Conversion from forests to pastures in the Colombian Amazon leads to contrasting soil carbon dynamics depending on land management practices

Running head: Soil carbon dynamics in the Colombian Amazon

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Abstract

Strategies to mitigate climate change by reducing deforestation and forest degradation (*e.g.* REDD+) require country- or region-specific information on temporal changes in forest carbon (C) pools to develop accurate emission factors. The soil C pool is one of the most important C reservoirs, but is rarely included in national forest reference emission levels due to a lack of data. Here we present the soil organic C (SOC) dynamics along 20 years of forest-to-pasture conversion in two sub-regions with different management practices during pasture establishment in the Colombian Amazon: high-grazing intensity (HG) and low-grazing intensity (LG) sub-regions. We determined the pattern of SOC change resulting from the conversion from forest (C3 plants) to pasture (C4 plants) by analysing total SOC stocks and the natural abundance of the stable isotopes ^{13}C along two 20-year chronosequences identified in each sub-region. We also analysed soil N stocks and the natural abundance of ^{15}N during pasture establishment. In general, total SOC stocks at 30 cm depth in the forest were similar for both sub-regions, with an average of 47.1±1.8 Mg C ha^{-1} in HG and 48.7±3.1 Mg C ha^{-1} in LG. However, 20 years after forest-to-pasture conversion SOC in HG decreased by 20%, whereas in LG SOC increased by 41%. This net SOC decrease in HG was due to a larger reduction in C3-derived input and to a comparatively smaller increase in C4-derived C input. In LG both C3- and C4-derived C input increased along the chronosequence. N stocks were generally similar in both sub-regions and soil N stock changes during pasture establishment were correlated with SOC changes. These results emphasize the importance of management

practices involving low-grazing intensity in cattle activities to preserve SOC stocks and to reduce C emissions after land-cover change from forest to pasture in the Colombian Amazon.

Introduction

Land-cover conversion is the second most important source of anthropogenic greenhouse gases (GHG) emissions (Don *et al*., 2011), generating around 7-14% of the total carbon dioxide (CO_2) emissions around the world (Harris *et al.*, 2012). Deforestation in the tropics has been estimated at ~1.1 million km^2 during the period 2000-2012 (Hansen *et al*., 2013), and conversion from forests to pasture has become the most common land-use change globally (Elmore & Asner, 2006; IPCC, 2006). Most of the deforested area in the Amazon has been occupied by cattle pasture (Fearnside & Barbosa, 1998; Asner *et al*., 2004; Desjardins *et al*., 2004), although since the beginning of the 21st century the area for the agricultural production has increased, mainly focused on soybean crops (Nepstad *et al*., 2008; Pacheco *et al*., 2012).

In the tropics, soil organic carbon (SOC) represents 30-60% of the total C stored in forest ecosystems (Don *et al*., 2011), and some studies have reported soil C emissions of 0.2 Pg C yr^{-1} due to deforestation in the tropics (Houghton, 1999; Achard *et al*., 2004). Most studies suggest that C content in forest soils decrease with depth. For instance, Malhi *et al*. (2009) reported SOC stocks at three sites of the Brazilian Amazon of 74-127 Mg C ha^{-1} in the top 1 meter depth, 28-63 Mg C ha^{-1} in the 1-2 m layer and 19-37 Mg C ha^{-1} in the 2-3 m layer. Conant *et al*. (2001) found that 64% of the SOC located in the top 50 cm, and Moraes *et al*. (1996) reported a total SOC content of 47 Pg C in the Brazilian Amazon, of which 21 Pg C are stored in the top 20 cm. Despite of the importance of soils as one of the largest organic C

pools in tropical forests, the impact of deforestation on this reservoir has been barely quantified (Don *et al*., 2011) and more information is required.

Management practices implemented in pastures are as important as land-cover changes in determining SOC dynamics and C emissions from human-modified tropical ecosystems (Berenguer *et al*., 2014), and among them, grazing intensity can significantly contribute to preserve or reduce SOC stocks (Uhl, *et al*., 1988). Depending on management, soils under grassland cover may act either as a C sink or source (Fearnside & Barbosa 1998; Dias-Filho *et al*., 2000). For example, Veldkamp (1994) found a net decrease in soil C content of 2-18% in degraded pastures 25 years after deforestation, and Fearnside (1997) found net average emissions of 3.9 Mg C ha^{-1} in 10-11 year-old pastures in poorly managed grasslands. On the other hand, Fisher *et al*. (1994) found that C content is higher in soils where management practices include the combination of introduced grasses with a nitrogen-fixing legume compared to nature grasses in Colombia, and Moraes *et al*. (1996) found an increase of 17% and 19% in SOC content in two 20-year-old chronosequences established in well managed pastures in Brazil.

Strategies for avoiding deforestation such as REDD+ could help to reduce anthropogenic C emissions by around 0.8-1.3 Pg C yr^{-1} (Don *et al*., 2011). According to the United Nations Framework Convention on Climate Change (UNFCCC) decisions (UNFCCC, 2010; UNFCCC, 2011; UNFCCC, 2014), countries willing to access result-based payments through REDD+ activities require developing forest reference emission levels (FRELs) as benchmarks for assessing country's performance (FAO, 2014). In general, FRELs comprise the emission factors, representing the emissions/removals of all important GHG associated with land-cover conversion in all relevant C pools (*i.e.* total changes in C stocks), and the activity data,

referring to the size of a deforested or degraded area (Verchot *et al*., 2012). Despite its importance as a C reservoir (Marin-Spiotta *et al*. 2009; Powers *et al*., 2011), the soil C pool was not included in any of the FRELs submitted to the UNFCCC in 2014 by Brazil, Colombia, Ecuador, Guyana, Malaysia and Mexico due to data scarcity (Conafor, 2014; GFC, 2014; MAE, 2014; MMA, 2014; MNRE, 2014). Colombia, in particular, included the above- and below-ground biomass C pool in forests in its FREL, but neither the SOC stock nor its change after conversion from forest to any post-deforestation land-use category were included (MADS, 2014). However, under the UNFCCC Stepwise Approach (UNFCCC, 2012), countries have the option to improve their initial FRELs by incorporating high-quality data, improved methodologies and additional C pools developed from country- or region-specific information and field measurements following an IPCC Tier 3 approach.

Development of emission factors to describe changes in SOC due to land-cover conversion can be done by using robust methods such as chronosequences (IPCC, 2006) combined with soil analysis of total C and nitrogen (N), and the natural abundance of the stable isotopes ^{13}C and ^{15}N (Marin-Spiotta *et al*., 2009; Elmore and Asner, 2006; López-Ulloa *et al*., 2005; Desjardins *et al*., 2004; Camargo *et al*., 1999; Moraes *et al*., 1996; Piccolo *et al*., 1996). Differences in discrimination against ^{13}C between C3 and C4 plants due to variations in their photosynthetic pathways (Dawson *et al*., 2002; Balesdent & Mariotti, 1996), as well as differences in the soil isotope composition of ^{15}N (δ^{15}N) associated with the rate of atmospheric N_2 fixation (Piccolo *et al*., 1994), can be used to establish the pattern of change in SOC and N stocks resulting from the conversion from forest to pasture and the impact of the management practices (*e.g*. grazing intensity) on C emissions or removals.

