



Land-use effects on leaf-litter breakdown in streams in a tropical lowland catchment

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Abstract

The expansion of oil palm and cattle grazing in the tropics continues to alter numerous ecosystem functions. The generated land-use change is potentially impacting stream leaf-litter breakdown, a fundamental process for freshwater ecosystems. To assess the effect of land-use change, we studied breakdown rates of forest (*Pachira aquatica*, *Pouroma aspera*, *Sloanea ampla*, and *Hippocratea volubilis*) and oil palm (*Elaeis guineensis*) leaves after a 26-day immersion in streams surrounded by rainforests, grazing lands, or oil palm plantations with and without riparian buffers. In addition, we assessed breakdown drivers by deploying litter bags (248) of two mesh sizes (15 mm and 0.5 mm) allowing or restricting macroinvertebrates' access (134 coarse-mesh bags and 114 fine-mesh bags). Forest leaf breakdown by microbes (fine-mesh) was lower by 55% in the plantations compared to forests; while microbial oil palm-leaf breakdown was lower by 32% in the unbuffered plantations compared to forests ($p < 0.05$). Total litter breakdown was lower ($p > 0.05$) in the plantations but not when these preserved riparian buffers. Litter breakdown was driven primarily by microbes in all land uses except in the buffered plantations, possibly due to increased shredder biomass. These results suggest that oil palm agriculture may decrease microbial stream leaf-litter breakdown, especially in streams with no riparian buffers.

Keywords Palm oil · Pasture · Riparian forest · Primary forest · Decomposition · Ecosystem service

Introduction

The global agricultural expansion has finally slowed down, from 4854 million ha in 2000 to less than 4832 million ha in recent years (Klein Goldewijk et al. 2017). However, farmlands still occupy 38% of the planet's ice-free surface and are responsible for nearly 90% of global deforestation (FAO 2022a), especially in numerous tropical countries (FAO 2022b) where farmlands expand at alarming rates, often at the expense of carbon-rich habitats such as tropical wet rainforests (FAO 2022a). Grazing lands, for example, replace 2.1 million hectares of tropical forest yearly (Ritchie and Roser 2021), and oil palm (*Elaeis guineensis* Jacq.) plantations

are responsible for the loss of 10.5 million ha of tropical forest in the last two decades (Goldman et al. 2020). Furthermore, oil palm plantations are expected to expand even further as the demand for vegetable oil continues to increase (Meijaard et al. 2020). These land-use shifts severely damage biodiversity and ecosystem functioning (Laurance et al. 2014). Agriculture can affect the soil's physical, chemical, and/or biological properties along with many vital processes, including nutrient cycling, carbon sequestration, and litter breakdown and decomposition (Sanaullah et al. 2020). In this regard, stream ecosystems are of particular concern due to their direct connectivity to their surrounding terrestrial landscapes (Allan 2004) and their pivotal role in supporting numerous vulnerable and endemic species (Dudgeon et al. 2006; Burlakova et al. 2011). Streams are impacted by agriculture through inputs of nutrients, sediments, and contaminants, as well as physical changes in habitats and microclimate and the replacement or removal of riparian vegetation (Sala et al. 2000).

To mitigate some of the agricultural impacts on streams, a growing number of farmers in tropical countries are being incentivized to conserve riparian buffers in their lands via

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crop certification schemes (Luke et al. 2019). Riparian buffers are native vegetation strips, which can include trees, shrubs, or other perennial vegetation adjacent to streams and rivers. These can bring several benefits to terrestrial and freshwater ecosystems, including runoff filtering, habitat structure and connectivity conservation, and stabilization of eroding banks (Hickey and Doran 2004; Cole et al. 2020). Riparian buffers thus bring an overall positive effect on the aquatic and terrestrial biota (Deere et al. 2022) and ecosystem functioning (Luke et al. 2019). Nevertheless, there are several research gaps in the tropics regarding riparian buffers, as most research comes from Europe and North America (Luke et al. 2019; Hughes et al. 2021). Additionally, the policies for riparian buffers are often poorly defined or even absent in several of these countries (Luke et al. 2019), and to this day, numerous streams in tropical agricultural lands remain unbuffered (Rojas-Castillo et al. 2024).

Litter breakdown is among the most critical ecosystem processes in streams, as it is essential for energy acquisition, especially in shaded streams where leaves from the riparian vegetation constitute the most significant energy source (Gessner et al. 1999; Benfield et al. 2017). Litter breakdown is considered an adequate measure of the functional integrity of the streams, as it incorporates physical, chemical, and biological elements (Benfield et al. 2017). The process includes both abiotic and biotic mechanisms, as it involves the leaching (dissolution of labile compounds), microbial conditioning and consumption, macroinvertebrate fragmentation, and environmental abrasion of the leaf litter (Webster and Benfield 1986; Peralta-Maraver et al. 2019). In addition, the process constitutes a key step in the carbon cycle and reincorporation of the nutrients into the ecosystem (Battin et al. 2008; Darmawan et al. 2021).

Due to the dependency of leaf-litter breakdown on both abiotic and biotic features, the process is highly vulnerable to land-use change. Overall, fast litter breakdown and decomposition rates are indicators of pristine stream conditions (Young et al. 2008; Silva-Junior et al. 2014). However, other variables associated with land-use change may also impact litter breakdown in a complex way. Soil and water temperature tend to increase litter breakdown and decomposition (Gonçalves et al. 2013), as does organic pollution, and the presence of stable beds is also associated with increased breakdown rates (Silva-Junior et al. 2014). Oppositely, decreased litter breakdown rates are often observed in channelized streams, at reduced flow, low pH, or with high presence of mud, silt, fine particles, insecticides, and heavy metals (Silva-Junior et al. 2014). Riparian buffer removal may increase litter breakdown rates through increased temperatures, yet this could be offset by concurrent factors: a reduction in shredder macroinvertebrates biomass (Rojas-Castillo et al. 2023), an upsurge in fine particles and erosion (Silva-Junior et al. 2014), and decreased microbial richness

(Chavarria et al. 2021), all prevalent in streams lacking riparian buffers.

Grazing lands for livestock in the neotropics have shown reduced litter breakdown compared to forests (Iñiguez-Armijos et al. 2016; Lemes da Silva et al. 2020). This reduction has been attributed to a loss of fungal biomass and shredders in impacted streams, increased water temperatures, phosphorus, and pH (Iñiguez-Armijos et al. 2016), and decreased dissolved oxygen and water velocity (Lemes da Silva et al. 2020). Other studies have found no significant differences between grazing lands and forests even when forests were hosting a higher abundance and diversity of macroinvertebrates (Gutiérrez-López et al. 2016). The oil palm expansion may also decrease litter breakdown rates, since forest soil microbiota are more effective in litter breakdown compared to that of oil palm plantations (Elias et al. 2020). Yet, other studies show no differences between treatments (Foster et al. 2011) or even opposite results attributed to an increase in microbial activity due to the increased water temperature in plantations (Chellaiah and Yule 2018a).

