



# Direct and indirect drivers of shredders biomass in an Amazonian stream: the roles of litter quantity, quality, and climate-mediated nutrient stoichiometry

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**Abstract** Tropical stream food webs are largely dependent on allochthonous litter, yet the relative importance of its quantity versus nutritional quality in limiting detritivore biomass remains poorly understood. We investigated the direct and indirect drivers of shredder biomass in an Amazonian stream over 16 months, focusing on litter quantity, stoichiometric quality (C:N, C:P), and climate-mediated effects. Biomass of shredders was primarily constrained by litter quantity, with nutrient availability having a secondary negative effect. Although precipitation had no direct influence, higher rainfall decreased litter C:N molar ratio, suggesting enhanced nitrogen availability. We conclude that biomass of shredders in this

Amazonian stream is regulated by the interaction between resource availability, nutrient balance, and climate dynamics. Litter storage quantity represents strong control, modulated by changes in litter chemistry linked to rainfall and temperature. Our results highlight the critical role of litter availability, chemistry and climate-driven nutrient dynamics in shaping detritivore communities and organic matter processing in tropical streams.

**Keywords** Amazon · Aquatic insects · Bottom-up control · Decomposition · Organic matter

## Introduction

Tropical streams are strongly supported by allochthonous inputs, particularly leaf litter from riparian vegetation, which represents the primary energy

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source for their food webs (Boyero et al. 2011; Tonin et al. 2017). Both the quantity and quality physical and chemical quality of food resources can limit the metabolism of consumers by restricting the acquisition of essential elements such as carbon (C), nitrogen (N), and phosphorus (P) (Sperfeld et al. 2016). This phenomenon, known as bottom-up control, is well-established in autotrophic systems but still lacks comprehensive understanding within detritus food webs. (Cross et al. 2006; Halvorson et al. 2017). The functioning of the detritus food web in forested headwater streams provides an example of an ecosystem potentially subject to bottom-up control driven by both the quantity and quality of available food resources (Halvorson et al. 2017), especially in megadiverse sites like tropical riparian forests.

Ecological stoichiometry provides a useful framework to understand how the balance between carbon and essential nutrients in detritus constrains consumers (Sterner and Elser 2002a, b). Litter elemental ratios, one of the litter chemical characteristics, have been recognized as an important factor in regulating leaf litter decomposition worldwide (Zhang et al. 2019). Moreover, they serve as valuable indicators for predicting nutrient limitations in aquatic ecosystems (Sterner and Hessen 1994). For instance, when leaf litter contains an excess of carbon, it can restrict the availability of other essential nutrients, thereby altering the overall balance of elements in food resources (Cross et al. 2003; Scott et al. 2013). Aquatic macroinvertebrates generally consume materials that are high in carbon but low in nutrients, resulting in elevated C:N and C:P ratios; this imbalance can hinder their growth and limit secondary production (Cross et al. 2003; Hladyz et al. 2009). Although research in temperate streams indicates that phosphorus often acts as a key limiting nutrient (Demi et al. 2018; Danger et al. 2021), our understanding of how nitrogen and phosphorus influence shredder biomass in tropical environments is still limited (Gonçalves et al. 2006; Rezende et al. 2016).

Beyond the quality of litter, its quantity entering in streams can also influence shredder biomass by affecting the availability of substrate for colonisation and food resources (Gulis and Suberkropp 2003; Boyero et al. 2015). Historically, research has largely emphasised leaf litter quality in explaining detritivore activity, frequently employing the litterbag method at both regional and global scales (e.g., Whiles and

Wallace 1997; Gonçalves and Callisto 2013; Zhang et al. 2019). More recently, studies have begun to investigate the joint effects of litter quantity and quality, often using laboratory experiments (e.g., Halvorson et al. 2017; Arias-Real et al. 2018; Sena et al. 2020). These works indicate that detritivore growth can be enhanced by increases in both litter quantity and quality (Halvorson et al. 2017; though see Cararo et al. 2023). Additionally, macroinvertebrates may preferentially feed on higher-quality litter even when it is less plentiful than lower-quality material (Arias-Real et al. 2018; Sena et al. 2020).

