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Land cover affects the breakdown of *Pinus elliottii* needles litter by microorganisms in soil and stream systems of subtropical riparian zones

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ABSTRACT

Riparian zones are important interface areas between soil and stream systems. Few studies carried out in tropical and subtropical regions evaluate litter decomposition in both stream water and riparian soils. Herein, we assessed the effects of land cover on microbial activity on the decomposition of an exotic litter (*Pinus elliottii* pine needles only) in water and soils of a subtropical riparian zone. Leaf litter breakdown rates (k in d^{-1}) were estimated for different land covers (Grassland without riparian vegetation, Grassland with riparian vegetation, Forest, and Silviculture). To assess the microbial influence on k, we used fine mesh litter bags with monospecific leaf litter of senescent pine needles. Streams in Silviculture land use showed high k values and orthophosphate, dissolved oxygen and water velocity accelerated the leaf litter breakdown in the stream system. The soil system of Silviculture, Forest, and Grassland with riparian vegetation land covers showed high k values due to the high moisture and litter stock on riparian soil. Only a minor difference between stream and soil systems highlights the significant changes and the negative effects of silviculture on subtropical riparian zones.

1. Introduction

Exotic plants largely used in monocultures are potential invaders and may affect riparian ecosystems (Castro-díez et al., 2017) by changing community structure attributes, such as species frequencies and occurrence (Fenoglio et al., 2016; Oficialdegui et al., 2019), and abiotic factors, such as fire regime, water depth, and soil properties (Castro-díez et al., 2017). As a consequence, changes in ecosystem functioning are expected due to alteration in nutrient and organic matter processing (Ferreira et al., 2019; Krevš et al., 2017; Kuglerová et al., 2017). Since 1950, the total area covered by *Eucalyptus* and *Pinus* in silviculture systems in Brazil has expanded rapidly (Carvalho et al., 2019), and *Pinus* silviculture now occupies extensive areas of South America (Olsson et al., 2019). Many of these exotic monocultures are currently managed close to or in riparian zones, areas with agriculture, and other land uses (Richardson et al., 2007).

Comparison of leaf litter breakdown of exotic monocultures and native plants is a useful tool for monitoring soil and stream ecosystems (Castro-díez et al., 2017; Kuglerová et al., 2017). Senescent leaves have a high contribution to biomass and energy input in riparian zones as a result of the leaf breakdown process (Tank et al., 2010; Tonin et al., 2017a; Wallace et al., 1997). This process is particularly important for stream metabolism, as photosynthetic rates are restricted by the vegetation canopy (Feio et al., 2018; Graça et al., 2015). Several factors increase the decay rates in the riparian zone, for example (Graça et al., 2015; Tiegs et al., 2019; Woodward et al., 2013): (i) litter diversity (Boyero et al., 2021); (ii) litter quality, determined by N and P concentrations and leaf toughness (Firmino et al., 2021; Sena et al., 2020); (iii) canopy cover (Fabian et al., 2018; Qu et al., 2021; Rezende et al., 2017); (iv) instream conditions including flow velocity, oxygen saturation and temperature (Martins et al., 2015; Rezende et al., 2020); and (v) biomass of microbial and invertebrate decomposers (Ayres et al., 2009; Graça et al., 2016; Rezende et al., 2021).

In general, low canopy cover in riparian zones increases the water temperature due to higher luminosity, and, consequently, the autochthonous production in stream channels (Rezende et al., 2017; Tank

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et al., 2010). The increased temperature and autochthonous production of open-canopy areas may result in higher leaf breakdown rates in both stream and soil systems compared areas with closed-canopy areas (Alvim et al., 2014; Rezende et al., 2017). The expected higher leaf breakdown rate in open-canopy riparian zones occurs mainly by microbial activity (Alvim et al., 2014; Marks, 2019). On the other hand, the soils of these areas may present reduced humidity, which decreases microbial and invertebrate activity, and reduced litter stock because of lower productivity and retention capacity (Carvalho et al., 2019; Olsson et al., 2019). Therefore, limited canopy cover may reduce leaf breakdown rate in the soil system of the riparian zone (Kurz et al., 2000; Principe et al., 2015). Furthermore, in desert systems, abiotic/physical breakdown *via* photodegradation is likely the most important contributor to decomposition (Ball et al., 2019; Day et al., 2018), a factor that might apply in systems with high canopy openness. The effects of changes in physical structure of riparian zones by anthropic alterations (Ferreira et al., 2019; Rezende et al., 2014) are well documented in Neotropical areas (Ferreira et al., 2019; Rezende et al., 2017). On the other hand, the information on the effects of alien plant invasion on leaf breakdown is still incipient in Neotropical riparian zones (Marks, 2019).

