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Drivers of soil carbon stocks along an elevational gradient in the tropical Andes

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To my family, friends, Yina and Romeo

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Abstract

Globally, soils represent the most important terrestrial carbon (C) stock of the planet and improving our understanding of how soil organic carbon (SOC) changes along elevational gradients can help us to inform the likely response of tropical SOC to climate change. In this study, we used field data and linear mixed effect models to assess the effects of temperature, soil fertility, root symbiont association, and aboveground biomass productivity on SOC alongside an elevational gradient in the northwestern region of Colombia. Samples were taken from nine permanent forest plots located in Antioquia, ranging from 167 to 2928 m asl. We found that SOC increased significantly with elevation, with highland forests (>2000 m asl) having approximately a twice of SOC stocks than their lowland counterparts. The best model explaining SOC stock retained mean annual temperature, soil nitrogen stock, soil N:P, and proportion of basal area of ectomycorrhizal tree in each plot. Our results demonstrate that current SOC stocks in tropical Andes forests are more strongly influenced by belowground and climatic effects rather than plant productivity, that did not change along elevation.

Keywords: Soil organic carbon; temperature; mycorrhizal fungi; soil nitrogen; nitrogen: phosphorus

Resumen

Determinantes del almacenamiento del carbono orgánico en el suelo a lo largo de un gradiente de elevación en los Andes tropicales.

Los bosques tropicales representan globalmente un importante sumidero de carbono (C). Por lo tanto, mejorar nuestro entendimiento sobre la variación del carbono orgánico en el suelo (COS) a través de un gradiente de elevación puede ayudarnos a esclarecer la posible respuesta del COS tropical al cambio climático. En este estudio, nosotros evaluamos el efecto de la temperatura, la fertilidad del suelo, los microorganismos asociados a las raíces, y la productividad de la biomasa aérea sobre el COS a lo largo de un gradiente de elevación, entre 167 y 2928 msnm, en el noroccidente de Colombia. Nosotros encontramos que el COS incrementa significativamente con la elevación. Adicionalmente, hallamos que el mejor modelo que explica el stock de COS esta dado por la temperatura, el stock de N y la relación N:P en el suelo y la proporción del área basal de los árboles con ectomicorrizas. En general, nuestros resultados demuestran que el stock actual de COS en los bosques tropicales de los Andes está más fuertemente influenciado por los efectos del clima y del suelo que por la entrada de C, ya que la productividad de las plantas no cambió con la elevación

Palabras clave: Carbono orgánico en el suelo; temperatura; hongos micorrizicos, nitrógeno en el suelo, relación nitrógeno: fósforo

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Symbols and abbreviations list

Symbols

Symbol	Description	SI units	Definition
AIC	Akaike information criterion	Dimensionless	Without definition
R^2	R square	Dimensionless	$1 - \frac{Unexplained\ Variation}{Total\ Variation}$
R^2c	R square conditional	Dimensionless	Without definition
R^2m	R square marginal	Dimensionless	Without definition
$S.E.$	Standard error	Dimensionless	$\sqrt{S_{total}/n}$
$S_{between}$	Uncertainty among plots	Dimensionless	Without definition
S_{total}	Total uncertainty	Dimensionless	$\sqrt{(S_{between})^2 + (S_{within})^2}$
S_{within}	Uncertainty within plots	Dimensionless	Without definition

Abbreviations

Abbreviation	Description
AGB	Aboveground biomass
AM	Arbuscular mycorrhizal
C	Carbon
DBH	Diameter at the breast height
ECM	Ectomycorrhizal
H	Tree height
LMM	Linear mixed model
MAP	Mean annual precipitation
MAT	Mean annual temperature
N	Nitrogen
NF	Nitrogen fixing
NPP	Net primary productivity
P	Phosphorus
SOC	Soil organic carbon
SON	Soil organic Nitrogen
SRA	Symbiont root associations
WD	Wood density

Introduction

Soil organic carbon (SOC) stocks (in Mg ha-1) represent about 70% of the total organic carbon stored in terrestrial ecosystems (Li et al., 2016), serving as a significant sink for atmospheric carbon dioxide concentrations (Li et al., 2016; Raich et al 2006). SOC stocks are driven by the balance between carbon (C) inputs from plant and microbial sources, including such as leaf litter fall, root production, and microbial turnover, and outputs from root respiration and microbial decomposition (Amundson, 2001; Davidson & Janssens, 2006; Li et al., 2016; Chen et al., 2017). These physiological processes, however, are strongly affected by changes in temperature and nutrient availability (Cao & Woodward, 1998; Amundson, 2001; Davidson & Janssens, 2006). Along gradients of temperature, increased net primary productivity (NPP) at warmer temperatures is typically balanced by increased rates of decomposition (Davidson & Janssens, 2006). The availability of key elements for photosynthesis and microbial activity, however, such as Nitrogen (N) and Phosphorus (P), in soils is expected to decline with increasing temperature due to greater NPP (Tashi et al., 2016). Because tropical forests are responsible for the majority of terrestrial C uptake on Earth (Pan et al., 2011), understanding their SOC dynamics has global importance. In particular, improving our understanding of SOC variation along elevational gradients can help inform the likely response of tropical SOC to climate change.