Although progress has been made, there remain few investigations into how natural, temporal changes in litter deposition on the streambed affect detritivore metabolism. The link between consumer biomass and detrital input is probably intricate, influenced by seasonal rainfall patterns and the phenology of riparian vegetation (Ardón et al. 2006; Tonin et al. 2017). Furthermore, detritivore responses may not be immediate, as time is needed for resource assimilation and population growth (Graça et al. 2015). Despite the significance of this topic, only a limited number of studies have considered both the temporal dynamics of shredders and the associated changes in litter storage quantity and stoichiometric quality in tropical streams. Crucially, it remains uncertain whether observed patterns are driven by limitations of a single nutrient or by interactions among multiple resources (Elser et al. 2007). Investigating such relationships, even without establishing direct causality, can yield important insights into the factors shaping detritivore communities and the flow of energy mediated by resources in detritus-dependent ecosystems.

Here, we examine temporal variation in shredder biomass in an Amazonian stream over 16 months, assessing how these patterns relate to changes in litter quantity and stoichiometric composition (C:N, N:P, C:P) of litter deposited on the streambed. Our approach is exploratory, aiming to identify patterns linking litter stoichiometry, quantity, and biomass of shredders, and to contribute to a broader understanding of how detrital resources shape consumer–resource interactions in tropical streams. Our study is based on two key premises: (i) the growth of shredders is co-limited by both litter quantity and quality (Halvorson et al. 2017); and (ii) macroinvertebrates tend to selectively consume resources with higher energy content for metabolism maintenance

(Kaspari et al. 2012; Arias-Real et al. 2018). Therefore, our hypothesis is (i) that biomass of shredders will show a positive associations with litter nutrient content (i.e. lower C:N and C:P ratios), reflecting potential nutrient limitation and no or weak association with litter quantity, which highlights the importance of litter chemistry in foliar consumption.

## Methods

### Study site

The experiment was performed in the Barro Branco stream, located in the Adolpho Ducke Reserve (03°01'S, 59°53' and 59°59'W), Manaus, Amazonas, Brazil. The reserve encompasses an area of 10,000 ha with vegetation composed of a dense ombrophilous forest of terra firme (Hopkins 2005). The climate is classified as "Af", constantly humid (Peel et al. 2007). Annual rainfall is approximately 2,200 mm, concentrated in the months of December to April, with an average annual temperature of 26 °C (Inmet 2023; Station Code: 82,331; <https://bdmep.inmet.gov.br/>; Fig. 1). The Barro Branco stream is surrounded by "terra firme" vegetation and features yellow latosol-type soils. The streambed is sandy and rich in abundant plant litter (Spironello et al. 2004). The stream water is acid (pH=4.6±0.1), well oxygenated (6.6±0.1 mg/L) and low levels of dissolved ions, as well as electrical conductivity (10.7±0.4 µS/cm) (Martins et al. 2014).