Recent studies in streams in oil palm and grazing lands found significant decreases in microbial diversity and shredder macroinvertebrates together with increases in water temperature and changes in water quality (Rojas-Castillo 2023; Rojas-Castillo et al. 2023). In addition, oil palm streams showed a significant decrease in wood decomposers and fungal taxa richness (Rojas-Castillo 2023). All these changes could potentially affect leaf-litter breakdown. These land uses also modify the material entering the streams and thus the litter quality itself, which influences litter breakdown rates (Manzoni et al. 2010). Despite the foreseeable adverse effects on stream litter breakdown and decomposition by these land uses, few studies address the process, the ecological drivers, and the mitigation strategies, especially in oil palm plantations.

This study aims at contrasting leaf-litter breakdown rates of local and introduced leaf species in streams in oil palm plantations, grazing lands, and primary rainforests (control group). It also explores the mitigating effect of riparian buffers on stream leaf-litter breakdown in plantations. To do so, we measured leaf breakdown of four local forest species (*Pachira aquatica*, *Pouroma aspera*, *Sloanea ampla*, and *Hippocratea volubilis*) and oil palm (*Elaeis guineensis*) in fine (0.5 mm, access only to microbes) and coarse-mesh bags (15 mm, easy access to macroinvertebrates) after a 26-day stream immersion on each land use. We sought to answer two research questions: (i) How do land use and riparian buffers affect total, microbial, and macroinvertebrate-mediated leaf-litter breakdown in the streams? and (ii) What are the drivers of leaf-litter breakdown in the different land uses? Based on previous findings of higher biomass of shredders in dense-canopy streams (Rojas-Castillo et al. 2023) and the lower richness of microbes in open-canopy

streams (Chavarria et al. 2021), we hypothesized that leaf-litter breakdown would be higher in rainforests and plantations with riparian buffers compared to grazing lands and oil palm plantations without buffers. However, we also hypothesized that the process would still be driven primarily by microbes while macroinvertebrates would only play a minor role, as shown in previous tropical studies (Chellaiah and Yule 2018b; Pérez et al. 2023).

Methods

Streams and study area

This study was conducted in the Lachuá region in Alta Verapaz, Guatemala. The region covers an area of 535 km² which includes a protected area (Lachuá Lake National Park) of tropical moist broadleaf rainforests (145 km²) which is part of the last and northernmost tropical hotspot in the neotropics (Mendoza and Dirzo 1999; Granados 2001). Lachuá also encompasses several smaller forest patches (143 km²), human settlements (5 km²), and agriculture and grazing lands (115 km²) (Escuela de Biología 2004). The region lies

within the Usumacinta basin, bounded to the north, west, and east by the Chixoy and Icbolay rivers, and to the south by the Sultana mountains. The area's physiographic context is defined by the Lacandón Fold Belt province and a karstic Upper Cretaceous geology. The region has a dominant seasonal climate with annual rainfall exceeding 2500 mm, an average 91% air humidity, and a 25 °C averaged temperature, experiencing two main seasons: a dry (February–April) and a rainy season (June–October) (CONAP 2003; Rojas-Castillo et al. 2023). The area possesses a number of aquatic ecosystems and floodplains, e.g., the 4-km² and 220 m deep Lachuá Lagoon, and the Lachuá, El Altar, and Peyán rivers that are recognized under the Ramsar Convention as wetlands of national and international significance (Escuela de Biología 2004).

Our experiment was conducted in the 19 streams described by Rojas-Castillo et al. (2023) (Fig. 1), seven of which were located in rainforests (F), six in grazing lands (G), and six in oil palm plantations (three with a riparian buffer [P_RF] and three without [P]). The additional stream in the rainforest treatment was included as a precautionary measure to mitigate the risk of losing a sample unit due to potential drought in the smaller streams during the study

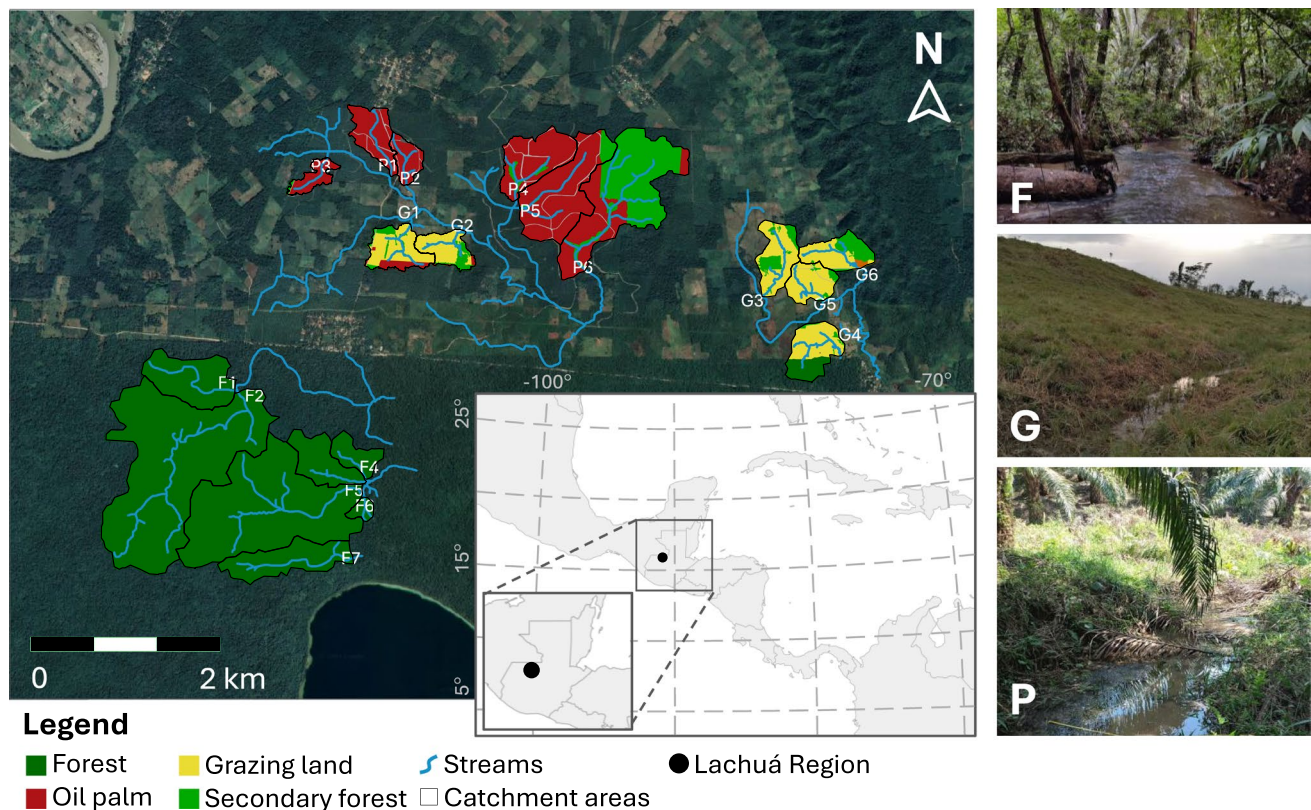


Fig. 1 Study area: stream network and land uses in catchment areas. Rainforest streams (F1–7), grazing land streams (G1–6), unbuffered streams in oil palm (P1–3), and buffered streams in oil palm (P4–6).

