an extensive set of satellites. TREES consists of subcontinental forest distribution maps for the early 1990s at 1: 5,000,000 derived from 1 km^2 spatial resolution satellite images. The assessment of forest change is based on fine spatial resolution images of 20–30 m-pixels acquired at two dates close to 1990 and 1997. We used this dataset to calculate the area occupied by TMCFs in the high tropical Andes (12° N–24° S) (>2000 m). This layer was then used to mask the MODIS fire polygons to exclusively focus on montane cloud forests and eliminate non-forest fires. GIS processes were run with MIRAMON v.6.4 (Pons, 2000) and with ArcGIS 9.3. ESRI Inc.

3. Results

3.1. Forest structure in burned and control plots

The Student's *t*-tests for related samples indicated non-significant differences for mean (± SE) tree heights and mean DBHs between the control and the burned plots (8.5 ± 0.7 vs. 7.7 ± 0.2 m for height, and 24.0 ± 2.5 vs. 22.8 ± 2.5 cm for DBH) ($t = 1.4$, $p = 0.3$, $n = 4$; $t = 0.9$, $p = 0.4$, $n = 4$). The similarity of these two variables was basic for non-skewed biomass estimations since the chosen allometric equations rely on them. Mean basal areas also showed non-significant differences (37.4 ± 4.5 vs. 43 ± 5 $m^2\,ha^{-1}$) between the control and the burned plots ($t = -2.9$, $p = 0.06$, $n = 4$). Tree densities were, however, significantly different (847 ± 100 vs. 1110 ± 177 trees ha^{-1}) ($t = -4.8$, $p = 0.02$, $n = 4$) (Table 1).

Sprouting was significantly higher in the burned plots than in their controls, with mean sprouting fractions of 9.8 ± 2.7 vs. 43.0 ± 11.7% in the control versus the burned plots. Maximum

Table 4
Carbon stocks for above and belowground compartments. Values represent mean ±SE, max and min for each variable. $n = 5$ for the control plots and $n = 4$ for the burned plots. n.a. indicates non-available data to display variability.

		Control			Burnt			Difference from control (MgC ha^{-1})
		Mean	Max	Min	Mean	Max	Min	Absolute difference (% of difference)
Standing	Live	69.2 ± 13.4	97.7	32.9	45.5 ± 17.4	83.5	13.4	−23.7 ± 22 (−34%)
	Dead	16.4 ± 4.4	24.2	4.3	45.2 ± 9.4	71.5	30.4	+28.8 ± 10.4 (+276%)
Fallen dead wood		6.7 ± 3.2	15.8	1.5	11.2 ± 5.0	26.2	4.4	+4.5 ± 6 (+167%)
CWD Standing dead + fallen dead		23.1 ± 5.4	37.2	7.5	56.4 ± 10.6	97.7	35.9	+33.3 ± 11.9 (+244%)
Percent of fallen dead in CWD		29%			19.9%			-9.1 (-31%)
Soil organic layer		54.1 ± 22.3	108	10.7	5.8 ± 5.3	21.7	0	−48.3 ± 22.9 (−89%)
Roots (<2 mm)		14.8 ± 0.8	n.a.	n.a.	n.a. ± n.a.	n.a.	n.a.	−14.8 ± 0.8 (−100%)

sprouting reached a value of 69% at the highest plot location, Laguna-Acjanaco (3400 m) (Table 1). The mean percent of dead stems was 19 ± 1.5% in the control versus 54.8 ± 9.8% in the burned plots. The percent of dead stems in the control plots ranged from 15 to 21% while in the burned plots it was 31–78%. Most trees in the burned plots were completely charred (maximum flame heights above 10 m) but many resprouted and were therefore counted as standing live biomass. Vigorous resprouting complicated carbon estimations.

Lianas were abundant in our control cloud forests especially with a maximum contribution of 16% of all stems supporting lianas in our highest elevation plot (Acjanaco 3400 masl) (Table 1).

