Tropical Agricultural Research and Higher Education Center

Graduate School

# Soil carbon stocks on a tropical forest altitudinal gradient are correlated with bioclimatic factors, soil properties and vegetation´s functional properties

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Thesis presented to the Graduate School

in partial fulfillment of the requirements for the degree

*Magister Scientiae*

in Management and Conservation of Tropical Forests and Biodiversity

Costa Rica, 2017

This Master's thesis has been accepted in its present form by the Division of Education and the Graduate School Program of CATIE and by the advisory committee of the student, considering that it fills the requirements necessary for the student to present the final defense as well as participate in the final exam.

***MAGISTER SCIENTIAE* IN MANAGEMENT AND CONSERVATION OF TROPICAL FORESTS AND BIODIVERSITY**

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This thesis subscribes to the regional program

CLIMIFORAD

Climate change, Iberoamerican Mountain Forests and Adaptation

Funded by the Inter-American Development Bank (BID)

The author received scholarships from:

Desarrollo de Programas y Proyectos de Investigación

Consejo de Ciencia y Tecnología del Estado de Puebla (CONCyTEP)

México

Fondo Sectorial para la Sustentabilidad Energética

Consejo Nacional de Ciencia y Tecnología (CONACyT)

Secretaría de Energía (SENER)

México

For those who walk the forests

For those who look down and find a world beneath their feet

## Acknowledgements

I would like to express my most sincere gratitude to my assessing committee.

To Bryan, for trusting my thesis project and guiding me throughout the process. For having your door always open to solve my concerns, indicate errors, suggest changes, apply knowledge of tropical ecology and above all, teach me how to be a better researcher (For those e-mails with interesting articles and happy faces). To Victor, for agreeing to be part of this committee and always providing such relevant contributions. For the opportunity to work again with him and all the time he gave me for the reviews and the formalities. To Ney, for being part of this committee and always checking progress, particularly in the field of the development of this thesis.

To Leonel Coto and Vicente Herra, for all the help they gave me in the field. I knew the rough side of working in tropical forests, and they helped me to endure everything: those climbs in Barbilla, that cold in Villa Mills, crossing that river, falling down... But always making the experience an adventure and not a martyrdom. Between them and the talks with the park rangers, I met another side of Costa Rica. For them I learned to cook and desperately need a café con leche, maduros con natilla, tortilla con queso, and the secret recipe of a good pinto.

To Sergio Vílchez, for his help in the statistical analyzes. To Diego Delgado for all the help with the research logistics and the work process. To Aranjid, Marce and Martita, who made all these complicated procedures so simple. To Javier, Juan, and Andrés, for making the library my favorite place.

To Daniel and Miguel, who helped me get that sampling core out. To Dr. Lanuza, for so many reflections together. To Manu, who helped me immeasurably with everything: logistics in the field, help with analysis, encouragement, but above all for always being very kind and willing to help.

To Alonso, Leo and Marco, who as always supported me. The first months in CATIE were long, but they always encouraged me to continue the fight. We missed us even more than before, but I also felt us so close. To all my family, who always looked after me from the distance and "apapachated" me when visiting them.

To Vane and Nati. To LP and Charlie Pacayas. To Daniel and Samu. To Oswaldo and Erick. To Rosita and Yami. To Mati. No need to say more, you already know.

To Henry.

To Andre and Male. To Mario.

## Contents

## Abstract

Tropical forests are recognized as the most diverse ecosystems in terms of their wealth and relative abundance. Within these, tropical mountain forests are acknowledged for their key role in the provision of ecosystem services and the serious threat posed by climate change upon them. Of the many ecosystem services offered by tropical forests, the climate regulation service provided by soil makes it the main terrestrial carbon sink and stock.

The response of soil carbon storage to elevation, environmental, soil, and biological conditions has been widely studied. However, factors affecting soil C have been studied separately, leaving aside the high correlation between these factors. This study quantifies the SOC stocks on a tropical forest altitudinal gradient (400 – 2900 masl) and aims to answer a key question: when interdependent bioclimatic factors, soil properties and vegetation functional properties are all taken into account, which of these sets of predictors best explain variation in SOC?

Total organic C and bulk density were determined to 1 m depth in soil samples from 28 primary forest plots (0.25 ha) distributed over the gradient. Complementary soil properties to 30 cm depth were also measured. Climatic data for each plot was obtained from WorldClim. Community weighted mean (CWM) values of six functional traits were obtained for 183 tree and palm species, which formed 73-99% of total basal area > 10 cm dbh in all plots.

SOC relations with elevation, bioclimatic factors, soil properties and CWM trait values were evaluated individually through GLMs, using spatial correlation functions and correcting for heterogeneous variances when this improved model fit. The relative influence of each set of predictors (climate, soil, CWM traits and space as represented by PCNM eigenfunctions) on SOC was then assessed using variance partitioning, including variables selected by Forward Selection in each of the four matrices.

Total soil C stocks to 1 m depth ranged from 6.8 to 43.1 kg $m^{-2}$. Total SOC and its variance increased with elevation (R2=0.64, p<0.0001). Variance partitioning for total SOC and SOC in four depth categories (0-5, 5-20, 20-60 and 60-100 cm) explained 55 to 65% of variation in SOC stocks, though the model was not significant for 5-20 cm soil depth. Forest functional properties, predominantly leaf dry matter content and wood density, had the strongest overall influence on total SOC, followed by bioclimatic and soil variables; the influence of PCNM eigenvalues was relatively low. However, no significant individual fractions were observed.

Elevation and therefore temperature have the expected strong positive correlations with SOC, though no clear patterns were found for soil depth 5-20 cm. CWM WD and LDMC were both positively correlated with SOC. These CWM traits are not correlated with elevation, suggesting that SOC accumulates in stands dominated by species that invest in tough, long-lived leaf and stem tissues.

The lack of significant individual fractions in variation partitioning, however, indicates that SOC is responding to interdependent climate, vegetation and soil factors. The lack of an effect of PCNM eigenvectors suggests that control of SOC is predominantly environmental. Changes in the significant explanatory variables indicate the variation of processes and the different working scales of soil C storage.

To our knowledge, this is the first study to go beyond elevation and determine the influence of a wide range of predictors on SOC in tropical mountain forest ecosystems. Our results strengthen understanding of pattern and process in these ecosystems and should enhance capacity to model the response of their properties to climate change.

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## Introduction

Of the many changes caused by humans in natural systems, climate change has become the main threat to our society (Mendelsohn et al. 2006). Its impact on natural systems, and our dependence on goods and services provided by them, makes it urgent to study current and future impacts in order to take the necessary measures to adapt to these possible changes and their consequences.

In recent decades, several changes in the dynamics and processes of natural forests attributed to anthropogenic climate change have been reported (IPCC, 2014). These changes, mainly caused by an increase in atmospheric temperature and changes in precipitation, indicate the movement of plant and animal species, increase in diseases and mortality of vegetation, reduction of primary productivity and fires (Thomas et al. 2004, Reto-Gian et al. 2002).

Given the likely changes in climate patterns, the analysis of tropical mountain forests dynamics is even more relevant because of their high vulnerability. Detailed information on the processes that occur in these ecosystems is crucial in order to have a better picture of the facing future of forests to climate change and, when possible, to have readily available information for decision making.

The world's tropical forests, especially tropical mountain forests, have been particularly threatened by the consequences of climate change. It is expected that alterations in rainfall regimes and higher temperatures will result in declining ecosystem functions, the greatest threat to mountain natural tropical forests (Parmesan & Yohe 2003, Girardin et al. 2013, Asner et al. 2014).

Tropical mountain forests have direct strong interaction with atmospheric phenomena that show significant changes in short ranges of elevation, making these ecosystems extremely sensitive to changes in climate (Spracklen & Righelato 2014). Thus, these forests are important indicators of the effects of climate change in the tropics (Dieleman et al. 2013, Körner 2007, Malhi et al. 2010).

Of the many ecosystem services offered by tropical forests, regulating ecosystem functions provided by soil makes it the main terrestrial C sink and stock (Scharlemann et al. 2014). The constant exchange of carbon between soil and atmosphere leads to the dependence of each stock to the other: C losses from the soil matrix will cause an increase in concentration of $CO_2$ in the atmosphere, while net accumulation of C in soil contributes to the reduction of this gas in the atmosphere (Lal et al. 2007).

The soil's ability to store carbon as stable organic matter makes it the main terrestrial C sink and stock, for it contains twice the C found in the atmosphere and three times the C content of all terrestrial vegetation (Scharlemann et al. 2014). It is estimated that about half of the C stored in the first meter of soil across the earth's surface is located in forests; about 25% is found on tropical forest ecosystems (Bonan 2008). According to Bernoux and Volkoff (2006), the global soil C stock reaches 1589 Pg, of which 277 Pg are distributed in Latin America, 6214 Tg in Central America and 653 Tg (0.6 Pg) in Costa Rica.

Although the carbon sequestration and storage service offered by aboveground biomass in natural tropical forests has been well documented (Poorter et al. 2015, Keith et al. 2009, Malhi et al. 2006, Mitchard et al. 2014), there is little analysis of stored C in tropical soils. A lack of evidence on how this C pool varies to combined and parallel changes, leaves insufficient information for future management of soil C stocks in tropical mountain ecosystems, especially in the context of climate change.

Therefore, this study attempts to quantify the soil C stocks along a tropical forest altitudinal gradient, and its relation with bioclimatic conditions, soil characteristics and vegetation functional properties. Furthermore, it attempts to determine the relative influence of these factors upon the stored soil C amounts and identify the most significant of them. The results will be a valuable contribution, both for the advancement of the scientific information collected in the studies of the dynamics of the forest and its role in the face of climate change, as well as for making better informed decisions.

## Main objective

To determine the amount of carbon stored in the soil and its relation with various ecosystem characteristics in an altitudinal gradient of tropical forests in Costa Rica.

### Specific objectives

- To determine the amount of stored organic soil carbon in an altitudinal gradient ranging 440 to 2950 mas.
- To relate and identify the relative influence of climatic conditions, soil characteristics, and vegetation functional properties on soil C storage.

## Hypotheses

- The amount of C stored in the soil increases as altitude rises above sea level.
- The amount of C stored in the soil increases as temperature declines.
- Sites that are characterized by higher weighted averages of traits associated with conservative strata would have higher levels of C in soil.

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# Soil carbon stocks along a tropical forest altitudinal gradient are determined by bioclimatic factors, soil properties and vegetation functional traits.

## Introduction

Tropical forests are recognized as the most diverse ecosystems in terms of their wealth and relative abundance (Gibson et al. 2011). Of the four billion hectares of forest cover on the earth's surface (FAO 2011), tropical forests represent only 10%, which host the majority of tree species on the planet (Fine et al. 2008), and are estimated to account for 34% of terrestrial primary productivity (Beer et al. 2010).

Within these, montane forests are acknowledged for their high alpha and beta diversity, their prominent number of endemic species (Kappelle and Brown 2001), their key role in the provision of ecosystem services and the serious threat posed by climate change upon them (Malhi et al. 2010), particularly natural tropical mountain ecosystems found along altitudinal gradients (Ghazoul and Sheil 2010).

The importance of tropical forests lies not only in the number of species found, but in the great functional diversity that allows them to provide a large number of ecosystem services, particularly those related to the C, water and nutrients cycles (Díaz et al. 2007). Of the many ecosystem services offered by tropical forests, those provided by the soil play a vital role for their proper functioning (Amundson et al. 2007). The soil matrix plays a major role in the regulation of different elements in the atmosphere, mainly $CO_2$, $N_2O$ and $CH_4$ (Dominati et al. 2010), providing the climate regulation service. Soil and the organic carbon found in it receive particular attention for its potential to mitigate the high concentrations of atmospheric $CO_2$ (Lal et al. 2007), particularly on tropical soils (Trumbore 1997, Powers and Schlesinger 2002).