### Field sampling

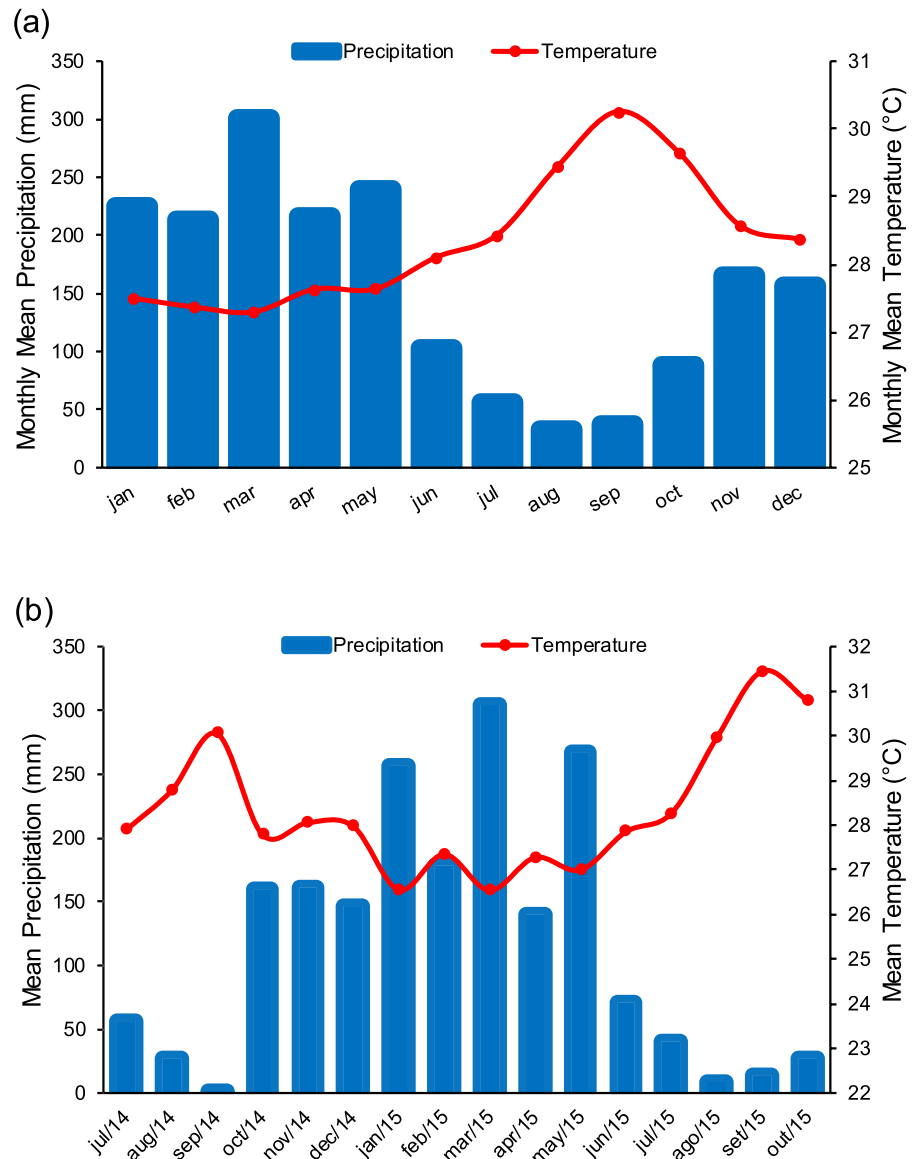
Leaf litter storage samples were collected monthly (30±3 d) from July 2014 to October 2015, totaling 16 sampling events. Nine litter storage samples were collected from three locations within a 120 m stream reach using a Surber® sampler (0.09 m<sup>2</sup> and 250-µm mesh). This 120-m stretch was divided into three 40-m sections. Three litter storage samples were collected from each section, totaling nine samples per month. Litter quantity was calculated by nine times the area of the Surber® sampler (0.09 m<sup>2</sup>×9 sections points). Both biomass of shredders and litter quantity were scaled to m<sup>2</sup>. To ensure a representative sample of the Barro Branco stream conditions, samples were randomly selected

from pool and riffle areas. The collected litter was sieved through a 1-mm mesh, enclosed into individual plastic bags, and transported to the laboratory. We specifically used the leaf litter fraction, separated from other detrital components like wood and seeds. In the lab, litter was cleaned with distilled water using a sieve (250 µm mesh) to retain any associated macroinvertebrates, which were then preserved in 70% ethanol for subsequent identification. This research was conducted with necessary permissions from the National Institute for Research in the Amazon—INPA and the Adolfo Ducke Forest Reserve—RFAD, allowing us to conduct the study and collect aquatic insects at the sampling site.