3.2. Carbon stock losses

Main carbon losses came from the large removal of soil organic carbon stocks (89% removals), with significant differences between control and burned plots (mean (± SE)): 54.1 ± 22.3 vs. 5.8 ± 5.3 MgC ha^{-1}) ($t = 4.6$, $p = 0.02$, $n = 4$). Mean soil losses were 48.3 ± 22.9 MgC ha^{-1}, with maximum values reaching 86 MgC ha^{-1} for Laguna-Acjanaco. Fine root biomass was completely absent from the burned plots, which represented a mean loss of 14.8 ± 0.8 MgC ha^{-1} as estimated for the control plots (Table 4).

Live standing carbon stocks were not significantly different between the control and the burned plots ($t = 1.7$, $p = 0.19$, $n = 4$) (means: 69.2 ± 13.4 vs. 45.5 ± 17.4). In our study sites, burned forests did not have significantly lower live tree biomass compared to their controls. The observed non-significant 37% biomass reduction in the burned plots was mainly compensated by vigorous resprouting. In the estimation of standing live tree biomass, Tanner's equation consistently offered the highest values, with ca. 25% more biomass than the other equations (results not shown).Chave et al.'s (Chave et al., 2005) equation frequently offered the lowest biomass values (between 5% lower (for live trees in burned plots) to 50% lower (for dead trees in control plots). Control plots had most of their Aboveground Carbon Stocks concentrated on live standing trees (75%), while burned plots showed an even distribution between live standing trees (45%) and CWD (55%) (Table 4).

Coarse woody debris (CWD = fallen dead wood + standing dead trees) was significantly higher in the burned plots than in the controls: 2.4-fold higher with a 33 MgC ha^{-1} difference from the control (56.4 ± 10.6 vs. 23.1 ± 5.4) ($t = -3.3$, $p = 0.04$, $n = 4$) (Table 4). This was related to higher carbon stocks for both dead standing trees and fallen dead wood in the burned plots versus their controls. Dead standing trees were, however, the main contributors to CWD final values (e.g. more than 70% for both burned and control plots). The carbon stocks of dead standing trees were significantly higher, in the burned plots than in their controls (45.2 ± 9.4 vs. 16.4 ± 4.4 in burned and control, respectively). Dead fallen wood was 1.7-fold higher in burned plots, with a mean difference of 4.5 MgC ha^{-1} from the control (11.2 ± 5 vs. 6.7 ± 3.2 in burned plots versus the control).

3.3. Preliminary results on biomass burning emissions in the Andes

After masking for elevation (>2000 m) and for forested areas (i.e. Puna fires are not considered), there were 6251 hotspots for the period 2000–2008, in the tropical high Andes. Considering a conservative fraction of burned area of 20%, this represents ca. 125,020 burned hectares for the region, for the considered period (Table 3) (A value from Eq. (2)). Our mean immediate carbon stock releases due to fire were 92 MgC ha^{-1} with a maximum of 126 MgC ha^{-1} and a minimum of 58 MgC ha^{-1} (Table 3) (Mb value from Eq. (2)).

Mean biomass burning emissions for the period 2000–2008 were 11.5 (15.8–7.3) TgC (mean, max–min), with annual emissions of 1.3 (1.8 − 0.8) TgC yr^{-1}. Fire showed, however, a marked cyclicity with some years regionally contributing the most to these values (2000, 2003, 2005). 2005 hold more than 50% of the total number of hotspots for the considered period.

4. Discussion

There is growing evidence that fire has profound implications for shaping ecological patterns and processes in the ecosystems of the Neotropical mainland (Horn et al., 2001). These fire impacts come associated with unaccounted for biomass burning emissions that we claim to be regionally important. This is particularly true considering that increasing human populations and land use pressures surrounding cloud forest ecosystems, combined with more rapid climate warming this century, are apparently leading to an intensification of fire regimes in montane cloud forest regions (see review at Asbjornsen and Wilcke, 2008).