Here we present new Tier 3 information and emission factors on SOC pool and its dynamics during 20 years of forest-to-pasture under different management practices in the Colombian Amazon. In our study we addressed the following general question: to what extent land-cover change from forest to pasture and subsequent land management practices affect SOC dynamics in the Colombian Amazon? Therefore, we aimed to better quantify SOC stocks and changes with forest-to-pasture conversion in support of REDD+ initiatives. Specifically, our objectives were to:

1. Quantify and describe the SOC dynamics in two sub-regions of the Colombian Amazon with high- and low-grazing intensity after 20 years of forest-to-pasture conversion.

2. Quantify the relative input of C derived from C3 and C4 plants to the total SOC, and its variation with soil depth and pasture age in both sub-regions.

3. Quantify the N stocks during 20 years of forest-to-pasture conversion in both sub-regions of the Colombian Amazon.

4. Determine the emission factors of the SOC pool in both sub-regions according to IPCC (2006), by applying region-specific equations developed in this study describing SOC dynamics.

Materials and methods

Site description

The study took place in two sub-regions of the Colombian Amazon where management practices after forest-to-pasture conversion differ in terms of grazing intensity. According to Maecha *et al*. (2002), the carrying capacity of pastures in the Colombian Amazon is 0.8-1.0 heads of forage-fed livestock per hectare (HFFL). Therefore, for this study we defined the high- and low-grazing intensity areas (hereafter HG and LG, respectively) as those pastures in

which the number of HFFL per hectare is above and below 1.0 head of livestock ha^{-1}, respectively (Fig. 1). High-grazing intensity management practices are evident in HG, where pastures cover ~662 000 ha from a total area of 18 237 519 ha (Ideam, 2014) and cattle density by 2013 was 1 777 549 heads of forage-fed livestock (HFFL), averaging 2.7 HFFL ha^{-1}, according to the National Livestock Inventory of Colombia (Fedegan, 2013). By contrast, pastures in LG in 2013 covered ~45 000 ha from a total area of 23 387 251 ha (Ideam, 2014), and cattle density by the same year was 5 328 HFFL (Fedegan, 2013), averaging 0.1 HFFL ha^{-1}. HG and LG also coincide with the division of the Colombian Amazon made by government, as high- and low-deforestation risk sub-regions, respectively (Gonzáles *et al*., 2014).

HG is located in the west of the Colombian Amazon where the major land forms are low-gradient foot slopes and dissected plains, extending eastward between 800-200 m above sea level, and the predominant soils are Haplic Ferralsols and Haplic Acrisols, respectively. However, Ferralsols occur only in a relatively small portion of the western side of HG, in the transition of the Andean and Amazon regions of Colombia. Mosquera *et al*. (2012) found no significant differences in total soil organic carbon and the content of other elements in pastures of the same age located in Ferralsols and Acrisols sites within HG. LG is located in the east of the Colombian Amazon where the land forms are dominated by dissected plains between 90-80 m above sea level, and the soils are mainly Haplic Acrisols (van Engelend & Dijkshoorn, 2013). For this study mean annual precipitation and temperature were calculated as the average between 1970 and 2013 in HG, and between 1972 and 2012 in LG. Mean annual precipitation and mean annual temperature in HG are 3723.9±408.6 mm and 26.6±0.6 °C, respectively, and in LG are 3351.1±341.7 mm and 25.9±0.4 °C, respectively. On average evapotranspiration never exceeds precipitation in either sub-regions. The dominant forest

within both sub-regions is the Tropical Moist Forest, which extends over ~39 million hectares, and stores 136.6 ± 4.9 Mg C ha^{-1} and 27.5 ± 0.9 Mg C ha^{-1} in the above- and below-ground biomass, respectively (Phillips *et al*., 2014). Pastures are the predominant post-deforestation land cover across the whole Colombian Amazon and are mostly located in HG (Cabrera *et al*., 2011). According to Bowman *et al*. (2012), up to 80% of the pasture area in the Colombian Amazon is occupied by farms implementing the extensive cattle ranching system. However, whereas in HG farmers tend to manage their pastures by planting *Brachiaria humidicola* or *B. decumbens*, or by mixing these species with legume species such as *Arachis pintoi* or *Desmodium ovalifolium* (Alarcón & Tabares, 2007; Mosquera *et al*., 2012), in LG it is common to find pasture areas where grasses (C4 vegetation) are mixed with shrubs and trees (C3 vegetation).

Chronosequence approach

One chronosequence of six sites representing forest-to-pasture conversion was identified in each of the two sub-regions of the Colombian Amazon, through the use of satellite images, official maps of deforestation in Colombia, and interviews with landowners and local people, who also provided information about the land-use history and management. Both chronosequences covered a period of 20 years of forest-to-pasture conversion, with the primary forest as the reference point (*i.e*. 0 years since deforestation). The chronosequences were established in areas of pasture that previously had a forest cover and have been kept as pasture ever since the deforestation event. In order to have a more representative sequence of the forest-to-pasture conversion, the chronosequences included the first stages of the pasture establishment, corresponding to areas recently deforested (*i.e*. around one year since deforestation) and areas recently burned to clean the biomass remaining from deforestation

(*i.e.* one to two years after deforestation). The rest of the chronosequence was established in pastures of around 5, 12 and 20 years old since deforestation in both sub-regions (Table 1).

The landscape of the area devoted to cattle ranching in HG is mainly dominated by extensive pastures established during the last decades, with the sporadic occurrence of small (< 1.0 ha), scattered patches of remnant forest. The distance from the selected pasture areas to the closest forest in HG was < 1.0 km in the case of the 1- and 2-year-old pastures, ~4.0 km in the case of the 5-year-old pasture and > 30 km in the case of the 12- and 20-year-old pastures. In contrast, the areas dedicated to cattle ranching in LG are embedded within the primary forest matrix, so selected pasture areas from all stages of the chronosequence in this sub-region are surrounded by the adjacent forest.