However, invertebrate decomposers tend to have low density in neotropical systems, making the microorganisms the most important group for the decomposition process in these areas (Alvim et al., 2015; Boyero et al., 2012; Rezende et al., 2014), especially for litter with tough tissue (Rezende et al., 2021; Sena et al., 2020), such as pine needles, the focus of this study. For this reason and because invertebrate decomposers have low preference for pine needles, here we investigate microbial breakdown only (Martínez et al., 2013a, 2013b). In this way, we aimed to assess land cover effects on decomposition of needles of the exotic silviculture species (*Pinus elliottii*) by microbial activity on stream and soil systems in subtropical riparian zones. We used fine mesh litter bags to assess microbial breakdown of senescent needles of *P. elliottii* in streams and riparian soils under different land covers in a region of the subtropics (Grassland without and with riparian vegetation, Mixed Ombrophilous Forest and Silviculture). Based on the premises that (i) environmental changes among different land covers alter the leaf breakdown rate and (ii) the *Pinus* sp. exotic silviculture leaves have low litter quality (high hardness and low nutrient concentration) compared to natural ones, our hypotheses are that the leaf breakdown of *Pinus elliottii* will be higher (i) in warm-water and nutrient-rich streams, compared to cold-water and nutrient-poor streams, and (ii) in riparian soils with high moisture and litter stock, compared to dry soils with low litter stock.

2. Methods

2.1. The study system

We selected 10 sampling sites in riparian zones distributed along the Wildlife Refuge of Campos de Palmas (16.582 ha; between 26°33′19.07 and 26°20′24.82″ S and 51°20′64″ and 51°43′8.82″ W) in Paraná State in Southern Brazil (Fig. 1). The study area is part of the Atlantic Rain Forest Biome, and its vegetation is composed of *stricto sensu* Steppe (clean field), Hygrophilous Steppe (wet field), and Mixed Ombrophilous Forest. In the riparian zones of the region there is a dominance of *Psychotria carthagenensis* Jacq.*,* *Daphnopsis fasciculata* (Meisn.)*,* *Vernonia discolor* (Spreng.) Less., and high occurrence of *Araucaria angustifolia* ((Bertol.) Kuntze, 1898)*,* *Ilex paraguariensis A. St. Hil., Psidium cattleianum* Sabine*,* *Ocotea porosa* (Nees & Mart.) Barroso, and *Inga uruguensis* Hook. & Arn. (ICMBio, 2013).

The climate is Cfa (c.f. Köppen, Humid subtropical), described as temperate subtropical. The altitude varies between 950 m and 1370 m above sea level. Rainfall and air temperature were obtained from meteorological station number 265 1035 of the National Agency of Waters of Brazil, located at 26°21′58.3″ S and 51°51′58.2″ W, available on the website hidroweb: http://hidroweb.ana.gov.br/. The mean

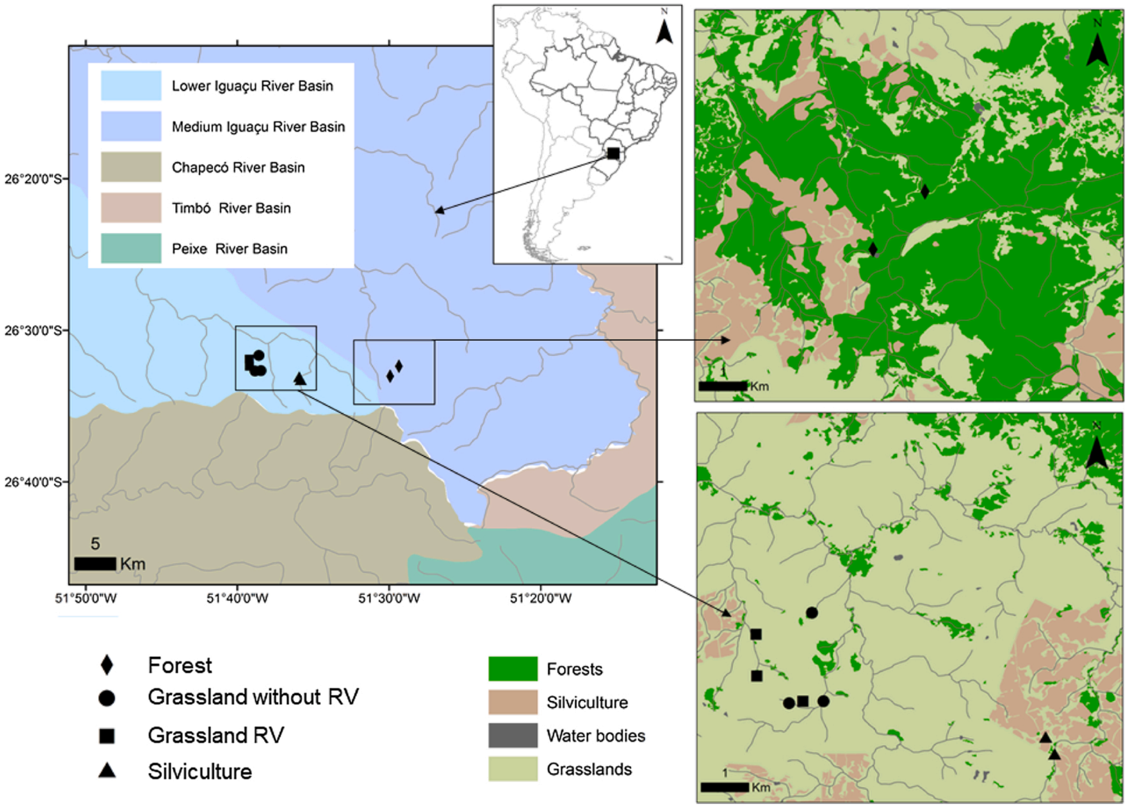

Fig. 1. Geographic location of sampling sites with different land covers (Forest, Silviculture, and Grasslands with and without riparian vegetation - RV) on Chopim river watershed, Paraná (Brazil).