Map from Google Earth (2021) edited in QGIS (Team QD 2015). Pictures on the right taken by Celia Diaz and Natalia Vargas, 2021

period, as suggested by a park ranger. The canopy cover varies across these areas, with streams in grazing lands retaining a mean 14% cover, unbuffered streams in oil palms retaining 37% cover, while buffered streams in the plantations and forested streams retaining 81% and 82% cover, respectively. Notably, no significant differences were observed by Rojas-Castillo et al. (2023) across the streams within different land uses in terms of watershed area (mean = 46 ha, CI 22–71), width (mean = 1.69 m, CI 1.44–1.95), or depth (mean = 0.17 m, CI 0.15–0.19). For further insights into the study site and streams, refer to Rojas-Castillo et al. (2023).

Leaf-litter breakdown

Using the litter bag method adapted from Boulton and Boon (1991), we measured stream leaf-litter breakdown during an immersion period of 26 days. We decided on this duration as previous studies have shown considerable weight loss after this period (Tschelaut et al. 2008; Blanco and Gutiérrez-Isaza 2014; Abelho and Descals 2019; Pérez et al. 2023). To quantify the role of macroinvertebrates and microbes in the litter breakdown, we used coarse-mesh (15 mm mesh size) and fine-mesh (0.5 mm) plastic bags (both 10 × 15 cm) either allowing or restricting the access of macroinvertebrates (adapted from Tiegs et al. 2009). In addition, we measured the effect of land use on introduced and local species by employing leaves from the exotic oil palm crop (*Elaeis guineensis* Jacq.) and four local forest species (*Pachira aquatica* Aubl., *Pouroma aspera* Trécul, *Sloanea ampla* I. M. Johnst., and *Hippocratea volubilis* L.). We selected these local species based on their high abundance in riparian areas in the national park during the study period.

The introduced species, *E. guineensis*, is a widespread tropical palm tree crop (Choudhary and Grover 2019). It features tough (472 g/mm² in penetrometer) compound pinnate leaves that are 3–5 m long and generally rich in nutrients ($N = 2\text{--}2.6\%$, $p = 0.12\text{--}0.22\%$, $K = 0.88\%$, lignin = 25%, cellulose = 18%) (Chellaiah and Yule 2018a; Behera et al. 2022). The local forest species include three trees and one vine, commonly found in riparian ecosystems. *Pachira aquatica* is a fast-growing evergreen tree reaching heights of 15–30 m. Its palmate, leathery tough (443 g/mm²), and thick (0.16 mm) leaves are rich in antibiotics (Blanco and Gutiérrez-Isaza 2014; Rodrigues and Pastore 2021; Yoshikawa et al. 2022). Members of *Pachira* show moderate levels of foliar nitrogen (2.2%) and high foliar carbon (45%) (Werden et al. 2018). *Pouroma* is a genus of evergreen trees that prefers sunny conditions and it is characterized by hollow stems and palmately compound leaves (Berg et al. 1990). It belongs to the Cecropiaceae family whose members typically show moderately high foliar nitrogen content (2.5%) and phosphorus (0.78–0.91 mg g⁻¹) and moderate to high levels of leaf

toughness (364 g/mm²) (dos Santos et al. 2006; Blanco and Gutiérrez-Isaza 2014). *Sloanea ampla* is a medium-sized evergreen climax tree (15–18 m tall) from the Elaeocarpaceae family, endemic to the wet tropical biome in Central America and Mexico (Grobbs 2022). It possesses alternate wide, ovoid, leathery leaves with wavy margins and pronounced venation. Members of this genus contain low foliar nitrogen (1.6%), high foliar carbon (50%), and leaf thickness of 0.18 mm (Umaña and Swenson 2019). *Hippocratea* is a climber vine with oblong-elliptic leaves, occasionally thin-coriaceous (Smith 1940) often found in riparian ecosystems and wetlands where they represent high litterfall productivity (up to 75%) (Infante Mata et al. 2012). Leaf material from this genus is high in lignin content and calcium oxalate crystals, and tends to decompose slowly (Gomes et al. 2005; Marín-Muñoz et al. 2014).

Forest leaves were picked up from the forest ground at the Lachuá Lake National Park, selecting only the freshly fallen brown ones and avoiding leaves with fungi colonization. These leaves were sourced from patches under one or two individual trees per species. In the oil palm plantations, we picked brown leaves that were cut 2 weeks before, and we then removed the leaflets from the rachis. We selected brown leaves over green ones to avoid the effect of defensive compounds which tend to be higher in green leaves (Burton et al. 2023). We collected the leaves in a large sack, separated by species, stored the leaves in hanging nets in a dry room for 1 week, air-dried them for 72 h (mean temperature 25–33 °C, max 40 °C), and cut and introduced 4–5 g of leaf material in each bag (one gram per each of the four forest species and 4–5 g of oil palms). We packed forest species together and oil palm leaves individually to recreate the natural conditions in which leaf litter is found in streams in forests and oil palm plantations. In total, we filled 247 plastic bags (133 coarse mesh and 114 fine mesh). In each stream, we placed 13 bags (seven coarse-mesh bags: three with oil palm and four with forest leaves; six fine-mesh bags: three with oil palm and three with forest leaves) separated by at least 10 m from each other. To ensure full immersion of the bags during the experiment, we secured them to the stream bed and placed them within pools and runs, deliberately avoiding riffles to prevent desiccation of the leaf litter (which could introduce additional confounding factors).

The litter bags were immersed in the streams in February 2021. We conducted the experiment during the dry season to minimize the risk of bag losses caused by flooding or mud covering and to catch the effect of the greater macroinvertebrate diversity found during this period compared to the rainy season (Pearson 2014; Mwaijengo et al. 2020). After their collection, the bags were immediately sealed in plastic Ziploc bags, preventing litter loss. These were then transported to the laboratory, where the leaves were carefully cleaned under water to remove macroinvertebrates and

sediment particles. The leaves were then air-dried under the sun for 24 h and weighed.

Water quality and shredder biomass

To address water quality and shredder biomass, factors that can potentially affect leaf-litter breakdown (Silva-Junior et al. 2014), we used the water quality and macroinvertebrate biomass datasets compiled by Rojas-Castillo et al. (2023) for each of the study streams (conducted concurrently with our study). The water quality dataset included dissolved oxygen (measured with a handheld multiprobe, Model 6000, YSI, Yellow Springs, OH, USA), turbidity (measured with a Eutech-100 turbidity meter, Nijkerk, Netherlands), pH (measured with a pH meter ecoTestr pH 2), water temperature and light (measured by installing HOBO Pendant® MX2202 temperature/light data loggers for 30 days in the streams), conductivity (measured by installing HOBO U24 conductivity data loggers for 15 days), water level (measured by installing HOBO U20L-01 water level data loggers for 15 days), stream discharge and current velocity (measured by dilution gauging of 1 kg NaCl in 10 L of water/15 m transect) (White 1978). The macroinvertebrate dataset included the average biomass (WWg) of the different functional feeding groups (FFG) per stream, e.g., shredders. The average represented the macroinvertebrates collected in each stream, each calculated from six Surber-net samples (20 × 25 cm, mesh size 200 µm). These individuals were identified to genus level (Domínguez 2009; Springer et al. 2010; Hamada et al. 2018), were then classified into functional feeding group (FFG) (Oliveira and Nessimian 2010; Merritt et al. 2017; Pereira et al. 2021), and weighed with a Mettler Toledo AE50 analytical balance after a standard drying procedure (20 s in a paper towel) (Rojas-Castillo et al. 2023).

