

## **WOOD PREDICTORS IN NEOTROPICAL STREAMS: ASSESSING THE EFFECTS OF REGIONAL AND LOCAL CONTROLS IN AMAZON AND CERRADO CATCHMENTS**

**SARAIVA, S. O.<sup>1\*</sup>, KAUFMANN<sup>2</sup>, P. R., RUTHERFURD, I<sup>3</sup>., LEAL<sup>4,5</sup>, C. G., LEITÃO<sup>6</sup>, R. P., MACEDO<sup>7</sup>, D. R., POMPEU, P. S<sup>8</sup>.**

<sup>1</sup> Programa de Pós-graduação em Ecologia Aplicada, Universidade Federal de Lavras, Lavras - MG, Brazil, 37.200-000.

<sup>2</sup> U.S. Environmental Protection Agency, Office of Research and Development, Center for Public Health and Environmental Assessment, Pacific Ecological Systems Division, 200 SW 35th Street, Corvallis, OR, and Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Corvallis, Oregon 97331, USA.

<sup>3</sup> School of Geography, Earth, and Atmospheric Sciences, The University of Melbourne, 221 Bouverie St, Carlton, 3010, Melbourne - VIC, Australia.

<sup>4</sup> Lancaster Environment Centre, Lancaster University, Lancaster, Lancashire, LA1 4YQ, United Kingdom.

<sup>5</sup> Escola Superior de Agricultura Luiz de Queiroz (ESALQ), Universidade de São Paulo, Piracicaba - SP, 13.418-900.

<sup>6</sup> Departamento de Genética Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil, 31270-901.

<sup>7</sup> Departamento de Geografia, Instituto de Geociências, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil, 31270-901.

<sup>8</sup> Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Lavras - MG, Brazil, 37.200-900.

\* Corresponding author (sarahsaraiva@hotmail.com)

### **ACKNOWLEDGEMENTS**

We thank the field crews involved in data collection in both Amazon and Cerrado streams. We also thank Rafaella T. Maciel Oliveira for her assistance in data analysis. We are grateful for financial support from Companhia Energética de Minas Gerais (CEMIG) and Agência Nacional de Energia Elétrica (P&D ANEEL/CEMIG GT 487), Instituto Nacional de Ciência e Tecnologia - Biodiversidade e Uso da Terra na Amazônia (CNPq; 574008/2008-0), Empresa Brasileira de Pesquisa Agropecuária (Embrapa; SEG: 02.08.06.005.00), the UK government Darwin Initiative (17-023), The Nature Conservancy, Natural Environment Research Council (NERC; NE/F01614X/1 and NE/G000816/1), and Fulbright Brasil. Individual funding included a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/esp.5506

(CAPES) scholarship in Brazil and a Science without Borders Grant in Australia (PDSE-88881.361954/2019-01) to SOS. Our manuscript was subjected to review by the U.S. Environmental Protection Agency National Health and Environmental Effects Research Laboratory's Western Ecology Division and approved for publication, benefitting greatly from reviews by Dr. Mark Meleason and Patti Meeks. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

### **AUTHOR CONTRIBUTIONS**

SOS, CGL, RPL and PSP conceived of the presented idea. SOS developed the conceptual model with support of PRK and IR. PSP, CGL and RPL provided the dataset. DRM obtained the geographical data and their respective metrics. SOS processed all data and calculated the channel metrics with assistance of PRK. SOS performed the structural equation modelling with assistance of RPF. PRK contributed to the interpretation of the results. SOS wrote the manuscript in consultation with PSP, IR and PRK. All authors discussed the results and contributed to the final manuscript.

### **DATA AVAILABILITY STATEMENT**

Raw and derived data supporting the findings of this study are available from the corresponding author SOS on request.

### **Abstract**

Large wood plays a critical role providing complex habitat structure in rivers and streams. The instream wood regime consists of wood recruitment, transport, retention, and decay in river corridors. In tropical streams, transport and decay are thought to be the dominant influences on the amount instream wood stored, and these are driven by upstream forest cover, as well as catchment hydroclimatic and geomorphic characteristics. Lack of studies of the tropical wood regime leave many uncertainties. Notably, the wood regimes in the neotropical Amazon and Cerrado biomes are not known, and rapidly changing land-use threatens efforts to understand their natural wood regime. We investigated predictors of instream wood in catchments of the Amazon and Cerrado subject to a wide range of agricultural land use to identify the critical factors controlling wood recruitment and load. Using the structural equation modelling technique, we disentangled the complex net of regional and local controls. Contrary to our expectations, local drivers, such as the relation between the piece size and channel dimensions, discharge, stream power and riparian forest were the most important predictors of instream wood. The amounts of wood found in these streams were primarily the result of the wood delivered by the local riparian forest and how much of that wood remains trapped. Therefore, the preservation of the forested riparian zones in Amazon and Cerrado streams is crucial for maintaining the sources of wood as well as the

channel morphology capable of trapping and retaining instream wood. Further research should compare reference and disturbed streams to quantify the influence of anthropogenic activities on instream wood and its primary influences. This information would facilitate assessing the extent of human alteration and developing mitigating measures to arrest or reverse changes that reduce instream wood and degrade aquatic and riparian habitat in neotropical rivers and streams.

**Keywords:** instream wood, wood budget, contemporary wood regime, channel features, agriculture landscape.

## 1. INTRODUCTION

Large wood derived from trees is among the most important contributors to instream habitat complexity, retention of nutrients, and stabilization of banks and bed sediments. Wohl et al. (2019) refer to natural water flow, sediment flux, and the wood regime as the three legs of a tripod of physical processes that support ecological processes in rivers and streams. Accelerating land-use change in riparian zones has disrupted wood recruitment and retention worldwide, reducing the amount of instream wood (Wohl et al., 2019). The conversion from forested uplands and riparian areas to agriculture and grazing have altered the flux of wood, water and sediment, resulting in profound impacts on the habitat quality, water quality, and biodiversity of rivers and streams. Despite the importance of tropical, and especially neotropical streams as hotspots of biodiversity, regional assessments of wood and other aspects of physical habitat supporting that biodiversity remain sparse. Instream wood is controlled by local and regional factors that act as sources and sinks to determine the recruitment, transport, and storage of wood in river corridors (Wohl et al., 2019). Notably, we are not aware of any studies examining the factors controlling the amount and size of wood in neotropical streams.

Instream wood sources and sinks are summarized in the equation proposed by Benda and Sias (2003), where the amount of wood in a stream reach at any point in time is the result of the balance between input (lateral and fluvial recruitment) and output forces (lateral deposit, downstream transport and decay processes). This model has been successfully applied worldwide, though the magnitude of the various terms of the equation differ by region. Cadol et al. (2009) demonstrated that the influence of fluvial transport on the amount of wood stored in channels was relatively more important in tropical streams than in temperate streams. They also pointed out that decay may be as important as transport in tropical wood budgets but recommended further investigations. Studies evaluating the decomposition of wood in tropical

streams still remain scarce (but see Jones et al., 2019). However, available information about wood decomposition on tropical forest floors (Barbosa et al., 2017; Clark et al., 2002; Delaney et al., 1998; Harmon et al., 1995; Lewis et al., 2004) suggest that wood in the tropics is very transient, being completely degraded in less than a decade, while in temperate river corridors wood remains stored for decades, centuries or even millennia (Guyette et al., 2008; Hyatt and Naiman, 2001).

It is generally thought that the wood regime in tropical streams is more dynamic than in temperate streams. However, this consensus is based on a small number of studies with limited and geographically uneven coverage (Swanson et al., 2020). To our knowledge, the wood regime has never been studied in rivers of the Amazon, the largest tropical forest and hydrographic basin in the world. Only a few studies have inventoried large wood on Amazon floodplains (Chao et al., 2008; Martius, 1997; Silva et al., 2016) and only one (Saraiva et al., 2022) quantified large wood (LW) in the streams themselves. Saraiva et al. (2022) is also the only study of instream wood in the Cerrado (the Brazilian Savanna), the second largest biome in South America. Further efforts to quantify wood naturally occurring in these neotropical streams are threatened by the recent high rates of deforestation in these two neotropical biomes in recent years, triggered mainly by expansion in agriculture and livestock grazing (Parente et al., 2021; Pereira et al., 2020; Silva Junior et al., 2021; Trigueiro et al., 2020). Unfortunately, we may well lose the natural wood regime in the neotropical streams before we are able to describe it.

Because of the transiency of wood in tropical streams, it is expected that they naturally contain less wood than comparable temperate streams (Wohl, 2017), and even less in human-impacted catchments. However, this is not always true in agricultural landscapes. Paula et al. (2011) found that LW abundance in Southeast Brazilian streams was similar to that in temperate secondary forested streams in Germany, and that LW volume was similar or greater than in temperate old-growth forested streams in New Zealand and Japan, respectively. Likewise, Saraiva et al. (2022) reported that amounts of LW in streams in Brazilian tropical forests and savannas were similar to those in temperate biomes in the USA. Both studies suggested that the differences between tropical and temperate wood stock were more related to the distribution of wood size than the total number of pieces of instream wood. Tropical streams tend to have more small-sized wood than the temperate ones, probably due to a high and unceasing rate of dropping branches (Cadot and Wohl, 2010), which is apparently intensified when the riparian forest was subjected to some level of degradation. However, with so limited knowledge from the tropical zone it is difficult to generalize, underscoring the need for further studies to expand the geographic range of both surveyed sites and sites where instream wood controls are intensively studied.

Given the importance of transport in the tropical wood regimes, the influence of large-scale regional hydrogeographic influences might be expected to dominate the instream wood budget. From a landscape perspective, the wood regime is determined by the drainage network, the surrounding forests and the processes that link both (Swanson, 2003). Thus, many large-scale variables such as geomorphic and hydroclimatic features of the catchment (Wohl and Jaeger, 2009b), network configuration, basin size and shape, drainage, and confluence density (Benda et al., 2004), and the areal cover and proximity of upstream forests (Paula et al., 2013; Swanson, 2003), might be important controls on wood transport. However, local controls cannot be disregarded, because they provide wood to the channel and affect its retention or transport, which may be enhanced in tropical streams given the high rate of wood replacement. Therefore, size, age, structure, density, proximity, extent, and health of the local riparian forest (Bilby and Bisson, 1998; Costigan et al., 2015; McDade et al., 1990; Van Sickle and Gregory, 1990), channel dimensions, gradient, discharge, confinement, bed material and bank erosion propensity (Bilby and Bisson, 1998; Comiti et al., 2016; Keller and Swanson, 1979; Martin et al., 2018; Wohl and Jaeger, 2009a) must also be considered as possible instream wood controls. Moreover, disturbances and episodic events, such as blowdowns and landslides are also important sources of wood that can prevail in some catchments (Robison and Beschta, 1990; Wohl et al., 2012b). Similarly, decay agents and enablers, such as environmental conditions, decomposing organisms, and wood species (Bärlocher and Boddy, 2016; Mackensen et al., 2003; Martius, 1997), may have significant roles in breaking down wood in tropical systems.

The task of understanding the effects of the many influences on wood storage in neotropical streams is challenging. We applied Structural Equation Modelling (SEM) to disentangle the complexity of the relationships between wood and the landscape and stream channel factors that influence its abundance in Cerrado and Amazon streams. SEM is a powerful path analysis technique that allows us to test and evaluate multivariate causal relationships (Fan et al., 2016). In a causal pathway, it is inevitable that variables along that pathway covary. SEM uses the covariance between variables to calculate the direct and indirect effects of each predictor in the model. According to Lefcheck (2016), two primary characteristics of SEM distinguish it from more traditional modelling approaches: (i) SEM paths represent hypothesized causal relationships among variables, whereas correlation alone may imply causation, but the direction of causality is unresolved, since one cannot know whether, for instance, A causes B, B causes A, or both A and B are a consequence of some third, unmeasured variable (Shipley 2000); (ii) variables can appear as both predictors and responses, allowing one variable to serve as a response in one path and as a predictor in another, making SEM useful for testing and quantifying indirect or cascading effects that would otherwise go unrecognized by examining the influence of each predictor in isolation

(e.g. Grace et al. 2007). Therefore, by applying SEM we believe that we have identified the main influences on wood in Amazon and Cerrado streams, contributing to fill the gap of knowledge on wood load in neotropical streams.

## **2. METHODS**

### **2.1 Study area**

This study is based on an instream habitat assessment performed in Brazilian catchments located in agricultural impacted landscapes of Cerrado and Amazon biomes. Although all the studied catchments are subject to some level of impact, some of them still have an impressive percentage of up to 100% native forest, while others were substantially cleared and have <1% remaining forest cover (Table 1 and supplementary material - S1). A total of 258 stream reaches (sites) were sampled, with sites distributed across six different regions: two in the Amazon and four in the Cerrado. The two Amazon regions are located in Pará state (Figure 1) and are characterized by a mosaic of mechanized agriculture, extensive and intensive pastures, forestry, densely populated colonies of small farms and settlements, and large areas of undisturbed and disturbed primary and secondary forest (Gardner et al., 2013) (Table 1). The four Cerrado regions are located in the centre of the country in Minas Gerais state and on the borders of this state with Goiás and São Paulo states (Figure 1), being subject to a high degree of anthropogenic influence mainly by agriculture and livestock, only having small fragments of native vegetation (Macedo et al., 2014) (Table 1). In the Amazon the study sites were chosen over a gradient of previously known anthropogenic impact to capture the full deforestation gradient as described in Gardner et al. (2013). In Cerrado, we selected sample sites within four contrasting basins using a randomized, spatially balanced draw within each basin to represent the range of wadeable stream sizes and to systematically cover the study areas as described in Macedo et al. (2014).