annual air temperature is 16 °C and monthly range from 5 °C to 27 °C. The mean monthly precipitation throughout the year is 142 mm, ranging from 105 mm to 182 mm, with a yearly total of 1700 mm.

2.2. *Exotic silviculture species and procedures*

Pinus is a plant genus with a native distribution comprising broad areas of northern hemisphere, occupying a latitudinal range from 72 °N to 0° (Nobis et al., 2012). Native from Florida to South Carolina, *Pinus elliottii* is the leading species of its genus in agroforestry production in Brazil, mainly for charcoal for steelmaking and pulp for papermaking. *P. elliiottii* has a needle-shaped leaf, hard wood and its timber, pulp, and resin are economically important. This species presents potential for biological invasion, and is considered one of the most pervasive invasive species in Brazil (Bechara et al., 2013). It was already recorded on 11 different phytophysiognomies, including Subtropical Ombrophilous Forest and Steppe (Bechara et al., 2013), where it brings potential impacts to the watersheds. Based on this, we selected leaves from *Pinus elliottii* as exotic silviculture litter to be used in the experiments.

The experiment was conducted during the spring season, from September to November 2018. The spring is a period in which the temperature and rainfall are close to the annual averages, with lower rainfall compared to summer, but higher temperatures compared to winter and autumn. Four types of land cover were selected: Grassland with riparian vegetation (Hygrophilous Steppe; 3 streams); Grassland without riparian vegetation (Hygrophilous Steppe; 3 streams); Forest (Mixed Ombrophilous Forest; 2 streams); and *Pinus* sp. area (monoculture/silviculture; 2 streams). In each riparian zone, 1 litter bag containing *P. elliottii* leaves (monospecific litter of senescent pine needles) was incubated *in situ* in the stream water and riparian soil system at 3 sampling points 10 m apart from each other (10 streams × 2 systems × 3 sampling points). In the soil system, the litter bags were arranged in 7–8 meters away from the stream bank, in the same disposition described earlier.

2.3. *Physicochemical parameters*

Water temperature (°C), electrical conductivity ($\mu S.cm^{-1}$), pH, total dissolved solids (g.L), turbidity (Nephelometric Turbidity Unity, NTU) and dissolved oxygen ($mg.L^{-1}$) were measured *in situ* using a multi-analyzer (model 85, YSI Incorporated). For each sampling period we estimated the stream water flow ($cm^3.s^{-1}$) based on the measure of the water velocity ($m.s^{-1}$) using a flow meter (Sigma Sports model FP101, Global Water), and the depth and width of the stream using a measuring tape (cm). The nitrate and ammonia (detection limit: 0.05 $mg.L^{-1}$) and orthophosphate (detection limit: 0.015 $mg.L^{-1}$) concentrations in water were analyzed according to Clesceri and Greenberg (1989).

The canopy openness was quantified using hemispherical photographs taken with a fisheye lens analyzed using the Gap Light Analyzer 2.0 software (Simon Fraser University, Burnaby, BC, Canada). The air temperature was measured *in situ* with a thermometer (°C). In each sampling point of the streams with riparian vegetation the litterfall was collected using nets (1 m^2), and the percentage of organic matter in the litter was estimated according to Graça et al. (2005). Also, we estimated the moisture in litter and riparian soil by oven-drying the samples at 105 °C for 72 h to determine its dry weight. The stock of organic matter of the riparian soil was measured from samples of total litter collected from areas of 1 m^2 until it reaches the clean ground by 3 sampling points per local.

The total nitrogen content was determined by the Kjeldahl method (Cantarella and Trivelin, 2001) and total phosphorus was measured by a reaction with ascorbic acid (Flindt and Lillebø, 2005). The hardness of intact leaves was assessed by measuring their resistance to rupture (Graça and Zimmer, 2005).

2.4. *Leaf breakdown process*

The experiment used 30 × 30 cm litter bags with a mesh size of 0.5 mm for a 42-day incubation period in riparian soil and streams' water. Each litter bag contained 2 g (±0.1 g) of dry leaves. Litter bags were incubated at a depth of 0.2 to 0.5 m in contact with the sediment in the stream system and placed directly on the ground in the riparian soil system. After the incubation time, all litter bags were removed and individually placed into insulated plastic bags and transported in thermal containers (±4 °C) to the laboratory. In the laboratory, leaves were washed with distilled water. Afterwards, for each litter bag, five needles were randomly selected for ash-free dry mass (AFDM) analysis. The AFDM was obtained after incinerating needles (550 °C for 4 h) and subtracting the mass of the remaining material, representing the inorganic fraction of the sample. The remaining leaf litter was placed in trays and was oven-dried at 60 °C for 72 h to determine the dry weight.

