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Hierarchical feedbacks of vegetation and soil carbon pools to climate constraints in Brazilian ecosystems

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ABSTRACT: It remains unclear whether temperature and precipitation exert independent control on tropical vegetation and soil C pools. Likewise, it is unknown whether the feedbacks of tropical C pools to climate constraints vary with nutrient availability. These aspects are critical to improving our ability to predict the response of tropical C pools to climate dynamics. This review aimed to assess climate data and the spatial distribution of vegetation and soil C pools across the Brazilian territory to investigate i) whether mean annual precipitation (MAP) and temperature (MAT) exert independent effects on tropical C pools; ii) whether vegetation and soil C pools exhibit hierarchical feedbacks to climate; and iii) how these feedbacks reflect soil nutrient availability. To account for MAP and MAT effects on tropical C cycling, we calculated Ecosystem Effective Moisture (EEM), i.e., the difference between MAP and potential evapotranspiration. We gathered substantial evidence suggesting that under high MAT and MAP controlling EEM, plants exchange more C for water and resorb more nutrients (especially P), which limitations in plant litter reduce microbial-derived C inputs into soil organic matter. Frequent soil saturation under high EEM favors denitrification rates (“open” N cycle), allowing continuous mineralization of litter and shallow soil C pools to release nutrients, sustaining high plant C pools. With decreasing MAP levels, ecosystem C pools depend on MAT controlling evapotranspiration and EEM. Accordingly, decreasing MAP under high MAT reduces EEM, with vegetation and soil C pools co-limited by low net primary productivity (NPP), frequent fire and/or nutrient losses. Otherwise, decreasing MAP and coupled to cool temperatures allow EEM to remain positive, forcing plants to increase deep-rooting and/or shed their leaves, which nutrients are immobilized with microbial-derived C into mineral-organic associations, favoring high soil C pools. Combined, the evidence gathered suggests that the sensitivity of tropical ecosystems to global increases in temperature should not be overlooked, especially if coupled to reductions in precipitation. Overall, the horizontal distribution of vegetation and soil C pools is best described by EEM rather than temperature or precipitation alone, whereas the vertical partition of C in plant-soil systems reflects biotic responses to climate-nutrient constraints.

Keywords: tropical ecosystems, terrestrial C dynamics, soil-plant-atmosphere, ecosystem C stocks, nutrient cycling.

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INTRODUCTION

Mounting evidence suggests that rising atmospheric levels of CO₂ increase the turnover rate of C in the plant-soil continuum even in the short-term (van Groenigen et al., 2017). In the long-term, rising CO₂ levels also should cause climate changes, but our ability to predict their impacts on terrestrial C pools remains limited, particularly for tropical ecosystems (Cavaleri et al., 2015). Critically, the mean residence time (MRT) of tropical C pools (vegetation and soils combined) appears to be less than 20 years (Carvalhais et al., 2014). Given that tropical C fluxes are already high, it is critical to assess the extent to which environmental changes may impact the size of vegetation and soil C pools, which combined represent approximately 846.0 Pg carbon (1 Pg C = 1.0 × 10¹⁵ g C) at global scales (Scharlemann et al., 2014). This is relevant because there are no clear spatial correlations between the MRT of tropical C pools and mean annual temperature (MAT) or precipitation (MAP) (Carvalhais et al., 2014). Furthermore, since both MAT and evapotranspiration rates increase towards the Equator (Huston and Wolverton, 2009), this aspect raises the question of the extent to which temperature and precipitation exert independent controls on tropical C pools.

Globally, vegetation and soil C pools show contrasting responses to temperature. Usually, both vegetation C pools and net primary productivity (NPP) increase with MAT at a rate varying between 5.0 and 13.0 Mg C ha⁻¹ yr⁻¹ °C⁻¹, and this relationship is mirrored by a decrease in soil C pools at a rate of 8.0 Mg C ha⁻¹ yr⁻¹ °C⁻¹ (Raich et al., 2006). Consequently, it has been suggested that the increase in NPP with MAT is dependent on the positive correlation between MAT and soil respiration at global scales (Raich and Schlesinger, 1992; Chapin et al., 2009). Despite the significance of these correlations, the processes and mechanisms underlying them remain poorly constrained. Moreover, because tropical regions are expected to undergo significant warming in the near future (Almazroui et al., 2021), the difference between MAP and evapotranspiration, i.e., ecosystem effective moisture (Kramer and Chadwick, 2018), may be significantly narrowed. Therefore, any rise in MAT should also bring consequences for the hydrological cycle.

Across the tropics, vegetation stores about 200–300 Pg C (Mitchard, 2018) and soils hold about 630 Pg C within their first 1.00 m depth (Jobbágy and Jackson, 2000). In this case, both vegetation and soil C pools show positive correlations with MAP levels up to 3000 mm (Schuur, 2003; Del Grosso et al., 2008). However, the control of moisture on soil C pools has long been considered indirect and dependent on the control of MAP levels on the vegetation (Post et al., 1982). Hence, MAP levels would primarily control NPP and vegetation C pools, which in turn, would determine C inputs into the soil and the size of its C pools. If so, vegetation and soil C pools should exhibit a strong spatial correlation. However, this view is contradicted by recent observations that high vegetation C pools are not necessarily spatially correlated with high soil C pools across the Brazilian territory (Englund et al., 2017; Gomes et al., 2019). Moreover, in a study across 147 sites in humid forests across the Amazon, no clear relationships between soil C and climate (i.e., MAT and MAP) or aboveground biomass were found (Quesada et al., 2020). Furthermore, correlations between soil C and MAP levels appear to depend on soil depth (Jobbágy and Jackson, 2000). These authors argue that the relative proportion of deep and shallow soil C pools is more dependent on plant C allocation than on climate itself. Overall, determining the extent to which vegetation and soil C pools respond independently to temperature, precipitation or ecosystem effective moisture is essential to predict the response of tropical C pools to environment changes, including rises in temperature and/or decreases in precipitation.

High temperatures and precipitation levels boost weathering rates and the development of deep soil profiles across the tropics (Huston and Wolverton, 2009). Additionally, tropical soils are highly leached, with low availability of base cations and high capacity for P fixation (Townsend et al., 2007; Vitousek et al., 2010). Consequently, restricted nutrient

availability may limit the responses of NPP to the “fertilization effect” of increasing levels of atmospheric CO₂ (Wieder et al., 2015). Seemingly, the least limiting element required for plant growth in tropical ecosystems is N, which availability may be even in excess relative to other elements (Martinelli et al., 1999; Hedin et al., 2009; Brookshire et al., 2012). The relative excess of N may be an important source of greenhouse gases such as nitrous oxide (N₂O), which emissions appear to increase with decreasing P availability in humid ecosystems (Hall and Matson, 1999). However, it remains unknown whether nutrient availability can impact the response of vegetation and soil C pools to climate constraints (Carvalhais et al., 2014). Moreover, the extent to which the differential availability of P and N across the tropics exerts independent or joint controls on terrestrial C pools remains unclear.

