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Stream Degradation: Direct and Indirect Impacts of Amazonian Deforestation

Gabriel Martins Cruz,^{1,2*} Ana Paula Justino Faria,³
Josinete Sampaio Monteles,^{2,4} Karina Dias-Silva,⁵ Lilian Casatti,⁶
Juan Mateo Rivera-Perez,^{2,4} Rafael Costa Bastos,^{2,4}
Victor Rennan Santos Ferreira,³ Leandro Schlemmer Brasil,⁷
Thaís Sala Michelin,² Lenize Batista Calvão,^{2,4} Everton Cruzda Silva,^{2,4}
Tainã Silvada Rocha,^{2,4} Maria Dayanne Limade Lucena,^{1,2}
Raimundo Luiz Morais de Sousa,¹³ Antônio Augustode Souza Costa,⁴
Joás Silva Brito,^{2,4} José Max Barbosa Oliveira-Júnior,⁴ Bethânia Oliveirade
Resende,^{2,4} Erlane José Cunha,⁸ Raphael Ligeiro,² Gabriel L. Brejão,⁹
Luciano F. A. Montag,² Robert M. Hughes,^{10,11} Cecília G. Leal,^{12,14} and
Leandro Juen²

¹Programa de Pós-Graduação em Zoologia, Universidade Federal do Pará – UFPA, Belém, PA, Brasil; ²Laboratório de Ecologia e Conservação, LABECO, Instituto de Ciências Biológicas, Universidade Federal do Pará – UFPA, Rua Augusto Corrêa, Nº 1 Bairro Guamá, CEP: 66.075-110, Belém, PA, Brasil; ³Universidade Estadual do Piauí – Campus Heróis de Jenipapo, Núcleo de Pesquisa em Insetos Aquáticos, Campo Maior, Brasil; ⁴Programa de Pós-Graduação em Ecologia, Universidade Federal do Pará – UFPA, Belém, Pará, Brasil; ⁵Laboratório de Ecologia, LABECO, Faculdade de Ciências Biológicas, Universidade Federal do Pará-UFPA, Rua Coronel José Porfírio, Nº 030 Bairro Recreio, Altamira, Pará CEP: 68372-040, Brasil; ⁶Departamento de Ciências Biológicas, Universidade Estadual Paulista - UNESP, Rua Cristóvão Colombo, 2265, São José do Rio Preto, SP CEP: 15054-000, Brasil; ⁷Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso - UFMT, Avenida Universitária, 3500, Pontal do Araguaia, MT CEP: 78698-000, Brasil; ⁸Instituto Tecnológico Vale, Rua Boaventura da Silva, 955, Belém, PA 66055-900, Brasil; ⁹Departamento de Biodiversidade, Universidade Estadual Paulista - UNESP, Avenida 24-A, 1515, Rio Claro, SP CEP: 13506-900, Brasil; ¹⁰Amnis Opes Institute, 2895 SE Glenn, Corvallis, OR 97333, USA; ¹¹Department of Fisheries, Wildlife, & Conservation Sciences, Oregon State University, Nash 104, Corvallis, OR 97331, USA; ¹²Lancaster University, Bailrigg, Lancaster LA1 4YW, UK; ¹³Programa de Pós-Graduação em Botânica Tropical, Museu Paraense Emílio Goeldi/Universidade Federal Rural da Amazônia, Av. Perimetral, 1901 - Terra Firme, Belém, PA 66077-830, Brasil; ¹⁴Programa de Pós-Graduação em Ecologia Aplicada, Universidade Federal de Lavras, Lavras, Brasil

ABSTRACT

The increasing demand for natural resources has accelerated deforestation in the tropics, resulting in impacts on freshwater ecosystems. The extent of

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In memoriam—Robert M. Hughes.

*Corresponding author; e-mail: gabrielcruz696963@gmail.com

deforestation is a critical factor in determining the stream's physical habitat status condition. We evaluated the direct and indirect impacts of catchment and riparian deforestation on stream physical habitat conditions. To do so, we assessed how deforestation reduces allochthonous inputs, altering channel morphology, and ultimately leading to a decline in physical habitat condition. We used structural equation modeling to evaluate the effects of deforestation on physical habitat variables in 269 stream sites across Eastern Amazonia. We found that sites exhibiting higher physical habitat integrity were associated with greater forest cover in both the catchment and the riparian zone. The loss of riparian vegetation reduced organic matter inputs, decreasing the amounts of organic substrates and dead wood. Those changes resulted in increased sand deposits and lower physical habitat condition scores. However, natural variation in catchment morphology also played an important role, especially in predicting stream morphology features. The effects of deforestation are complex and depend on its extent. Nonetheless, riparian vegetation proved to be an important buffer against the effects of catchment deforestation, and its preservation is essential for maintaining good physical habitat conditions.

Key words: Allochthonous resources; Anthropogenic pressure; Catchment morphology; Channel structure; Riparian vegetation; Water security.

HIGHLIGHTS

- Deforestation affects stream physical habitat structure.
- Local deforestation has greater impact than at the catchment scale.
- Stream slope and altitude correlate with habitat conditions.

INTRODUCTION

Deforestation is the primary driver of habitat loss and fragmentation in many terrestrial ecosystems and is also a major threat to freshwater biodiversity and ecosystem functioning (Almond and others 2020). Rapid human population growth and the increasing demand for food and raw materials have accelerated deforestation, leading to the conversion of large areas of natural forest to agriculture and

livestock farming (Barbier and Burgess 2001; Hosonuma and others 2012; Maja and Ayano 2021). In regions rich in natural resources, such as Amazon, the expansion of activities like crop monoculture (Yanai and others 2022), livestock farming (Cantanhêde and others 2021), logging (Jacob and others 2021), and mining (Bastos and others 2021) have transformed forests into highly altered landscapes (Fearnside 2021). These activities have escalated rapidly over the past decade, leading to approximately 110,000 km² of deforestation in the Brazilian Amazon between 2011 and 2022 (Projeto MapBiomas 2023), with a peak of 11,088 km² of forest loss recorded in 2020 (Silva-Junior and others 2021). Similar trends have been reported in other biodiversity-rich tropical forests, such as the Congo Basin and the forests of Southeast Asia, particularly in Borneo and Sumatra (Megevand and Monsier 2013; Gaveau and others 2014; Margono and others 2014).