Soil microbial communities drive fundamental biogeochemical processes through their mineralization of organic matter (Crowther et al., 2019). As noted above, microbial mineralization is generally constrained by temperature and nutrient availability, as these factors influence both microbial abundance and enzymatic activity. For example, high N concentration can reduce microbial abundance and activity, as observed in N addition experiments (Treseder, 2008). Therefore, if N concentration increases with elevation, decomposition rate may decrease, resulting in an increase in SOC content. These two factors may also have additive effects along elevational gradients, i.e. cold temperatures and high N concentrations both reducing decomposition rates of highland soil microbial communities, leading to large SOC contents. Importantly, however, these negative effects on decomposition rate could be counteracted by the effect of P concentration relative to N concentration. Due to the involvement of P in many basic cellular processes (Sterner and Elser, 2002), N:P relationships can affect microbial metabolic activity, with an increase in decomposition rate when N:P decreases (Li et al., 2014). Since tropical mountains are generally characterized as P limited ecosystems (Camenzid et al., 2018), and soil P concentration depends on leaf nutrient content and microbial mineralization, the N:P ratio could change independent of temperature, thereby influencing the decomposition rate and ultimately SOC accumulation in highland communities.

In addition to microbial abundance and activity, there is also growing appreciation that microbial community composition can also strongly affect organic matter decomposition rates and SOC accumulation (Crowther et al., 2019). In particular, different groups of root-associated fungi are increasingly well-recognized to influence rates of soil nutrient cycling due to differential metabolic capacities (Tedersoo and Bahram, 2019). For example, arbuscular mycorrhizal (AM) fungi aid plants in acquiring inorganic nutrients from soils, while ectomycorrhizal (ECM) fungi have greater enzymatic capacities to assist plants in directly acquiring N and P from soil organic matter (Phillips et al., 2013). Variation in mycorrhizal associations have shown to significantly alter SOC and soil C:N ratios at both local and global scales (Averill et al., 2014; Cheeke et al., 2017; Zhu et al., 2018; Soudzilovskaia et al., 2020). Because these effects are also linked with temperature-related changes in decomposition rate (‘Read’s Rule’; Steidinger et al., 2019), it is likely the changes along elevational gradients in forest mycorrhizal composition (i.e. dominated by AM- versus EM-associated trees) may have significant effects on SOC.

Independent of microbial activity and composition, net plant primary productivity (NPP) largely regulates the amount of C that enters an ecosystem. Although NPP is reduced by decreasing temperature along elevational gradients (Girardin et al., 2010), recent studies have shown that both aboveground biomass (AGB) stocks and aboveground biomass productivity can sometimes be as high in montane tropical forests as those reported in lowlands (Peña et al., 2018; Girardin et al., 2014). The implications of changes in AGB productivity will have direct effects on litterfall productivity, and thus, on the potential amount of carbon (C) input and SOC accumulation (Reich and Tufekcioglu, 2000). Similarly, changes in root production along elevation gradients may also influence plant organic matter inputs, although this variable has received less study (Mahli et al., 2017). Assessing the effect of primary productivity in concert with temperature allows for better separation of the climatic controls on SOC input and output processes. In particular, if one assumes AGB dynamics ($AGB_{recruitment}$ + AGB_{growth}) as a surrogate of litterfall productivity (see Malhi et al., 2017), SOC stocks should be expected to increase along with AGB productivity because it may determine the potential amount of C to be stored in the soils (but see Phillips et al., 2019).

In this study, we assessed the effect of temperature, soil fertility, root symbiont association, and aboveground biomass productivity on SOC along an elevational gradient in the northwestern region of Colombia, which includes the northern region of the Andes. Based on samples and measurements carried out in 9 permanent plots located along an elevational gradient ranging from 167 and 2928 m asl, we aim to answer the following research questions: i) Are there systematic changes in SOC stocks along the elevational gradient? ii) What are the main drivers of SOC stocks along the elevational gradient? We hypothesize that SOC increases with elevation due to the main effect of temperature on decomposition rate (i.e. microbial activity). However, this expected augmentation may be reduced by lower AGB primary productivity (i.e. reduced SOC inputs) as well as decreases in the availability of specific nutrients that constrain microbial activity.

Methods

Study area

This study was conducted using soil samples data collected at 9 different sites in the northwest region of Colombia. The sampled sites were located between 6º0' and 8º65' North and 74°61' and 77º 35' West (Figure 1). This region encompasses an elevational gradient from 167 m asl to 2928 m asl. The mean annual precipitation (MAP) varies between 1971 and 4937 mm year^{-1}, while mean annual temperature (MAT) ranges between 11.5 and 27.6 °C (Table 1). Topography and geology of the area are highly variable as a result of volcanic and alluvial sediments that rise to the diversity of soil and geomorphological properties of the region (Malagón et al., 2003).

