

Uncovering aquatic diversity patterns in Plecoptera and Trichoptera (Insecta) immatures in the riffles of the Xingu River

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Abstract

Environmental gradients can directly structure Plecoptera and Trichoptera (PT) assemblages in Amazonian rivers by modifying habitat conditions such as flow, substrate composition, water depth, and the availability of organic resources and suitable microhabitats. This study evaluated how environmental gradients are associated with genus richness, taxonomic composition, and functional feeding group (FFG) distribution in riffle sections, and quantified variation among sites using β -diversity partitioning. We hypothesized that (i) PT genus richness, taxonomic composition, and FFG composition would vary along environmental gradients; (ii) taxonomic β -diversity would be dominated by genus replacement; and (iii) FFG-based β -diversity would be mainly driven by balanced changes in abundance.

Macroinvertebrates were collected from submerged rocky substrates using a Surber net, preserved in 70% alcohol, identified to genus, and classified into FFGs. Environmental variation was summarized using principal component analysis, while relationships with biological metrics were evaluated using multiple regression and distance-based redundancy analyses. Environmental gradients did not significantly explain PT genus richness, taxonomic composition, or FFG abundance structure. Taxonomic β -diversity was primarily associated with genus replacement ($\beta_{\text{total}} = 0.758$; $\beta_{\text{repl}} = 0.614$; 80.98%), whereas FFG-based β -diversity was mainly associated with balanced variation in abundance ($\beta_{\text{total}} = 0.744$; $\beta_{\text{bal}} = 0.431$; 57.92%). These findings indicate substantial variation in PT assemblages among riffle sections and highlight the importance of taxonomic and functional β -diversity when assessing aquatic insect assemblages in Amazonian rivers.

1. Introduction

Riffles are naturally heterogeneous lotic habitats characterized by shallow water, high current velocity, turbulence, and generally well-oxygenated conditions. This environmental complexity increases the diversity of refuges, feeding sites, and attachment surfaces available to aquatic insect assemblages (Bispo et al. 2004; Oliveira and Nessimian 2010; Schmitt et al. 2020). Aquatic insects persist in these habitats through morphological, behavioral, and trophic adaptations, including flattened or streamlined bodies, claws and other attachment structures, crawling and clinging habits, case and retreat construction, and filtering or predatory strategies suited to flowing waters (Hamada et al. 2014; Merritt et al. 2019). Such adaptations allow taxa to occupy different microhabitats within riffles, potentially producing marked compositional differences even among nearby sites.

At broader spatial scales, the River Continuum Concept predicts that changes in channel structure, hydrology, and resource availability along river networks are accompanied by shifts in aquatic communities (Vannote et al. 1980). The distribution of functional feeding groups (FFG) is consequently related to the availability and transport of allochthonous and autochthonous food resources (Luiza-Andrade et al. 2020). At the local scale, differences in current velocity, depth, substrate configuration, and physicochemical conditions may alter habitat suitability and the relative abundance of feeding groups among riffle sections.

In addition to local richness, beta diversity provides information about how assemblages vary among sites. Taxonomic beta diversity can be partitioned into replacement and richness-difference components, which represent, respectively, the substitution of taxa among communities and differences in their number of taxa (Podani and Schmera 2011; Legendre 2014). Similarly, abundance-based beta diversity of FFG can be decomposed into balanced variation in abundance and abundance gradients. Balanced variation represents compensatory changes in the abundances of feeding groups among sites, whereas abundance gradients indicate directional differences in their total abundance (Baselga 2013).

Plecoptera and Trichoptera (PT) are particularly suitable for investigating these patterns because their immature stages are strongly associated with flowing-water habitats and encompass contrasting morphological, behavioral, and feeding strategies. Both orders include taxa adapted to rocky substrates, current exposure, resource capture, and refuge construction, making them important components of riffle assemblages. Their distributions may respond to local variation in habitat structure and water conditions, and several representatives are also used in biomonitoring because of their sensitivity to environmental alteration (Buss et al. 2002; Martins et al. 2014; Brasil et al. 2020; Faria et al. 2021). Plecoptera nymphs inhabit lotic environments and are commonly associated with well-oxygenated water and rocky substrates. The Amazonian genera commonly include predatory organisms with crawling and clinging habits (Alencar et al. 1999; Lecci and Froehlich 2007; Merritt et al. 2019). Trichoptera is considerably more diverse and includes genera with multiple feeding and habitat-use strategies. Its larvae may construct cases, retreats, or capture nets, or live freely on the substrate, allowing them to occupy a broad range of microhabitats in lotic systems (Pes et al. 2005; Bentes et al. 2008; Santos et al. 2023). They constitute a significant portion of the insect biomass in lotic systems.

Despite their ecological relevance, PT in large-river riffles remain comparatively understudied in Amazonian freshwater ecology. In fact, available studies on aquatic insects in these habitats are still limited, restricting broader understanding of how assemblages vary among riffle sections and how taxonomic and trophic organization changes across space (Silva et al. 2021; Leal et al. 2023). Consequently, the processes underlying beta-diversity patterns in Amazonian large-river riffles remain poorly understood. Examining these complementary dimensions is essential for interpreting how ecological processes structure communities and for supporting management strategies in freshwater ecosystems (Dey et al. 2024). Thus, we assessed how local environmental variation is associated with genus richness, taxonomic composition, and functional feeding-group composition of Plecoptera and Trichoptera in riffles of the Xingu River, and quantified taxonomic and feeding-group beta diversity among sites. We tested the following hypotheses: (i) PT genus richness, taxonomic composition, and FFG compositions are affected by environmental variation among riffle sections because hydrodynamic and physicochemical conditions determine habitat and microhabitat availability; (ii) taxonomic beta diversity is high and dominated by genus replacement rather than richness differences because microhabitat heterogeneity among riffles promotes spatial replacement of PT genera; and (iii) beta diversity based on FFGs is high and mainly driven by balanced changes in FFG abundances because local riffle conditions alter the proportional dominance of feeding groups without necessarily eliminating functional categories.