### Chemical analysis of litter

Dried litter samples were ground in a vibratory ball mill (Fritsch Pulverisette, Model 0, Idar-Oberstein, Germany) prior to chemical analysis. Total C and N concentrations (% of dry mass) were determined through total combustion (950 °C) in an elemental analyzer (Leco Instruments Ltda, Model Truspec CHN628, San José, USA). Total P concentration was measured spectrophotometrically (absorbance at 882 nm) using the ascorbic acid method following combustion (550 °C for 4 h) and digestion (with hydrochloric acid) of litter samples (Flindt et al. 2020). All chemical analyses were performed in triplicate on 100-mg portions of litter powder from each sample. The masses of litter chemical constituents were estimated by multiplying the proportion of each constituent by the litter storage mass. The dry mass of litter chemical elements (in grams) was then multiplied by three times the area of the Surber® sampler (0.27 m<sup>2</sup>×3 sample points). Carbon (C), nitrogen (N), and phosphorus (P) contents were calculated from the elemental percentages (%C, %N, %P) of dried leaf litter. Elemental masses were converted to molar units (mol m<sup>-2</sup>) using atomic weights (C=12.011, N=14.007, P=30.974 g mol<sup>-1</sup>). Molar ratios (C:N and C:P molar ratios) were then computed (Eq. S1). Conversion to molar units was used to ensure element comparisons on a per-atom basis, which better reflects nutrient balance and bioavailability in decomposer–litter relationships (Sterner and Elser 2002a, b).

**Fig. 1 a** Climatogram of the Amazon using records of monthly mean precipitation (blue bars) and temperature (red line) over 59 years. **b** Climatogram of the Amazon using records of mean precipitation (blue bars) and temperature (red line) from July 2014 to October 2015. Data from INMET (1961–2020), Station Code: 82,331. Available in: <https://bdmep.inmet.gov.br/>



## Identification of invertebrates

The macroinvertebrates were identified to the genus or family level using the identification keys provided by Pes et al. (2005), Domínguez and Fernández (2009), and Hamada et al. (2014). These organisms were further categorized into functional feeding groups (FFGs): shredders, collectors, scrapers, and predators (Cummins et al. 2005). In the present study, we focused on shredders, which directly consume litter (Cummins et al. 2005). Chironomid larvae were excluded from the FFGs classification due to their

generalist feeding habits but should be acknowledged as a potential underestimation of macroinvertebrate biomass. We estimated shredders total biomass based on mean body size, using published equations to each family with shredding habits, using published length-mass equations from the literature (see Table S1).

## Data analysis

Prior to model fitting, multicollinearity among predictor variables was evaluated using variance inflation factors (VIF; car package; Fox and Weisberg

2019) and pairwise correlations. Temperature and precipitation were strongly and negatively correlated (Pearson  $r = -0.84$ ,  $p < 0.001$ ), indicating severe climatic collinearity. This was also reflected in moderate VIF values when both variables were included in linear models (VIF = 4.72 for temperature and 4.15 for precipitation). To avoid unstable smooth estimation and inflated uncertainty in GAMMs, temperature and precipitation were not included simultaneously. Precipitation was retained as the climatic predictor in GAMMs due to its direct relevance to hydrological variability in tropical streams, whereas temperature was excluded from these models. Generalized additive mixed models (GAMMs; mgcv package) were used to examine relationships between shredder biomass and litter characteristics (quantity and chemical quality). Competing models included litter mass, C:N and C:P molar ratios, and precipitation as predictors, with month included as a random intercept to account for repeated temporal sampling. Temporal autocorrelation was evaluated by comparing models with and without an AR(1) correlation structure; AR(1) did not improve model support ( $\Delta AIC = -1.65$ ) and was therefore not retained. Model selection was based on AICc, comparing candidate models differing in litter stoichiometric predictors (C:N vs. C:P) and temporal structure. In addition to models including only a random intercept for month, we explicitly tested a by-month smooth term [s(Month)] to capture potential nonlinear temporal patterns. All GAMMs were fitted using restricted maximum likelihood (REML). In addition to the synchronous analysis, we assessed the possibility of lagged responses of shredders to litter quantity, litter chemical quality (C:N and C:P molar ratios) using linear mixed models comparing synchronous and one-month lagged responses. The AIC comparison did not indicate an improvement in fit with the inclusion of time lags. Finally, temporal variation in shredder biomass was examined with a separate GAMM including month as a smoothed term, while maintaining the AR1 correlation structure. We used a model with a two-dimensional tensor interaction (te function, mgcv package) to examine how litter quantity and C:N molar ratio interact, then analysed responses on the boundary surfaces.