Figure 1 Location of 9 1-ha plots in Antioquia and its regional location within Colombia and South America (maps inset). Colors indicate the elevational gradients of the plots. The circles sizes show the SOC stock storage in each plot where the smallest corresponds to 43.54 ± 3.98 Mg SOC h-1 and the biggest corresponds to 125.31 ± 9.63 Mg SOC h-1.

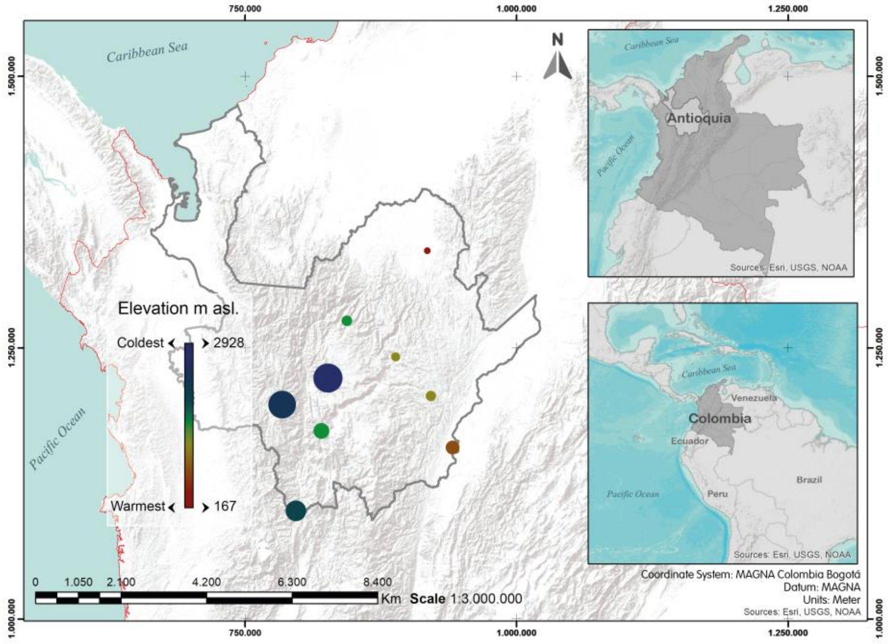


Table 1 Location and description of the 9 sites located in northwestern Colombia. The sites are ordered according to elevation (m asl). Mean values followed by parentheses represent the mean and S_{within} of 15 0.04-ha subplots. MAT (°C) = Mean annual temperature. C (%) = Soil organic Carbon concentration. SOC stock (Mg ha^{-1}) = Soil organic carbon stock. N stock (Mg ha^{-1}) = Soil Nitrogen stock. P stock (Mg ha^{-1}) = Phosphorus stock. N:P = Nitrogen and Phosphorus ratio. EM = Ectomycorrhizal. AM = Arbuscular mycorrhizal. NF = Nitrogen fixing. AGB productivity (Mg ha^{-1} y^{-1}) = aboveground biomass productivity between censuses.

Site	Latitude	Longitude	Elevation (m asl)	Rainfall (mm y^{-1})	MAT (°C)	C (%)	SOC stock (Mg ha^{-1})	N stock (Mg ha^{-1})	P stock (Mg ha^{-1})	N:P	EM	AM	NF	AGB productivity (Mg ha^{-1} y^{-1})
1	7.66	-74.82	167	2783	27	1.66	43.54	5.00	0,0046	0.11	0.08	0.7	0.05	6.60
						(0.15)	(3.98)	(0.38)	(0.00037)	(0.0003)	(0.020)	(0.058)	(0.011)	(0.89)
2	6.01	-74.61	550	1971	23.2	3.35	65.82	6.6	0.007	0.1	0.1	0.74	0.14	3.68
						(0.28)	(3.88)	(0.42)	(0.00041)	(0.0004)	(0.037)	(0.056)	(0.028)	(1.27)
3	6.46	-74.79	928	3145	22.2	2.95	56.98	4.76	0,0036	0.16	0.00	0.89	0.03	8.34
						(0.20)	(2.06)	(0.18)	(0.00041)	(0.0004)	(0.00)	(0.020)	(0.011)	(0.70)
4	6.78	-75.08	977	2108	21.9	2.88	56.87	5.17	0.0088	0.06	0.00	0.8	0.07	7.88
						(0.23)	(2.79)	(0.20)	(0.00043)	(0.0004)	(0.00)	(0.024)	(0.023)	(0.43)
5	6.15	-75.7	2027	2197	16.2	7.81	74.52	6.17	0.0143	0.06	0.16	0.74	0.03	11.4
						(0.83)	(5.61)	(0.44)	(0.00217)	(0.0022)	(0.055)	(0.053)	(0.009)	(1.05)
6	7.08	-75.48	2056	3868	16.1	11.08	57.79	4.16	0.0019	0.44	0.00	0.93	0.02	7.44
						(3.31)	(5.25)	(0.31)	(0.00021)	(0.0002)	(0.00)	(0.017)	(0.007)	(0.65)
7	5.49	-75.9	2527	2819	14.3	16.29	86.88	5.03	0.0027	0.36	0.00	0.85	0.00	6.24
						(2.39)	(5.47)	(0.37)	(0.00092)	(0.0009)	(0.00)	(0.036)	(0.00)	(1.17)
8	6.38	-76.03	2646	2124	13.2	16.08	113.34	6.88	0,0025	0.32	0.00	0.92	0.01	5.71
						(2.45)	(4.94)	(0.51)	(0.00026)	(0.0003)	(0.00)	(0.011)	(0.008)	(0.54)
9	6.61	-75.65	2928	2339	11.5	8.16	125.31	5.85	0.0056	0.21	0.84	0.15	0.00	9.28
						(1.05)	(9.63)	(0.47)	(0.00108)	(0.0011)	(0.037)	(0.034)	(0.00)	(0.93)

