Soil microbial carbon and activity along with land use and geographic gradients

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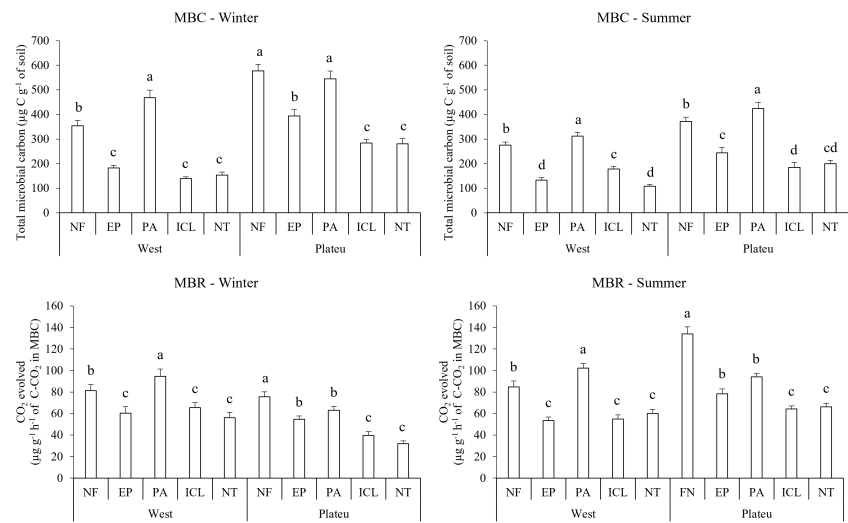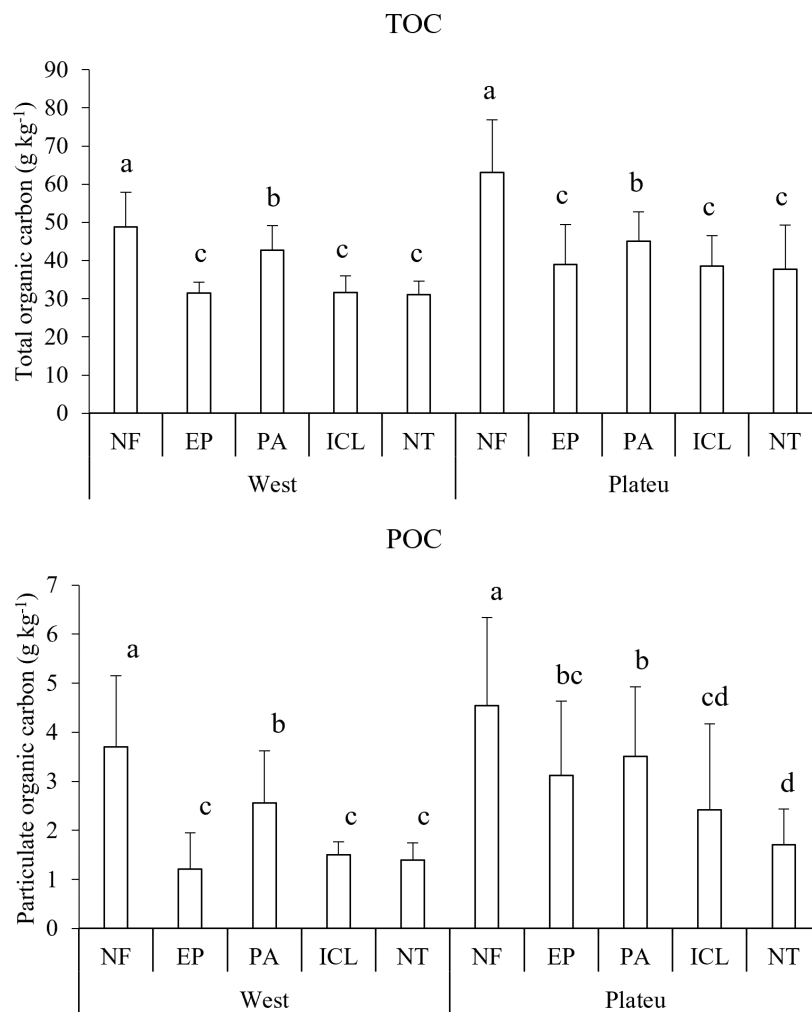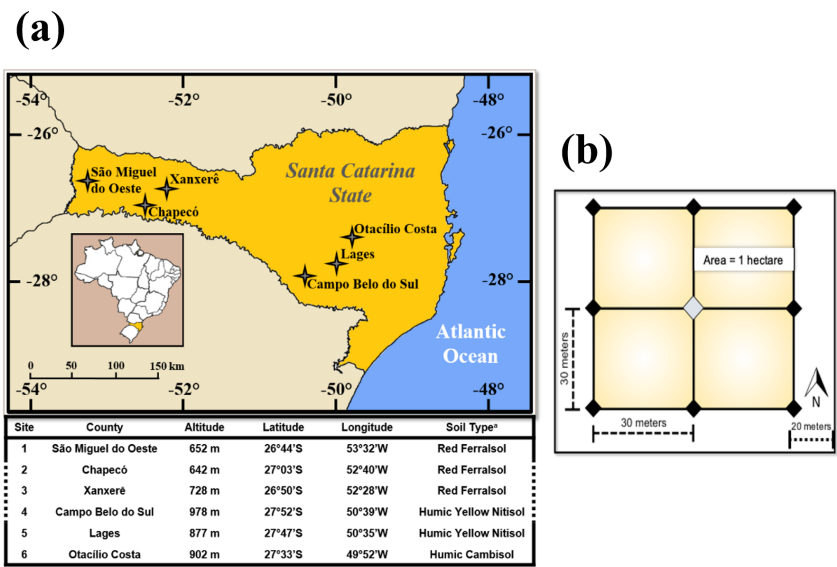[4]University of Coimbra,University of Coimbra

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Abstract

Soil carbon is intimately related to the living part of the organic matter, as represented by the soil microbial biomass, which mediates the decomposition, mineralization, and immobilization of organic carbon available in soils under different land-use systems. Forest-to-agriculture conversion and land-use change often lead to a loss in microbial biomass carbon (MBC) and shifts in microbial activity, directly influencing the soil carbon dynamics. The main aim of this study was to evaluate the effects of land-use change and geographical distribution on the microbial and environmental patterns related to soil C-dynamics. We evaluated MBC and microbial respiration in soils under five different land-use systems and two contrasting seasons, at a regional scale in Santa Catarina State, Southern Brazil. At the west mesoregion, changes in the MBC were correlated to sampling season in forest and grassland systems. Yet at the plateau mesoregion, we observed a land-use effect, as MBC decreased in no-till and crop-livestock integration systems. At the two mesoregions, forest and grassland had presented the highest values of MBC and microbial activity, as represented by microbial respiration. The grassland sites have presented lower values of the metabolic quotient (qCO_2) and higher values of the microbial quotient (qMic). The qCO_2 was lower in winter for all land-use systems. The forest sites have shown the highest total and particulate organic carbon values. The chemical-physical characteristics have shown correlations with microbiological variables related to the soil microbial C-dynamics. The land-use intensity, season, and geographic location were the main drivers of changes in microbial C-dynamics.

