Decomposition and stabilization of the organic matter in an old-growth tropical riparian forest: effects of soil properties and vegetation structure

Pedro Fernandes  
Universidade Federal de Sao Carlos Centro de Ciencias Biologicas e da Saude

Andrea Teixeira Souza  
Universidade Federal de Sao Carlos Centro de Ciencias Biologicas e da Saude

Marcel Tanaka  (marcel@ufscar.br)  
Universidade Federal de Sao Carlos Centro de Ciencias Biologicas e da Saude  
https://orcid.org/0000-0001-5924-1886

Renata Sebastiani  
Universidade Federal de Sao Carlos Centro de Ciencias Biologicas e da Saude

Research

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Abstract

Background: Nutrient cycling in tropical forests has large importance for primary productivity, and decomposition of litterfall is a major process influencing nutrient balance in forest soils. Although large-scale factors strongly influence decomposition patterns, small-scale factors can have major influences, especially in old-growth forests that have high structural complexity and strong plant-soil correlations. We evaluated decomposition rates and stabilization of soil organic matter using the Tea Bag Index in an old-growth riparian forest in southeastern Brazil to evaluate the effects of forest structure and soil properties on decomposition processes. These data sets were described separately using Principal Components Analysis (PCA). The main axes for each analysis, together with soil physical properties (clay content and soil moisture), were used to construct different structural equations models that evaluated the different parameters of the TBI, decomposition rates and stabilization factor. The best model was selected using Akaike's criterion.

Results: Forest structure and soil physical and chemical properties presented large variation among plots within the studied forest. Clay content was strongly correlated with soil moisture and the first PCA axis of soil chemical properties, and model selection indicated that clay content was a better predictor than this axis. Decomposition rates presented a large variation among tea bags (0.009 and 0.098 g g\textsuperscript{-1} day\textsuperscript{-1}) and were positively related with forest structure, as characterized by higher basal area, larger trees, and tree density. The stabilization factor varied between 0.211 – 0.426 and was related to forest stratification and soil clay content.

Conclusions: The old-growth forest studied presented high heterogeneity in both forest structure and soil properties at small spatial scales, that influenced decomposition processes and probably contributed to small-scale variation in nutrient cycling. Decomposition rates were only influenced by forest structure, whereas the stabilization factor was influenced by both forest structure and soil properties. Heterogeneity in ecological processes can contribute to the resilience of old-growth forests, highlighting the importance of restoration strategies focused on the spatial variation of ecosystem processes.

Background

Tropical forests generally occur on nutrient poor soils, and the maintenance of primary productivity strongly depends on nutrient cycling within these ecosystems (Sayer and Banin 2016). Litterfall is the major route of nutrient return to the soil, so that litter decomposition provides organic and inorganic compounds for the plant community (Osman 2013; Pausas and Bond 2020). This process includes the physical fragmentation of the biological structures, chemical transformations, and synthesis of new compounds, enabling the mineralization of the organic matter (Berg and McClaugherty 2014). Litter decomposition processes progress gradually, since the organic matter is composed by fractions that may be chemically labile and recalcitrant, resulting in molecules with short and long duration in the soil, influencing carbon fixation and soil structure (Berg 2018). Therefore, the decomposition of the organic...
matter can strongly influence local and global biogeochemical cycles (Benbow et al. 2019; Sayer et al. 2020).

During the decomposition process, part of the nutrients is released and made available for plant use, and part is immobilized during decomposer growth (Berg and Mc Claugherty 2014; Wachendorf et al. 2020). However, not all litter residue is necessarily mineralized, and can stabilize or decompose at very slow rates, contributing for the soil organic matter (Berg 2018). The fraction that is not effectively decomposed and the speed of the decomposition depend on litter quality, temperature and humidity, and on soil nutrient availability, since they influence decomposer activity (Berg 2014; Bradford et al. 2016; Lajtha et al. 2018; Wiesmeier et al. 2019).