The Amazon basin is the largest in the world, serving as a crucial source of freshwater and biodiversity (Cantonati and others 2020). However, the rapid expansion of deforestation is altering various aspects of the physical habitat structure in lotic ecosystems, especially small streams (for example, Leal and others 2018; Maués-Silva and others 2024). Those small streams are estimated to comprise approximately 90% of its total drainage network (McClain and Elsenbeer 2001; Tonkin and others 2018). Deforestation can directly reduce the availability of organic matter such as leaves, branches, and dead wood, which are important resources for aquatic biota and act as retention structures, creating hydraulic resistance within the stream channel (Vannote and others 1980; Faria and others 2017; Lima and others 2022). Reduced large wood inputs directly modify stream morphology and hydraulics by increasing width, decreasing depth, and reducing habitat complexity and heterogeneity (Kaufmann and others 1999; Montag and others 2019; Moi and others 2024). These combined impacts in stream physical structure decrease the amount of available habitats for biodiversity (Moi and others 2024), undermining ecological processes and the forest and freshwater essential ecosystem services (Dodds and others 2013). Additionally, an alarming data from *Plataforma MapBiomas* (Projeto MapBiomas 2023) indicates a 32% reduction in the extent of surface water in the Amazon over the past 35 years, based on satellite-detected water pixels. This decline reflects the contraction of the visible dendritic network, threatening freshwater availability.

Deforestation extent is a key factor in determining the stream's physical habitat condition because riparian vegetation helps maintain bank stability, limnological conditions, and buffers anthropogenic impacts in the channel (Juen and others 2016; Kaufmann and others 2022; Faria and others 2023). However, deforestation in stream catchments beyond the riparian zone can create a mosaic of land uses that potentially affect the input of organic resources and sediments, as well as other stream physical habitat features across different spatial scales (Frissell and others 1986; Leal and others 2016; Paiva and others 2021; Brito and others 2021a). Previous studies have examined anthropogenic effects on local stream structure (Juen and others 2016) and catchments (Cruz and others 2022), but these relationships remain complex and can operate across multiple spatial scales, as shown for benthic insects in the Eastern Amazon (Monteles and others 2021). This complexity arises from the indirect influence of intermediate structural features, such as channel morphology and the input of allochthonous resources, which mediate the effects of deforestation (Leal and others 2016; Leitão and others 2018). In addition, these effects can vary depending on broader landscape features such as catchment morphology and land-use patterns (Almeida and others 2023; Fahrig 2024). Furthermore, the scope of observations in ecological studies is often too limited to fully address conservation policy needs (Herlihy and others 2020; Almeida and others 2023; Fahrig and others 2024). Given the hierarchical nature of catchment and stream predictor variables, assessments of anthropogenic impacts solely on riparian vegetation are insufficient to evaluate the potential effects of deforestation on lotic ecosystems (Leal and others 2018; Leitão and others 2018; Tonkin and others 2018; Herlihy and others 2020).

Ecological integrity, in its strictest sense, refers to an unmodified natural environment (Cairns 1977; Karr 1991). However, in human-modified landscapes such as the Amazonian frontier, truly pristine conditions are increasingly rare or extremely remote. Therefore, we considered physical habitat structure as a continuum from nearly pristine to highly altered environments. This approach is essential to understand the effects of deforestation on Amazonian streams, thereby influencing the continuity of key ecosystem services, including organic matter processing, water purification, and habitat provision (Dodds and others 2013). Here, our objective is to evaluate how deforestation, across multiple spatial scales, directly and indirectly influences the physical habitat structure of Ama-

zonian streams. We further investigate how anthropogenic impacts interact with natural variation in catchment morphology—an aspect that has received limited attention in broad-scale assessments. To address these questions, we applied a hierarchical modeling approach that disentangles spatially structured processes and assesses multiple stressors within a unified framework, thereby revealing how the impacts of deforestation accumulate and propagate across stream physical characteristics. Specifically, we hypothesize that deforestation triggers a series of changes in stream physical characteristics, beginning with i) a reduction in allochthonous input, leading to ii) changes in stream morphological features (for example, width and depth), and ultimately resulting in iii) a decline in physical habitat condition—here understood as lower habitat integrity, reflecting the combined degradation of streams structural features.

MATERIAL AND METHODS

Study Area

We studied 269 1st–3rd-order stream sites distributed across Eastern Amazonia (Figure 1). The predominant climate in the region is humid tropical, with precipitation ranging from 1,800 to 2,200 mm and average air temperatures between 24.2 and 27.2 °C (Peel and others 2007). Catchment deforestation ranged from 0 to 100%. Physical habitat was characterized once in each stream site between 2010 and 2023, always during dry season, June to November, when stream conditions tend to be more stable and representative of the underlying habitat structure. This study design minimized the influence of high wet season flows on stream physical habitat and maximized site access (Hughes and Peck 2008).

STREAM PHYSICAL HABITAT AND FOREST COVER

We followed the U.S. Environmental Protection Agency (EPA) wadeable streams protocol (Kaufmann and others 1999, 2022; Peck and others 2006; Hughes and Peck 2008), adapted to the Neotropics (Callisto and others 2014) to characterize physical habitat. In each stream, we delimited a continuous 150 m reach, subdivided into 10 longitudinal sections of 15 m, which were delimited by 11 cross-channel transects labeled from A (downstream) to K (upstream). This design allows the collection of variables from two complementary

