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Ecological Structure of Fish Assemblages in the Colombian Piedemonte Llanero Region: Patterns of Diversity and Habitat Association in the Humea River Sub-basin

Estructura ecológica de los ensamblajes de peces en la región del Piedemonte Llanero colombiano: patrones de diversidad y asociación con el hábitat en la subcuenca del río Humea

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Abstract

The Llanero Piedmont of the Colombian Orinoco basin is a complex biogeographic transition zone characterized by high freshwater fish diversity and marked environmental heterogeneity. However, ecological information on fish assemblages in this region remains limited. We characterized fish assemblages in five rivers of the Humea River sub-basin to assess patterns of diversity, abundance, community composition, and their association with environmental variability. Sampling was conducted

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at 20 sites between May and October 2019, covering an altitudinal gradient from 357 to 1,100 m a.s.l. We recorded 3,866 individuals belonging to 50 species. Although some rivers exhibited high species richness, these assemblages were frequently dominated by a few widely distributed taxa, particularly *Knodus deuterodonoides*, *Hemibrycon metae*, and *Chaetostoma dorsale*. These differences may be primarily associated with variation in physical habitat characteristics, including channel dimensions, water velocity, and substrate composition. Our results indicate that fish assemblages in the Humea River sub-basin are structured primarily by spatial species turnover associated with habitat heterogeneity rather than by nested species loss. This pattern highlights the importance of maintaining habitat complexity and environmental heterogeneity across interconnected tributaries to conserve regional fish diversity in river systems of the Llanero Piedmont.

Keywords: Biodiversity, Habitat heterogeneity, Species dominance, Andean-Orinoco transition.

Resumen

El Piedemonte Llanero de la cuenca del Orinoco colombiano es una zona de transición biogeográfica compleja, caracterizada por una alta diversidad de peces de agua dulce y una marcada heterogeneidad ambiental. Sin embargo, la información ecológica sobre los ensamblajes de peces en esta región sigue siendo limitada. Caracterizamos los ensamblajes de peces en cinco ríos de la subcuenca del río Humea para evaluar los patrones de diversidad, abundancia, composición de las comunidades y su asociación con la variabilidad ambiental. El muestreo se realizó en 20 sitios entre mayo y octubre de 2019, cubriendo un gradiente altitudinal de 357 a 1.100 m s. n. m. Registramos 3.866 individuos pertenecientes a 50 especies. Aunque algunos ríos presentaron una alta riqueza de especies, estos ensamblajes estuvieron frecuentemente dominados por unos pocos taxones ampliamente distribuidos (particularmente *Knodus deuterodonoides*, *Hemibrycon metae* y *Chaetostoma dorsale*). Estas diferencias pudieron estar asociadas principalmente con la variación en las características físicas del hábitat, incluidas las dimensiones del canal, la velocidad del agua y la composición del sustrato. Los resultados indican que los ensamblajes de peces de la subcuenca del río Humea están estructurados principalmente por el reemplazo espacial de especies asociado con la heterogeneidad del hábitat, más que por la pérdida anidada de especies. Este patrón resalta la importancia de mantener la complejidad del hábitat y la heterogeneidad ambiental a lo largo de tributarios interconectados para conservar la diversidad regional de peces en los sistemas fluviales del Piedemonte Llanero.

Palabras clave: Biodiversidad, Heterogeneidad del hábitat, Dominancia de especies, transición Andino-Orinoco.

INTRODUCTION

The Piedemonte Llanero region, located in the eastern foothills of the Andes in Colombia, marks a biogeographic transition zone between the Andean highlands and the Orinoco lowlands and plays a crucial role in connecting upland and lowland aquatic systems. Its dynamic topography and climatic gradients give rise to a diverse mosaic of freshwater habitats that support high levels of ichthyological diversity and endemism (Barrios-Alonso et al., 2025; Moreno-Burbano et al., 2025). Riverine systems in the piedmont serve as ecological corridors, hosting structurally diverse fish assemblages shaped by habitat heterogeneity and hydrological complexity (Briceño et al., 1998; Usma et al., 2016).

Despite its ecological and conservation value, the fish fauna of the Colombian Llanos piedmont has been studied mostly through taxonomic surveys or regional checklists (Galvis et al., 2007; Urbano-Bonilla et al., 2009; Ramírez-Gil et al., 2011; Urbano-Bonilla et al., 2014; DoNascimento et al., 2017; Urbano-Bonilla et al., 2018; Zamudio et al., 2018; Cortés-Hernandez et al., 2023; Ramírez-Gil et al., 2023; Barrios-Alonso et al., 2025; Moreno-Burbano et al., 2025). Ecological surveys into community structure remain scarce (Briceño, 2015; Urbano-Bonilla et al., 2014; Urbano-Bonilla et al., 2018; Cortés-Hernandez et al., 2023; Ramírez-Gil et al., 2023), particularly within the piedmont zone. Moreover, existing studies often lack integrative frameworks that account for spatial heterogeneity or compare assemblages across nested hydrographic units, such as sub-basins.