These factors can be strongly influenced by the vegetation and soil properties, which can vary at local spatial scales (Bradford et al. 2016, 2017). Soil properties present large variation among ecosystems even at small spatial scales, and can be related with the structure and composition of plant communities (Spielvogel et al. 2016; Metzger et al. 2017). Forest structure can vary at different spatial scales due to differences in species composition, internal dynamics, and physical factors (Wekesa et al. 2019; Muñoz Mazón et al. 2020). The structural heterogeneity found within forests can influence local microclimate conditions, hydrological movements, litterfall spatial patterns, and also the soil physical and chemical properties (Krishna and Mohan 2017; Bélanger et al. 2019). For example, forest sites with more developed canopies and higher tree density produce more leaf litter (Nunes and Pinto 2007) increasing the availability of resources to decomposers. Local differences in the biomass of deposited litter could promote heterogeneity in decomposer activity (Lajtha et al. 2018; Silva-Sánchez et al. 2019). Further, higher forest stratification can provide higher radiation input, increasing temperatures and reducing soil moisture (Yeong et al. 2016), factors that can also influence decomposition rates (Petraglia et al. 2019). Therefore, decomposition processes can be spatially variable in unmanaged old-growth forests due to higher heterogeneity, differences in litter spatial distribution, and variation in surface and subsurface hydrological pathways.

Riparian forests may present large spatial variation, related to the distance from watercourses, topography, geomorphology, and internal processes (Rot et al. 2000; Naiman et al. 2005). In response to this heterogeneity, there may be large spatial variation in soil properties and composition of plant communities, which then contribute with spatial variation in processes such as nutrient and carbon cycling (Parron et al. 2011; Woodward et al. 2015).

The evaluation of environmental factors that influence the decomposition and stabilization of the organic matter can be carried out by using leaf litter with different qualities, since different factors can influence the decomposition of the labile and recalcitrant fractions of the organic matter (Manzoni et al. 2012). With these considerations, Keuskamp et al. (2013) proposed the Tea Bag Index method (TBI), which uses standard leaf litter with higher (green tea) and lower (rooibos tea) quality to obtain estimates of decomposition and stabilization of the organic matter, using an asymptotic model of mass loss (Wider and Lang 1982). The usage of standard material enables the evaluation of environmental factors on the
decomposition process, independently of leaf litter quality (Keuskamp et al. 2013). Also, the TBI material (green and rooibos tea) is representative of the leaf litter found in natural ecosystems (Duddigan et al. 2020).

In this study, we evaluated the decomposition rates and stabilization of the organic matter in a tropical old-growth riparian forest in southeastern Brazil. We evaluated whether forest structure and soil properties could influence these processes using standard TBI methods (Keuskamp et al. 2013). In this way, we aimed to identify which factors at small spatial scales influence decomposition processes in old-growth forests, contributing for the identification of indicators for the monitoring of restored forests.

**Methods**

**Study area**

This study was carried out in a highly preserved remnant of riparian forest that belongs to the Air Force Base of Pirassununga (FAYS) in central São Paulo state (21°59’39.98” S, 47°20’12.73” W), Southeastern Brazil. FAYS includes a total forest area of 2,608 ha, where about 45% is composed of semideciduous seasonal forest and transition with riparian forest. The studied forest is adjacent to the Mogi-Guaçu River, in the upper Paraná River watershed, and is part of a 140 ha forest fragment at 620 meters above sea level. Geologically, the region is in the residual plateaus of Franca/Batatais and is composed by intrusive Serra Geral, with deep distroferric red latosols, and a wavy relief (Rossi 2017).

Climate is Cwa following Köppen's classification, with wet summer and dry winter (Rolim et al. 2007). Between 1976 and 2008, the mean minimum and maximum temperatures recorded at FAYS were 10.6 and 32.8 ºC, respectively, and mean annual rainfall was 1,290 mm (Ferrari et al. 2012). The experiment was carried out in the early dry season (24 April to 24 June 2019). Mean temperatures and monthly rainfall recorded in May were 23.7 ºC and 39.4 mm, and in June 21.2 ºC and 16.2 mm, respectively, in the meteorological station of University of São Paulo, campus Pirassununga, located about 15 km from FAYS.

