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

Keywords: Tea bag index, forest structure, carbon fixation, nutrient cycling

Posted Date: August 27th, 2020

DOI: https://doi.org/10.21203/rs.3.rs-61797/v1

Version of Record: A version of this preprint was published on February 9th, 2021. See the published version at https://doi.org/10.1186/s40663-021-00293-0.

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.

Methods: We evaluated decomposition rates and stabilization of soil organic matter using the Tea Bag Index in an old-growth riparian forest in southeastern Brazil. We buried 50 pairs of green and red tea at two distances from the watercourse to evaluate the effects of forest structure and soil properties on decomposition processes. Forest structure and soil properties were described using Principal Components Analysis (PCA). The main axes for each analysis were considered predictors of decomposition processes using a structural equations model.

Results: Decomposition rates presented a large variation among tea bags and were positively correlated with forest structure, as characterized by higher basal area, larger trees, and tree density. Higher decomposition rates were probably correlated with higher litter production and microbial activity. On the other hand, stabilization factor was related mainly to soil chemical properties, with higher values with increased soil fertility as indicated by the PCA axes. Further analyses evaluated the effects of clay content, soil moisture, soil organic matter, soil base saturation, and soil fertility as predictors of the stabilization factor. These predictors were highly correlated, but clay content was the best predictor, explaining 79% of the variation among plots.

Conclusions: These results showed that this old-growth forest presented high heterogeneity in both forest structure and soil properties at small spatial scales, that influenced decomposition processes and contributed to small-scale variation in nutrient cycling. Heterogeneity in ecological processes can contribute to the resilience of old-growth forests, strengthening ecosystem functions such as nutrient cycling and carbon fixation, and highlighting the importance of restoration strategies focused in the recovery 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 substances 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 progresses 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) .

The energy source used in the microbial activity during decomposition consists of organic carbon, so that part of the nutrients is released and made available for plant use, and part is immobilized during microbial growth (Berg and McClaugherty 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 effectively decomposed and the speed of the decomposition process generally increase with temperature and humidity, stimulating microbial activity (Bradford et al. 2016). On the other hand, litter quality is strongly related to the amount of lignin and other recalcitrant compounds (Duddigan et al. 2020). High-quality litter is more easily decomposed due to the lower C:N ratio, whereas the decomposition of low-quality litter, with higher amounts of lignin, is slower and may need specialized organisms to be decomposed (Berg 2014), or higher availability of soil nutrients that can be transferred to leaf litter (Bonanomi et al. 2017).

The stabilization of soil organic matter (SOM) is a complex process, and can be influenced by the available nutrients, soil texture and aggregation, and biological activity (Lajtha et al. 2018; Wiesmeier et al. 2019). The recalcitrant fraction of leaf litter that is not decomposed can contribute to SOM stocks (Berg and McClaugherty 2014). On the other hand, part of the labile fraction can be incorporated in the microbial biomass or their byproducts, and can be stabilized in SOM (Cotrufo et al. 2013). The stabilization of SOM is also favored by higher clay surfaces, oxides of iron and aluminum, and by the formation of aggregates (Wiesmeier et al. 2019).

Several factors influence litter decomposition processes, especially local climatic conditions, litter quality, and the composition of microbial communities (Aerts 1997; Bradford et al. 2016, 2017; Djukic et al. 2018), which are strongly influenced by the vegetation structure and soil physical and chemical properties. Soil fertility present large variation among ecosystems, and even at small spatial scales, since fertility is strongly related with soil texture and the structure and composition of plant communities (Spielvogel et al. 2016; Metzger et al. 2017). The structure of the vegetation directly influences the microclimate conditions, hydrological movements, and soil properties (Krishna and Mohan 2017; Bélanger et al. 2019). For example, higher forest stratification can provide higher radiation input, increasing temperatures and reducing soil moisture (Yeong et al. 2016), which are positively related with decomposition rates (Petraglia et al. 2019). Further, forests with more developed canopies and higher tree density produce more leaf litter, and this greater input can promote local microbial activity (Nunes and Pinto 2007; Silva-Sánchez et al. 2019). This process can be more complex in unmanaged old-growth forests due to the higher structural complexity on the soil surface, litter spatial distribution, stronger relationships between plants and soil, and responses of soil properties to this variation (Austin et al. 2014; Lajtha et al. 2018; Soares et al. 2020).

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).

Riparian forests have large importance for the environmental quality of watersheds, contributing for important ecosystem functions such as the maintenance of biodiversity and water quality, cycling of nutrients and carbon, and contributing to regional climate (Naiman et al. 2005). These 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 (Woodward et al. 2015). Due to their ecological importance and strong deforesting pressure, the restoration of riparian forests has been stimulated worldwide (Hjältén et al. 2016; Dybala et al. 2019). However, the recovery of canopy cover may be not enough for ecosystem recovery, and establishing references is necessary to evaluate the recovery of ecosystem functions (Boudell et al. 2015; Matzek et al. 2016).