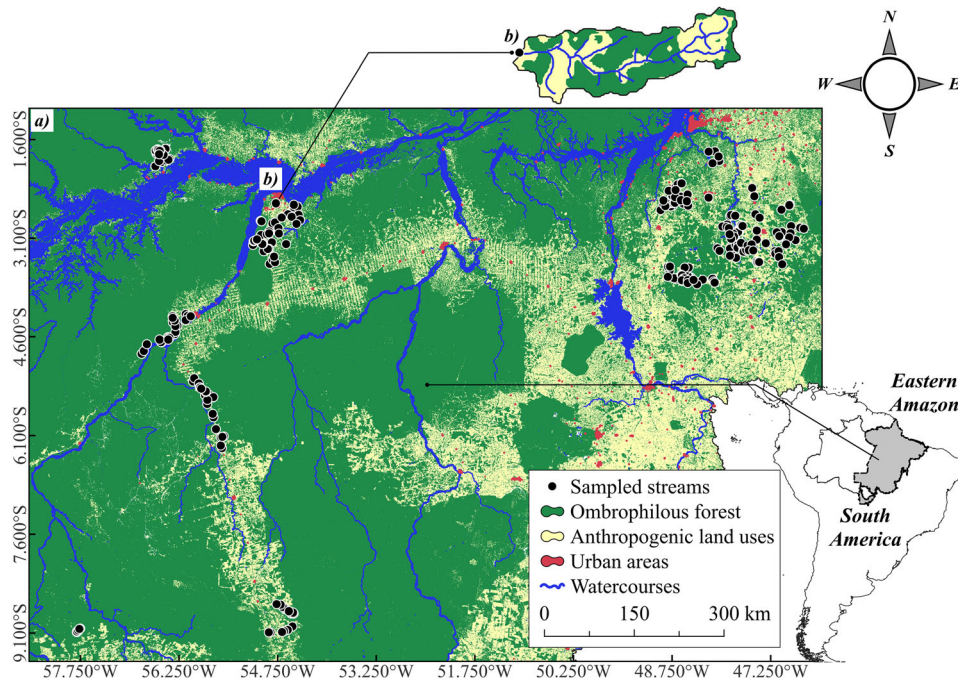


Figure 1. Locations of the 269 stream sites in Eastern Amazonia across different deforestation intensities **a** and in a representative stream site catchment **b**.

perspectives: along the longitudinal dimension of the stream and across channel transects. This full evaluation protocol generates approximately 240 environmental variables describing multiple aspects of stream habitat. To address our objective, we retained a smaller subset of variables most directly related to the ecological mechanisms through which deforestation alters stream habitats—such as reductions in allochthonous input, loss of retention structures, and changes in channel morphology (for example, Juen and others 2016; Leal and others 2018). In addition, the retained variables are based on straightforward and replicable visual observations, which makes them particularly suitable for large-scale assessments (Maués-Silva and others 2024). From the longitudinal dimension, we retained stream depth (cm), large wood (m^3), and fast flow (%). From the channel transects, we retained organic substrates (%), stream width (m), and sand (%) (Table 1, Figure 2).

We measured forest cover at two spatial extents—riparian zone and catchment—for each stream site as a proxy for deforestation (Table 1). For the riparian zone, we used a convex densiometer to measure channel shading (hereafter “canopy cover”) (Figure 2, Table 1), which is considered a cost-efficient proxy for forest cover (for example, Peck and others 2006; Cruz and others 2022). For the catchment scale, we used

QGIS geoprocessing software (version 3.34) to measure the catchment forest proportion. Initially, we delineated the catchment upstream from each stream site (Section A, see Figure 2) using a digital elevation model (DEM, with a spatial resolution of 30 m), obtained from the *Instituto Nacional de Pesquisas Espaciais* (INPE, <http://www.webmapit.com.br/inpe/topodata/>) and the *QGIS* algorithms *r.watershed* and *r.outlet*. We then extracted the forest proportion for each catchment from MapBiomass Collection 8 land use and cover raster (MapBiomass, <https://brasil.mapbiomas.org/map/colecao-8/>), considering the year each site was sampled.

Finally, we calculated the Habitat Integrity Index (HII, Nessimian and others 2008), which provides a composite measure of physical habitat condition. The HII is independent of the U.S. EPA protocol and integrates 12 items grouped in four main categories: i) land-use patterns (dominant land-use type surrounding the stream reach), ii) riparian vegetation (for example, riparian buffer width and composition), iii) channel structure (for example, bank stability and flow heterogeneity), and iv) organic matter (for example, aquatic vegetation and detritus availability). The 12 items are visually evaluated and scored, and the index is calculated as the mean of all items, ranging from 0 to 1, with higher values indicating more intact habitats (Nessimian and others 2008). This index has been

Table 1. Environmental Features Representing the Physical Habitat and Integrity of Stream Sites

Feature	Variable	Definition
Catchment morphology	Catchment area (km ²)	The total drainage area of each stream was defined from the geographic coordinates of the downstream sampling section (Section “A”) and calculated from a Digital Elevation Model (DEM) in <i>QGIS</i> using the <i>r.watershed</i> algorithm
	Catchment slope (%)	The longitudinal slope of each stream catchment was calculated from the Digital Elevation Model (DEM), expressed as $\text{slope\%} = \tan(\text{angle}) \times 100$
	Catchment altitude (m)	Altitude of each site’s downstream section (Section “A”) based on the digital elevation model
Deforestation	Catchment forest (%)	Proportion of forest cover in each stream catchment, calculated in <i>QGIS</i> by overlaying the catchment boundaries (delineated for each stream) with the MapBiomas land-use raster corresponding to the sampling year
	Canopy cover (%)	Measured using a convex densiometer at the center of each transect (from A to K), oriented in four different directions (i.e., upstream, downstream, left, and right from the center). This resulted in 44 measurements per site, and the final value represents the mean canopy cover (%) of these observations for each stream
Flow dynamics	Fast flows (%)	Water velocity was visually assessed every meter along the thalweg (the deepest point in the channel) and classified according to the U.S. EPA protocol (for example, glide, pool, riffle, rapid, cascade, waterfall). Fast-flowing sections were defined as observations classified as riffle, rapid, cascade, or waterfall. The percentage of fast flows was calculated as the proportion of these fast-flowing observations out of the total 150 measurements per stream. The final value represents the mean percentage of fast-flowing sections across the stream
Allochthonous input	Large wood (m ³)	The mean wood volume in the streambed and along the banks was estimated by counting all woody fragments (branches or trunks) in each longitudinal section. Each fragment was visually assigned to one of 12 size categories, ranging from diameter ≥ 10 cm and length ≥ 1.5 m to diameter ≥ 80 cm and length ≥ 15 m. Only fragments meeting these minimum size criteria were included. The final value for each stream represents the sum of estimated volumes across all 12 categories
	Organic substrates (%)	Substrate composition was visually assessed at fixed points along each transect (at both banks and at 1/4, 1/2, and 3/4 of the channel width) and at the midpoints between transects, totaling 105 observations per stream. At each point, the dominant substrate type on the streambed surface was classified following the U.S. EPA protocol. Whenever possible, a small portion of the substrate was collected by hand to confirm the visual classification. Observations classified as leaf litter, small wood fragments (smaller than the “large wood” threshold), roots, or particulate organic matter were grouped as organic substrates. The final value represents the mean percentage of organic substrate observations per stream
Channel morphology	Depth (cm)	The thalweg depth (the deepest point between the banks) was measured every meter along the 150-m transect from downstream to upstream using a graduated rod. The final value represents the mean depth across all 150 measurements for each stream
	Width (m)	Wetted channel width was measured with a graduated rod at 11 transects and at the midpoint between consecutive transects. The final value represents the mean width across all measurements for each stream
	Sand (%)	Measured in the same way as organic substrates (105 visual observations per stream). Substrates were classified according to granulometric categories in the U.S. EPA protocol; here, we focused on sand, which was by far the most common inorganic substrate in the study area. The final value represents the mean percentage of sand observations per stream
Physical habitat integrity	Habitat integrity index (HII)	Composite index of physical habitat condition, ranging from 0 (degraded) to 1 (well-preserved). Integrates 12 items grouped into four categories: land use, riparian vegetation, channel structure, and organic matter. Each item is scored ordinally (0–3 or 0–5, depending on the item) based on theoretical impact levels defined in Nessimian and others (2008). The score for each item is divided by its maximum possible value, so all items contribute equally to the final index. The HII is calculated as the average of the 12 normalized items