The soil's ability to store carbon as stable organic matter makes it the main terrestrial C sink and stock, for it contains twice the C found in the atmosphere and three times the C content of all terrestrial vegetation (Scharlemann et al. 2014). It is estimated that about half of the C stored in the first meter of soil across the earth's surface is located in forests; about 25% found on tropical forest ecosystems (Bonan 2008). According to Bernoux and Volkoff (2006), the global soil C stock reaches 1589 Pg, of which 277 Pg are distributed in Latin America, 6214 Tg in Central America and 653 Tg (0.6 Pg) in Costa Rica.

Although the carbon sequestration and storage service offered by aboveground biomass in natural tropical forests has been well documented (Poorter et al. 2015, Keith et al. 2009, Malhi et al. 2006, Mitchard et al. 2014), there is little analysis of stored C in tropical soils.

In mountain environments, understood as any land mass elevation >300 m above sea level (Körner 2007), soil C stocks depend greatly on spatial variability (Hoffmann et al. 2014), but they are also influenced by site-specific parameters, such as temperature, soil type, and vegetation (McCarl et al. 2007). The elevation gradient on a mountain, as an important spatial factor influencing temperature and precipitation, influence soil processes involved with carbon cycling, particularly its sequestration (Heneghan et al. 1999). However, variations in biological and environmental factors that are not necessarily altitude-specific are observed to largely influence soil C storage (Wang et al. 2016, Lavigne et al. 2004).

In tropical mountain forests, soil properties change with altitude (Wilcke et al. 2008). As C stocks are mainly based on SOM levels and their formation processes, the soil conditions and characteristics (such as humidity, temperature, acidity, among others) greatly determine the soil's ability to store carbon as stable organic matter (Parajuli and Duffy 2013). Furthermore, physical properties of soil determine its exchange rates with the atmosphere, controlling the soil C pool contents (Dilustro et al. 2005).

Finally, vegetation attributes, specifically net primary productivity and litter quality, are considered to largely determine the level of carbon in soils, for they are the main controlling factors of litterfall and its decomposition rates (Davidson and Janssens 2006).

Although soil C storage response to elevation, environmental, soil, and biological conditions has been studied, it's been done separately, leaving aside the high correlation between these factors (Malhi et al. 2010). A lack of evidence on how this C pool varies to combined and parallel changes leaves insufficient information for future management of soil C stocks in tropical mountain ecosystems, especially in the context of climate change.

This study attempts to quantify the soil C stocks along a tropical forest altitudinal gradient, and its relation with bioclimatic conditions, soil characteristics and vegetation functional properties. Furthermore, it attempts to determine the relative influence of these factors upon the stored soil C amounts and identify the most significant of them.

## Methods

### Study area

The study was conducted in a 400 to 2900 masl altitudinal transect across a 226.700 ha area within the Caribbean slope of the Cordillera de Talamanca, Costa Rica. The sampled plots belong to a long-term research network of unlogged primary forests, representing eight Holdridge (2000) life zones and three transition life zones (Appendix 9).

The Cordillera de Talamanca is the highest in Central America, reaching up to 3820 masl, with elongated tops, steep ridges and long straight slopes (Berner 1992); of volcanic origin and formed in the Cenozoic era. Soils are mainly Ultisols (85%) and Inceptisols (15%), usually deep, well drained, red or yellow, strongly acid, with relatively low fertility, and an elevated content of organic matter, mainly in highlands (ITCR 2008).

The study area has no dry season; precipitation shows unimodal behaviour with a low rainfall season during the first quarter, a slight increase in July and August and a peak in November and December. The annual rainfall ranges from 2805 mm $yr^{-1}$ (Cerro de la Muerte station at 3100 masl) to 6120 mm yr-1 (Destierro station at 1800 masl). The average annual temperature ranges from 7.5°C to about 25.2°C (data from Worldclim climate layers).

The gradient higher lands are described as Holdridge's montane rainforest; followed by lower montane and premontane rainforests, located at Tapantí-Macizo de la Muerte National Park and El Copal Biological Reserve. The lower lands, found at Barbilla National Park, are described as very humid montane forests. The floristic composition shows a reduction of species along the gradient, especially from 1800 to 2800 masl, with a dominance of *Quercus* and other genres such as *Ilex* and *Magnolia*, little presence of palms, and plenty of bamboo (Blaser and Camacho 1991).

The study area, within the La Amistad Biosphere Reserve, presents several conservation areas with different protection categories. Barbilla National Park has a recognized presence of Cabecar indigenous groups and co-adjoins Alto Chirripó and Nairi Awari Indigenous Reserves.

## Determination of soil organic carbon

The study was conducted in 28 plots, each one standing in 0.25 ha of primary forest (Appendix 1). Field work occurred from May to July 2016, following the USDA (2011) sampling protocol.

For soil organic carbon concentrations, each plot was divided in four, collecting one 100 cm deep soil core at the centre of each quadrant. All soil cores were divided in four depths (0-5 cm, 5-20 cm, 20-60 cm, and 60-100 cm). Mixed samples per depth were analysed for total organic C using the weight loss after ignition method (*LOI*). Fresh 100g samples are dried at 40°C, homogenized and sieved through a 2mm mesh; an aliquot is then taken and sieved through a 0.25mm mesh. For analysis, 30-40 mg weighed samples are prepared in tin capsules for combustion in a C and N elemental analyzer (Flash EA 1112, ThermoFinnigan, Italy).

In order to report SOC stocks at 1 m deep (where $C\ stock(kg\ m^{-2}) = SOC(kg\ kg^{-1})\ bulk\ density(kg\ m^{-3})\ depth(m3\ m^{-2})$), samples for bulk density were taken next to every collected core, one of 0-10 cm and another of 30-40 cm. They were carefully stored, oven-dried (Soiltest INC, Illinois, USA) at 105°C for 24 hr and weighted.

Soil temperature was measured with a common soil thermometer at 5 cm deep, measuring once in every quadrant; all measurements occurred between 9 to 11 am and 1 to 4 pm. Complementary soil data of physical and chemical properties was obtained from a previous study (Veintimilla Ramos 2013), including texture, pH, acidity, nutrients, total C, N and SOM (Appendix 2).

## Climate data

Climatic data for each plot was obtained from the WorldClim database (Appendix 3). This base is a set of global climate layers with a spatial resolution of 1 km$^2$ (30 arc- second). It contains gridded mean climate values from global meteorological stations for the 1950–2000 period

(Hijmans et al. 2005). Data layers were generated through interpolation of average monthly temperature and precipitation data, resulting in 19 derived bioclimatic variables representing annual trends, seasonality and extreme or limiting environmental factors (http://www.world-clim.org/bioclim).

## Community functional traits

Functional traits values were obtained for 183 species forming 73-99% of the total plot basal area >10 cm dbh in at least one of the 28 plots (Appendix 4), following Pérez-Harguindeguy et al. (2013) protocol. For 28 species that couldn't be sampled, an estimated value was given based on genre or family means.

For each plot, community weighted mean values were calculated for each trait using the formula given by Violle et al. (2007) with the species basal area as weighting variable. Calculations were performed using FDiversity software (Casanoves et al. 2010).

## Statistical modelling

Soil C relations with elevation, bioclimatic factors, soil properties and community weighted mean trait values were evaluated individually through a general linear model analysis using Infostat software (Di Rienzo et al. 2016). GLMs were performed with a Gaussian correlation function using Euclidean distances (*corGaus*), although it did not improve every model. Variance increased with higher elevation and heteroscedasticity was corrected with an exponential variance function (*varExp*).

The importance of each predictive variable in explaining the variation of soil C was then assessed with a variance partitioning analysis (*VarPart*) (Borcard et al. 1992, Legendre et al. 2009), performed using QEco software (Di Rienzo et al. 2010).

Previous to this, the spatial distribution was expressed as significant eigenvalues generated by a Principal Coordinates of Neighbour Matrices analysis (*PCNM*). These values are constructed from a matrix of geographical distances (X coordinates, Y coordinates, and elevation) assessed by distance-based Moran´s Eigenvector Maps (*db-MEM*). Both positive and negative eigenvectors were retained; for positive eigenvectors describe positive autocorrelation and large scale spatial structure, whilst negative ones describe negative autocorrelation and local spatial structure (Borcard and Legendre 2002).

Matrixes constructed for the *VarPart* analysis were separated by spatial, bioclimatic, soil, and vegetation factors. Variables used in each matrix were previously selected with a Forward Selection analysis (Jones et al. 2008), choosing those with a significant ($p<0.05$, 999 random permutations) contribution to explaining variation in soil C stocks.

## Results

Soil C stocks ranged from 6.8 to 43.1 kg $m^{-2}$ (Appendix 5). Vertical distribution of C increased with depth only from 0 to 60 cm deep. Total C stocks and at each depth were different for every life zone, increasing with altitude.

Table 1. Soil C total stocks means and changes by life zones. Different letters indicate statistically significant models in bold (p<0.05).

| | Humid | | Premontane | | Lower montane | | Montane | | F | p-value |
|---|---|---|---|---|---|---|---|---|---|---|
| *SOC 0-5cm (kg $m^{-2}$)* | 1.04±0.2 | A | 1.2±0.16 | AB | 1.62±0.16 | BC | 2.07±0.24 | C | 4.85 | **0.0089** |
| *SOC 5-20cm (kg $m^{-2}$)* | 1.81±0.43 | A | 2.11±0.35 | A | 2.16±0.35 | A | 2.32±0.53 | A | 0.21 | 0.8857 |
| *SOC 20-60cm (kg $m^{-2}$)* | 3.66±1.53 | A | 6.86±1.25 | AB | 9.79±1.88 | B | 14.97±1.25 | C | 12.63 | **<0.0001** |
| *SOC 60-100cm (kg $m^{-2}$)* | 1.86±0.91 | A | 3.4±0.74 | A | 6.68±1.12 | B | 7±0.74 | B | 8.51 | **0.0005** |
| *SOC stock 1m (kg $m^{-2}$)* | 8.38±2.38 | A | 14.04±1.94 | AB | 20.86±2.91 | BC | 25.28±1.94 | C | 11.77 | **0.0001** |

Total soil C content (Figure 1) increased with elevation ($R^2=0.62$, p<0.0001), with higher variance within plots above 2000 masl. When divided by depth (Figure 2), soil C behaved differently on the profile. From 0 to 5 cm deep, soil C increases as it reaches 1800 masl and then drops to contents similar from those at lower elevations. While soil C between 5 and 20 cm deep showed no clear trends ($R^2=0.01$, p=0.5605), contents from 20 to 100 cm increased with elevation, with a stronger relation in the 20 to 60 cm profile ($R^2=0.67$, p<0.0001).