Therefore, an understanding of the functioning of preserved ecosystems is necessary to select adequate indicators for the monitoring of restored ecosystems, such as the processes of organic matter decomposition (Pollock et al. 2012; Dey and Schweitzer 2014). Some studies found that decomposition processes can be very different in old-growth and degraded forests (Borders et al. 2006; Yeong et al. 2016). However, comparative studies may not allow the evaluation of the factors that have most local influence on decomposition rates, and more detailed studies on old-growth riparian forests are necessary to understand the decomposition processes in these preserved systems (Bradford et al. 2016). For example, Saint-Laurent and Arsenault-Boucher (2020) did not find effects of environmental variables or soil properties on the decomposition and stabilization of the organic matter in Canadian riparian forests. On the other hand, Oliveira et al. (2019) found both soil and plant functional diversity effects on leaf litter decomposition of a tropical Atlantic Forest in Brazil, suggesting that factors with effects at small spatial scales can be important. Further, the structure of old-growth Atlantic forests can be very complex, contributing for higher microclimate heterogeneity (Ottermanns et al. 2011), as well as influencing patterns of litterfall, nutrient cycling and carbon fixation (Teixeira 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 the standard TBI methods (Keuskamp et al. 2013). In this way, we aimed to identify which factors at small spatial scales influence the 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 high preserved remnant 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 by 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 (masl). Geologically, the region is in the residual plateaus of Franca/Batatais and is composed by intrusive Serra Geral, with deep distroferric red latosols, very deep, 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 attributes 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 (R plots) and five plots at a 30 m distance from the river (I plots). 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 composed to form a single sample. In the laboratory, a subsample was obtained from each compound sample and put up in containers. We determined soil moisture by initially determining the subsample wet mass and after drying at 65 ºC in an oven until dry mass stabilized. Soil moisture was then obtained as h = (wet mass – dry mass)/dry mass × 100. 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 (V%) 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):

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

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:

$$a_r = H_r(1 - S) \tag{2}$$

where $H_r = 0.552$ 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:

$$S = 1 - \frac{a_g}{H_g} \tag{3}$$

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

$$a_g = 1 - \frac{Wf_g}{W0_g} \tag{4}$$

where Wf_g and $W0_g$ 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).

The PCA soil and vegetation axes 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). 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).

We found a strong effect of PCA Soil axis 1 on the stabilization factor *S* (see Results), and previous studies also found an effect of soil base saturation in natural remnants of riparian forest (Soares et al. 2020). Therefore, we evaluated the following variables as predictors of mean *S* per plot: soil organic matter, soil base saturation, clay content, soil moisture, and PCA Soil axis 1. Different linear regression models were fit for each predictor variable, and we selected the model with the lowest Akaike Information Criterion calculated for small samples (Burnham and Anderson 2002). Analyses were carried out using Systat 13 software, except SEM analyses as noted above, with significance levels considering a = 0.05.

Results

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 related with CEC, OM, V%, pH, N, and P (Fig. 1). The second axis (Soil 2) explained 25.2% of the variation (eigenvalue = 2.27) and was positively related with K and N:P ratios, and negatively related with CN ratios (Fig. 1). The ordination indicates a soil fertility gradient, with plots nearer the river less fertile than those in the forest interior, but with intermediate fertility plots in both distances (Fig. 1). The second PCA axis contributed to variation at the same distance from the river, with no apparent pattern (Fig. 1).

Fig. 1. Ordination of plots near the river (squares) and in the forest interior (circles) by Principal Components Analysis in relation to soil chemistry: cation exchange capacity (CEC), soil base saturation (V), soil organic matter (OM), nitrogen (N), phosphorus (P), potassium (K), N:P and C:N ratios.

Soil fertility as indicated by the first PCA axis (Soil 1) was strongly correlated with clay content and soil moisture, as well as with soil base saturation and soil organic matter (Table 1). In fact, all these variables were correlated with each other (Table 1).

Table 1.

Pearson’s correlation coefficients between soil predictor variables. ** $P < 0.01$, *** $P < 0.001$.

Predictor variables	Clay content	Soil moisture	Soil base saturation	Soil organic matter
Soil moisture	0.973***			
Soil base saturation	0.875**	0.871**		
Soil organic matter	0.972***	0.943***	0.798**	
PCA Soil 1	0.968***	0.939***	0.889**	0.965***

The PCA on forest structure variables explained 82.7% of the variation in the first two axes. The first axis (Veg 1) explained 51.2% 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, to a lesser degree, negatively correlated with mean DBH and tree density (Fig. 2). Both axes contributed to separate plots at different distances from the river, so that plots nearer the river presented higher forest stratification and basal area than those in the forest interior (Fig. 2). Tree density and mean tree sizes contributed to variation in forest structure among plots located at the same distance from the river (Fig. 2).