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MBC - Winter

MBC - Summer

MBR - Winter

MBR - Summer

TOC

POC

(a)

Site	County	Altitude	Latitude	Longitude	Soil Typeᵃ
1	São Miguel do Oeste	652 m	26°44'S	53°32'W	Red Ferralsol
2	Chapecó	642 m	27°03'S	52°40'W	Red Ferralsol
3	Xanxerê	728 m	26°50'S	52°28'W	Red Ferralsol
4	Campo Belo do Sul	978 m	27°52'S	50°39'W	Humic Yellow Nitisol
5	Lages	877 m	27°47'S	50°35'W	Humic Yellow Nitisol
6	Otacílio Costa	902 m	27°33'S	49°52'W	Humic Cambisol

(b)

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Keywords: Land-use change; Microbial biomass C; Microbial activity; $q\mathrm{CO_2}$; Soil C-dynamics.

1. INTRODUCTION

Most organic C is stored in soils (Scharlemann et al., 2014; Trivedi et al., 2018) and plays a leading role in the global biogeochemical cycles of several nutrients (Stevenson et al., 2016; Wang et al., 2020). The soil organic carbon (SOC) storage results from the dynamic feedback between its input and output through assorted microbial-mediated processes, such as organic matter decomposition, mineralization, and greenhouse gas emissions (McClean et al., 2015; Beillouin et al., 2022). The land-use change has a pronounced influence on SOC stocks and carbon cycling, with numerous studies pointing out soil management, cropping systems, and environmental conditions as the main drivers of C-dynamics in agriculture soils (Bayer et al., 2011; Spohn et al., 2016; Xue et al., 2017).

Soil microbial biomass and activity are sensitive biological indicators and rec-

ognized as pivotal tools for soil quality assessment (Benintende et al., 2015; Sun et al., 2018), due to their rapid response to environmental perturbations (Kabiri et al., 2016), such as land-use change (Prout et al., 2022). Studies have shown the importance of microbiological properties when evaluating the effects of management intensification and land use (Carvalho et al., 2010; Frazão et al., 2010; Silva et al., 2014; Kabiri et al., 2016). These bioindicators are also important for monitoring ecosystem services (Maxwell and Silva, 2020) such as water and nutrient cycling, plant-pathogen suppression, and decomposition of residues (Kaschuk et al., 2010). As soil quality emerges as a fundamental concept for sustainable soil management to produce food, wood, and fiber (Silva et al., 2011), the biological quality of soil is a potentially effective indicator to measure soil functional resilience due to changes related to disturbances (Dinesh and Chaudhuri, 2013), which may reflect the suitability of different soils for agricultural or conservation purposes (Benintende et al., 2015).

Land-use change and management intensification can modify soil microbial carbon dynamics and their levels (Silva et al., 2014). Cultivated soils often support lower microbial biomass and biodiversity than forest soils (Jantz et al., 2015), although they can present high efficiency in promoting the growth of plants (Kaschuk et al., 2010). In addition, soil temperature and moisture variation directly influence soil microbes (Fang and Moncrieff, 2001; Lupatini et al., 2019), and are considered key factors explaining geographical variation in microbial biomass and enzymatic activity (Paz-Ferreiro et al., 2011). Microbial biomass and soil respiration are robust and sensitive indicators to measure the long-term C-dynamics in soils (Dinesh and Chaudhuri, 2013; Stevenson et al., 2016). Yet the metabolic quotient, related to the ratio of CO_2-C evolved and the microbial C pool is indicative of the biological activity and substrate quality, signaling conditions of disturbance or stability of the soil (Boechat et al., 2012).

We hypothesized that (i) the soil microbial biomass C and activity would vary at a regional scale, shaped by land-use change and management intensification, as represented by soil characteristics. A secondary hypothesis stated that (ii) there would be a seasonal effect on microbial C and activity patterns, emphasized by the regional constraints. We aimed to evaluate the effects of land-use change and management intensification on soil microbial biomass and activity related to the C-dynamics at a regional scale.

2. MATERIALS AND METHODS

2.1. Study sites and soil sampling

The study sites were located within the subtropical Atlantic Forest Biome, in two different mesoregions (West and Plateau) of the Santa Catarina State, Brazil, to establish a climatic gradient (Figure 1). The climate in the west mesoregion was classified as *Cfa* subtropical climate, with hot summers, while the plateau mesoregion presented the subtropical type *Cfb*, mesothermal and humid, ac-

cording to Köppen-Geiger climate classification (Alvares et al., 2013). Average monthly temperature and rainfall are shown as supplementary information (Supplementary Figure S1). At each mesoregion, three municipalities were selected, as follows: São Miguel do Oeste (SMO), Chapecó (CHA) and Xanxerê (XAN) in the West mesoregion, and; Lages (LAG), Campo Belo do Sul (CBS) and Otacílio Costa (OTC) in the Plateau. At each municipality, five different land uses were selected, representing a gradient of land-use intensification: native forest (NF), *Eucalyptus* plantations (EP), pastureland (PA), no-tillage cropping (NT), and integrated crop-livestock (ICL).
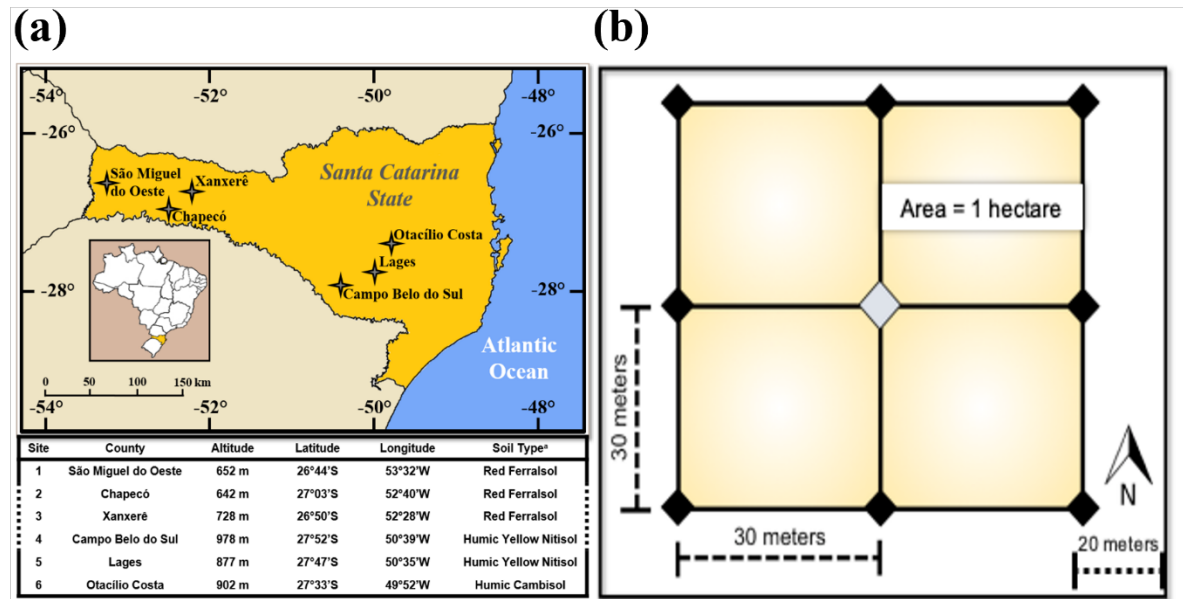