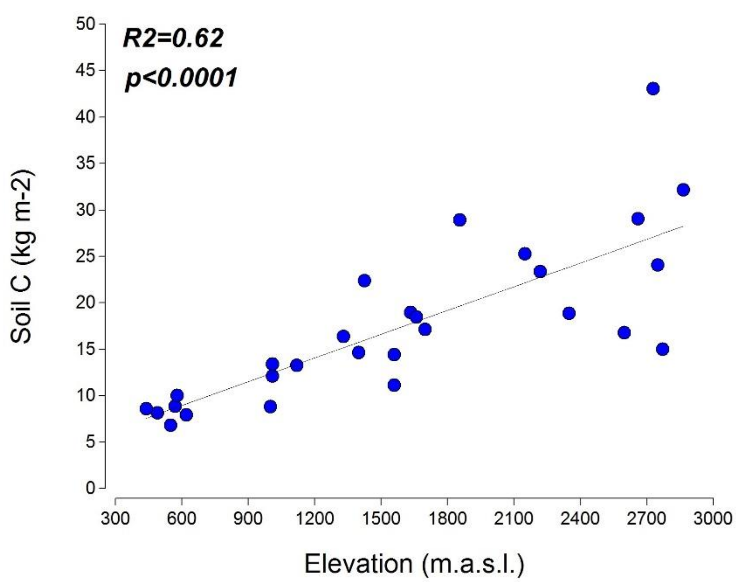


Figure 1. Soil C stock response to changes in elevation *(n=28, with varExp function).*

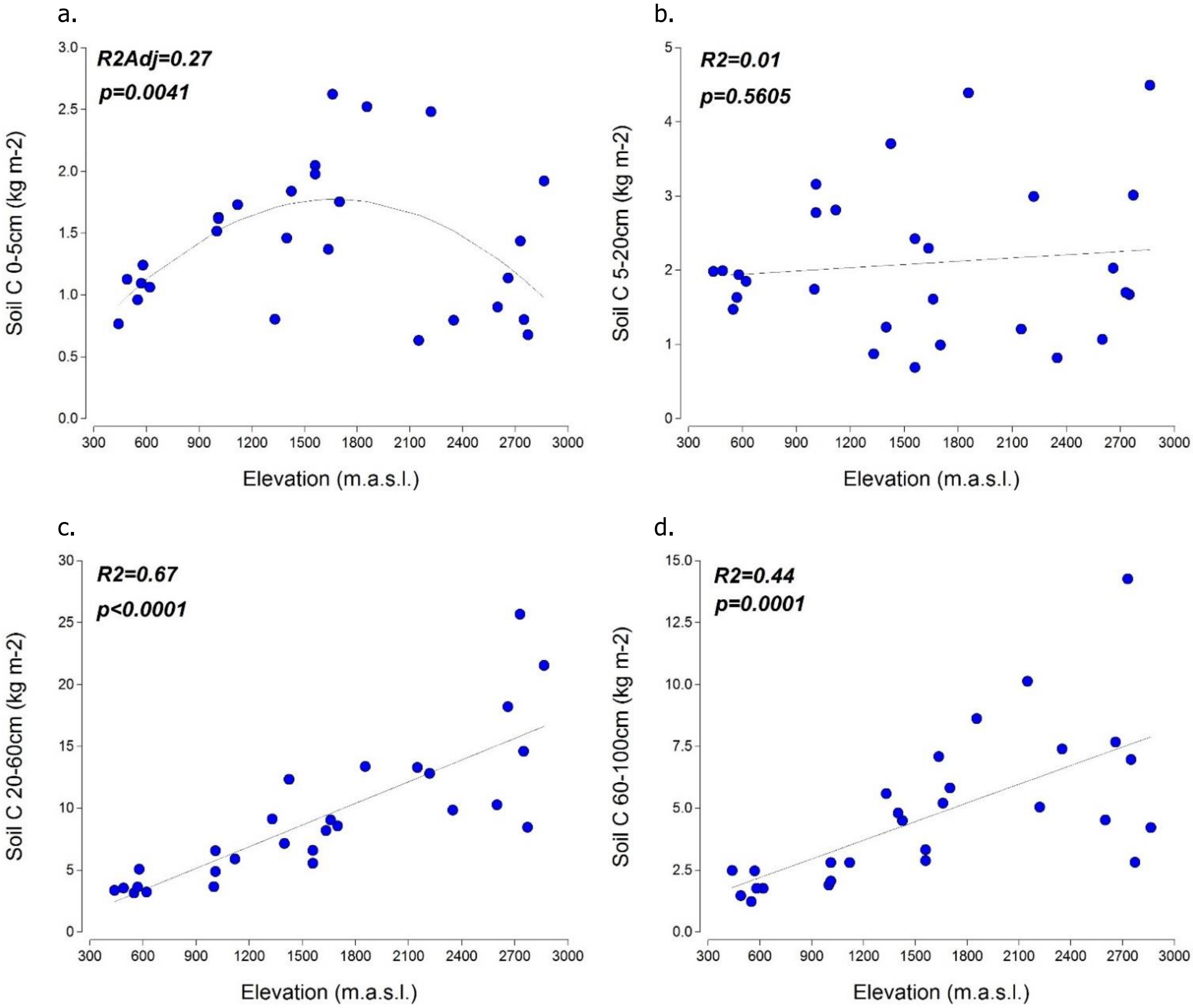


Figure 2. Soil C response to changes in elevation at (a.) the first 5 cm; (b.) 5 to 20 cm; (c.) 20 to 60 cm (*with varExp function*); and (d.) 60 to 100 cm (*with corGaus function*).

Soil C contents, as expected from the observed response to elevation, showed a strong relation with bioclimatic variables (Table 2). All temperature variables showed that the amount of C stored in soil decreases with increasing temperature (Figure 3). Precipitation variables behaved differently. Pearson's correlation matrix for all bioclimatic variables can be found in Appendix 6.

Table 2. Soil C stocks relationships with bioclimatic factors. Statistically significant models in bold (p<0.05).

| | n | F-value | p-value | $R^2$ |
|---|---|---|---|---|
| *Annual mean temperature (°C)* | 28 | 65.97 | <0.0001 | **0.58** |
| *Mean diurnal range (°C)* | 28 | 5.46 | 0.0278 | **0.34** |
| *Isothermality (°C)* | 28 | 38.25 | <0.0001 | **0.03** |
| *Temperature seasonality (SD)* | 28 | 40.75 | <0.0001 | **0.49** |
| *Max temperature of warmest month (°C)* | 28 | 68.06 | <0.0001 | **0.58** |
| *Min temperature of coldest month (°C)* | 28 | 71.65 | <0.0001 | **0.59** |
| *Temperature annual range (°C)* | 28 | 5.64 | 0.0256 | **0.34** |
| *Mean temperature of wettest quarter (°C)* | 28 | 58.26 | <0.0001 | **0.59** |
| *Mean temperature of driest quarter (°C)* | 28 | 70.19 | <0.0001 | **0.59** |
| *Mean temperature of warmest quarter (°C)* | 28 | 71.26 | <0.0001 | **0.59** |
| *Mean temperature of coldest quarter (°C)* | 28 | 85.72 | <0.0001 | **0.59** |
| *Annual precipitation (mm)* | 28 | 20.77 | 0.0001 | **0.33** |
| *Precipitation of wettest month (mm)* | 28 | 5.78 | 0.0236 | **0.01** |
| *Precipitation of driest month (mm)* | 28 | 4.97 | 0.0347 | **0.40** |
| *Precipitation seasonality (CV)* | 28 | 38.05 | <0.0001 | **0.54** |
| *Precipitation of wettest quarter (mm)* | 28 | 4.47 | 0.0450 | **0.003** |
| *Precipitation of driest quarter (mm)* | 28 | 4.91 | 0.0356 | **0.40** |
| *Precipitation of warmest quarter (mm)* | 28 | 5.36 | 0.0288 | **0.06** |
| *Precipitation of coldest quarter (mm)* | 28 | 7.93 | 0.0092 | **0.40** |

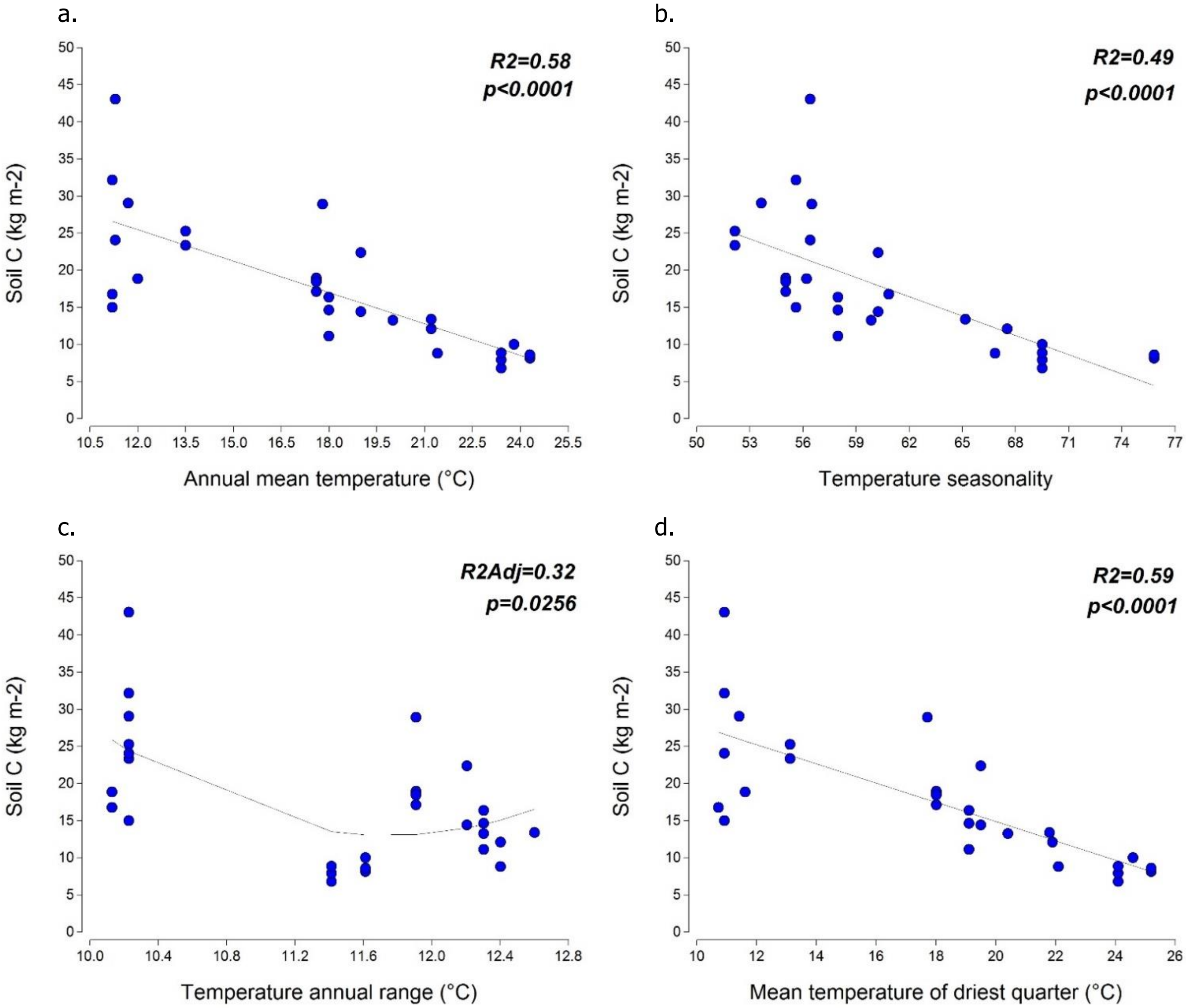


Figure 3. Four most significant and less correlated variables of soil C response to changes in (a.) annual mean temperature (*with ExpVar function*); (b.) temperature seasonality (*with varExp function*); (c.) temperature annual range (*with corGaus and varExp function*); and (d.) mean temperature of driest quarter (*with varExp function*).

Soil C showed a concave relationship with annual precipitation with the best fit to a quadratic model (Figure 4). When divided by quarters, those variables related with temperature (e.g. precipitation of coldest quarter) showed a decrease with precipitation. Seasonality of precipitation presented the strongest relation ($R^2=0.54$, $p<0.0001$) with soil C content.