### **2.2 Data collection**

We surveyed 99 wadeable streams in the Amazon (51 in Paragominas - PGM and 48 in Santarém - STM), and 159 streams in Cerrado (40 in Nova Ponte - NP, 40 in Três Marias - TM, 40 in Volta Grande - VG, and 39 in São Simão - SS). In each stream we made standardized measurements of wood, stream channel morphology, bed substrate, riparian vegetation cover and structure during the dry season, using the USEPA methodology (Hughes and Peck, 2008; USEPA, 2013) with minor adaptations for tropical streams (see Junqueira et al., 2016; Leal et al., 2016). Sample

reach lengths at each site were set proportional to the stream mean wetted width (40 times the mean width), with a minimum of 150 m.

Along the reach we counted all the large wood pieces (LW), which were defined as being all the pieces located inside the bankfull channel with a length  $\geq 1.5$  m and diameter  $\geq 0.1$  m at the small end (note, if small end diameter was  $< 0.1$  m, the wood piece was defined as the length between large end and the point where the diameter = 0.1 m). Each piece was categorized into one of five size classes (Table 2) to calculate a nominal mean volume for each piece of LW according to its diameter-length class membership (Robison and Beschta, 1990; Kaufmann et al. 1999; Hughes and Peck, 2008; USEPA, 2013). For more details on the wood quantification methods, see Kaufmann et al. (1999). Because logjams were rare in the study streams, we did not explicitly identify them. Instead, we measured LW pieces individually when logjams appeared.

In order to identify the main wood controls, we measured multiple variables at local and regional scale. At the local scale, still following USEPA methods, we measured thalweg depth, wetted width, incision height, bankfull width, and bankfull depth. The determination of bankfull channel dimensions was on the basis of bank morphology, substrate, and vegetation, reflecting channel-forming flood events with a recurrence interval of 1.5 to 2 years. For thalweg depth determination we measured the water depth at 100 evenly-spaced locations along the thalweg in each sample stream reach, and we describe the mean and SD of thalweg depth (XDepth and SDDepth). The bankfull height is the height of the bankfull water level (inferred from channel morphology) above the wetted surface at the time of sampling. The bankfull depth is the sum of the mean thalweg depth plus the bankfull height. The incision height is the vertical distance from the water surface (at the time of sampling) to the first floodplain terrace above the bankfull surface.

We also measured the channel slope and sinuosity and characterized the bed material based on classifying 105 systematically-spaced particles as bedrock, concrete, boulder, cobble, coarse gravel, fine gravel, sand, silt and clay, hardpan, fine litter, coarse litter, wood, roots, macrophyte or algae. To characterize the riparian vegetation, we made a visual estimation of the areal cover of each one of the three vegetation layers (canopy, understory, and ground cover) located on both banks within a 10-meter field of view, accounting by tree size (big (DBH  $> 0.3$  m), small (DBH  $< 0.3$  m), woody shrubs and herbs) and vegetation type (deciduous, conifer, broadleaf evergreen, mixed, or none). The maximum cover in each layer is 100%, so the sum of the areal covers for the combined three layers could add up to 300% (USEPA, 2013). Because we are interested in the riparian forest as a source of LW, in the present study we focused on the woody riparian vegetation, excluding herbs, grasses and non-woody shrubs. As there are no stream gauges in any of the sampled catchments, we measured discharge at the time of sampling (during the low flow season) by the floating object technique and also

estimated bankfull discharge using a slope-area method of Kaufmann et al. (2008) and Kaufmann et al. (2009). The detailed field methods for each variable measured on channels are available in Hughes and Peck (2008) and USEPA (2013).

To obtain the regional variables, we first delimited the catchment area upstream of each sample site from a digital elevation model (DEM) with 30 m resolution for all study regions (generated using TopoData-IBGE; Valeriano and Rossetti, 2012), except for STM, for which we used a DEM with 90 m resolution (SRTM-NASA; Jarvis et al., 2008). Having the upstream catchments for each site, then we obtained the drainage network from a national database available for Cerrado regions (spatial resolution 1:25,000; FBDS, 2009). For Amazon regions, we estimated the contributing drainage boundaries for each site by applying the hydrological tool ArcSWAT on ArcGIS software (Di Luzio et al., 2004) with subsequent manual correction. We used satellite images (Landsat TM and ETM+ images, 30 m resolution, year 2010) to map land use and quantify the native vegetation cover. Regardless of whether the native vegetation is tropical forest or savanna phytophysiology, depending on the biome analyzed, we refer to all of them as forest throughout this article to facilitate understanding and comparisons. We considered forest cover at the catchment scale, which includes the forest in the whole catchment upstream of the site. Finally, we obtained historical data on the temperature, precipitation, and humidity averages from the WorldClim data website (<https://www.worldclim.org/>) for each study site catchment. All the spatial data were processed in geographic information systems (ArcMap 10.5 and QGIS 3.4). The complete list of measured variables and their descriptions is presented on Table 3.

### **2.3 Conceptual model**

To understand the controls on wood in the study sites, we used the wood budget model proposed by Cadol et al. (2009) - the Benda and Sias (2003) model adapted for tropical headwaters streams - as our starting point (Equation 1). A better understanding of the wood budget would allow us to identify the critical factors that maintain wood recruitment and stock into those streams. Following the same approach as Comiti et al. (2006) and Cadol et al. (2009), we did not directly measure recruitment, transport, or decay in our assessment of wood loads. Instead, we inferred each of the wood budget variables by examining correlations between wood volume and its potential predictors in a large sample of stream reaches. As the wood load is the result of the sum of lateral ( $L_i$ ) and downstream input ( $Q_i$ ) and subtraction of decay ( $D$ ), lateral ( $L_o$ ) and downstream output ( $Q_o$ ), knowing the factors that affect each one of these equation terms and the relationship between them will enable us to understand the wood regime. As we only sampled each stream once, we

do not know the variation of wood load over time. We are aware that we are missing the time variation term from the wood budget equation. Thus, we are looking at equilibrium wood stock based on long-term average rates of input, output, and decay. This is an approximation of the dynamics of wood flux but is necessary in order to examine potential controls on wood volumes.

$$S_c = \left[ L_i - L_o + \frac{Q_i}{\Delta x} - \frac{Q_o}{\Delta x} - D \right] \Delta t$$

Equation 1: The model of the wood budget initially proposed by Benda and Sias (2003) and later modified by Cadol et. al (2009) for tropical streams, where the transport terms have prominent importance.  $S_c$  = wood load;  $L_i$  = lateral input of wood from tree mortality and bank erosion;  $L_o$  = lateral output of wood by flood events;  $Q_i$  = fluvial input of wood from upstream reaches;  $Q_o$  = fluvial output of wood to downstream reaches;  $D$  = wood decay;  $\Delta x$  = reach length.

We used LW volume scaled by channel dimensions as our instream wood metric. We adopted two variables, the wood volume per 100 m stream length ( $m^3/100m$ ) (WOOD1) and the wood volume per 100  $m^2$  of stream surface area ( $m^3/100m^2$ ) (WOOD2), because of their different applications. The former is more appropriate when analyzing the incoming or outgoing flux of wood, the latter is more suitable once the wood is in the channel affecting habitat, sediment, and flows. Therefore, the delivery of wood should be represented by WOOD1 and the wood storage by WOOD2. To facilitate this understanding, throughout this article we will refer to WOOD1 as wood load and to WOOD2 as wood stock. Importantly, WOOD2 is influenced by WOOD1 jointly with stream size, depth, flow variables, etc.

In this study we consider  $L_i$  as the wood delivered by tree mortality and bank erosion. Landslides and wind throw were not considered here since we have not observed evidence of such events in the study sites. Furthermore, the scarcity and the low density of riparian forest in most of Cerrado sites, and the mild slope particularly in Amazon sites, discount any significant importance of these events even if they occurred. Thus, we considered riparian forest cover and bank erosion as positive and direct influences on  $L_i$ . The first because the presence of trees near-bank and the forest characteristics such as size, density, age, and structural integrity affect tree mortality rate (Costigan et al., 2015; McDade et al., 1990; Van Sickle and Gregory, 1990). The second, because bank erosion fells trees into the stream channel (Comiti et al., 2016; Wohl et al., 2011). In addition to these direct effects, we also accounted for indirect effects on  $L_i$ . Discharge, stream power, channel slope and riparian forest may affect bank erosion, which in turn affect  $L_i$  (Keller and Swanson, 1979). Climate (i.e., humidity, temperature, and precipitation) and deforestation affect forest cover in the catchment scale and also the

amount and quality of the riparian forest on the channel banks, which may affect  $L_i$  directly, or indirectly through bank erosion.

The lateral output ( $L_o$ ) consists of logs exported from the stream to the riparian zone during flood events. Therefore,  $L_o$  may be affected mainly by the discharge because an increase in water level would be needed for the logs to be carried up onto the floodplain by the flow (Ruiz-Villanueva et al., 2016b). However, this type of wood loss may be significantly reduced in confined channels (Bilby and Bisson, 1998; Martin et al., 2018), because a greater increase in discharge and, thus, in the water level would be necessary before the flow reached the riparian zone, possibly depositing wood on it.

The confinement of the channel may also indirectly affect the downstream transport terms ( $Q_i$  and  $Q_o$ ), but in the opposite direction. Confinement leads to greater depth, velocity, and shear stress, and consequently to a greater unit stream power. As confined channels will have deeper flow for a given discharge, and because flow depth relative to piece diameter is such an important transport metric, narrow channels would be expected to have higher fluvial transport rates, both in and out. The stream power is also affected by channel slope, but this variable may also directly influence wood mobilization since wood pieces are more prone to move downstream in steep channels (Cadol and Wohl, 2010; Wohl and Jaeger, 2009a). Regarding only  $Q_i$ , the input of wood from upstream regions depends on the presence and amounts of forests in upstream reaches, since those forests are important sources of wood (Paula et al., 2013; Swanson, 2003). So, the forest cover in the upstream catchment may directly and positively affect the fluvial input of wood ( $Q_i$ ). And the greater the number of tributaries in a catchment, the greater the potential incoming flux of wood from upstream forest patches. Therefore, the drainage and confluence density in the upstream catchment may result in higher  $Q_i$ .

The probability of a piece of wood being trapped in the channel is the inverse of its chance of being transported downstream. The ratio between wood dimensions (length and diameter) and channel dimensions (width and depth) is frequently used as an indicator of wood stability (the inverse of wood mobility) (Cadol and Wohl, 2010; Dixon and Sear, 2014), since the larger the piece size relative to the channel, the less the chance of it being carried downstream (Lienkaemper and Swanson, 1987). Therefore,  $Q_o$  would be negatively affected by wood stability.

The last term of the equation, the decay ( $D$ ), includes both physical and biochemical decomposition and varies according to the environmental conditions, wood species, and the diversity of decomposer organisms (Harmon et al., 1986; Martius, 1997). The physical decomposition includes breakage and abrasion resulting from the friction between the wood and the water flow and sediment transport. Therefore, the wood stability and resistance to breakage and the stream discharge should be the most important variables influencing physical decomposition. The

biochemical decomposition is dependent on the abundance and diversity of decomposers, as well as the wood species. As we neither have data about the wood quality and species nor about the decomposer community, we did not include these variables in our conceptual model. As a surrogate to infer the influence of decay on wood load we used environmental conditions, since the wood decay is highly and positively influenced mainly by temperature and moisture (Boddy, 1983; Liu et al., 2013). The variation in the discharge may also influence the decay through both physical and biochemical decomposition. Repeated submersion and exposure of logs may accelerate the decay process, since the submersion events provide moisture to the wood and the exposure provides oxygen and heat to the decomposing organisms, enhancing the biochemical processes (Cadol and Wohl, 2010; Jones et al., 2019; Martius, 1997). In addition, the alternation between submerged and non-submerged conditions enables the occurrence of joint effects of physical and biochemical agents, in which the microorganisms decompose the organic matter, and the water flow washes it out (Bärlocher and Boddy, 2016; Harmon et al., 1986). Therefore, besides temperature and humidity we also considered precipitation averages and discharge variation as surrogates for the decomposer agents that may affect wood decay.

Besides the variables mentioned above, there are many other factors indirectly affecting the wood budget terms and thus the wood load. In order to understand the wood regime in the studied streams, we built our conceptual model as a flow chart (Figure 2). We included all the available variables that we expected to affect the wood budget directly or indirectly, based on the published literature and personal knowledge. Because we did not measure the wood budget terms, we showed them in the flow chart merely for illustrative purposes, to understand the expected relationships between predictors and instream wood. Instead of using the wood budget terms themselves in the pathway analysis (see data analysis section), we simply used wood volume, represented by wood load (WOOD1 –  $\text{m}^3/100\text{m}$ ) and stock (WOOD2 –  $\text{m}^3/100\text{m}^2$ ).