Understanding how species richness, evenness, and composition vary across piedmont river systems, and how they respond to environmental gradients, is important for characterizing patterns of freshwater fish diversity and community structure. In particular, the use of diversity frameworks incorporating species dominance and turnover remains largely unexplored in this region, despite their wide application in Neotropical freshwater systems. These gaps are pressing considering the increasing anthropogenic pressures on piedmont rivers, including agricultural expansion, deforestation, mining, and biotic homogenization (Van Ausdal, 2009; Machado-Allison et al., 2010; Gutiérrez et al., 2012; Briceño, 2015; Lasso et al., 2016; Zamudio & Maldonado-Ocampo, 2022). Understanding and protecting fish diversity in piedmont river systems is crucial for maintaining the ecological integrity of these freshwater ecosystems, highlighting the value of studies that characterize how fish diversity is structured across environmental gradients.

In this study, we characterize fish assemblages in five rivers of the Humea sub-basin (Cundinamarca), a representative piedmont system within the upper Orinoco basin in Colombia. We aim to describe patterns of ichthyofaunal diversity, composition, and dominance across these rivers and to explore how these patterns are influenced by environmental variability.

MATERIAL AND METHODS

Study area

We conducted fieldwork in the municipality of Medina (Cundinamarca, Colombia), situated in the Piedemonte Llanero, a transitional area between the eastern Andean foothills and the Orinoquía region (Figure 1, Table S1). Sampling took place between May and October 2019, covering an altitudinal range from 357 to 1,100 m a.s.l. We surveyed 20 localities distributed across five streams: Gazaduje, Gazaguán, Gazamumo, Gazaunta, and Humea rivers. The sampling localities were selected to provide broad spatial coverage of the study area and to capture variation in altitude and local environmental conditions among the five rivers. The rivers surveyed are characterized by heterogeneous habitats, alternating riffles, runs, and pools with variable channel morphology. Substrates include predominantly rocks, cobbles, gravel, and sand. These characteristics generate a diverse mosaic of aquatic microhabitats, with differences in water depth, flow conditions, and substrate type occurring along the sampled reaches.

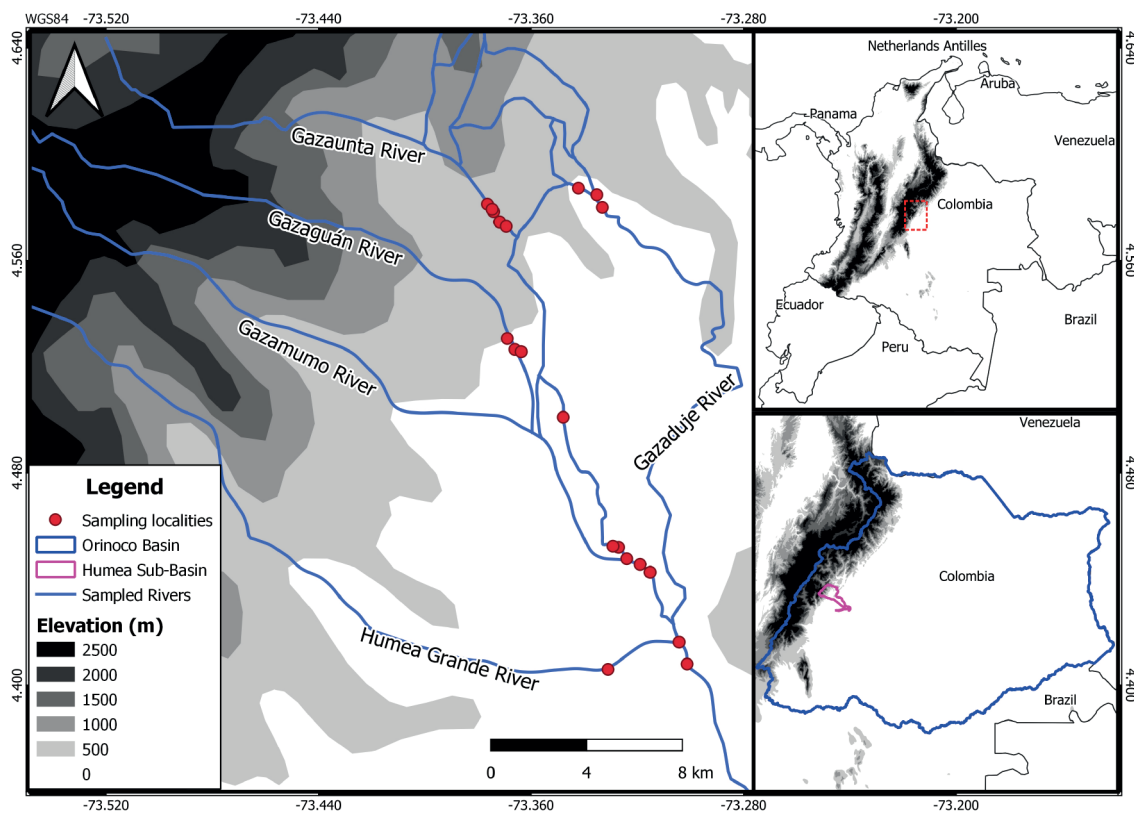


Figure 1. Study area and sampling sites ($n = 20$) in the Humea Sub-Basin, Medina (Cundinamarca, Colombia) across five rivers: Gazaduje, Gazaguán, Gazamumo, Gazaunta, and Humea at the Orinoco Basin.