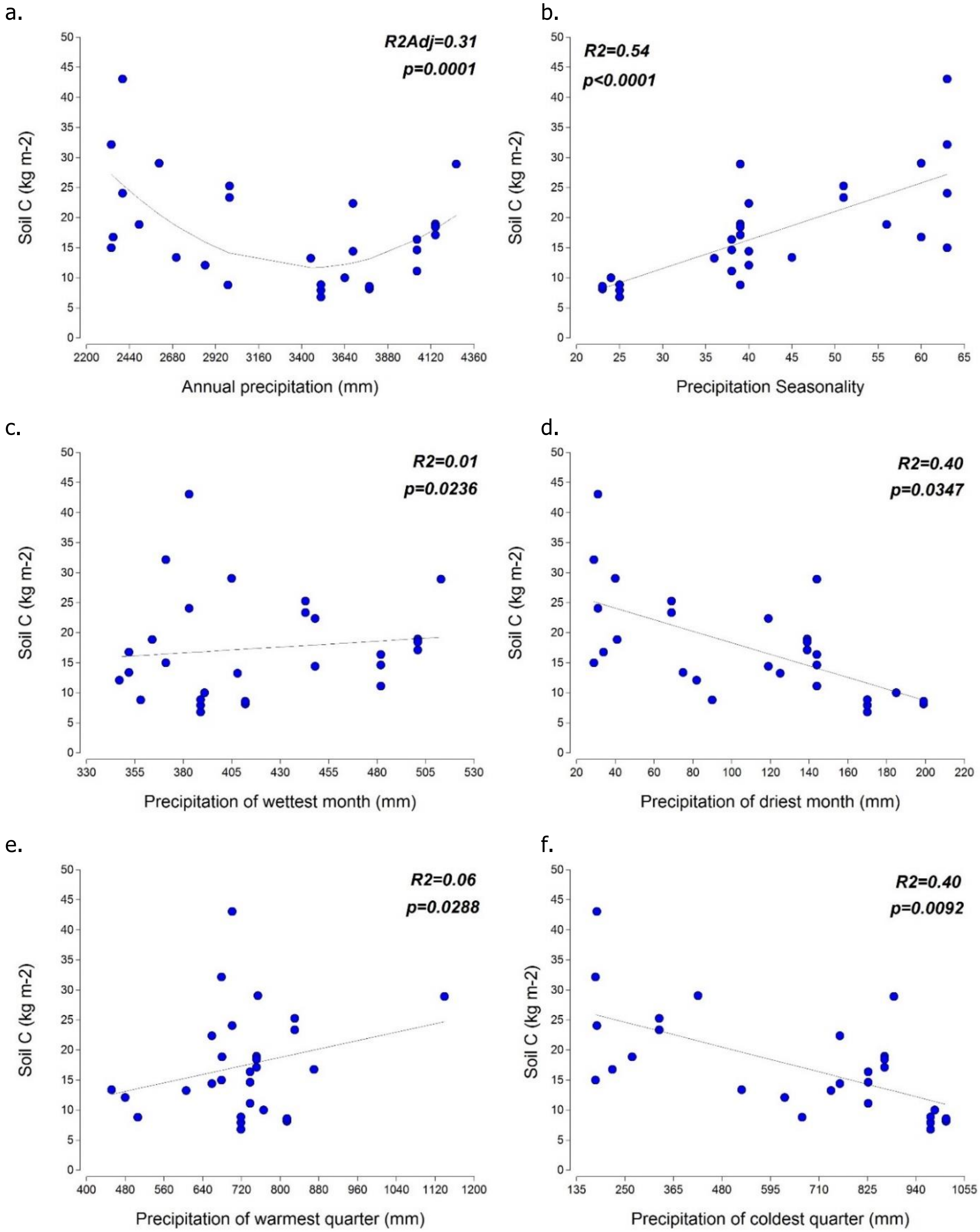


Figure 4. Soil C response to changes in (a.) annual precipitation (with corGaus and varExp function); (b.) precipitation seasonality (with varExp function); (c.) precipitation of wettest month (with corGaus and varExp function); (d.) precipitation of driest month (with corGaus and varExp function); (e.) precipitation of warmest quarter; and (d.) precipitation of coldest quarter (with corGaus and varExp function).

Soil properties showed certain relation with soil C contents, for some variable showed really strong relations whilst others are very weak (Table 3). Congruently to soil C sensitivity to bio-climatic conditions, soil temperature showed the strongest relation with C content (R2=0.62, p<0.0001). Soil C stocks decreased in soils with higher pH (R2=0.31, p=0.0213) and ECEC (R2=0.31, p=0.0003), and were greatly explained by C:N (R2=0.62, p<0.0001) and SOM (R2=0.48, p=0.437) (Figure 5). Pearson's correlation matrix for soil variables with elevation can be found in Appendix 7.

Table 3. Soil C stocks relationships with physical and chemical soil factors. Statistically significant models in bold (p<0.05).

| | n | F-value | p-value | $R^2$ |
|---|---|---|---|---|
| *Soil temperature (°C)* | 25 | 54.88 | <0.0001 | **0.62** |
| *Slope (%)* | 25 | 1.96 | 0.1750 | 0.08 |
| *Sand (%)* | 25 | 12.00 | 0.0021 | **0.05** |
| *Silt (%)* | 25 | 0.56 | 0.4603 | 0.02 |
| *Clay (%)* | 25 | 15.49 | 0.0007 | **0.08** |
| *pH* | 25 | 6.15 | 0.0213 | **0.31** |
| *Acidity (cmol+ $L^{-1}$)* | 25 | 11.78 | 0.0023 | **0.13** |
| *ECEC (cmol+ $L^{-1}$)* | 25 | 18.15 | 0.0003 | **0.31** |
| *Base saturation (%)* | 25 | 2.49 | 0.1281 | 0.10 |
| *C (%)* | 25 | 4.57 | 0.0434 | **0.48** |
| *N (%)* | 25 | 4.29 | 0.0504 | 0.15 |
| *P (mg $L^{-1}$)* | 25 | 11.59 | 0.0024 | **0.35** |
| *C:N* | 25 | 37.05 | <0.0001 | **0.62** |
| *SOM (%)* | 25 | 4.56 | 0.0437 | **0.48** |
| *Ca (cmol+ $L^{-1}$)* | 25 | 5.55 | 0.0274 | **0.31** |
| *Mg (cmol+ $L^{-1}$)* | 25 | 10.53 | 0.0037 | **0.48** |
| *K (cmol+ $L^{-1}$)* | 25 | 8.07 | 0.0093 | **0.24** |
| *Mn (mg $L^{-1}$)* | 25 | 6.87 | 0.0156 | **0.45** |
| *Fe (mg $L^{-1}$)* | 25 | 7.58 | 0.0116 | **0.28** |
| *Cu (mg $L^{-1}$)* | 25 | 0.54 | 0.4690 | 0.02 |
| *Zn (mg $L^{-1}$)* | 25 | 7.37 | 0.0124 | **0.05** |

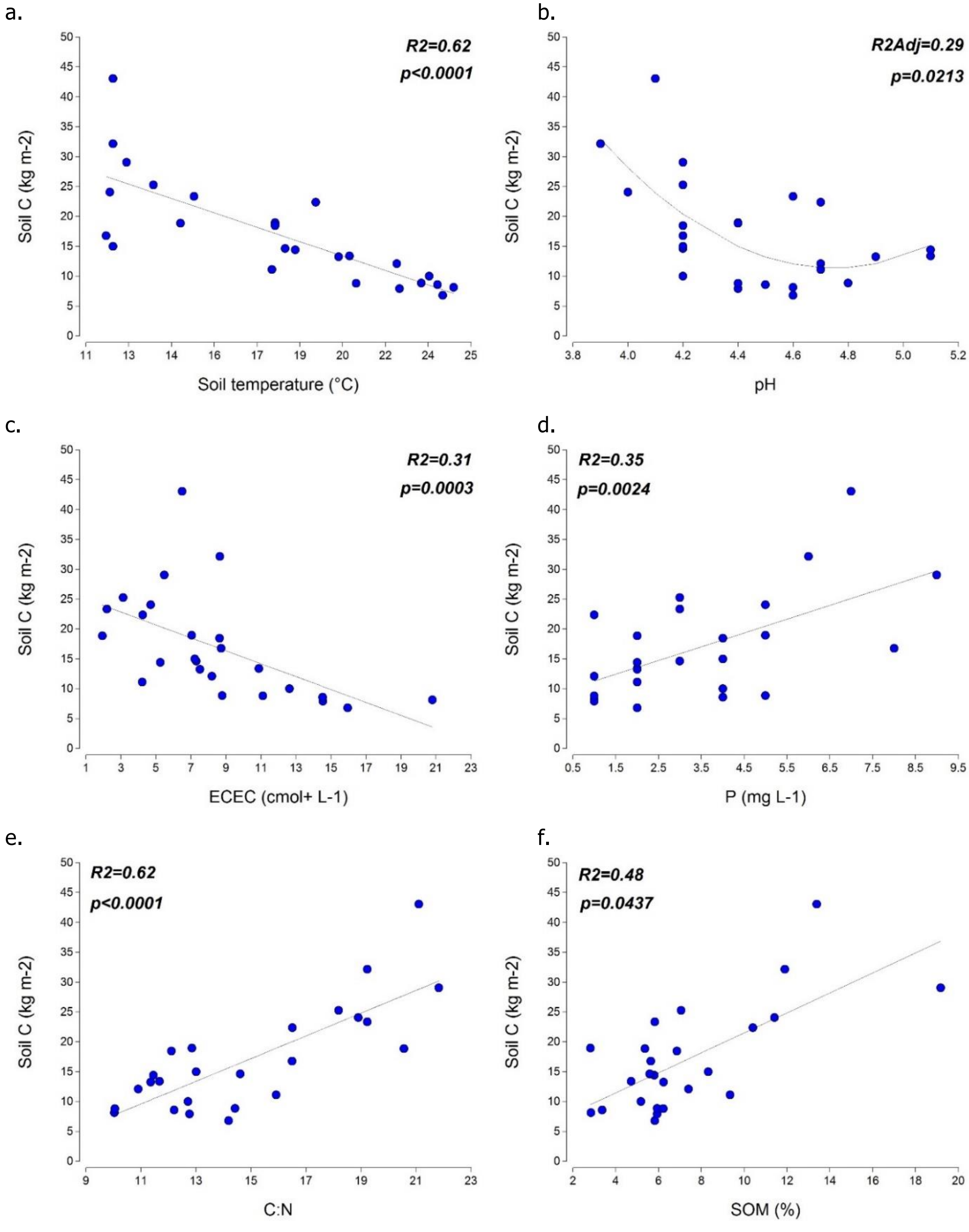


Figure 5. Six most significant and less correlated variables of soil C response to changes in (a.) soil temperature (with varExp function); (b.) pH (with varExp function); (c.) CEC (with varExp function); (d.) P (with corGaus function); (e.) C:N; and (f.) SOM (with corGaus and varExp function).

Community weighted means of vegetation functional traits for each plot showed certain relation with soil C contents (Table 4). Leaf area (R2=0.40, p=0.0003), and foliar N:P (R2=0.5, p<0.0001) were the most significant variables (Figure 6). Pearson's correlation matrix for soil variables with elevation can be found in Appendix 8.