Fig. 2. Ordination of plots near the river (squares) and in the forest interior (circles) by Principal Components Analysis in relation to forest structure: basal area, tree density, mean DBH, and forest stratification (CV DBH).

The structural equations model showed a good fit to the covariance matrix (c^2 = 0.021, df = 2, P = 0.990; CFI = 1.000; RMSEA = 0.000, P = 0.991). Veg 1 (which was positively related with basal area and tree sizes) was weakly correlated with Soil 1 (P = 0.057), whereas Veg 2 (which was more related with forest stratification) was negatively correlated with Soil 1, indicating that higher forest stratification was found nearer the watercourse, in less fertile plots (Fig. 3). 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). 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 presented lower variation (0.211 – 0.426, CV = 0.15) than decomposition rates. The model explained 53% of the variation in the stabilization factor. The stabilization of the organic matter was strongly influenced by soil chemistry, with positive effects of soil fertility, as well as K concentrations and N:P ratios (Fig. 3). There was also a trend for a negative effect of Veg 2 (P = 0.054), suggesting lower stabilization of the organic matter in areas with higher forest stratification (Fig. 3).

Fig. 3. Structural equation model depicting the effects of forest structure (Veg 1, Veg 2) and soil chemical attributes (Soil 1, Soil 2) on decomposition rates (*k*) and stabilization factor (*S*) as calculated by the Tea Bag Index. Arrow widths are proportional to the standardized coefficients, which are also indicated next to the line. Dashed arrows indicate that $P = 0.054$ (Veg 2 ® S) and $P = 0.057$ (Veg 1 « Soil 1). ** $P < 0.01$, *** $P < 0.001$. Green arrows indicate positive effects, red arrows negative effects, and grey lines indicate non-significant effects ($P > 0.25$).

Considering the mean values per plot, these five soil variables that were proposed as predictors were positively related with the stabilization factor *S* (Table 2). However, the best predictor was soil clay content, with the lowest AICc value, explaining 79% of the variation in the stabilization factor; the probability that this model was the best explanation for the variation in *S* was almost three times higher than for the second best model (Table 2).

Table 2.

Results of model selection on the effects of different predictor variables on the stabilization factor (*S*). Adj-R^2 = adjusted coefficient of determination, AICc = Akaike Information Criterion for small samples, w_i = Akaike weights.

Predictor variable	Equation	*P*	Adj-R^2	AICc	w_i
Clay content	0.291 + 0.006x	< 0.001	0.79	-46.02	0.594
Soil moisture	0.281 + 0.004x	0.001	0.74	-43.85	0.201
Soil base saturation	0.131 + 0.003x	0.002	0.69	-42.08	0.083
PCA Soil 1	0.350 + 0.013x	0.002	0.68	-41.88	0.075
Soil organic matter	0.281 + 0.001x	0.003	0.65	-40.95	0.047

Discussion

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). In the present study, we found a large variation in leaf litter decomposition rates, spanning almost an order of magnitude even at a small spatial scale, which was related 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. Although forest structure and soil properties were correlated, the structural equations model allowed to separate the effects of each driver on the processes involved in the decomposition of the organic matter.

Forest structure was weakly correlated with soil fertility as represented by the first PCA axis (Soil 1). The correlation between Soil 1 and Veg 1 can be due to higher production of leaf litter in areas with higher basal area, larger trees, and higher tree density, as observed in other studies on semideciduous seasonal forests (Werneck et al. 2001; Nunes and Pinto 2007; Pinto et al. 2008). Higher leaf litter input can promote microbial activity and influence SOM stocks (Lajtha et al. 2018; Silva-Sánchez et al. 2019), whereas litter mineralization release important nutrients for tree growth. On the other hand, soil fertility was negatively correlated with forest stratification, which was related with distance from the river. Plots near the river presented higher forest stratification, but also lower clay content and soil moisture. Clay content, soil moisture, and soil fertility were highly correlated with each other. 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).

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 produce higher amounts of leaf litter, which can positively influence microbial activity (Nunes and Pinto 2007; Silva-Sánchez et al. 2019), increasing decomposition rates (Lajtha et al. 2018). Further, some studies suggest that soil microbial respiration is highly related with photosynthetic rates of the plant community, because with increased photosynthesis and primary production, the availability of root substrates increase and promote microbial activity, since the highest microbial biomass is found in the rhizosphere (Ryan and Law 2005; Tang et al. 2005).

Although significant, the correlation with Veg 1 explained few of the variation of decomposition rates (19%) in relation to pure error, since our data indicate a high variation in the individual estimates of *k*, varying almost an order of magnitude. High individual variation in *k* estimates was also found by Saint-Laurent and Arsenault-Boucher (2020) in their study on riparian forests, but decomposition rates were not related with soil properties or other environmental variables. Our data showed that decomposition rates were related with forest structure, 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).