Statistical analysis

We calculated the leaf-litter breakdown coefficient (K) for each sample from the formula $m_f/m_i = e^{-Kt}$ where m_f and m_i are the final and initial litter mass (g), respectively, t is time in days, and K is the breakdown rate coefficient (Olson 1963). We obtained the total ($K \text{ day}^{-1}$ in coarse-mesh bags) and the microbial ($K \text{ day}^{-1}$ in fine-mesh bags) leaf-litter breakdown coefficients. Additionally, we calculated shredder and physical leaf-litter breakdown by subtracting the average microbial litter breakdown from the average overall litter breakdown per stream, as follows: $(K \text{ day}^{-1}_{\text{Total}} - K \text{ day}^{-1}_{\text{microbial}})$.

We explored the effect of land use, leaf litter, and mesh size on leaf-litter breakdown ($K \text{ day}^{-1}$) by contrasting different linear mixed-effect models (with and without interactions) performed in the nlme package (Pinheiro et al. 2022); these included the stream as a random effect following

repeated measurements sampling (Forman 2019). We selected the best-fitting model based on the Akaike information criterion (AIC) and performed a marginal analysis of variance (ANOVA) on the best-fitting one employing the R stats package (R Core Team 2022). To address specific differences on the total and microbial breakdown between land uses, we performed post hoc Tukey tests on linear mixed-effect models for each leaf litter type in the multcomp package (Hothorn et al. 2008). For exploring land-use effect on shredder and physical leaf-litter breakdown, we performed ANOVAs on linear mixed-effect models including the stream as a random effect. For addressing specific differences across land uses, we ran ANOVAs on linear models for each type of leaf litter (rainforest and oil palm leaves), followed by Tukey analyses. We contrasted the average stream shredder biomass (WWg in 500 m²) from Rojas-Castillo et al. (2023) by performing an ANOVA followed by a post hoc Tukey test employing the stats package (R Core Team 2022). To explore the relation between macroinvertebrates, microbes, and litter breakdown, we performed a series of linear regressions (lm) between shredder biomass and total leaf-litter breakdown and between microbial leaf-litter breakdown and total leaf-litter breakdown employing the stats package (R Core Team 2022). Additionally, we compared $K_c \text{ day}^{-1}$ against $K_f \text{ day}^{-1}$ within each land use employing ANOVAs on linear mixed-effect models to quantify the importance of macroinvertebrates and physical factors on the total leaf-litter breakdown. Finally, we performed a series of linear regressions between the water and habitat quality parameters reported in Rojas-Castillo et al. (2023) and each stream's average litter breakdown ($K_c \text{ day}^{-1}$ and $K_f \text{ day}^{-1}$) to determine potential environmental factors associated with total and microbial leaf-litter breakdown. All statistical analyses were performed in R version 4.1.3 (R Core Team 2022) and RStudio version 2022.2.1.461 (RStudio Team 2022).

Results

Land use and riparian buffer effect on leaf-litter breakdown rates

During the 26 days of the study, forest leaves lost, on average, 6.4% (CI 5.6–7.1%) of their mass, reporting a mean breakdown rate of $0.0026 K \text{ day}^{-1}$ (CI 0.0022–0.0029). The weight loss in oil palm leaves was higher, 21% (CI 19.9–22.0%) on average, with a rate of $0.009 K \text{ day}^{-1}$ (CI 0.0086–0.0096). Litter, mesh, and land use showed a significant effect on $K \text{ day}^{-1}$ (Table 1). Total breakdown rate of oil palms and forests did not differ significantly among land uses (Table 2). Nevertheless, microbial breakdown rate ($K_f \text{ day}^{-1}$) of forest litter was higher in rainforests compared to oil palm plantations, and the one for oil palm litter was

Table 1 ANOVA on best fitting model: lme ($K \sim$ land use + litter + mesh size, random = ~ 1|river)

	numDF	denDF	<i>F</i> value	<i>p</i> value	Cohen's <i>d</i>	
Litter	1	219	655.041	< 0.001	−3.32	
Mesh size	1	219	21.892	< 0.001	−0.608	
Land use	3	15	3.882	0.031	G − F	−0.20
					P − F	−1.10
					P_RF − F	−0.64

Significant values (*p* values < 0.05) in bold**Table 2** Post hoc Tukey tests on total and microbial leaf-litter breakdown

Land use		Mean difference <i>A − B</i>	Std. error	<i>p</i> value	CI 95%	
Oil palm litter coarse mesh						
G	F	−0.0004	0.0009	0.963	−0.0019	0.0017
P		−0.0015	0.0011	0.526	−0.0038	0.0008
P_RF		−0.0011	0.0011	0.758	−0.0019	0.0026
P	G	−0.0011	0.0011	0.780	−0.0038	0.0010
P_RF		−0.0007	0.0011	0.938	−0.0018	0.0028
P_RF	P	0.0004	0.0013	0.989	−0.0008	0.0046
Oil palm litter fine mesh						
G	F	−0.0006	0.0010	0.922	−0.0019	0.0017
P		−0.0036	0.0012	0.021	−0.0038	0.0008
P_RF		−0.0027	0.0012	0.138	−0.0019	0.0026
P	G	−0.0029	0.0013	0.097	−0.0038	0.0010
P_RF		−0.0020	0.0013	0.378	−0.0018	0.0028
P_RF	P	0.0009	0.0015	0.928	−0.0008	0.0046
Rainforest litter coarse-mesh						
G	F	−0.0001	0.0007	0.999	−0.0019	0.0017
P		−0.0015	0.0009	0.355	−0.0038	0.0008
P_RF		0.0004	0.0009	0.971	−0.0019	0.0026
P	G	−0.0014	0.0009	0.441	−0.0038	0.0010
P_RF		0.0005	0.0009	0.946	−0.0018	0.0028
P_RF	P	0.0019	0.0011	0.285	−0.0008	0.0046
Rainforest litter fine-mesh						
G	F	−0.0003	0.0005	0.950	−0.0019	0.0017
P		−0.0018	0.0006	0.023	−0.0038	0.0008
P_RF		−0.0021	0.0006	0.006	−0.0019	0.0026
P	G	−0.0015	0.0007	0.091	−0.0038	0.0010
P_RF		−0.0018	0.0007	0.031	−0.0018	0.0028
P_RF	P	−0.0002	0.0008	0.988	−0.0008	0.0046

Land use: grazing land (G), oil palm without riparian buffer (P), oil palm with riparian buffer (P_RF), and rainforest (F). Significant differences (Tukey test, $p \leq 0.05$) in bold and marginally significant in bold italic (Tukey test, $p \leq 0.1$)

higher in rainforests compared to the plantations without buffers, but not compared to the buffered ones (Fig. 2). Surprisingly, microbial leaf-litter breakdown surpassed total leaf-litter breakdown for oil palm and forest litter (ANOVA, $p = 3.97 \times 10^{-6}$, $p = 0.082$, respectively). The breakdown rate estimated for physical abrasion and macroinvertebrate activity ($K_c - K_f \text{ day}^{-1}$) for oil palm leaves did not differ among land uses (Table 3); however, the Tukey test showed

significant differences for forest litter $K_c - K_f \text{ day}^{-1}$ between buffered plantations and all other land uses (Table 4 and Fig. 3).