2. Materials and Methods

2.1. Study area

Sampling was conducted in October 2015 during the dry season. Eight sampling points were randomly selected in the Volta Grande do Xingu (Fig. 1). The Xingu River, spanning approximately 2,500 km in length, encompasses a catchment area of about 504,000 km². It originates from the confluence of the Culuene and Sete de Setembro rivers in the state of Mato Grosso and flows into the Amazon River in the state of Pará (Goulding et al., 2003). According to Sioli (1956), the Xingu River is classified as a “clearwater” river, a typology characterized by high water transparency and acidic pH. Moreover, it is the second-largest clearwater tributary of the Amazon River and one of the largest in South America (Sawakuchi et al., 2015). It is characterized by low concentrations of suspended solids, mineral elements, and nutrients. Additionally, it exhibits a neutral to slightly acidic pH and low electrical conductivity (mean 30 $\mu\text{S}/\text{cm}^{-1}$) (Goulding et al., 2003; Camargo and Ghilardi Jr., 2009; Nascimento et al., 2021).

The course of the Xingu River takes a significant turn near the city of Altamira, Pará (northern region of Brazil), leading to the formation of the Volta Grande of the Xingu River. This stretch, covering a distance of only 160 km, features a remarkable altitudinal gradient of 85 m. This geological configuration gives rise to multiple flow channels characterized by waterfalls cascading over fractured rocks (Sawakuchi et al. 2015), a particular characteristic of the Xingu River. The rapids are composed of rocky substrate of various sizes (Salomão et al. 2007). Within the Volta Grande region, the dry season spans from July to October. During this period, there is a reduction in suspended solids, resulting in decreased turbidity and subsequently increased water transparency. Water transparency can exceed 2.5 meters between the months of August and November (Sabaj-Pérez 2015).

2.2. Collection of PT

The present study focuses specifically on Plecoptera and Trichoptera because these orders are closely associated with riffle habitats, represent contrasting taxonomic and trophic strategies. Ephemeroptera and the remaining macroinvertebrate groups were not included because the study was designed a priori to investigate Plecoptera and Trichoptera assemblages in rocky riffle habitats. Individuals were collected from submerged rocky outcrops at a maximum depth of 1.30 m. This depth limit was established to ensure proper functioning of the benthic macroinvertebrate sampling. An area of 0.25 m² was demarcated, and a Surber net (a square net covered with 250 μm nylon mesh) was positioned against the water current and swept across the substrate. Using tweezers and a soft bristle brush, macroinvertebrates adhering to the substrate were carefully removed and placed in 100 ml polyethylene jars containing 70% alcohol. The specimens were appropriately labeled.

In the laboratory, the organisms were separated from the sediment using a stereoscopic microscope (Leica®, ZOOM 2000). They were then stored in 50 ml polyethylene bottles with 70% alcohol and appropriately labeled. Identification was conducted at the taxonomic levels of order, family, and genus,

with reference to specific literature (Hamada et al. 2014), and consultation with experts was pursued when necessary. The classification of Functional Feeding Groups (FFG) was based on specific literature sources (Merritt et al. 2019; Castro et al. 2017; Brito et al. 2018). The identified material was deposited in the Laboratório de Ecologia do Campus Universitário de Altamira, Universidade Federal do Pará.

2.3. Environmental variables

We measured a set of environmental variables at each riffle site, including water temperature (TMA), dissolved oxygen (OD, mg/L), pH, and electrical conductivity (CMA, $\mu\text{S}/\text{cm}$), using a multiparameter probe (Horiba® U-50). Channel depth (DEP, m) was measured with a 3-m rope weighted at one end; three measurements were taken per site, and the mean value was used in the analyses. Surface current velocity (VSC, m/s) was estimated with a Styrofoam buoy, recording the time required to travel a 10-m distance; the final velocity value corresponds to the mean of three repetitions. Substrate roughness (RUG) was estimated using the chain-and-tape method adapted from coral reef assessments (Risk 1972; Luckhurst et al. 1978; Aronson and Precht 1995; Knudby et al. 2007). A metal chain (3/32-inch links, 2 m long) was laid along the streambed following the natural contour. Roughness was calculated as the ratio between the contoured chain length and the linear distance covered (Luckhurst et al. 1978). This procedure was performed three times at each site, and the mean roughness value (dimensionless index) was used in the analyses.

2.4. Data analysis

Environmental variables were examined using Pearson correlation matrices to assess pairwise associations among variables. Prior to principal component analysis (PCA), all environmental variables were centered and standardized to account for differences in measurement scales. The PCA included electrical conductivity, pH, water temperature, dissolved oxygen, surface current velocity, depth, and substrate roughness. Then, to address hypothesis (i), environmental variation among riffle sections was summarized using PCA. Components were retained according to the Kaiser-Guttman criterion, which retains axes with eigenvalues greater than 1. Three components met this criterion and were retained for interpretation and subsequent analyses.

The influence of the retained environmental gradients on PT genus richness was assessed using multiple linear regression, with PC1, PC2, and PC3 as explanatory variables. The normality of model residuals was evaluated using the Shapiro-Wilk test. Relationships between environmental gradients and taxonomic composition were tested using distance-based redundancy analysis (dbRDA), implemented with the *capscale* function. Taxonomic composition was converted to presence-absence data, and Jaccard dissimilarity was used to represent differences in genus composition among sites. Relationships between environmental gradients and functional feeding-group (FFG) composition were also tested using dbRDA, using the FFG abundance matrix and Bray-Curtis dissimilarity. In both dbRDA analyses, PC1, PC2, and PC3 were included as explanatory variables, and an additive correction for negative eigenvalues was applied. The significance of the global models, individual environmental

components, and constrained axes was evaluated using permutation ANOVA with 999 permutations ($p < 0.05$).

Taxonomic and FFG composition among sites were additionally explored using hierarchical cluster analysis. Taxonomic composition was based on Jaccard dissimilarity calculated from the presence-absence genus matrix, whereas FFG composition was based on Bray-Curtis dissimilarity calculated from the FFG abundance matrix. In both cases, clustering was performed using the UPGMA algorithm ("average" linkage). The representational quality of the resulting dendrograms was evaluated using the cophenetic correlation coefficient (Sokal and Rohlf 1962). Cluster analyses were interpreted as exploratory representations of biological similarity among riffle sections. Additionally, genus-sharing matrices were computed to describe the number of genera shared among sites.