Overall, the Brazilian territory provides a unique study area to analyze the feedbacks of tropical C pools to climate constraints. As such, Brazilian ecosystems are very diversified, including dry forests, semideciduous and humid forests, grasslands and mixed vegetation types (Arruda et al., 2018). These ecosystems occur in an area spanning a latitude gradient between 5° N and 35° S and a longitude range between 35 and 75° W, where MAT varies between 10 and 26 °C and MAP levels can be less than 700 up to more than 3100 mm yr⁻¹ (Alvares et al., 2013). Therefore, our overarching goal in this review is to rationalize the drivers of the horizontal distribution of vegetation and soil C pools as well as the vertical partitioning of C in the plant-soil continuum across the major Brazilian biomes.

MATERIALS AND METHODS

In this review, we searched the literature to investigate i) whether temperature and precipitation exert independent effects on C pools in Brazilian biomes; ii) the extent to which vegetation and soil C pools exhibit hierarchical feedbacks to climate, and iii) how these feedbacks are related to nutrient availability, especially P and N. To address the first question, we obtained data for MAP and MAT from the WorldClim Project, encompassing a temporal range from 1970 to 2000 (Fick and Hijmans, 2017). For evapotranspiration, the data obtained was based on the calibration of the MOD16 product for the period between 2000 and 2014 (Dias et al., 2021). Subsequently, we calculated the ecosystem effective moisture (EEM), that is, the difference between MAP and potential evapotranspiration (Kramer and Chadwick, 2018). According to these authors, the major weakness of this method is that the redistribution of water across the landscapes cannot be accurately accounted for in the calculation. Nonetheless, EEM should allow us to evaluate the interaction between precipitation and temperature in determining moisture availability considering the large area of the Brazilian territory. To address the second question, we combined the spatial distribution of vegetation (Englund et al., 2017) and soil C pools (Gomes et al., 2019) across the Brazilian territory with 1 km spatial resolution. Our maps and figures were plotted using the R software. Aboveground vegetation C pools included an up-to-date land use/cover determined in 2016 with a spatial resolution of 50 m as part of the communication to the United Nations Framework Convention on Climate Change (UNFCCC) (Englund et al., 2017). Soil C pools were based on a data set that included 8,227 soil profiles and the analysis of 37,693 samples. This soil survey and sampling was conducted by the RADAM Project in the period between 1973 and 1986 (Gomes et al., 2019). For this reason, we could not restrict our discussion to natural ecosystems and patterns associated to land-use change had to be considered to some extent. Although the data for vegetation and soil C pools were not obtained in the same timeframe, it is expected that latter is much less sensitive to land-use change than the former (Boy et al., 2018). Based on the data obtained for MAT, MAP, EEM, vegetation and soil C pools, we obtained Pearson’s correlation coefficients among these variables for each biome (Amazon, Caatinga, Cerrado, Atlantic Forest, Pampa, and Pantanal) as shown in table 1.

We addressed the third question by searching the literature for studies evaluating i) nutrient resorption preceding leaf senescence, ii) nutrient mineralization in plant litter and soil organic matter, and iii) plant responses to seasonal variations in moisture availability. This step allowed us to infer a relationship between nutrient dynamics as constrained by climate, the horizontal distribution and vertical partition of C in plant-soil systems. A synthesis of the information gathered in those studies is given in table 2 and was used to support a conceptual framework to link climate constraints

Table 1. Pearson's correlation coefficients (r) for the spatial distribution of mean annual precipitation (MAP), temperature (MAT), ecosystem effective moisture (EEM), plant and soil C pools across the six Brazilian biomes and the whole country

Biome	Variables	MAT	EEM	Plant C pools	Soil C pools	Ecosystem C pools
Amazon	MAP	0.20	0.99	0.40	0.50	0.50
	MAT		0.20	0.10	-0.10	0.10
	EEM			0.40	0.50	0.50
	Plant C pools				0.20	0.99
	Soil C pools					0.50
Atlantic Forest	MAP	-0.50	0.90	0.20	0.50	0.40
	MAT		-0.70	-0.20	-0.80	-0.60
	EEM			0.20	0.70	0.60
	Plant C pools				0.20	0.80
	Soil C pools					0.70
Caatinga	MAP	0.30	0.80	0.20	0.30	0.30
	MAT		0.00	-0.10	-0.60	-0.50
	EEM			0.20	0.50	0.50
	Plant C pools				0.30	0.70
	Soil C pools					0.80
Cerrado	MAP	0.20	0.90	0.00	0.10	0.10
	MAT		-0.10	0.20	-0.60	-0.20
	EEM			-0.10	0.20	0.10
	Plant C pools				-0.20	0.70
	Soil C pools					0.60
Pampa	MAP	0.50	0.80	0.00	-0.10	-0.10
	MAT		0.30	-0.10	-0.20	-0.30
	EEM			0.00	-0.20	-0.20
	Plant C pools				0.10	0.70
	Soil C pools					0.80
Pantanal	MAP	-0.20	0.90	-0.30	-0.10	-0.30
	MAT		0.00	0.20	-0.30	0.00
	EEM			-0.20	0.00	-0.10
	Plant C pools				0.20	0.90
	Soil C pools					0.60
Brazil	MAP	0.40	0.99	0.70	0.30	0.80
	MAT		0.20	0.40	-0.50	0.20
	EEM			0.70	0.40	0.80
	Plant C pools				0.10	0.90
	Soil C pools					0.40

The spatial correlation between the selected variables is based on the data shown in figures 1, 2 and 3 in the main text (annual basis).