Plot data and soil sampling

In each of the 9 study sites, a continuous 100 m × 100 m (1-ha) plot was established in areas covered by natural forests. Each plot was divided in 25 contiguous subplots of 20 m × 20 m (0.04 ha), and all trees and palms larger than 10 cm of diameter at the breast height (DBH) were tagged, mapped, measured, and collected. Plot were censused at least twice between 2006-2009 and 2013-2014, respectively (see Duque et al., 2015; Peña et al., 2018).

In each plot, we used a systematic sampling design to select 15 out of 25 20 m × 20 subplots and took sample a centrally located soil core from the superficial layer (i.e. A horizon, 0-20 cm). For each soil core, we removed the organic litter layer and extracted a sample using a cylinder of 4 cm wide and 5 cm long (62.83 cm^3). The samples were preserved in paper bags while were carried out to the laboratory. These soil cores were oven-dried at 105 °C to a constant mass. The samples were then crushed and sieved to 2 mm to remove all roots and stones and measured again. A 5-10 g subsample from every core was ground and both C and N concentrations determined after dry combustion with a FLASH 2000 Elemental Analyzer. P concentration was determined employing spectrophotometry based on a Bray II /L-Ascorbic acid dilution. All soil samples were determined to be carbonate free. Analyses were made at the National University of Colombia at Medellin.

Bulk soil densities (soil particles < 2 mm) were quantified using the stone-free dry weights and the sampling tube volumes corrected for the stone volumes (g cm^{-3}). Soil C, N and P stocks (Mg ha^{-1}) were then calculated according to the soil densities for each 20 cm soil layer. Then, we obtained SOC, N and P stock values for each subplot and calculated the N:P ratio of N and P concentration as a broad indicator of soil nutrient availability. To check for collinearity between N stock and N:P, we employed a Pearson correlation test and found that they are independent (r = -0.04, p > 0.05).

Temperature data

We extracted the mean annual temperature (MAT °C) from CHELSA database (Karger et al., 2017) employing the geographic coordinates of each plot. The CHELSA database is a topographically weighted interpolation of weather stations that improves the climatic prediction in mountain regions, such as the Tropical Andes. The MAT values are the same for all subplots because of the coarse resolution of CHELSA database. As expected, MAT was highly correlated with elevation (r = 0.99; P < 0.001).

Symbiont root microbial association

All stems, when possible, were assigned the following symbiont root associations (SRA): ectomycorrhizas (EM), arbuscular mycorrhizas (AM) and nitrogen fixing (NF), based on the genus -or family- level designations provided in Steidinger et al. (2019). Overall, the number of genera assigned was >90% (227/249). We chose these two taxonomic levels for three reasons: 1) assigning species-level taxonomy is difficult for some individuals in our plots, 2) using these taxonomic levels greatly increases the ability to provide SRA assignments, and 3) SRA is a trait largely conserved at the plant genus and family level (Maherali et al., 2016). Here, we restricted matches for our genera and families to only those present in North and South America in the compiled list of Steidinger et al. (2019). Any genera or families lacking symbiotic root assignment were manually checked and, when possible, given SRA assignments based on primary literature searches. Following SRA assignment, we estimated the proportion of basal area per subplot of each one of the three symbiont groups.

Aboveground biomass productivity

We calculated the AGB of each tree using an allometric equation that relates DBH, tree height (H) and wood density (WD) (Chave et al., 2014). AGB productivity was calculated as the sum of AGB growth and AGB recruitment. The AGB growth of each subplot was calculated as the sum of the AGB differences of each tree between censuses, divided by the elapsed time (in years) between them. The AGB recruitment was defined as the sum of the AGB of all trees that reached DBH ≥ 10cm between censuses.