2.5. *Statistical analysis*

The breakdown rate ($k\ d^{-1}$) of pine needles was calculated using the negative exponential model of percent mass lost over time ($W_t = W_0 e^{-kt}$; Wt = remaining weight; W_0 = initial weight; -k = decay rate; t = time). We also expressed the k in degree days (dd^{-1}) by computing the thermal sums for each sampling site according to Gessner and Peeters (2020), based on a reference temperature of normalization of 1 in degree-day model. Water temperature was used for litter correction in the stream and air temperature for litter correction in riparian forest, respectively, at each sampling point.

To evaluate the effects of different land covers (Grassland without riparian vegetation, Grassland with riparian vegetation, Forest, and Silviculture; explicative variable) on the percentage of remaining mass (response variable), we used Generalized Linear Models (GLM; by "*glm*" function of "*vegan*" R-package; Crawley, 2007). All models were tested for error distribution by "*hnp*" function from "*hnp*" R-package and corrected for over or under-dispersion. Therefore, initial models were built using binomial (link = logit, test = Chi-square) distribution, but later corrected to quasi-binomial (link = logit, test = Chi-square) distribution for stream water and riparian soil (Crawley, 2007).

The contrast analysis was used to assess differences among different land covers (explicative variable). In the contrast analysis (orthogonal), the explicative variable was ordered by increasing input values and pairwise tested (with the treatments with the closest values). Stepwise model simplification was performed by sequentially adding treatment values that did not affect the model, and testing against the next variable in the sequence (for more details, see chapter 9 in Crawley, 2007).

A Principal Component Analysis (PCA; "*princomp*" function of "stats" R-package) based on the correlation matrix of eigenvalues and eigenvectors was used for i) ordination of the physical and chemical parameters of water and k in the stream system, and ii) ordination of the physical parameters of soil and k in the soil system, at different land covers. The significance of the axes was measured according to the broken-stick model (Legendre and Legendre, 1998). The associations between physicochemical parameters and k were analyzed using Spearman's correlations ("*cor*" function of "stats" R-package; Crawley, 2007). All analyses were performed using R software (R Core Team, 2021).

3. Results

3.1. *Physical and chemical parameters*

Water temperature was higher in Grassland without RV and Grassland with riparian vegetation compared to other sampling sites (GLM; Resid. Dev.$\%_{(3,56)} = 61.4$; $p < 0.01$; Table 1). Water velocity (Resid. Dev.$\%_{(3,56)} = 18.1$; $p < 0.01$), conductivity (Resid. Dev.$\%_{(3,56)} = 86.1$; $p < 0.02$), pH (Resid. Dev.$\%_{(3,56)} = 85.1$; $p = 0.02$) and concentration of

Table 1
Mean and standard error (± SE) values of environmental parameters among different land covers (Grasslands without riparian vegetation -RV, Grassland with RV, Forest and Silviculture).

	Grassland without RV	Grassland with RV	Forest	Silviculture
Canopy opening (%)	87.00 ± 1.39	6.00 ± 0.00	5.00 ± 0.00	83.97 ± 1.21
Temperature (°C)	17.88 ± 0.69	19.09 ± 0.80	16.09 ± 0.33	15.59 ± 0.17
pH	4.39 ± 0.29	4.92 ± 0.26	4.70 ± 0.23	5.23 ± 0.19
Conductivity (µS.cm)	0.01 ± 0.00	0.01 ± 0.00	0.02 ± 0.00	0.04 ± 0.02
NTU	24.76 ± 17.94	0.18 ± 0.10	0.85 ± 0.24	7.78 ± 4.10
Dissolved oxygen (mg.l)	8.21 ± 0.38	9.01 ± 0.42	8.73 ± 0.32	8.91 ± 0.20
TDS (g.l)	0.01 ± 0.00	0.01 ± 0.000.00	0.01 ± 0.00	0.02 ± 0.00
Nitrite (mg.l)	0.02 ± 0.00	0.02 ± 0.00	0.02 ± 0.00	0.02 ± 0.00
Orthophosphate (mg.l)	6.07 ± 0.06	7.23 ± 0.06	8.06 ± 0.03	7.00 ± 0.17
Ammonia (mg.l)	0.23 ± 0.03	0.21 ± 0.02	0.24 ± 0.02	0.08 ± 0.01
Water velocity (cm.s)	2.50 ± 0.38	3.01 ± 0.42	3.92 ± 0.35	6.17 ± 1.81
Water flow (cm^3.s)	0.57 ± 0.23	0.45 ± 0.08	4.42 ± 0.79	0.30 ± 0.00
Soil moisture (%)	14.58 ± 2.74	33.62 ± 2.66	45.21 ± 2.33	32.55 ± 4.41
Litter stock (g. m^2)	18.60 ± 6.60	146.5 ± 42.5	180.80 ± 27.40	208.9 ± 17.00
Litterfall input (g. m^2)	0.00 ± 0.00	70.31 ± 13.32	56.70 ± 8.01	0.00 ± 0.00