On the other hand, the SEM model explained 53% of the variation in the stabilization factor *S*, which was strongly influenced by soil properties. The strong correlation 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. Clay surfaces, as well as oxides of iron and aluminum, tend to stabilize the organic matter (Schmidt et al. 2011). 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 be 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 carbon fixation in the soil.

The variation in the stabilization factor *S* was not significantly influenced by Veg 2 although a marginal value was found ($P = 0.054$), suggesting that forest stratification can negatively influence *S*. This is an expected result, since forest stratification can provide higher radiation input, increasing soil temperature and reducing humidity (Yeong et al. 2016). Our results showed that soil moisture was positively related with the decomposition process, although the model considering clay contents had a higher probability of explaining variation in *S*. Therefore, both soil properties and microbial activity can contribute for the stabilization of SOM.

The drivers of decomposition in forests can be related with vegetation structure, which influences microclimate conditions and local hydrological movements, and therefore forest soil properties and decomposition rates (Krishna and Mohan 2017; Bélanger et al. 2019). 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. Cations such as Ca^{2+} and Mg^{2+} can reduce the organic matter mass loss (Lukumbuzya et al. 1994), as well as contribute for aggregate formation and consequent stabilization of SOM (Powers and Salute 2011). Our study suggests that the stabilization of SOM can be strongly influenced by microbial composition, which should differ according to soil clay content, but future experiments are necessary to directly test this hypothesis.

Conclusions

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). This heterogeneity at small spatial scales can contribute to the resilience of old-growth forests (e.g., Feit et al., 2019), strengthening ecosystem functions such as nutrient cycling and carbon fixation, and highlighting the importance of restoration strategies focused in the recovery of ecosystem processes. Studies comparing the stabilization factor in soils within preserved and degraded forests could test these hypotheses and contribute on restoration techniques that aim to increase carbon fixation in the soil.

Declarations

Acknowledgments

We thank the Air Force Base of Pirassununga (FAYS) for the permission to work at Guarnição da Aeronáutica de Pirassununga. We also thank Gustavo Galetti, Débora Bessi and José Victor Silva for help in the field and lab work.

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.

Funding

This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES) – Code Financing 001, and FAPESP (proc. 2018/21913-8).

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

References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449. https://doi.org/10.2307/3546886

Aprile F, Lorandi R (2019) Cation Exchange Capacity in Tropical Soils. Lambert Academic Publishing

Austin AT, Vivanco L, González-Arzac A, Pérez LI (2014) There's no place like home? An exploration of the mechanisms behind plant litter-decomposer affinity in terrestrial ecosystems. New Phytol 204:307–314. https://doi.org/10.1111/nph.12959

Bélanger N, Collin A, Ricard-Piché J, et al (2019) Microsite conditions influence leaf litter decomposition in sugar maple bioclimatic domain of Quebec. Biogeochemistry 145:107–126. https://doi.org/10.1007/s10533-019-00594-1

Benbow ME, Barton PS, Ulyshen MD, et al (2019) Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecol Monogr 89:e01331. https://doi.org/10.1002/ecm.1331

Berg B (2018) Decomposing litter; limit values; humus accumulation, locally and regionally. Appl Soil Ecol 123:494–508. https://doi.org/10.1016/j.apsoil.2017.06.026

Berg B (2014) Decomposition patterns for foliar litter – A theory for influencing factors. Soil Biol Biochem 78:222–232. https://doi.org/10.1016/j.soilbio.2014.08.005

Berg B, McClaugherty C (2014) Plant Litter. Springer Berlin Heidelberg, Berlin, Heidelberg

Berkelmann D, Schneider D, Engelhaupt M, et al (2018) How rainforest conversion to agricultural systems in Sumatra (Indonesia) affects active soil bacterial communities. Front Microbiol 9:1–13. https://doi.org/10.3389/fmicb.2018.02381

Bonanomi G, Cesarano G, Gaglione SA, et al (2017) Soil fertility promotes decomposition rate of nutrient poor, but not nutrient rich litter through nitrogen transfer. Plant Soil 412:397–411. https://doi.org/10.1007/s11104-016-3072-1

Borders BD, Pushnik JC, Wood DM (2006) Comparison of leaf litter decomposition rates in restored and mature riparian forests on the Sacramento River, California. Restor Ecol 14:308–315. https://doi.org/10.1111/j.1526-100X.2006.00133.x

Boudell JA, Dixon MD, Rood SB, Stromberg JC (2015) Restoring functional riparian ecosystems: Concepts and applications. Ecohydrology 8:747–752. https://doi.org/10.1002/eco.1664

Bradford MA, Berg B, Maynard DS, et al (2016) Understanding the dominant controls on litter decomposition. J Ecol 104:229–238. https://doi.org/10.1111/1365-2745.12507

Bradford MA, Ciska GF, Bonis A, et al (2017) A test of the hierarchical model of litter decomposition. Nat Ecol Evol 1:1836–1845. https://doi.org/10.1038/s41559-017-0367-4