## 2.4 Data analysis

To test whether our conceptual model fits our dataset, we used structural equation modelling (SEM) to confirm whether the potential predictors of wood load do explain the instream wood in Amazon and Cerrado streams. In the SEM statistical framework, it is possible to deal simultaneously with multiple processes to explain the functioning of a whole system (Shipley, 2000), including the direct and indirect effects between variables. In SEM, theoretically justified models are parameterized to find a solution that minimizes the difference between the model predictions and the observed data (Grace, 2008). This is made by combining regression and factorial analysis, enabling us to identify not only what explains the response variable, but how much of its variance is explained. To do so, we first applied the strictly confirmatory approach, in which we tested our

conceptual model, concluding by its acceptance or refutation. Depending on whether the initial conceptual model is refuted in this step, we then proceed to the model development approach in which we set out to search for the most parsimonious model that better fits our dataset. This is made by including or excluding paths and variables in the initial model to improve its fit to the data.

We used the local estimation method (also called piecewise SEM) proposed by Shipley (2000) and ran the SEM in R software applying the 'piecewiseSEM' package (Lefcheck, 2016). In a SEM model, endogenous variables are those that have paths entering them, regardless of whether they also have paths emanating from them. Conversely, exogenous variables only have paths emanating from them, in which case we do not try to explain what generates them. In the local estimation method, relationships for each endogenous variable are estimated separately, fitting a linear model for each response, and then stringing together the inferences rather than trying to estimate all relationships at once (as in global estimation method) (Lefcheck, 2016). Through the test of directed separation (TDS), the 'piecewiseSEM' indicates to us whether or not we are missing paths in our model, so that we can include those paths if the model does not fit well. In the same way, we can exclude paths with non-significant relationships in the linear regression analyses. Therefore, with the caution to always ensure that each path is consistent with plausible ecological mechanisms, the search for the most suitable model is not arbitrary but guided by the strength of statistical evidence.

As piecewise SEM is a series of concatenated linear regressions, our data must meet the same assumptions as those for linear regression analysis ('lm' = function command to run linear regression in R software) otherwise we must specify the distribution of each response variable running a generalized linear model ('glm' = function command to run generalized linear regression in R software). Because of the great number of variables and the high complexity of our initial model, we had difficulty in running 'glm' function in 'piecewiseSEM' package. Thus, we decided to transform our non-normal distributed response variables using square root or log transformations and simply apply 'lm' function.

After running the SEM for our conceptual model, we verified that the data fit was poor ( $p < 0.05$ , meaning that the observed data significantly differed from the modelled). Thus, we started the search for a better model by first excluding the non-significant paths between predictors and wood volume variables (direct paths), and then between the predictors themselves (indirect paths). Once our model had only significant pathways, we then analyzed the "missing" paths indicated by TDS and added the ones we judged to represent plausible ecological mechanisms. The procedure of adding or removing paths was made one by one, always running the SEM again after each one. We analyzed the results of each SEM iteration, sequentially choosing the next path to be excluded or included to the model. We stopped changing the model once we met

three conditions: (i) a good fit ( $p > 0.05$ , meaning that the observed data do not significantly differ from the modelled); (ii) all the specified paths were significant; and (iii) no ecologically plausible paths were missing, that is, no significant relationships detected on TDS for the independence claims.

From the final model, we calculated the indirect and total effects for each pathway. The indirect effect is calculated by multiplying the direct effects linking a given pathway (e.g., to calculate the indirect effect of precipitation on wood load mediated by catchment forest, we multiplied the effect of precipitation on catchment forest by the effect of catchment forest on wood load), and the total effect is given by summing all direct and indirect effects linking a predictor (e.g., precipitation) and a response variable (e.g., wood load). After running the SEM for the global model (Amazon and Cerrado streams without grouping), we also ran a multigroup analysis per biome, in order to investigate whether wood predictors change or not depending on the biome. Finally, we plotted the predictors that differed between biomes against the wood volume metrics.

### **3. RESULTS**

We organize our results by presenting the overall SEM model performance, the causal pathways influencing wood in neotropical streams, the major influences on wood load (WOOD1) and on wood stock (WOOD2), and lastly the regional differences streams between Amazon and Cerrado streams.

#### **3.1 SEM model fit**

The most parsimonious model and closest to the conceptual model to explain instream wood in both Amazon and Cerrado regions contains 15 variables (seven exogenous, eight endogenous), 47 links and 235 pathways. The TDS indicated a number of 43 independence claims (mathematically possible paths but unspecified in the model), none of them showing significant relationship between the variables involved, indicating that we were justified in excluding those relationships from our path diagram. Thus, we obtained a model-wide  $P = 0.356 (>0.05)$  implying that the hypothesized structure is supported by the data. The global goodness-of-fit Fisher's  $C = 90.24$  and  $AIC = 220.24$  (Figure 3). From this global model we calculated the direct, indirect, and total effect of each predictor variable on the response variables (Table 4). All the pathways and the partial effects of each predictor variable on the response variables are detailed in the supplementary material (S2).

### 3.2 Causal pathways on wood

As predicted in the conceptual model, bankfull discharge (QBF), stream power (STR\_PWR), discharge variation (Q\_VAR), temperature (TEMP), precipitation (PRECIP), humidity (HUMID), riparian forest (RIP\_FOR), and wood stability (WSTAB-L and WSTAB-D) directly affected instream wood (WOOD1 or WOOD2). The channel depth (CHAN\_DEPTH) and channel width (CHAN\_WIDTH) also directly affected wood volume, although we expected that the effect of depth and width would be only indirect, mediated by WSTAB-L and WSTAB-D and also by WOOD1 on WOOD2 (because  $WOOD2 = WOOD1 / CHAN\_WIDTH$ ). Channel slope (CHAN\_SLOPE) and forest cover in the catchment (CAT\_FOR) had a small and indirect effect on wood (-0.10 and 0.01 respectively), whereas bank erosion (BANK\_ERO), channel confinement (CHAN\_CONF), confluence density (CONFL\_DEN) and drainage density (DRAIN\_DEN) apparently did not affect wood load and so were removed from the model. Likewise, wood volume did not respond to variables measured at a broader, catchment, scale (i.e., CAT\_AREA, CAT\_SHAPE, CAT\_SLOPE, CAT\_ELEV, CAT\_DEFOR). Figure 3 shows all variables influencing wood in Cerrado and Amazon streams according to SEM. In order to show the strength of SEM in disentangling the effects of predictors on instream wood, we included a Spearman correlation matrix as a supplementary material (supplementary material, S3). The correlation analysis is not capable of detecting the effects of some of the main wood predictors such as the discharge and stream power.

### 3.3 Major influences on Wood Load (WOOD1)

The variables that most directly explained wood load (WOOD1) was WSTAB-L (0.53), bankfull discharge (0.34), channel depth (0.33) and stream power (-0.32), where the numbers in parentheses are the SEM standardized coefficients, which indicate the direct effect of one variable on another. The indirect effects are obtained by multiplying the direct effects of each variable included within a given pathway from the predictor to the response variable. The total effect is obtained by summing all direct and indirect effects of each variable. Thus, in the case of WSTAB-L, its direct effect on WOOD1 was 0.53, its indirect effect was 0.17, and its total effect was 0.70 (see Table 4 for all effects).

The channel width also affected wood load directly (0.15), but the channel slope only indirectly (-0.10) mainly through stream power ( $0.28 * -0.32 = -0.09$ ) and bankfull discharge ( $0.35 * 0.34 = 0.12$ ). Considering the direct and indirect effects altogether, WSTAB\_L is by far the most important variable to explain wood load ( $0.53 + 0.17 = 0.70$ ), followed by the riparian forest ( $0.20 + 0.23 = 0.43$ ). The indirect effect of the riparian forest was through WSTAB\_L ( $0.26 * 0.53 = 0.14$ ) and WSTAB\_D ( $0.15 * 0.29 = 0.04$ ), further emphasizing the importance of the stability of wood. The direct effect of riparian forest on wood load reflects the lateral

recruitment in the wood budget equation ( $L_i$ ), while the indirect effect reflects the hindrance to the transportation ( $Q_o$ ), since it was positively related to the wood stability. Greater stability of instream wood was associated with larger riparian trees that contributed larger pieces of wood. Regarding the downstream transportation ( $Q_i$ ), we did not detect any direct effect of CAT\_FOR on wood load, but we did detect an indirect effect of CAT\_FOR on wood stock (WOOD2) through discharge variation ( $0.29 * 0.02 = 0.01$ ).

### 3.4 Major influences on Wood Stock (WOOD2)

The wood load itself was the variable that most influenced wood stock (0.88). QBF, STR\_PWR and WSTAB\_D had direct effects opposite to that observed for wood load (-0.19, 0.08, and -0.07 respectively). The riparian forest only affected wood stock indirectly through wood stability and wood load (0.40). The wood stock was also directly affected by the climatic predictors, which we used as surrogates for wood decay agents. We did expect that these variables had a negative effect on the wood stock. However, only humidity reduced WOOD2 (-0.17), whereas precipitation and temperature affected it positively (0.05 and 0.10 respectively), as well as discharge variation (0.02). This result shows that those variables tend to affect wood volume through other wood budget terms,  $L_i$  or  $Q_i$ , rather than decay (D), different from what we initially expected. Despite not affecting wood load (WOOD1) directly, climatic variables acted indirectly (HUMID = 0.15, PRECIP = 0.24 and TEMP = -0.23) in many ways, through riparian forest (TEMP =  $-0.54 * 0.20 = 0.11$ , HUMID =  $0.91 * 0.20 = 0.18$ ), bankfull discharge (PRECIP =  $0.18 * 0.34 = 0.06$ , HUMID =  $-0.28 * 0.34 = 0.09$ ) and WSTAB-L (PRECIP =  $0.27 * 0.53 = 0.14$ , HUMID =  $-0.42 * 0.53 = 0.22$ ).

### 3.5 Regional Differences

Based on the final global model we ran the multi-group analysis per biome (Fisher's C = 74.95;  $p = 0.80$ ) (Table 5). With regard to wood load (WOOD1), we found that examining the biomes separately only affected the role of wood stability (WSTAB\_D), with this predictor ceasing to be important to explain wood in Amazon streams (Figure 4a). Regarding WOOD2, biome affected the relationships between wood and CHAN\_WIDTH, QBF, STR\_PWR, Q\_VAR, HUMID, TEMP, WSTAB-L and WSTAB-D (Figure 4b-i). STR\_PWR, HUMID, TEMP and WSTAB\_D were no longer important to explain WOOD2 in Cerrado and Q\_VAR in neither of the two biomes, when considering biome as a grouping variable. Biome also affected the relationship between predictor variables themselves, such as PRECIP on CAT\_FOR, Q\_VAR and QBF; HUMID and TEMP on RIP\_FOR; CHAN\_WIDTH on QBF; CHAN\_DEPTH, CHAN\_WIDTH and WSTAB\_L on WSTAB\_D; CHAN\_SLOPE on STR\_PWR; and CAT\_FOR on Q\_VAR (supplementary material, S4).

## 4. DISCUSSION

We first discuss our findings concerning the main controls on wood in neotropical streams overall and then compare results from the Amazon and Cerrado regions.

### 4.1 Main drivers of wood in neotropical streams

The most important controls on wood in Amazon and Cerrado streams were wood stability, bankfull discharge, stream power, channel dimensions and riparian forest (Figure 5). The last one is the primary source of wood to the channels, delivering directly through dropping pieces or by floating downed wood from the riparian zone. However, wood amounts are more strongly determined by how much streams can retain than by how much wood is falling into the channel. Wood retention is controlled firstly by the piece size relative to the channel (wood stability) and channel dimensions, and secondly by the stream power to move it downstream. As we can see in the conceptual model (Figure 2), wood stability, bankfull discharge and stream power are expected to be linked to the fluvial transport terms ( $Q_i$  and  $Q_o$ ) of the wood budget equation. Our results confirmed these relationships (Figure 3), showing that the transport capacity or the resistance to transportation are the most important mechanisms influencing wood load in streams of both the Amazon and Cerrado regions. Discharge and stream power act by bringing wood from floodplain and upstream regions or removing it to downstream reaches, and the size of wood pieces relative to the channel size influences wood stability (mainly WSTAB-L and WSTAB-D) by keeping big pieces trapped within the channel. The importance of wood stability is also evidenced by the absence of direct effect of channel slope on wood load, indicating that even in steep streams the wood pieces remain stable if they are trapped.

As expected, the greater the stream power, the smaller the wood volume per length of channel, indicating that more wood is transported downstream. Wohl and Jaeger (2009a) reported that wood load is inversely correlated with stream power and despite some variations, it works well as a proxy indicator of relative transport capacity. Surprisingly, the bankfull discharge had a direct positive effect on wood, indicating that it augments wood inputs. Bankfull floods likely import downed LW from the lateral seasonal bed or from banks by scouring and causing tree fall or excavating buried wood. Indeed, the floodplain can become one of the main sources of wood to forested streams through overbank flow (Latterell and Naiman, 2007). This occurs because the floodplain attenuates peak flows, reducing downstream transport, while floating downed wood into the stream channel or exhuming buried pieces from alluvial channel beds (Wohl, 2013). This seems to apply to the streams we studied, especially those in the Amazon biome. Therefore, we expect the predominance of downstream transport forces in reaches with steeper

slopes, and thus, higher stream power, while in low gradient reaches the wood supply might have come from the riparian zone during overflow events.