FIGURE 1 Description of sampling areas, coordinates, and sampling method. (a) Samples were collected in six counties of Santa Catarina State, Brazil. The sampling sites are located on the Atlantic Forest Biome, following a land use change, after deforestation. (b) Sampling Cartesian geogrid. Each diamond represents an individual soil sample. At each sampling site, we collected nine individual soil samples, later used for microbial, physical, and chemical analyses. Map created with Google Earth/Maps version 7.1 (Map data ©2020 Google) and modified in Adobe Photoshop version 11. [a]Soil types were classified according to the World Reference Base for Soil Resources (Anjos et al., 2015).

The NF sites represented small fragments (ranging from 1.2-10.8 ha) of a mixed ombrophilous forest at the Plateau or a transition to the semi-deciduous seasonal forest (West mesoregion). Signs of cattle grazing and human paths were observed in some forest patches. The EP ranged from 1-6 ha with plantations between 4-21 years old, often established in previous native grasslands. The PA ranged from 1.9-7.6 ha in size and 12-50 years in age and were all native pastures

at the Plateau mesoregion while in the West they were introduced or mixed pastures. The NT involved minimum soil disturbance, permanent soil cover, and crop rotation (at least four crops in three years), with fields ranging from 1.1 to 6.2 ha in size and 4 to 18 years old. The ICL patches ranged from 1.8-14 ha in size and 8-25 years of age. ICL is an agricultural management system with annual crops (using no-tillage) in summer and cover crops (oat, wheat, ryegrass, and millet) in winter used for livestock grazing. Both ICL and NT were more intensified systems due to the frequent use of chemical inputs such as herbicides, fungicides, and insecticides.

The soil sampling campaigns were performed in August and January, comprising the winter and the summer seasons of the southern hemisphere, respectively. Each sample was collected in a 3×3 Cartesian square-geogrid scheme, equidistantly by 30 m from each other, with 20 m of the border, totalizing an area of one hectare per sampling site. Twelve subsamples around each geogrid point composed the samples for physical and chemical analysis (explanatory variables). All samples were collected at 0-10 cm depth, wrapped in a thermal box, and transported to the laboratory. A total of 540 composite soil samples were collected (9 composite samples per geogrid $\times$ 5 land uses $\times$ 6 municipalities $\times$ 2 sampling seasons). Details about site management history, sampling, and environmental analyses are available in previous studies from our group (Bartz et al., 2014; Goss-Souza et al., 2017, 2022; Ceola et al., 2021), and as supporting information joining this manuscript (Supplementary Table ST1).

2.2. Soil microbial analysis

The soil microbial carbon (MBC) was determined using the Chloroform Fumigation-Extraction (CFE) method (Vance et al., 1987) and calculated by applying the extraction coefficient $(K_{EC}) = 0.33$ (Sparling and West, 1988). The microbiological activity was determined by soil basal respiration of samples (MBR; CO_2-C) using 50 g of soil incubated for 10 days at 28°C in biological oxygen demand (BOD) incubator (Alef and Nannipieri, 1995). The eco-physiological parameters such as metabolic quotient ($q CO_2$) (Anderson and Domsch, 1993) and microbial quotient (qMic) (Sparling, 1992) were calculated by the ratio between basal respiration and MBC, and MBC:TOC, respectively. The $q CO_2$ represents the C use efficiency of microbial biomass while qMic is the biotic carbon percentage of organic C in soil.

2.3. Soil analysis

To determine Total Organic Carbon (TOC) soil samples were dried at 60°C and grounded in a porcelain mortar. Particulate Organic Carbon (POC) was determined with 20 g of the ground sample following the routine methodology (Cambardella and Elliott, 1992). The TOC and POC content were determined by dry combustion in Autoanalyzer Elementary Vario El Cube equipment. Samples for chemical analysis were dried at 60°C and sieved through a 2 mm mesh

sieve, and certain pH_{H2O}, pH_{SMP}, soil organic matter (SOM), P, K, Ca, Mg and their relations, Al, H+Al, Cation exchange capacity at pH 7.0 (CEC), and bases sum, according to the routine methodology (Tedesco et al., 1995).

Soil moisture was determined on the samples dried in an oven at 105°C for 24 hours. The bulk density (Bd) was determined with the samples undisturbed by the volumetric ring method. The particle density was determined by the volumetric flask method (Teixeira et al., 2017). The soil microporosity (MI) was determined in the sand suction to the voltage table of 60 cm (6 kPa) and total porosity (TP) was calculated by the ratio between the bulk density and the particle density [E = 1-(ds/Dp)]. The macroporosity (MA) was obtained as the difference between TP and MI (Teixeira et al., 2017). The soil aggregate stability was determined by wet-sieving methodology according to (Kemper and Chepil, 1965), represented by the weighted average diameter (WAD). Soil granulometry was determined by the pipette method, using a sodium hydroxide solution as a chemical dispersant (Gee and Bauder, 1986). The soil penetration resistance was evaluated in volumetric samples (Dexter et al., 2007). [a]Soil types were classified according to the World Reference Base for Soil Resources (Anjos et al., 2015). Details regarding soil physical-chemical characteristics are shown as supplementary information and Supplementary Table ST1.