To address hypothesis (ii), that taxonomic β -diversity would be primarily driven by genus replacement rather than differences in richness, taxonomic β -diversity was quantified from the site $\times$ genus presence-absence matrix using a Jaccard-based partitioning framework (Podani and Schmera 2011; Legendre 2014). Total β -diversity (β_{total}) was decomposed into replacement (β_{repl}) and richness-difference (β_{rich}) components. Pairwise β_{total} , β_{repl} , and β_{rich} values were calculated for all combinations of riffle sites.

To address hypothesis (iii), that β -diversity of FFG composition would be primarily driven by balanced changes in abundance rather than abundance gradients, a site $\times$ FFG abundance matrix was used to quantify abundance-based β -diversity (Baselga 2013). Bray-Curtis dissimilarity was partitioned into balanced variation in abundance (β_{bal}) and abundance-gradient (β_{grad}) components. Pairwise β_{total} , β_{bal} , and β_{grad} values were calculated for all combinations of riffle sites. All analyses were performed in R using the packages *vegan*, *betapart*, *cluster*, *dendextend*, *dplyr*, *tidyr*, *ggplot2*, and *ggrepel*.

3. Results

3.1. Environmental variables

Environmental variables showed considerable variation among the riffle sections sampled in the Xingu River (Table 1). Overall, riffles exhibited normal CMA values, with the highest measurement recorded at site 11PEM. Water temperature was consistently high, and OD and pH showed little variation, indicating predominantly well-oxygenated and neutral to slightly alkaline conditions. Current velocity (VSC) varied moderately across sites, as did mean depth (DEP), with site 07PEM representing the deepest section, reaching 1.09 m.

Table 1
Environmental variables recorded in the riffle sections of the Xingu River. CMA = electrical conductivity ($\mu\text{S}/\text{cm}$); TMA = water temperature ($^{\circ}\text{C}$); OD = dissolved oxygen (mg/L); VSC = current velocity (m/s); DEP = mean depth (m).

SECTIONS	CMA	pH	TMA	DO	VSC	DEP	RUG
01PEM	24.000	8.900	30.500	7.900	0.429	0.553	0.873
02PEM	13.500	7.620	28.000	5.900	0.273	0.610	0.877
04PEM	11.000	7.950	29.700	7.800	0.353	0.370	0.763
05PEM	12.000	8.000	30.100	8.200	0.638	0.953	0.680
06PEM	23.000	8.800	31.300	6.100	0.517	0.623	0.623
07PEM	24.000	7.460	31.400	7.500	0.353	1.090	0.707
11PEM	67.000	8.580	29.900	7.900	0.455	0.923	0.803
13PEM	11.000	8.250	29.100	7.600	0.556	0.810	0.717

The Kaiser-Guttman criterion indicated the retention of three principal components with eigenvalues greater than 1. PC1 had an eigenvalue of 2.46 and explained 35.21% of the environmental variation, PC2 had an eigenvalue of 1.47 and explained 20.97%, and PC3 had an eigenvalue of 1.27 and explained 18.21%. Together, the three retained components accounted for 74.38% of the total environmental variation (Fig. 2).

3.2. PT collection and diversity

A total of 178 individuals were collected, representing two orders, eight families, and 14 genera. Hydropsychidae was the most abundant family ($n = 76$; 42.69%), while *Marilia* Müller, 1880 was the most abundant genus ($n = 45$; 25.28%) (Table 2). Trichoptera showed the highest richness, comprising seven families and 12 genera. Plecoptera was represented exclusively by the family Perlidae, with two genera, *Anacroneuria* Klapálek, 1909 and *Macrogynoplax* Enderlein, 1909. Among the FFGs, predators were the most abundant group, followed by shredders and filterers, whereas collector-filterers and scrapers showed lower abundances in the sampled riffles (Table 2).

Table 2
Abundance of genera and functional feeding groups of PT sampled in the riffles of the Xingu River.

Order/ Family/ Genus	Abundance	Functional feeding groups
Plecoptera		
Perlidae		
<i>Anacroneuria</i> Klapálek, 1909	29	Predator
<i>Macrogynoplax</i> Enderlein, 1909	10	Predator
Trichoptera		
Hydropsychidae		
<i>Leptonema</i> Guérin-Méneville, 1843	24	Filterer
<i>Blepharopus</i> Kolenati, 1859	3	Filterer
<i>Macrostemum</i> Kolenati, 1859	10	Filterer
<i>Smicridea</i> McLachlan, 1871	14	Collector-filterer
<i>Synoestropsis</i> Ulmer, 1906	25	Predator
Philopotamidae		
<i>Chimarra</i> Stephens, 1829	2	Collector-filterer
Polycentropodidae		
<i>Polyplectropus</i> Ulmer, 1905	2	Collector-filterer
<i>Cyrnellus</i> Banks, 1913	2	Collector-filterer
Hydroptilidae		
<i>Flintiella</i> Angrisano, 1995	1	Scraper
Helicopsychidae		
<i>Helicopsyche</i> von Siebold, 1856	10	Scraper
Odontoceridae		
<i>Marilia</i> Müller, 1880	45	Shredder
Leptoceridae		
<i>Oecetis</i> McLachlan, 1877	1	Predator
Total individuals	178	

We found no significant relationship between the retained environmental PCA axes and PT genus richness in the Xingu River riffles (adjusted $R^2 = 0.340$; $F = 2.202$; $p = 0.230$). Similarly, the retained environmental components did not significantly explain overall PT taxonomic composition (dbRDA: adjusted $R^2 = 0.203$; $F = 1.596$; $p = 0.081$) or FFG abundance structure (dbRDA: adjusted $R^2 = 0.165$; $F = 0.669$; $p = 0.799$).

The taxonomic cluster analysis adequately represented the original distance matrix, as indicated by a cophenetic correlation coefficient of 0.747. The dendrogram revealed variation in taxonomic similarity among riffle sections. Site 07PEM showed the greatest separation from the remaining sites, followed by 01PEM and 02PEM, whereas 04PEM and 06PEM showed the highest similarity in genus composition (Fig. 3). The FFG-based cluster analysis showed a strong correspondence with the original Bray-Curtis dissimilarity matrix, with a cophenetic correlation coefficient of 0.849. Most riffle sections showed comparatively similar FFG abundance structure, whereas 01PEM and 05PEM clustered together but were separated from the remaining sites at a relatively high dissimilarity level (Fig. 4).