**Experimental design**

We evaluated the effects of spatial variation in soil properties and forest structure on the decomposition and stabilization of the organic matter by establishing ten 10 × 10 m plots in the riparian forest, five plots distant 5 m from the Mogi-Guaçu River and five plots at a 30 m distance from the river. We selected these areas to maximize the variation in soil physical properties, since areas near the river generally have more sand and less clay than those in the forest interior (Woodward et al. 2015; Rodrigues et al. 2018; Saint-Laurent and Arsenault-Boucher 2020). Also, we expected that forest structure would differ between these areas due to higher incidence of light near the river. Within each distance, each plot was 30 m distant from each other.
Soil sampling and description of forest structure were carried out just before the experiment began. Soil samples from each plot were obtained by randomly collecting three 0-20 cm depth subsamples with an auger, which were then composited to form a single sample. In the laboratory, a subsample (50 g) was obtained from each compound sample to determine soil moisture by initially determining the subsample wet mass and then reweighting after drying at 65 ºC in an oven until dry mass stabilized. Soil moisture was then obtained as \( h = \frac{\text{wet mass} - \text{dry mass}}{\text{dry mass}} \times 100 \). Clay content was determined with the pipette method (Embrapa 1997). Soil chemical analyses were carried out following Embrapa (1997) and Raij et al. (2001): available phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were determined with the anion exchange method; soil organic matter was determined with the Walkley-Black method, pH was determined with CaCl\(_2\) solution at 0.01 mol L\(^{-1}\); nitrogen (N) was determined with the Kjeldahl method, and potential acidity (H + Al) was determined with a buffered solution of calcium acetate at pH = 7. Cation exchange capacity (CEC) was obtained from the sum K + Ca + Mg + (H + Al), and soil base saturation (BS) was calculated by dividing the sum of bases (K + Ca + Mg) by CEC.

Forest structure characterization was adapted from Souza et al. (2013) by measuring all trees in each plot with circumference at breast height (CBH) > 10 cm, which was determined with a measuring tape. For each plot we determined mean diameter at breast height (DBH), tree stratification (calculated as the coefficient of variation of DBH), tree density (individuals ha\(^{-1}\)), and plot basal area (m\(^2\) ha\(^{-1}\)).

We estimated the decomposition rates and stabilization of the organic matter using the TBI method (Keuskamp et al. 2013). In this method, a pair of tea bags is buried at 8 cm depth, and each tea bag differs in litter quality: green tea (sencha tea, C:N ratio = 12.2) and red tea (rooibos tea, C:N = 42.9), as manufactured by Lipton ® (Keuskamp et al. 2013). The tea bags are made of polypropylene, have a tetrahedral shape with 5 cm sides, and contain about 2.0 g of tea. Within each pair, each tea bag type is buried 15 cm from each other. Five pairs were randomly buried in each plot at a minimum distance of 2.0 m from the plot sides, for a total of 100 tea bags buried in 24 April 2019. One day before the experiment was set up, 55 bags from each tea type were weighed in the lab with a spring (precision = 0.0001 g). The five extra bags from each tea type were carried to the field but were not buried and were used as manipulation controls. After returning from the field, they were weighed, dried in an oven at 60 ºC for 72 h, and weighed again. We combined both measures to obtain a single correction factor to account for mass losses during transportation and humidity losses: 0.9433 for the green tea, and 0.9318 for the red tea. All initial mass values from the 100 tea bags were multiplied by the corresponding correction factor to obtain initial dry mass values for each bag.