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York

Cotrufo MF, Wallenstein MD, Boot CM, et al (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? Glob Chang Biol 19:988–995. https://doi.org/10.1111/gcb.12113

Dey DC, Schweitzer CJ (2014) Restoration for the Future: Endpoints, Targets, and Indicators of Progress and Success. J Sustain For 33:37–41. https://doi.org/10.1080/10549811.2014.883999

Djukic I, Kepfer-Rojas S, Schmidt IK, et al (2018) Early stage litter decomposition across biomes. Sci Total Environ 628–629:1369–1394. https://doi.org/10.1016/j.scitotenv.2018.01.012

Duddigan S, Shaw LJ, Alexander PD, Collins CD (2020) Chemical underpinning of the Tea Bag Index: an examination of the decomposition of tea leaves. Appl Environ Soil Sci 2020:. https://doi.org/10.1155/2020/6085180

Dybala KE, Matzek V, Gardali T, Seavy NE (2019) Carbon sequestration in riparian forests: A global synthesis and meta-analysis. Glob Chang Biol 25:57–67. https://doi.org/10.1111/gcb.14475

Embrapa (1997) Manual de Métodos de Análise de Solo. Emprapa, Rio de Janeiro

Feit B, Blüthgen N, Traugott M, Jonsson M (2019) Resilience of ecosystem processes: a new approach shows that functional redundancy of biological control services is reduced by landscape simplification. Ecol Lett 22:1568–1577. https://doi.org/10.1111/ele.13347

Ferrari AL, Vecchia FADS, Colabone RDO (2012) Tendência e variabilidade anuais da temperatura e da pluviosidade em Pirassununga-SP. Rev Bras Climatol 10:30–46. https://doi.org/10.5380/abclima.v10i1.30585

Grace JB (2006) Structural Equation Modeling and Natural Sstems. Cambridge University Press, New York

Hjältén J, Nilsson C, Jørgensen D, Bell D (2016) Forest–stream links, anthropogenic stressors, and climate change: Implications for restoration planning. Bioscience 66:646–654. https://doi.org/10.1093/biosci/biw072

Hooper D, Coughlan J, Mullen M (2008) Structural equation modelling: guidelines for determining model fit. Electron J Bus Res Methods 6:53–60

Keuskamp JA, Dingemans BJJ, Lehtinen T, et al (2013) Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. Methods Ecol Evol 4:1070–1075. https://doi.org/10.1111/2041-210X.12097

Krishna MP, Mohan M (2017) Litter decomposition in forest ecosystems: a review. Energy, Ecol Environ 2:236–249. https://doi.org/10.1007/s40974-017-0064-9

Lajtha K, Bowden RD, Crow S, et al (2018) The detrital input and removal treatment (DIRT) network: Insights into soil carbon stabilization. Sci Total Environ 640–641:1112–1120. https://doi.org/10.1016/j.scitotenv.2018.05.388

Legendre P, Legendre L (2012) Numerical ecology, 3rd edn. Elsevier

Lukumbuzya TK, Fyles JW, Côté B (1994) Effects of base-cation fertilization on litter decomposition in a sugar maple forest in southern Quebec. Can J For Res 24:447–452. https://doi.org/10.1139/x94-061

Manzoni S, Piñeiro G, Jackson RB, et al (2012) Analytical models of soil and litter decomposition: Solutions for mass loss and time-dependent decay rates. Soil Biol Biochem 50:66–76. https://doi.org/10.1016/j.soilbio.2012.02.029

Matzek V, Warren S, Fisher C (2016) Incomplete recovery of ecosystem processes after two decades of riparian forest restoration. Restor Ecol 24:637–645. https://doi.org/10.1111/rec.12361

Metzger JC, Wutzler T, Dalla Valle N, et al (2017) Vegetation impacts soil water content patterns by shaping canopy water fluxes and soil properties. Hydrol Process 31:3783–3795. https://doi.org/10.1002/hyp.11274

Naiman RJ, Décamps H, McClain ME (2005) Riparia: ecology, conservation, and management of streamside communities. Elsevier Academic Press, London

Nunes FP, Pinto MTC (2007) Produção de serapilheira em mata ciliar nativa e reflorestada no alto São Francisco, Minas Gerais. Biota Neotrop 7:97–102. https://doi.org/10.1590/S1676-06032007000300011

Oliveira RAC, Marques R, Marques MCM (2019) Plant diversity and local environmental conditions indirectly affect litter decomposition in a tropical forest. Appl Soil Ecol 134:45–53. https://doi.org/10.1016/j.apsoil.2018.09.016

Osman KT (2013) Nutrient Dynamics in Forest Soil. In: Forest Soils: Properties and Management. Springer, Cham, pp 97–121

Ottermanns R, Hopp PW, Guschal M, et al (2011) Causal relationship between leaf litter beetle communities and regeneration patterns of vegetation in the Atlantic rainforest of Southern Brazil (Mata Atlântica). Ecol Complex 8:299–309. https://doi.org/10.1016/j.ecocom.2011.06.001