Figura 1. Área de estudio y sitios de muestreo ($n = 20$) en la subcuenca del río Humea, Medina (Cundinamarca, Colombia), abarcando cinco ríos: Gazaduje, Gazaguán, Gazamumo, Gazaunta y Humea, pertenecientes a la cuenca del Orinoco.

Sampling and specimen processing

We collected the fish using an electrofishing technique with three depletion passes at each site (Lobón-Cerviá, 1991; Sostoa et al., 2005; Zippin, 1958; Lockwood and Schneider, 2000). To estimate sampling constancy, we established a fixed protocol applied at all sites. This included: (1) using the same electrofisher and generator; (2) maintaining a fixed voltage range (500–700 V); (3) working with the same number of operators and roles; (4) sampling stream sections of equal length; and (5) applying the same duration of active sampling. During sampling, we swept the anode upstream to immobilize fish, which were then captured manually using hand nets.

Captured specimens were anesthetized with eugenol (300 mg/L) following ethical guidelines for fish euthanasia (AVMA, 2020). They were then fixed in formalin (10%) for 48 hours and subsequently transferred to ethanol (70%) for preservation. Specimens were deposited in the Ichthyology Collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN-MHN). Specimen identifications were performed using specialized taxonomic literature and original species descriptions (Taphorn, 2003; Van der Sleen & Albert, 2018). We followed updated taxonomic classifications according to Thomaz et al. (2015), Mirande et al. (2018), and Van der Sleen & Albert (2018) for Characidae, and Fricke et al. (2026) and DoNascimento et al. (2024) for other fish families.

At each sampling site, we characterized habitat structure by measuring stream channel morphology, substrate composition, and water velocity to assess their relationships with fish diversity (Simonson et al., 1994; Bain & Stevenson, 1999; Gordon et al., 2004). We measured wetted width and depth along perpendicular transects every 10 meters across the channel (covering its total width) and estimated total sampled area by summing the cross-sectional transect surfaces (Simonson et al., 1994). Depth was measured at one-meter intervals along each transect using a calibrated cylindrical probe. At the same points, we visually estimated substrate composition based on particle size, categorized it as silt, sand, fine gravel, coarse gravel, cobble, or rock, and averaging the values for each sampling area (Bain & Stevenson, 1999). For each point, we assigned estimated percentage values summing to 100% across substrate categories (Bain & Stevenson, 1999). Then, we calculated the average percentage of each substrate type across all sampling points at the site. Water velocity was estimated using a float method: a custom-built hydrodynamic float with adjusted volume and mass was released, and the time to traverse a 10-meter section was recorded (Gordon et al., 2004).

Data analysis

Sampling completeness was evaluated using individual-based rarefaction–extrapolation analyses based on Hill numbers with 500 bootstrap resampling to estimate 95% confidence intervals (CI). We quantified diversity as Hill numbers representing species richness (q_0), Shannon diversity (q_1), and Simpson diversity (q_2) using the *iNEXT* package (Chao et al., 2014; Hsieh et al., 2016). In addition, coverage-based rarefaction–extrapolation analyses for species richness (q_0) were performed separately for each river. Sample coverage was used as a measure of inventory completeness, allowing comparisons among rivers. To emphasize sampling completeness rather than projected richness, only the rarefaction component of the coverage-based curves was presented.

We assessed dominance and community structure by generating rank–abundance curves using the *rankabuncomp* function in the *BiodiversityR* package (Kindt, 2025). Species abundance was organized by river, and the most abundant species were used to evaluate richness, evenness, and dominance patterns among locations. Plots were generated using *ggplot2* (Wickham, 2009) and annotated using *ggrepel* to improve label readability. Abundance data were log-transformed ($\text{Log}_{10}[x]$) to improve interpretability.

We estimated fish diversity in each river by calculating Simpson's ($D = 1/\sum P_i^2$) and Shannon-Wiener ($H' = -\sum P_i \ln p_i$) indices, where P_i represents the relative abundance of species i . Calculations were performed in the software PAST v4.03 (Hammer et al., 2001). To facilitate comparisons among communities, we transformed these indices into Hill numbers following Chao et al. (2014): species richness (q_0), the exponential of the Shannon index (q_1 : $D = \exp[H']$), and the inverse of Simpson's index (q_2 : $D = 1/\sum P_i^2$). These metrics provided a unified framework for interpreting diversity in terms of species richness, common species, and dominant species.