Table 4. Soil C stocks relationships with CWM functional traits. Statistically significant models in bold (p<0.05).

| | n | F-value | p-value | $R^2$ |
|---|---|---|---|---|
| *Wood density (g cm$^{-3}$)* | 28 | 6.79 | 0.0150 | **0.01** |
| *Leaf dry matter content (g)* | 28 | 5.69 | 0.0249 | **0.14** |
| *Leaf area (mm$^2$)* | 28 | 17.53 | 0.0003 | **0.40** |
| *Specific leaf area (mm$^2$ mg$^{-1}$)* | 28 | 6.69 | 0.0156 | **0.26** |
| *N (%)* | 28 | 4.40 | 0.0462 | **0.02** |
| *P (%)* | 28 | 7.81 | 0.0096 | **0.24** |
| *N:P* | 28 | 31.46 | <0.0001 | **0.50** |

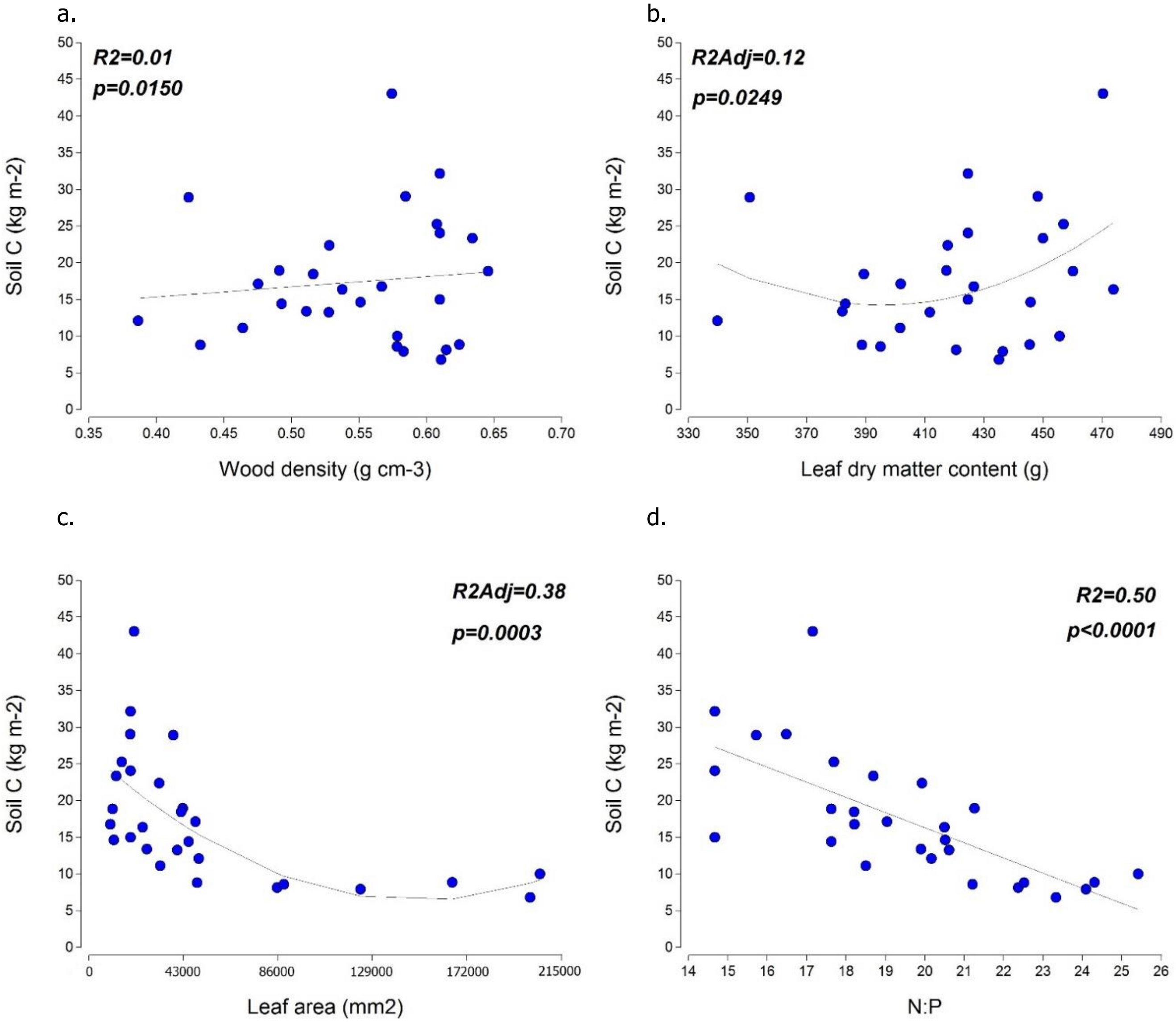


Figure 6. Soil C response to changes in (a.) CWM wood density (*with corGaus and varExp function*); (b.) CWM LDMC (*with corGaus and varExp function*)); (c.) CWM leaf area; and (d.) CWM foliar N:P (*varExp function*).

In order to explain the determinant factor of soil C stocks, a variance partitioning analysis was performed considering four explanatory matrixes (Table 5). Variables included in each matrix are: Spatial (PCNM2), Bioclimatic (Mean temperature of warmest quarter), Soil (ECEC, P, and Mn) and Vegetation (CWM wood density, CWM leaf dry matter content, and CWM foliar N/P). Variables included are those selected by forward selection; for the soil matrix, forward selection was run without SoilTemperature, C, C:N and SOM variables.

This model explained 63% of variation in soil C stocks. Vegetation showed the strongest overall influence on soil C, followed by bioclimatic and soil variables; spatial influence was not significant. When analysed individually, however, not a single matrix had a statistically significant relation ($p<0.05$) on soil C stocks. Results when controlling only one other matrix showed that bioclimatic, soil and vegetation were significant without the influence of space. Vegetation showed significant relations without space, soil, and both space and soil matrices.

Table 5. Variance partitioning for soil C stocks at 1 m deep. Bold cases indicate statistically significant fractions ($p<0.05$).

| | Explanatory matrix | Df | Adj. $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| *Model* | All | 8 | **0.63** | 6.02 | 0.003 |
| *Partition* | Spatial | 1 | 0.04 | 1.90 | 0.205 |
| | Bioclimatic | 1 | **0.62** | 39.57 | 0.001 |
| | Soil | 3 | **0.54** | 10.50 | 0.001 |
| | Vegetation | 3 | **0.67** | 16.95 | 0.001 |
| *Individual fractions* | Spatial | 1 | 0.00 | 0.18 | 0.695 |
| | Bioclimatic | 1 | 0.00 | 0.02 | 0.888 |
| | Soil | 3 | 0.00 | 0.70 | 0.583 |
| | Vegetation | 3 | 0.04 | 1.67 | 0.208 |
| *Controlling* | Spa \| Bio | 1 | 0.00 | 0.0001 | 0.993 |
| | Spa \| Soil | 1 | 0.00 | 0.02 | 0.908 |
| | Spa \| Veg | 1 | 0.00 | 0.48 | 0.516 |
| | Bio \| Spa | 1 | **0.56** | 33.28 | 0.001 |
| | Bio \| Soil | 1 | 0.06 | 4.39 | 0.057 |
| | Bio \| Veg | 1 | 0.00 | 0.20 | 0.667 |
| | Soil \| Spa | 3 | **0.48** | 8.73 | 0.001 |
| | Soil \| Bio | 3 | 0.00 | 0.80 | 0.507 |
| | Soil \| Veg | 3 | 0.00 | 0.95 | 0.438 |
| | Veg \| Spa | 3 | **0.62** | 14.91 | 0.001 |
| | Veg \| Bio | 3 | 0.04 | 1.80 | 0.182 |
| | Veg \| Soil | 3 | **0.12** | 3.52 | 0.046 |
| | Veg \| Spa+Soil | 3 | **0.13** | 3.41 | 0.038 |

The same analysis was conducted for soil C concentration at different depths (Figure 7). For soil C in the top 5 cm, variables included in each matrix are: Spatial (PCNM2), Bioclimatic (Isothermality), Soil (Slope and Sand) and Vegetation (CWM Foliar N). Bioclimatic factors showed the strongest influence on soil C stocks, followed by soil variables, space and vegetation; explaining 37% of variation in soil C stocks (Table 6). When analysed individually, not a single matrix was statistically significant ($p<0.05$). When controlling only one other matrix, bioclimatic factors showed significant relations without the influence of all the other matrices.

Table 6. Variance partitioning for soil C stocks at 0 to 5 cm deep. Bold cases indicate statistically significant fractions (p<0.05).

| | Explanatory matrix | Df | Adj. $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| *Model* | All | 5 | **0.37** | 3.88 | 0.010 |
| *Partition* | Spatial | 1 | **0.27** | 9.98 | 0.003 |
| | Bioclimatic | 1 | **0.36** | 14.53 | 0.001 |
| | Soil | 2 | **0.29** | 5.86 | 0.015 |
| | Vegetation | 1 | **0.20** | 7.14 | 0.016 |
| *Individual fractions* | Spatial | 1 | 0.00 | <0.0001 | 0.989 |
| | Bioclimatic | 1 | 0.08 | 3.53 | 0.090 |
| | Soil | 2 | 0.00 | 0.58 | 0.586 |
| | Vegetation | 1 | 0.00 | 0.37 | 0.565 |
| *Controlling* | Spa \| Bio | 1 | 0.03 | 2.01 | 0.192 |
| | Spa \| Soil | 1 | 0.00 | 0.77 | 0.381 |
| | Spa \| Veg | 1 | **0.13** | 5.64 | 0.029 |
| | Bio \| Spa | 1 | **0.12** | 5.32 | 0.028 |
| | Bio \| Soil | 1 | **0.13** | 6.14 | 0.020 |
| | Bio \| Veg | 1 | **0.18** | 7.79 | 0.011 |
| | Soil \| Spa | 2 | 0.01 | 1.13 | 0.355 |
| | Soil \| Bio | 2 | 0.06 | 2.25 | 0.117 |
| | Soil \| Veg | 2 | 0.10 | 2.64 | 0.088 |
| | Veg \| Spa | 1 | 0.06 | 3.26 | 0.090 |
| | Veg \| Bio | 1 | 0.02 | 1.92 | 0.168 |
| | Veg \| Soil | 1 | 0.01 | 1.46 | 0.224 |
| | Bio \| Soil+Veg | 1 | **0.10** | 4.94 | 0.036 |
| | Bio \| Spa+Veg | 1 | **0.11** | 4.65 | 0.042 |

VarPart analysis for soil C content from 5 to 20 cm deep (Table 7) seemed to explained 8% of its variation. Variables included in each matrix are: Spatial (PCNM3), Bioclimatic (Precipitation of warmest quarter), Soil (Fe) and Vegetation (CWM LDMC); however, a model including all this variables was not significant (p=0.242). Only the soil matrix was statistically significant (p=0.039), but showed no individual effect.

Table 7. Variance partitioning for soil C stocks from 5 to 20 cm deep. Bold cases indicate statistically significant fractions ($p<0.05$).

| | Explanatory matrix | Df | Adj. $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| *Partition* | Spatial | 1 | 0.08 | 3.17 | 0.102 |
| | Bioclimatic | 1 | 0.11 | 3.91 | 0.071 |
| | Soil | 1 | **0.13** | 4.61 | 0.039 |
| | Vegetation | 1 | 0.04 | 1.98 | 0.187 |
| *Model* | All | 4 | 0.08 | 1.54 | 0.242 |
| *Individual fractions* | Spatial | 1 | 0.00 | 0.12 | 0.752 |
| | Bioclimatic | 1 | 0.00 | 0.11 | 0.746 |
| | Soil | 1 | 0.03 | 1.70 | 0.205 |
| | Vegetation | 1 | 0.00 | 0.34 | 0.591 |

For soil C from 20 to 60 cm deep, variables included are: Spatial (PCNM13), Bioclimatic (Max temperature of warmest month), Soil (P and Mn) and Vegetation (LDMC and Foliar N:P). Bioclimatic factors showed the strongest influence on soil C stocks, followed by vegetation and soil variables, explaining 76% of variation in soil C stocks (Table 8). Although space showed no significant relation in the complete model, it was the only significant variable when analysed individually ($p=0.018$). Results when controlling only one other matrix showed that space could be separated from the bioclimatic and vegetation matrices. Bioclimatic, soil and vegetation were significant without the influence of space. Vegetation showed significant relations without space, soil, and both space and soil matrices.