Table 2. Major climate constraints (temperature and precipitation) on ecosystem effective moisture (EEM) and their impacts on ecosystem C pools (vegetation and soils) across the major Brazilian biomes and supporting evidence from the literature consulted

Precipitation and temperature constraints on ecosystem effective moisture	Impact on ecosystem C pools	Occurrence	Supporting evidence from the literature
High moisture availability due to the control of precipitation on EEM, regardless of temperature	Carbon pools can be much higher in vegetation than in soils, which C sink strength is reduced; Transport of C by water percolating through the soil profile could contribute significantly for mineral-organic associations in subsoil horizons; Ecosystem C pools are determined by the vegetation.	Predominantly humid forests across the Amazon domain	Plants invest C in organs with long time span (Herrera et al., 1978; Aerts, 1995; Wardle et al., 2004; Körner, 2017); High resorption rates of nutrients in senescing leaves, especially P (Vitousek and Sanford, 1986; Cleveland and Liptzin, 2007; Vergütz et al., 2012); Wide C-to-nutrient ratios reduce microbial C use efficiency during litter decay in the soil (Cleveland et al., 2002; Manzoni et al., 2010; Schneider et al., 2012; Zechmeister-Boltenstern et al., 2015; Camenzind et al., 2018); Microbial succession during the decay of plant litter alleviates nutrient stoichiometric constraints, but respiration rates increase (Kaiser et al., 2014; Maynard et al., 2017); Carbon use efficiency by soil microbes is low under high temperatures (Manzoni et al., 2012; Frey et al., 2013; Qiao et al., 2019); High denitrification rates (“open” N cycle) are linked to wide N:P ratios (Martinelli et al., 1999; Breuer et al., 2002; Davidson et al., 2007); In permanent or temporarily water-saturated soils, nitrate can be used as an alternative electron acceptor to oxygen, keeping soil C mineralization at high rates (Bollmann and Conrad, 1998; Houlton et al., 2006; Butterbach-Bahl et al., 2013; Keiluweit et al., 2016); Shallow root mats optimize nutrient recycling at or close to the soil surface (Stark and Jordan, 1978; Jordan and Escalante, 1980; Kingsbury and Kellman, 1997).
Moderate to high restrictions in moisture availability with high temperatures controlling EEM owing to seasonal and/or low precipitation levels	Carbon inputs to soils may be limited by low primary productivity; Vegetation C sink strength is weakened, and plants contribute little for total ecosystem C pools.	Dry forests (Caatinga), grasslands (Pampa), Brazilian savanna (Cerrado), mixed vegetation in the Pantanal and deciduous forests of the Atlantic Forest and Cerrado domains	Soil C pools may be limited by shallow soil profiles (Corrêa et al., 2019); Vegetation C pools may be limited by seasonal precipitation and/or low primary productivity (Bond and Keeley, 2005; Dexter et al., 2018); Part of the biomass produced during the humid season may dry out once precipitation declines under high temperatures (Coutinho, 1990; Sarmiento, 1992; Moritz et al., 2005); Dried biomass may be burnt upon ignition events depending on the amount of combustible available (Bond and Keeley, 2005); Fire events trigger biomass mineralization and can favor nutrient volatilization and/or transport of particles by wind, particularly N and S, but not only these elements (Pivello and Coutinho, 1992; Pivello et al., 2010); Frequent burning of aboveground biomass, increases the relative importance of belowground C inputs to soils (Hoffmann and Franco, 2003); Nutrients can be stored in roots or other belowground organs with long timespan (Hoffmann and Franco, 2003; Appezzato-da-Glória et al., 2008; Simon and Pennington, 2012); High nutrient resorption favors graminoids under frequent fire (Aerts, 1996).

Continue

Continuation

Moderate restrictions in moisture availability with reducing precipitation levels coincident with decreasing temperatures limiting evapotranspiration

Soil C sink strength is greater than that of the vegetation;
 Deep rooting should contribute more for mineral-organic associations than transport by percolating water to form subsoil C pools;
 Vegetation may account for a significant fraction of the whole ecosystem C pool.

Predominantly across the semideciduous and mixed forests of the Atlantic Forest domain

Plants that keep their leaves during the dry season should increase C allocation into roots (Markesteijn et al., 2010);
 Leaf-shedding plants represent between 25 and 50 % of the vegetation (Arruda et al., 2018);
 Leaf-shedding may be followed by root senescence (Kummerow et al., 1990; Eissenstat and Yanai, 1997; Campo et al., 1998; Brunner et al., 2015);
 Plants that keep their leaves under reduced moisture availability may invest C in deep rooting (Markesteijn and Poorter, 2009; Brunner et al., 2015);
 Aboveground C inputs are added to the soil surface when the potential for fast mineralization rates is low (Sayer et al., 2006);
 Reduced evapotranspiration under cool temperatures during the dry season limits the risk of fire (Duff et al., 2018);
 Soil C pools are favored by deep rooting (Jobbágy and Jackson, 2000; Markesteijn et al., 2010; Brunner et al., 2015);
 Positive annual EEM favors the formation of mineral-organic associations (Kleber et al., 2015; Doetterl et al., 2015; Kramer and Chadwick, 2018);
 Soil microbes act as a nutrient sink during the cool-dry season (Singh et al., 1989; Campo et al., 1998; Manzoni et al., 2010; Cotrufo et al., 2013).

EEM is the ecosystem moisture, that is, the difference between MAP and potential evapotranspiration (Kramer and Chadwick, 2018).

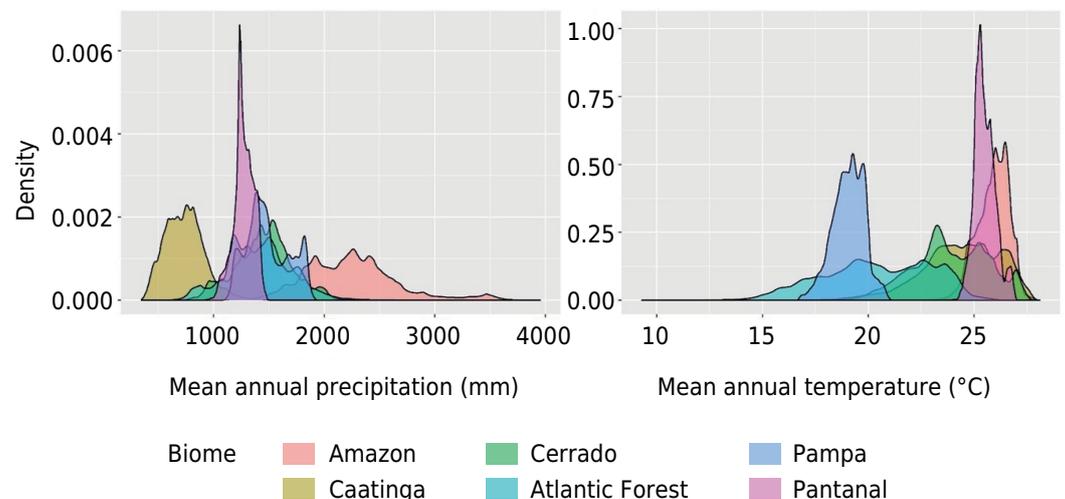


Figure 1. Distribution of frequency for mean annual precipitation (MAP) and mean annual temperature (MAT) across the six major Brazilian biomes, namely Amazon, Caatinga, Cerrado, Atlantic Forest, Pampa and Pantanal.

and terrestrial C pools in Brazil. Not all studies included in this analysis were conducted in Brazilian biomes, but we tried to be as specific as possible.