Statistical analyses

We used a linear mixed model (LMM) to evaluate the effect of elevation and soil conditions on determining SOC stocks. We included MAT, N stock, N:P ratio, the three SRA indexes and net AGB change as fixed effects. Plot identity was included as a random effect to control for site-specific features. We retained the significant variables and interactions (significance levels ≤ 0.05) to define the final model based on 2 units of difference of the Akaike information Criteria (AIC) among assessed models. These models were run employing *lme* function in the *nlme* R package.

In addition, we calculated the AIC weight, which is a measure derived from the weighting of the relative likelihoods obtained from the difference between the AIC of the best model and others. This measure allows us comparisons among models and estimate the relative importance of the explanatory variables by summing the AIC weights across all models that contain the target variable (Burnham and Anderson, 2004). The AIC weights were run using the *akaike.weights* function available in the *qpcR* R package.

We obtained the conditional R^2 (R^2c) and the marginal R^2 (R^2m) for the final model. The former indicates the total explained variance for fixed and random effects simultaneously, while the latter indicates the total explained variance for only fixed effects (Nakagawa and Schielzeth, 2013). The R^2 values were obtained using *rsquare* function in the *piecewiseSEM* R package.

Finally, we estimated the total uncertainty (S_{total}) around the variables used in the model divided into two components: The variation between ($S_{between}$) and within (S_{within}) plots. The first, was calculated as the mean standard deviation (SD) of 1000 random draws including the 80% of total data (i.e. bootstrapping procedure). The second, was estimated as the mean SD of 1000 draws of a bootstrapping applied for each plot. S_{total} was estimated as the square root of the sum of squares of $S_{between}$ and S_{within} (Sierra et al., 2007).

All analyses were performed using R 3.5.1 (R Core Team 2018).

Results

Variation of SOC and nutrient stocks along elevational gradient

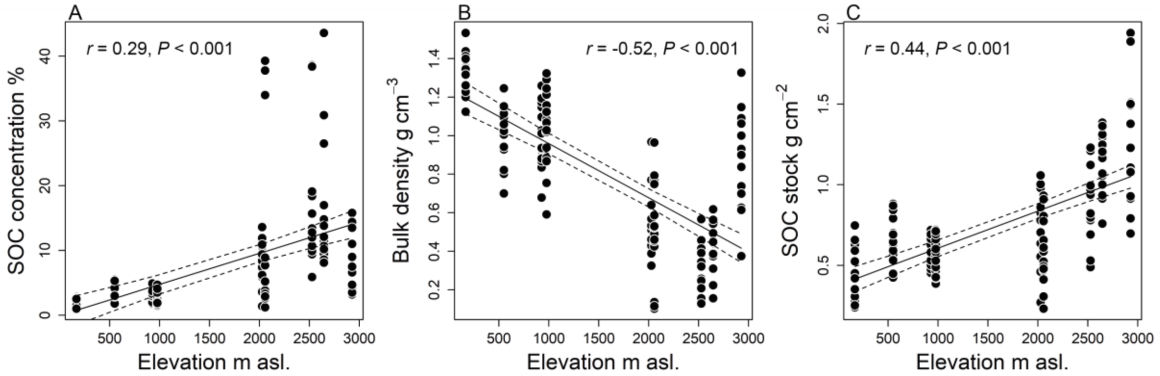
Across all sites and subplots, the mean soil C concentration (± 1 *S.E.*) was 7.80 ± 0.52 %, the mean soil N concentration was 0.51 ± 0.03 %, and the mean soil P concentration was 4.31 ± 0.34 ppm (Table 2). Both soil C and N concentrations were positively correlated with elevation ($r = 0.29$, $P < 0.001$, Figure 2a; $r = 0.21$, $P < 0.001$, respectively). In contrast, soil bulk densities (0.78 ± 0.03 g cm^{-3}, Table 2) were negatively correlated to elevation ($r = -0.52$, $P < 0.001$; Figure 2b). Mean soil C, N, and P stocks were 75.30 ± 2.48 Mg C ha^{-1}, 5.51 ± 0.09 Mg N ha^{-1} and 0.0056 ± 0.0004 Mg P ha^{-1}, respectively (Table 2). SOC stocks were positively correlated with elevation ($r = 0.44$, $P < 0.001$; Figure 2c), while neither N nor P stocks were significantly correlated with elevation ($r = 0.08$ $P > 0.05$; $r = 0.01$, $P > 0.05$, respectively). The ratio of N:P, however, was positively correlated with elevation ($r = 0.24$, $P < 0.01$).