In addition, we examined patterns of beta diversity among rivers using Non-metric Multidimensional Scaling (NMDS) based on Bray–Curtis dissimilarities calculated from log-transformed fish density matrices ($\text{Log}_{10}[x + 1]$). This transformation reduces the disproportionate influence of dominant species and stabilizes variance across sites containing zero values. The optimal dimensionality for the ordination was evaluated using a broken-stick model, which supported a three-dimensional solution ($k = 3$). NMDS analyses were implemented using the *vegan* package (Oksanen et al., 2019) with 100 random starts to ensure a stable configuration. Site scores from the final NMDS solution were plotted for the first two axes, and group structure was visually assessed using convex hulls drawn around sites belonging to the same river.

To statistically evaluate differences in community composition among rivers, we applied a permutational multivariate analysis of variance (PERMANOVA) using Bray–Curtis distances and 999 permutations. Before interpreting PERMANOVA results, we tested the assumption of multivariate homogeneity of dispersion, which allowed us to distinguish location effects (differences in centroid position) from differences in group dispersion.

We further quantified the components of beta diversity following the abundance-based decomposition (Baselga, 2010). For this analysis, we used the untransformed species density matrix to avoid distortion of relative abundance structures. Beta diversity was partitioned into three components using the *betapart* package (Baselga & Orme, 2012): (1) total Bray–Curtis dissimilarity, (2) the balanced variation in species abundances, which reflects reciprocal changes in abundance between sites, and (3) the abundance gradient component, which captures nested differences caused by directional loss or gain of individuals across assemblages. Pairwise dissimilarities were calculated for all site combinations, together with the proportion of total dissimilarity explained by balanced variation and abundance gradients. To evaluate spatial patterns, we compared within-river and between-river dissimilarities to distinguish whether beta diversity was primarily driven by abundance replacement (balanced variation) or by nestedness-like gradients in total abundance.

We evaluated the relationships between fish assemblage structure and environmental gradients using Canonical Correspondence Analysis (CCA), based on a log-transformed species density matrix ($\text{Log}_{10}[x + 1]$). Analyses were performed using the *vegan* package (Oksanen et al., 2019). Canonical axes were interpreted according to their eigenvalues and the proportion of explained variance, retaining the first two canonical axes. Environmental variables showing the strongest correlation with the canonical axes were considered the principal drivers of assemblage structure (Lepš & Šmilauer, 2021). All statistical analyses and figures were generated in R v4.2.3 (R Core Team, 2023).

RESULTS

A total of 3,866 individuals representing 50 fish species were recorded across the 20 sampling sites (Table S3). Sampling completeness was high for the pooled dataset, reaching an estimated sample coverage of 99.8% (Figure 2A). Abundance-based rarefaction–extrapolation analyses indicated that effective diversity was nearly asymptotic for common and dominant species, with observed and estimated values differing only marginally. In contrast, species richness (q_0) remained below the asymptotic estimate (50 observed vs. 70.99 estimated), indicating that additional sampling would be expected to primarily increase the detection of rare species.

Despite differences in the number of individuals collected among rivers, sampling coverage exceeded 98% in all cases, supporting comparable sampling completeness across the five assemblages (Figure 2B).

The rank-abundance curves (Figure 3) reveal distinct patterns of species dominance and richness across river systems. All assemblages exhibit a typical pattern of low evenness, with a few dominant species (*Knodus deuterodonoides*, *Hemibrycon metae*, and *Chaetostoma dorsale*) accounting for most individuals, followed by a long tail of rarer taxa. This pattern is most pronounced in the Gazamumo River, where the steepest curve suggests a strong dominance by a few species and lower relative abundance of subordinate taxa.