Wood stability is not indicative of wood transport itself, instead, it indicates the resistance to transport. Mobile pieces are usually shorter than the bankfull width; therefore, pieces that are large relative to the channel tend to remain trapped (Gurnell et al., 2002; Lienkaemper and Swanson, 1987). This agrees with our results, since the ratio between piece length and channel width was in fact the most important factor explaining wood volume. Channel dimensions also affected wood volume. Because of the reduced transport capacity and the high wood retentiveness, small streams are known to have comparatively more wood than larger streams (Harmon et al., 1986; Martin and Benda, 2001; Swanson, 2003). However, in our study, channel width and depth had a positive effect on wood volume when wood is scaled by channel length (WOOD1). Nevertheless, when we scaled wood volume per channel area (WOOD2) this positive effect of channel depth disappeared and the effect of channel width and became negative, confirming that larger streams do tend to have lower densities of instream wood. The explanation for the different relationship detected between channel dimensions and wood volume for the two different wood metrics is precisely the difference in the metric scaling by channel width. As we adopted bankfull, rather than wetted measures, a significant part of the wood volume is located outside the water, in the frequently flooded zone. The same amount of wood volume per length of channel will have greater instream volume per bankfull channel surface area in a small narrow stream than in a large wide stream.

Local recruitment of wood from riparian sources was also important in predicting wood load in the studied streams, although to a lesser extent than the stability of instream wood. The denser the riparian forest cover, the greater the wood load. The influence of the riparian forest in predicting wood was not only direct, but also indirect through wood stability. The larger size of fallen trees in mature riparian forests contribute larger, more stable wood pieces that tend to remain trapped in the stream channel. Many previous studies have shown that old-growth forest streams contain instream wood with greater diameters and volumes than found in streams draining second-growth forest, reflecting the more complex structure of old growth forests (e. g. Beckman and Wohl, 2014; Benda et al., 2002; Keeton et al., 2007). Besides the development stage of the riparian forest, its proximity to the channel also affects wood volumes (McDade et al., 1990). Moreover, pieces may travel long distances downstream, so the wood stock in a reach may reflect the riparian forest in upstream parts of their drainage (Iroumé et al., 2010; Paula et al., 2013; Ravazzolo et al., 2015).

In surprising contrast with the influence of riparian forest cover, we did not detect any direct effect of the forest in the upstream catchment

(CAT\_FOR) on wood load, but we found an indirect effect on wood stock (WOOD2) through discharge variation. Thus, the instream wood in our streams may have been somewhat sensitive to the forest cover in the basin because it affects the hydrological regime, rather than its potential to provide wood. Indeed, catchments with sparse forest typically have altered disbalanced hydrological regimes (Kang et al., 2001; Mahe et al., 2005; Sriwongsitanon and Taesombat, 2011). Also, the lack of relationship between wood load (WOOD1) and catchment forest may indicate that relatively few LW pieces recruited in upstream regions are arriving in the studied reaches. This is different from what was found in another Brazilian biome, the Atlantic Forest, in streams also located in an agriculture-impacted landscape, where most of the wood was coming from upstream reaches (Paula et al., 2013). Despite that, the predominantly small size of LW in the study streams (Saraiva et al., 2022) indicates that they can be easily transported. Thus, if LW pieces are not arriving from upstream it is probably because they are being degraded along the way, as expected for small sized instream wood (Haga et al., 2002; Lienkaemper and Swanson, 1987; Merten et al., 2013). Alternatively, could it be because the Atlantic Forest streams have more topographic relief than our streams, especially the Amazon ones (see Paula et al., 2013). In streams draining basins with steep hillsides, wood can be contributed by mass-failures (landslides), which bring a lot of wood from outside the riparian zone (Wohl et al., 2012b).

Unfortunately, our ability to estimate the role of wood decay was weak because we did not measure it, instead using climatic variables as surrogates. Still, we inferred the direct effects of wood decay through humidity reducing wood stock (WOOD2), since water is a limiting factor to decomposing organisms (Bärlocher and Boddy, 2016). Conversely, temperature and precipitation tended to increase wood stock, likely being more related to input sources than decay. The inferred indirect effects of climatic variables on instream wood provide us some relevant insights. The negative relationship between temperature and riparian forest results in higher average temperatures in deforested streams, which in turn have less wood as demonstrated by Leal et al. (2016) for the same Amazon streams. Higher precipitation averages result in higher bankfull discharge, but higher average humidity levels are associated with lower bankfull discharges. Streams located in more humid sites have denser riparian forest which contributes to greater wood loads (WOOD1), but also in less stable pieces probably due to breakage caused by decay agents that reduce the wood stock. Fragmentation and leaching are particularly important mechanisms of wood decomposition in streams leading to significant mass loss (Jones et al., 2019).

#### **4.2. Regional differences in wood predictors**

Analyzing the results per biome, we found that Amazon and Cerrado differ in some aspects. The interaction between biome and wood predictors is

rarely important to explain wood load (WOOD1), but commonly important to explain wood stock (WOOD2). This means that the mechanisms influencing wood load (the wood sources) are basically the same in tropical streams independent of the biome, but the channel features that determine wood stock by storage and transport can vary considerably between biomes. Regarding wood load, the general pattern detected in the combined-region model (i.e., the transport variables being the most important wood predictor and the riparian forest playing a secondary role) persisted independent of the biome. Nevertheless, the influence of riparian forest is greater in the Amazon than in Cerrado, probably as a result of naturally denser forest due to climatic conditions, but also to better conservation status, as reflected in the lower rates of deforestation in the Amazon region (Saraiva et al., 2022).

Wood stability based on the piece diameter and water depth (WSTAB\_D) was the only predictor of wood load that differed between biomes, ceasing to be important to explain wood in Amazon. Amazon streams have greater and more variable values of WSTAB\_D than those in the Cerrado. This difference in wood stability is caused not by the piece diameter differences between biomes, but by differences in bankfull dimensions, since Amazon streams had wider and shallower channels (Saraiva et al., 2022). The reduced channel depth would provide greater stability to the wood in Amazon, but as these streams are also wide, a piece of wood will not remain trapped even in shallow channels, as they are wide enough to decrease anchoring and allow the piece to be rolled down even during mild flood events.

Precipitation and wood load (WOOD1) were the only predictors that did not differ in their influence on wood stock (WOOD2) between the two biomes; they had a positive influence of similar magnitude in both Amazon and Cerrado streams. Discharge variation, which was a minor influence on wood stock in the combined regional model, was not important when we considered biomes separately. Therefore, the expected influence of discharge variation in reducing wood stock through decay, because of repeated episodes of submersion and exposition of wood (Cadot and Wohl, 2010; Martius, 1997) was not detectable in our data. This may be due to the limitations of our variable since we calculated discharge variation from the ratio between low flow and bankfull discharge. This variable does not exactly correspond to the submersion and exposure episodes since wood pieces may be submerged even in floods smaller than the bankfull. To better measure the influence of these episodes in wood decay we would need flow records of the frequency and duration of low and high flows to use as a better indirect (surrogate) variable than the one we used, but unfortunately this kind of data is not available for the study catchments. Combined with measurements of the discharge level at which most of the instream wood pieces are submerged, further studies could provide a precise measure of the frequency and duration of submersion and exposure episodes.

Humidity affected wood stock negatively and air temperature affected it positively in the Amazon, but not in the Cerrado. This is understandable because both humidity and temperature are markedly higher in the Amazon. Therefore, the high and constant humidity and temperature levels in the Amazon (Fisch et al., 1998) as well as the high diversity of decomposing microorganisms (Bustamante and Martius, 1998; Lodge, 1995; López-Quintero et al., 2012) might contribute to faster wood decay compared with the Cerrado. The high temperatures associated with high humidity in the Amazon are responsible for the typical high primary productivity of this biome. These two climatic factors influenced wood volume both by providing greater quantity of pieces and by supplying streams with large sized pieces of wood, which are harder to break down than small ones (Merten et al., 2013).

Channel width negatively affected wood stock (WOOD2) in both Amazon and Cerrado streams (Table 4), confirming the universal pattern that larger streams tend to store less wood (Harmon et al., 1986; Martin and Benda, 2001; Swanson, 2003). However, in Cerrado this relationship was stronger. The pattern with bankfull discharge was reversed, affecting wood stock negatively in streams of both biomes, but in this case, the relationship was stronger in Amazon. Stream power affected wood stock positively in the Amazon, but not in the Cerrado. These variables are related to wood transport such their influence is exerted through mobilizing and trapping pieces, which may be limited by the channel characteristics. Amazon streams have low slope and stream power, predominantly glide flow, and less confined channels (Saraiva et al., 2022). In the Cerrado, slope and stream power are much greater, but it is also important to consider the influence of anthropogenic activities.

In comparison with the Amazon, the greater amounts of deforestation and conversion to human land uses in the Cerrado (Saraiva et al., 2022) not only reduce the input of wood, but may increase the frequency and magnitude of flood events (Kang et al., 2001; Mahe et al., 2005; Sriwongsitanon and Taesombat, 2011). These anthropogenic influences favor downstream wood output ( $Q_o$ ) in the Cerrado, which explains why the relationship between channel width and wood stock was stronger and why there was no effect of stream power on the wood stock in this biome. It is apparent that most of the wood that enters into the reaches is transported downstream, nullifying the stream power effect. The effect of bankfull discharge in reducing wood stock in Amazon streams derived not only directly from downstream transport ( $Q_o$ ), but also indirectly through its effects on lateral output ( $L_o$ ) and decay ( $D$ ), which are potentially favored by the shallower channel characteristics and wetter environmental conditions. Unconfined channels allow the overflow to easily inundate adjacent areas, so LW may be exported more easily onto the seasonally flooded riparian areas. Furthermore, forested floodplains are able to trap floating LW (Wohl, 2017), keeping it out of the water in the riparian zone floor, where there is a high density of decomposing organisms (Martius, 1997). Therefore, bankfull discharge is likely to be a

negative influence on in-stream wood in the Amazon biome through three mechanisms instead of only one.

Finally, wood stock was also influenced by wood stability based on piece length in both biomes. The longer the transported piece relative to channel width, the greater the wood volume per channel area (WOOD2) in both biomes. The strength of this influence is twice as strong in the Amazon streams because they are wider and shallower and also bordered by denser riparian forest than in the Cerrado (Saraiva et al., 2022). Conversely, the influence of the wood piece diameter relative to channel depth was significant only in Amazon, where it was a small negative influence in contrast with its strong positive influence on WOOD1 in both biomes. This shows that when we consider the wood volume in the channel area, the thicker the wood related to channel depth, the lower the wood volume. This may be pointing out a soft effect of decay on wood stability, since more stable pieces tend to remain trapped in the same place, providing better opportunities to the decomposing organisms, which already have favorable conditions in the floodplain of Amazon streams (Martius, 1997). Alternatively, this could be only a mathematical consequence, since WSTAB\_D and WOOD2 both have channel width in their denominator, such their association just reveals that LW volume per area with equal WOOD1 increases as width (therefore also area) decreases.

## **5. CONCLUSIONS**

### **5.1. Summary**

We examined the association of instream wood with potential drivers of the wood budget in large sample of neotropical streams experiencing very low to very high levels of agricultural influence. Our results indicate that variation in the amount of instream wood among these streams was more strongly influenced by variation in downstream transport than by differences in the amount of recruitment. Specifically, transport of wood recruited from the local riparian forest along these streams is controlled primarily by channel dimensions and the size of wood pieces relative to the channel size. Basically, the amount of wood found in the streams is the result of the wood delivered by the local riparian forest and how much of this wood remains trapped.

### **5.2. Implications for land and river management**

Local factors dominated the wood regime in Amazon and Cerrado streams, whereas regional factors only showed influence through climatic controls. Our findings support the preservation of forested riparian zones to ensure both the maintenance of standing forest (the wood source) and the integrity of the channel morphology (the wood trap). Both of these riparian forest functions are crucial for maintaining adequate amounts of

wood in neotropical streams to maintain their physical and biological integrity.

### 5.3. Topics for further work

Wood decay may play an important role, but unfortunately our ability to detect its effect was limited, indicating that the use of surrogate wood decay variables is not ideal. To clearly show the decay effect on wood budget future studies should focus on measuring the decay rates ( $D$ ). The most desirable scenario to fully understand the wood regime would be to directly measure all terms of the wood budget equation, which also includes the recruitment rates from the local riparian forest ( $L_i$ ), the export to the riparian zone ( $L_o$ ) and the rates of fluvial transport in ( $Q_i$ ) and out ( $Q_o$ ) the reach. However, this would never be possible in a study of a spatial scale as extensive as ours. The SEM analysis proved to be a powerful tool in disentangling such complex systems when applied to a large regional dataset. Further research should focus on comparing reference and disturbed streams to more fully assess anthropogenic influences and to investigate whether the predominance of local controls persists in both the contemporary and the natural wood regime in Amazon and Cerrado river corridors. Thereafter, we might be able to infer the magnitude of the problem and then propose management measures to maintain the wood regime in neotropical river corridors.

### REFERENCES

- Bagnold, R.A. (1966) An Approach to the Sediment Transport Problem from General Physics. *Physiographic and Hydraulic Studies of Rivers*, 422(1), 1–37. Available from: <https://doi.org/10.3133/pp4221>
- Barbosa, R.I., Castilho, C.V., Perdiz, R.O., Damasco, G., Rodrigues, R. & Fearnside, P.M. (2017) Decomposition rates of coarse woody debris in undisturbed Amazonian seasonally flooded and unflooded forests in the Rio Negro-Rio Branco Basin in Roraima, Brazil. *Forest Ecology and Management*, 397, 1–9. Available from: <https://doi.org/10.1016/j.foreco.2017.04.026>
- Bärlocher, F. & Boddy, L. (2016) Aquatic fungal ecology - How does it differ from terrestrial? *Fungal Ecology*, 19, 5–13. Available from: <https://doi.org/10.1016/j.funeco.2015.09.001>
- Beckman, N.D. & Wohl, E. (2014) Effects of forest stand age on the characteristics of logjams in mountainous forest streams. *Earth Surface Processes and Landforms*, 39(11), 1421–1431. Available from: <https://doi.org/10.1002/esp.3531>
- Benda, L.E., Bigelow, P. & Worsley, T.M. (2002) Recruitment of wood to streams in old-growth and second-growth redwood forests, northern

California, U.S.A. *Canadian Journal of Forest Research* 32(8), 1460–1477. Available from: <https://doi.org/10.1139/x02-065>

Benda, L.E., Poff, N.L., Miller, D., Dunne, T., Reeves, G., George, P. & Pollock, M. (2004) The Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats. *BioScience* 54(5), 413–427.