Drivers of leaf-litter breakdown

Overall, the leaf-litter breakdown was almost exclusively driven by microbial activity measured in fine-mesh bags

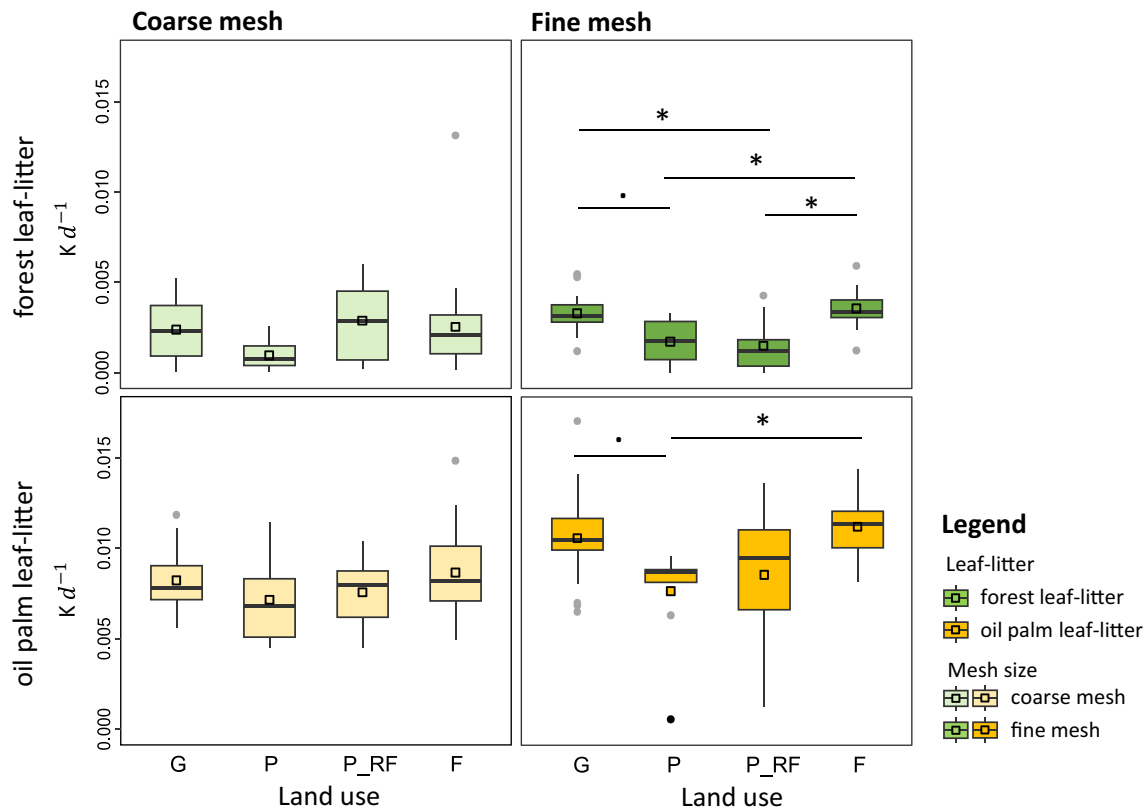


Fig. 2 Leaf breakdown ($K \text{ day}^{-1}$) by land use, mesh, and litter type. Boxplots: box (interquartile range), vertical lines (maximum and minimum values), small squares (mean), horizontal lines (median), circles (outliers). Land use: grazing land (G), oil palm without riparian

buffer (P), oil palm with riparian buffer (P_RF), and rainforest (F). Significant differences (Tukey test, $p \leq 0.05$) between treatments represented by different letters

Table 3 ANOVA on best-fitting model: $\text{lme}((K_c - K_f \text{ day}^{-1}) \sim \text{land use} + \text{litter}, \text{random} = \sim | \text{river})$

	numDF	denDF	F value	p value	Cohen's d
Land use	3	15	2.16	0.135	
Litter	1	18	6.06	0.024	-0.799

Significant values (p values < 0.05) in bold

(lm , $R^2 = 0.76$, $p = 5.96 \times 10^{-13}$) (Fig. 4). However, shredders and physical breakdown ($K_c - K_f \text{ day}^{-1}$) appear to play an important role only in the leaf-litter breakdown of forest leaves in oil palm plantations with riparian buffers. This was the only land use where K_c was significantly higher than K_f (ANOVA, $p = 0.05$); here, microbes conducted $\sim 52\%$ of the total leaf-litter breakdown as opposed to the rest of land uses where the role of shredders and physical breakdown was negligible. Furthermore, shredder biomass was significantly higher in rainforests and oil palm plantations with riparian buffers compared to grazing lands and oil palm plantations without buffers (ANOVA, $p = 0.03$) (Fig. 3).

Turbidity correlated positively with total and microbial breakdown of forest litter. Physical properties, such as watershed area, depth, water current and discharge, and dissolved oxygen, correlated positively with total breakdown of oil palm litter, while turbidity and scrapper biomass correlated negatively with the oil palm microbial breakdown which correlated positively with silica (Table 5).

Discussion

Our findings suggest potential alterations in the stream ecosystem functioning associated with the oil palm expansion. However, even though we found statistical differences in the leaf-litter breakdown rate among land uses, the actual numerical differences were very small compared to estimates from other studies and systems (Petersen and Cummins 1974; Torres and Ramírez 2014; Rezende et al. 2017; Chellaiah and Yule 2018b). Furthermore, our results differed from the only other study that we know of that compares leaf-litter breakdown in oil palm plantations and forests, as this found higher leaf-litter breakdown rates in

Table 4 Post hoc Tukey tests results for shredder and physical leaf-litter breakdown (K_c – K_f day^{−1})

Land use		Mean difference <i>A – B</i>	Std. error	<i>p</i> value	CI 95%	
<i>A</i>	<i>B</i>				Lower	Upper
Rainforest litter						
G	F	0.0005	0.0006	0.832	–0.0011	0.0021
P		0.0004	0.0007	0.925	–0.0016	0.0024
P_RF		0.0025	0.0007	0.013	0.0005	0.0045
P	G	0.0000	0.0007	1.000	–0.0021	0.0020
P_RF		0.0020	0.0007	0.054	0.0000	0.0041
P_RF	P	0.0021	0.0008	0.097	–0.0003	0.0044
Oil palm litter						
G	F	0.0002	0.0013	0.999	–0.0036	0.0040
P		0.0021	0.0016	0.603	–0.0027	0.0068
P_RF		0.0016	0.0016	0.773	–0.0031	0.0063
P	G	0.0019	0.0017	0.691	–0.0030	0.0067
P_RF		0.0014	0.0017	0.845	–0.0035	0.0062
P_RF	P	–0.0005	0.0019	0.994	–0.0061	0.0051

Land use: grazing land (G), oil palm without riparian buffer (P), oil palm with riparian buffer (P_RF), and rainforest (F). Significant differences (Tukey test, $p \leq 0.05$) in bold and marginally significant in bold italic (Tukey test, $p \leq 0.1$)

the plantations (Chellaiah and Yule 2018b). It is thus not possible to conclude on a general leaf-litter breakdown decline based solely on the existing studies, highlighting the need for more research of leaf-litter breakdown in oil palm plantations.