After two months (24 June 2019), the tea bags were recovered and taken to the lab, where they were dried at 60 ºC in an oven for 72 h. Each bag was then carefully cleaned from soil particles and plant roots using a brush and weighed. The final tea dry mass was obtained by subtracting 0.2424 g for the red tea and 0.2449 for the green tea, which was the mass related to the bag, threads, and label. We left the tea bags for only two months instead of three months as suggested by Keuskamp et al. (2013) because in another experiment carried out in 2018 in the same region, we lost many tea bags due to excessive decomposition (Soares et al. 2020). In these cases, Keuskamp et al. (2013) recommend a reduced
incubation time because decomposition rates can be underestimated. The method assumes that the red tea is in the first phase of the decomposition, so that if the red tea decomposes excessively, entering the second phase of decomposition, it is not possible to calculate $k$ (http://www.teatime4science.org/faq/). Even though the tea bags stayed for only 60 days, we still lost seven tea pairs due to the high decomposition of the red tea.

The TBI model estimates the stabilization factor ($S$) based upon the green tea decomposition, and the decomposition rate ($k$) considering the red tea decomposition as fitted by the asymptotic model (Keuskamp et al. 2013):

$$W_r(t) = a_r e^{-kt} + (1 - a_r)$$

where $W_r(t)$ is the remaining mass of red tea after $t$ days, $a_r$ is the labile fraction of the red tea, and $(1 - a_r)$ is the recalcitrant fraction. The labile fraction is estimated by:

$$a_r = H_r (1 - S)$$

where $H_r = 0.552 \text{ g g}^{-1}$ and is the chemically hydrolysable fraction of the red tea, and $S$ is the stabilization factor (Keuskamp et al. 2013), estimated by:

$$S = 1 - \frac{a_g}{H_g}$$

where $H_g = 0.842 \text{ g g}^{-1}$, and is the chemically hydrolysable fraction of the green tea, and:

$$a_g = 1 - \frac{W_f}{W_0}$$

where $W_f$ and $W_0$ are the final and initial masses of the green tea, respectively.

**Data analysis**

We used a Principal Components Analysis (PCA) to reduce the dimensionality of soil chemical variables. Concentrations of K and P were ln-transformed to obtain normal distributions, which were verified using Shapiro-Wilk tests. All variables were then standardized for zero means and unity variance. We also used PCA to evaluate forest structure variables; forest stratification (coefficient of variation of DBH) was transformed using the Box-Cox method to obtain a normal distribution. For both PCA analyses we used the Kaiser criterion and selected axes with eigenvalues > 1 (Legendre and Legendre 2012). We calculated the correlation between the resulting soil PCA axes and soil physical properties (soil moisture and clay content) with the Pearson Correlation Coefficient. Both variables were strongly correlated with the PCA first axis of chemical variables (Soil 1), as well as between each other (see Results – Table 2).

The physical and chemical soil variables and vegetation structure were then used in a Structural Equations Model (SEM) as exogenous variables to evaluate their direct effects on decomposition rates.
(k) and stabilization factors (S) (Grace 2006). Vegetation structure was evaluated considering the first two PCA axes (Veg1 and Veg 2, see Results). To evaluate the effects of soil, we constructed three SEM models, each considering different effects of the physical variables. We used only clay content to summarize the physical variables because it was strongly correlated with soil moisture (see Results – Table 2). The models were I) Clay content, Soil 1, Soil 2 (chemical and physical variables); II) Clay content, Soil 2 (chemical and physical variables); III) Soil 1, Soil 2 (only chemical variables). Model II considered that clay content and Soil 1 were highly correlated, but since clay content directly influences soil chemical properties, clay content would be enough to predict litter decomposition. We used model selection methods by considering AICc criterion to select the best model.

Considering that soil and vegetation covary, we also included correlations between soil and vegetation variables. Model fit was evaluated considering differences between the observed and predicted covariance structure, the Comparative Fit Index (CFI), and the Root Mean Square Error of Approximation (RMSEA) following (Hooper et al. 2008). These analyses were carried out using the lavaan package (Rosseel 2012) in R (R Core Team 2018).

**Results**

Soil physical and chemical properties and forest structure presented large variation among plots (Table 1).