Available from: [https://doi.org/10.1641/0006-3568\(2004\)054\[0413:TNDHHC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2)

Benda, L.E. & Sias, J.C. (2003) A quantitative framework for evaluating the mass balance of in-stream organic debris. *Forest Ecology and Management*, 172(1), 1–16. Available from:

[https://doi.org/10.1016/S0378-1127\(01\)00576-X](https://doi.org/10.1016/S0378-1127(01)00576-X)

Bilby, R.E. & Bisson, P.A. (1998). Function and Distribution of Large Woody Debris. In: Naiman, R.J. & Bilby, R.E. (Eds.) *River ecology and management: lessons from the Pacific Coastal Ecoregion*. New York: Springer, pp. 324–346.

Bilby, R.E. & Wasserman, L.J. (1989) Forest practices and riparian management in Washington State: Data based regulation development. In: Gresswell, R.E., Barton, B.A. & Kershner, J.L. (Eds.) *Practical approaches to riparian resource management: an educational workshop*. Billings: U.S. Bureau of Land Management.

Boddy, L. (1983). Carbon dioxide release from decomposing wood: Effect of water content and temperature. *Soil Biology and Biochemistry*, 15(5), 501–510. Available from: [https://doi.org/10.1016/0038-0717\(83\)90042-1](https://doi.org/10.1016/0038-0717(83)90042-1)

Bustamante, N.C.R. & Martius, C. (1998) Nutritional preferences of wood-feeding termites inhabiting floodplain forest of the Amazon River, Brazil. *Acta Amazonica*, 28(3), 301–307. Available from: <https://doi.org/10.1590/1809-43921998283307>

Cadol, D. & Wohl, E. (2010) Wood retention and transport in tropical, headwater streams, La Selva Biological Station, Costa Rica.

*Geomorphology*, 123(1-2), 61–73. Available from: <https://doi.org/10.1016/j.geomorph.2010.06.015>

Cadol, D., Wohl, E., Goode, J.R. & Jaeger, K.L. (2009) Wood distribution in neotropical forested headwater streams of La Selva, Costa Rica. *Earth Surface Processes and Landforms*, 34(9), 1198–1215. Available from:

<https://doi.org/10.1002/esp.1800>

Chao, K.J., Phillips, O.L. & Baker, T.R. (2008) Wood density and stocks of coarse woody debris in a northwestern Amazonian landscape. *Canadian Journal of Forest Research*, 38, 795–805. Available from:

<https://doi.org/10.1139/X07-163>

Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F. & Veldkamp, E. (2002) Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *Forest Ecology and Management*,

164, 237–248. Available from: [https://doi.org/10.1016/S0378-1127\(01\)00597-7](https://doi.org/10.1016/S0378-1127(01)00597-7)

Comiti, F., Andreoli, A., Lenzi, M.A. & Mao, L. (2006) Spatial density and characteristics of woody debris in five mountain rivers of the Dolomites (Italian Alps). *Geomorphology*, 78(1-2), 44–63. Available from: <https://doi.org/10.1016/j.geomorph.2006.01.021>

Comiti, F., Lucía, A. & Rickenmann, D. (2016) Large wood recruitment and transport during large floods: A review. *Geomorphology*, 269, 23–39. Available from: <https://doi.org/10.1016/j.geomorph.2016.06.016>

Costigan, K.H., Soltesz, P.J., Jaeger, K.L. (2015) Large wood in central Appalachian headwater streams: Controls on and potential changes to wood loads from infestation of hemlock woolly adelgid. *Earth Surface Processes and Landforms*, 40(13), 1746–1763. Available from: <https://doi.org/10.1002/esp.3751>

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A. & Quintero, N.B. (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica*, 30(1), 2–11. Available from: <https://www.jstor.org/stable/2389209>

Dixon, S.J. & Sear, D.A. (2014) The influence of geomorphology on large wood dynamics in a low gradient headwater stream. *Water Resources Research*, 50(12), 9194–9210. Available from: <https://doi.org/10.1002/2014WR015947>

Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S.R., Park, H. & Shao, C. 2016. Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecological Processes*, 5, 1-12. Available from: <https://doi.org/10.1186/s13717-016-0063-3>

FBDS - Fundação Brasileira para o Desenvolvimento Sustentável (2009) *Mapeamento em Alta Resolução dos Biomas Brasileiros*. Rio de Janeiro, Brasil. Available from FBDS web page: <http://geo.fbds.org.br/>. Date accessed: 2021-10-29.

Ferraz, S.F.B., Cassiano, C.C., Begotti, R.A. & Tranquilin, A.R. (2012) Land use change analysis tools (LUCAT). II Congresso Brasileiro de Ecologia de Paisagens.

Fick, S.E & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302–4315. Available from: <https://doi.org/10.1002/joc.5086>

Fisch, G., Marendo, J.A. & Nobre, C.A. (1998) Uma revisão geral sobre o clima da Amazônia. *Acta Amazonica*, 28, 101–126. Available from: <https://doi.org/10.1590/1809-43921998282126>

Gardner, T.A. et al. (2013) A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences*,

368, 20120166–20120166. Available from:

<https://doi.org/10.1098/rstb.2012.0166>

Grace, J.B. et al. (2007) Does species diversity limit productivity in natural grassland communities? *Ecology Letters* 10, 680–689. Available from: <https://doi.org/10.1111/j.1461-0248.2007.01058.x>

Grace, J.B. (2008) Structural Equation Modeling for Observational Studies. *Journal of Wildlife Management*, 72, 14–22. Available from: <https://www.jstor.org/stable/25097499>

Gurnell, A.M., Piégay, H., Swanson, F.J. & Gregory, S. V. (2002) Large wood and fluvial processes. *Freshwater Biology*, 47, 601–619. Available from: <https://doi.org/10.1046/j.1365-2427.2002.00916.x>

Guyette, R.P., Dey, D.C. & Stambaugh, M.C. (2008) The temporal distribution and carbon storage of large oak wood in streams and floodplain deposits. *Ecosystems*, 11, 643–653. Available from: <https://doi.org/10.1007/s10021-008-9149-9>

Haga, H., Kumagai, T., Otsuki, K. & Ogawa, S. (2002) Transport and retention of coarse woody debris in mountain streams: An in-situ field experiment of log transport and a field survey of coarse woody debris distribution. *Water Resources Research*, 38, 1–16. Available from: <https://doi.org/10.1029/2001WR001123>

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S. V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G. & Sedell, J.R. (1986) Ecology of Coarse Woody Debris in Temperate Ecosystems. *Advances in Ecological Research*, 15, 133–302. Available from: [https://doi.org/10.1016/S0065-2504\(03\)34002-4](https://doi.org/10.1016/S0065-2504(03)34002-4)

Harmon, M.E., Whigham, D.F., Sexton, J. & Olmsted, I. (1995) Decomposition and Mass of Woody Detritus in the Dry Tropical Forests of the Northeastern Yucatan Peninsula, Mexico. *Biotropica*, 27, 305–316. Available from: <https://doi.org/10.2307/2388916>

Hughes, R.M. & Peck, D.V. (2008) Acquiring data for large aquatic resource surveys: the art of compromise among science, logistics, and reality. *Journal of the North American Benthological Society*, 27, 837–859. Available from: <https://doi.org/10.1899/08-028.1>

Hyatt, T.L. & Naiman, R.J. (2001) The residence time of large woody debris in the Queets River, Washington, USA. *Ecological Applications*, 11, 191–202. Available from: <https://doi.org/10.2307/3061066>

Iroumé, A., Andreoli, A., Comiti, F., Ulloa, H. & Huber, A. (2010) Large wood abundance, distribution and mobilization in a third order Coastal mountain range river system, southern Chile. *Forest Ecology and Management*, 260, 480–490. Available from: <https://doi.org/10.1016/j.foreco.2010.05.004>

- Jarvis, A., Reuter, H.I., Nelson, A., & Guevara, E. (2008) Hole-filled SRTM for the globe Version 4. Available from the CGIAR- CSI SRTM 90m Database. Available from: <http://srtm.csi.cgiar.org>
- Jones, J.M., Heath, K.D., Ferrer, A., Brown, S.P., Canam, T. & Dalling, J.W. (2019). Wood decomposition in aquatic and terrestrial ecosystems in the tropics: contrasting biotic and abiotic processes. *FEMS Microbiology Ecology*, 95, 1–13. Available from: <https://doi.org/10.1093/femsec/fiy223>
- Junqueira, N.T., Macedo, D.R., Souza, R.C.R., Hughes, R.M., Callisto, M. & Pompeu, P.S. (2016) Influence of environmental variables on stream fish fauna at multiple spatial scales. *Neotropical Ichthyology*, 14(3), e150116. Available from: <https://doi.org/10.1590/1982-0224-20150116>
- Kang, S, Zhang L, Song X. (2001) Runoff and sediment loss responses to rainfall and land use in two agricultural catchments on the Loess Plateau of China. *Hydrological Processes*, 15, 977–988. Available from: <https://doi.org/10.1002/hyp.191>
- Kaufmann, P. R., Faustini, J.M., Larsen, D.P. & Shirazi, M.A. (2008) A roughness-corrected index of relative bed stability for regional stream surveys. *Geomorphology*, 99, 150–170. <https://doi.org/10.1016/j.geomorph.2007.10.007>
- Kaufmann, P.R., Larsen, D.P. & Faustini, J.M. (2009) Bed stability and sedimentation associated with human disturbances in Pacific Northwest streams. *Journal of the American Water Resources Association*, 45, 434–459. Available from: <https://doi.org/10.1111/j.1752-1688.2009.00301.x>
- Kaufmann, P.R, Levine, P., Robison, E.G., Seeliger, C. & Peck, D. V. (1999) Quantifying Physical Habitat in EPA/620/R-99/003. U.S. Environmental Protection Agency: Washington, DC
- Keeton, W.S., Kraft, C.E. & Warren, D.R. (2007) Mature and old-growth riparian forests: Structure, dynamics, and effects on Adirondack stream habitats. *Ecological Applications*, 17, 852–868. Available from: <https://doi.org/10.1890/06-1172>
- Keller, E.A. & Swanson, F.J. (1979) Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes and Landforms*, 4, 361–380. Available from: <https://doi.org/10.1002/esp.3290040406>
- Latterell, J.J. & Naiman, R.J. (2007) Sources and dynamics of large logs in a temperate floodplain river. *Ecological Applications*, 17: 1127–1141. Available from: <https://doi.org/10.1890/06-0963>
- Leal, C.G. et al. (2016) Multi-scale assessment of human-induced changes to Amazonian instream habitats. *Landscape Ecology*, 31, 1725–1745. Available from: <https://doi.org/10.1007/s10980-016-0358-x>
- Lefcheck, J.S. (2016) piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology*

*and Evolution*, 7: 573–579. Available from:  
<https://doi.org/10.1111/2041-210X.12512>

Lewis, S.L. et al. (2004) Tropical forest tree mortality, recruitment and turnover rates: Calculation, interpretation and comparison when census intervals vary. *Journal of Ecology*, 92, 929–944. Available from:  
<https://doi.org/10.1111/j.0022-0477.2004.00923.x>

Lienkaemper, G.W. & Swanson, F.J. (1987) Dynamics of large woody debris in streams in old-growth Douglas-fir forests. *Canadian Journal of Forest Research*, 17, 150–156. <https://doi.org/10.1139/x87-027>

Liu, W., Schaefer, D., Qiao, L. & Liu, X. (2013). What controls the variability of wood-decay rates? *Forest Ecology and Management*, 310, 623–631. Available from: <https://doi.org/10.1016/j.foreco.2013.09.013>

Lodge, D.J. (1995) A survey of patterns of diversity in non-lichenized fungi. *Mitt. Eidgenöss. Forsch.anst. Wald Schnee Landsch*, 70, 157–173.

López-Quintero, C.A, Straatsma, G., Franco-Molano, A.E. & Boekhout, T. (2012) Macrofungal diversity in Colombian Amazon forests varies with regions and regimes of disturbance. *Biodiversity and Conservation*, 21, 2221–2243. Available from: <https://doi.org/10.1007/s10531-012-0280-8>

Di-Luzio, M., Srinivasan, R. & Arnold, J.G. (2004) A GIS-coupled hydrological model system for the watershed assessment of agricultural nonpoint and point sources of pollution. *Transactions in GIS*, 8, 113–136. Available from: <https://doi.org/10.1111/j.1467-9671.2004.00170.x>

Macedo, D.R., Pompeu, P.S., Morais, L., Castro, M.A., Alves, C.B.M., França, J.S., Sanches, B.O., Uchôa, J. & Callisto, M. (2014) Sampling site selection, land use and cover, field reconnaissance, and sampling. Ecological conditions in hydropower basins. In: Callisto, M., Hughes, R.M., Lopes, J.M. & Castro, M. A. (Eds.) *Ecological Conditions in Hydropower Basins*. Belo Horizonte, Brazil: Companhia Energética de Minas Gerais, pp. 61–83.