RESULTS AND DISCUSSION

Temperature and precipitation across the Brazilian territory

Across the Amazon, most of its ecosystems occur in areas where MAT is above 22 °C and MAP levels are predominantly higher than 1800 mm (Figure 1). According to the Köppen classification system, the most common climate classes in these areas are Af

and Am (Alvares et al., 2013). In sharp contrast with the Amazon, the Caatinga domain is marked by high MAT (above 22–24 °C) overlapping with very low MAP levels, usually varying between 700 and 1000 mm yr⁻¹ (Figure 1). In this biome, As and Bs climates predominate (Alvares et al., 2013). Hence, the Amazon and the Caatinga represent the sharpest contrast in MAP levels in Brazil.

Across the Cerrado, MAT is consistently higher than 22 °C, while MAP levels vary between 1000 and 1900 mm yr⁻¹. This upper limit in MAP levels marks the northwest border between the Cerrado and the Amazon domain (Figure 1). Although precipitation levels are relatively high in the Cerrado, rainfall has a strong seasonality, with humid and dry seasons lasting approximately six months each. In the northeast, deciduous forests mark the border between the Cerrado and the Caatinga (Arruda et al., 2018). At the southwest border of the Cerrado occurs the Pantanal biome, which is marked by high MAT (mostly 24–27 °C) and MAP levels varying between 1000–1500 mm yr⁻¹ (Figure 1). Typically, the predominant climate class in the Cerrado are Aw and Am, whereas, both Aw and Af can occur across the Pantanal (Alvares et al., 2013).

Generally, the Atlantic Forest shows the widest MAT range (15–25 °C) relative to the other Brazilian biomes (Figure 2). In this biome, deciduous, semideciduous, and mixed forests predominate (Arruda et al., 2018). In the SE-NE transect across the Atlantic Forest domain, deciduous forests determine a border with the Caatinga, coinciding with reduced EEM levels (Figure 2). Similar levels of EEM also occur at the southwest border between the Atlantic Forest and the Cerrado, but semideciduous forests predominate (Arruda et al., 2018). At latitudes higher than 20° S, both the Atlantic Forest and the Pampa occur in areas where MAT is consistently below 25 °C, with MAP varying between 1000 and 1900 mm yr⁻¹ (Figure 1). Across the Atlantic Forest domain, MAT showed a relatively strong negative correlation with both MAP and EEM levels (Table 1). Mixed forests mark the southern border between the Atlantic Forest and the Pampa (Arruda et al., 2018). In contrast to the Atlantic Forest, the Pampa

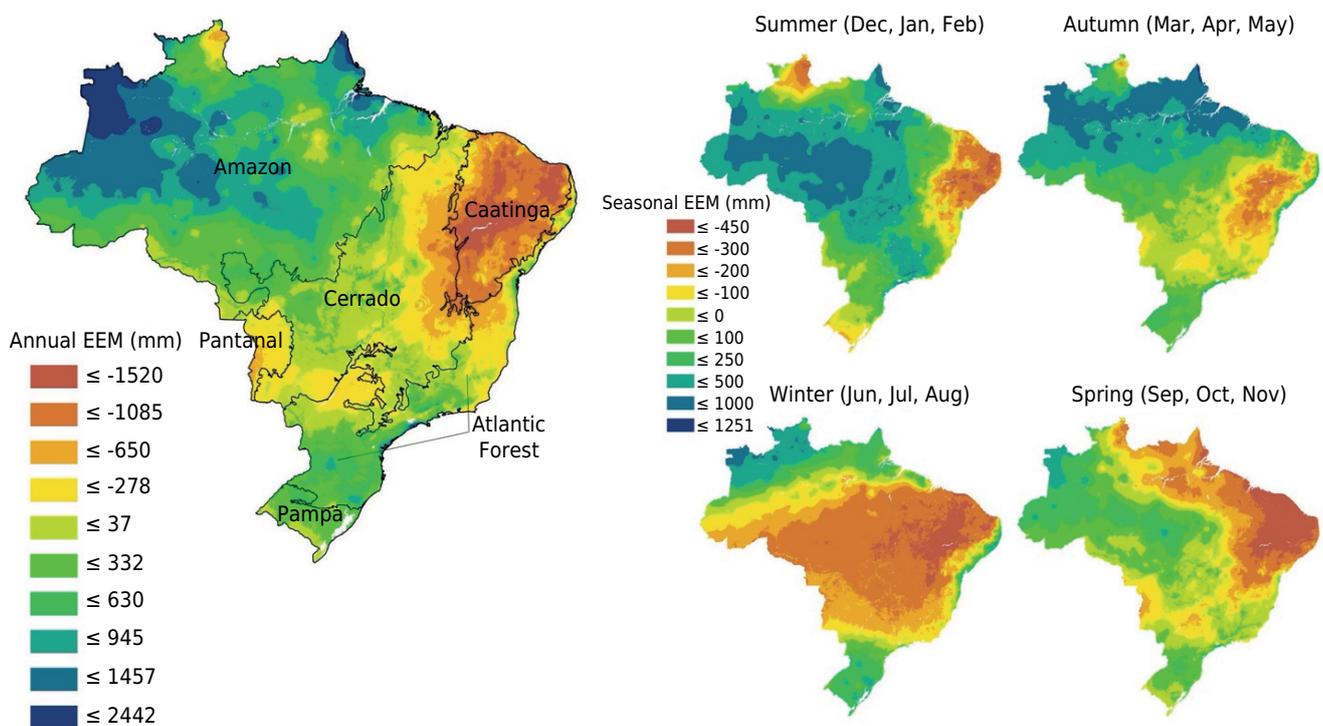


Figure 2. Spatial distribution of annual and seasonal ecosystem effective moisture (EEM), i.e., the difference between mean annual precipitation and potential evapotranspiration (Kramer and Chadwick, 2018) across the Brazilian territory. Summer: December–February; Autumn: March–May; Winter: June–August; and Spring: September–November.

domain is marked by a narrow temperature range (17–20 °C), as shown in figure 1. For the Atlantic Forest, the predominant climate classes are Cwa, Cwb, Cfa and Cfb, whereas Cfa predominates across the Pampa (Alvares et al., 2013). Overall, there is a substantial overlap in MAP levels for the Cerrado, Pantanal, Atlantic Forest, and the Pampa in the range between 1000 and 1800 mm yr⁻¹ (Figure 1).