Structural equation modeling (SEM; Grace 2006; Rosseel 2012) was used to examine direct and indirect associations among litter quantity, litter chemical quality (C:N and C:P molar ratios), climatic variables,

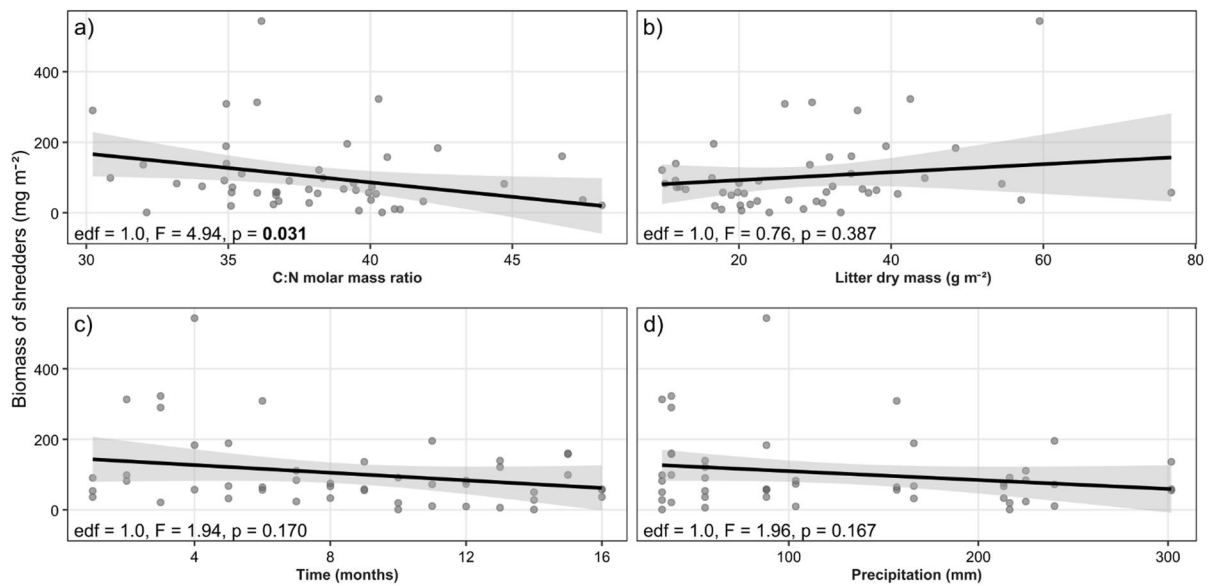
and shredder biomass using the lavaan package (Rosseel 2012). Monthly means were calculated for all variables (litter mass, C:N and C:P molar ratios, precipitation, temperature, and shredder biomass) prior to analysis to match the temporal resolution of biological responses.