Mackensen, J., Bauhus, J. & Webber, E. (2003) Decomposition rates of coarse woody debris - A review with particular emphasis on Australian tree species. *Australian Journal of Botany*, 51, 27–37. Available from: <https://doi.org/10.1071/BT02014>

Mahe, G., Paturel, J.E., Servat, E., Conway, D. & Dezetter, A. (2005) The impact of land use change on soil water holding capacity and river flow modelling in the Nakambe River, Burkina-Faso. *Journal of Hydrology*, 300, 33–43. Available from: <https://doi.org/10.1016/j.jhydrol.2004.04.028>

Martin, D.J. & Benda, L.E. (2001) Patterns of Instream Wood Recruitment and Transport at the Watershed Scale. *Transactions of the American Fisheries Society*, 130, 940–958. Available from:  
[https://doi.org/10.1577/1548-8659\(2001\)130<0940:poiwra>2.0.co;2](https://doi.org/10.1577/1548-8659(2001)130<0940:poiwra>2.0.co;2)

Martin, D.J., Harden, C.P., Tran, L., Pavlowsky, R.T. (2018) Investigating patterns of in-channel wood deposition locations in a low-gradient,

variably-confined alluvial river system. *Progress in Physical Geography*, 42, 139–161. Available from:  
<https://doi.org/10.1177/0309133318759613>

Martius, C. (1997) Decomposition of Wood. In: Junk, W.J. (Ed.) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Plön, Germany: Springer, pp. 267–276.

McDade, M.H., Swanson, F.J., McKee, W.A., Franklin, J.F. & Van Sickle, J. (1990) Source distances for coarse woody debris entering small streams in western Oregon and Washington. *Canadian Journal of Fisheries and Aquatic Science*, 20, 326–330. Available from:  
<https://doi.org/10.1139/x90-047>

Merten, E.C., Vaz, P.G., Decker-Fritz, J.A., Finlay, J.C. & Stefan, H.G. (2013) Relative importance of breakage and decay as processes depleting large wood from streams. *Geomorphology*, 190, 40–47. Available from:  
<https://doi.org/10.1016/j.geomorph.2013.02.006>

Parente, L., Nogueira, S., Baumann, L., Almeida, C., Maurano, L., Affonso, A.G. & Ferreira, L. (2021) Quality assessment of the PRODES Cerrado deforestation data. *Remote Sensing Applications: Society and Environment*, 21, 100444. Available from:  
<https://doi.org/10.1016/j.rsase.2020.100444>

Paula, F.R., Ferraz, S.F.B., Gerhard, P., Vettorazzi, C.A. & Ferreira, A. (2011) Large woody debris input and its influence on channel structure in agricultural lands of Southeast Brazil. *Environmental Management*, 48, 750–763. Available from: <https://doi.org/10.1007/s00267-011-9730-4>

Paula, F.R., Gerhard, P., Wenger, S.J., Ferreira, A., Vettorazzi, C.A. & Ferraz, S.F.B. (2013) Influence of forest cover on in-stream large wood in an agricultural landscape of southeastern Brazil: A multi-scale analysis. *Landscape Ecology*, 28, 13–27. Available from:  
<https://doi.org/10.1007/s10980-012-9809-1>

Pereira, E.J.A.L., Ribeiro, L.C.S., Freitas, L.F.S. & Pereira, H.B.B. (2020) Brazilian policy and agribusiness damage the Amazon rainforest. *Land Use Policy*, 92, 104491. Available from:  
<https://doi.org/10.1016/j.landusepol.2020.104491>

Ravazzolo, D., Mao, L., Garniga, B., Picco, L. & Lenzi, M.A. (2015) Volume and Travel Distance of Wood Pieces in the Tagliamento River (Northeastern Italy). In: Lollino, G., Arattano, M., Rinaldi, M., Giustolisi, O., Marechal, J.C., Grant, G. (Eds) *Engineering Geology for Society and Territory*. Cham: Springer, pp. 135–138. Available from:  
[https://doi.org/10.1007/978-3-319-09054-2\\_26](https://doi.org/10.1007/978-3-319-09054-2_26)

Robison, E.G. & Beschta, R.L. (1990) Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 1684–1693. Available from:  
<https://doi.org/10.1139/f90-193>

Ruiz-Villanueva, V., Wyzga, B., Hajdukiewicz, H. & Stoffel, M. (2016) Exploring large wood retention and deposition in contrasting river morphologies linking numerical modelling and field observations. *Earth Surface Processes and Landforms*, 41, 446–459. Available from: <https://doi.org/10.1002/esp.3832>

Shipley, B. (2000) *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge: Cambridge University Press. Available from: <https://www.cambridge.org/core/product/identifier/9780511605949/type/book>

Van Sickle, J. & Gregory, S. V. (1990) Modeling inputs of large woody debris to streams from falling trees. *Canadian Journal of Forest Research*, 20, 1593–1601. Available from: <https://doi.org/10.1139/x90-211>

Saraiva, S.O., Rutherford, I.D., Kaufmann, P.R., Leal, C.G., Macedo, D.R., Pompeu, P.S. (2022) Wood stock in neotropical streams: quantifying and comparing instream wood among biomes and regions. *PLoS ONE*, 17(10), e0275464. Available from: <https://doi.org/10.1371/journal.pone.0275464>

Silva-Junior, C.H.L., Pessôa, A.C.M., Carvalho, N.S., Reis, J.B.C., Anderson, L.O. & Aragão, L.E.O.C. (2021) The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nature Ecology and Evolution*, 5, 144–145. Available from: <http://dx.doi.org/10.1038/s41559-020-01368-x>

Silva, L.F.S.G., Castilho, C.V., Cavalcante, C.O., Pimentel, T.P., Fearnside, P.M. & Barbosa, R.I. (2016) Production and stock of coarse woody debris across a hydro-edaphic gradient of oligotrophic forests in the northern Brazilian Amazon. *Forest Ecology and Management*, 364, 1–9. Available from: <https://doi.org/10.1016/j.foreco.2015.12.045>

Sriwongsitanon, N. & Taesombat W. (2011) Effects of land cover on runoff coefficient. *Journal of Hydrology*, 410, 226–238. Available from: <http://dx.doi.org/10.1016/j.jhydrol.2011.09.021>

Swanson, F.J. (2003) Wood in Rivers: A Landscape Perspective. *American Fisheries Society Symposium*, 37: 299–313.

Swanson, F.J., Gregory, S.V., Iroumé, A., Ruiz-Villanueva, V. & Wohl, E. (2020) Reflections on the history of research on large wood in rivers. *Earth Surface Processes and Landforms*, esp.4814. Available from: <https://doi.org/10.1002/esp.4814>

Trigueiro, W.R., Nabout, J.C. & Tessarolo, G. (2020) Uncovering the spatial variability of recent deforestation drivers in the Brazilian Cerrado. *Journal of Environmental Management*, 275, 111243. Available from: <https://doi.org/10.1016/j.jenvman.2020.111243>

USEPA - United States Environmental Protection Agency (2013) National Rivers and Streams Assessment 2013-2014: *Field Operations Manual – Wadeable*. EPA-841-B-12-009b. Washington: Office of Water. Available

from: [https://www.epa.gov/sites/production/files/2016-04/documents/nrsa1314\\_fom\\_wadeable\\_version1\\_20130501.pdf](https://www.epa.gov/sites/production/files/2016-04/documents/nrsa1314_fom_wadeable_version1_20130501.pdf)

Valeriano, M.M. & Rossetti D.F. (2012) Topodata: Brazilian full coverage refinement of SRTM data. *Applied Geography*, 32, 300–309. Available from: <http://dx.doi.org/10.1016/j.apgeog.2011.05.004>

Wohl, E. et al. (2012a) The hydrology of the humid tropics. *Nature Climate Change*, 2, 655–662. Available from: <http://dx.doi.org/10.1038/nclimate1556>

Wohl, E. (2013) Floodplains and wood. *Earth-Science Reviews*, 123, 194–212. Available from: <https://doi.org/10.1016/j.earscirev.2013.04.009>

Wohl, E. (2017) Bridging the gaps: An overview of wood across time and space in diverse rivers. *Geomorphology*, 279: 3–26. Available from: <https://doi.org/10.1016/j.geomorph.2016.04.014>

Wohl, E. et al. (2019) The natural wood regime in rivers. *BioScience*, 69, 259–273. Available from: <https://doi.org/10.1093/biosci/biz013>

Wohl, E., Bolton, S., Cadol, D., Comiti, F., Goode, J.R. & Mao, L. (2012b) A two end-member model of wood dynamics in headwater neotropical rivers. *Journal of Hydrology*, 462–463, 67–76. Available from: <https://doi.org/10.1016/j.jhydrol.2011.01.061>

Wohl, E. & Jaeger, K. (2009a) A conceptual model for the longitudinal distribution of wood in mountain streams. *Earth Surface Processes and Landforms*, 34, 329–344. Available from: <https://doi.org/10.1002/esp.1722>

Wohl, E. & Jaeger, K.L. (2009b) Geomorphic implications of hydroclimatic differences among step-pool channels. *Journal of Hydrology*, 374, 148–161. Available from: <https://doi.org/10.1016/j.jhydrol.2009.06.008>

Wohl, E., Polvi, L.E. & Cadol, D. (2011) Wood distribution along streams draining old-growth floodplain forests in Congaree National Park, South Carolina, USA. *Geomorphology*, 126, 108–120. DOI: Available from: <https://doi.org/10.1016/j.geomorph.2010.10.035>

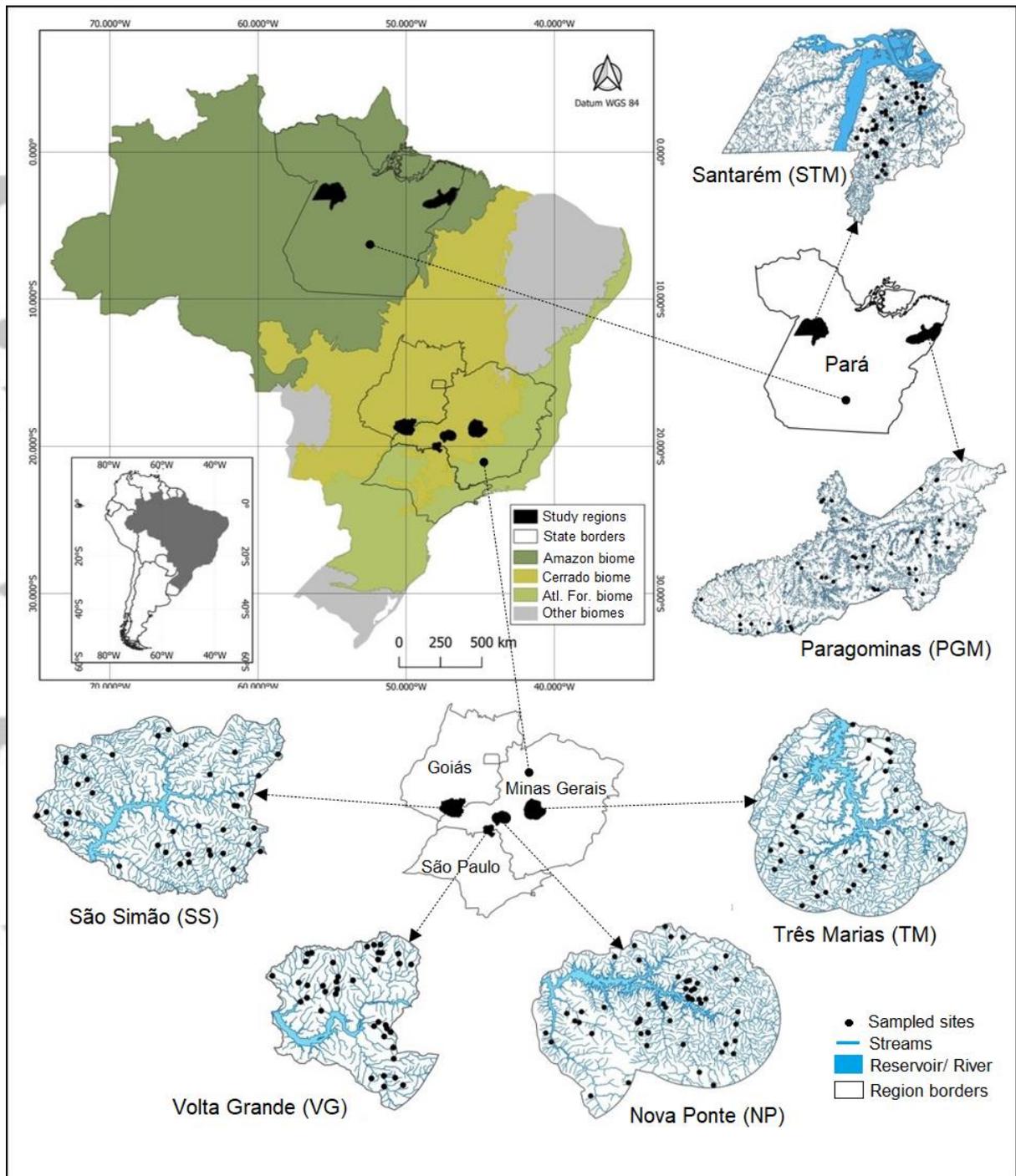


Figure 1: Map of the study sites in six study regions across Brazilian biomes. Adapted from Saraiva et al. (2022).