3.3. Beta diversity

Taxonomic β -diversity among riffle sites was $\beta_{\text{total}} = 0.758$. Most of this dissimilarity was associated with the replacement component ($\beta_{\text{repl}} = 0.614$), which accounted for 80.98% of total β -diversity, whereas differences in genus richness ($\beta_{\text{rich}} = 0.144$) accounted for 19.02%. Pairwise replacement values varied considerably among riffle sections, with the greatest dissimilarity observed between 01PEM and 07PEM. Comparatively lower replacement values were observed among several pairs involving 04PEM, 05PEM, 06PEM, and 13PEM (Fig. 5). Overall, these results indicate that taxonomic differentiation among the sampled riffles was primarily associated with the replacement of genera among sites.

FFG-based β -diversity among riffle sites was $\beta_{\text{total}} = 0.744$. Balanced variation in abundance was the largest component of this dissimilarity ($\beta_{\text{bal}} = 0.431$), accounting for 57.92% of total β -diversity, whereas the abundance-gradient component ($\beta_{\text{grad}} = 0.313$) accounted for 42.07%. Pairwise dissimilarity varied among riffle sections, with comparatively lower values observed for some site pairs and greater differences in FFG abundance structure among others (Fig. 6). Thus, these results indicate that differences in FFG composition among the sampled riffles were associated mostly by balanced changes in the abundances of feeding groups.

4. Discussion

The taxonomic composition of PT recorded here is consistent with other studies in lotic environments in the Amazon, where these groups are commonly associated with small streams (Santos et al. 2024). However, it differs from studies conducted in the Xingu River, which have reported higher abundance and richness of Plecoptera genera (Leal et al. 2023).

Our first hypothesis, that environmental gradients would structure PT richness, taxonomic composition, and functional feeding groups, was not supported. Although riffles are inherently dynamic and heterogeneous habitats, the physicochemical variables measured in this study may not have captured the fine-scale complexity influencing PT assemblages (Boyero et al. 2011; Heino et al. 2015). This pattern is consistent with findings from tropical lotic systems in which broad-scale environmental variables may not fully reflect the microhabitat-scale heterogeneity associated with the community structure (Boyero et al. 2011; Bispo et al. 2004; Shimano et al. 2012). Interestingly, other aquatic communities in the Xingu River system have shown significant relationships with environmental variables, which emphasizes that, despite the absence of detectable environmental effects on PT assemblages in the present study, habitat characteristics can play an important role in structuring aquatic communities and may respond to a different or finer-scale set of environmental variables than those measured here (Souza et al. 2026).

Naturally, it is important to note that variability in aquatic environmental data may also reflect seasonality, unmeasured climatic fluctuations, and other local factors that may influence genus composition (Mathers et al. 2023). For this reason, sampling was conducted during the dry season to reduce the influence of abrupt hydrological shifts and sudden chemical changes associated with intense rainfall, although occasional rain-induced effects may still occur. These unmeasured factors may help explain patterns that diverge from those reported for other aquatic assemblages, suggesting that additional drivers not accounted for in this study may influence PT genera in riffle habitats (Da Silva et al. 2021; Leal et al. 2023).

The cluster analyses revealed variation in biological similarity among riffle sections. The taxonomic dendrogram showed greater separation of 07PEM from the remaining sites, followed by 01PEM and 02PEM, whereas 04PEM and 06PEM showed the greatest similarity in genus composition. These patterns may reflect differences among local assemblages. Similarly, the FFG-based clustering indicated variation in FFG abundance structure among riffle sections, with 01PEM and 05PEM clustering together but remaining comparatively separated from the other sites. Although microhabitat variability can influence assemblage organization in lotic systems (Heino et al. 2015; Schneck et al. 2017), the environmental variables measured here did not significantly explain PT richness, overall taxonomic composition, or FFG structure.

Our hypothesis (ii) predicted that β -diversity among riffle sites would be dominated by genus replacement and was supported, as indicated by the high contribution of the replacement component ($\beta_{\text{repl}} = 0.614$). This pattern is consistent with ecological expectations for heterogeneous riffle habitats, where variation in hydraulic and substrate conditions may contribute to taxonomic replacement among sites (Heino et al. 2015; Schneck et al. 2017; Dey et al. 2024). Pairwise replacement was greatest between 01PEM and 07PEM, indicating marked differences in genus composition between these two riffle sections. The dominance of the replacement component nevertheless indicates that differences among riffle assemblages were driven primarily by changes in genus identity rather than by differences in genus richness.

The functional structure of PT assemblages reflected patterns reported for tropical and subtropical lotic systems (Schmitt et al. 2020). Predators were the most abundant functional feeding group (FFG), followed by shredders and filter feeders, whereas collector-filterers and scrapers were less represented. Predator dominance may be associated with the structural complexity of rocky lotic habitats, which can provide suitable conditions for predatory taxa (Bispo et al. 2004). Riffle microhabitats also provide conditions favorable to organisms associated with flowing water, including filter-feeding taxa that use suspended resources transported by the current (Schmitt et al. 2020). Genera recorded here, such as *Smicridea*, *Leptonema*, and *Chimarra*, are commonly associated with flowing-water habitats (Oliveira and Nessimian 2010). The comparatively low abundance of scrapers may reflect differences in resource availability and habitat conditions among riffle sections. In contrast, shredders were well represented in the assemblage, constituting the second most abundant FFG, indicating that this feeding strategy was an important component of the PT assemblages sampled in the Xingu riffles.

FFG-based β -diversity was substantial ($\beta_{\text{total}} = 0.744$) and was associated primarily with balanced variation in abundance ($\beta_{\text{bal}} = 0.431$), supporting hypothesis (iii). This type of reorganization in feeding-group abundance has been reported in lotic habitats (Miserendino et al. 2023), where variation in hydraulic and microhabitat conditions can influence the relative representation of different feeding strategies (Maasri et al. 2021; Leal et al. 2023). Thus, understanding variation in the taxonomic and FFG-based β -diversity of PT may contribute to the development of more targeted conservation strategies for riffle sections of Amazonian rivers. The predominance of genus replacement indicates that different riffle sections may contribute distinct components of PT diversity. Consequently, changes in flow regime, sediment dynamics, or substrate stability have the potential to alter riffle habitat conditions and, in turn, affect assemblage composition (Calapez et al. 2021; Pompeu et al. 2022). Given ongoing anthropogenic pressures in the Volta Grande region, maintaining habitat heterogeneity among riffle sections may therefore contribute to the conservation of PT taxonomic and functional diversity.