Table 1. Mean, standard deviation (SD) and range of measured variables describing soil chemical and physical variables and forest structure, and variables estimated by the Tea Bag Index.
Variables | Mean | SD | Range
---|---|---|---
**Soil chemical properties (n = 10)**
P pH (CaCl$_2$) | 5.71 | 0.543 | 5.00 – 6.70
N (mg kg$^{-1}$) | 3,627 | 1,413 | 1,974 – 6,538
P (mg dm$^{-3}$) | 18.9 | 8.12 | 11.0 – 34.0
K (mmol$_{c}$ dm$^{-3}$) | 3.84 | 0.714 | 3.2 – 5.1
N:P | 198.0 | 44.27 | 123.4 – 247.5
C:N | 9.47 | 1.184 | 7.06 – 11.72
OM (g dm$^{-3}$) | 59.6 | 26.09 | 34.0 – 113.0
CEC (mmol$_{c}$ dm$^{-3}$) | 133.0 | 61.83 | 67.2 – 224.7
BS (%) | 82.1 | 11.45 | 64.0 – 95.1

**Soil physical properties (n = 10)**
Soil moisture (%) | 18.5 | 8.49 | 5.6 – 30.9
Clay content (%) | 9.4 | 5.20 | 3.0 – 18.4

**Forest structure (n = 10)**
Basal area (m$^{2}$ ha$^{-1}$) | 46.2 | 21.88 | 19.1 – 97.0
Mean DBH (cm) | 8.15 | 1.161 | 6.30 – 9.85
Forest stratification – CV DBH | 1.006 | 0.197 | 0.846 – 1.442
Tree density (ind ha$^{-1}$) | 4,200 | 666.7 | 3,200 – 5,100

**Tea Bag Index (n = 43)**
Decomposition rate – $k$ (g g$^{-1}$ day$^{-1}$) | 0.028 | 0.017 | 0.009 – 0.098
Stabilization factor – $S$ | 0.350 | 0.051 | 0.211 – 0.426

The two PCA axes related to soil chemical attributes explained 85.4% of the variance. The first axis (Soil 1) explained 60.2% of the variation (eigenvalue = 5.42) and was positively correlated with CEC, OM, BS, pH, N, and P (Fig. 1). The second axis (Soil 2) explained 25.2% of the variation (eigenvalue = 2.27) and was positively correlated with K and N:P ratio, and negatively correlated with the C:N ratio (Fig. 1). The ordination indicates that the studied area included plots that presented a large variation in soil chemical properties, forming a gradient (Table 1, Fig. 1).

Soil chemical properties as indicated by the first PCA axis (Soil 1) was strongly correlated with clay content and soil moisture, whereas Soil 2 was not correlated with either variable (Table 2). Also, clay content and soil moisture were strongly correlated with each other (Table 2).

Table 2. Pearson’s correlation coefficients between soil physical properties and soil chemical variables summarized by PCA axes 1 (Soil 1) and 2 (Soil 2). *** $P < 0.001$. 
The PCA on forest structure variables explained 82.7% of the variation in the first two axes. The first axis (Veg 1) explained 51.9% of the variance (eigenvalue = 2.07) and was positively correlated with mean DBH, tree density, and basal area (Fig. 2). The second axis (Veg 2) explained 30.8% of the variation (eigenvalue = 1.23) and was positively correlated with forest stratification and negatively correlated with mean DBH and tree density (Fig. 2). Therefore, the PCA indicated a large spatial variation in relation to tree sizes, density, and forest stratification (CV DBH).

The three structural equations models showed a good fit to the covariance matrix ($c^2 < 0.022; P > 0.900$), with adequate values of the other model evaluation indicators (CFI = 1.000; RMSEA = 0.000, $P > 0.630$). Model II presented the lowest AICc (537.7) when compared to models I (575.3) and III (664.4), and thus best explained the covariance matrix. In model II, Veg 1 (which was positively correlated with basal area and tree sizes) was not correlated with soil properties, whereas Veg 2 (which was correlated with forest stratification) was negatively correlated with clay content, indicating that higher forest stratification was found in less fertile plots that had lower clay content (Fig. 3). There was also a significant but weak positive correlation between the decomposition rate and the stabilization factor ($r = 0.354, P = 0.028$), suggesting that where decomposition is slower, more organic matter is stabilized.