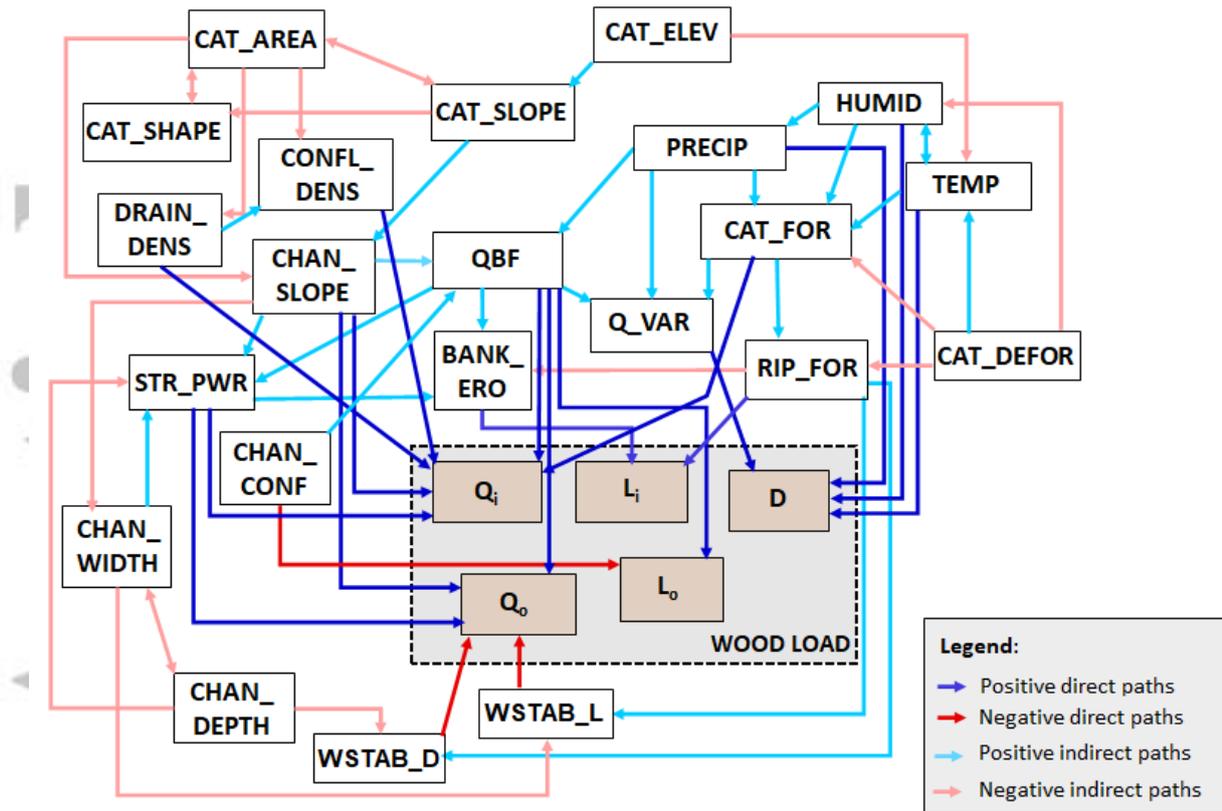


Figure 2: Conceptual model considering the potential predictors of instream wood in a tropical stream. One-way arrows indicate the expected effect of one variable on another and two-way arrows indicate expected correlations between them. The direct effects on wood load are indicated by dark blue and red arrows which link any potential causal variable to a response variable (the wood budget terms). The indirect effects are indicated by light blue and rose arrows which link one explanatory variable to another.



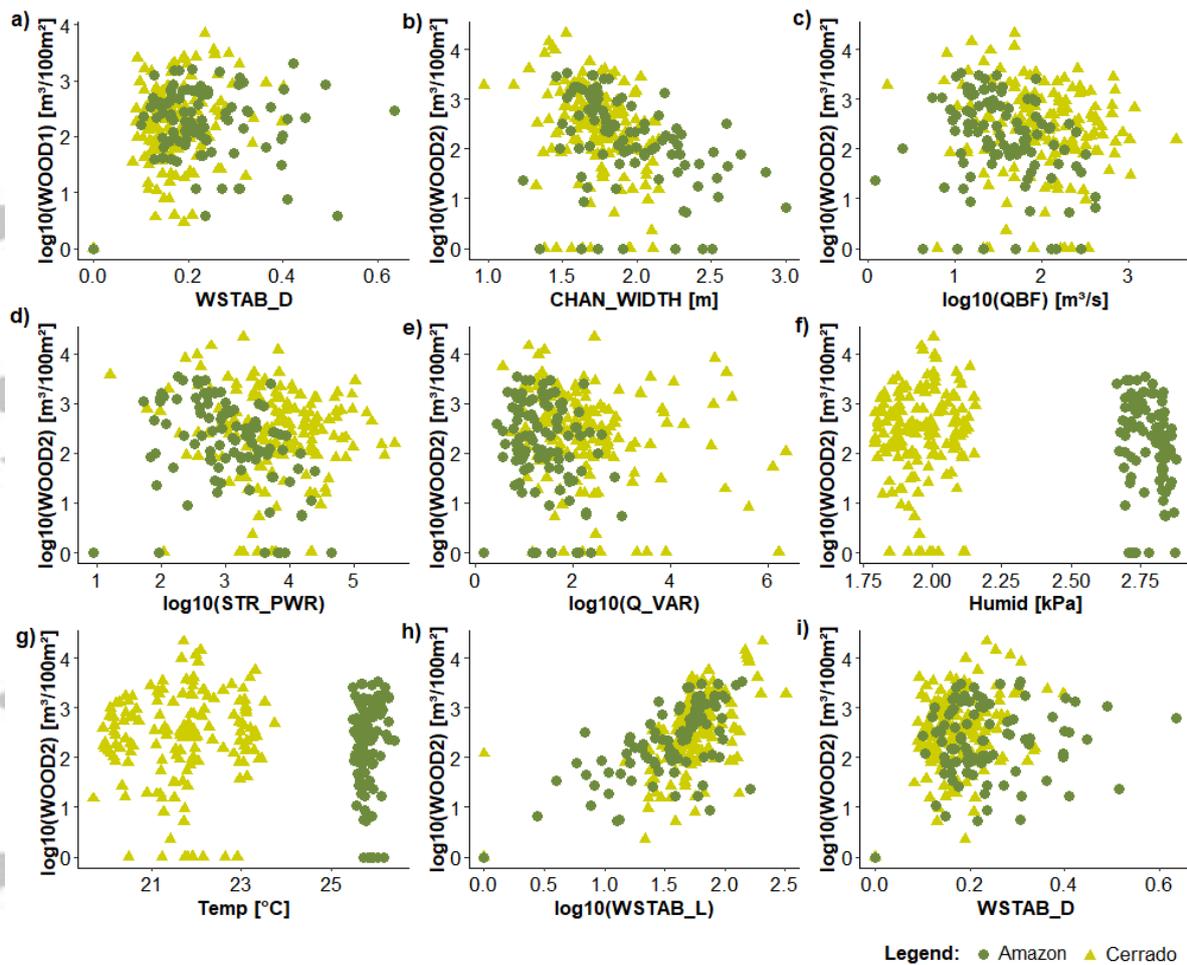


Figure 4: Dispersion plots between variables that differed on the SEM multigroup analysis per biome. a) wood volume per channel length (WOOD1) versus wood stability from piece length (WSTAB\_D) and b) channel width (CHAN\_WIDTH), c) bankfull discharge (QBF), d) stream power (STR\_PWR), e) discharge variation (Q\_VAR), f) humidity (Humid), g) temperature (Temp), h) wood stability from piece length (WSTAB-L), i) wood stability from piece diameter (WSTAB-D), all of them versus wood volume per channel area (WOOD2).

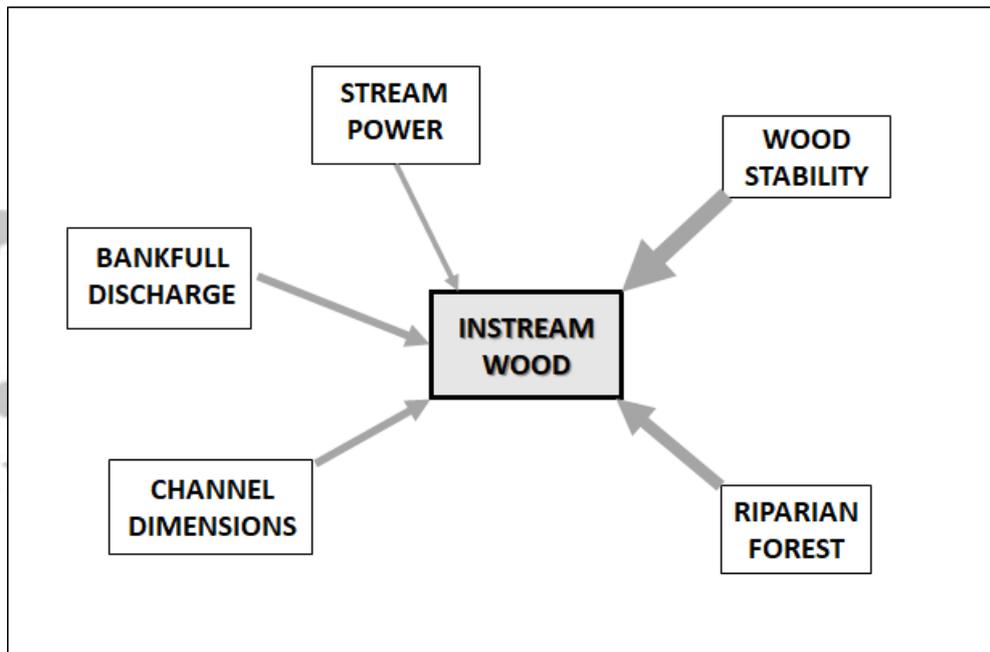


Figure 5: Flowchart summarizing the most important predictors of instream wood in Amazon and Cerrado streams.

Accepted

Table 1: Summary description of the study catchments grouped by region. Mean, standard deviation and range are presented.

Region name	Region Code	Biome	Number of study sites	Area (Km <sup>2</sup> )	Forest cover (%)	Agricultural land cover (%)
				Mean ± SD (range)	Mean ± SD (range)	Mean ± SD (range)
Paragominas	PGM	Amazon	51	12.55 ± 12.39 (0.44 - 50.37)	68.85 ± 27.02 (2.71 - 100)	2.52 ± 7.40 (0 - 44.03)
Santarém	STM	Amazon	48	28.70 ± 47.07 (0.83 - 227.13)	60.15 ± 31.18 (4.79 - 100)	7.66 ± 13.87 (0 - 59.45)
Nova Ponte	NP	Cerrado	40	10.74 ± 10.70 (1.38 - 50.74)	36.57 ± 24.98 (7.84 - 99.19)	63.06 ± 24.76 (0.81 - 91.83)
Três Marias	TM	Cerrado	40	45.23 ± 47.21 (0.45 - 164.97)	45.57 ± 18.03 (14.78 - 100)	53.81 ± 17.36 (0 - 80.27)
Volta Grande	VG	Cerrado	40	27.53 ± 30.22 (2.64 - 116.43)	11.56 ± 5.32 (0.10 - 22.78)	86.22 ± 9.21 (37.87 - 96.82)
São Simão	SS	Cerrado	39	30.23 ± 26.93 (0.37 - 108.45)	12.99 ± 6.35 (0.81 - 27.37)	85.94 ± 8.85 (48.79 - 99.19)

Table 2: The five wood size classes from LW assessment USEPA protocol described according to length and diameter.

Diameter	Length		
	1.5 - 5 m	> 5 - 15 m	> 15 m
0.1 - 0.3 m	<b>T</b>	<b>S</b>	<b>M</b>
> 0.3 m - 0.6 m	<b>S</b>	<b>M</b>	<b>L</b>
> 0.6 m - 0.8 m	<b>S</b>	<b>L</b>	<b>L</b>
> 0.8 m	<b>M</b>	<b>L</b>	<b>X</b>

\* T = tiny, S = small, M = medium, L = large and X = extra-large

Table 3: Summary of variables measured in the field assessments or obtained through geographic information systems (GIS).

Variable	Code	Unit	Directly Measured?	Description	Reference
Catchment elevation	CAT_ELEV	m	Yes	Altitude measured through GPS in field assessment.	-
Catchment slope	CAT_SLOPE	%	Yes	Slope obtained through GIS tools.	Valeriano and Rossetti (2012)
Catchment area	CAT_AREA	Km <sup>2</sup>	Yes	Area measured through GIS tools.	Valeriano and Rossetti (2012)
Catchment shape	CAT_SHAPE	-	No	$\frac{(\text{Main stem length}^*)^2}{\text{CAT\_AREA}}$	Benda et al. (2004)
Confluence density	CONFL_DEN	confl /Km <sup>2</sup>	No	$\frac{\text{Confluence number}^\dagger}{\text{CAT\_AREA}}$	Benda et al. (2004)
Drainage density	DRAIN_DEN	Km <sup>-1</sup>	No	$\frac{\text{Network length}^\ddagger}{\text{CAT\_AREA}}$	Benda et al. (2004)
Deforestation in the catchment	CAT_DEFOR	years	Yes	Land-use intensity index = time since last deforestation event obtained through GIS tools.	Ferraz et al. (2012)
Forest cover in the catchment	CAT_FOR	%	Yes	Mature forest located at the catchment scale measured through GIS tools.	Gardner et al., (2013)
Riparian forest on the banks	RIP_FOR	%	Yes	Summed areal cover of woody riparian forest in 3 layers within 10m of the banks (mean of 22 visual estimates in the field)	Kaufmann et al. (1999)

\* Length (Km) of the main stem of the studied stream measured through GIS tools.