Table 8. Variance partitioning for soil C stocks from 20 to 60 cm deep. Bold cases indicate statistically significant fractions ($p<0.05$).

| | Explanatory matrix | Df | Adj. $R^2$ | F | Pr(>F) |
|---|---|---|---|---|---|
| *Model* | All | 6 | **0.76** | 39.56 | 0.001 |
| *Partition* | Spatial | 1 | 0.08 | 3.15 | 0.102 |
| | Bioclimatic | 1 | **0.65** | 44.71 | 0.001 |
| | Soil | 2 | **0.51** | 13.59 | 0.002 |
| | Vegetation | 2 | **0.64** | 22.59 | 0.001 |
| *Individual fractions* | Spatial | 1 | **0.11** | 9.87 | 0.018 |
| | Bioclimatic | 1 | 0.00 | 0.47 | 0.478 |
| | Soil | 2 | 0.00 | 0.74 | 0.498 |
| | Vegetation | 1 | 0.01 | 1.32 | 0.287 |
| *Controlling* | Spa \| Bio | 1 | **0.12** | 12.35 | 0.013 |
| | Spa \| Soil | 1 | 0.03 | 2.61 | 0.124 |
| | Spa \| Veg | 1 | **0.12** | 12.45 | 0.007 |
| | Bio \| Spa | 1 | **0.68** | 66.94 | 0.001 |
| | Bio \| Soil | 1 | **0.15** | 10.74 | 0.006 |
| | Bio \| Veg | 1 | 0.002 | 1.13 | 0.291 |
| | Soil \| Spa | 2 | **0.46** | 12.71 | 0.002 |
| | Soil \| Bio | 2 | 0.02 | 1.55 | 0.240 |
| | Soil \| Veg | 2 | 0.03 | 1.85 | 0.195 |
| | Veg \| Spa | 2 | **0.68** | 34.42 | 0.001 |
| | Veg \| Bio | 2 | 0.0006 | 0.98 | 0.379 |
| | Veg \| Soil | 2 | **0.16** | 6.19 | 0.012 |
| | Veg \| Spa+Soil | 2 | **0.23** | 11.37 | 0.001 |

Finally, the VarPart analysis for soil C from 60 to 100 cm deep was run including: Spatial (PCNM13), Bioclimatic (Mean temperature of warmest quarter), Soil (P and K) and Vegetation (Wood density, LDMC and Foliar N:P). Bioclimatic factors showed the strongest influence on soil C stocks, followed by soil variables, space and vegetation; explaining 37% of variation in soil C stocks (Table 9). When analysed individually, not a single matrix was statistically significant ($p<0.05$). Results when controlling only one other matrix showed that bioclimatic and soil were significant without the influence of space. Vegetation was separated from the other matrices, even bioclimatic factors.

Table 9. Variance partitioning for soil C stocks at 60 to 100 cm deep. Bold cases indicate statistically significant fractions ($p<0.05$).

| | **Explanatory matrix** | **Df** | **Adj. $R^2$** | **F** | **Pr(>F)** |
|---|---|---|---|---|---|
| *Model* | All | 7 | **0.63** | 6.96 | 0.002 |
| *Partition* | Spatial | 1 | 0.07 | 2.86 | 0.088 |
| | Bioclimatic | 1 | **0.47** | 22.17 | 0.001 |
| | Soil | 2 | **0.46** | 11.21 | 0.001 |
| | Vegetation | 3 | **0.62** | 14.08 | 0.001 |
| *Individual fractions* | Spatial | 1 | 0.06 | 3.97 | 0.075 |
| | Bioclimatic | 1 | 0.00 | 0.03 | 0.855 |
| | Soil | 2 | 0.00 | 0.13 | 0.877 |
| | Vegetation | 3 | 0.06 | 2.17 | 0.138 |
| *Controlling* | Spa \| Bio | 1 | 0.10 | 6.21 | 0.050 |
| | Spa \| Soil | 1 | 0.04 | 3.00 | 0.102 |
| | Spa \| Veg | 1 | **0.06** | 4.98 | 0.034 |
| | Bio \| Spa | 1 | **0.49** | 27.27 | 0.001 |
| | Bio \| Soil | 1 | 0.03 | 2.49 | 0.137 |
| | Bio \| Veg | 1 | 0.00 | 0.14 | 0.732 |
| | Soil \| Spa | 2 | **0.43** | 11.04 | 0.001 |
| | Soil \| Bio | 2 | 0.03 | 1.57 | 0.226 |
| | Soil \| Veg | 2 | 0.00 | 0.38 | 0.698 |
| | Veg \| Spa | 3 | **0.61** | 15.63 | 0.001 |
| | Veg \| Bio | 3 | **0.14** | 3.63 | 0.038 |
| | Veg \| Soil | 3 | **0.14** | 3.49 | 0.034 |
| | Spa \| Bio+Veg | 1 | **0.06** | 4.86 | 0.037 |
| | Veg \| Bio+Soil | 3 | **0.08** | 3.24 | 0.046 |
| | Veg \| Spa+Soil | 3 | **0.15** | 4.04 | 0.020 |

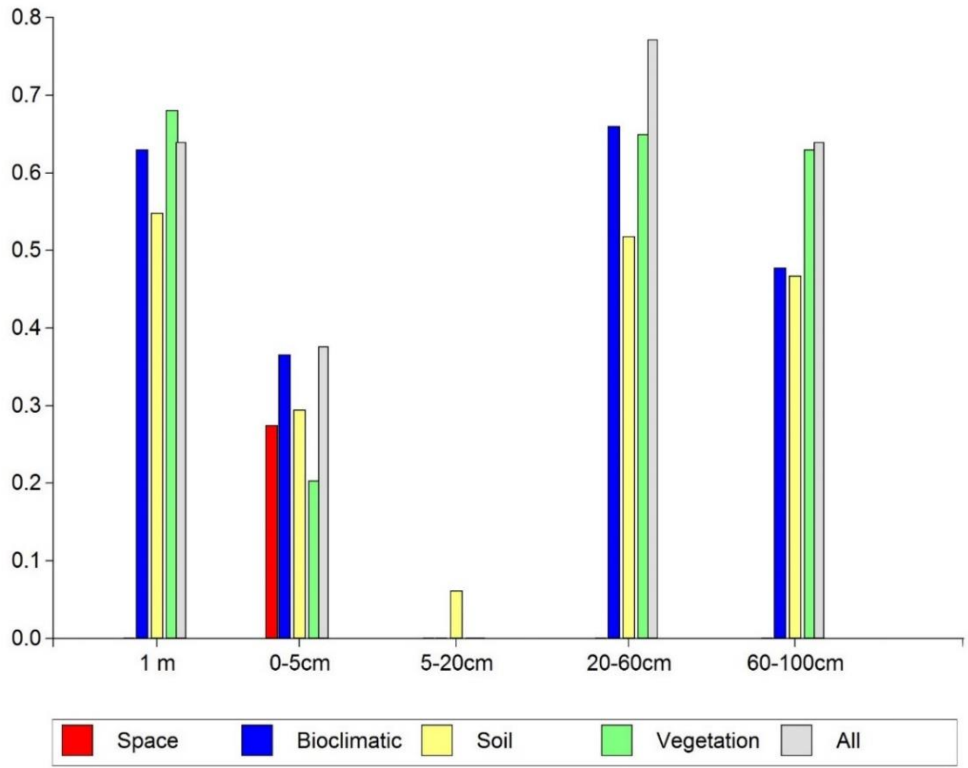


Figure 7. Variance partitioning for soil C stocks at different depths. All bars, except Soil for 5-20cm, are general effects. Missing bars showed no significant Adj$R^2$.

## Discussion

Soil C stocks in the study area (440-2865 masl) ranged from 6.8 to 43.1 kg $m^{-2}$, increasing with altitude. Previous soil C estimations for another tropical forest elevation gradient in Costa Rica ranged from 5.1 to 11.2 kg $m^{-2}$ (Powers y Veldkamp 2005), though the sampled sites were located between 40 to 800 masl. Compared to another tropical gradient of similar length in Papua New Guinea, values in this study are relatively high, for this study recorded stocks ranging between 4.8 and 19.4 kg $m^{-2}$. In all these, and other studies (Du et al. 2014), stored soil C showed a positive response to increase in elevation, mainly because of differences strongly marked by the gradient.

Vertical distribution of soil C did not respond the same way. From 20 to 100 cm, C contents followed the same trend as total C stocks, but soil C distributions in the first top centimeters showed not clear patterns. Soil C changes with depth have been previously reported (Jobbágy and Jackson 2000), concluding that differences in root distributions affect the vertical placement of C, and above and belowground allocation affects the relative amount of C that eventually falls to the soil´s surface.

No significant differences with elevation, particularly from 5 to 20 cm, accounts for C cycling processes and soil C exchanges that are not directly influenced by altitude (Hoffmann et al. 2014). In the first 5 cm, the quadratic relationship with elevation may reveal the presence of an enabling factor that contributes to soil C but is then limited by a controlling factor, presumably low temperature or site-specific characteristics, such as slope. Soil C concentrations in the following 15 cm showed high variations along the gradient; however, contents in the lowest plots (Barbilla National Park) are very much alike, and may indicate a balanced soil C exchange.

Our results suggest that temperature has a strong relation with soil C. The amount of stored C soil increases as the temperature is reduced (see also Wang et al. 2016). This may be influenced by two main factors: litter decomposition rates and soil respiration. Lowlands with high temperatures present larger primary production, greater litter production, and faster decomposition rates; opposed to forests in higher lands (Salinas et al. 2011).

As litter decomposition is considered the main soil C input (Post and Kwon 2000), high temperatures influences soil C content for its direct regulation of decomposition rates (Salinas et al. 2011), as it creates enabling environments for microbial activity. Despite this, lowland forests do not present elevated soil C stocks because high temperatures generate an exponential increase of detritivore activity and microbial respiration, accelerating the transformation of organic carbon to $CO_2$ (Wang et al. 2000, González and Seastedt 2001). On the other hand, forests at higher elevations function at slower rates, allowing C accumulation in soil (Rustad et al. 2001).

Precipitation seemed to have relatively low influence on soil C; probably because water is not a limiting factor anywhere on the gradient. However, relations with soil C are better observed during extreme periods (i.e. driest month and coldest quarter) than in annual trends. Although water availability changes throughout the year are low, precipitation seasonality showed the strongest statistical relationship to soil C, presenting elevated C contents in higher grounds. However, we believe that this is a simple consequence of the correlation of precipitation seasonality with elevation and not a causal relationship.

Although the effect of precipitation on soil carbon storage was not clearly perceived on this work, its importance must not be set aside as a controlling factor in other ecosystem processes. For example, decomposition rates, and thus C accumulation, increase with soil moisture, and decomposing organisms are more productive under hot and humid conditions (Gholz et al. 2000).

Our results indicate three main soil factors that are correlated with soil C stocks: soil temperature, P, and CEC. Although data obtained during this study may not lead to substantial conclusions, for soil temperature was not thoroughly measured, it exposes the soil C sensitivity to bioclimatic conditions. Changes in physical conditions within the soil matrix determine the rates of all processes in soil, specially fluxes and exchanges with the atmosphere (Lavigne et al. 2004).

Increasing soil C with P suggests differences in nutrient availability along the gradient (Alvarez-Clare y Mack 2011). This changes may respond to known P limitation in tropical forests at lower elevations, thus influencing nutrient cycling, C accumulation and reduced SOM turnover (Wang et al. 2000). Additionally, P concentrations increase with SOM levels, associated with clay particles and minerals that stabilize and store C (Jobbágy y Jackson 2000).

The vegetation community-weighted mean functional trait with the strongest statistical relationship with soil C stocks was CWM foliar N:P. This nutrient concentration trait also indicates nutrient limitation in the ecosystem. It may also be an indicator of nutrient resorption and re-translocation efficiency (Rentería-Rodríguez et al. 2005), that may influence C retention time on the soil matrix.

CWM LDMC has a quadratic relationship with SOC, increasing at higher soil C concentrations; C stocks are therefore higher under vegetation with leaves with high dry matter content, similar to the ones found by Manning et al. (2015). Since CWM LDMC is not correlated with elevation, we can suspect of a real ecological relationship between vegetation functional traits and soil C storage.