Ecosystem effective moisture: the interaction between temperature and precipitation

For most of the area under the Amazon domain, the relatively well distributed annual volume of precipitation is translated into EEM levels predominantly positive (>630 mm yr⁻¹) (Figure 2). Although high temperatures favor high evapotranspiration rates, EEM showed the strongest spatial correlation with MAP ($r = 0.99$) across the Amazon (Table 1). Otherwise, high temperatures and low precipitation rates combined led to EEM levels varying between -650 and -1250 mm yr⁻¹ across the Caatinga (Figure 2).

Across the Cerrado, EEM levels can vary between negative (-280 mm yr⁻¹) and positive values (+330 mm yr⁻¹) as shown figure 2. The overall variability in EEM levels for the Cerrado is consistent with its geographic distribution in central Brazil, bordering with the Amazon in northwest, the Caatinga in northeast, the Atlantic Forest in southeast, and the Pantanal to the west (Figure 2). Across the Pantanal domain, EEM levels are predominantly negative (0 to -1000 mm yr⁻¹), which is likely an underestimation because many ecosystems occurring in this biome are wetlands located in depressional areas. Hence, the redistribution of water within landscapes cannot be well represented in the EEM estimates (Kramer and Chadwick, 2018).

Atlantic Forest and the Pampa show similar EEM levels at latitudes higher than approximately 20° S, as shown in figure 2. Given the overall wide range in temperature observed for the Atlantic Forest (Figure 1) and its reduced precipitation levels during the winter, EEM levels in this area can vary between -1000 up to 500 mm yr⁻¹ (Figure 2). Geographically, the negative levels of EEM occur predominantly across a SW-NE transect bordering with the Cerrado and the Caatinga in the northeast (Figure 2). The exception in this case is a narrow strip of land located along the coast of the Atlantic Ocean. Across the Pampa, where precipitation levels are usually reduced during the summer, annual EEM is predominantly positive (0 to 500 mm yr⁻¹). Several lines of evidence indicate that the predominant native vegetation of the Pampa, that is, Campos das Missões or Campos de Barba-de-Bode (*Aristida jubata*), reflects past climates conditions that were dryer than the current climate (Behling et al., 2009; Verdum et al., 2019).

As expected, EEM showed stronger spatial correlation with MAP than with MAT in all biomes considered (Table 1). Overall, the Atlantic Forest domain stands out as the biome where MAT and EEM showed the strongest negative correlation ($r = -0.70$) (Table 1).

Under high MAT-EEM constraints, nutrient dynamics determine the relative C sink strength of vegetation and soil

Because many elements can limit NPP in tropical regions (Townsend et al., 2011), plants growing in humid ecosystems appear to invest proportionally more C in organs with long timespan to increase their nutrient use efficiency (Herrera et al., 1978; Aerts, 1995; Wardle et al., 2004; Körner, 2017). Further, high resorption rates of nutrients often precede leaf senescence (Vergütz et al., 2012), whereas some nutrients are recycled during the breakdown of plant litter in the soils. These traits can have at least three major consequences for terrestrial C dynamics in humid ecosystems under high MAT coupled to high MAP controlling EEM levels.

Firstly, owing to the high resorption of nutrients, especially P (Vitousek and Sanford, 1986), tropical plants growing in humid ecosystems produce litter showing wide C:P

and/or N:P ratios (Cleveland and Liptzin, 2007). These wide elemental relations have a negative impact on the C use efficiency of soil decomposers (Cleveland et al., 2002; Camenzind et al., 2018). Generally, it is well known that microbes growing on substrates with wide C-to-nutrients ratios exhibit low C use efficiency due to stoichiometric constraints (Manzoni et al., 2010; Zechmeister-Boltenstern et al., 2015). This means that a given microbial community attempts to narrow C-to-nutrients ratios by eliminating the relative “excess” of C in the substrate. Alternatively, stoichiometric constraints can be minimized by means of succession among distinct microbial communities in soil food webs (Kaiser et al., 2014; Maynard et al., 2017). In this case, different microbial communities drive substrate breakdown as the C-to-nutrients ratio narrows down. Hence, whether a single microbial community attempts to narrow C-to-nutrients ratios via increased respiration or engage in microbial succession, proportionally more C should be lost as CO₂. Moreover, soil microbes should use C less efficiently under high temperatures (Manzoni et al., 2012; Frey et al., 2013; Qiao et al., 2019). Therefore, under these environmental and biological constraints, the contribution of microbial-derived products to form soil C pools should be significantly reduced (Cotrufo et al., 2013).

The second aspect concerning nutrient cycling is that a relative excess of N in humid ecosystems may help to keep fast mineralization rates of plant litter. The most recurrent evidence supporting this inference is that humid tropical ecosystems are marked by significant losses of gaseous N, especially via denitrification (Martinelli et al., 1999; Breuer et al., 2002; Davidson et al., 2007). These losses characterize an “open N cycle” in many tropical humid forests (Martinelli et al., 1999). We interpret such “openness” in the N cycle as a mechanism to keep high rates of litter mineralization in ecosystems where soil water content is frequently above field capacity or high enough to saturate the soil pore space (Bollmann and Conrad, 1998). In such circumstances, nitrate can be used as an alternative electron acceptor when the levels of oxygen drop significantly and aerobic respiration cannot proceed normally, especially within soil aggregates (Houlton et al., 2006; Butterbach-Bahl et al., 2013; Keiluweit et al., 2016). This reasoning is also consistent with increases in denitrification rates with decreasing P availability (Hall and Matson, 1999). Thus, denitrification would allow high mineralization rates of plant litter, soil organic matter to favor fast P cycling that sustain high vegetation C pools in ecosystems under high EEM (Figure 3).