2.4. Data analysis

The results were submitted to analysis of variance (ANOVA F), considering the means of nine samples for each of the five land-use systems, two sampling seasons, and three municipalities. The means were compared by Tukey's HSD test at 5% probability, using the statistical software Statistica 7.0 (Hill and Lewicki, 2007). Pearson's correlations were established to assess any significant pattern between response and environmental variables. The concordance analysis was performed for the microbiological data according to mesoregion, season, and LUS (Li and Schucany, 1975).

3. RESULTS

The MBC soil pools varied among the LUS in west and plateau mesoregions with the influence of season (Figure 2). For the qMic, variation in LUS depending on the season (Table 1) was observed only in the west. In this mesoregion, we observed a decrease of 23, 32, 26, and 31% in MBC in the summer, for the NF, PA, EP, and NT, respectively, in comparison to the winter. Yet for ICL, we observed an increase of 30% in the summer. The highest MBC values were observed in PA, followed by NF, in the winter. Based on TOC and POC, the NF areas had the highest levels of soil carbon, followed by PA (Figure 3). In general, the levels of MBC, TOC, and POC in the EP west did not differ from the ICL and NT systems.
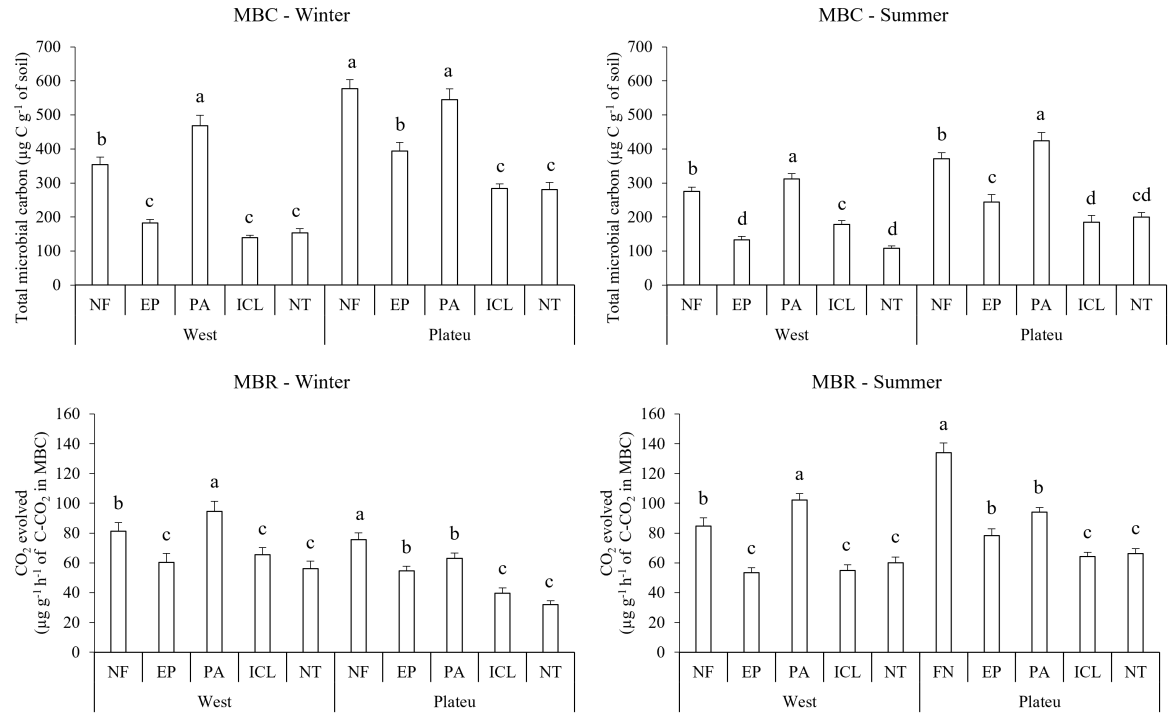
FIGURE 2 Microbial biomass carbon (MBC) and soil microbial basal respiration (MBR) in land-uses systems across West and Plateau mesoregions, for winter and summer. NF – Native Forest, EP – *Eucalyptus* plantation, PA – Pasture, ICL – Integrated crop-livestock, and NT – No-tillage. Means followed by the same letter do not differ with Tukey's HSD test at 5% probability into each mesoregion. Lowercase letters compare the land-use systems for the West and Plateau mesoregions.
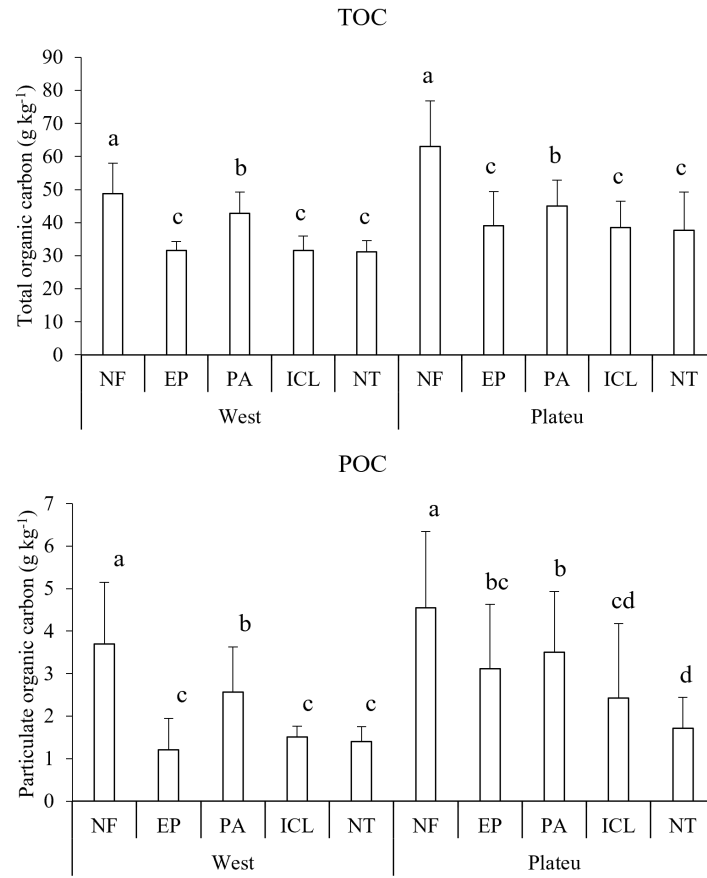
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TOC

POC

FIGURE 3 Total organic carbon (TOC) and particulate organic carbon (POC) in land-use systems of West and Plateau mesoregions. NF – Native Forest, EP – *Eucalyptus* plantation, PA – Pasture, ICL – Integrated crop-livestock, and NT – No-tillage. Means followed by the same letter do not differ with Tukey's HSD test at 5% probability.