Leaf-litter breakdown rates

The overall breakdown rates observed for forest species in fine-mesh bags (k day^{−1} mean = 0.0029), and particularly in coarse-mesh bags (K day^{−1} mean = 0.0023), were considerably lower than those reported for forest species in tropical lowland streams elsewhere, such as *Cecropia schreberiana* Miq. (K day^{−1} = 0.017) in Puerto Rico (Torres and Ramírez 2014); *Mauritia flexuosa* L. fil. (K day^{−1} = 0.037) in southeastern Brazil (Rezende et al. 2017); *Theobroma cacao* L. (K day^{−1} = 0.008) and *Hymenaea courbaril* L. (K_c day^{−1} = 0.005; K_f day^{−1} = 0.004) in northern Brazil (Firmino et al. 2021); *Dryobalanops beccarii* Dyer (K_c day^{−1} = 0.0110, K_f day^{−1} = 0.0159), *Koompassia malaccensis* Maingay (K_c day^{−1} = 0.0112, K_f day^{−1} = 0.0264), and *Shorea* sp. (K_c day^{−1} 0.0129, K_f day^{−1} 0.0089) in a dipterocarp forest in Malaysia (Jinggut and Yule 2015); and *Macaranga* sp. (K day^{−1} = 0.06–0.08) in oil palm plantations in Borneo, Malaysia (Chellaiah and Yule 2018b).

The studied forest leaf litter consisted of four species, including *Pachira aquatica*, whose leaf extracts are rich in antimicrobial, antifungal, and nematocidal compounds (Rodrigues and Pastore 2021), potentially explaining the slow breakdown rates of our forest leaf mix. Additionally, leaf extracts from members of the genus *Hippocratea* have

shown antimicrobial (Sojini et al. 2022) and insecticidal activity (Obobo et al. 2022). Our mix also contained *Sloanea* leaves, known for their thickness and unpalatability to macroinvertebrates (K day^{−1} = 0.0094) (Tschelaut et al. 2008). The low breakdown rates observed in our forest mix may be attributed to factors such as high content of cellulose and leaf toughness, low nutritional value (Giweta 2020), and the presence of inhibitors or antimicrobials (Karavin et al. 2016; Luo et al. 2023). However, other studies have reported decomposition rates for species of the genus *Pachira* to be much higher (K_c day^{−1} = 0.0205 ± 0.016) than those reported in our study (Blanco and Gutiérrez-Isaza 2014). The same is true for *Cecropia* sp. (K_c day^{−1} = 0.0234) (Tschelaut et al. 2008), although *Pouroma* tends to decompose slower than *Cecropia* in land (Bakker et al. 2011).

The low breakdown rates observed in the forest mix may be attributed to several factors. Firstly, to the overall low nutritional value of brown leaves. Sampling brown leaves from the forest floor allows for the reabsorption of nutrients by the tree before leaf fall. This process is particularly efficient in nutrient-deficient soils (Xiong et al. 2022), such as those found in Lachuá. Additionally, the process of grouping several species together may impact decomposition rates. In mixed bags, antibiotic or inhibitory compounds released by one species could affect the overall decomposition process (Hättenschwiler et al. 2005). However, leaf mixing can also diversify limiting nutrients, potentially leading to accelerated decomposition (Cassart et al. 2020). But it is worth noting that brown leaves generally have lower concentrations of defensive compounds and nutrients compared to green leaves (Burton et al. 2023), which should theoretically

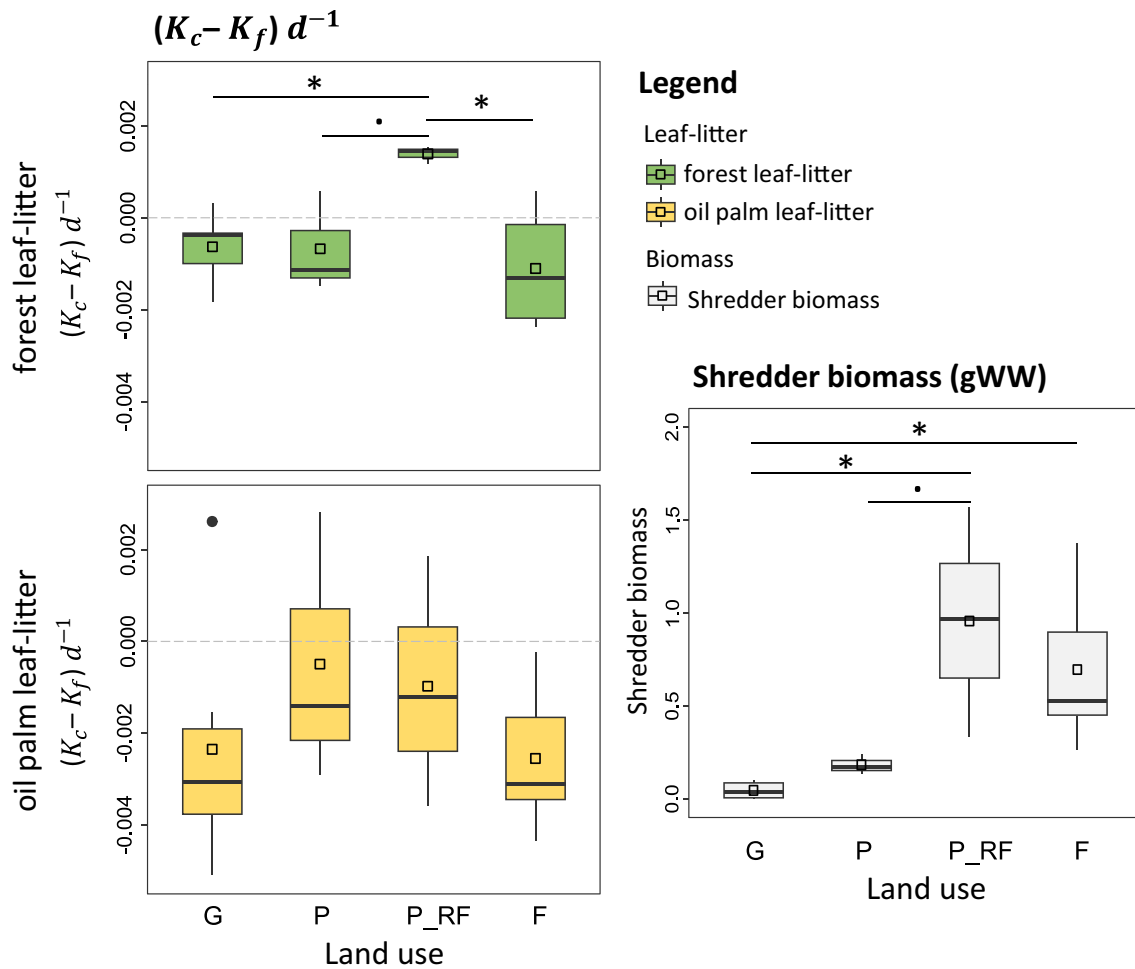


Fig. 3 K coarse mesh– K fine mesh (day^{-1}) and shredder biomass ($\text{WWg per } 0.05 \text{ m}^2$). Boxplots: box (interquartile range), vertical lines (maximum and minimum values), small squares (mean), horizontal black lines (median), gray-circles (outliers). Land use: grazing land