nitrate (Resid. Dev.%$_{(3,56)} = 78.9$; $p < 0.01$) and ammonia (Resid. Dev.%$_{(3,56)} = 55.6$; $p < 0.01$) were higher in Silviculture compared to other sampling sites (Table 1). Forest showed the highest values of orthophosphate concentration (Resid. Dev.%$_{(3,56)} = 11.6$; $p < 0.01$) and water flow (Resid. Dev.%$_{(3,56)} = 40.7$; $p < 0.01$) compared to other sampling sites (Table 1). Turbidity (Resid. Dev.%$_{(3,56)} = 88.3$; $p = 0.06$) and dissolved oxygen (Resid. Dev.%$_{(3,56)} = 90.7$; $p < 0.12$) did not differ among the four treatments (Table 1).

The canopy opening was low in Forest and Grassland RV compared to other sampling sites (GLM; Resid. Dev.%$_{(3,56)} = 10.1$; $p < 0.01$; Table 1). Riparian soil moisture was higher in Forest, followed by Grassland RV and Silviculture land cover, with the lowest values in Grassland without RV (Resid. Dev.%$_{(3,26)} = 12.6$; $p < 0.01$; Table 1). The litter stock was higher on the Silviculture riparian soil, followed by Grassland RV and Forest, and lower in Grassland without RV (Resid. Dev.%$_{(3,26)} = 34.1$; $p < 0.01$; Table 1) land cover. The litterfall was higher in Grassland RV and Forest compared to other sampling sites (Resid. Dev.%$_{(3,26)} = 24.4$; $p < 0.01$; Table 1). Finally, the mean amount of nitrogen on *Pinus elliottii* leaf litter before incubation was 1.20 g.g^{-1} (± 0.011), the total phosphorus was 0.22 g.g^{-1} (± 0.10), and the initial leaf litter hardness was 0.97 cm.g^{-1} (± 0.11).

3.2. *Leaf breakdown in stream*

The mean leaf breakdown rate (k) for *P. elliottii* was −0.0029 per day (d^{-1}) and −0.0094 per degrees day (dd^{-1}) in stream system (Fig. 2). Higher values were observed on Forest ($k = -0.0047$ d^{-1} and −0.0137 dd^{-1}), followed by Silviculture ($k = -0.0040$ d^{-1} and −0.0117 dd^{-1}), Grasslands without RV ($k = -0.0026$ d^{-1} and −0.0071 dd^{-1}), and with RV ($k = -0.0022$ d^{-1} and −0.0061 dd^{-1}) land covers. Higher remaining mass was found in Grasslands with and without RV compared to Forest and Silviculture land covers (Table 2; Fig. 2). Spearman's correlation analyses indicated a significant positive association between k (d^{-1}) and water velocity ($n = 10$; $r = 0.9$; $p = 0.047$), concentration of nitrate and ammonia ($n = 10$; $r = 0.8$; $p = 0.048$) and electrical conductivity (n =

Table 2
Generalized Linear Models (GLM) comparing the remaining mass of *P. elliottii* leaf litter on aquatic (A) and terrestrial (B) compartments of riparian zones with different land covers (Forest, Silviculture, and Grasslands with and without riparian vegetation (RV)).

GLM	Df	Dev. Res.	Dev. Res. %	Pr (>Chi)	Analysis of contrast
A. Aquatic					
Null	29	1.11	100.00		
Land use	3	0.68	61.16	< 0.001	Forest = Silviculture < Grassland without RV = Grassland with RV
Residual	27	0.43	38.84		
B. Terrestrial					
Null	29	1.36	100.00		
Land use	3	1.04	76.51	0.049	Forest = Silviculture = Grassland with RV < Grassland without RV
Residual	27	0.32	23.49		