An initial, full SEM included direct paths from litter mass and litter chemical traits (C:N and C:P molar ratios) to shredder biomass, as well as indirect paths mediated by climatic variables (precipitation and temperature) acting on litter mass and litter chemical traits. Covariance between C:N and C:P molar ratios was specified. Model parameters were estimated using maximum likelihood, and standardized path coefficients were obtained to facilitate comparison of relative effect magnitudes. To address potential overparameterization, a simplified SEM was subsequently fitted by reducing model complexity while retaining the core hypothesized pathways. Model fit was evaluated using multiple global fit indices ( $\chi^2$ , degrees of freedom, p-value, CFI, TLI, RMSEA with confidence intervals, and SRMR), and standardized path coefficients with 95% confidence intervals were reported. Direct and indirect effects were derived analytically within the SEM framework. Path diagrams were visualized using the lavaanPlot package (Lishinski 2025). All data and R scripts used in this study are archived and will be made publicly available upon acceptance of the manuscript, ensuring full reproducibility of the analyses. All statistical analyses were conducted in R software (version 4.5.1.; R Core Team 2025).

## Results

### Effects of litter quantity and quality on shredder biomass

Litter quantity (litter dry mass) and litter quality (C:N molar ratio) were evaluated as predictors of shredder biomass. In the generalized additive mixed models (GAMMs), shredder biomass was significantly associated with the litter C:N molar ratio (Fig. 2a). In contrast, litter dry mass showed no significant association with shredder biomass (Fig. 2b). Precipitation and time (month) also did not exhibit statistically significant effects on shredder biomass (Fig. 2c, d). The absence of a temporal pattern in shredder biomass (Fig. 2c)



**Fig. 2** Relationship between shredder biomass and its temporal and environmental predictors, and summary of generalized additive mixed model (GAMM) results: **a** shredder biomass vs. C:N molar ratio; **b** shredder biomass vs. litter dry mass; **c** shredder biomass vs. time (month) and **d** shredder biomass vs.

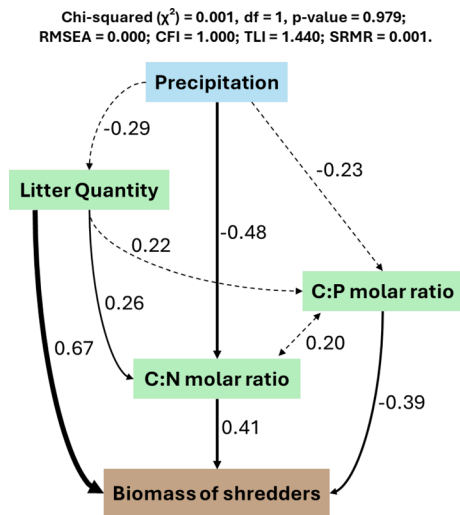
precipitation. Effective degrees of freedom (edf) equal to 1.0 indicate linear relationships. Black lines represent the fitted smoothers for shredder biomass, and grey shaded areas denote 95% confidence intervals derived from the model

did not coincide with abrupt hydrological changes (Fig. 1), indicating no clear association with seasonal dynamics.

The structural equation model (SEM) exhibited excellent global fit to the data ( $\chi^2=0.001$ ,  $df=1$ ,  $p=0.979$ ; RMSEA=0.000; CFI=1.000; TLI=1.440; SRMR=0.001; Fig. 3), explaining a large proportion of the variance in shredder biomass ( $R^2=0.731$ ). In SEM, Shredder biomass was directly and positively associated with litter dry mass (standardized coefficient  $\beta=0.67$ ) and litter C:N molar ratio ( $\beta=0.41$ ), and negatively associated with litter C:P molar ratio ( $\beta=-0.39$ ). Precipitation showed indirect associations with shredder biomass by influencing litter characteristics, being negatively related to C:N molar ratio ( $\beta=-0.48$ ). While Litter dry mass was positively associated with both C:N molar ratio ( $\beta=0.26$ ). Covariance between C:N and C:P molar ratios was not statistically significant. Climatic effects on shredder biomass were therefore primarily indirect and mediated through changes in litter quantity and chemical composition, whereas litter traits showed strong direct associations with shredder biomass.