Soil sampling and laboratory analysis

One 200 m transect was established at every stage of each chronosequence in both sub-regions. The starting point of each transect was randomly selected and 11 sampling points were established every 20 m. At every sample point the litter was removed and soil samples were collected at 0-10 cm, 10-20 cm and 20-30 cm depth using an AMS Soil Core Sampler. A total of 33 samples were collected at every stage of each chronosequence, for a grand total of 198 samples per sub-region. Additionally, six samples of leaf litter were collected from both forests and another six samples of plant material were collected from the 20-yr pastures at both sub-regions, in order to establish reference values for isotope analyses. Soil samples were used to determine dry weight, bulk density, and C and N content in the Analytical Services Laboratory at the International Center of Tropical Agriculture (CIAT/CGIAR). Soil samples were oven-dried at 60 °C, and sub-samples of 18.0 mg were taken after soils were ground and passed through a 2 mm sieve. Total organic C and N contents were determined by

the dry combustion method (at 900 °C), using a PE 2400 Series II CHNS/O Analyzer

calibrated with certified acetanilide (C_8H_9NO).

In order to compare SOC and N stocks from forest and pasture areas in an equivalent

weight (Fearnside & Barbosa, 1998), corrections for soil compaction due to cattle trampling

were applied according to the methodology proposed by Ellert & Bettany (1995). Total SOC

stocks (SOC_T; Mg C ha^{-1}) to 30 cm depth were thus calculated as the sum of the SOC stocks

at 0-10 cm, 10-20 cm and 20-30 cm depth, obtained as the product of the C content, bulk

density and soil thickness at every depth j, as follows:

$$SOC_T = \Sigma(C_j \times \rho_j \times L_j)$$
(1)

where C_j (kg C kg^{-1} soil) is the C content, ρ_j (g cm^{-3}) is the soil bulk density, and L_j (cm) is the

soil thickness adjusted for compaction at the depth j. Total N stocks (N_T; Mg N ha^{-1}) to 30 cm

depth were calculated similar to SOC_T, but replacing C_j by N_j in Eqn (1) as the N content at

the depth j (kg N kg^{-1} soil).

Isotope analysis

Soil sub-samples and plant material were used to establish the stable isotope composition

of ^{13}C (δ^{13}C) and ^{15}N (δ^{15}N) at forests and pastures of all stages in both sub-regions. The

analyses of δ^{13}C and δ^{15}N were carried out in the Stable Isotope Facility at the University of

California–Davis, using an Elementar Vario EL Cube elemental analyser, interfaced to a PDZ

Europa 20-20 isotope ratio mass spectrometer

(http://stableisotopefacility.ucdavis.edu/index.html). Soil δ^{13}C (‰) results are relative to the

VPDB standard, and are expressed as:

$$\delta^{13}C = \left(\frac{R_{sample} - R_{std}}{R_{std}}\right) \times 1000, \tag{2}$$

where R_{std} is the standard $^{13}C{:}^{12}C$ ratio. Variation in $\delta^{13}C$ composition due to differences in the photosynthetic pathway between C3 vegetation (mostly trees and shrubs) and C4 vegetation (mostly tropical grasses), and the resulting differentiated discrimination against ^{13}C, can be used to determine the fraction of soil C derived from C3-plants (C3-C) and C4-plants (C4-C) to total SOC as a result of the forest-to-pasture conversion. The fraction of C4-C and C3-C at each depth j at every stage of the forest-to-pasture conversion was calculated using a two-compartment mixing model (Balesdent & Mariotti, 1996):

$$F_{C4-cj} = \left[\frac{(\delta_{Sj} - \delta_F)}{(\delta_{Vp} - \delta_{Vf})}\right] \times SOC_j, \tag{3}$$

where F_{C4-Cj} (Mg C ha^{-1}) is the fraction of C4-C, δ_{Sj} is the $\delta^{13}C$ of the soil sample, δ_F is the average $\delta^{13}C$ of the soil at forests (-27.5±0.7‰, in this study), δ_{Vp} is the average $\delta^{13}C$ of C4 plant material from pastures (-17.4±2.0‰, in this study) and δ_{Vf} is the average $\delta^{13}C$ of the forest litterfall (-31.2±0.7‰, in this study). Moreover, the fraction of C3-C at the same depth j (F_{C3-Cj}) was calculated as:

$$F_{C3-cj} = SOC_j - F_{C4-cj}, \tag{4}$$

Total C4-C$_T$ and C3-C$_T$ fractions to 30 cm depth were thus calculated as the sum of F_{C4-Cj} and F_{C3-Cj}, respectively, at each depth j. Soil isotope composition of $\delta^{15}N$ (‰) was calculated as:

$$\delta^{15}N = \left[\left(R_{sample} - R_{standard}\right) - 1\right] \times 1000, \tag{5}$$

where R represents the sample and standard $^{15}N{:}^{14}N$ ratio. Atmospheric $R_{standard} = 0.0036765$ (Piccolo et al., 1994).

All data were tested for normality and homogeneity of variance. Analysis of variance (ANOVA) were performed to establish differences in mean soil bulk density, SOC_T and N_T stocks, C:N ratio, $\delta^{13}C$, $\delta^{15}N$, C3-C and C4-C among the six stages of each chronosequence, and between similar stages of the forest-to-pasture conversion between the two sub-regions. Additional ANOVA tests were performed to determine differences of these variables with increasing depth within every stage of each chronosequence. *Post hoc* Tukey-HSD tests were made when significant differences were found. Linear, exponential and logarithmic regression analyses were tested to establish the pattern of variation of SOC_T stocks, C3-C, and C4-C to a depth of 30 cm, and within every depth (*i.e.* 0-10 cm, 10-20 cm and 20-30 cm), during the forest-to-pasture conversion at both sub-regions, and the model which best fitted the data in every case was selected. Selection of the best model depended on the resulted r^2 and *P*-value of each model. Pearson's correlation analyses between SOC and N stocks were performed to assess similarities in the pattern of variation along the forest-to-pasture conversion at both sub-regions. All the analyses were evaluated with a significance level of $P < 0.05$. The equations selected to describe the pattern of variation of SOC_T to 30 cm depth were used to establish the emission factors for the total change in SOC stocks due to the forest-to-pasture conversion after 20 years of deforestation at both sub-regions, according to the IPCC (2006) Tier 3 approach. Thus, the results expressed in Mg C ha^{-1} were converted to tonnes of CO_2 equivalent per hectare (t CO_2e ha^{-1}) by using the C-to-CO_2e conversion factor of 44/12 (UNFCCC, 2012), and were assessed at a 95% confidence interval.

Results

Bulk density

Soil bulk density (ρ) was significantly different ($P < 0.05$) during the forests-to-pasture conversion in each sub-region, as well as between pastures with similar age from the different sub-regions. While in HG ρ progressively increased with time within the 30 cm profile, in LG it remained almost constant at the same depth (Table 2). A total increase in soil ρ in the top 0-10 cm layer of 27% in HG and 14% in LG with respect to the original forest were registered at the end of both chronosequences. Values of ρ at the 0-10 cm layer were significantly different from those in the deeper 10-20 cm and 20-30 cm layers at the forest and at the 1- and 2-year-old pastures in LG. In contrast, there were no differences with depth along the chronosequence in HG, except for the 20-year-old pasture (Table S1). Soil ρ showed a similar increasing pattern across the soil profile and along the chronosequence in HG, with a peak during the 12-year-old pasture at the 10-20 cm and 20-30 cm layers, and during the 20-year-old pasture at the 0-10 cm layer. After 12 years of pasture establishment in HG there was a pronounced decline in ρ at the 20-30 cm layer. For LG, while soil ρ increased along the whole chronosequence in the top 0-10 cm layer, it tended to decrease with time since disturbance in the 10-20 cm and the 20-30 cm layers (Fig. 2a).