The absence of significant environmental effects in regression and dbRDA analyses suggests that unmeasured processes, such as biotic interactions or fine-scale hydraulic variation, may contribute to the replacement patterns observed among riffle sites (Suhaila et al. 2012). Because several of the recorded genera were predators, variation in prey availability may also have contributed to assemblage patterns. However, prey availability was not quantified in the present study, preventing us from separating potential trophic effects from those of abiotic habitat conditions. Overall, our results show substantial taxonomic and FFG variation among riffle sections of the Xingu River and highlight the importance of considering habitat heterogeneity when evaluating aquatic insect diversity in large tropical rivers.

5. Conclusions

This study expands current knowledge of PT assemblages in Amazonian riffle habitats by integrating taxonomic and functional feeding-group perspectives. Contrary to hypothesis (i), the environmental gradients measured in this study did not significantly explain PT genus richness, overall taxonomic

composition, or FFG abundance structure, indicating that the variables considered here were insufficient to account for the observed biological variation among riffle sections. Taxonomic β -diversity was primarily driven by genus replacement, supporting hypothesis (ii), whereas FFG-based β -diversity was mainly associated with balanced variation in abundance, supporting hypothesis (iii). Together, these results show that differences among riffle assemblages were expressed mainly through changes in genus identity and in the abundance structure of feeding groups rather than through simple differences in richness or directional abundance gradients. The maintenance of environmental heterogeneity among riffle sections may therefore be important for conserving PT diversity in the Volta Grande do Xingu. Future studies incorporating fine-scale hydraulic and habitat descriptors, biotic interactions, and temporal replication will be important for clarifying the processes underlying these patterns and for assessing the potential use of PT assemblages as indicators of environmental change in large Amazonian rivers.

Declarations

Competing Interests

The authors declare that they have no relevant financial or non-financial interests to disclose.

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Author Contribution

All authors contributed to the study conception and design. Data collection was performed by Alany Pedrosa Gonçalves, material preparation and analysis were performed by Eduarda Silva de Lima, Jaciane Correa, Ana Caroline Leal-Nascimento, Alany Pedrosa Gonçalves, and Karina Dias-Silva. The first draft of the manuscript was written by Karina Dias-Silva; Emilly Vieira Drosdosky, Iluany Silva da Costa and all the other authors commented, discussed and contributed to previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability

The data used in this study are available from the corresponding author upon request.