## Discussion

Our results demonstrate that biomass of shredders in this Amazonian stream is shaped by the combined influence of resource quantity, nutrient stoichiometry, and indirectly climatic conditions. Biomass of shredders declined progressively over time, apparently independent of hydrological fluctuations. Both litter quantity and chemical quality were important predictors of biomass, with higher biomass associated with abundant and nitrogen-rich litter. However, it is important to emphasize that litter quantity and C:N molar ratio exerted higher direct positive effects on biomass of shredders and was tightly linked (C:N molar ratio) to climate, while C:P molar ratio had a negative effect. These strong climatic influences on litter chemistry indicate that rainfall indirectly modulate shredder productivity through their effects on nutrient availability, particularly phosphorus (Ardón et al. 2006; Tonin et al. 2021). These finding goes against with previous studies conducted in tropical streams (Martins et al. 2015; Gonçalves et al. 2017; Sena et al. 2020), that underscores litter chemical composition as main factor in governing litter



**Fig. 3** Structural equation modeling (SEM) showing the direct and indirect relationships between climatic factor (blue) and litter characteristics (green) on biomass of shredder (brown). Solid arrows indicate statistically significant relationships ( $p < 0.05$ ), while dashed arrows indicate statistically non-significant relationships ( $p > 0.05$ ). The width of each arrow is proportional to the strength of the relationship, and values next to the arrows indicate standardized coefficients ( $\beta$ ). C:N=Carbon: Nitrogen; C:P=Carbon: Phosphorous. SEM fit indices: Chi-squared ( $\chi^2$ ) tests overall model fit ( $p > 0.05$  indicates good fit); RMSEA (Root Mean Square Error of Approximation,  $\leq 0.08$  indicates acceptable fit); CFI (Comparative Fit Index,  $\geq 0.90$  indicates good fit compared to a null model); TLI (Tucker-Lewis Index,  $\geq 0.90$  indicates good fit while penalizing model complexity); SRMR (Standardized Root Mean Square Residual,  $\leq 0.08$  indicates small differences between observed and predicted correlations)

biological fragmentation and, by extension, ecological processes in these ecosystems. But collectively, our results highlight that biomass of shredders in tropical streams could emerge from the interplay between resource abundance, nutrient balance, and climate-driven variation in litter stoichiometry, rather than from nutrient limitation alone.

The absence of a significant relationship between shredder biomass and time indicates that biomass dynamics were not driven by a consistent temporal trend over this sampling period. This result suggests that variations in shredder biomass are more strongly associated with changes in resource availability and quality than with progressive temporal processes such as consumer depletion or life-cycle turnover (Richardson 2001; Schmera et al. 2007). Similar patterns have been reported in tropical

streams where detritivore biomass shows high temporal variability but no directional change over time, reflecting dynamic responses to litter inputs and microbial conditioning rather than successional or hydrological forcing (Richardson 2001; Wantzen and Wagner 2006; Boyero et al. 2011). The lack of a clear response to rainfall suggests that, in this headwater stream, temporal changes in shredder biomass are primarily driven directly by biological and resource-related processes rather than by short-term hydrological fluctuations. (Gonçalves et al. 2006; Martins et al. 2015; Rezende et al. 2016). Furthermore, shredder phenology and species-specific life histories, which can drive temporal patterns of biomass independent of the litter characteristics measured here, should also be considered in future studies aiming to fully predict detritivore dynamics.