Additional guidelines on the definitions can be found in Kaufmann and others (1999), Peck and others (2006), Nessimian and others (2008), and Callisto and others (2014).

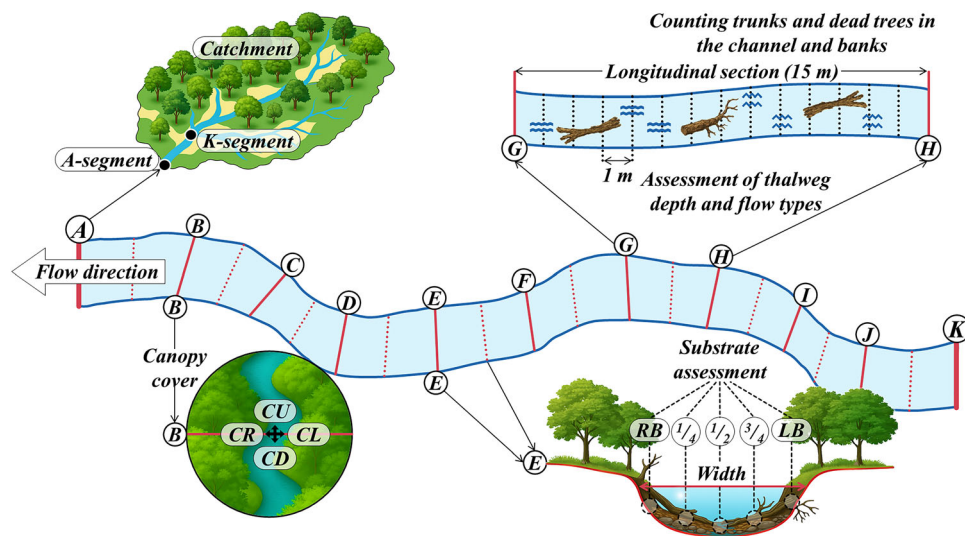


Figure 2. Site sampling design. Solid red lines labeled “A” to “K” represent the transects, and dashed red lines represent the midpoint between two transects. Dotted black lines indicate the positions where depth measurements and flow-type assessments were made. RB = right bank; LB = left bank; CU = center upstream; CD = center downstream; CL = center left; and CR = center right. Left and right banks are relative to flow direction.

successfully used in Amazonian aquatic biomonitoring studies (Brasil and others 2020). Additionally, we included catchment morphology features—area, slope, and altitude—derived from DEM data (Table 1) as natural controls, because these geomorphological characteristics can influence stream physical habitat independently of anthropogenic disturbance (Leal and others 2016; Benone and others 2017) (Figure 3). Including these variables allowed us to distinguish the effects of natural variation from those of deforestation on stream habitat conditions.

Details on variable definitions, measurement units, and procedures are provided in Table 1 and follow the methods of Kaufmann and others (1999, 2022) and Peck and others (2006).

DATA ANALYSIS

Each stream site represented a sampling unit. We performed a principal component analysis (PCA; Peres-Neto and others 2006) to visualize the stream site physical habitat considering the relationships among deforestation and the other variables. Before the analysis, we standardized variables using the z-score method (Legendre and Legendre 2012) and inspected multicollinearity among them; all Pearson coefficients were $|r| \leq 0.65$, so no variables were excluded.

We assessed the effect of deforestation on stream physical habitat condition by using structural equation modeling (SEM) (Arhonditsis and others

2006). The SEM approach is based on linear models. It allows for evaluating direct and indirect effects between predictor and response variables. This approach requires the prior formulation of a conceptual model (Arhonditsis and others 2006). Our conceptual model was developed based on results observed in previous studies (for example, Juen and others 2016; Leitão and others 2018; Montag and others 2019), field observations of environmental changes, and it represents our hypotheses (Figure 3). To capture the cascading effects of deforestation on stream physical habitat, variables were organized into six hierarchical levels, each one influenced by those above (except for deforestation): i) catchment morphology—area, slope, and altitude, exogenous to deforestation effects; ii) deforestation—catchment forest and canopy cover, the main driver of habitat change; iii) flow dynamics—fast flows, potentially shaped by catchment morphology and deforestation, driving sediment and allochthonous retention; iv) allochthonous input—large wood and organic substrates, contributing to v) channel morphology—width, depth, and sand; and vi) habitat integrity—HII, reflecting the cumulative effects of all preceding levels.