Soil organic carbon (SOC) stocks

Total soil organic carbon (SOC_T) stocks down to 30 cm depth in the primary forest were similar between both sub-regions, with an average of 47.1 ± 1.8 Mg C ha^{-1} in HG and 48.7 ± 3.1 Mg C ha^{-1} in LG. After deforestation SOC_T stocks significantly varied with pasture age in both sub-regions, although the patterns of soil C change were notably opposite between HG and LG (Table 2). During the first year of the forest-to-pasture conversion, SOC_T increased by the same magnitude in HG and LG (53.0 ± 2.7 Mg C ha^{-1} and 55.9 ± 3.6 Mg C ha^{-1},

respectively), but after the use of fire the variation of SOC_T at pastures was significantly different between HG and LG (Table 2). In HG, SOC_T was 37% higher at the 2-year-old pasture, and then 28%, 20% and 20% lower at the 5-, 12- and 20-year-old pastures, respectively, compared to the original forest. Oppositely, SOC_T in LG was 11% lower at the 2-year-old pasture with respect to the forest, and 18%, 13% and 41% higher at the 5-, 12- and 20-year-old pastures, respectively.

The vertical distribution of SOC showed significant differences among forests and pastures at most stages in both sub-regions, except for the 1- and 2-year-old pastures in LG (Table S1). As expected, the largest proportion of SOC was found in the top 0-10 cm layer in all stages of the forest-to-pasture conversion in both sub-regions, followed by a reduction towards the 10-20 cm and 20-30 cm layers, with the exception of the 1-year-old pasture in LG (Fig. 2b). After five years of forest-to-pasture conversion in HG, the proportion of SOC in the top 0-10 cm soil layer increased to the detriment of the proportion in the deeper layers. This pattern was not registered in LG, where the proportions of SOC were similar across the soil profile during the post-deforestation time (Fig. 2b). In both sub-regions SOC was higher at the end of the 20 years of pasture establishment in the top 0-10 cm layer compared to the forest.

Nitrogen (N) stocks and C:N ratio

Total soil nitrogen (N_T) stocks at 30 cm depth were only significantly different between HG and LG at the 2-year-old pastures. The average N_T content in the soil of forests at this depth was 4.19 ± 0.12 Mg N ha^{-1} in HG, and 3.72 ± 0.14 Mg N ha^{-1} in LG, but the values increased to 5.76 ± 0.42 Mg N ha^{-1} and 4.76 ± 0.23 Mg N ha^{-1} after two and one years since deforestation, respectively (Table 2). While N_T stocks at 30 cm depth were significantly different in almost all stages of the chronosequence in LG, it was only significantly different

at the 2-year-old pasture in HG. There were also significant differences in N stocks among the
soil layers in all stages of the forest-to-pasture conversion in HG, and in the forest, 5- and 20-
year-old pastures in LG (Table S1). As in SOC, the largest proportion of soil N was found in
the top 0-10 cm layer in both sub-regions, although in HG the difference between the 0-10 cm
layer and the deeper layers increased to ~50% after the fifth year of pasture establishment
(Fig. 2c).

Variation in soil N_T at 30 cm depth and in N stocks at 0-10 cm, 10-20 cm and 20-30 cm
depth were highly correlated with variation in SOC_T at 30 cm depth and with SOC stocks at
every soil layer, respectively (Fig. 3). These results indicate both that losses in C stocks
occurring during the forest-to-pasture conversion are concomitant with losses in N stocks, as
well as gains in soil N are associated with gains in soil C. C:N ratios ranged from 9.4 to 11.4
in HG and from 11.5 to 19.2 in LG, and were significantly higher in the forest and the 5-, 12-
and 20-year-old pastures in LG compared to the same stages in HG (Table 2). There were also
significant differences in C:N ratios with depth in most of the stages of the forest-to-pasture
conversion in both sub-regions (Table S1), but whereas in HG C:N tended to increase with
depth and keep around constant along the forest-to-pasture conversion, in LG it tended to
decrease with depth and to increase with time (Fig. 2d).

Natural abundance of ^{13}C and ^{15}N

Soil isotopic composition of ^{13}C ($\delta^{13}C$) at 30 cm depth at the forest, 1-, 2- and 20-year-old
pastures was significantly different between both sub-regions (Table 2). There was a
significant increase of $\delta^{13}C$ during the forest-to-pasture conversion at this depth in HG,
ranging from -27.6‰ at the forest stage, to -21.5‰ at the 20-year-old pasture. In LG,
although variation of $\delta^{13}C$ was not so evident along the chronosequence (*i.e.* between -25.3‰

and -24.7‰), there was a significant increase at the 5-year-old pasture which reached a value of -24.2‰.

There were also significant differences of $\delta^{13}C$ going down the soil profile in both sub-regions. In LG, $\delta^{13}C$ in the 0-10 cm and 10-20 cm layers were similar along the chronosequence, whereas in HG there was a large, significant increase in soil $\delta^{13}C$ in the top 0-10 cm layer with stage, which decreased in magnitude with depth to 30 cm (Table S2).

Natural abundance of ^{15}N in soils at 30 cm depth was significantly different between all stages of the forest-to-pasture conversion in both sub-regions (Table 2). Higher values ^{15}N were found at LG compared to HG, ranging from 11.1‰ to 12.5‰ and from 5.8‰ to 8.9‰, respectively. A decrease in natural abundance of soil ^{15}N occurred during the slash and burn events in HG, after which a gradual increase up to 31% of the original content was recorded at the end of the 20 years of pasture establishment. In LG, on the other hand, soil $\delta^{15}N$ at 30 cm depth remained relatively stable during the entire chronosequence. Values of soil $\delta^{15}N$ were always lower in the top 0-10 cm layer in both sub-regions and significantly different from the values recorded in the deeper layers (Table S2).