TABLE 1 Microbial quotient (qMic; %) and metabolic quotient (qCO$_2$; µg g^{-1} h^{-1} of C in the MBC) in land-use systems of West and Plateau mesoregions.

Land use	qMic		qCO$_2$		qMic	qCO$_2$	
	Winter		Summer		Winter	Summer	
	----------------------- West -----------------------		------------ Plateau ------------				
NF	0.74 bA		0.60 bA		0.25 cdA	0.32 bA	
EP	0.60 bcA		0.43 cA		0.36 bcA	0.42 bA	
PA	1.16 aA		0.73 aB		0.21 dA	0.34 bA	
ICL	0.44 cA		0.57 bA		0.51 aA	0.36 bA	

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Land use	qMic	qCO$_2$	qMic	qCO$_2$	
NT	0.49 cA	0.34 cA	0.48 abA	0.62 aA	

In the plateau mesoregion, the NF and PA areas showed the highest levels of MBC, with 479.6 and 484.4 µg C g^{-1} of soil, respectively. The EP areas showed lower levels of MBC than those observed in the NF and PA areas, with a decrease of around 34% over the pastures in the plateau (Figure 2). EP presented POC similar values to PA. The qMic decreased in the ICL and NT areas when compared to PA. The TOC and POC showed higher levels in the NF, with 63.1 and 4.6 g kg^{-1}, respectively. The activity of soil micro-organisms and their efficiency of C utilization, represented by soil microbial basal respiration (MBR) and metabolic quotient (qCO$_2$), varied with the LUS and sampling seasons for the two studied mesoregions (Figure 2, Table 1).

In the west, the soil microbial respiration was correlated with the season. The highest MBR values were observed in the pasture areas, the same as found for MBC (98.3 µg g^{-1} h^{-1} of C-CO$_2$) (Figure 2). However, the qCO$_2$ values were 14% higher on average in the summer, with the highest contents found in NT (0.62 µg g^{-1} h^{-1}) in the MBC.

In the Plateau, the C-CO$_2$ evolution increased 64% from winter to summer. The NF areas had the highest MBR in both winter and summer, with 78.98 and 134.08 µg g^{-1} h^{-1} of C-CO$_2$ in MBC, respectively (Figure 2). The PA and EP presented the same behavior for MBR for times sampled with values for C-CO$_2$ emission in the winter 62.98 and 54.00 µg g^{-1} h^{-1} of C-CO$_2$ in MBC, as ICL and NT presented in winter values in the range of 32.04 and 39.60 µg g^{-1} h^{-1} of C-CO$_2$ in MBC, respectively. The NF, PA, EP, ICL, and NT no-showed changes in the metabolic quotient for the winter, ranging from 0.13 to 0.16 µg µg^{-1} h^{-1} of C-CO$_2$ in MBC.

A concordance analysis considering all land-use systems and seasons was performed for the microbial parameters (MBC, MBR, qCO$_2$, and qMic). Results showed a high similarity between the two mesoregions (Table 2 and Supplementary Table ST2). The highest concordance was found for the MBC, with 85% of concordance between mesoregions. The microbial carbon was correlated with soil chemical and physical variables for the two seasons (Table 3). The same was not observed for the other microbial parameters (MBR, qCO$_2$, qMic). We found positive correlations for MBC with total organic carbon, total nitrogen, organic matter, and soil moisture. Meanwhile, negative correlations were observed with phosphorus and bulk soil density. The MBR had higher correlations with TOC.

The qCO$_2$ and qMic showed few and lower correlations with the explanatory variables.

TABLE 2 Concordance analysis of microbial parameters among West and Plateau mesoregions, considering all land-use systems and seasons.

Parameter	W	X^2	P-value
MBC	0.85	13.6	< 0.001
MBR	0.76	12.2	< 0.005
qCO$_2$	0.77	12.4	< 0.005
qMic	0.81	13.0	< 0.001

Footnote: MBC – Microbial biomass carbon. MBR – Microbial basal respiration. qCO$_2$ – Metabolic quotient. qMic – Microbial quotient. W – Kendall W rank-based coefficient. X^2 – Friedman's test qui-squared with two degrees of freedom.

TABLE 3 Significant Pearson's correlation factors (r^2) for microbial biomass carbon (MBC) and microbial respiration (RB) and soil characteristics considering the seasons or overall data. Analysis encompassing the two mesoregions and five land-use systems.

MBC	Total Organic Carbon	Total Nitrogen	Available P	Soil moisture	Bulk density
	r^2				
Winter	0.63***	0.57**	-0.59**	0.71***	-0.56**
Summer	0.66***	0.62***	-0.56*	0.50*	-0.52*
Overall	0.52***	0.56***	-0.54***	0.66***	-0.51***
RB	r^2				
Summer	0.75***	0.65***	NS	0.54*	NS
Overall	0.64***	0.52***	NS	NS	NS

Footnote: Significance codes, *** *p-value* < 0.001; ** < 0.01; * < 0.05; NS (non-significant) > 0.05; (n = 27, winter or summer; n = 54, winter + summer).

4. DISCUSSION

Great losses of soil C have been observed with increased land-use intensity (Sanderman et al., 2017; Wiesmeier et al., 2019; Sharma et al., 2019; Ji et al., 2020). In our study, under subtropical conditions, we have also observed this pattern for ICL and NT systems, with decreased TOC and POC, when compared to systems with lower land-use intensification (NF and PA). Accordingly, microbial carbon has decreased in ICL and NT systems in comparison to PA for the two studied mesoregions (Figure 2). The systems with lower land-use intensification (NF and PA) have presented the highest values of MBC and qMic

(Figure 2, Table 1), which would be related to the diversification of organic matter incorporated into the soil, particularly via plant deposition (Matoso et al., 2012) along time. Indeed, the higher presence of roots, and enhanced organic compound exudation, would lead to an increase in MBC, because of increased C and energy source for the microbial biomass (Souza et al., 2010; Merino et al., 2015).

The land-use effect on soil carbon changes has varied between the Plateau and West mesoregions, confirming the hypothesis of a regional pattern of microbial C pools. Similarly, a seasonal pattern has also been observed in land uses for each mesoregion, emphasizing the differences in the efficiency of utilization of organic among seasons. In the West, the decrease in C was more pronounced, reaching more than half the qMic on the same system (PA). Climatic conditions such as prolonged drought would alter the active pool of MBC (Sherrod et al., 2018), with the variability also conditioned to temperature, as it is one of the main factors driving the fluctuation of microbial C, influencing soil respiration (Wei et al., 2016).