Pausas JG, Bond WJ (2020) On the three majorrecycling pathways in terrestrial ecosystems. Trends Ecol Evol in press. https://doi.org/10.1016/j.tree.2020.04.004

Petraglia A, Cacciatori C, Chelli S, et al (2019) Litter decomposition: effects of temperature driven by soil moisture and vegetation type. Plant Soil 435:187–200. https://doi.org/10.1007/s11104-018-3889-x

Pinto SIC, Martins SV, Barros NF, Dias HCT (2008) Produção de serapilheira em dois estádios sucessionais de floresta estacional semidecidual na reserva mata do paraíso, em Viçosa, MG. Rev Arvore 32:545–556. https://doi.org/10.1590/s0100-67622008000300015

Pollock MM, Beechie TJ, Imaki H (2012) Using reference conditions in ecosystem restoration : an example for riparian conifer forests in the Pacific Northwest. Ecosphere 3:1–23. https://doi.org/Unsp 98\rDoi 10.1890/Es12-00175.1

Powers JS, Salute S (2011) Macro- and micronutrient effects on decomposition of leaf litter from two tropical tree species: inferences from a short-term laboratory incubation. Plant Soil 346:245–257. https://doi.org/10.1007/s11104-011-0815-x

R Core Team (2018) R: A language and environment for statistical computing. In: R Found. Stat. Comput. Vienna, Austria. URL https//www.R-project.org/. url: http://www.R–project.org

Raij B van, Andrade JC, Cantarella H, Quaggio JA (2001) Análise química para avaliação da fertilidade de solos tropicais. Instituto Agronômico, Campinas

Rolim G de S, Camargo MBP de, Lania DG, Moraes JFL de (2007) Classificação climática de Köppen e de Thornthwaite e sua aplicabilidade na determinação de zonas agroclimáticas para o estado de são Paulo. Bragantia 66:711–720. https://doi.org/10.1590/S0006-87052007000400022

Rosseel Y (2012) lavaan: An R Package for Structural Equation Modeling. J Stat Softw 48:1–36

Rot BW, Naiman RJ, Bilby RE (2000) Stream channel configuration, landform, and riparian forest structure in the Cascade Mountains, Washington. Can J Fish Aquat Sci 57:699–707. https://doi.org/10.1139/f00-002

Ryan MG, Law BE (2005) Interpreting, measuring, and modeling soil respiration. Biogeochemistry 73:3–27. https://doi.org/10.1007/s10533-004-5167-7

Saint-Laurent D, Arsenault-Boucher L (2020) Soil properties and rate of organic matter decomposition in riparian woodlands using the TBI protocol. Geoderma 358:113976. https://doi.org/10.1016/j.geoderma.2019.113976

Sayer EJ, Banin LF (2016) Tree Nutrient Status and Nutrient Cycling in Tropical Forest—Lessons from Fertilization Experiments. In: Goldstein G, Santiago LS (eds) Tropical Tree Physiology. Springer International Publishing, pp 275–297

Sayer EJ, Rodtassana C, Sheldrake M, et al (2020) Revisiting nutrient cycling by litterfall—Insights from 15 years of litter manipulation in old-growth lowland tropical forest. Adv Ecol Res 62:173–223. https://doi.org/10.1016/bs.aecr.2020.01.002

Schmidt MWI, Torn MS, Abiven S, et al (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56. https://doi.org/10.1038/nature10386

Schoenholtz S., Miegroet HV, Burger J. (2000) A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. For Ecol Manage 138:335–356. https://doi.org/10.1016/S0378-1127(00)00423-0

Silva-Sánchez A, Soares M, Rousk J (2019) Testing the dependence of microbial growth and carbon use efficiency on nitrogen availability, pH, and organic matter quality. Soil Biol Biochem 134:25–35. https://doi.org/10.1016/j.soilbio.2019.03.008

Soares JAH, Souza ALT de, Pestana LF de A, Tanaka MO (2020) Combined effects of soil fertility and vegetation structure on early decomposition of organic matter in a tropical riparian zone. Ecol Eng 152:105899. https://doi.org/10.1016/j.ecoleng.2020.105899

Souza ALT, Fonseca DG, Liborio RA, Tanaka MO (2013) Influence of riparian vegetation and forest structure on the water quality of rural low-order streams in SE Brazil. For Ecol Manage 298:12–18. https://doi.org/10.1016/j.foreco.2013.02.022

Spielvogel S, Prietzel J, Kögel-Knabner I (2016) Stand scale variability of topsoil organic matter composition in a high-elevation Norway spruce forest ecosystem. Geoderma 267:112–122. https://doi.org/10.1016/j.geoderma.2015.12.001

Tang J, Baldocchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. Glob Chang Biol 11:1298–1304. https://doi.org/10.1111/j.1365-2486.2005.00978.x