Soil C turnover

Conversion from forests to pasture modified the original SOC_T stocks in both sub-regions (Fig. 4a). Whereas SOC_T down to 30 cm depth decreased with time since conversion in HG ($r^2 = 0.24$; $P < 0.0001$), in LG SOC_T tended to increase ($r^2 = 0.20$; $P = 0.0002$). While C3-C_T in HG followed a similar decline over the chronosequence ($r^2 = 0.51$; $P < 0.0001$) with a pronounced decrease after the second year of deforestation (*i.e.* after the fire event), C4-C_T tended to increase ($r^2 = 0.75$; $P < 0.0001$) (Fig. 4b, 4c). There was a clear dominance of C3-

C_T over C4-C_T inputs to SOC$_T$ during the forest stage in HG (C3-C_T = 46.4±1.8 Mg C ha^{-1}; C4-C_T = 0.7±0.3 Mg C ha^{-1}), that progressively reduced as C3-C_T declined and C4-C_T increased along the chronosequence (C3-C_T = 21.2±0.8 Mg C ha^{-1}; C4-C_T = 16.7±1.0 Mg C ha^{-1} at the 20-yr pasture). Both sources of soil C input in LG tended to increase after deforestation (C3-C_T: r^2 = 0.14; P = 0.0017; C4-C_T: r^2 = 0.16; P = 0.0007), with no large change after the fire event (Fig. 4b, 4c). The dominance of C3-C_T over C4-C_T during the forest stage in LG was less pronounced than in HG (C3-C_T = 39.1±2.8 Mg C ha^{-1} and C4-C_T = 9.6±0.5 Mg C ha^{-1}), although C3-C_T increased in 26% at the end of the forest-to-pasture conversion.

No trend was found in SOC in the upper 0-10 cm layer in HG along the chronosequence, with an average of 20.8±1.7 Mg C ha^{-1}, reflecting both a strong decrease in the C3-C content (r^2 = 0.56; P < 0.0001) and the pronounced increase of C4-C (r^2 = 0.77; P < 0.0001) at this depth. SOC and C3-C tended to decrease with time in the 10-20 cm layer (r^2 = 0.29; P < 0.0001, and r^2 = 0.42; P < 0.0001, respectively) as well as in the 20-30 cm layer (r^2 = 0.35; P < 0.0001, and r^2 = 0.43; P < 0.0001, respectively), with a marked reduction after the fire event at both depths. C4-C increased in the 10-20 cm (r^2 = 0.67; P < 0.0001) and 20-30 cm layers (r^2 = 0.54; P < 0.0001), although in a lower proportion compared to the top 0-10 cm layer. Significant differences in C3-C were found among the three depths in all stages of the forest-to-pasture conversion in HG (P < 0.0001), and in most of the stages in the case of C4-C, except for the forest and the 2-years-old pasture (Table S3).

There was a weak but still significant increase in SOC (r^2 = 0.20; P = 0.0002), C3-C (r^2 = 0.11; P = 0.006) and C4-C (r^2 = 0.09; P = 0.01) in the top 0-10 cm layer in LG, as well as in SOC (r^2 = 0.22; P < 0.0001), C3-C (r^2 = 0.21; P < 0.0001) and C4-C (r^2 = 0.09; P = 0.01) at

the 10-20 cm layer along the forest-to-pasture conversion. However, no trend was found in SOC, C3-C and C4-C in the 20-30 cm layer in this sub-region, where stocks averaged 13.6 ± 1.9, 10.6 ± 1.5, and 3.0 ± 0.6 Mg C ha^{-1}, respectively. There were significant differences in C3-C stocks among soil layers in most stages of LG, except for the 2-year-old pasture, and only the 5-year-old pasture showed differences in C4-C among depths (Table S3).

Emission factors for changes in SOC_T stocks (IPCC Tier 3 approach)

IPCC (2006) recommends developing emission factors for changes in SOC pool for lands converted to grasslands, including the forest-to-pasture conversion, and the long term effects of land-use management within a Tier 3 approach. Accordingly, the following equations and parameters were fitted to the data in order to describe the change in SOC_T stocks to 30 cm depth with time due to the forest-to-pasture conversion after 20 years of deforestation in HG and LG, respectively:

$$SOC_T = 52.1024 \, exp \, (-0.216yr) \tag{6}$$

and the equation

$$SOC_T = 49.0154 + 0.8807yr \tag{7}$$

Table S5 presents the resulting emission factors for changes in SOC_T stocks for the forest-to-pasture conversion in both sub-regions.

Discussion

The results indicate that forest-to-pasture conversion modified SOC_T in the Colombian Amazon, although the pattern of C variation after deforestation in each sub-region was very different. SOC_T increased shortly following deforestation as a result of a large input from litter, then SOC_T quickly declined to previous levels in both sites within 5 years of

deforestation, after which the change in SOC_T diverged among land management regimes, decreasing in HG and increasing in LG (Fig. 2). A few causal mechanisms for changes in SOC as a consequence of land management are expanded upon below, and include the changes in decomposition rates following deforestation, the effects of fires on C inputs to soil, C losses from erosion and runoff and loss of C from deeper soils as a consequence of greater C in the light fraction of soil, which is easily lost.

It has been demonstrated that the slash-and-burn system widely used in the Amazon to prepare land for pasture establishment contributes to transfer large amounts of C and nutrients from forest biomass to the soil (Buschbacher, 1986; Buschbacher *et al*., 1988; Fearnside *et al*., 2001; Fearnside & Barbosa, 1998; Aragão & Shimabukuro, 2010), and that, as a result, decomposition rates increase during the first months after deforestation due to the high availability of readily decomposable organic matter at the soil surface, and increases in surface temperatures and aeration (Lavelle *et al*., 1993; Kauffman *et al*., 1995; Kauffman *et al*., 1998; Yakimenko, 1998; Chapin *et al*. 2002; Powers *et al*., 2009; Conant *et al*., 2011).

The use of fire as a management practice of pasture establishment contributed to elevate SOC_T stocks in HG and LG. In fact, depending on burning efficiency, fire contributes to eliminate on average 38% of the remnant dead wood and other non-readily-decomposable material left after deforestation in the Amazon (Kauffman *et al*., 1995; Kauffman *et al*., 1998; Fearnside *et al*., 2001; IPCC, 2006). As a consequence, in some areas of the Amazon region where burning efficiency is low due to short or non-existent dry seasons (Armenteras-Pascual *et al*., 2011), or associated with chemical or physical properties of organic matter such as wood density or moisture content (Araujo *et al*., 1999), farmers usually implement fire more than once in order to eliminate the greatest possible amount of woody debris (Fearnside *et al*.,

2001) or to control the growth of secondary vegetation (Aragão & Shimabukuro, 2010). Navarrete *et al.* (2016) found that fire does not totally consume the remnant woody debris left after cutting the forest in HG, so farmers tend to burn the deforested areas in two to three fire events.