A third important aspect is that many plants in humid ecosystems have shallow root mats to optimize nutrient recycling from decaying plant litter (Stark and Jordan, 1978; Jordan and Escalante, 1980; Kingsbury and Kellman, 1997). Critically, shallow root mats

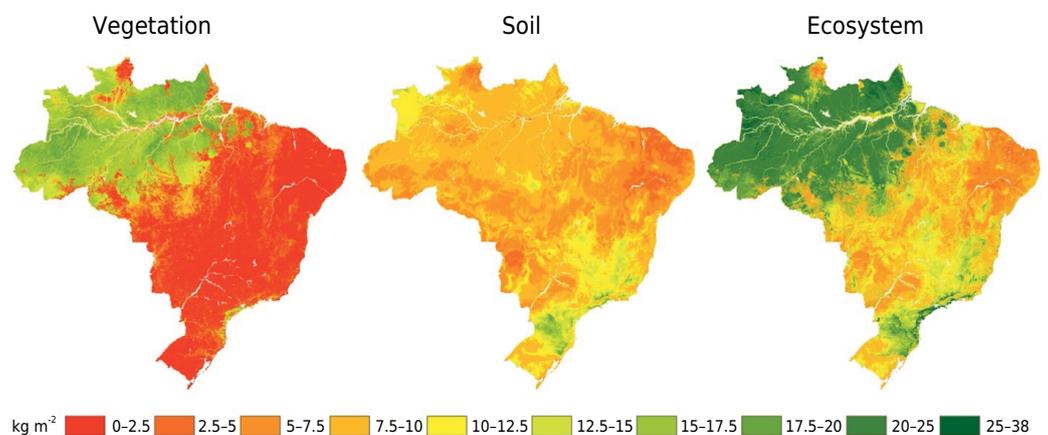


Figure 3. Spatial distribution of vegetation and soil C pools, and their sum to yield the ecosystem C pool in Brazil. The spatial distribution of vegetation C pools has been published by Englund et al. (2017). Soil C pools included observations from more than 8,200 soil profiles as described elsewhere by Gomes et al. (2019).

are not restricted to low fertility soils across the tropics (Sayer et al., 2006), suggesting that high MAP-EEM is essential for this trait to be effective (Figure 2). As the plant material decomposes on the soil surface, a shallow and thick root mat also would help to reduce P fixation in the oxidic soils underneath tropical forests (Herrera et al., 1978). However, because the roots are concentrated on the soil surface, their contact with soil minerals is reduced, and so should be their contribution to soil C pools (Lavallee et al., 2018). Hence, with increasing MAP and EEM levels, proportionally more soil C is stored within the first 0.30 m of topsoil (Moraes et al., 1995; Jobbágy and Jackson, 2000). This also may help to explain why the correlations between soil C pools and MAP tend to decrease with soil depth (Jobbágy and Jackson, 2000). Otherwise, the retention of soil C in mineral-organic associations at depths below 0.30 m should depend proportionally more on water transport than on deep rooting (Kalbitz et al., 2000; Schwendenmann and Veldkamp, 2005; Kramer and Chadwick, 2018). All these factors contribute to weaken the soil C sink strength in humid ecosystems, while favoring the vegetation C pool (Figure 3). As such, across the Amazon domain, soil C pools vary in the range between 7.5 to 10 kg m⁻², whereas vegetation C pools can be as high 27 kg m⁻² (Figure 3). Our study highlights that vegetation C pools showed the strongest spatial correlation with both MAP and EEM across the Amazon domain compared to the other Brazilian biomes (Table 1).

Our analysis indicates a potential mechanistic connection to explain the correlation between soil respiration and NPP in moist tropical ecosystems (Raich and Potter, 1995; Chapin et al., 2009). Further, the dependence of a strong vegetation C pool on a weakened soil C sink strength under high EEM contributes to explain the lack of correlations between the MRT of tropical C pools and MAT or MAP as isolate variables (Carvalhais et al., 2014). It is important to point out that these correlations may be low because vegetation and soil C combined may overestimate the MRT of the latter pool, and this aspect warrants further research. Hence, it seems reasonable that only in areas where high temperatures cannot override the control of precipitation on EEM, high throughput rates of C and water maximize both vegetation and ecosystem C pools (Figure 4; Table 1). However, this feature comes at 'a price' of a weak soil C sink. Thus, vegetation and soil C pools in humid ecosystems show opposite, but essentially hierarchical responses to climate. Therefore, the overall high turnover rates of litter and soil organic matter are ultimately the driver of high ecosystem C pools dominated by the vegetation.

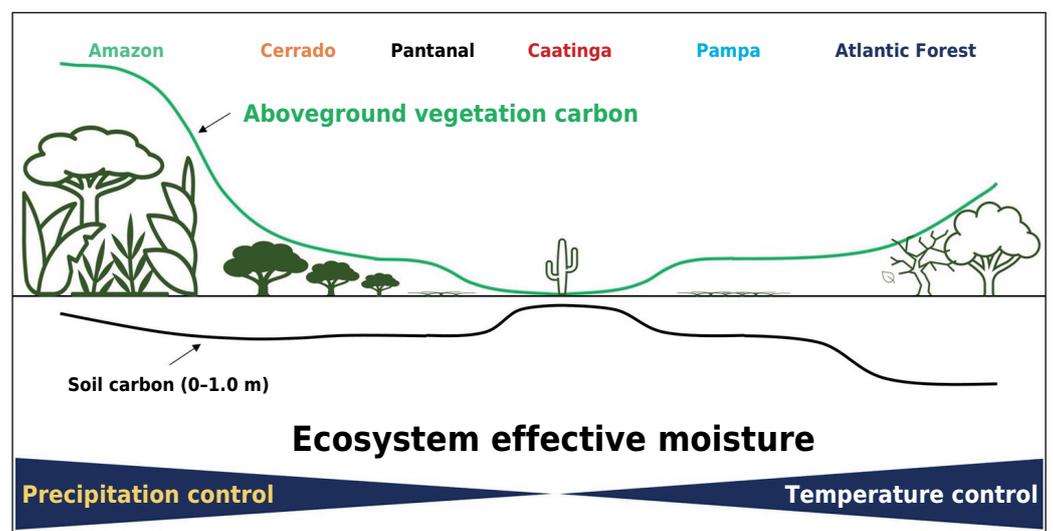


Figure 4. Conceptual model to describe the control of temperature and precipitation on ecosystem effective moisture (EEM), which in turn determines the partition of C and vegetation and soils across the six major Brazilian biomes: Amazon, Cerrado, Pantanal, Caatinga, Pampa and Atlantic Forest.