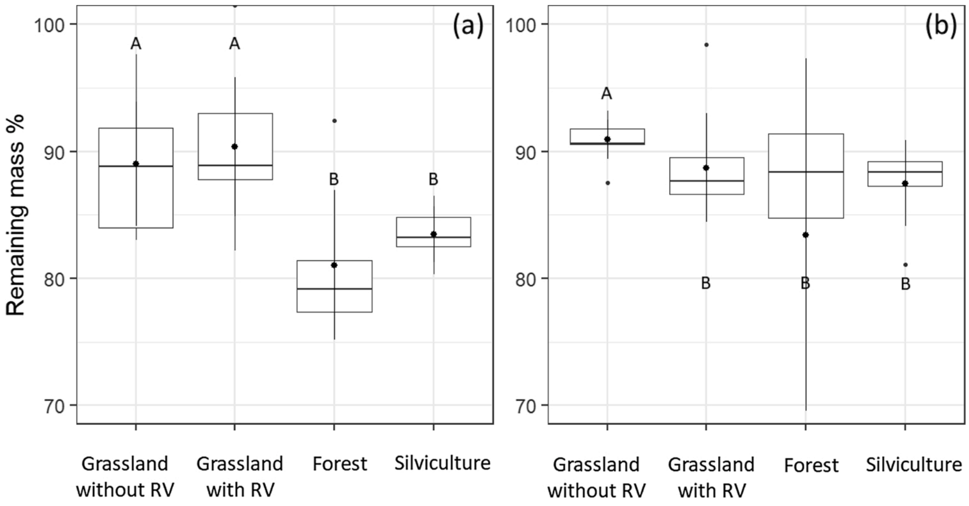

Fig. 2. Percentage of remaining mass of *Pinus elliotti* leaf litter after microbial decomposition in stream (a) and soil (b) systems under different land covers (Grassland without riparian vegetation, Grassland with riparian vegetation, Forest and Silviculture - riparian vegetation = RV). Boxes represent quartiles, the bold line is the median, large circles are means, vertical dashed lines are the upper and lower limits, and small circles are outliers. Different numbers (A and B) indicate significant differences by orthogonal contrast post hoc tests.

10; r = 0.8; p = 0.045) in streams. On the other hand, a significant negative association was found between *k* and water temperature (n = 10; r = −0.9; p = 0.044).

In the PCA, the first two axes explained 60 % and 21 % of variance, respectively. Eigenvalues of both first (7.7) and second axes (2.8) were significant after comparison with the Broken-stick model (6.4 and 2.3; first and second axes, respectively; Fig. 3a). Silviculture was positively correlated with axes 1 and 2 and was associated with orthophosphate, dissolved oxygen, and *k* in the stream system. Grassland without RV was negatively correlated with axes 1 and 2 associated with temperature and turbidity. Grassland RV was negatively correlated with axis 1 and positively with axis 2, associated with ammonia, canopy opening, water flow, and OPR. Forest was negatively correlated with axis 2 and positively with axis 1, and was associated with electrical conductivity, water velocity, concentration of nitrate and ammonia, and pH.

3.3. *Leaf litter breakdown in the soil*

In the riparian soils, the mean leaf breakdown rate (*k*) for *P. elliottii* was -0.0033 d^{-1} and -0.0079 degrees per day (dd^{-1}). Higher values were observed on Forest soil ($k = -0.0040$ d^{-1} and -0.0126 dd^{-1}), followed by Silviculture ($k = -0.0030$ d^{-1} and -0.0087 dd^{-1}), and similar values between Grasslands without RV ($k = -0.0027$ d^{-1} and -0.0058 dd^{-1}), and with RV ($k = -0.0021$ d^{-1} and -0.0077 dd^{-1}) land covers. The higher remaining mass was observed in Grassland without RV compared to the other land covers (Table 2; Fig. 2). Spearman's correlation analysis showed that *k* was significantly positively correlated with the percentage of organic matter in the leaf litter (n = 10; r = 0.8; p = 0.048).

In the PCA, the first two axes explained 63 % and 32 % of variance, respectively. Eigenvalues of both first (3.8) and second axes (1.9) were significant after comparison with the Broken-stick model (3.6 and 1.7 for first and second axes, respectively; Fig. 3b). Silviculture was positively correlated with axes 1 and 2 and was associated with *k* value. Grassland RV was negatively correlated with axes 1 and 2 and was associated with temperature. Grassland without RV was negatively correlated with axis 2 and positively correlated with axis 1, and was associated with canopy opening and the percentage of organic matter in the leaf litter. Forest was negatively correlated with axis 1 and positively with axis 2, in an association with moisture and litter stock in the riparian soil.

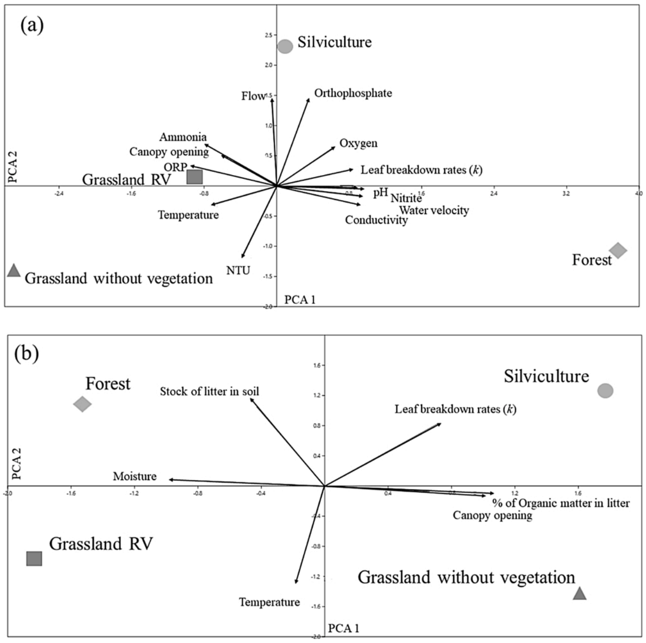

Fig. 3. Results of the PCA based on the physicochemical variables and breakdown coefficient rates (*k* in d^{-1}) of the stream (a) and soil (b) systems of riparian zones under different land covers (Forest, Silviculture, and Grasslands with and without riparian vegetation, represented by the grey symbols).