SOC variation with forest-to-pasture conversion in HG

The high-intensity post-deforestation grazing occurring in HG, represented by a high density of cattle population (*i.e.* 2.7 HFFL ha^{-1}) in pastures with low carrying capacity (*i.e.* 0.8-1.0 HFFL ha^{-1} according to Maecha *et al.*, 2002), poor maintenance of the introduced grasses and the use of machinery, has increased the soil susceptibility to lose organic C through erosion and runoff. C loss due to soil erosion has been well documented (Lal, 1998; Wairu & Lal, 2003; Fonte *et al.*, 2014). Soil erosion contributes to deplete the organic C associated to the free and occluded light-density fractions in soils (Marin-Spiotta *et al.*, 2009; Wagai *et al.*, 2009), mainly composed of plant and animal material at different stages of decomposition, and gradually also affects the soil organic C in the high-density fraction consisting of organic matter attached to minerals (Schrumpf *et al.*, 2013). Some authors have suggested that soil organic matter is related to soil clay content (Moraes *et al*,. 1996; Moraes *et al.*, 2002), and that susceptibility to soil erosion is higher in clayey soils where high-intensity grazing, cattle trampling, mechanization and high annual precipitation values contribute to remove small particles composing soil (Lal, 1977; Fearnside & Barbosa, 1998). While clay content was not measured directly in this study, van Engelend & Dijkshoorn (2013) suggested that the predominant soils in HG (*i.e.* Haplic Ferralsols and Haplic Acrisols) have high clay contents, indicating the high risk of erodibility in pastures established in this sub-region, which increases when considering that mean annual precipitation exceeds 3700 mm. Guo & Gifford (2002) suggested that land-cover change from forest to pasture in areas

where annual rainfall is >3000 mm, precipitation leads to soil erosion and associated C loss. The use of machinery to eliminate the remnant dead wood after fire also contributed to reduce the SOC in HG, through the removal of part of the dead root C pool. The dead root C pool is the main source of organic C to the deeper soil layers (Ludovici *et al*., 2012), and the use of machinery during pasture establishment reduces the C stocks stored in roots by ~90% (Navarrete *et al*., in preparation).

Soil compaction due to cattle trampling after 20 years of forest-to-pasture conversion in HG was also notable at the three depths assessed in this study, evidenced by an increase in soil bulk density of 36% in the top 0-10 cm layer, 27% in the 10-20 cm layer and 17% in the 20-30 cm layer compared to the original forest. As bulk density increased, a resulting decreased of soil porosity might have limited the productivity of improved pastures, consequently leading to a reduction in the SOC stocks in late stages after pasture establishment (Ellert & Bettany, 1995; Martinez & Zink, 2004). Fonte *et al*. (2014) found that productivity in pastures declined progressively after poor maintenance, resulting in the occurrence of patches of bare soil, invasion of non-palatable vegetation and progressive loss of the improved grass *Brachiaria spp*.

SOC_T in the original forest, and its increment during the first two years after deforestation, were strongly influenced by the high input of C3-derived C to the entire soil profile, as a result of the high organic matter input through litterfall and the implementation of slash-and-burn practices. However, the rapid loss of C3-derived C during the early years of pasture establishment and its deceleration during the later stages, could reflect the high susceptibility of the C associated to the free, unprotected light fraction of soil (Marin-Spiotta *et al*., 2009) and the progressive depletion of the occluded light and heavy fractions (Desjardins *et al*.,

2004; Wagai *et al*., 2009). Camargo *et al*. (1999) found that ~90% of bulk soil at 10 cm depth corresponds to the heavy fraction at degraded and improved pastures and also at primary and secondary forests of the Brazilian Amazon, but C concentration associated to that fraction was low ($2.8\pm0.3\%$) compared to the high C concentration found in the light fraction ($22.8\pm3.4\%$). Pastures under well-managed practices have the potential to sequester more C in soils than forests and to store it even below 30 cm depth (Fisher *et al*., 1994; Murty *et al*., 2002); in HG, however, where pastures are poorly maintained, soil C4-derived C is increasing mostly in the 0-10 cm layer.

SOC variation with forest-to-pasture conversion in LG

Unlike HG, low intensity grazing led to a net gain of 41% in SOC_T stocks to 30 cm depth after 20 years of forest-to-pasture conversion, mainly as a consequence of the significant increase of C3- and C4-derived C input to soil at the 0-10 cm and 10-20 cm layers. The management practices implemented in LG, in which secondary vegetation is rarely eliminated from the pasture matrix, could explain the pattern of increase of C3-derived C during the entire chronosequence. In fact, due to the low cattle density (0.1 HFFL ha^{-1}) and the possibility to establish new pastures areas in the adjacent forest, it is a common practice in LG to abandon the pasture when its productivity declines allowing the reestablishment of secondary vegetation. Camargo *et al*. (1999) reported the contribution of C3- and C4-derived C to SOC_T in a degraded pasture in the Brazilian Amazon (*i.e.* the early stages of secondary succession), where C3 shrubs grew within a matrix of C4 grasses. Some other studies have also reported the transition from abandoned pastures to the different stages of secondary forest growth in the tropics (Uhl *et al*., 1988; Brown & Lugo, 1990; Marin-Spiotta *et al*., 2009).

Forest clearing in LG also resulted in a large transfer of organic matter to the soil surface, which increased the availability of readily decomposable material and allowed the input of large amounts of C3-derived C to soils. Decomposition rates increase just after deforestation in pastures and in early stages of secondary succession, because disturbance allocates large amounts of labile nutrients as C and N to the soil (Lavelle *et al*., 1993; Ewel, 1976). The increase in SOC_T stocks and in C3-derived C input continued until the end of the 20 years of forest-to-pasture conversion in LG, which could be related to an increase in NPP due to the rapid colonization and high growth rates of C3 vegetation supported by a high availability of light, water, and nutrients (Chapin *et al*., 2002; Grace, 2004). The proximity of the pastures areas to the forest matrix in LG would facilitate seed dispersal and seedling establishment of C3-plant species into the opened areas, enhancing secondary succession (Cavelier *et al*., 1996; Maza-Villalobos *et al*., 2011; Mora *et al*., 2015; Norden *et al*., 2015). In the competition for light and nutrients in areas such as abandoned pastures where early stages of succession could occur, plants have developed strategies to allocate a large fraction of C to construct leaves with high turnover rates (Selaya *et al*., 2008), or to increase leaf area index (Ryan *et al*., 1997). Brown & Lugo (1990) found larger amounts of C allocated to highly-decomposable organic matter during the first 20 years of secondary succession in humid areas of the tropics, which then was recycled through litter decomposition.

Compared to HG, the susceptibility to lose organic C through erosion and runoff is lower in LG. Soil compaction due to cattle trampling in this sub-region was only evident in the top 0-10 cm layer during 20 years of forest-to-pasture conversion, reducing the impact on soil porosity and structure (Ellert & Bettany, 1995; Martinez & Zink, 2004). The lower average values of precipitation in LG (*i.e.* 3351.1±341.7 mm) also could contribute to reduce the risk of C loss through erosion and runoff (Guo & Gifford, 2002).