4.1. Carbon stocks in control plots

In order to ensure that our carbon estimates from biomass burning were in a range of "normality", we framed the carbon stocks of our control sites in the range of other montane forests: The mean standing live biomass in our control TMCFs (69.2 ± 13.4 MgC ha^{-1}) were lower than Southern Mexican and Venezuelan values (98–155 MgC ha^{-1} and 147–167 MgC ha^{-1} (Asbjornsen et al., 2005; Delaney et al., 1997); but higher than Ecuadorian values for undisturbed TMCFs: 50–66 (MgC ha^{-1}) (Leuschner and Moser, 2008). Mean CWD values for our control plots (23.1 ± 5.4 MgC ha^{-1}) were in the upper range of other undisturbed montane cloud forest studies: 8.5–21 MgC ha^{-1} in Mexican TMCFs (Asbjornsen et al., 2005), 6.5–28 MgC ha^{-1} in Venezuelan montane forests (Delaney et al., 1998), and 0.2–12 MgC ha^{-1} in Ecuadorian montane forests (Wilcke et al., 2002). Our CWD contributed up to 29% to the aboveground carbon stocks, a bit higher than other CWD contributions in undisturbed TMCFs: 5–20% in Venezuela and 5–17% in Mexico. These unusually high CWD values could relate to high mean values of dead fallen wood (6.7 ± 3.2 MgC ha^{-1}) compared to Venezuela: 3.5–4.5 MgC ha^{-1} (Delaney et al., 1998), although not to Mexico:

5.5–8.5 MgC ha^{-1} (Asbjornsen et al., 2005); and most likely to high values of dead standing wood (16.4 MgC ha^{-1}) which were high compared to Mexico: 3–12.5 MgC ha^{-1} (Asbjornsen et al., 2005), although not to Venezuela: 3–23 MgC ha^{-1} (Delaney et al., 1998).

4.2. Carbon stock differences due to fire in tropical montane cloud forests

Tropical peatlands are one of the largest near-surface reserves of terrestrial organic carbon, and hence their stability has important implications for climate change, through the regional release of biomass burning emissions (Page et al., 2002). Peat soils with thick waterlogged organic layers are frequent along montane cloud forests in the Andes (Stadmüller, 1987) and Mesoamerica (Asbjornsen et al., 2005; Sherman et al., 2008). Cold temperatures, slowed decomposition, high humidity levels, and large litterfall, favour the formation of these soils under montane cloud forest ecosystems.

Our mean organic soil carbon values (54 ± 22.3 MgC ha^{-1}) and our local maximum value of 108 MgC ha^{-1} were in the range of other organic soils: Ecuadorian montane forests (25 cm): 3–140 MgC ha^{-1} (Wilcke et al., 2002). Zimmermann et al. (2009) reported, for our study area, a total soil carbon stock of 272 MgC ha^{-1} for the first 75 cm of soil, where the last 50 cm were mineral layers. This large stock is in the range of other reported soils in montane forests in Ecuador: 15–306 MgC ha^{-1} (Oi, Oe,Oa, Wilcke et al., 2002); and Venezuela: 237–276 MgC ha^{-1} (1 m, Delaney et al., 1997).

Andean organic soils were the carbon pool with larger differences after fire, and the one that contributed the most to the regional emissions (52% of the emissions, Tables 2 and 3). Our 89% reduction of the organic soil layer is very frequent in burned peatsoils. Asbjornsen et al. (2005) reported 89% losses of soil layers after fire in TMCFs in Mexico; Dikici and Yilmaz (2006) saw a 90% decrease in burned peatlands in Turkey, and Rein et al. (2008) a 90% damage of their soil due to a smouldering fire in a Scottish peatland. Complete removal of organic horizons has also been reported in Colombian Andean slopes affected by fires (Cavelier et al., 1998). Under low moisture conditions these deep organic soil horizons provide additional fuel, often sustaining slow-burning smouldering ground fires with potentially severe impacts on the belowground biological system (Neary et al., 1999; Sherman et al., 2008). Besides the direct role of fire over these highly volatile soil carbon layers, carbon could have easily been eroded. With slopes frequently above 60% and rainfall levels between 1500–3200 mm yr^{-1}, the unstructured and exposed soils of our burned plots easily got eroded.