Soil C stocks showed a negative relation with CWM leaf area, although it may respond to the high presence of palms in the lowland wet forest, where SOC is low. Combined with CWM LDMS, these properties indicate slow decomposition rates, understood as low C inputs. However, this leaf traits also indicate more stable and longer residence time of C in soils (Wieder et al. 2009, Schimel et al. 2001).

Wood density showed no significant relationship with soil C stocks. This must be due to C cycling differences between functional type forests (Finegan et al. 2015). On sites where species with high WSG dominate, C is retained on aboveground biomass and its decomposition is slow, limiting C entrance to soil. Contrastingly, species with intermediate WSG are characterized by high growth and mortality rates, accelerating C movement within the ecosystem, and restricting its accumulation on soil.

The *VarPart* analysis for total SOC to 100 cm soil depth indicated that of the 63% of explained variation, vegetation, bioclimatic factors and soil properties have similar effects on soil C stocks, probably because of the inseparable interactions among these variables. Surprisingly, the spatial arrangement of plots had a relative small influence on SOC concentrations, even though the study area is a gradient with characteristics strongly marked by elevation, and distances between plots ranging between 256 m and 60 km. This evidences the high correlation between space, elevation, temperature and soil characteristics.

Assessed individually, not a single matrix had a significant relationship with soil C stocks. Significant general effects and not significant pure ones, account for all the interactions that cannot be separated and truly explain and determine the amounts of stored C on soils.

Changes in the significant explanatory matrices when soil C is divided by depths indicate the variation of processes and the different working scales of soil C storage. The most varying fraction is 0 to 5 cm, where Isothermality, Slope and CWM Foliar N are greatly related to soil C stocks. This variables are highly associated to soil interactions with the atmosphere and decomposition rates. The influence of slope may indicate a C loss caused by runoff, though further assessment is needed.

A not significant partition for soil C at 5 to 20cm, combined with an unclear relation with elevation, may indicate that other variables not measured in this study may have a significant effect on soil C distribution and interactions on soil, such as litter quality, root activity, soil fauna, microorganisms, enzymatic rates, soil aggregates, and so on. Soil properties tend to be strongly correlated with environmental conditions contributing to ecosystem arrangements, but it is difficult to unravel the causal relationships responsible for this correlation (Brokaw 2004).

Wang et al. (2016) found SOM decomposition rates along an altitudinal gradient were individually correlated with temperature and soil moisture, as well as a significant effect from the interaction between the two factors. Furthermore, partial correlation analysis showed that the relative importance of the three factors was in the following order: temperature > soil moisture > elevation.

It is important to acknowledge that our study has a functional-trait approach, and vegetation variables used go beyond diversity or composition. This may emphasize the importance of vegetation in the ecosystem, explaining soil C stocks, particularly at deep layers, to more extent than space, climate, and soil. Recognized limiting resources, such as space, light and water, determinate plant species composition, but are probably not directly causal. Still, we should not forget that C cycling, as other ecosystem processes, is controlled by a hierarchy of factors (Díaz et al. 2007).

Established the latter, *VarPart* analysis must be interpreted taking this into consideration. In this study's context, controlling factors are examined as a circle, rather than a pyramid. Spatial characteristics, majorly altitude, determine climate, vegetation distributions and soil properties. At the same time, climate controls the metabolism of plants and determines rates of soil matrix processes, thus influencing soil properties. Next, soil abiotic properties, such as texture and pH, influence soil C storage by affecting plant growth and microbial activity. Moreover, climate and soil properties influence the vegetation composition and growth, which in turn affect the amount and quality of litter inputs, and the turnover of soil organic matter (Manning et al. 2015).

## Conclusion

As expected, results clearly showed a strong relationship between soil C stocks and altitude. However, findings suggest that soil C stocks in mountain tropical forests are controlled by a wide range of factors beyond elevation. Changes with elevation and its variations in temperature have strong correlations with soil C contents. As expected, plots with high weighted means of functional traits associated to conservative species presented higher levels of C in soil.

When assessed individually, vegetation presented the greatest influence on soil C stocks, followed by bioclimatic variables and soil properties. Space showed no significant influence on soil C stocks. This study gives an insight on the relative influence and importance of these factors on soil C stocks. However, the biggest influence come from all the interactions that cannot be separated and truly explain and determine the amounts of stored C on soils.

These results offer a better understanding of mountain tropical forests ecosystem dynamics, valuable contribution for this ecosystem extremely vulnerable to climate change. A first insight on how soil C changes and its controlling factors bring information for making better-informed decisions for conservation and management facing climate change strategies.

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## Appendixes

Appendix 1. Sample plots within study area, Costa Rica

| Plot | ID | Site | Life zone | CoordX | CoordY | masl | Sampling date |
|---|---|---|---|---|---|---|---|
| 1 | B1 | PN Barbilla | Super-humid tropical rain forest | 560610 | 1101413 | 490 | May-10 |
| 2 | B2 | PN Barbilla | Super-humid tropical rain forest | 560715 | 1101056 | 550 | May-11 |
| 3 | B3 | PN Barbilla | Super-humid tropical rain forest | 560912 | 1100767 | 620 | May-11 |
| 4 | B4 | PN Barbilla | Super-humid tropical rain forest | 561140 | 1100308 | 570 | May-24 |
| 5 | B5 | PN Barbilla | Super-humid tropical rain forest | 561013 | 1101390 | 440 | May-17 |
| 6 | B6 | PN Barbilla | Super-humid tropical rain forest | 561221 | 1100598 | 580 | May-18 |
| 7 | A1 | ZPCRT Atirro | Humid premontane tropical wet forest | 538740 | 1082737 | 1000 | Jun-09 |
| 8 | A2 | ZPCRT Atirro | Humid premontane tropical wet forest | 538338 | 1083140 | 1010 | Jul.29 |
| 9 | C1 | RB El Copal | Humid premontane tropical wet forest | 527475 | 1081183 | 1010 | Jun-15 |
| 10 | C2 | RB El Copal | Humid premontane tropical wet forest | 526760 | 1081567 | 1120 | Jun-02 |
| 11 | T1 | PN Tapantí | Humid premontane tropical rain forest | 522072 | 1079639 | 1425 | May-31 |
| 12 | T2 | PN Tapantí | Humid premontane tropical rain forest | 522288 | 1079211 | 1560 | May-31 |
| 13 | T3 | PN Tapantí | Humid lower montane tropical rain forest | 522284 | 1078881 | 1635 | May-31 |
| 14 | T4 | PN Tapantí | Humid lower montane tropical rain forest | 522108 | 1078548 | 1700 | Jun-01 |
| 15 | T5 | PN Tapantí | Humid premontane tropical rain forest | 523484 | 1077813 | 1400 | Jun-07 |
| 16 | T6 | PN Tapantí | Humid premontane tropical rain forest | 522935 | 1078099 | 1560 | Jun-07 |
| 17 | T7 | PN Tapantí | Humid lower montane tropical rain forest | 522480 | 1078142 | 1660 | Jun-08 |
| 18 | T8 | PN Tapantí | Humid lower montane tropical rain forest | 522104 | 1078043 | 1856 | Jun-08 |
| 19 | T9 | PN Tapantí | Humid premontane tropical rain forest | 523163 | 1077473 | 1331 | Jul-05 |
| 20 | E1 | PN Tapantí-La Esperanza | Humid lower montane tropical wet forest | 515616 | 1074178 | 2150 | Jun-21 |
| 21 | E2 | PN Tapantí-La Esperanza | Humid lower montane tropical wet forest | 515749 | 1073770 | 2220 | Jun-21 |
| 22 | E3 | PN Tapantí-La Esperanza | Humid lower montane tropical wet forest | 515510 | 1073296 | 2350 | Jun-21 |
| 23 | E4 | PN Tapantí-La Esperanza | Humid montane tropical rain forest | 514165 | 1070765 | 2600 | Jun-21 |
| 24 | V2 | RFRM Villa Mills | Humid montane tropical rain forest | 532320 | 1059094 | 2773 | Jun-22 |
| 25 | V3 | RFRM Villa Mills | Humid montane tropical rain forest | 533346 | 1058573 | 2660 | Jul-20 |
| 26 | V4 | RFRM Villa Mills | Humid montane tropical rain forest | 532479 | 1058848 | 2865 | Jun-22 |
| 27 | V5 | RFRM Villa Mills | Humid montane tropical rain forest | 534132 | 1057111 | 2750 | Jun-22 |
| 28 | V6 | RFRM Villa Mills | Humid montane tropical rain forest | 534435 | 1057075 | 2730 | Jun-22 |

Appendix 2. Descriptive statistics of complementary soil variables. All variables, except soil temperature, taken from Veintimilla Ramos (2013).

| **Variable** | **Mean** | **SD** | **Min** | **Max** |
|---|---:|---:|---:|---:|
| Soil temperature | 18.02 | 4.32 | 11.75 | 24.60 |
| Slope (%) | 26.52 | 5.95 | 16.00 | 37.00 |
| Sand (%) | 43.44 | 15.65 | 16.00 | 75.00 |
| Silt (%) | 23.28 | 5.71 | 15.00 | 38.00 |
| Clay (%) | 33.28 | 15.48 | 10.00 | 61.00 |
| pH | 4.45 | 0.32 | 3.90 | 5.10 |
| Acidity (cmol+ $L^{-1}$) | 6.41 | 4.29 | 1.09 | 18.78 |
| ECEC (cmol+ $L^{-1}$) | 8.36 | 4.59 | 1.88 | 20.79 |
| Base saturation (%) | 77.12 | 24.79 | 17.00 | 96.00 |
| C (%) | 5.35 | 2.49 | 2.29 | 13.46 |
| N (%) | 0.36 | 0.11 | 0.18 | 0.63 |
| P (mg $L^{-1}$) | 3.48 | 2.26 | 1.00 | 9.00 |
| C:N | 14.68 | 3.52 | 10.00 | 21.37 |
| SOM (%) | 7.65 | 3.57 | 3.27 | 19.25 |
| Ca (cmol+ $L^{-1}$) | 1.22 | 1.62 | 0.05 | 6.30 |
| Mg (cmol+ $L^{-1}$) | 0.65 | 0.62 | 0.07 | 2.55 |
| K (cmol+ $L^{-1}$) | 0.08 | 0.05 | 0.01 | 0.19 |
| Mn (mg $L^{-1}$) | 41.24 | 39.55 | 1.00 | 146.00 |
| Fe (mg $L^{-1}$) | 660.68 | 465.89 | 220.00 | 1807.00 |
| Cu (mg $L^{-1}$) | 5.4 | 3.04 | 1.00 | 13.00 |
| Zn (mg $L^{-1}$) | 2.37 | 0.84 | 1.10 | 4.10 |

Appendix 3. Descriptive statistics of Worldclim bioclimatic variables

| ID | Variable | Mean | SD | Min | Max |
|---|---|---|---|---|---|
| Bio1 | Annual mean temperature (°C) | 17.71 | 4.64 | 11.2 | 24.3 |
| Bio2 | Mean diurnal range (°C) | 9.27 | 0.93 | 7.9 | 10.4 |
| Bio3 | Isothermality (°C) | 8.07 | 0.22 | 7.7 | 8.4 |
| Bio4 | Temperature seasonality (SD) | 61.03 | 7.08 | 52.2 | 76.2 |
| Bio5 | Max temperature of warmest month (°C) | 23.71 | 5.14 | 16.3 | 30.5 |
| Bio6 | Min temperature of coldest month (°C) | 12.30 | 4.46 | 6.1 | 18.9 |
| Bio7 | Temperature annual range (°C) | 11.40 | 0.91 | 10.1 | 12.6 |
| Bio8 | Mean temperature of wettest quarter (°C) | 17.86 | 4.46 | 11.5 | 24.4 |
| Bio9 | Mean temperature of driest quarter (°C) | 17.84 | 5.12 | 10.5 | 25.0 |
| Bio10 | Mean temperature of warmest quarter (°C) | 18.53 | 4.85 | 11.7 | 25.4 |
| Bio11 | Mean temperature of coldest quarter (°C) | 17.00 | 4.63 | 10.3 | 23.4 |
| Bio12 | Annual precipitation (mm) | 3315.57 | 668.60 | 2338.0 | 4261.0 |
| Bio13 | Precipitation of wettest month (mm) | 418.57 | 52.97 | 347.0 | 513.0 |
| Bio14 | Precipitation of driest month (mm) | 109.61 | 56.64 | 29.0 | 199.0 |
| Bio15 | Precipitation seasonality (CV) | 42.32 | 13.38 | 23.0 | 63.0 |
| Bio16 | Precipitation of wettest quarter (mm) | 1180.07 | 172.72 | 983.0 | 1500.0 |
| Bio17 | Precipitation of driest quarter (mm) | 377.71 | 184.02 | 108.0 | 648.0 |
| Bio18 | Precipitation of warmest quarter (mm) | 722.96 | 128.84 | 452.0 | 1139.0 |
| Bio19 | Precipitation of coldest quarter (mm) | 653.00 | 303.94 | 180.0 | 1012.0 |