Nitrogen and C:N ratio

N_T stocks to 30 cm depth remained relatively similar between HG and LG during the forest-to-pasture conversion. However, notably changes in N stocks occurred in soil profiles in HG where an increase of 17% in N stocks was recorded at the end of the 20 years of pasture establishment in the top 0-10 cm layer, and a decrease of 33% and 36% was registered in the 10-20 cm and 20-30 cm layers, respectively, compared to the original forest. These results are supported by the results of the natural abundance of ^{15}N presented here that show lower values of $\delta^{15}N$ in the 0-10 cm layer compared to the deeper profiles, indicating high rates of N_2 fixation at the soil surface in the pasture sites of HG. Assessing the effects of land-cover conversion from forest to pasture on the natural abundance of ^{15}N in the western Brazilian Amazon, Piccolo *et al*. (1994) found that $\delta^{15}N$ values of soil surface in pastures are lower than those in forests and decrease with pasture age, which could be related to atmospheric N_2 fixation by free-living nitrogen fixing bacteria associated with pasture grasses (Piccolo *et al*., 1996). Grasses of the genus *Brachiaria spp*. obtain ~40% of their nitrogen from N_2 atmospheric fixation through the association with free-living nitrogen fixing bacteria (Boddey & Victoria, 1986; Moraes *et al*., 2002), explaining the high values of soil N stocks in the top 0-10 cm of HG where *Brachiaria spp*. is commonly planted. Some farmers in HG mix *Brachiaria spp*. grasses with the nitrogen fixing legumes *Arachis pintoi* or *Desmodium ovalifolium* (Alarcón & Tabares, 2007; Mosquera *et al*., 2012), in order to improve the N transfer to the grasses (He *et al*., 2009). The difference in N stocks among soil layers is less noticeable in LG, although N stocks decreased with depth in all stages of forest-to-pasture conversion. As in HG, decreasing N stocks were supported by the increase of $\delta^{15}N$ with depth in LG, but in this sub-region the reduction of $\delta^{15}N$ with pasture age was not as evident as in HG. Values of $\delta^{15}N$ in LG were greater than in HG, suggesting that atmospheric N_2 fixation is lower in LG presumably due to the absence of introduced grasses. The strong correlation

between soil C and N variation during the pasture establishment in both sub-regions indicates that soil N stocks are also highly susceptible to grazing intensity. In a review of different studies, Murty *et al*. (2002) also found that changes in soil C and N were strongly correlated when forest is converted to agricultural land, including the forest-to-pasture conversion. SOC and N change also affected C:N ratios in each sub-region, represented by a small decrease of C:N ratios in HG and an increase in LG (see Table 2). Low C:N ratios are related to high rates of decomposition (Chapin *et al*., 2002), for example during the first year following deforestation, which is particularly evident in LG (see Fig 2d).

The chronosequence approach

The chronosequence approach is a practical and commonly used method to monitor changes in C stocks due to land-use change from, for example, forest to pasture (*e.g.* Moraes *et al*. 1996; Camargo *et al*., 1999; Marin-Spiotta *et al*., 2009), or from abandoned agricultural lands to secondary forests (*e.g.* Kennard, 2000; Lebrija-Trejos *et al*., 2008), in the absence of long-term information from fixed locations. However, the method has received some criticism in studies of secondary succession in tropical forests, particularly because of the lack of information on land-use and management histories from the assessed sites (Feldpausch *et al*., 2007; Maza-Villalobos *et al*., 2011; Mora *et al*., 2015). The sites selected to represent the chronosequence of conversion from forest to pasture in this study share a similar land-use and management history in each sub-region, according to information from remote sensing, official maps of deforestation in Colombia, interviews with landowners and local people, and information on accessibility in terms of mobility and security. The assessment of the last criterion limited the availability of potential sampling sites located in remote or high-risk areas in both sub-regions, which may reduce the possibility of capturing the whole variability on SOC with forest-to-pasture conversion in unexplored areas in HG and LG. The lack of

information on SOC stocks dynamics after deforestation from long-term studies in fixed sites, makes the chronosequence approach a suitable alternative to improve the information required in support of REDD+ initiatives. Nevertheless, a complementary set of long-term dynamic studies on SOC dynamics after deforestation should be established in fixed sites, in order to cover the high variability in landscape and soil properties occurring within extensive regions such as the Colombian Amazon, and to reduce the uncertainty on SOC estimates associated with land-use and management history.

In conclusion, to our knowledge, the results presented here are the first Tier 3 information and emission factors on SOC pool and its dynamics during 20 years of forest-to-pasture under different management practices in the Colombian Amazon. Our results emphasize the dual importance of land conversion and subsequent management practices for SOC dynamics in the Amazon and contribute to improve the accuracy of SOC stocks data for REDD+ initiatives in the region. They also highlight the necessity to implement low-grazing intensity practices during cattle activities, in order to preserve SOC stocks and to reduce C emissions after land-cover change from forest to pasture in the Colombian Amazon. Consequently, in order to accurately estimate the impact of land-cover change on soil C dynamics, it is essential to develop a detailed description of all the land uses and associated management practices occurring in deforested areas, and spatially-explicit maps describing their location.

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Supporting information captions

Table S1 Mean soil bulk density (g cm^{-3}), soil organic carbon (SOC; Mg C ha^{-1}) and nitrogen (N; Mg N ha^{-1}) stocks, and C:N ratio to 0-10 cm, 10-20 cm and 20-30 cm depth. Values in parenthesis represent the standard error of the mean (n = 11). Letters indicate significant differences among depths within each stage of the forest-to-pasture conversion ($P < 0.05$).

Table S2 Mean soil isotopic composition of δ^{13}C (‰) and δ^{15}N (‰) to 0-10 cm, 10-20 cm and 20-30 cm depth. Values in parenthesis represent the standard error of the mean (n = 11). Letters indicate significant differences among stages within each sub-region ($P < 0.0001$). HG: high-grazing intensity sub-region; LG: low-grazing intensity sub-region.

Table S3 Mean soil C derived from C3 plants (C3-C; Mg C ha^{-1}) and C derived from C4 plants (C4-C; Mg C ha^{-1}) to 0-10 cm, 10-20 cm and 20-30 cm depth. Values in parenthesis represent the standard error of the mean (n = 11). Letters indicate significant differences among depths within each stage of the forest-to-pasture conversion ($P < 0.05$).

Table S4 Results of the linear, exponential and logarithmic regression analyses test to establish the pattern of variation of SOC$_T$ stocks, C3-C, and C4-C to a depth of 30 cm during the forest-to-pasture conversion at the high- and low-grazing intensity sub-regions

Table S5 Emission factors (t CO$_2$e ha^{-1}) for changes in soil organic C pool after 20 years of forest-to-pasture conversion in the high-grazing intensity (HG) and the low-grazing intensity (LG) sub-regions of the Colombian Amazon. Values in parenthesis represent the Confidence Interval (95%).

Tables

Table 1 Location and time after deforestation of the identified sites comprising both chronosequences at the high-grazing intensity (HG) and the low-grazing intensity (LG) sub-regions in the Colombian Amazon.