Live standing biomass was altered by fire in our study region. However, it can hardly be compared to other studies since resprouting has been observed but not considered in other carbon estimates in these ecosystems (Asbjornsen, personal communication). Vigorous resprouting partly compensated for our carbon losses and was an evidence of fire resilience of certain Andean cloud montane forest species, contrary to other reports in the Andes (Kessler, 2000). Resprouting has been reported in Mesoamerican (Fig. 3) TMCFs before (Matelson et al., 1995; Arriaga, 2000) but to our knowledge not in the Andes. In spite of this evidence, there is a widespread agreement of montane cloud forests' susceptibility to fire (May, 1997; Young and Keating, 2001), partly due to very slow recovery rates as found for disturbed TMCFs in Puerto Rico (e.g. 200–300 years) (Weaver, 1989; Olander et al., 1998) and partly due to an extrapolation of fire susceptibility from wet lowland rainforest's research, where thin barks and lack of ecological adaptation to fire (such as resprouting strategies) result in large forest die-backs even with low fire intensities. Fire is, however, an important ecological disturbance factor on both historical and modern time scales in cloud forests (Asbjornsen and Wilcke, 2008; DiPasquale et al., 2008). While fire presence *per se* might not retreat the treeline, *fire frequency* quite likely does. Thus, the effect of fire on Andean cloud forests is both (i) species dependent (e.g. *Polylepis* are poorer resprouters than *Chletra*) (*pers. observation*) and (ii) fire-return-interval dependent (e.g. low but currently unknown fire return intervals will likely remove many of our resprouting trees and eliminate seedlings such as those of *Clusia*). More information is therefore needed to estimate TMCF resilience to repeated fire disturbances.

While live tree biomass was not significantly different between the control and burned plots, carbon stocks from standing dead trees showed higher values in the burned plots than in their controls (2.7-fold difference), similarly to Asbjornsen et al.'s (Asbjornsen et al., 2005) results. Fallen dead wood also showed higher values in the burned plots than in their controls (1.7-fold difference), which is slightly lower than the values reported in Asbjornsen et al. (2005). Total CWD was also higher in the burned plots than in their controls (2.4-fold difference), almost identical to burned Mexican TMCFs (Asbjornsen et al., 2005). The role of dead trees and especially the role of fallen dead wood have been reported in lowland Amazonian forests in relation to carbon cycling (Chambers et al., 2000), nutrient release (Wilcke et al., 2002, 2005), carbon partitioning (Delaney et al., 1998; Clark et al., 2002) and fire risk (Kauffman et al., 1988; Cochrane et al., 1999; Barlow and Peres, 2008). However, little information exists for montane cloud forests. Under severe drought conditions (e.g. year 2005 in the Andes), large stocks of CWD might increase fire spread and intensity, favouring more harmful fire events as those registered in the 1998/2003 El Niño years in southern Mexico (Asbjornsen et al., 2005). Moreover, Wilcke et al. (2002) reported leaves shedding under the unusual drought conditions of El Niño 1998 for Ecuadorian montane forests, increasing the stock of dry litter to help spread the fires.

4.3. Regional estimates of biomass burning emissions in the Andes

As it is the case in other tropical peatlands, such as Indonesia (Page et al., 2002), fire in the Andes is mainly of an anthropogenic nature, is exacerbated by climatic extremes such as the severe regional drought of 2005 (North Atlantic warming), and is conditioned by a human management component that results in cloud forests being affected by different levels of disturbance, and therefore different susceptibilities to fire (i.e. ecotonal and fragmented cloud forests suffer from much more severe fires than undisturbed and non-fragmented ones (Page et al., 2002).

Since montane cloud forest peat soils hold the largest carbon stocks, large stock reductions through fire represent major unaccounted for emissions in tropical carbon budgets. These underground fires also present the largest management challenge since, once started, only persistent rainfall will put them out.

Our preliminary regional estimates of biomass burning emissions from Andean TMCFs (2000–2008): 1.3 (1.8–0.8) TgC yr^{-1}, suggests the need for further fire research in the region and better understanding of the regional contribution of TMCFs to biomass burning emissions. Hence, our mean annual estimated emissions are in the same order of magnitude than South American annual fire emissions (300 TgC yr^{-1}) for the period 1997–2009 (Van der Werf et al., 2010), or for the annual mean net emissions in the Amazon as estimated by Achard et al. (2004): 220 ± 146 (TgC yr^{-1}) and by Houghton (2003): 180 ± n.a. (TgC yr^{-1}). Our estimates are an order of magnitude larger than the biomass burning emissions reported for Indonesian peatland fires in 1997/1998 El Niño (0.81 and 2.57 Gt), as estimated by Page et al. (2002), which clearly offered very conservative values.