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Figures

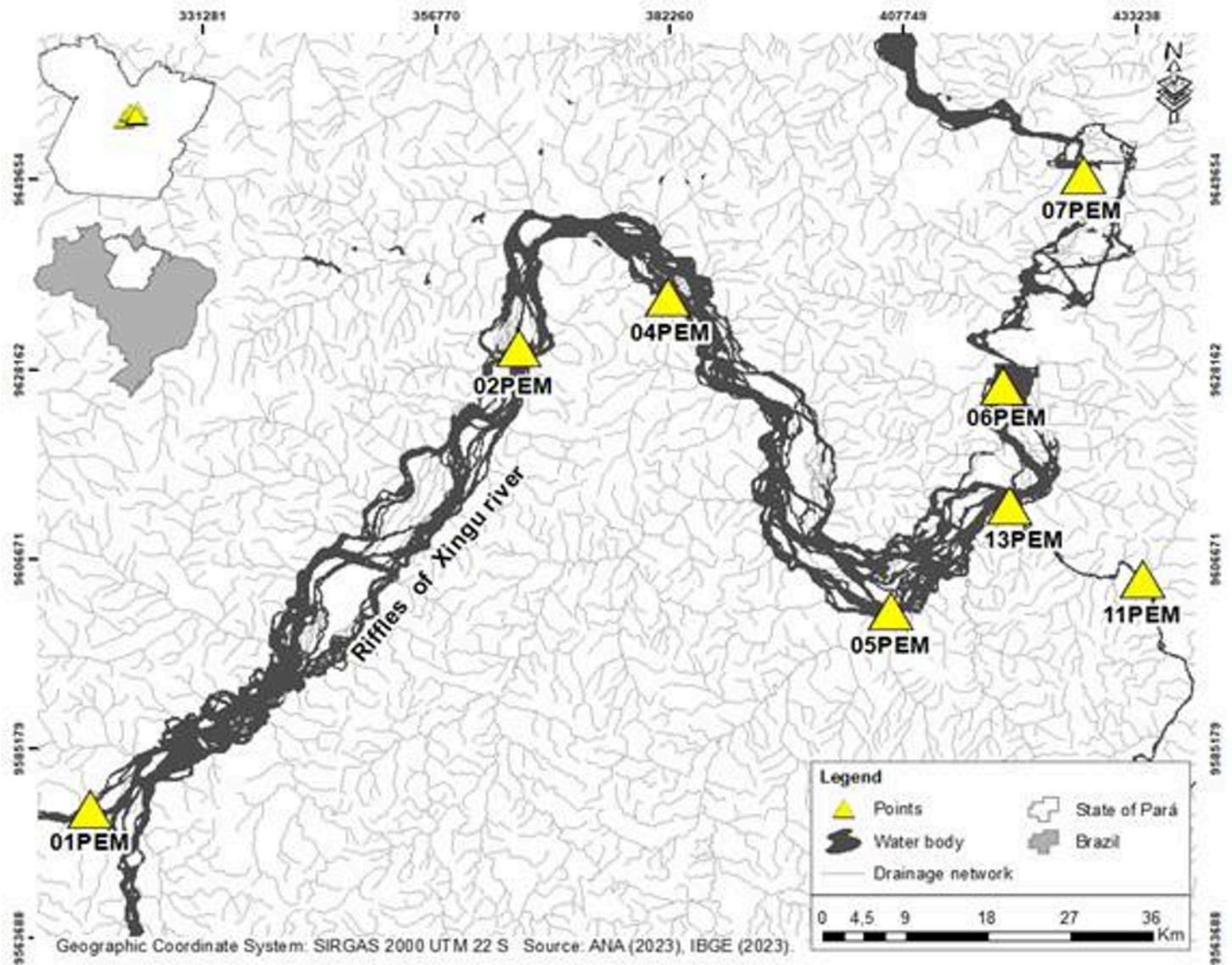


Figure 1

Locations where PT collections were made in the riffles of Xingu river

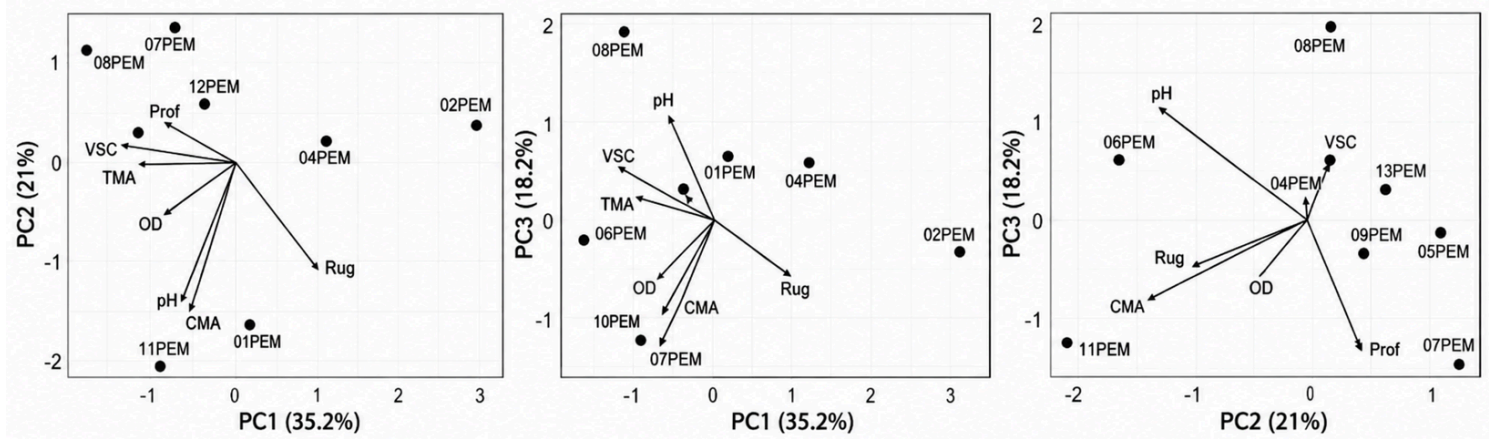


Figure 2

Principal component analysis of environmental variables measured at eight riffle sites in the Xingu River. The three components retained by the Kaiser-Guttman criterion accounted for 74.38% of the total environmental variation: (A) PC1 versus PC2, (B) PC1 versus PC3, and (C) PC2 versus PC3. Arrows indicate the direction and relative association of environmental variables with the ordination axes. Abbreviations: CMA = electrical conductivity; TMA = water temperature; OD = dissolved oxygen; VSC = surface current velocity; Prof = depth; and RUG= substrate roughness

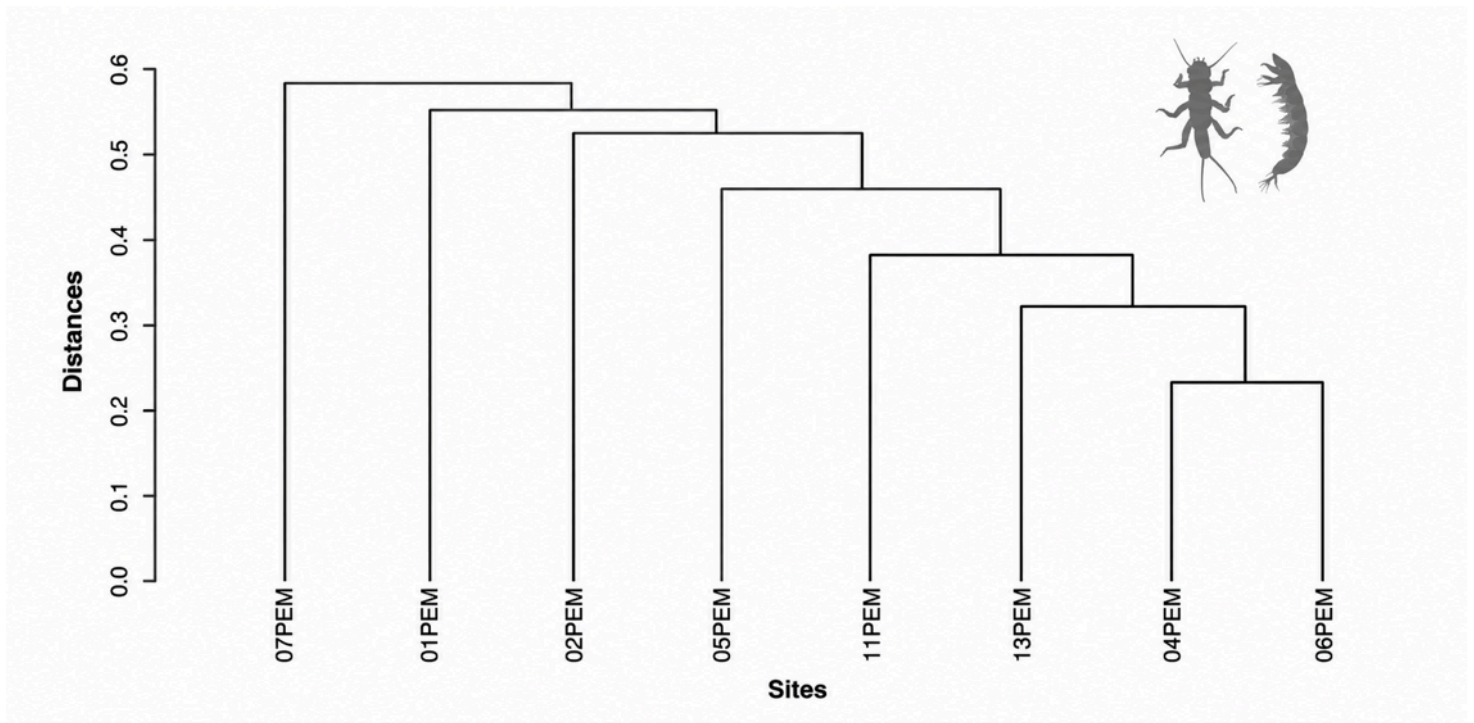


Figure 3

Hierarchical clustering of PT genus composition among riffle sites in the Xingu River based on Jaccard dissimilarity and UPGMA linkage