4. Discussion

4.1. *Leaf breakdown in the stream*

Our data indicate that riparian zones surrounded by a matrix of silviculture converted to land have the highest breakdown rates for *Pinus* needles. In areas dominated by *Pinus elliottii,* a high leaf litter input of this species is expected over the years since the establishment of the plantations. As a consequence, the dominance of one species as of litter input in the streams may result in modifications on the metabolism of the local microbiota (Boyero et al., 2021; McInerney and Rees, 2017). This this is expected as a long period of exposure to monospecific litter may lead to extinction or adaptation of sensitive species and prevalence of resistant species in the decomposer community (McInerney and Rees, 2017; Principe et al., 2015). Adaptations on local microbiota may increase the breakdown rate of the alien invader pine species in riparian zones within a matrix of silviculture land use compared to other land covers (Ferreira et al., 2019; Rezende et al., 2014). Increase in leaf breakdown rates, associated with high concentration of orthophosphate and dissolved oxygen in streams water under silviculture indicate the potential negative effect of replacing natural habitats with *P. elliottii* plantations on subtropical stream systems. Negative impacts may be represented by the increased contribution of microbial activity on the breakdown process (Graça et al., 2015; Tank et al., 2010) as a response to the synergetic effect of high concentration of orthophosphate (Lopez et al., 2001; Medeiros et al., 2015; Rezende et al., 2014) and dissolved oxygen (Graça et al., 2016; Medeiros et al., 2009) in areas under the influence of silviculture.

The positive correlation between the leaf breakdown rate, and water velocity, and electrical conductivity could explain the high mass loss in native forest areas. Water velocity increases the physical fragmentation of the litter by high abrasion (Rezende et al., 2014, 2017). Moreover, high water velocity increases the water turbulence favoring fungal sporulation (Gessner and Newell, 2002; Rezende et al., 2016), consequently increasing microbial decomposer activity (Ferreira and Graça, 2006; Wellnitz, 2014). Our results showed that the studied streams were nutrient-poor such that even a slight nutrient increase might be sufficient to raise ecosystem metabolism and, consequently, litter breakdown (Medeiros et al., 2015; Rezende et al., 2014, 2021).

The leaf breakdown rates showed negative relation with water temperature, contrary to most results from tropical and subtropical stream systems (Alvim et al., 2015; Rezende et al., 2016, 2017; Tiegs et al., 2019). Sampling points are in a geographical range that presents low temperatures throughout the year due to a high-altitude gradient. Constant low temperatures can promote adaptation of the microbial community (Follstad et al., 2017), increasing their sensitivity to higher temperatures (Martins et al., 2016, 2017). In a global synthesis by meta-analysis of litter breakdown, Follstad et al. (2017) evidenced that microbial contribution to the litter breakdown in stream water is increased by physiological adaptation (*e.g.*, properties of enzymes, maximum growth rate) during peak periods of litter input despite low temperatures, supporting our explanation (Tiegs et al., 2019).

The mean breakdown rates (*k*) of *P. elliottii* leaf litter were −0.0029 in the streams of the studied riparian zones. The leaf breakdown rates in this study were close to other Subtropical (*k* of −0.043 in Principe et al., 2015) and Mediterranean streams (*k* of −0.0033 in Graça and Pereira, 1995), probably due to climate similarity. Global studies have shown that temperature has a greater influence than other variables such as nutrients on decomposition (Tiegs et al., 2019). On the other hand, the leaf breakdown rates are in the low range compared to Temperate streams (*k* of −0.0015 to −0.0370 in Collen et al., 2004; Díez et al., 2002; Lopez et al., 2001; Martínez et al., 2013a, 2013b; Webster et al., 1999; Whiles and Wallace, 2001). We did not find studies evaluating pine needle decomposition in streams of tropical zones (Table SM1). However, the *k* values were in low range compared to the decomposition rates of native litters in others subtropical streams (*k* of −0.0021 to −0.238 in Biasi et al., 2013, 2016; Tonin et al., 2014, 2017b), and intermediary range compared to neotropical savanna streams (*k* of −0.0001 to −0.077 in Gonçalves et al., 2012; Moretti et al., 2007; Rezende et al., 2014, 2017).