The significant relationships between litter quantity and quality, and biomass of shredders highlight the dual importance of resource abundance and stoichiometry in sustaining consumer communities (Graça 2001; Hladyz et al. 2009; Rosemond et al. 2015). However, these results partially refuted our hypothesis that biomass of shredders would show positive associations with litter nutrient content (i.e. lower C:N and C:P ratios), reflecting potential nutrient limitation and no or weak association with litter quantity. Litter quantity exerted the strongest direct influence on biomass of shredders, indicating that litter storage availability may be a preponderant driver of detritivores consumer in tropical streams. (Wallace et al. 1997; Boyero et al. 2011; Sena et al. 2020). Higher resource availability may stimulate consumption by shredders, meeting their nutritional demands and promoting higher biomass (Covich et al. 1999; Graça 2001). Moreover, higher litter storage accumulation provides habitat and energy substrates, while nitrogen-rich litter enhances microbial colonization and accelerates decomposition, thereby increasing food availability and palatability for shredders (Hladyz et al. 2009; Ardón et al. 2013; Sena et al. 2021). This finding revealed a joint influence of the litter quantity and quality on the biomass of shredders. The response-surface model reinforces this synergy, showing that maximum biomass of shredders occurs when both quantity and quality thresholds are met—a pattern consistent with resource co-limitation in detrital food webs (Ferreira et al. 2015; Leroy and Marks 2006).

Nonetheless, C:N and C:P molar ratios also played a significant role. The biomass of shredders was primarily constrained nutritiously by N litter availability, indicating its predominant role in controlling the biomass of tropical shredders (Sena et al. 2020; Cararo et al. 2023). It corroborates the Nitrogen Limitation Hypothesis (NLH) which claims that consumer growth and biomass are limited by N availability in resources (Sterner and Elser 2002a, b; Bergström et al. 2015). This is due to the importance of N for the formation of proteins, nucleic acids and other cellular components (Gruber and Galloway 2008). Furthermore, the path between C:P molar ratio and biomass indicates that phosphorus-rich litter enhances the biomass of shredders. It is consistent with the growth rate hypothesis (GRH), which suggests that higher P availability to consumers also results in higher body sizes (Main et al. 1997; Elser et al. 2003). This is mainly attributed to the critical role of P in rRNA synthesis and in the physiological processes involved in tissue and cellular growth, maintenance, and repair. (Elser et al. 2003).

Moreover, the strong negative relationships between climate, and litter C:N molar ratio suggest that climate modulates litter stoichiometry, likely through effects on riparian plant nutrient resorption before leaf senescence (Sardans et al. 2017). This finding reinforces that litter chemical characteristics are influenced by trade-offs between plant metabolism, resource availability, and plant-environment relationships (Weiher et al. 1999; Craine et al. 2001), with P identified as a main limiting element in tropical riparian zones (Boyero et al. 2017; Tonin et al. 2021). These climatic effects indirectly favor biomass of shredders by promoting more phosphorus-enriched litter under warmer and wetter conditions (Boyero et al. 2017).

In summary, these results emphasize that biomass of shredders in an Amazonian stream emerges from the interplay of litter quantity and chemical quality, and climate-mediated nutrient dynamics. While litter quantity exerts strong direct effect, climatic modulation of litter chemistry represents a key indirect mechanism linking environmental variability to the biomass of shredders in this Amazonian stream. However, it is crucial to cautiously interpret these results. Our study was conducted in a single stream in the Amazon basin over a relatively short period of one and a half years. Furthermore, other potential

factors could influence biomass increments by shredders, such as the influence of biofilm on the litter, the organisms tested not being exclusive shredders, density-dependent effects, and competition (Rezende et al. 2019; Allen et al. 2020). These results deepen our understanding of the functioning Amazonian streams and can contribute to policies for the conservation and restoration of riparian zones in the Amazon River Basin. Understanding these combined effects is essential for predicting changes in trophic dynamics and organic matter processing under climate change in tropical ecosystems.

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**Author Contributions** A.M.T., J.F.G., N.H. and R.T.M conceived the study; G.S. analyzed the data; G.S. led the writing of the manuscript with substantial inputs from A.M.T., N.H., R.S.R., J.F.G. and R.T.M.; R.T.M. collected. All authors contributed critically to the drafts and gave final approval for publication.

**Data Availability** No datasets were generated or analysed during the current study.

## Declarations

**Conflicts of interest** The authors declare no competing interests.

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