We believe our estimates to be conservative for the following reasons: (1) We masked all the abundant Puna fires (which also burn over peat soils); (2) It is currently unknown how much area of

TMCFs burns annually. Persistent cloud cover, low fire intensities, early/late pass of the satellites, etc., make them difficult to detect (Bradley and Millington, 2006). However, field verification in our study area consistently reported much more fire than detected by the satellites (i.e. there was not a single satellite-reported fire in our study area for the period 2000–2008, in spite of abundant fire presence). Our estimates of total burned area are, therefore, conservative; (3) Our estimated mean removal of carbon stocks due to severe fires in TMCFs (Mb = 92 MgC ha^{-1}) was also conservative compared to values of slashed and burned tropical moist forests (80 MgC ha^{-1}) (IPCC 2006), which only consider aboveground carbon stocks.

4.4. Methodological constraints and assumptions

1) Our study represents the first effort to account for biomass burning emissions from TMCF along the tropical Andes. It is, however, a rough approach that only considers mature forests and severe fires, which respond to a maximum threshold of biomass emissions. These values can therefore be considered the upper bound of biomass burning estimations for montane Andean forests. On-going research is currently addressing intermediate burning intensities and different TMCFs successional stages, to offer a more complete view of biomass burning estimates in the high tropical Andes.
2) While our forests are representative of Andean conditions, our number of replicates is low ($n = 4$ paired-samples). If we calculate the number of plots we would need to take into account internal variability of the key variables (a 95% confidence with an allowed error of 10%), values would rise to $n = 9$ for standing live biomass, $n = 32$ for standing dead biomass, $n = 36$ for fallen dead wood, and $n = 45$ for organic soil biomass. More sampling sites are therefore required for higher confidence estimates.
3) The Andes are missing updated, high quality vegetation maps to inform about real forest areas and their locations. Moreover, the proportion of mature and successional stands of TMCFs is currently unknown. By extrapolating our field site data to a regional scale we have assumed that all burned pixels were forests with similar mature properties and similar fire responses to those of our plots. This is an overestimation of real forest emissions in the area. We believe, however, that this overestimation gets compensated by conservative burnt area estimates, conservative biomass stocks losses (we considered resprouting in our estimations), and the masking of the very abundant, non-forest fires in the region which are also over peat soils.
4) Time since last disturbance would have been an important factor to measure in our Andean study area since it plays an important role on AGB and BGB (Vargas et al., 2008). This factor is currently included in emission calculations such as Houghton's model (Houghton et al., 1983, 1999). Identifying time since last disturbance through MODIS data is, however, a challenging task, and the protected Area authorities do not have a record on past fires that could compensate the lack of satellite data.

4.5. Andean fire management

By the end of the 21st century, and following the SRES A2 emission scenario (IPCC, 2007), the tropical Andes are expected to experience substantial warming with maximum temperature increases predicted in the high mountains of Ecuador, Peru, Bolivia and northern Chile (Bradley et al., 2006; Vuille et al., 2008).

The fragile interaction of tropical mountain cloud forests with cloud dynamics and the already on-going fast climatic changes at high tropical altitudes have positioned these ecosystems as the miner's canary of climate change impacts on tropical forests (Pounds et al., 1999; Still et al., 1999). Fire is one factor that is prone to increase as a result of rising temperatures and changing hydrological properties in Andean mountain ecosystems.

Several initiatives have already started in the region to improve fire research, to promote adaptive fire management, and to favour economic alternatives through land use diversification. One of these initiatives is currently searching for ways to promote landowner participation into conservation activities through positive incentives such as the REDD+ mechanism (www1). The heart of this initiative is reforestation of degraded lands with green fire breaks enriched with economically valuable Andean plant species planted by local foresters and half-dozen local and indigenous communities. Such fire breaks should prevent the spread of fire into Manu National Park and adjacent community-held forests. Other initiatives have been proposed for the montane forests of Southern Ecuador (Knoke et al., 2010). These authors suggested the improvement of local household economies through land use diversification, with the reforestation of tropical "wastelands" as a key activity and as a main way to halt local montane deforestation.

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