† Number of confluences in the upstream catchment counted through GIS tools.

‡ Total length of network accounting the length of all the streams located in the upstream catchment.

Precipitation	PRECIP	mm	Yes	Historical average precipitation (1970-2000) on the catchment upstream to the site.	Fick and Hijmans (2017)
Humidity	HUMID	kPa	Yes	Historical average water vapor pressure (1970-2000) on the catchment upstream to the site.	Fick and Hijmans (2017)
Temperature	TEMP	°C	Yes	Historical average temperature (1970-2000) on the catchment upstream to the site.	Fick and Hijmans (2017)
Channel slope	CHAN_SLOPE	%	Yes	The water surface slope measured in field assessment.	Kaufmann et al. (1999)
Bankfull discharge	QBF	m <sup>3</sup> /s	No	$Q_{bf}^{\S} = \left(\frac{1}{C_t}\right)^{\frac{1}{2}} A_{xs} (gR_{bf}S)^{\frac{1}{2}}$	Kaufmann et al. (2008)
Discharge variation	Q_VAR	-	No	$\frac{\text{low flow discharge}^{**}}{Q_{bf}}$	-
Stream power	STR_PWR		No	$\Omega = \rho g Q_{bf} S^{\dagger\dagger}$	Bagnold (1966)
Bank erosion	BANK_ERO	-		$\frac{\log D_{cbf}^{\ddagger\ddagger}}{(RIP\_FOR + 1)}$	-
Channel confinement	CHAN_CONF	m	No	$XINC\_H^{\S\S} - CHAN\_DEPTH$	-
Channel width	CHAN_WIDTH	m	Yes	Bankfull channel width measured in field assessment.	Kaufmann et al. (1999)

§ Where  $Q_{bf}$  = bankfull discharge;  $C_t = 1.21d_{res}^{1.08} (d_{res} + WOOD2/100)^{0.638} (d_{th\_bf}^{-3.32})$ ; from Kaufmann et al. (2008);  $d_{res}$  = residual depth according to Kaufmann et al. (1999);  $d_{th\_bf}$  = CHAN\_DEPTH;  $A_{xs}$  = cross-sectional area;  $R_{bf} = 0.65d_{th\_bf}$ ;  $g$  = acceleration due to gravity (9.8 m/s<sup>2</sup>);  $S$  = CHAN\_SLOPE

\*\* low flow discharge = discharge measured by velocity-area method in field assessment during the dry season.

†† Where  $\Omega$  = the stream power,  $\rho$  = the density of water (1000 kg/m<sup>3</sup>),  $g$  = acceleration due to gravity (9.8 m/s<sup>2</sup>),  $Q_{bf}$  = discharge (m<sup>3</sup>/s), and  $S$  = channel slope.

‡‡ Where  $D_{cbf} = 0.604 \cdot [(R_{bf}) \cdot (\text{slope})] / \theta$ ;  $R_{bf} = 0.65 \cdot \text{bankfull depth}$ ;

$\theta = 0.04 \cdot R_{ep}^{-0.24}$  if  $R_{ep} \leq 26$  or  $\theta = 0.5[0.22R_{ep}^{-0.6} + 0.06(10^{-(7.7R_{ep}^{-0.6})})]$  if  $R_{ep} > 26$

§§ XINC\_H = Incision height measured in field assessment according to Kaufmann et al. (1999).

Channel depth	CHAN_DEPT H	cm	Yes	Bankfull channel depth measured in field assessment.	Kaufmann et al. (1999)
Wood stability from piece length	WSTAB_L	-	No	$\frac{\text{LW length}}{\text{Bkf. Channel width}}$	Cadol et al. (2009)
Wood stability from piece diameter	WSTAB_D	-	No	$\frac{\text{LW diameter}}{\text{Bkf. Channel depth}}$	Cadol et al. (2009)
Wood volume per 100m reach length	WOOD1	m <sup>3</sup> /100m	No	$\frac{\text{Wood volume}^{***}}{\text{Reach length}} \times 100$	Kaufmann et al. (1999)
Wood volume per 100 m <sup>2</sup> of channel area	WOOD2	m <sup>3</sup> /100m <sup>2</sup>	No	$\frac{\text{Wood volume}}{\text{Reach area}^{+++}} \times 100$	Kaufmann et al. (1999)

\*\*\* Wood volume is calculated for each wood size class according to Kaufmann et al. (1999).

+++ Reach planform area is the result of the average bankfull width multiplied by the reach length.

Table 4: Direct, indirect, and total effect of each predictor variable on the response variables (wood metrics).

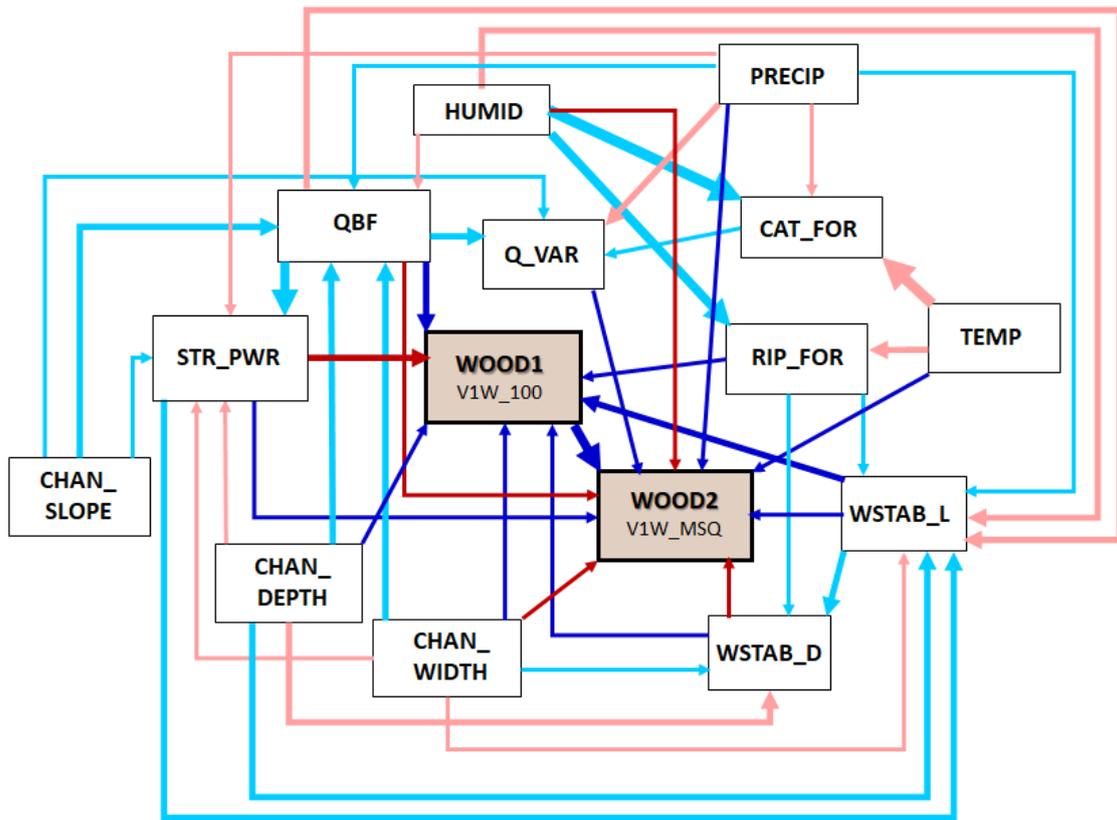
Predictor	WOOD1			WOOD2		
	Direct effect	Indirect effect	Total effect	Direct effect	Indirect effect	Total effect
<b>HUMID</b>	0.00	0.15	0.15	-0.17	0.21	0.04
<b>PRECIP</b>	0.00	0.24	0.24	0.05	0.21	0.26
<b>TEMP</b>	0.00	-0.23	-0.23	0.10	-0.21	-0.11
<b>CAT_FOR</b>	0.00	0.00	0.00	0.00	0.01	0.01
<b>RIP_FOR</b>	0.20	0.23	0.43	0.00	0.40	0.40
<b>QBF</b>	0.34	-0.54	-0.20	-0.19	-0.13	-0.32
<b>STR_PWR</b>	-0.32	0.23	-0.09	0.08	-0.04	0.04
<b>Q_VAR</b>	0.00	0.00	0.00	0.02	0.00	0.02
<b>CHAN_SLOPE</b>	0.00	-0.10	-0.10	0.00	-0.10	-0.10
<b>CHAN_WIDTH</b>	0.15	-0.20	-0.05	-0.11	-0.11	-0.22
<b>CHAN_DEPTH</b>	0.33	-0.05	0.28	0.00	-0.05	-0.05
<b>WSTAB_L</b>	0.53	0.17	0.70	0.17	0.57	0.74
<b>WSTAB_D</b>	0.29	0.00	0.29	-0.07	0.26	0.19
<b>WOOD1</b>	-	-	-	0.88	0.00	0.88

Accepted Article

Table 5: Parameters estimated for the wood variables in the SEM multigroup analysis per biome. The predictors that differed in explaining wood between biomes are indicated by an asterisk. The significant relationship between predictor and wood metrics within biomes is highlighted in bold.

Predictor	Amazon				Cerrado			
	Estim.	Std. error	p-value	Std. estim.	Estim.	Std. error	p-value	Std. estim.
WOOD1								
CHAN_WIDTH	<b>0.013</b>	<b>0.005</b>	<b>0.008</b>	<b>0.226</b>	<b>0.013</b>	<b>0.005</b>	<b>0.008</b>	<b>0.046</b>
CHAN_DEPTH	<b>0.699</b>	<b>0.199</b>	<b>&lt;0.001</b>	<b>0.267</b>	<b>0.699</b>	<b>0.199</b>	<b>&lt;0.001</b>	<b>0.312</b>
QBF	<b>0.504</b>	<b>0.236</b>	<b>0.034</b>	<b>0.303</b>	<b>0.504</b>	<b>0.236</b>	<b>0.034</b>	<b>0.321</b>
STR_PWR	<b>-0.329</b>	<b>0.121</b>	<b>0.007</b>	<b>-0.279</b>	<b>-0.329</b>	<b>0.121</b>	<b>0.007</b>	<b>-0.302</b>
RIP_FOR	<b>0.003</b>	<b>0.001</b>	<b>&lt;0.001</b>	<b>0.244</b>	<b>0.003</b>	<b>0.001</b>	<b>&lt;0.001</b>	<b>0.145</b>
WSTAB_L	<b>0.865</b>	<b>0.109</b>	<b>&lt;0.001</b>	<b>0.557</b>	<b>0.865</b>	<b>0.109</b>	<b>&lt;0.001</b>	<b>0.498</b>
WSTAB_D*	2.028	1.060	0.059	0.283	<b>5.953</b>	<b>1.141</b>	<b>&lt;0.001</b>	<b>0.527</b>
WOOD2								
CHAN_WIDTH*	<b>-0.006</b>	<b>0.001</b>	<b>&lt;0.001</b>	<b>-0.097</b>	<b>-0.044</b>	<b>0.003</b>	<b>&lt;0.001</b>	<b>-0.146</b>
QBF*	<b>-0.429</b>	<b>0.075</b>	<b>&lt;0.001</b>	<b>-0.232</b>	<b>-0.076</b>	<b>0.035</b>	<b>0.032</b>	<b>-0.044</b>
STR_PWR*	<b>0.132</b>	<b>0.041</b>	<b>0.002</b>	<b>0.101</b>	0.025	0.019	0.182	0.021
Q_VAR*	0.049	0.030	0.105	0.030	-0.003	0.007	0.665	-0.004
HUMID*	<b>-0.962</b>	<b>0.242</b>	<b>&lt;0.001</b>	<b>-0.064</b>	0.039	0.158	0.807	0.004
PRECIP	<b>0.0002</b>	<b>0.0001</b>	<b>&lt;0.001</b>	<b>0.018</b>	<b>0.0002</b>	<b>0.0001</b>	<b>&lt;0.001</b>	<b>0.031</b>
TEMP*	<b>0.200</b>	<b>0.073</b>	<b>0.007</b>	<b>0.046</b>	0.002	0.015	0.893	0.002
WSTAB_L*	<b>0.350</b>	<b>0.043</b>	<b>&lt;0.001</b>	<b>0.203</b>	<b>0.200</b>	<b>0.021</b>	<b>&lt;0.001</b>	<b>0.105</b>
WSTAB_D*	<b>-0.761</b>	<b>0.196</b>	<b>&lt;0.001</b>	<b>-0.096</b>	0.006	0.148	0.967	0.001
WOOD1	<b>0.970</b>	<b>0.012</b>	<b>&lt;0.001</b>	<b>0.875</b>	<b>0.970</b>	<b>0.012</b>	<b>&lt;0.001</b>	<b>0.886</b>

Graphical Abstract



Accepte