Our conceptual model specifically considers organic substrates affecting sand, as sand is the dominant inorganic substrate in Amazonian lowland streams. In these streams, sand is often buried beneath the accumulated organic matter, rather than the reverse, as consistently observed during

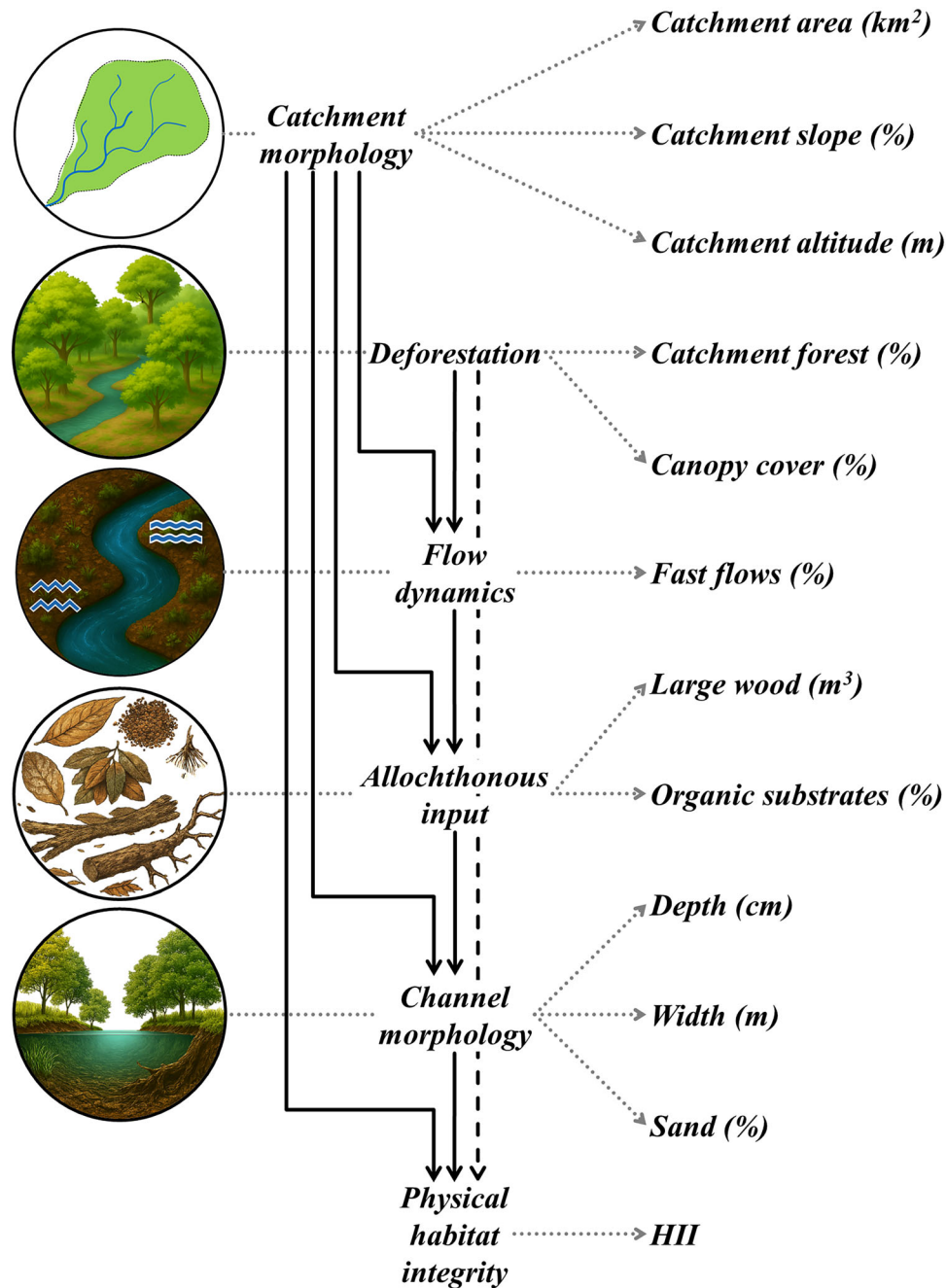


Figure 3. Conceptual model of the relationships between forest cover and site physical habitat. Solid black arrows represent hypothesized causal effects between hierarchical levels of variables, while dashed black arrows represent effects spanning multiple levels. Dotted gray arrows indicate the variables grouped within each hierarchical level. We expect direct effects from higher- to lower-level variables across the hierarchy; however, not all possible paths are shown to simplify visualization. Deforestation influences all lower-level processes but is not affected by anyone. HII = Habitat Integrity Index.

field sampling (Figure 3). To account for the spatial arrangement of the sampled streams (Figure 1), we considered the possibility of spatial nesting. Therefore, we constructed our SEM by including the mesoscale basin in which each stream is

embedded (that is, Baixo Tocantins, Gurupi, Tapajós, Trombetas, and Xingu rivers) as a random effect. This approach allowed us to control for potential spatial dependence among streams within

the same mesobasin and to reduce the risk of pseudoreplication.

The adequacy of the conceptual model to the collected data was assessed using an iterative method considering the global D-separation p value and model parsimony, based on global Akaike information criterion (AIC) (Shipley 2009; Lefcheck 2016). Our conceptual model (model-0) already included all theoretically plausible paths among variables from different defined hierarchical levels. The possible relationships among variables within the same hierarchical level are then tested and modeled as correlations. Next, model refinement followed a stepwise procedure restricted to the removal of non-significant paths (based on their individual p values), one at a time, starting with the least significant. A path was removed only when its exclusion reduced the global AIC, while maintaining model plausibility (that is, global D-separation p value > 0.05). Through this stepwise pruning, progressively simpler models were generated (that is, model-1, model-2, and so on). The final model was selected as both plausible and the most parsimonious among candidates. In addition, we assessed potential indirect pathways linking deforestation across spatial scales to physical habitat integrity. Indirect effects were quantified as the product of standardized path coefficients along the causal pathways linking forest cover to HII through mediator variables (Murphy 2024). As mediators, we retained only variables that exhibited significant direct associations with forest cover.

We performed all analyses using *R* software version 4.1.2 (R Development Core Team 2021), the *vegan* package (Oksanen and others 2023) for PCA, *piecewiseSEM* (Lefcheck 2016) and *lme4* (Bates and others 2015) for structural equation modeling, and *semEff* (Murphy 2024) for indirect effect analysis.