The pasture has stood out from the other LUS, with higher qMic values in both mesoregions, with values greater than 1% in terms of contribution to the total C content in the soil. This pattern has indicated that the C microbial compartment (MBC) is more important for these systems, pointing out to the increase of nutrients in pasture areas through the soil microbial carbon, which has presented a faster turnover ratio (Glaeser et al., 2010). In general, high MBC values have been found in no-till compared to conventional tillage, demonstrating the influence of soil management on microbial parameters (Hungria et al., 2009; Silva et al., 2010; Babujia et al., 2010).

The decrease in MBC with land-use intensification would be a consequence of the largest soil exposure, with the pronounced effect of sunlight, increasing soil temperature, and decreased moisture, leading to a decrease in soil microbial biomass (Souza et al., 2010) (Curtin et al., 2012). In NF and PA, the continuous soil protection due to the presence of plants and different organic sources would improve the soil water retention, as the straw would protect the soil from direct solar radiation, decreasing the temperature on the soil subsurface, and inhibiting the OM mineralization rate, with consequences to soil MBC (Guimarães et al., 2013). The land-use intensification has been found to affect the soil organic carbon (Wang et al., 2011; Xiao et al., 2019), due to the decreased contribution of crop residues, coupled with erosion losses (Hickmann and Costa, 2012; Aziz et al., 2013; Wiesmeier et al., 2019), and the accelerated OM mineralization, decreasing their soil levels (Loss et al., 2010; Trivedi et al., 2013, 2018). A decrease in the C use efficiency or a decline in microbial turnover would cause soil C losses, as factors that trigger increases in microbial efficiency or the microbial return time may increase soil sequestration (Spohn et al., 2016).

The native forest and pasture systems have presented lower C-CO_2 losses. These results suggest more C is assimilated to microbial growth, which would be related to factors such as accessibility to the substrate, soil physical-chemical

conditions, or even changes in the metabolic patterns and composition of the microbial biomass (Souza Nunes et al., 2011). The higher microbial respiration rates would culminate in higher productivity in those ecosystems (Silva et al., 2012). Microbial respiration is often increased in the SOM fraction, while the C efficiency is not compromised, suggesting that despite the high C-nutrient ratio, microbial activity has been found not limiting (Spohn et al., 2016).

In the Plateau mesoregion, the PA system has presented lower stress conditions, as verified by the lowest level of C-CO_2 (Table 1). The EP, ICL, and NT systems have shown elevated levels of the metabolic quotient, indicating loss of C, because the smaller soil microbial population often needs a larger amount of C as a source of energy for maintenance (Carneiro et al., 2008; Primieri et al., 2017), which has indicated those microbial populations have been under metabolic stress (Anderson and Domsch, 1993).

Yet in the West, microbial soil respiration has not differed between seasons, the temperature and soil moisture may have influenced this behavior, with higher temperatures in winter. Since the climatic conditions have affected both the soil organic and microbial C (Luo et al., 2017). In this study, the results of MBC and TOC were influenced by soil temperature and moisture, with a positive correlation with soil moisture and a negative correlation with soil temperature (Almeida et al., 2009). The decomposition of soil C presents hydrothermal sensitivity, assuming significant importance to predict the correlation between land-use change the global climate change (Biswas et al., 2018). We argue that the total organic carbon could be a better predictor of microbial carbon than the particulate organic C (Rudrappa et al., 2006), as the last accounts for the organic C fraction quickly decomposable and constitutes a transient C reserve in soils (Souza et al., 2016).

The land-use intensification has decreased the C immobilization by soil biomass for the ICL and NT in the winter, and for NT in the summer. The least intensified systems (NF and PA) had presented a lower metabolic quotient in winter. The EP, ICL, and NT were less effective in sequestering C, and have lost more C-CO_2 to the atmosphere, in the winter. Those results would be correlated to the negative influence of the most intensive management practices, which often cause stress on soil microbial biomass, catalyzing the release of C-CO_2 into the atmosphere (Xiao et al., 2019). Moreover, soil management intensification often favors the decomposition of OM, besides root and microbial respiration, leading to increased loss of C-CO_2 to the atmosphere (Xu and Yuan, 2017). Higher temperatures are often recorded together with higher C-CO_2 emissions (Campos et al., 2011).

Native forests and pastures have presented higher microbial activity, based on the release of C-CO_2 (Xavier et al., 2006; Jiang et al., 2009), which would be assigned to the constant incorporation of straw and the accumulation of organic matter, promoting biomass diversity and the consequent biological activity, releasing C-CO_2 (Singh and Gupta, 2018). The *Eucalyptus* reforestation is a system that settles over time, the culture time on the ground and without their

preparation after planting. However, failed to increase the C content in the soil when compared to the more conservation systems (NF and PA). This can be attributed to the diversity, quality, and quantity of litter culture that provides the soil.

The $q\text{CO}_2$ would also reflect a change in the microbial structure and composition differing in C use efficiency following land-use change and management practices (Kabiri et al., 2016). Long-term land-use systems have had the lowest values of $q\text{CO}_2$, which may reflect lower stress conditions and biomass stabilization (Pereira et al., 2013). The significant decreases in MBR and $q\text{CO}_2$ would indicate that the microbial C use efficiency has been improved with low respiration and high microbial synthesis (Xue et al., 2017). Erroneous agricultural practices and wrong management would reflect in OM loss and represent a sink of C to the atmosphere (Schmidt et al., 2011; Ontl and Schulte, 2012). In addition, the C emissions are found to be positively correlated with the temperature (Ding et al., 2016). Studies comparing land-use systems with higher intensification compared to the native vegetation have found no significant differences in $q\text{CO}_2$ (Neves et al., 2009; Glaeser et al., 2010), which demonstrates greater efficiency of MBC to avoid loss of $C\text{-}\text{CO}_2$ to the atmosphere with higher carbon incorporation into microbial biomass (Fialho et al., 2006; Melo et al., 2017).