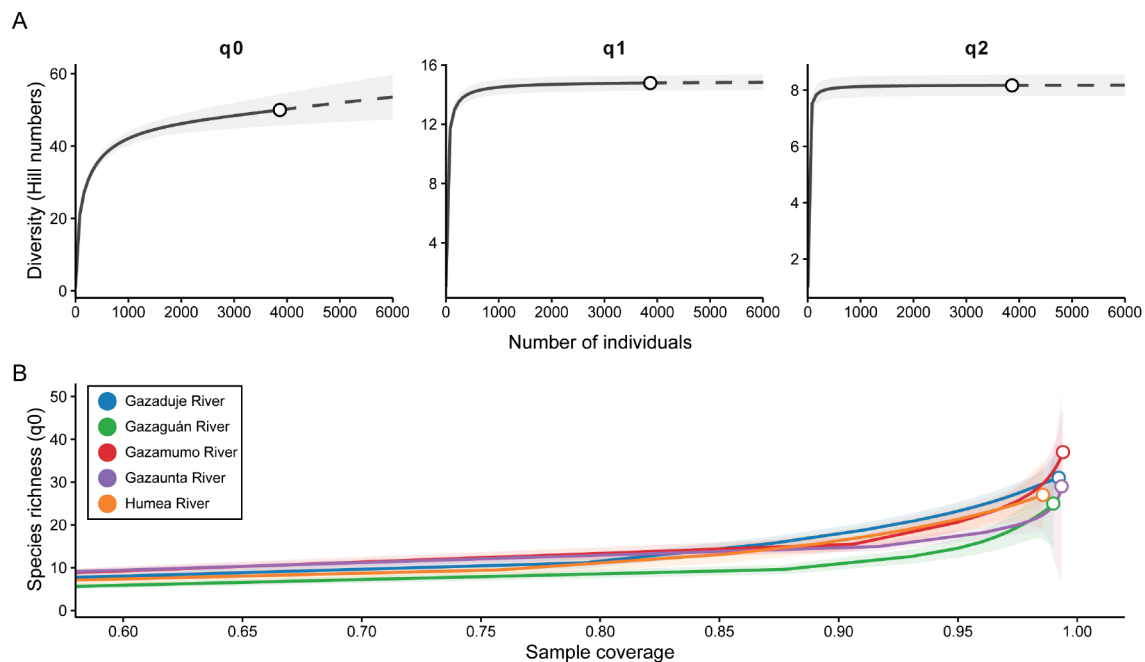


Figure 2. Sampling completeness of fish assemblages in the study area. (A) Individual-based rarefaction–extrapolation curves for species richness (q_0), Shannon diversity (q_1), and Simpson diversity (q_2) for all 20 sampling sites. Solid lines represent rarefaction, dashed lines represent extrapolation, shaded areas indicate 95% bootstrap confidence intervals, and open circles denote the observed sampling effort. (B) Coverage-based rarefaction curves for species richness (q_0) for each river, showing the high sampling completeness achieved across assemblages. Open circles indicate the observed sample coverage, and shaded areas represent 95% bootstrap confidence intervals.

Figura 2. Completitud del muestreo de los ensamblajes de peces en el área de estudio. (A) Curvas de rarefacción y extrapolación basadas en individuos para la riqueza de especies (q_0), la diversidad de Shannon (q_1) y la diversidad de Simpson (q_2) en los 20 sitios de muestreo. Las líneas continuas representan la rarefacción, las líneas discontinuas representan la extrapolación, las áreas sombreadas indican los intervalos de confianza del 95 % mediante bootstrap y los círculos vacíos señalan el esfuerzo de muestreo observado. (B) Curvas de rarefacción basadas en la cobertura para la riqueza de especies (q_0) en cada río, que muestran la alta completitud de muestreo lograda en los distintos ensamblajes. Los círculos vacíos indican la cobertura de muestreo observada, y las áreas sombreadas representan los intervalos de confianza del 95 % mediante bootstrap.

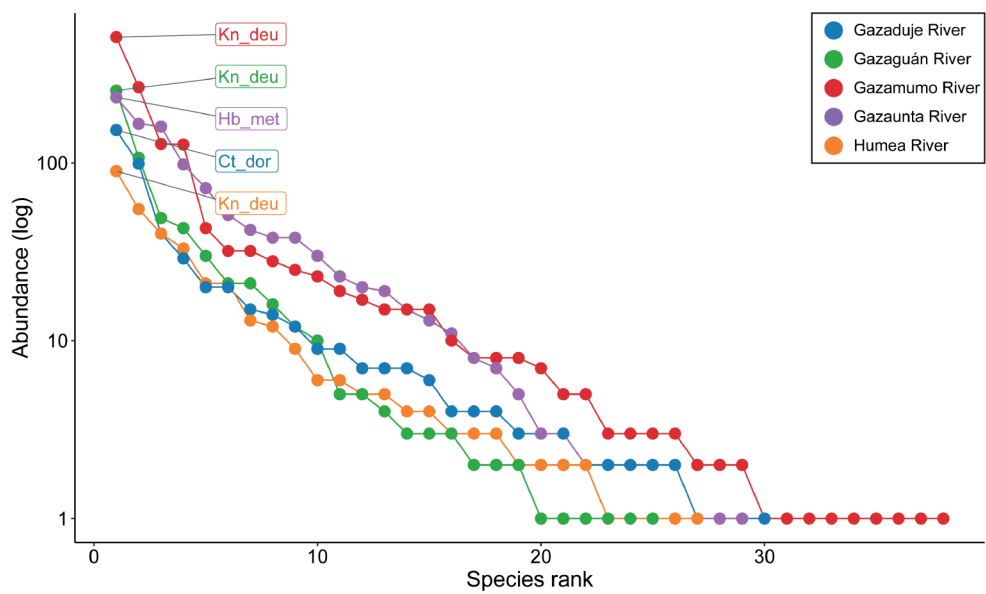


Figure 3. Rank-abundance curves of fish assemblages in the five rivers of the Humea River sub-basin, showing patterns of species dominance. Dominant taxa—*Knodus deuterodonoides* (Kn_deu), *Hemibrycon metae* (Hb_met), and *Chaetostoma dorsale* (Ct_dor)—are highlighted, illustrating consistent patterns across sites.