RESULTS

Stream sites exhibited high variation in catchment forest (0–100%, mean 68.3%) and canopy cover (0–100%, mean 81.9%). Stream depth ranged from 4.5 to 116 cm, and stream width from 0.5 to 12.4 m. Additionally, catchment morphology, flow dynamics, allochthonous input, channel morphology, and physical habitat integrity features showed high variation (Table 2). Sites with higher HII scores had greater catchment forest and canopy cover. Channel morphology features like width and depth were strongly related to catchment area, whereas sand and fast flows were related to catchment altitude (Figure 4). Additionally, or-

ganic substrates were negatively associated with sand and catchment altitude.

Deforestation negatively altered the HII scores both directly and indirectly (D-separation: $p = 0.478$, Figure 5; Table S1). Our results indicate that the cumulative effects of deforestation on HII were considerable, with a conditional $R^2 = 0.58$. At the upper level, canopy cover exerted a positive effect on organic substrates ($\beta = 0.24$). Organic substrates, in turn, strongly reduced sand cover ($\beta = -0.62$), while sand was also negatively affected by large wood ($\beta = -0.29$) and positively influenced by canopy cover ($\beta = 0.11$). Ultimately, organic substrates, sand, and canopy cover all had direct positive effects on HII ($\beta = 0.17$, 0.16, and 0.49, respectively). Catchment forest, on the other hand, influenced HII only directly, with a medium effect ($\beta = 0.28$), but without mediation by other variables.

Catchment morphology features also played a significant role in shaping habitat integrity through both direct and indirect pathways. The catchment area had a strong positive effect on stream depth ($\beta = 0.47$), which in turn negatively affected HII ($\beta = -0.17$). Catchment altitude positively influenced fast flows ($\beta = 0.15$) and large wood ($\beta = 0.31$), while negatively affecting organic substrates ($\beta = -0.35$). In addition, large wood also directly influenced HII ($\beta = 0.12$). Catchment altitude also showed a direct positive relationship with HII ($\beta = 0.21$), whereas catchment slope had no significant relationships retained in the final model. To aid interpretation, we highlight only the main pathways, whereas the complete set of direct effects is provided in Figure 5 and Table S1 (Supplementary Material).

Regarding the indirect effects of deforestation (here represented solely by canopy cover, since catchment forest affected HII only directly), these reflect how changes in one variable propagate through mediators to influence HII. Organic substrates were the primary mediator, followed by sand. Canopy cover influenced HII indirectly through three pathways: i) via organic substrates directly ($\beta = 0.012$), ii) via organic substrates and subsequently through sand ($\beta = -0.135$), and iii) via sand alone, independent of organic substrates ($\beta = -0.004$).

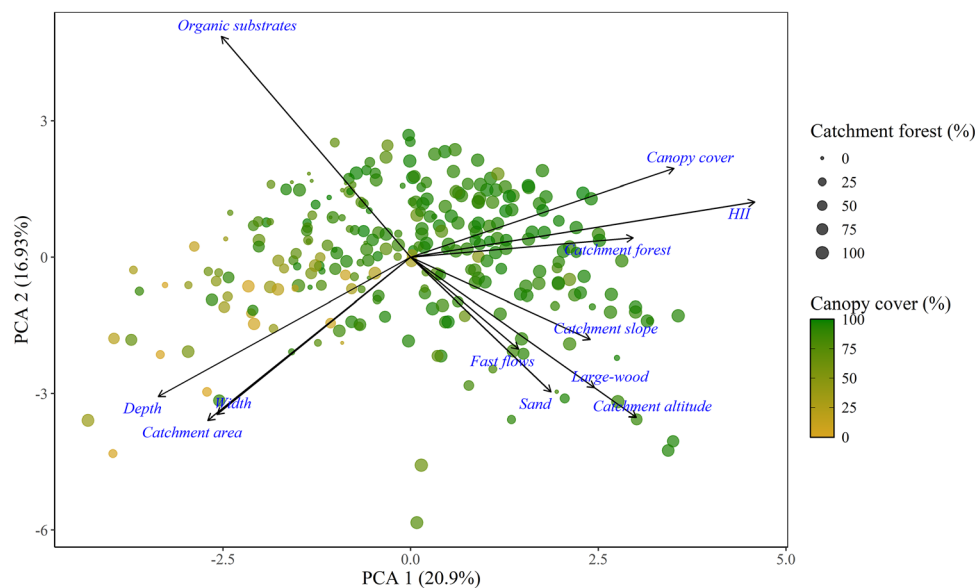
DISCUSSION

Our results support the hypothesis that deforestation generates cascading impacts on the physical habitat structure and condition on Amazonian streams. These impacts occurred both indirectly

Table 2. Site Environmental Characteristics

Feature	Minimum	Maximum	Mean	SD	CV
Catchment area (km ²)	0.11	64.81	8.64	11.55	133.74
Catchment slope (%)	0.01	0.37	0.12	0.07	54.77
Catchment altitude (m)	13.99	568.38	101.23	96.19	95.02
Catchment forest (%)	0.00	100.00	68.34	33.31	48.74
Canopy cover (%)	0.00	100.00	81.86	23.09	28.20
Fast flows (%)	0.00	100.00	27.89	28.43	101.94
Large wood (m ³)	0.00	83.64	4.43	11.96	269.95
Organic substrates (%)	0.00	100.00	44.62	23.30	52.22
Depth (cm)	4.49	115.88	36.92	19.34	52.39
Width (m)	0.49	12.35	3.08	1.65	53.43
Sand (%)	0.00	87.62	29.48	23.17	78.61
HII	0.07	0.99	0.68	0.19	28.31

HII = Habitat Integrity Index

**Figure 4.** Relationships between forest cover and the stream site physical habitat structure. HII = Habitat Integrity Index.

(that is, mediated by changes in habitat structure) and directly. However, the canopy cover had an impact almost twice as big as the catchment forest on stream physical habitat conditions, highlighting that local riparian vegetation plays a stronger role than catchment-scale forest in maintaining stream integrity (Brejão and others 2024). This emphasizes that the effects of deforestation depend on the location and spatial scale at which it occurs (Jackson and Fahrig 2015; Leal and others 2016).