Teixeira HM, Cardoso IM, Bianchi FJJA, et al (2020) Linking vegetation and soil functions during secondary forest succession in the Atlantic forest. For Ecol Manage 457:117696. https://doi.org/10.1016/j.foreco.2019.117696

Wachendorf C, Piepho H-P, Beuschel R (2020) Determination of litter derived C and N in litterbags and soil using stable isotopes prevents overestimation of litter decomposition in alley cropping systems. Pedobiologia (Jena) 81–82:150651. https://doi.org/10.1016/j.pedobi.2020.150651

Werneck MS, Pedralli G, Gieseke LF (2001) Produção de serapilheira em três trechos de uma floresta semidecídua com diferentes graus de perturbação na Estação Ecológica do Tripuí, Ouro Preto, MG. Rev Bras Botânica 24:195–198. https://doi.org/10.1590/s0100-84042001000200009

Wider RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642

Wiesmeier M, Urbanski L, Hobley E, et al (2019) Soil organic carbon storage as a key function of soils - A review of drivers and indicators at various scales. Geoderma 333:149–162. https://doi.org/10.1016/j.geoderma.2018.07.026

Woodward KB, Fellows CS, Mitrovic SM, Sheldon F (2015) Patterns and bioavailability of soil nutrients and carbon across a gradient of inundation frequencies in a lowland river channel, Murray-Darling Basin, Australia. Agric Ecosyst Environ 205:1–8. https://doi.org/10.1016/j.agee.2015.02.019

Yeong KL, Reynolds G, Hill JK (2016) Leaf litter decomposition rates in degraded and fragmented tropical rain forests of Borneo. Biotropica 48:443–452. https://doi.org/10.1111/btp.12319

Zhou Z, Wang C, Luo Y (2018) Effects of forest degradation on microbial communities and soil carbon cycling: A global meta-analysis. Glob Ecol Biogeogr 27:110–124. https://doi.org/10.1111/geb.12663

Figures

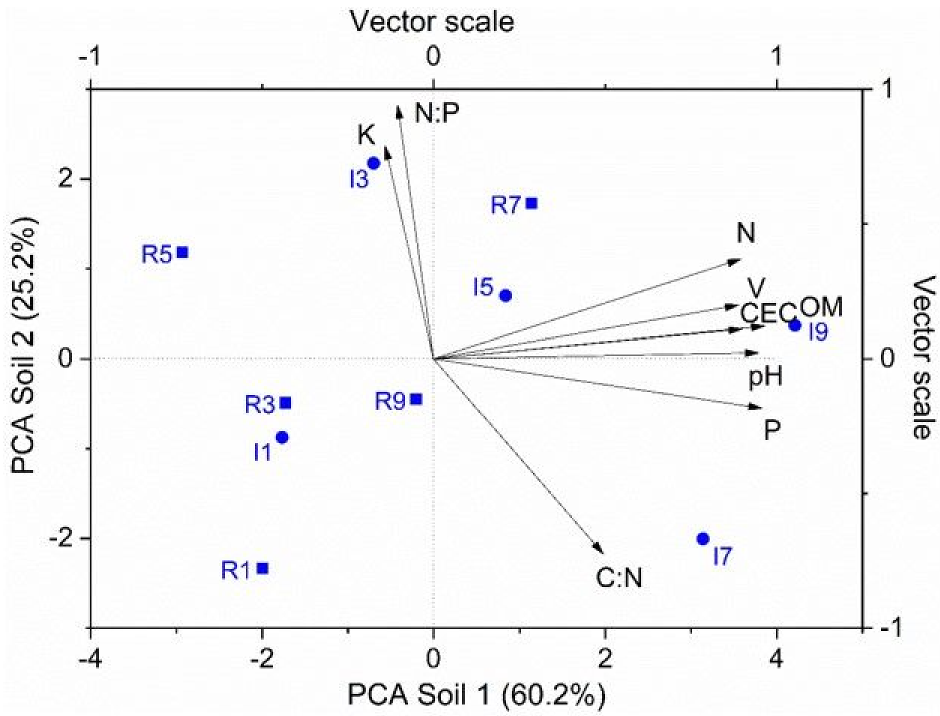

Figure 1

Ordination of plots near the river (squares) and in the forest interior (circles) by Principal Components Analysis in relation to soil chemistry: cation exchange capacity (CEC), soil base saturation (V), soil organic matter (OM), nitrogen (N), phosphorus (P), potassium (K), N:P and C:N ratios.