Site	Post-deforestation time (yr)	Location (Lat., Long.)
HG		
Primary forest	0.0	01°39'41.8''N, 75°37'41.8''W
1-yr-old pasture	0.6	01°39'53.8''N, 75°37'30.0''W
2-yr-old pasture	1.7	01°39'38.7''N, 75°37'28.1''W
5-yr-old pasture	5.4	01°44'02.8''N, 75°38'03.1''W
12-yr-old pasture	12.0	01°27'30.4''N, 75°37'34.8''W
20-yr-old pasture	20.0	01°27'22.5''N, 75°37'57.9''W
LG		
Primary forest	0.0	04°10'10.1''S, 69°55'17.0''W
1-yr-old pasture	0.7	04°09'53.6''S, 69°54'50.0''W
2-yr-old pasture	1.5	04°09'49.3''S, 69°55'02.8''W
5-yr-old pasture	5.0	04°09'51.5''S, 69°54'41.2''W
12-yr-old pasture	12.0	04°09'58.8''S, 69°54'10.5''W
20-yr-old pasture	20.0	04°10'02.2''S, 69°55'17.9''W

Forest-to-pasture conversion	Bulk density		SOC$_T$		N$_T$		C:N ratio		δ^{13}C		δ^{15}N	
HG												
Primary forest	0.75	(0.03)^{a*}	47.1	(1.8)^{bc}	4.19	(0.12)^{a}	11.2	(0.2)^{a*}	-27.6	(0.1)^{a*}	6.8	(0.2)^{a*}
1-yr pasture	0.75	(0.02)^{a*}	53.0	(2.7)^{c}	4.65	(0.19)^{a}	11.4	(0.2)^{a}	-27.7	(0.1)^{a*}	6.5	(0.1)^{ab*}
2-yr pasture	0.82	(0.03)^{ab*}	64.6	(3.7)^{d*}	5.76	(0.42)^{b*}	11.4	(0.3)^{a}	-27.6	(0.3)^{a*}	5.8	(0.2)^{b*}
5-yr pasture	0.89	(0.04)^{bc}	33.9	(2.4)^{a*}	3.62	(0.28)^{a}	9.4	(0.2)^{c*}	-24.2	(0.3)^{b}	7.5	(0.2)^{c*}
12-yr pasture	1.01	(0.02)^{c}	37.5	(1.8)^{ab*}	3.80	(0.14)^{a}	9.9	(0.3)^{bc*}	-24.3	(0.3)^{b}	8.4	(0.2)^{d*}
20-yr pasture	0.96	(0.02)^{c}	37.9	(1.6)^{ab*}	3.69	(0.17)^{a}	10.3	(0.1)^{b*}	-21.5	(0.2)^{c*}	8.9	(0.1)^{d*}
LG												
Primary forest	1.03	(0.03)^{ab*}	48.7	(3.1)^{a}	3.72	(0.14)^{ab}	13.0	(0.5)^{a*}	-24.8	(0.1)^{a*}	11.8	(0.3)^{ab*}
1-yr pasture	0.96	(0.02)^{ab*}	55.9	(3.6)^{ab}	4.76	(0.23)^{c}	11.7	(0.4)^{a}	-25.1	(0.2)^{a*}	12.0	(0.2)^{ab*}
2-yr pasture	1.06	(0.03)^{b*}	43.5	(3.6)^{a*}	3.73	(0.19)^{ab*}	11.5	(0.4)^{a}	-25.3	(0.1)^{a*}	11.8	(0.2)^{ab*}
5-yr pasture	0.95	(0.03)^{a}	57.4	(3.7)^{ab*}	4.51	(0.20)^{bc}	12.6	(0.3)^{a*}	-24.2	(0.3)^{a}	11.8	(0.3)^{ab*}
12-yr pasture	1.04	(0.02)^{ab}	55.0	(1.7)^{ab*}	4.30	(0.11)^{abc}	12.9	(0.5)^{a*}	-25.1	(0.4)^{a}	12.5	(0.3)^{a*}
20-yr pasture	1.01	(0.03)^{ab}	68.8	(5.7)^{b*}	3.58	(0.24)^{a}	19.2	(0.7)^{b*}	-24.7	(0.2)^{b*}	11.1	(0.3)^{b*}

Figure captions

Fig. 1 Location of the high- and low-grazing intensity sub-regions in the Colombian Amazon (HG and LG, respectively). Panels on the right side show the location of Colombia within South America and the squares within HG and LG represent the area where both chronosequences are located (Navarrete *et al.*, 2016).

Fig. 2 Mean a) soil bulk density, b) soil organic carbon (SOC) stocks, c) nitrogen (N) stocks, and d) C:N ratio to 0-10 cm (solid line), 10-20 cm (dotted line), and 20-30 cm (dashed line) depth, during the forest-to-pasture conversion in the high-grazing intensity (HG) and the low-grazing intensity (LG) sub-regions of the Colombian Amazon. Bars represent the standard error of the mean (n = 11).

Fig. 3 Correlation analyses between SOC stocks and soil N stocks at the whole 0-30 cm soil profile and at the 0-10 cm, 10-20 cm and 20-30 cm layers in HG (black circles) and LG (grey triangles) during 20 years of pasture establishment ($P < 0.0001$ in all analyses. r: Pearson's correlation coefficient; the black and grey straight lines represent the best-fit line obtained by linear regression analyses in HG and LG, respectively; n = 66). HG: high-grazing intensity sub-region; LG: low-grazing intensity sub-region.

Fig. 4 Variation of a) total soil organic carbon (SOC_T), b) C derived from C3 plants ($C3\text{-}C_T$), and c) C derived from C4 plants ($C4\text{-}C_T$) to a depth of 30 cm during the forest-to-pasture conversion in the high-grazing intensity (HG) and the low-grazing intensity (LG) sub-regions of the Colombian Amazon. Significance of all regressions was evaluated at $P < 0.05$. The dotted lines represent the 95% confidence interval.

(a)

$SOC_T = 52.1024 \exp(-0.0216yr)$
$r^2 = 0.24; P < 0.0001$

$SOC_T = 49.0154 + 0.8807yr$
$r^2 = 0.20; P = 0.0002$

SOC$_T$ (Mg C ha^{-1})

HG

LG

(b)

$C3\text{-}C_T = 52.8852 \exp(-0.0541yr)$
$r^2 = 0.51; P < 0.0001$

$C3\text{-}C_T = 39.8546 + 0.6546yr$
$r^2 = 0.14; P = 0.0017$

C3-C$_T$ (Mg C ha^{-1})

HG

LG

(c)

$C4\text{-}C_T = 24.9409 (1 - \exp(-0.0508yr))$
$r^2 = 0.75; P < 0.0001$

$C4\text{-}C_T = 9.1608 + 0.2261yr$
$r^2 = 0.16; P = 0.0007$

C4-C$_T$ (Mg C ha^{-1})

HG

LG

Post-deforestation time (yr)