Table 2 Estimates of uncertainty for each variable. C (%): Soil organic Carbon concentration. N (%): Soil Nitrogen concentration. P (ppm): Phosphorus concentration. SOC stock (Mg ha^{-1}): Soil organic Carbon stock. N stock (Mg ha^{-1}): Soil Nitrogen stock. P stock (Mg ha^{-1}): Soil Phosphorus stock. EM: Ectomycorrhizal. AM: Arbuscular mycorrhizas. NF: Nitrogen fixing. AGB productivity (Mg ha^{-1}): aboveground biomass productivity between census. S.E.: Standard error, estimated as $S_{total}/\sqrt{n}$.

Variable	S_{within}	$S_{between}$	S_{total}	n	S.E.	Mean
C (%)	1.23	5.90	6.02	134	0.5204	7.81
N (%)	0.07	0.30	0.31	134	0.0266	0.51
P (ppm)	0.73	3.82	3.89	134	0.3362	4.31
Soil bulk density (g cm^{-3})	0.04	0.35	0.35	134	0.0301	0.78
SOC stock (Mg C ha^{-1})	4.90	28.25	28.67	134	2.4766	75.30
N stock (Mg N ha^{-1})	0.37	0.98	1.05	134	0.0905	5.51
P stock	0.00	0.00	0.00	134	0.0004	0.01

Variable	S_{within}	$S_{between}$	S_{total}	n	S.E.	Mean
(Mg P ha^{-1})						
EM	0.02	0.27	0.28	134	0.0238	0.13
AM	0.03	0.24	0.24	134	0.0210	0.75
NF	0.01	0.05	0.05	134	0.0041	0.04
AGB productivity (Mg C ha^{-1} y^{-1})	0.84	2.36	2.50	134	0.2163	7.38

Figure 2 Soil organic carbon concentration (A). bulk density (B) and soil organic carbon stock (C) along elevational gradient. The solid line is a lineal model between variables and dashed lines represent the confidents intervals.



Symbiont root association

Across sites and subplots, the mean proportional basal area of EM trees was 0.13 ± 0.02, AM trees 0.75 ± 0.02 and NF trees was 0.038 ± 0.004, respectively (Table 2). Proportional basal area of EM trees was positively correlated with elevation ($r = 0.04$, $P < 0.001$), while AM and NF proportional basal area were negatively correlated with elevation ($r = -0.32$, $P < 0.05$ and $r = -0.19$, $P < 0.001$, respectively).

AGB productivity

Mean AGB productivity (± *S.E.*) was 7.38 ± 0.22 Mg C ha^{-1} year^{-1} (Table 2) and not significantly correlated with elevation ($r = 0.05$, $P > 0.05$).

Drivers of SOC accumulation along the elevational gradient

The best model explaining SOC stock retained MAT, soil N stock, soil N:P and EM proportional basal area. These variables captured a high proportion of the total variance (R^2m = 0.79; Table 3) and including non-significant variables did not notably increase the total amount of variance explained (R^2c = 0.85; Table 3). MAT had a negative effect on SOC stock (Figure 3a), while both N stock and N:P have positive effects on SOC stock (Figure 3b and 3c). Increasing EM basal area also had a positive effect on SOC stock (Figure 3d). Contrary to the expectations, AGB productivity was not significant different across elevation, and had no significant effect on SOC (Figure 4). Among the various explanatory variables, soil N stock was considered the most significant based on the sum of AIC weights excluding the full model (AIC_w = 0.0179), followed by MAT (AIC_w = 0.0158), EM (AIC_w = 0.0130), and N:P (AIC_w = 0.00682).

Table 3 Linear mixed models including significant variables. The best model is bolded. MAT (°C): Mean annual temperature. N stock (Mg ha^{-1}): Soil Nitrogen stock. N:P: Nitrogen and Phosphorus ratio. EM: Ectomycorrhizal. N:P is log transformed.

Model	R^2 marginal	R^2 conditional	AIC	AIC weight
MAT + N stock + N:P + EM	**0.79**	**0.85**	**1071.43**	**0.9821322**
MAT + N stock + N:P	0.74	0.85	1082.09	0.0047551
MAT + N stock + EM	0.78	0.85	1080.42	0.0109707
MAT + N:P + EM	0.47	0.65	1190.89	0.0000000
N stock + N:P + EM	0.42	0.82	1083.77	0.0020518
MAT + N stock	0.74	0.84	1090.99	0.0000555
MAT + N:P	0.44	0.67	1197.54	0.0000000
MAT + EM	0.46	0.61	1203.53	0.0000000
N stock + N:P	0.32	0.84	1093.50	0.0000158
N stock + EM	0.41	0.83	1093.16	0.0000187
N:P + EM	0.07	0.61	1199.15	0.0000000
MAT	0.43	0.62	1210.38	0.0000000
N stock	0.31	0.84	1103.25	0.0000001
N:P	0.04	0.65	1205.90	0.0000000
EM	0.03	0.59	1213.46	0.0000000

Figure 3 Soil carbon stock variation along mean annual temperature (A). N stock (B). N:P ratio (C) and proportion of basal area belonging to EM trees (D). The solid line is a lineal model between

variables and dashed lines represent the confidents intervals. Heat colors indicate high temperatures and cold colors indicate low temperatures (see panel A).