4.2. *Leaf breakdown in the soil*

Riparian soils under Silviculture showed breakdown rate higher than Forest and Grassland with riparian vegetation (RV) land covers. We suppose that the high leaf breakdown rate in Silviculture was probably due to the aforementioned process of extinction or adaptation of sensitive species and prevalence of resistant species in the decomposer community as a consequence of long periods exposed to a single litter type (Ayres et al., 2009; Principe et al., 2015; Tiegs et al., 2019). The Silviculture land use also showed changes and negative effects on the breakdown rates on riparian ecosystems of subtropical riparian zones (Carvalho et al., 2019). On the other hand, high values of moisture and litter stock on the riparian soil (Sánchez et al., 2018) may explain the high breakdown rate of pine needles by an increase in the microbial activity in Forest land cover (Carvalho et al., 2019; Kiser et al., 2013; Tiegs et al., 2019). These findings highlight the importance of preserving the riparian vegetation for the functioning of subtropical riparian zones (Inhamuns et al., 2021).

Grassland RV showed intermediate values of moisture and litter stock in soil and showed a high breakdown rate. These intermediate values associated with warm temperatures may have increased the microbial metabolism in the soil (Carvalho et al., 2019; Olsson et al., 2019; Sánchez et al., 2018). The acceleration of microbial metabolism increases the decomposition, and consequently increases the breakdown of the alien leaf litter (Carvalho et al., 2019; Olsson et al., 2019; Sánchez et al., 2018). The control of moisture and litter stock in the riparian soil is provided by the maintenance of the riparian vegetation microclimate, highlighting the importance of preserving the riparian zone on the functioning of subtropical riparian zones (Inhamuns et al., 2021).

P. elliottii had a mean leaf breakdown rate of −0.0033 in the riparian zones' soil. The mean leaf breakdown rate reported here shows a similar value compared to thw Subtropical region of Neotropics (*k* of −0.023; Sánchez et al., 2018) and to Mediterranean areas (*k* of −0.038; Kurz et al., 2000), probably because of climate similarity. This result demonstrates the importance of the climate, not only for streams, but also for riparian soils (Tiegs et al., 2019). On the other hand, *k* values were low compared to those observed in the soils of Temperate (*k* of −0.110; Ayres et al., 2009; Kiser et al., 2013; Ribeiro et al., 2008), Tropical (*k* of −0.688; Carvalho et al., 2019; Olsson et al., 2019), and Chinese Subtropical areas (*k* of −0.541; Wang et al., 2015). Tiegs et al. (2019), in a global study, similarly shows that the decomposition process slows down across latitudes, with faster rates in lower latitudes.

Sample design of this study aimed to be spatially diverse and was confined to one period of the year. We may have ceased this study too soon to fully assess leaf mass loss, especially on the soil. Further studies are required to investigate temporal patterns.

5. Conclusions

The difference between the leaf breakdown in stream and on the adjacent soil was 4% in Silviculture, 3% in Forest and 2% in both Grasslands land covers. The low breakdown rate and the small difference between the rate in the stream and on the soil of the riparian zones are consistent with the expected for environments at high altitudes (Tiegs et al., 2019). The breakdown rate of pine needles was higher on the stream probably due to the higher leaching of compounds and to the absence of hydric stress on the decomposing community (Tank et al., 2010; Tiegs et al., 2019). The small difference between the breakdown the rate the rate in the stream and on the soil may be due to the low palatability of the pine needles for the microbial community. The low palatability of pine needles may decrease the environmental importance for breakdown processes (Rezende et al., 2014, 2016; Tiegs et al., 2019). Therefore, these conditions may lead to much greater importance of physical and chemical characteristics of the litter in decomposition (Rezende et al., 2014, 2021).

As a consequence of these issues, litter input of alien invasive plants, such as pine may slow down the organic matter cycle on subtropical stream and soil systems of the riparian zones. The increase in leaf litter breakdown rate and orthophosphate concentration and dissolved oxygen in the stream water demonstrate that silviculture land use may change the organic matter cycle of subtropical streams. The leaf litter breakdown in the stream system was also positively correlated with water velocity through increasing physical fragmentation and electrical conductivity (the increasing nutrients), which supporting our hypothesis. In soil system, highest moisture and litter stock in the riparian soil accelerate the breakdown of pine needles, also supporting our hypothesis. The control of moisture and litter stock in the riparian soil is provided by riparian vegetation. Therefore, preserving the riparian vegetation is a key factor to the maintenance of the ecosystem functioning and organic matter cycle.

Author statement

Renan de Souza Rezende and José Francisco Gonçalves Jr conceived the study. Renan de Souza Rezende, Emanuel Rampanelli Cararo, João Pedro Bernardi, Valeria Chimello and Cássia Alves Lima-Rezende performed the experiments. Daniel Albeny Simões, Jacir Dal Magro performed the limnological analysis. Renan de Souza Rezende performed statistical analysis. Renan de Souza Rezende, Emanuel Rampanelli Cararo, João Pedro Bernardi, Valeria Chimello, Cássia Alves Lima-Rezende, Daniel Albeny Simões, Jacir Dal Magro and José Francisco Gonçalves Jr wrote

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.limno.2021.125905.

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