(G), oil palm without riparian buffer (P), oil palm with riparian buffer (P_RF), and rainforest (F). Significant differences between treatments (Tukey test: $p < 0.05^*$, $p < 0.1^\bullet$)

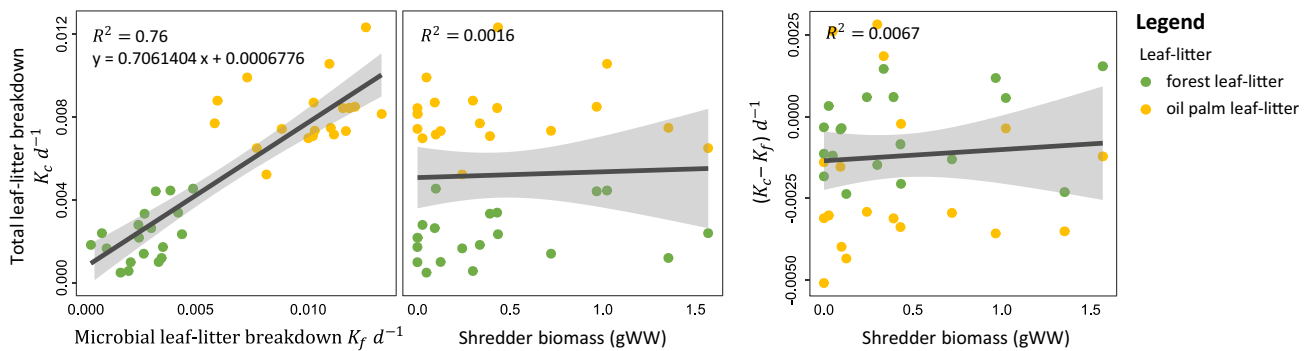


Fig. 4 Total leaf-litter breakdown as a function of microbial leaf-litter breakdown (left) and shredder biomass (middle), and $(K_c - K_f) \text{ day}^{-1}$ vs. shredder biomass ($\text{WWg per } 0.05 \text{ m}^2$) (right)

Table 5 Potential environmental factors affecting leaf-litter breakdown

	R2	pval	Slope	AIC
Rainforest leaf-litter				
Kc~turb	0.23	0.036	−9.4E−05	−199.3
Kf~turb	0.36	0.006	−1.1E−04	−204.4
Oil palm leaf-litter				
Kc~shed	0.28	0.020	1.5E−05	−192.5
Kc~depth	0.27	0.023	1.9E−02	−192.2
Kc~speed	0.29	0.018	4.6E−02	−192.7
Kc~flow	0.39	0.004	6.6E−02	−195.8
Kc~DO	0.40	0.004	7.6E−04	−195.9
Kc~DO_d	0.29	0.017	6.2E−04	−192.9
Kf~SiO₂	0.22	0.044	7.2E−05	−179.0
Kf~turb	0.40	0.004	−2.0E−04	−184.0
Kf~SC	0.21	0.049	−4.0E−04	−178.8

Total leaf-litter breakdown (K_c) and microbial leaf-litter breakdown (K_f), water turbidity (turb.), catchment area (shed), stream depth (depth), stream current (speed), stream discharge (flow), dissolved oxygen (DO), stream bed dissolved oxygen (DO_d), silica (SiO₂), macroinvertebrate scraper biomass (SC). Significant values (p values < 0.05) in bold

decrease both effects. Another factor to consider is that oil palm leaves were cut from the trees and likely contained higher levels of nutrients compared to the forest mix, which naturally fell from the trees.

Litter breakdown rates can vary considerably among species and regions (Allan and Castillo 2007), and many factors can influence these rates (Giweta 2020), making comparisons between studies problematic. Even when comparing the same species, substantial differences in breakdown rates may also exist. In this study, oil palm leaves lost 21% of their mass after 26 days of immersion ($K \text{ day}^{-1} = 0.009$). Conversely, in Malaysia, these leaves had a mass loss of 41–47% after a month of immersion ($K \text{ day}^{-1} = 0.01\text{--}0.02$) (Chellaiah and Yule 2018b), and in northern Brazil, Firmino et al. (2021) reported an average loss of 26% after 60 days ($K_c \text{ day}^{-1} = 0.006$; $K_f \text{ day}^{-1} = 0.005$). Our values are comparable to those in Brazil during the dry season. However, the observed higher rates in Malaysia may be partially ascribed to increased physical abrasion in the streams during sampling, which occurred in the rainy season. In contrast, our study took place during the dry season, resulting in highly stagnant stream conditions (0.019 m s^{-1} ; 95% CI = $0.011\text{--}0.028$). The fact that the breakdown in coarse mesh did not surpass that in fine mesh emphasizes the predominant role of microbes in leaf-litter breakdown. This finding aligns with the widely accepted notion that microbes are the primary drivers of litter breakdown in tropical streams, especially in the neotropics (Dobson et al. 2002; Yule et al. 2009; Boyero et al. 2016), while the role of

shredders is often negligible due to their low diversity and low abundance (Boyero et al. 2012; Jinggut and Yule 2015; Chellaiah and Yule 2018b; Firmino et al. 2021).

The relative importance of shredders on litter breakdown varies dramatically among tropical streams, from studies reporting highly diverse and abundant shredder assemblages (e.g., Cheshire et al. 2005; Yule et al. 2009) to studies registering shredder scarcity (Dobson et al. 2002; Jacobsen et al. 2008; Chellaiah and Yule 2018a). Our streams seem to follow an intermediate pattern with highly variable biomass among land uses, from representing 31% and 56% of the total biomass in rainforests and oil palm plantations with riparian buffers, respectively, to 7% and 2% in the plantations lacking buffers and grazing lands (Rojas-Castillo et al. 2023). Shredder richness in our streams was very modest, especially in pools and runs (overall, 0.2–7.7 taxa per stream; 0.5–2.7 taxa per Surber sample); rainforest and plantations with buffer hosted on average 2–3 more taxa than the plantations with no buffers and the grazing lands. Among the most common shredders in our streams were the caddisflies *Phylloicus* (Mueller, 1880) and *Triplectides* (Kolenati, 1859), the beetle *Anchytarsus* (Guérin-Méneville, 1843), and unidentified species of shrimps (Caridae) (Rojas-Castillo et al. 2023).

Still, the overall slightly lower leaf-litter breakdown in coarse-mesh bags compared to the fine-mesh ones was surprising. The reason for this is not clear, but it could be attributed to a higher amount of “anoxic mud” entering the coarse mesh bags, as dissolved oxygen accelerates carbon and nitrogen release and promotes litter breakdown (Liu et al. 2022). This would also explain the overall low breakdown rates. The stream bed was particularly low in oxygen and rich in mud, and several of the bags were completely buried in mud when collected, which could have slowed down the breakdown process, especially in coarse-mesh bags. It is worth noting that other factors might have contributed to these findings, as previous studies have reported faster breakdown rates in fine-mesh bags compared to coarse-mesh bags, even in systems where mud is less abundant (Jinggut and Yule 2015; Gutiérrez-López et al. 2016).