Figura 3. Curvas de rango-abundancia de los ensamblajes de peces en los cinco ríos de la subcuenca del río Humea, que muestran patrones de dominancia de especies. Se destacan los taxones dominantes —*Knodus deuterodonoides* (Kn_deu), *Hemibrycon metae* (Hb_met) y *Chaetostoma dorsale* (Ct_dor)—, ilustrando patrones consistentes entre los sitios.

Variation in dominance and evenness among rivers reflects spatial heterogeneity in community structure, potentially driven by differences in habitat conditions or localized ecological processes. The recurrent dominance of the same three species across all systems suggests broad environmental tolerance and potential competitive advantages, underscoring their ecological importance in piedmont river fish assemblages.

Alpha diversity patterns across rivers revealed contrasting community structures, reflecting differences in evenness and species dominance (Table 1).

Table 1. Fish abundance and Hill diversity numbers (q0 = species richness, q1 = common species, and q2 = dominant species) for the five analyzed rivers of the Humea River sub-basin.

Tabla 1. Abundancia de peces y números de diversidad de Hill (q0 = riqueza de especies, q1 = especies comunes y q2 = especies dominantes) para los cinco ríos analizados de la subcuenca del río Humea.

Individuals	Individuals	q0	q1	q2
Gazaduje	482	30	11.01	1.19
Gazaguán	599	25	7.45	1.30
Gazamumo	1374	38	9.17	1.25
Gazaunta	1065	29	12.15	1.13
Humea	346	27	11.99	1.15

Although the Gazamumo River displayed the highest species richness, its relatively lower diversity of common and dominant species suggests a strong prevalence of a few taxa, indicative of low evenness. In contrast, Gazaunta and Humea rivers harbored more balanced assemblages, with higher effective numbers of common and dominant species, despite slightly lower richness. Gazaguán River exhibited the most skewed structure, with low evenness and marked dominance, while the Gazaduje River showed intermediate values across metrics, suggesting a moderately structured assemblage.

The NMDS ordination revealed clear compositional differences among rivers (Figure 4A). Sites from each river tended to form distinct clusters, indicating non-random structuring of assemblages at the basin scale, with the Gazaunta River showing the most pronounced separation from the remaining rivers along the first two NMDS axes. Overall stress was low (0.075), and fit diagnostics indicated a high-quality ordination (non-metric $R^2 = 0.994$; linear $R^2 = 0.955$). PERMANOVA revealed significant compositional differences in fish communities among rivers ($F = 2.04$, $R^2 = 0.35$, $p = 0.002$), indicating spatial variation in assemblage structure. However, groups also differed in their multivariate dispersion ($F = 4.09$, $p = 0.028$), suggesting that part of the variation between rivers reflects differences in within-river heterogeneity. Overall, compositional dissimilarity across sites was high, with a median Bray-Curtis dissimilarity of 0.735.

The abundance-based decomposition of beta diversity revealed contrasting patterns of community heterogeneity (Figure 4B-C). Balanced variation in species abundances (β BAL) was the dominant component of Bray-Curtis dissimilarity, with between-river comparisons showing the highest median values (Figure 4B). In contrast, none of the rivers exhibited within-group medians exceeding the average β BAL, indicating that species-abundance replacement is stronger between rivers than within them. On the other hand, the abundance-gradient component (β GRA) showed consistently low medians for most rivers (Figure 4C); only the Gazamumo River displayed a median above the global mean. This pattern suggests that nestedness-like gradients contribute relatively little to overall dissimilarity, except for a moderate contribution in the Gazamumo River. The generally low β GRA values further indicate that directional gains or losses of individuals across sites are not the primary driver of beta diversity in the basin. Together, these patterns indicate that differences among rivers are characterized mainly by reciprocal changes in species abundances, whereas within-river assemblages tend to be more compositionally homogeneous and exhibit limited abundance gradients.