The increase in organic substrates is primarily influenced by the input of allochthonous organic matter from the riparian vegetation (Vannote and others 1980; Paula and others 2011). Our results highlight that maintaining riparian vegetation en-

sures an important supply of organic substrates to streams. Interestingly, we did not find a direct relationship between large wood and catchment forest or canopy cover. Given that forests are the primary natural source of wood (Paula and others 2011), this result suggests a possible threshold response (Baker and King 2010), in which a minimum level of forest cover may be required before wood input is significantly affected. This nonlinearity illustrates the complexity of wood dynamics in Amazonian streams. While riparian vegetation is key to maintaining resource availability, catchment-scale forest cover contributes to regulating hydrological regimes, modulating local climate, and reducing sediment and nutrient inputs, all of which

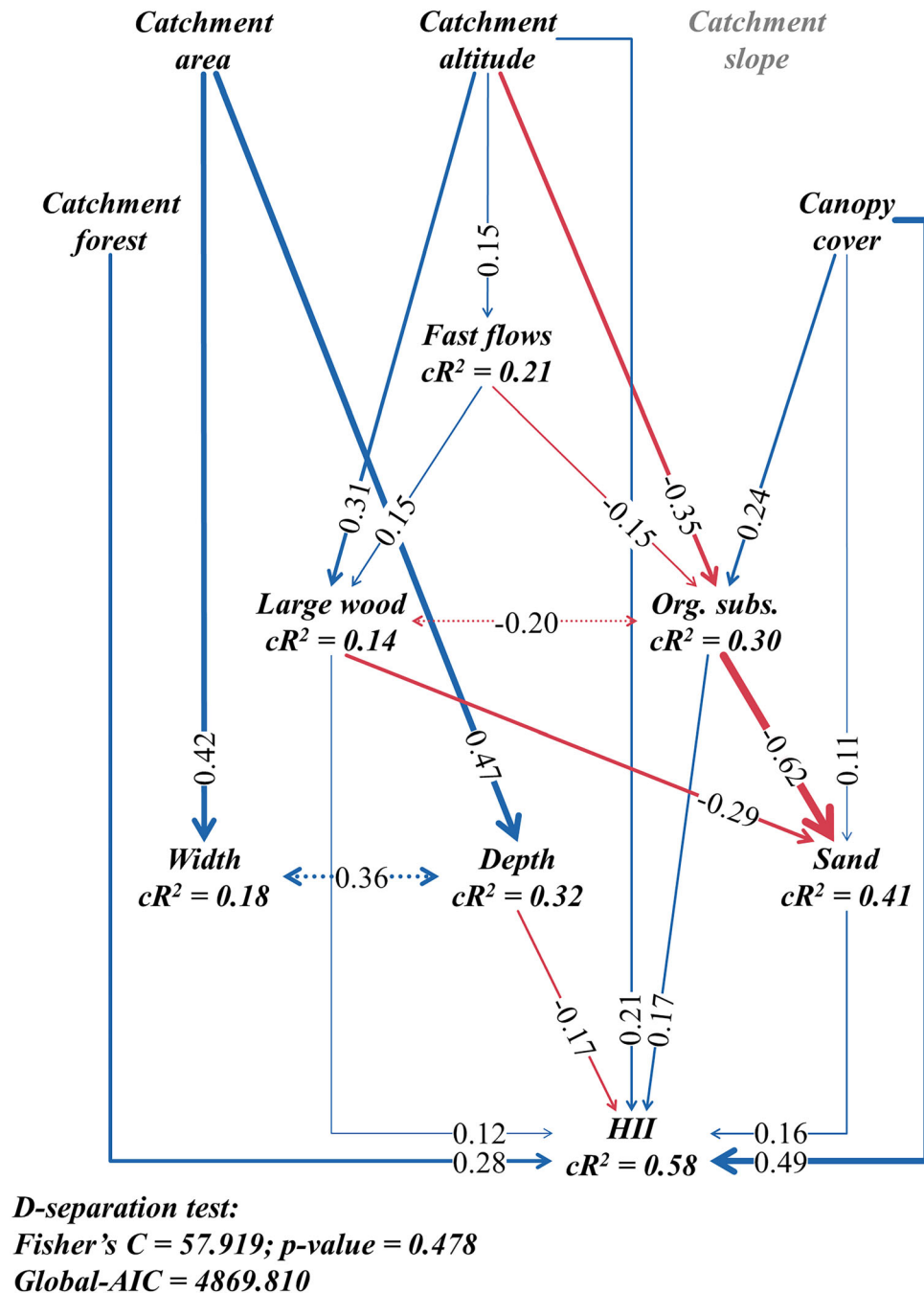


Figure 5. Structural equation models considering the effects of deforestation on the physical habitat of Amazonian streams sites. Continuous arrows indicate linear relationships (cause and effect), and double and dotted arrows indicate Pearson correlations. Blue and red indicate positive and negative relationships, respectively. Arrow thickness and values indicate the effect size (standardized- β , or Pearson- r). Only direct and significant relationships are shown. Org. subs. = Organic substrates. HII = Habitat Integrity Index. cR^2 = conditional R -squared.

are essential for stream resilience (Creed and others 2011; Sun and others 2016; Martins and others 2021).

Large wood and organic substrates are well-known drivers of habitat complexity, providing shelter and food resources for aquatic biota (Can-

hãde and others 2021; Cruz and others 2022). Our results further demonstrate that these components mediate the effects of deforestation, shaping channel morphology and enhancing physical heterogeneity. The accumulation of woody debris, leaves, and other plant fragments in the streambed

reduces the exposed sand and increases physical complexity and environmental heterogeneity (Leal and others 2016; Benone and others 2017), creating a greater diversity of microhabitats. Greater physical heterogeneity, in turn, has been shown to buffer anthropogenic impacts on fish and insect diversity (Leitão and others 2018; Moi and others 2024). The accumulation of these allochthonous materials also contributes to bank stabilization and reduces siltation (Juen and others 2016; Montag and others 2019), supporting physical habitat integrity, as we observed in our study.