Appendix 4. Descriptive statistics of community weighted means by functional trait

| Variable | Mean | SD | Min | Max |
|---|---|---|---|---|
| Wood density (g $cm^{-3}$) | 0.55 | 0.07 | 0.39 | 0.65 |
| Leaf dry matter content (g) | 420.67 | 33.67 | 339.79 | 473.85 |
| Leaf area ($mm^2$) | 48971.57 | 56686.20 | 4046.99 | 204862.47 |
| Specific leaf area ($mm^2$ $mg^{-1}$) | 2937.80 | 1704.23 | 886.95 | 6508.71 |
| Foliar N (%) | 2.19 | 0.25 | 1.77 | 2.82 |
| Foliar P (%) | 0.12 | 0.03 | 0.08 | 0.19 |
| Foliar N:P | 19.47 | 2.96 | 14.67 | 25.42 |

Appendix 5. Soil C contents at four different depths and total stock (kg $m^{-2}$)

| Plot | Soil C 5-20cm | Soil C 5-20cm | Soil C 20-60cm | Soil C 60-100cm | Soil C stock |
|---|---|---|---|---|---|
| B1 | 1.12509 | 1.99355 | 3.53688 | 1.46336 | 8.11887 |
| B2 | 0.96181 | 1.47356 | 3.15382 | 1.22129 | 6.81048 |
| B3 | 1.06274 | 1.85036 | 3.24153 | 1.76083 | 7.91546 |
| B4 | 1.09531 | 1.63465 | 3.63861 | 2.46556 | 8.83413 |
| B5 | 0.76697 | 1.98211 | 3.35550 | 2.48713 | 8.5917 |
| B6 | 1.23992 | 1.93910 | 5.05799 | 1.76076 | 9.99776 |
| A1 | 1.51626 | 1.74523 | 3.64666 | 1.89385 | 8.80200 |
| A2 | 1.62715 | 2.77553 | 4.87565 | 2.80048 | 12.07881 |
| C1 | 1.61656 | 3.15882 | 6.56119 | 2.04864 | 13.38521 |
| C2 | 1.72875 | 2.81094 | 5.89265 | 2.80501 | 13.23735 |
| T1 | 1.83841 | 3.70495 | 12.32113 | 4.49588 | 22.36038 |
| T2 | 2.04744 | 2.42298 | 6.59763 | 3.3233 | 14.39134 |
| T3 | 1.36922 | 2.29382 | 8.19528 | 7.08867 | 18.94699 |
| T4 | 1.75443 | 0.99421 | 8.55716 | 5.81392 | 17.11972 |
| T5 | 1.45913 | 1.23400 | 7.14249 | 4.80069 | 14.63631 |
| T6 | 1.97823 | 0.69119 | 5.54934 | 2.88766 | 11.10642 |
| T7 | 2.62381 | 1.61242 | 9.03866 | 5.20787 | 18.48276 |
| T8 | 2.52207 | 4.39111 | 13.37016 | 8.6208 | 28.90414 |
| T9 | 0.80435 | 0.87138 | 9.12248 | 5.58519 | 16.3834 |
| E1 | 0.63263 | 1.20759 | 13.28037 | 10.13228 | 25.25286 |
| E2 | 2.48106 | 2.99203 | 12.8112 | 5.0478 | 23.3321 |
| E3 | 0.79511 | 0.81739 | 9.84695 | 7.39135 | 18.8508 |
| E4 | 0.90111 | 1.06788 | 10.27688 | 4.52879 | 16.77466 |
| V2 | 0.67731 | 3.01128 | 8.46895 | 2.8136 | 14.97114 |
| V3 | 1.13585 | 2.02894 | 18.20296 | 7.67827 | 29.04602 |
| V4 | 1.92133 | 4.49131 | 21.54227 | 4.22356 | 32.17847 |
| V5 | 0.80198 | 1.67272 | 14.60827 | 6.96738 | 24.05034 |
| V6 | 1.43514 | 1.70117 | 25.66757 | 14.25976 | 43.06364 |

Appendix 6. Pearson's correlation matrix for Worldclim bioclimatic variables. Missing values below the diagonal were not significant ($p<0.05$).

| | Bio1 | Bio2 | Bio3 | Bio4 | Bio5 | Bio6 | Bio7 | Bio8 | Bio9 | Bio10 | Bio11 | Bio12 | Bio13 | Bio14 | Bio15 | Bio16 | Bio17 | Bio18 | Bio19 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bio1 | - | | | | | | | | | | | | | | | | | | |
| Bio2 | 0.66 | - | | | | | | | | | | | | | | | | | |
| Bio3 | | 0.85 | - | | | | | | | | | | | | | | | | |
| Bio4 | 0.83 | | | - | | | | | | | | | | | | | | | |
| Bio5 | 0.99 | 0.73 | 0.40 | 0.79 | - | | | | | | | | | | | | | | |
| Bio6 | 1.00 | 0.64 | | 0.83 | 0.99 | - | | | | | | | | | | | | | |
| Bio7 | 0.74 | 0.99 | 0.77 | | 0.8 | 0.71 | - | | | | | | | | | | | | |
| Bio8 | 0.99 | 0.70 | | 0.81 | 1.00 | 1.00 | 0.77 | - | | | | | | | | | | | |
| Bio9 | 1.00 | 0.69 | | 0.82 | 1.00 | 1.00 | 0.76 | 1.00 | - | | | | | | | | | | |
| Bio10 | 1.00 | 0.68 | | 0.82 | 1.00 | 1.00 | 0.75 | 1.00 | 1.00 | - | | | | | | | | | |
| Bio11 | 0.99 | 0.69 | | 0.80 | 1.00 | 1.00 | 0.76 | 1.00 | 1.00 | 1.00 | - | | | | | | | | |
| Bio12 | 0.60 | 0.73 | 0.74 | | 0.65 | 0.61 | 0.70 | 0.64 | 0.62 | 0.62 | 0.63 | - | | | | | | | |
| Bio13 | | 0.45 | 0.73 | -0.40 | | | | | | | | 0.81 | - | | | | | | |
| Bio14 | 0.87 | 0.60 | 0.41 | 0.61 | 0.88 | 0.88 | 0.64 | 0.88 | 0.88 | 0.88 | 0.88 | 0.86 | 0.44 | - | | | | | |
| Bio15 | -0.96 | -0.62 | | -0.73 | -0.95 | -0.96 | -0.68 | -0.96 | -0.96 | -0.96 | -0.96 | -0.75 | | -0.96 | - | | | | |
| Bio16 | | 0.55 | 0.78 | | | | 0.46 | | | | | 0.84 | 0.99 | 0.45 | | - | | | |
| Bio17 | 0.87 | 0.64 | 0.46 | 0.59 | 0.88 | 0.88 | 0.67 | 0.89 | 0.88 | 0.88 | 0.88 | 0.88 | 0.46 | 1.00 | -0.96 | 0.48 | - | | |
| Bio18 | | | | | | | | | | | | | 0.52 | | | 0.46 | | - | |
| Bio19 | 0.88 | 0.72 | 0.54 | 0.58 | 0.90 | 0.89 | 0.74 | 0.90 | 0.89 | 0.89 | 0.90 | 0.88 | 0.45 | 0.97 | -0.95 | 0.48 | 0.98 | | - |

Appendix 7. Pearson's correlation matrix for physical and chemical soil variables with elevation. Missing values below the diagonal were not significant (p<0.05).

| | masl | Slope | Sand | Silt | Clay | pH | Acidity | ECEC | Base sat | C | N | P | C:N | SOM | Ca | Mg | K | Mn | Fe | Cu | Zn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| masl | - | | | | | | | | | | | | | | | | | | | | |
| Slope | | - | | | | | | | | | | | | | | | | | | | |
| Sand | | | - | | | | | | | | | | | | | | | | | | |
| Silt | | | | - | | | | | | | | | | | | | | | | | |
| Clay | | | -0.93 | | - | | | | | | | | | | | | | | | | |
| pH | 0.58 | | | | | - | | | | | | | | | | | | | | | |
| Acidity | 0.45 | | -0.80 | | 0.84 | | - | | | | | | | | | | | | | | |
| ECEC | 0.68 | | -0.67 | | 0.77 | | 0.87 | - | | | | | | | | | | | | | |
| Base sat | | | -0.42 | | | -0.79 | 0.42 | | - | | | | | | | | | | | | |
| C | -0.59 | | | | | | | -0.41 | | - | | | | | | | | | | | |
| N | | | | -0.42 | | | | | | 0.82 | - | | | | | | | | | | |
| P | -0.61 | | | | | -0.57 | | | 0.48 | 0.54 | | - | | | | | | | | | |
| C:N | -0.75 | | | | | -0.50 | | -0.61 | 0.51 | 0.67 | | 0.57 | - | | | | | | | | |
| SOM | -0.59 | | | | | | | -0.41 | | 1.00 | 0.82 | 0.54 | 0.67 | - | | | | | | | |
| Ca | 0.46 | | | | | 0.70 | | | -0.92 | | | -0.45 | -0.57 | | - | | | | | | |
| Mg | 0.65 | | | | | 0.69 | | 0.54 | -0.80 | | | -0.53 | -0.66 | | 0.94 | - | | | | | |
| K | 0.69 | | | | 0.41 | 0.44 | 0.48 | 0.72 | | | | | -0.48 | | 0.47 | 0.68 | - | | | | |
| Mn | 0.61 | | | | | | | 0.48 | | | | | -0.53 | | | | | - | | | |
| Fe | | | | | | -0.44 | | | 0.47 | | | 0.45 | | | -0.48 | -0.53 | -0.51 | | - | | |
| Cu | | -0.52 | | | | | | | | | | | | | | | -0.41 | | 0.49 | - | |
| Zn | | | -0.64 | | 0.78 | | 0.67 | 0.61 | | | | | | | | | | 0.46 | | | - |

Appendix 8. Pearson's correlation matrix for CWM functional traits with elevation

| | masl | CWM WD | CWM LDMC | CWM LA | CWM SLA | CWM N | CWM P | CWM N:P |
|---|---|---|---|---|---|---|---|---|
| masl | - | | | | | | | |
| CWM WD | | - | | | | | | |
| CWM LDMC | | 0.77 | - | | | | | |
| CWM LA | -0.71 | | | - | | | | |
| CWM SLA | -0.62 | | -0.45 | | - | | | |
| CWM N | | -0.79 | -0.63 | | | - | | |
| CWM P | 0.56 | -0.46 | -0.48 | -0.58 | | 0.67 | - | |
| CWM N:P | -0.89 | | | 0.76 | 0.40 | | -0.77 | - |

Appendix 9. Study area. Protected areas and types of soil are shown. A cross section of changes in elevation is included