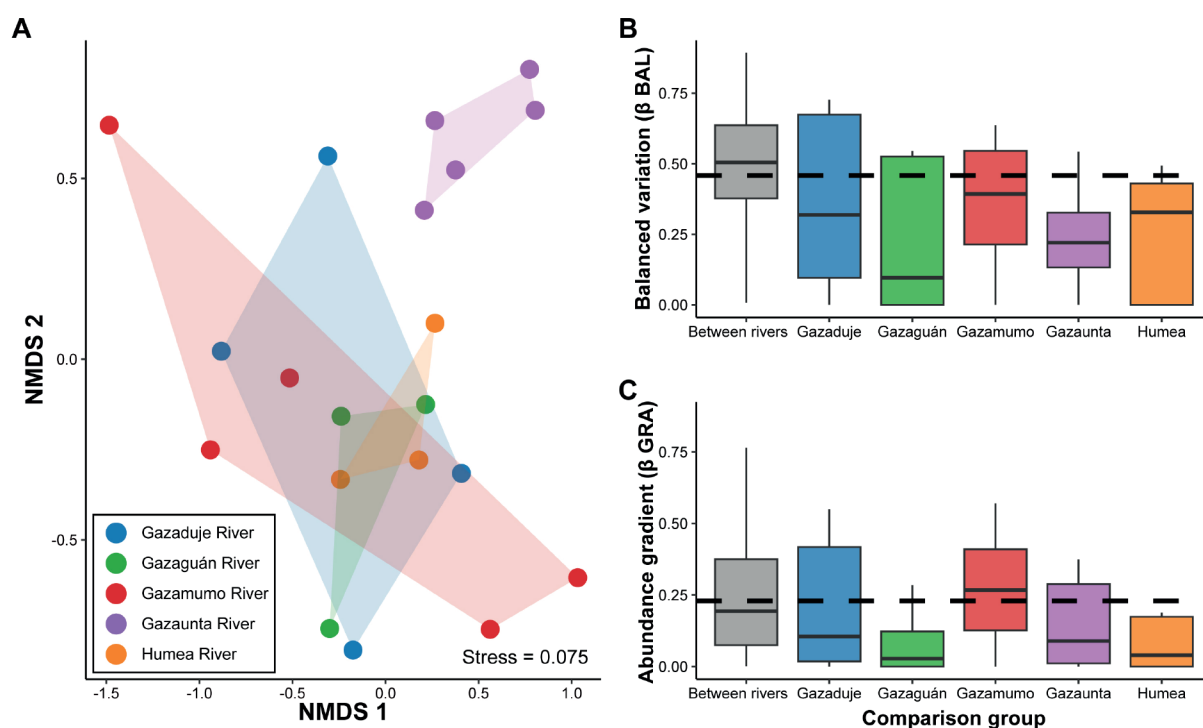


Figure 4. Differences in fish assemblage composition and abundance-based beta diversity among rivers of the Humea River sub-basin. (A) NMDS ordination based on Bray–Curtis dissimilarities. Points represent individual sampling sites and convex hulls delineate the multivariate dispersion of sites within each river. (B) Boxplots of the balanced variation component (β BAL) comparing within-river dissimilarities (colored boxes) and between-river dissimilarities (grey). (C) Boxplots of the abundance gradient component (β GRA) for the same comparison groups. Dark dashed horizontal line in B and C represents the overall mean across all pairwise comparisons.

Figura 4. Diferencias en la composición de los ensamblajes de peces y en la diversidad beta basada en la abundancia entre los ríos de la subcuenca del río Humea. (A) Ordenación NMDS basada en las disimilitudes de Bray-Curtis; los puntos representan los sitios de muestreo individuales y las envolventes convexas delimitan la dispersión multivariante de los sitios dentro de cada río. (B) Diagramas de caja del componente de variación equilibrada (β BAL) que comparan las disimilitudes dentro de los ríos (cajas de colores) y las disimilitudes entre ríos (gris). (C) Diagramas de caja del componente de gradiente de abundancia (β GRA) para los mismos grupos de comparación. La línea horizontal discontinua oscura en B y C representa la media general de todas las comparaciones por pares.

The Canonical Correspondence Analysis (CCA) revealed a strong association between fish assemblage composition and physical habitat characteristics related to channel dimensions, water velocity and substrate composition (Figure 5; see Table S3 for species abbreviations). The first two canonical axes explained 53.1% of the total variation, with the first axis reflecting a primary physical gradient separating localities characterized by larger channel dimensions (width and depth) and higher water velocity, associated with coarse substrate types such as sand and gravel, from sites dominated by fine gravel and rock substrates. The second axis further structured species occurrences along a gradient of substrate coarseness, mainly driven by coverage of cobble.