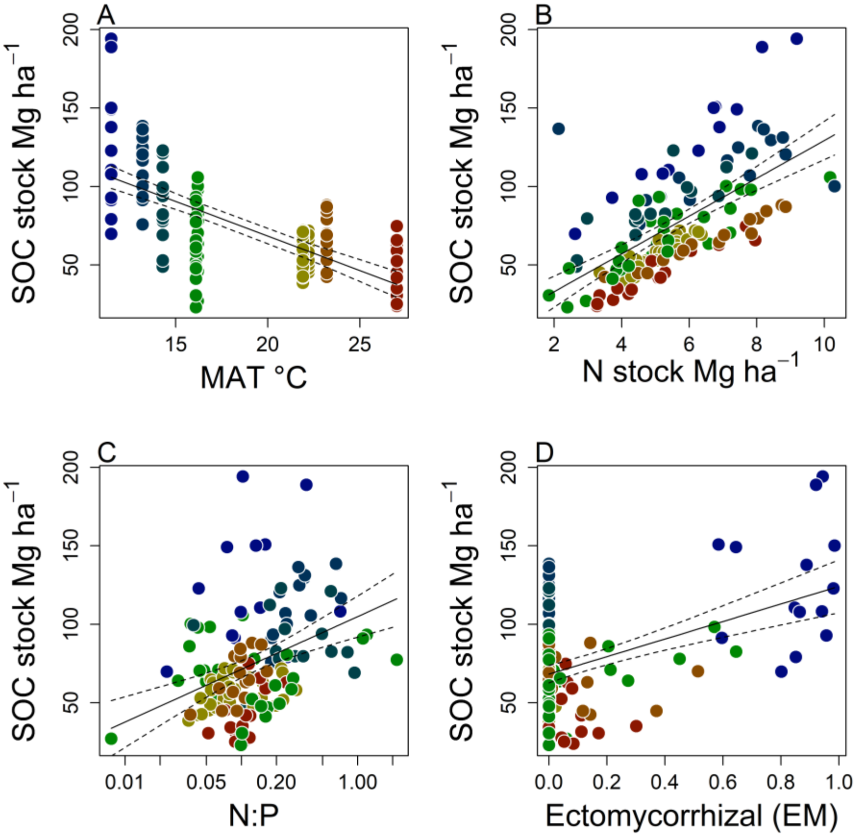
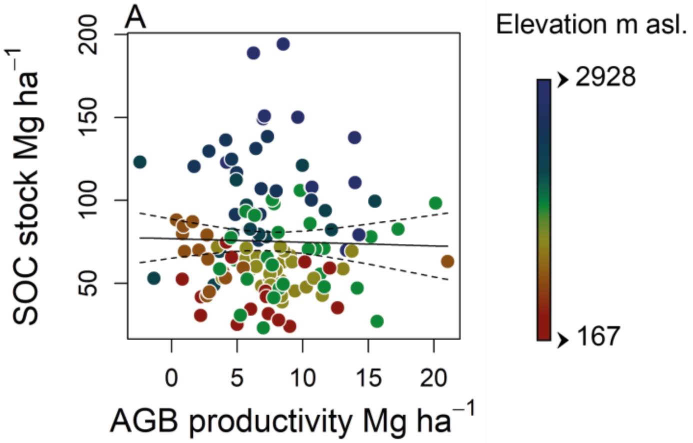


Figure 4 Soil carbon stock variation along AGB productivity (A). The solid line is a lineal model between variables and dashed lines represent the confidents intervals. Colors indicates the elevational gradient.



Discussion

Are there systematic changes in SOC stocks along the elevational gradient?

We found that SOC changed systematically along our tropical elevational gradient, increasing with elevation (Figure 2). These results correspond well with global observations across latitudes showing that cooler regions have a greater accumulation of soil organic matter stocks (Crowther et al., 2019; Dieleman et al., 2013). These results also match with other studies of SOC dynamics in different parts of the Andes (Phillips et al. 2019), suggesting the results we obtained are broadly representative of neotropical montane ecosystems. Additionally, our results indicate that highland mountain ecosystems can have SOC stocks that are approximately two times greater than their counterparts in lowlands, suggesting they act as major soil C sinks in tropical regions.

What are the main drivers of SOC stocks along the elevational gradient?