Temperature as a key factor for EEM with increasing seasonality of precipitation

Across the Brazilian territory, temperature appears to exert an increasing control on EEM as the seasonality of precipitation increases. However, the strongest negative correlation between MAT and EEM was observed for the Atlantic Forest (Table 1), probably owing to its wider temperature range as compared to the other biomes (Figure 1). Nonetheless, two major subregions can be identified: one region includes areas where temperatures remain elevated as precipitation rates decrease, and another region where both temperatures and precipitation decrease approximately simultaneously.

Decreasing precipitation under constantly high temperatures

In areas under persistently high temperatures and seasonal precipitation, the reduction in EEM is critical for C cycling in large areas of the Cerrado and the Caatinga (Figure 2). In some areas of the Caatinga, water limitation is so severe that it can even restrict weathering and pedogenesis, and consequently, soil C pools can be constrained by shallow soil profiles (Corrêa et al., 2019). Hence, because MAP levels limit the leaching of soil nutrients, their availability to plants in ecosystems across the Caatinga can be sufficient during the short humid season (Figure 2). Owing to the overall low MAP, high MAT and the resulting low EEM observed across the Caatinga domain, NPP is so low that it may limit C inputs into the soils (Dexter et al., 2018). Thus, both vegetation and soil C pools are low (Figure 3) and they show unidirectional responses to climate.

For ecosystems occurring across the Cerrado domain, periods of high precipitation and EEM levels are intercalated by equally long dry seasons (Figure 2). Therefore, high temperatures can favor C fixation during the humid season, despite the widespread occurrence of low fertility soils (Coutinho, 1990; Sarmiento, 1992). Subsequently, decreases in precipitation coupled to persistently high temperatures cause EEM levels to drop significantly and part of the living vegetation may dry out (Moritz et al., 2005). Dried plant material becomes flammable and can fuel wildfires (Bond and Keeley, 2005), leading to significant loss of nutrients by volatilization, particularly N and S (Pivello and Coutinho, 1992). Other elements such as K, Ca, and Mg are usually concentrated in the ashes on the soil surface (Coutinho, 1990), and these elements can be transported by wind during the dry season or by runoff in the subsequent humid season. In long-term, the impact of fire on soil fertility could be a deterrent to the size of vegetation C pools in such ecosystems (Figure 3). According to a survey across 70 sites in the Cerrado, total biomass production varied from 24 Mg ha⁻¹ in grasslands up to 98 Mg ha⁻¹ in forestlands (Miranda et al., 2014). These values would represent only a small fraction of the plant biomass observed across the Amazon under similar temperatures (Figure 3). Seemingly, Cerrado trees allocate a significant amount of C in organs such as thick barks to withstand fire (Simon and Pennington, 2012), but these adaptations ultimately may contribute to reduce their overall NPP.

Although fire events can quickly convert more than 80 % of the plant litter into CO₂ (Kauffman et al., 1994), pyrogenic carbonaceous materials can be added to the soil C pool. However, there is limited information about their contribution to soil C pools in the Brazilian Cerrado (Justi et al., 2017). Thus, in ecosystems submitted to frequent fire, the dependence of soil C on belowground C inputs increases substantially (Hoffmann and Franco, 2003), although some plants of the Cerrado allocate C belowground aiming to store water and nutrients in specialized organs (Apezzato-da-Glória et al., 2008; Simon and Pennington, 2012). In part of the Brazilian Cerrado and the Pampa, graminoids are favored by fire partially because they have a high capacity to resorb leaf nutrients and store them in their rhizomes (Aerts, 1996). Generally, the total belowground biomass in Cerrado grasslands is about 16.3 Mg ha⁻¹ and can be as high as 52.9 Mg ha⁻¹ in Cerrado forests (Castro and Kauffman, 1998). Soil C pools under the Cerrado and the Amazon are quite similar, despite the huge difference in biomass production between them (Figure 3). Hence, vegetation C pools are not a good indicator of the size of soil C pools in the tropics.

Overall, it can be inferred that i) vegetation C is much more sensitive to fire than soil C pools, ii) high NPP cannot be seen as an indicator of the size of soil C pools in tropical ecosystems, and iii) fire suppression may benefit soil C pools, but it comes at a cost of reduced plant biodiversity (Abreu et al., 2017). Similarly, liming and fertilization to sustain intensive agriculture with multiple crops grown in succession under no-tillage (Pavinato et al., 2020) also should favor increasing soil C pools, particularly across the Cerrado. Based on the evidence gathered, in ecosystems where precipitation levels are low or suffer strong seasonality, high temperatures can override the control of MAP on EEM levels (Figure 2). In line with these constraints, the C sink strength of Cerrado plants and remnants of the Pampa vegetation may be weakened by fire, whereas low NPP might play a bigger role across the Caatinga. In such biomes, vegetation C pools should not increase with temperature primarily because MAP levels are not high enough to control EEM.

Coupled decreases in temperature and precipitation levels

Across the SE-S transect of the Atlantic Forest domain, the reduction in precipitation is coincident with decreasing temperatures, allowing annual EEM to remain positive in this area (Figure 2; Table 1). In these ecosystems, the relative C sink strength of vegetation and soils also can be framed by considering i) plant C allocation (e.g., above and belowground), ii) nutrients dynamics, and iii) the formation of mineral-organic associations.

In terms of plant C allocation, as both temperature and precipitation rates decrease, the reduced levels of soil water should force part of the plants growing under these constraints to shed their leaves to reduce transpiration (Markesteyn et al., 2010). This is a typical response of the semideciduous vegetation that occurs within the Atlantic Forest domain in Brazil (Morellato et al., 2000). Quantitatively, between 25 and 50 % of the plants growing in semideciduous forests of the Atlantic Forest domain lose their leaves during the winter/dry season (Arruda et al., 2018). Possibly, these plants also shed part of their roots as the soil moisture level decreases (Kummerow et al., 1990; Eissenstat and Yanai, 1997; Campo et al., 1998; Brunner et al., 2015), but little is known about this aspect in most tropical ecosystems. This is certainly another subject that warrants further research. Given that 25 to 50 % of the plants in semideciduous forests lose their leaves during the cold-dry season, it is reasonable that 75 to 50 % of the vegetation can keep their leaves (Arruda et al., 2018). Since EEM should decrease with decreasing precipitation (Table 1), plants keeping their leaves must increase root growth to extract water from a larger volume of soil (Markesteyn and Poorter, 2009; Brunner et al., 2015).