Decomposition rates estimated from each pair of tea bags varied tenfold, between 0.009 and 0.098 g g$^{-1}$ day$^{-1}$ ($CV = 0.60$, Table 1). Decomposition rates were related with Veg 1, indicating higher rates in plots with higher basal areas and larger trees (Fig. 3), although this relationship explained relatively few (19%) of the variation.

The stabilization factor $S$ varied between 0.211 and 0.426 ($CV = 0.15$, Table 1). The model explained 54% of the variation in the stabilization factor. The stabilization of the organic matter was strongly influenced positively by clay content, with a negative effect of Veg 2, indicating lower stabilization of the organic matter in areas with higher forest stratification (Fig. 3).

**Discussion**

Decomposition processes can be very different in old-growth when compared to degraded forests (Borders et al. 2006; Yeong et al. 2016). However, comparative studies may not allow to evaluate the factors that influence local decomposition processes, because the large variation between natural and degraded forests can obscure more subtle variations found in natural, preserved forests (Bradford et al. 2016). For example, Oliveira et al. (2019) found both soil and plant functional diversity effects on leaf
litter decomposition in a tropical Atlantic Forest (Brazil), suggesting that effects at small spatial scales can be important.

Drivers of leaf litter decomposition at small spatial scales can influence the decomposition and stabilization of the organic matter, sometimes with effects as large as those of drivers that influence decomposition at large spatial scales (Bradford et al. 2016, 2017). We found a large variation (an order of magnitude) in leaf litter decomposition rates, at a small spatial scale, which was related only with the structure of an old-growth riparian forest. The stabilization of the organic matter was less variable and was strongly related with soil properties and also with forest structure.

The exogenous variables used as predictors of the decomposition process were not correlated with each other, except for the correlation between Veg 2 and clay content. However, since this forest structure axis was highly correlated with forest stratification ($r = 0.936$), the correlation between forest structure and clay content should be evaluated with caution. Plots near the river presented higher forest stratification which may be due to higher light penetration when compared to plots in the forest interior. Since plots near the river tended to present lower clay content, the correlation between forest stratification and soil clay content can be spurious because these effects may be confounded with distance from the river. Although a correlation between forest structure and soil properties was found, the structural equations model allowed to separate the effects of each driver on the processes involved in the decomposition of the organic matter.

Decomposition rates of the organic matter were correlated with the first axis of forest structure (Veg 1), which was represented by areas with higher tree density, mean DBH, and basal area. Forests with more developed canopies and higher tree densities present higher primary production and produce higher amounts of leaf litter (Teixeira et al. 2020). The additional leaf litter produced contributes to larger amounts of resources available for decomposers, which can positively influence their activity (Nunes and Pinto 2007; Silva-Sánchez et al. 2019), increasing decomposition rates (Lajtha et al. 2018). The tea bags were initially made of 0.25 mm woven nylon mesh and now are made of unwoven polypropylene; the bag material may limit the access of macro and most mesofauna (Setälä et al. 1996), so that most decomposition observed is due to microbial activity (Keuskamp et al. 2013).

Although significant, the correlation with Veg 1 explained few of the variation of decomposition rates (19%), since our data indicate a high variation in the individual estimates of $k$, varying an order of magnitude. High individual variation in $k$ estimates was also found by Saint-Laurent and Arsenault-Boucher (2020) in their study on temperate riparian forests, but decomposition rates were not related with soil properties or other environmental variables. The fitted SEM model showed that decomposition rates were directly related with forest structure while maintaining the other variables constant, suggesting that at this spatial scale the variation in vegetation is more important than other environmental factors such as differences in soil properties. The composition of old-growth forests may have more influence on soil communities, with the development of more specialized microbial communities depending on the leaf litter traits of different plant species, contributing to the heterogeneity in decomposition rates at this
spatial scale (e.g., Austin et al., 2014). In addition, soil nutrient availability and soil fertility recorded in this old-growth forest could be very high when compared with other riparian forests in the region (e.g., Soares et al. 2020), and it is possible that soil properties were not important for decomposition rates in our studied forest because there were no limiting resources for decomposition, although further studies are necessary to test this hypothesis.