The land-use effects on microbial biomass and their activity have followed similar patterns when the two mesoregions were compared. Although the two mesoregions present edaphoclimatic differences, the microbial indicators used here have shown consonant patterns regarding land-use change and management intensification. This study also demonstrated the positive correlation of MBC with the TOC, N, and moisture, and negative with P and bulk density, thus confirming once more the importance of chemical properties as drivers of carbon dynamics in the different land uses. Other studies also have found a negative correlation between MBC and P, indicating that an increase in MBC results in a decrease of this nutrient in the soil, led by the competition for this nutrient with the plants (Li et al., 2004). Microbial biomass of soil reflects the degree of immobilization of carbon and nitrogen, where organic matter is a crucial factor in their accumulation and development (Jia et al., 2005; Wiesmeier et al., 2019). Together, those results have highlighted the wide capacity of the soil microbial indicators used here to identify changes caused by land-use change and management intensification in an earlier stage, regardless of edaphoclimatic conditions, the same as found in other microbial and faunal studies at the same subtropical soils and land uses (Bartz et al., 2014; Goss-Souza et al., 2017; Ceola et al., 2021).

Forest conversion to agricultural systems has been often regarded as detrimental to soil biodiversity, activity, and their related ecosystem services (Goss-Souza et al., 2017). Most studies evaluate microbial carbon and activity patterns resulting from this conversion without examining the consequences of long-term land-use change across geographical scales and time. We have shown that soil microbial biomass and activity are dependent on land use and influenced by the management intensification and time, regardless of mesoregion. The SOC

transformations by micro-organisms are key processes of the terrestrial C-cycle and relevant supporting ecosystem service (Modernel et al., 2016) acting on the sequestration and decomposition of C (Spohn et al., 2016). Underlying microbial biomass and activity patterns bring us relevant insights into ecosystem modeling and C stock conservation within the Atlantic Forest and other subtropical and tropical hotspots of biodiversity around the globe.

5. CONCLUSIONS

The microbial C pools and dynamics have varied along the land uses and seasons, with similar patterns found along the two contrasting edaphoclimatic mesoregions. The no-till and the crop-livestock integration systems, as more intensified, have presented the lowest levels of C pools. Among the managed areas, the pasture areas have presented the highest potential for C sequestration by soil microbial biomass. The microbial biomass carbon was the most sensitive microbiological parameter, being found a suitable microbiological indicator regardless of edaphoclimatic conditions or land uses.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest that could have appeared to influence the work reported in this paper.

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SUPPLEMENTARY MATERIAL

2 * Names and affiliations omitted for double-blind.

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5 **MATERIALS AND METHODS**

6 **SUPPLEMENTARY FIGURE**   **1**

7 **SUPPLEMENTARY TABLES**   **1 to 2**

8 **REFERENCES**

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MATERIALS AND METHODS

Soil physical-chemical analyses

Soil pH was measured in a 1:2.5 soil/water suspension. Exchangeable Al^{3+}, Ca^{2+}, and Mg^{2+} were extracted with KCl 1M. After that, calcium and magnesium were determined by atomic absorption spectrometry and aluminum by acid-base titration. Phosphorus and K^+ were extracted by ion-exchange resin and determined by atomic absorption spectrometry. Potential acidity (H+Al) was estimated by an equation based on the pH determined in the SMP buffer solution (pH SMP). Some of the results allowed the calculation of other parameters such as exchangeable bases (SB), the sum of Ca, Mg, and K; cation exchange capacity (CEC), the sum of Ca, Mg, K, Al, and H; bases saturation (V%), the percentage relation between SB and CEC; and Al saturation (m%), the percentage relation between exchangeable Al and CEC. Soil texture was determined using a Bouyoucos densimeter, after shaking the soil vigorously with NaOH 1M as a dispersant. The gravimetric moisture was obtained in percentage, through the difference between the weight of the sample at the moment of sampling and its dry weight, after 48 hours in an incubator at 105°C. Soil density was measured by Kopecky's ring method. Biopores were calculated by measuring the pores' continuity. Total porosity was calculated through the saturation method. Microporosity was obtained by the tension table method. Macroporosity was calculated by difference, deducting the microporosity from the total porosity. Those parameters were analyzed at the Soils Laboratory, Santa Catarina State University, Lages, Brazil, following a routine methodology (Kemper and Chepil, 1965; Gee and Bauder, 1986; Dexter, 1988; Tedesco et al., 1995; Claessen et al., 1997; Dexter et al., 2007; Dhaliwal et al., 2011).

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Soil classification

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51 Soils were classified according to the World Reference Base for Soil Resources (Anjos et al.,

52 2015), as follows:

53 - Red Ferralsols - Soils distinguished by Fe/Al chemistry; Dominance of kaolinite and Fe

54 oxides; These were the soils found in all counties of western sampling counties (See Figure S1,

55 sites 1, 2, and 3), regardless of land use;

56 - Humic Yellow Nitisols - Soils distinguished by Fe/Al chemistry; low-activity clay, P fixation,

57 many Fe oxides, strongly structured, with the accumulation of organic matter on the surface.

58 - Humic Cambisols - Soils with little or moderately developed profile differentiation; with the

59 accumulation of organic matter on the surface.