We posit that either plants shedding their leaves/roots or increasing root growth can contribute to explain the spatial distribution of soil C pools across the Atlantic Forest domain (Figure 3). In the areas where plants shed their leaves, decreasing temperatures and precipitation combined may limit the mineralization rates of the plant litter added to the soil surface (Sayer et al., 2006). Owing to the negative correlation between MAT and EEM (Figure 2; Table 1), these C inputs added to the soil surface should be less prone to fire (Duff et al., 2018). Belowground, root-derived C inputs are added at greater soil depth and/or over a larger volume of soil (Markesteyn et al., 2010; Brunner et al., 2015). In contrast to the Amazon, where water fluxes through the soil profile can transport C towards the subsoil, plant C allocation into roots should be much more important for soil C pools across the domain of semideciduous vegetation of the Atlantic Forest. This inference also helps to explain why the correlation between soil C pools and clay content increases with depth (Jobbágy and Jackson, 2000). Although we have not considered clay content in our analysis, this factor should be considered in future studies. Apparently, in both ecosystems (Amazon and Atlantic Forest), plant feedbacks to climate exert a strong control on soil C pools, which responses are overwhelmingly opposite. As such, high MAP levels determine high EEM, which in turn

favors vegetation C pools in the Amazon, whereas low winter temperature is critical for the occurrence of areas under positive EEM levels across the Atlantic Forest domain, where soil C pools are favored (Figures 2 and 3). Consequently, whether precipitation or temperature exerts primary control on EEM has major effects on C pools' size and its vertical partition in plant and soils. For instance, aboveground C pools can vary between 110–150 Mg ha⁻¹ in humid ecosystems of the Atlantic Forest (Vieira et al., 2011). Thus, the overall NPP and vegetation C pools in these areas are much lower than those observed across the Amazon domain (Figure 3). The opposite is true for soil C, which pool corrected per unit area (Gomes et al., 2019), is much lower across the Amazon than in the Atlantic Forest, at least in areas where EEM is positive. Another important aspect is that the Pampa shows EEM levels similar to those occurring across a SE-S transect of the Atlantic Forest (Figure 2). However, soil C pools in the Pampa are very similar to those observed for the Cerrado. One possibility is that this pattern is caused by the summer dry season across the Pampa, where the highest EEM levels occur in the winter (Figure 2).

We also infer that not only plant feedbacks to climate ultimately control the vertical partition of C in plants and soils, but also the persistence of soil C pools should depend on positive EEM. This is particularly relevant for mineral-organic associations, which are among the major drivers of the persistence of soil C pools (Doetterl et al., 2015; Kleber et al., 2015; Kramer and Chadwick, 2018). Accordingly, mineral-organic associations primarily depend on i) moisture availability, ii) the presence of living plants; iii) active soil microbial biomass, iv) reactive minerals, and v) the acidification generated by the biotic factors involved (Kleber et al., 2015). In areas under Köppen C climates such as the Atlantic Forest, plants tend to produce leaf litter enriched in P, K, Ca, and Mg relative to plants growing under warm and humid climates (e.g., Köppen A) (Vergütz et al., 2012). Consequently, microbial C use efficiency should be favored by nutrient availability and cool Köppen C climates, with more microbial-derived products added into the soil C pool to form soil organic matter (Singh et al., 1989; Campo et al., 1998; Manzoni et al., 2010; Cotrufo et al., 2013). Otherwise, plants growing under Köppen C climates should resorb more C (+4.3 %) and N (+7.9 %) relative to plants growing under Köppen A climates (Vergütz et al., 2012). Although this pattern may be an indicator of the remobilization of C and N from senescing leaves to increase root growth during the cold/dry season, more research is needed on this topic.

Overall, leaf senescence and/or increased root growth may represent important pathways that regulate C inputs to soils in ecosystems dominated by semideciduous forests across the Atlantic Forest where the average annual EEM is positive. Thus, the transport of C by the percolating water should be much less relevant for soil C pools in these areas as compared to humid ecosystems occurring across the Amazon. Nonetheless, the persistence of soil C pools will ultimately depend on the mechanisms regulating C processing, such as microbial C use efficiency and its protection in mineral-organic associations.

Determinants of the ecosystem C pool: vegetation and soil as a function of climate constraints

Based on the evidence presented above and synthesized in table 2, we propose a tentative conceptual model to describe the horizontal and vertical partition of C in plant-soil systems across the major Brazilian biomes (Figure 4). Accordingly, as the precipitation level overrides the control of temperature on evapotranspiration and determines EEM levels, vegetation C pools are favored at the expense of a weak soil C sink. Such dynamics should be primarily relevant for the Amazon domain (Figure 4), which covers approximately 50 % of the Brazilian territory. Otherwise, with increasing seasonality of precipitation, EEM is controlled by temperature, and consequently, vegetation C pools are weakened relative to soil C pools (Figure 4). Thus, soil C can account for most of the ecosystem C pool because the vegetation C sink strength is weakened under high temperatures and

low precipitation, as observed across the Caatinga, Cerrado, Pantanal, and Pampa (dry summer). Alternatively, decreasing temperatures limiting evapotranspiration allows positive EEM (Figure 4), with some plants shedding their leaves and/or promoting deep rooting. In these areas, positive EEM levels also should favor mineral-organic associations, allowing the storage of C and nutrients in soil organic matter until increasing temperatures and precipitation favor their mineralization. This dynamic is probably more relevant for the mixed and semideciduous forests in the Atlantic Forest domain.

CONCLUSIONS

The enforcing effects of temperature and precipitation on Brazilian C pools are essentially hierarchical and can be quantitatively expressed by Ecosystem Effective Moisture (EEM). Accordingly, as precipitation rates increase, annual EEM levels are less affected by temperature and plants can trade more C for water. As a result, the vegetation C pool increases, but it depends on a weak soil C sink strength and fast mineralization rates of nutrients, especially P. With decreasing precipitation, EEM levels depend proportionally more on temperature. High temperatures reduce EEM, and vegetation C pools are limited by low net primary productivity (NPP), frequent fire and/or high nutrient losses. Decreasing temperatures allows EEM to remain positive even where precipitation undergoes seasonality, but plants either shed their leaves/roots or increase root production to explore a larger soil volume. Thus, the soil C sink is strengthened by the formation of mineral-organic associations, with more nutrients and microbial cell by-products stored in soil organic matter. Overall, the horizontal distribution of vegetation and soil C pools is best described by EEM, rather than temperature or precipitation alone. Likewise, the vertical partition of C in plant-soil systems reflects biotic responses to climate-nutrient constraints. Hence, the sensitivity of Brazilian C pools to temperature and its control on EEM should not be overlooked, especially as precipitation levels decrease. In other words, the projected increases in global temperatures and shifts in precipitation patterns may be relevant threats to Brazilian C pools.

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