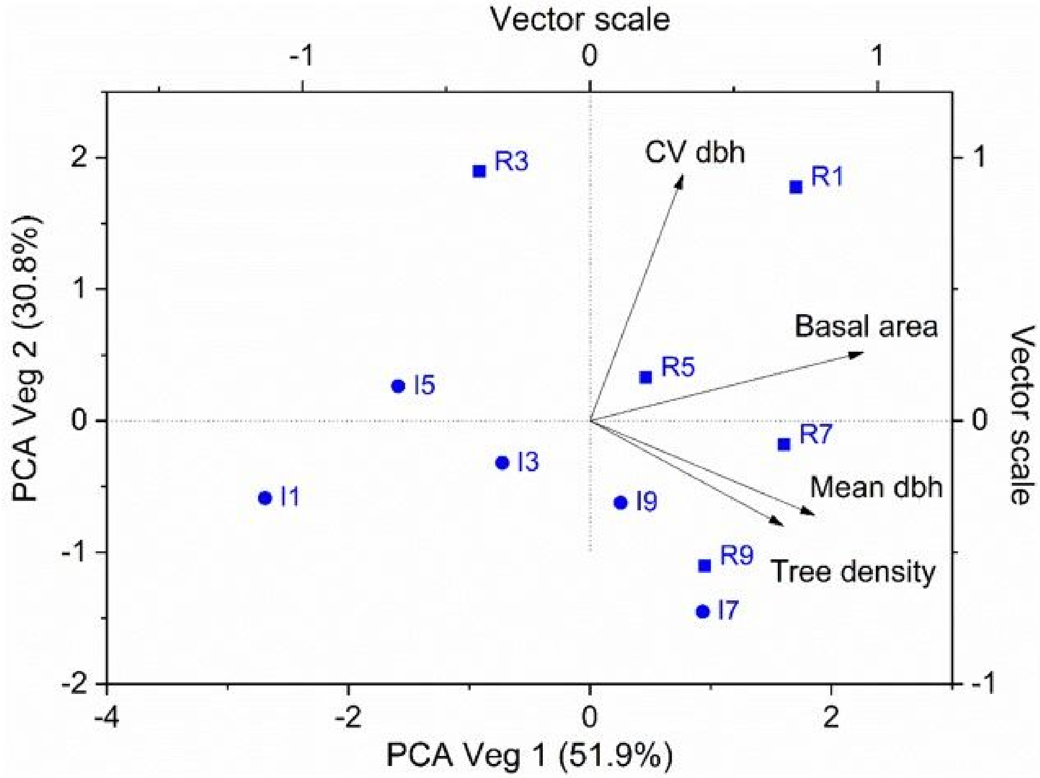

Figure 2

Ordination of plots near the river (squares) and in the forest interior (circles) by Principal Components Analysis in relation to forest structure: basal area, tree density, mean DBH, and forest stratification (CV DBH).

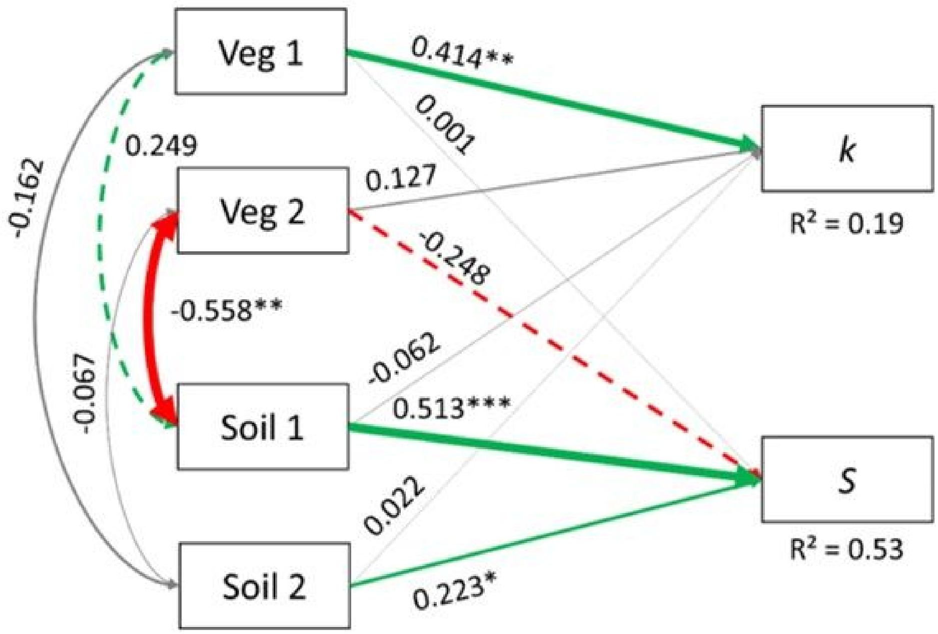

Figure 3

Structural equation model depicting the effects of forest structure (Veg 1, Veg 2) and soil chemical attributes (Soil 1, Soil 2) on decomposition rates (k) and stabilization factor (S) as calculated by the Tea Bag Index. Arrow widths are proportional to the standardized coefficients, which are also indicated next to the line. Dashed arrows indicate that P = 0.054 (Veg 2 → S) and P = 0.057 (Veg 1 → Soil 1). ** P < 0.01, *** P < 0.001. Green arrows indicate positive effects, red arrows negative effects, and grey lines indicate non-significant effects (P > 0.25).