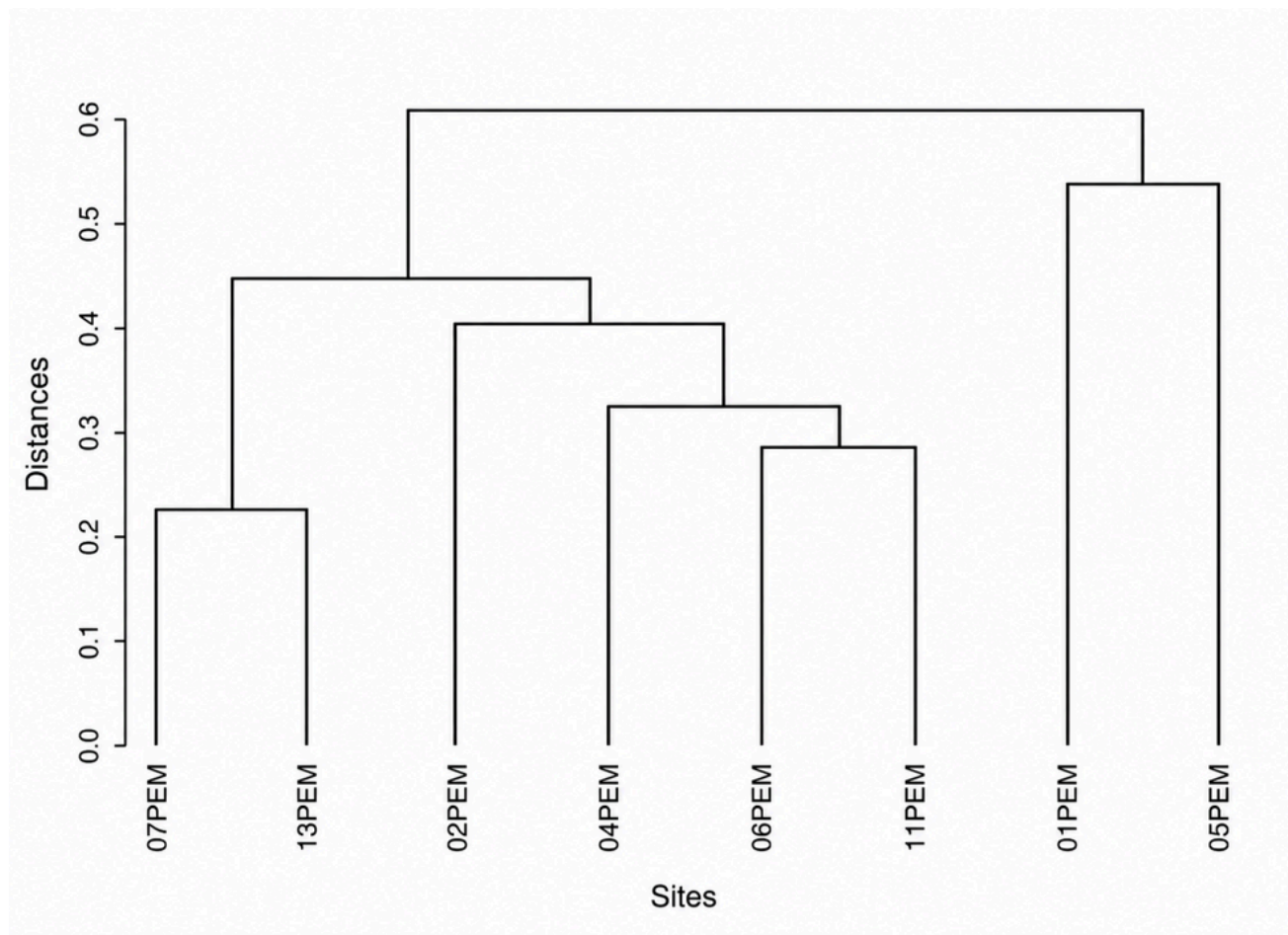


Figure 4

Hierarchical clustering of FFG abundance structure among riffle sites in the Xingu River based on Bray-Curtis dissimilarity and UPGMA linkage