On the other hand, the SEM model explained 54% of the variation in the stabilization factor $S$, which was strongly influenced by soil properties. The selected model included clay content instead of Soil 1 as a predictor of $S$, even though these variables were highly correlated (Table 2). The strong correlation of clay content with Soil 1 indicates that areas that presented higher $S$ values were those with higher SOM, CEC, and soil base saturation, variables that were strongly correlated with each other and with clay content. Also, several nutrients are correlated with clay content, including major cations, CEC, N, and P (Schoenholtz et al. 2000; Woodward et al. 2015; Aprile and Lorandi 2019). Since the tea was not in direct contact with clay surfaces, clays may have not directly influenced SOM formation, but may have had indirect effects by influencing the microbial community. The decomposition of the labile fraction enables the incorporation of this substrate in microbial biomass and in byproducts, which may constitute a large part of stabilized soil organic matter (Cotrufo et al. 2013). Considering that the stabilization factor is directly related with the transformation of the labile fraction into recalcitrant fraction (Keuskamp et al. 2013), these results suggest that this mechanism can contribute strongly with the stabilization of the organic matter and consequently carbon fixation in the soil.

The variation in the stabilization factor $S$ was also significantly influenced by Veg 2, suggesting that forest stratification can negatively influence $S$. Although Veg 2 was correlated with clay content, the SEM model suggests an independent, negative effect of forest stratification. This effect can be related with the increased penetration of light into the forest, which can influence microclimatic factors such as temperatures at the soil level, increasing litter decomposition (Ottermanns et al. 2011; Mayer et al. 2017). Higher soil temperatures can reduce the stabilization factor $S$ independently of soil moisture (Petraglia et al. 2019). Our study showed that even at a small spatial scale within the same forest, differences in forest structure can influence the stabilization factor.

The contribution of soil properties for the stabilization of the organic matter can be lower in managed forests when compared to natural forests (Lukumbuzya et al. 1994; Berkelmann et al. 2018). In a study carried out in the same region, Soares et al. (2020) found a strong relationship between $S$ and soil base saturation in a riparian forest remnant, but did not find this relationship in a riparian forest under restoration. The factors that contribute to the variation on decomposition processes within old-growth forests can differ from those in degraded forests or those under restoration (Borders et al., 2006; Yeong et al., 2016; Zhou et al., 2018), pointing to the importance of understanding these processes at small spatial scales (Bradford et al. 2016). Therefore, natural forests may have mechanisms of organic matter stabilization that differ in relation to managed or degraded forests that needs to be better understood.

**Conclusions**
Our study showed that the drivers of decomposition in forests can be related with both vegetation structure and soil properties, although their relative influence depends on the decomposition parameter evaluated. Tree sizes and plot basal area positively influenced decomposition rates but did not influence the stabilization factor. On the other hand, forest stratification had negative effects, whereas clay content had strong positive effects on the stabilization factor. This heterogeneity at small spatial scales can contribute to the resilience of old-growth forests, strengthening ecosystem functions such as nutrient cycling and carbon fixation, and highlighting the importance of small-scale variation in monitoring restored areas to evaluate the recovery of ecosystem processes. Studies comparing the stabilization factor in soils within preserved and degraded forests could test these hypotheses and contribute to restoration techniques that aim to increase carbon fixation in the soil.

Declarations

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Authors’ contributions

All authors contributed to the study conception and design. Material preparation, data collection, and writing initial draft: PHGF. Data analysis, writing final version, review and editing: ALTS and MOT. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests
The authors declare that they have no competing interest

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