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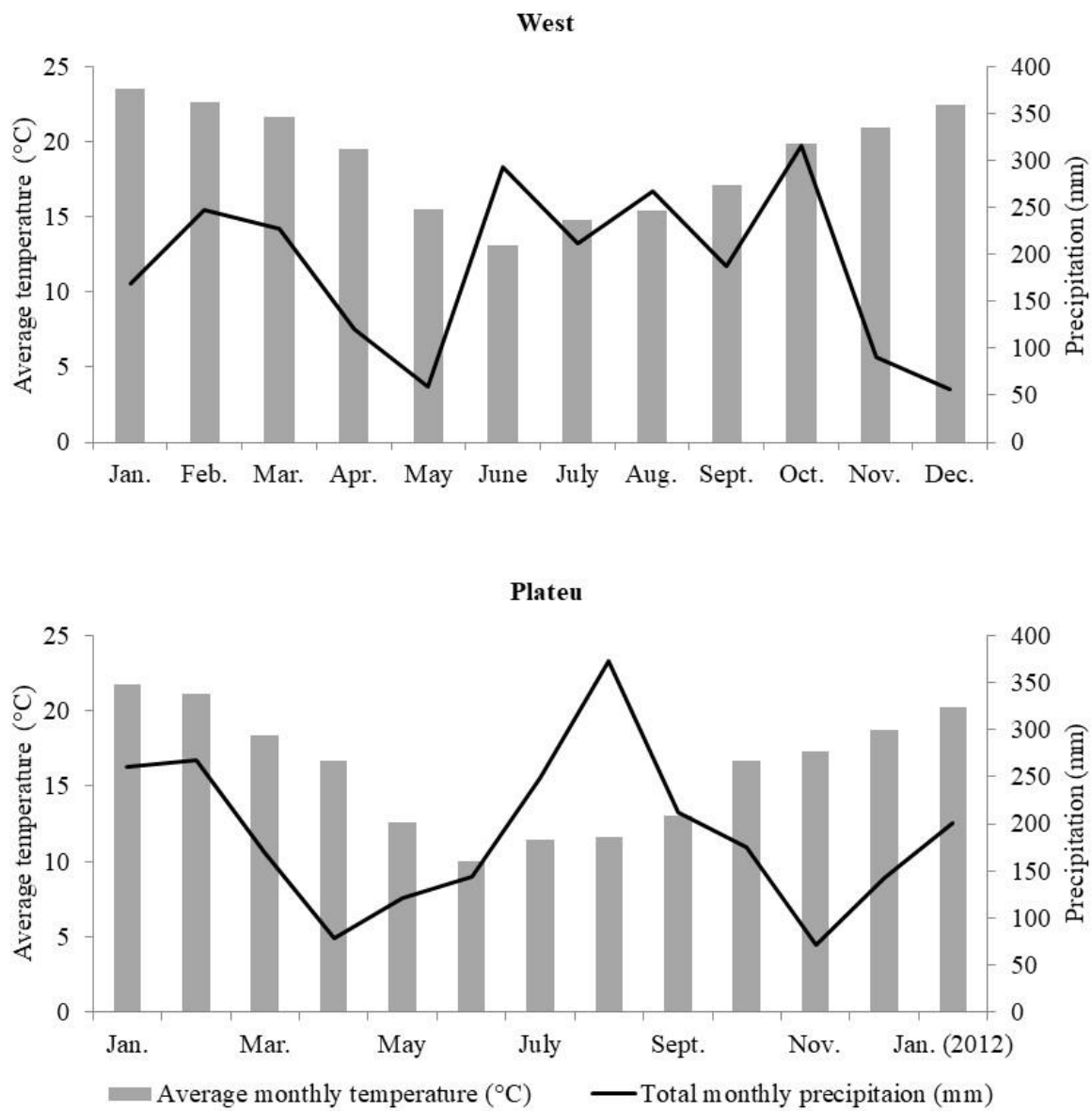
78   **FIGURE S1** Average monthly temperature (°C) and rainfall (mm) for the West (2011) and

79   Plateau mesoregions (2011 and January 2012). Source: Epagri – Ciram, 2013.

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SUPPLEMENTARY TABLES

82 **TABLE ST1** Soil chemical and physical properties of Native Forest (NF), *Eucalyptus*

83 plantation (EP), Pasture (PA), Integrated crop-livestock (ICL), and No-tillage cropping (NT) in

84 the West and Plateau mesoregions of Santa Catarina State.

Characteristics	Land use									
	NF	EP	PA	ICL	NT	NF	EP	PA	ICL	NT
	-------------- West --------------					------------ Plateau ------------				
pH $_{H_2O}$	4.3	4.8	5	5.2	5.6	4.6	4.8	4.8	5.3	5.5
P (mg dm^{-3})	5.2	5.1	4.7	12	14.9	4.3	3.9	3.6	8.7	5.8
K (mg dm^{-3})	82	105	145	178	262	112	84	190	135	128
SOM (%)	4.9	4.1	4.9	4	4	6.2	4.4	5.2	4.7	4.5
Al (cmol$_c$ dm^{-3})	3.5	2.2	1	0.8	0.3	3.9	2.8	3	0.4	0.1
Ca (cmol$_c$ dm^{-3})	1.8	3	3.6	5.3	7.2	5.2	2	2.1	7.2	7.5
Mg (cmol$_c$ dm^{-3})	0.7	1.2	1.8	2.3	2.8	1.7	1.8	1.4	3.8	3.8
H+Al (cmol$_c$ dm^{-3})	19.6	10.7	7.4	5.7	4.2	20.8	17	17.5	6.2	4.9
CTC pH$_7$ (cmol$_c$ dm^{-3})	22.3	15.2	13.2	13.8	14.8	27.9	21	21.5	17.5	16.5
Moisture (%)	54.0	33.8	43.6	32.3	32.4	57.7	42.4	50.8	39.8	38.7
Bd (g cm^{-3})	0.94	1.05	1.09	1.17	1.15	0.89	0.98	0.95	1.01	1.01
TP (m^3 m^{-3})	0.64	0.62	0.6	0.57	0.59	0.65	0.65	0.66	0.65	0.65
MA (m^3 m^{-3})	0.39	0.43	0.53	0.44	0.48	0.56	0.5	0.49	0.47	0.45
MI (m^3 m^{-3})	0.25	0.19	0.07	0.14	0.12	0.09	0.15	0.17	0.19	0.2
BP (m^3 m^{-3})	0.11	0.06	0.03	0.07	0.05	0.03	0.03	0.02	0.01	0.02
PR (MPa)	0.6	1.6	2.1	1.5	1.4	1.1	1.5	1.8	1.9	1.8
WAD	5.2	5.1	5.7	5.6	5.4	5.6	5.6	5.7	5.5	5.6
Sand (%)	29.7	29.5	27.1	27.2	32.6	42.8	35.5	34.3	25.9	19.1
Silt (%)	42.2	36.7	38.3	40.6	41.6	37.7	46.2	46.5	49.9	47.1
Clay (%)	22.3	26.7	30.8	31.2	25.8	19.4	18.3	19.2	24.1	33.8

85 Footnote: Bd – bulk density, TP – total porosity, MA – macroporosity, MI – microporosity,

86 BP – biopores, PR – penetration resistance, WAD – weighted average diameter.

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93   **TABLE ST2** Concordance analysis of microbial parameters according to the season for each

94   mesoregion.

Mesoregion	West						Plateau					
Season	Winter			Summer			Winter			Summer		
Parameter	W	X^2	P-value	W	X^2	P-value	W	X^2	P-value	W	X^2	P-value
MBC	0.80	9.6	< 0.005	0.95	11.5	< 0.001	0.91	10.9	< 0.001	0.84	10.1	< 0.001
BR	0.82	9.9	< 0.005	0.96	11.5	< 0.001	0.84	10.1	< 0.001	0.87	10.4	< 0.001
qCO$_2$	0.44	5.3	NS	0.78	9.4	< 0.05	0.16	1.9	NS	0.36	4.3	NS
qMic	0.82	9.9	< 0.05	0.89	10.7	< 0.001	0.69	8.3	< 0.05	0.42	5.1	< 0.05

95   Footnote: MBC – Microbial biomass carbon. BR – Microbial respiration. qCO$_2$ – Metabolic

96   quotient. qMic – Microbial quotient. W – Kendall W rank-based coefficient. X^2 – Friedman's

97   test qui-squared with two degrees of freedom.

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