Our statistical modeling indicates that SOC stocks are driven by multiple factors (Table 3). The variation in SOC along elevation could be due in part to temperature-induced effects on microbial abundance and activity (Lloyd and Taylor, 1994). For example, along latitudinal gradients, the accumulation of microbial biomass increases poleward, which has been linked to the effects of temperature on metabolic activity (Crowther et al., 2019). In our data, there was a near perfect correlation between temperature and elevation ($R^2 = 0.97$), which has been observed in other studies (Körner, 2007), including in the Andes (Mahli et al., 2017). However, a closer look at our data suggests that the relationship between SOC stock and temperature is not equal at lower and higher elevations. For example, in the four plots located at less than 1000 m, the amount of variation in SOC stock explained by temperature ($R^2 = 0.16$) is notably lower than that in plots located at higher than 1000 m ($R^2 = 0.46$). This suggests that while temperature is an important effector of SOC stock throughout our elevational gradient, its relative importance increases as temperature decreases. One might also predict that the variance of SOC would likely decrease with elevation, due to increasing limitation on microbial activity in highlands. However, we found that the variance of SOC stock increased with elevation (Figure 2c). We hypothesize that this difference may be caused by the lowland soil microbial communities having consistently high activity due to optimal thermal conditions (Lloyd and Taylor, 1994), resulting in greater similarity in SOC content in lowland forests. In contrast, greater variation in cold limitation on decomposition, may result in greater variation in SOC stock at higher elevations.

We found that SON stock was also a significant predictor of SOC (Table 2). This positive relationship between SOC and SON could result because N stock is the output of microbial decomposition rate in a similar fashion to SOC stock. Specifically, if both processes are temperature dependent, their covariation would not be causal. However, we found that unlike SOC, SON was not related to temperature, suggesting that variable is not the primary driver of N accumulation. One possible explanation is that high N concentration may reduce microbial activity by inhibiting the enzymes involved in soil recalcitrant C decomposition (Gallo et al., 2004; Liu et al., 2015). A second possibility for the parallel changes in SON and SOC we observed is variation in forest mycorrhizal composition across the elevational gradient. In both temperate and tropical forests (Waring et al., 2015,; Cheeke et al., 2017), forests dominated by EM associations have slower soil C and N cycles, resulting in greater accumulation of SOC associated with soil N being cycled in a primary organic form (Phillips et al., 2013). Our higher elevation sites had a consistently higher amount of basal area occupied EM trees, matching global trends that EM associations are favored where litter decomposition is slowed by less favorable climatic conditions (Steidinger et al., 2019). A third factor is that P availability may have influenced microbial activity, which may in turn drive SOC and SON. Supporting this possibility, we found that decreasing soil N:P also resulted in lower SOC, suggesting that more balanced soil fertility stimulates microbial activity, which decreases SOC.

To our surprise, the input of organic C by plants, as estimated by AGB productivity, did not change along elevation and was therefore unrelated to the SOC accumulation trends we observed (Figure 4). This suggests that the systematic decline in SOC with decreasing elevation (Figure 2) is not closely related to C input, supporting the alternative mechanisms discussed above. However, it is important to note that our surrogate of plant productivity is an indirect indicator of litterfall and maybe underestimating litterfall, particularly because there is growing recognition that SOC is strongly affected by belowground plant inputs (Sokol et al., 2019). As such, future studies should include litterfall estimations, both above- and belowground. We also recognize that changes in plant species composition changes along elevation could affect leaf nutrient content, particularly recalcitrant elements or secondary compounds that affect decomposition rates, which may also obscure trends in aggregate measures such as AGB productivity. Disentangling this latter effect, will take reciporal transplant experiments of different litter types across the elevation gradients, although climatic effects may mask the effects of leaf type as a filter on microbial community composition (Keiser and Bradford, 2017).

Caveats and future perspectives

Although our analyses clearly link SOC variation to various abiotic and biotic factors that change with elevation in the tropical Andes mountains, we acknowledge that there are important caveats to our results that must be considered regarding. While we feel generally confident that the assignment of tree genera to various symbiotic root associations, there are a number of species in tropical forests that for which specific root association is not yet identified (Corrales et al., 2017). With regard to potential changes in microbial abundance and activity, we did not directly measure either of these variables, so our inferences for both are based on broad patterns identified in other systems (Nottingham et al., 2019). Similarly, measuring decomposition rate of a common substrate in all of our sites would benefit in determining how changes in decomposition rate are influenced by both biotic and abiotic factors (Pioli et al., 2020). Despite these caveats, our study provides much needed baseline information on SOC variation in the Northern Andes, which is important given the sensitivity of these ecosystems to shifting climatic conditions (Duque et al., 2014).

Conclusion

In conclusion, we found that the SOC stocks along elevational gradients in Northern Andes are dynamic. Their increase with elevation appears to reflect a combination of abiotic and biotic factors that likely work in synergy to alter C cycling. Importantly, our results demonstrate that current SOC stocks are more influenced by belowground and climatic effects than plant C inputs, as plant productivity did not change along elevation. Given the increasing temperatures associated with ongoing increases in atmospheric carbon dioxide concentrations, the large amount of C stored in the soils of these montane systems make their conservation a global priority.

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