We detected a more subtle direct effect of deforestation on channel morphology, with only a direct and positive effect from canopy cover to sand. This may be related to the relatively high average percentage of canopy cover (81%) around streams, that make catchment morphology features the main drivers of channel morphology. On the other hand, the catchment area had a strong positive effect on stream depth and width, which is not surprising given that larger catchment areas tend to increase the number of tributaries (for example, Leopold and others 1995; Montgomery and Buffington, 1993). Additionally, catchment altitude influences allochthonous material retention in streams by increasing hydraulic forces. Higher flow speeds favor downstream transport of small vegetative fragments, reducing organic substrates (Grabowski and others 2014; Sutfin and others 2016), and can destabilize stream banks, promoting tree fall and the input of large wood into the channel. At the same time, the positive response of large wood to altitude may also be related to some level of anthropogenic activity. In some Amazonian regions, large wood is commonly removed to facilitate water flow in small streams (for example, Faria and others 2017), a practice more frequent in easily accessible streams, particularly those at lower elevations, as we also observed in the field. These findings highlight that the effects of deforestation on physical habitat structure and condition are shaped not only by anthropogenic activities but also by natural variations in catchment morphology features (Leal and others 2016; Benone and others 2017).

Lotic ecosystems are hierarchical and complex systems, where the effects of anthropogenic changes vary depending on spatial extent. The Habitat Integrity Index (HII), a proxy for physical habitat integrity, has been widely applied in Amazonian biomonitoring (Brasil and others 2020), and our study demonstrates a positive relationship between HII and both catchment forest and site canopy cover. However, the relatively high average canopy

cover of the stream sites likely buffered the more pronounced effects of catchment-scale deforestation, helping to maintain higher HII scores. Moreover, the full effects of extensive deforestation may take years to manifest, as allochthonous material (for example, large wood) can persist in the environment long after deforestation (Zeni and others 2019). This persistence could explain why the effects of catchment deforestation appeared less pronounced compared to site-riparian deforestation.

Human-induced changes associated with deforestation are not random processes and are often correlated with catchment morphology. Higher-altitude and/or steeper-slope regions generally involve higher financial costs for implementing and maintaining activities such as agriculture and livestock grazing, making them less favorable for land use. These costs stem from factors such as road construction, irrigation, mechanization, and increased soil erosion (Jasinski and others 2005; Gimenes and others 2017). In contrast, lower-altitude regions, typically valleys or lowlands, offer reduced costs for these activities, especially near water bodies. This aligns with our results, which showed a positive effect of catchment altitude on HII. Therefore, while disentangling the effects of natural variation from anthropogenic activities remains complex, our results shed new light on these interactions and advance our understanding of their influence on stream physical habitat (Whittier and others 2007; Stoddard and others 2008; Steel and others 2010).

These findings have important implications for monitoring and conservation. In Brazil, the Native Vegetation Protection Law (Law No. 12,651, May 25, 2012, also known as the Forest Code) establishes Permanent Preservation Areas (APPs, in Portuguese)—riparian buffer strips along natural watercourses, with a minimum width of 30 m on each bank. However, even when legal requirements are met, deforestation beyond these strips can still degrade stream habitats and threaten aquatic biodiversity (Leitão and others 2018; Faria and others 2021; Monteles and others 2021; Rivera-Perez and others 2024). Protected areas (for example, National Forests, National Parks, and Extractive Reserves) provide an additional safeguard by restricting land use and preventing severe habitat loss (Azevedo-Santos and others 2019; Brito and others 2024). Yet, these regulations are often disregarded in regions heavily impacted by agriculture, mining, or logging (Monteiro and others 2016; Preto and others 2022), emphasizing the urgent need for stricter enforcement. More-

over, terrestrial protected areas alone are insufficient to safeguard stream ecosystems (Azevedo-Santos and others 2019; Leal and others 2020). In fact, we found deforested stream sites even within National Parks and National Forests. Strengthening monitoring and enforcement is essential to prevent further habitat degradation and sustain aquatic biodiversity resilience amid growing anthropogenic pressures.

Although our findings indicate that riparian vegetation exerts a stronger influence on site-scale physical habitat than catchment deforestation, the broader role of catchment forest cover should not be underestimated. Extensive forested areas regulate climate, maintain water balance, and support metacommunity dynamics, all of which are crucial for ecosystem resilience and regional biodiversity (Ellison and others 2017; Chase and others 2020; Martins and others 2021). While we did not directly evaluate these processes, they are well documented as key factors for species persistence, recolonization, and connectivity in fragmented landscapes (Chase and others 2020; Riva and Fahrig 2022, 2023). In our study, even sites with low catchment forest cover often maintained relatively high canopy cover, which may buffer environmental changes (Naiman and others 1993; Hughes and Vadas 2021; Brito and others 2021b). Canopy predictor of aquatic assemblages, influencing fish (Leitão and others 2018; Cantanhêde and others 2021), aquatic insects (Cardoso and others 2015; Calvão and others 2016; Cruz and others 2022), and aquatic macrophytes (Fares and others 2020; Bomfim and others 2023), and stream physical structure (Juen and others 2016; Leal and others 2016; Leitão and others 2018). However, riparian vegetation in deforested catchments may not be sustainable in the long term, as large-scale ecological processes—such as seed bank maintenance and animal-mediated seed dispersal—are essential for its persistence (Naiman and others 1993).

CONCLUSION

Our results demonstrate that the effects of anthropogenic activities, particularly deforestation, on the physical structure and HII scores of Amazonian streams depend on the spatial scale of the disturbance. Site canopy cover emerged as a key factor in stream physical structure, underscoring the importance of riparian vegetation in mitigating the impacts of catchment deforestation by sustaining organic matter inputs and providing retention structures. Additionally, these impacts are not random but are shaped by catchment

morphology, including factors such as altitude and slope, which affect the feasibility and costs of anthropogenic alterations and environmental conservation. Such characteristics should be carefully considered in future studies, as they may indirectly shape biodiversity patterns and the delivery of ecosystem services. We also acknowledge that, in studies with a broad geographic scope such as ours, climatic variables may exert significant effects on the physical structure of streams, particularly on water volume. These factors, despite increasing the complexity of the models, should be considered in future studies.

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DATA AVAILABILITY

The data and code that support the findings of this study are openly available in Zenodo repository at <https://doi.org/10.5281/zenodo.15115427>.

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