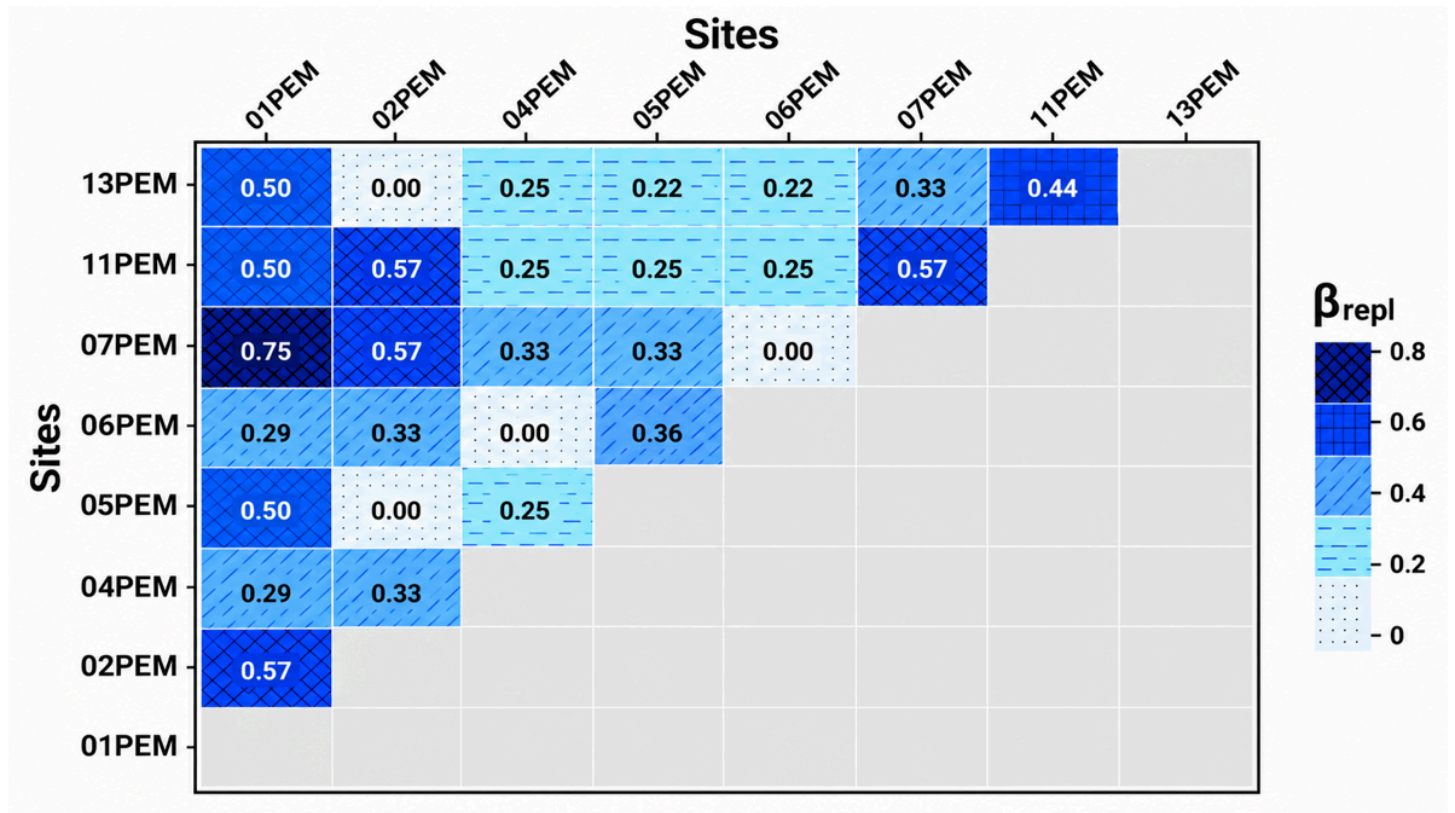


Figure 5

Pairwise taxonomic beta-diversity replacement among riffle sites in the Xingu River. β_{repl} = replacement component of beta diversity (Podani). Darker colors indicate higher genus replacement between site pairs, whereas lighter colors indicate lower replacement. Different texture patterns were added to distinguish value classes

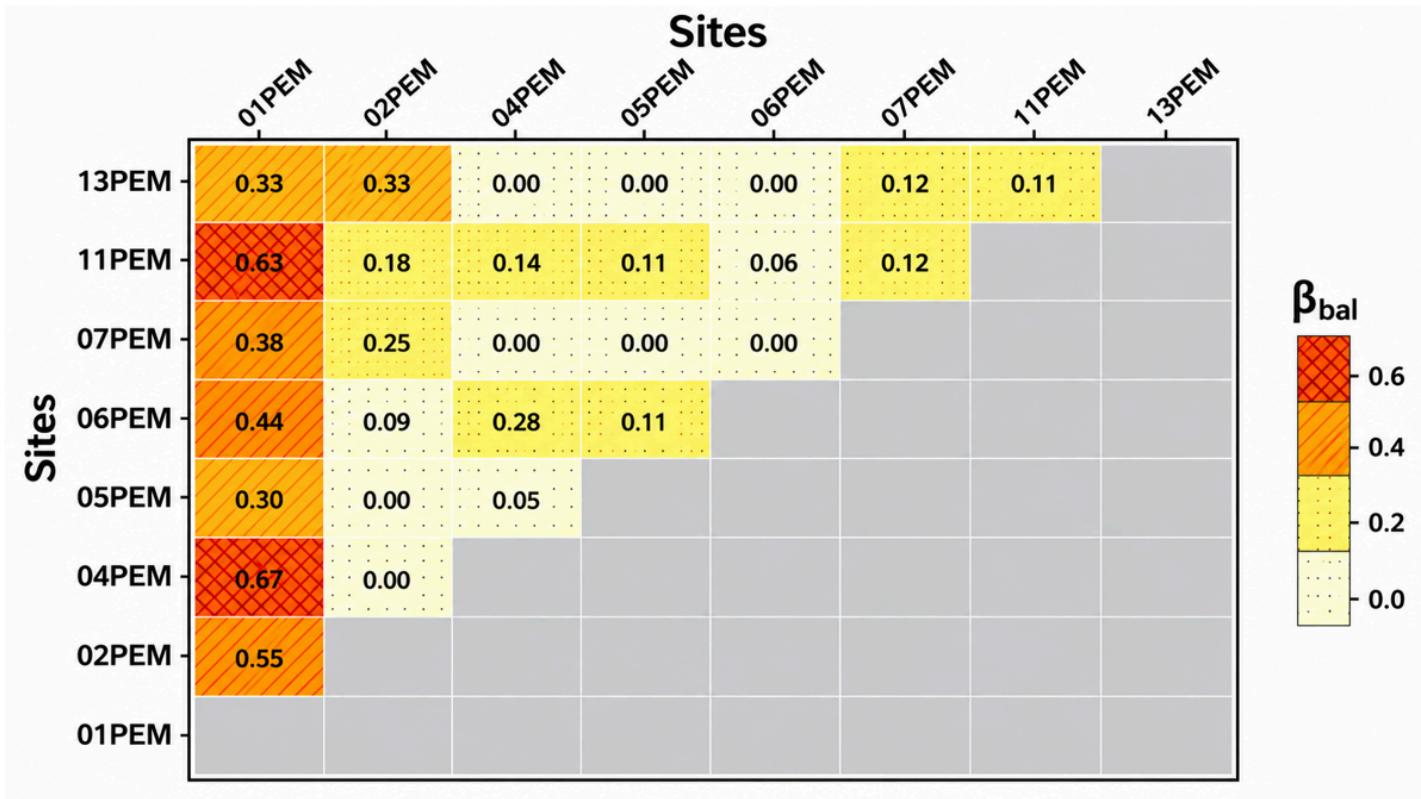


Figure 6

Pairwise functional β -diversity among riffle sites in Xingu River. β_{bal} represents the balanced abundance component of functional β -diversity (Baselga). Darker colors indicate greater proportional differences in the relative abundances of FFGs among sites, whereas lighter colors indicate more similar functional structures. Different texture patterns were added to distinguish value classes