Effect of land use and riparian buffer on leaf-litter breakdown rates

Microbial leaf-litter breakdown ($K_f \text{ day}^{-1}$) of forest and oil palm leaves was significantly lower by 55% (CI 32–84) and by 28% (CI 0.11–0.47), respectively, in oil palm plantations compared to rainforest. This could be due to a different bacterial and fungi community in the plantations. Even though we did not sample the microbial community here, a more recent study in the region performed in the rainy season found differences in the communities across these land uses, reporting lower wood and leaf saprotroph species of fungi

in the plantations lacking buffers (Rojas-Castillo 2023). It is possible that the fungi community in the plantations with riparian buffers resembled the community of the plantations lacking buffers in the dry season, as observed in the bacterial communities from intermediate-impacted streams (e.g., streams in silvopasture). These silvopasture communities resembled forest communities during the rainy season but grazing land communities in the dry season (Chavarria et al. 2021). This could explain why in our study, the riparian buffers appeared not to have an effect on the stream microbial leaf-litter breakdown of forest leaves. The lower breakdown by microbes in the plantations may also be attributed to the use of herbicides and pesticides in this agriculture, as this restricts aquatic hyphomycetes colonization (Sridhar et al. 1992). This would, however, also have affected litter breakdown in grazing lands, which was not the case.

The absence of significant differences between grazing lands and forests was highly surprising, as grazing lands typically exhibit slower breakdown rates (Zúñiga-Sarango et al. 2020; de Mello Cioneck et al. 2021). This slower decomposition in grazing lands often results from riparian vegetation removal, frequent siltation (increasing leaf burial), and grass proliferation along the margins, which homogenize habitats, intensify solar exposure, and causes flow disruption. Consequently, these conditions lead to reduced richness and abundance of shredders (de Mello Cioneck et al. 2021), findings consistent with observations in our streams within grazing lands (Rojas-Castillo et al. 2023). However, several studies have reported similar breakdown rates in grazing lands compared to forests (McTammany et al. 2008; Hladysz et al. 2010). These studies attribute the lack of differences to shifts in biological drivers, such as an increase in microbial activity alongside a decrease in invertebrate abundance (Hladysz et al. 2010). Microbes respond positively to environmental factors like temperature and nutrients, which are often higher in grazing lands. However, they respond negatively to high sediment load (McTammany et al. 2008), conditions present in our grazing lands, potentially explaining the lack of difference in microbial breakdown in these land uses. Another factor potentially minimizing differences in shredder and total leaf-litter breakdown could be the habitats sampled. To avoid leaf-litter desiccation, we did not sample riffles, which typically harbor the richest and most abundant shredder communities (Wang et al. 2023). The complex dynamics and high variability of litter breakdown in grazing lands underscore the importance of local studies for tailored livestock production farm management. Furthermore, it emphasizes the need for studies that compile and organize global data regionally to establish standardized management practices that consider location-specific variables.

In our study, the total leaf-litter breakdown rate ($K_c \text{ day}^{-1}$) of oil palm leaves was similar among land uses, and the breakdown rate of forest leaves was lower (not significantly)

only in the plantations with no riparian buffers. These results differed from a Malaysian study, where the decay rates of oil palm and *Macaranga* leaves were higher in the plantations than in forests (Chellaiah and Yule 2018b). This variability may be associated with regional or local factors, highlighting the need for additional research both locally and globally. The higher forest-leaf breakdown rates in buffered plantations (as opposed to the unbuffered ones) may be associated with shredder activity, as the stream current and water flow (and thus physical abrasion) did not differ among land uses, while shredder biomass did. Shredders may play a role in the forest-leaf breakdown in the plantations conserving riparian buffers, as these streams hosted a higher biomass and diversity of shredders compared to the ones lacking these buffers (Rojas-Castillo et al. 2023). The low $K_c - K_f$ (day^{-1}) in rainforests could be attributed to the presence of preferable food sources in these streams, considering that the biomass of macroinvertebrate shredders was as high as in the plantations with riparian buffers.

Drivers of leaf-litter breakdown

Leaf-litter breakdown appeared to be driven primarily by microbial activity, which is known to be affected by factors such as temperature and water-quality parameters (nutrient concentrations, dissolved oxygen, and pH) (Suberkropp and Chauvet 1995; Rezende et al. 2017; Trevathan-Tackett et al. 2020; Liu et al. 2022). In our study, breakdown rates were not correlated with water temperature, pH, or any nutrient other than silica, which correlated positively. Litter breakdown showed a negative relation with turbidity and a positive relation with dissolved oxygen. Liu et al., (2022) found that litter breakdown levels in anaerobic conditions tend to be half of those at low oxygen levels (4 mg L^{-1}) and one-third of those at higher levels (7 mg L^{-1}). Thus, in our low-oxygenated streams, a difference of 2 mg L^{-1} in the stream bed could have had an effect. In addition, litter breakdown showed a positive relation with many physical factors including catchment area, stream depth, and water current and discharge. These parameters are associated with physical abrasion, but the gradients between the streams are very small (CI 95%: area = 22–70 ha, depth = 15–19 cm, current = $0.7\text{--}14 \text{ L s}^{-1}$, current = $1.1\text{--}2.8 \text{ cm s}^{-1}$).

The effect of shredder macroinvertebrates in rainforest streams appeared to be negligible, even if shredder biomass was significantly higher than in grazing lands and oil palm plantations with no buffers. This may be due to the abundance of leaf litter in the buffered streams in the plantations, especially during the dry season, when the lack of flow accumulates the resource. It may be that the shredders were not interested in the leaf litter from the bags since the streams were already rich in diverse leaf litter with already conditioned material (algae, fungi, and bacteria in the leaf litter),

which is preferred by the shredders (Trochine et al. 2021). Streams surrounded by riparian buffers in the plantations were the only ones where $K_f \text{ day}^{-1}$ was significantly lower than $K_c \text{ day}^{-1}$. This difference of 48% could be attributed to the effect of shredders in these streams, as the biomass was as high as in rainforests ($6.3 \times 10^{-3} \text{ g/m}^2$ in pools and runs). These riparian buffers provide abundant leaf material to the streams, but in contrast to what happens in rainforests, it is possible that there is less conditioned material (less fungi) in these plantations, and therefore the macroinvertebrate did not prefer the stream leaf litter over the material in the bags.

This study has several limitations, including the absence of a microbial community analysis, which restricts the detection of biological drivers. Additionally, the sampling was restricted to a limited number of streams and habitats, and breakdown rates for individual forest species were not measured. These limitations constrain, to some extent, the statistical power and the ability to compare results with previous studies. Despite these constraints, this research offers valuable insights into the potential impacts of land-use change on freshwater ecosystems. It underscores the urgent need to expand research on how activities such as oil palm plantations and other agricultural practices affect leaf-litter breakdown and their underlying biological processes.

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Data availability Data and R-code are available upon reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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