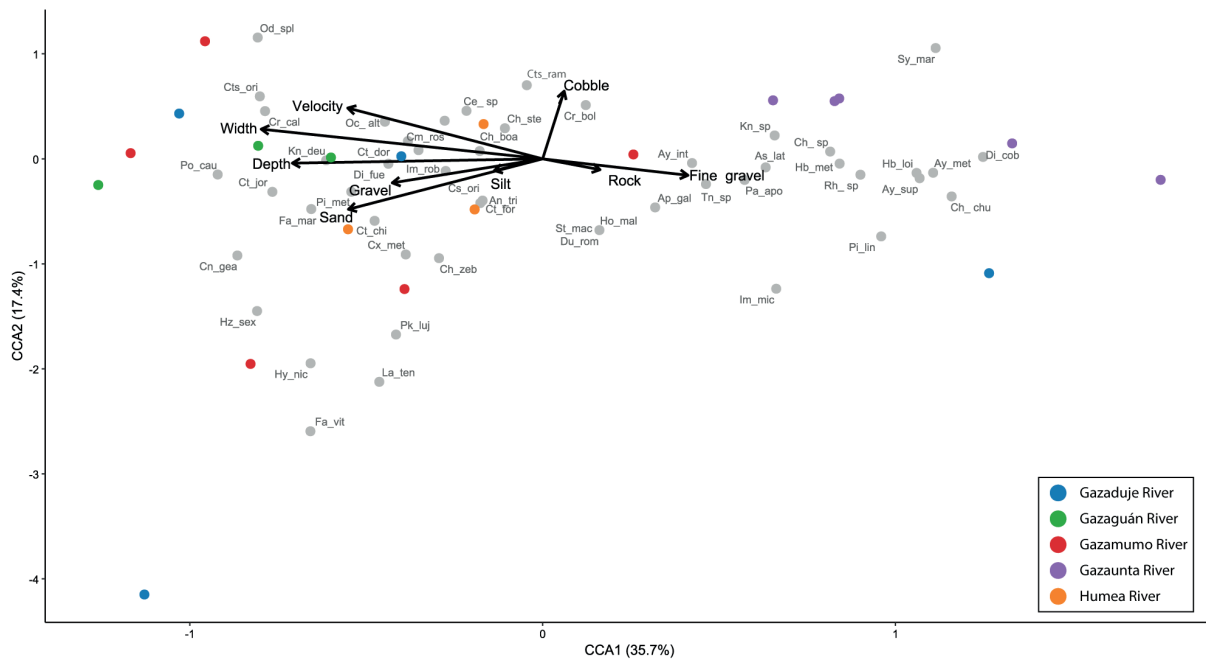


Figure 5. Canonical Correspondence Analysis (CCA) showing relationships between fish assemblages in relation to environmental variables in the five rivers of the Humea River sub-basin. Gray points denote species scores, indicating their distribution along the constrained environmental gradients. Black arrows represent environmental variables, with arrow direction indicating the direction of increasing values and arrow length reflecting the relative strength of each variable's association with assemblage structure.

Figura 5. Análisis de Correspondencia Canónica (CCA) que muestra las relaciones entre los ensamblajes de peces y las variables ambientales en los cinco ríos de la subcuenca del río Humea. Los puntos grises representan las puntuaciones de las especies, indicando su distribución a lo largo de los gradientes ambientales restringidos. Las flechas negras representan las variables ambientales; la dirección de la flecha indica el sentido de los valores crecientes y su longitud refleja la fuerza relativa de la asociación de cada variable con la estructura del ensamblaje.

The spatial distribution of sampling sites along these physical gradients highlighted distinct patterns across rivers. All localities from the Gazaunta and Gazaguán rivers clustered within a narrow region of the ordination space, reflecting relatively uniform physical channel dimensions and substrate conditions. In contrast, sites from Gazaduje and Gazamumo rivers displayed broader dispersion along CCA1 and CCA2, reflecting higher local heterogeneity in substrate composition and channel hydraulics. Localities from the Humea River occupied intermediate positions in the ordination, consistent with mixed substrate conditions.

DISCUSSION

The taxonomic composition of fish assemblages in the Humea River sub-basin was dominated by Characiformes and Siluriformes (Table S3), particularly within Characidae and Loricariidae families. This pattern aligns with previous reports across Colombian Orinoco sub-basins (e.g., Galvis et al., 2007; Urbano-Bonilla et al., 2014; Cortés-Hernández et al., 2023) and reflects historical biogeographic dispersal dynamics alongside the high ecomorphological versatility of these lineages (Albert et al., 2011; Carvajal-Quintero et al., 2015).

Despite shared taxonomic orders, abundance distributions across rivers revealed marked asymmetries in community structure (Figure 3). While observed species richness was moderately high across sites, effective diversity dropped drastically when incorporating relative abundances (Table 1). Such decline across all rivers highlights assemblages hyper-dominated by very few species; however, the identity of these dominant taxa shifted geographically: *K. deuterodonoides* dominated the Gazamumo, Gazaguán, and Humea rivers, whereas main dominance shifted to *H. metae* in Gazaunta and *C.* in Gazaduje rivers (Figure 3), resembling patterns observed in adjacent Orinoco tributaries (Ramírez-Gil et al., 2023; Barrios-Alonso et al., 2025; Becerra-Infante, et al., 2025) where different species of the genus *Knodus* domine the assemblages in the basin.

These shifts in dominant species explain the primary mechanism underlying spatial differentiation across the sub-basin (Figure 4). The partitioning of beta diversity demonstrated that dissimilarity among rivers was driven by balanced variation in abundance (turnover) rather than abundance gradients (nestedness). This turnover was primarily propelled by the spatial replacement of dominant taxa across rivers alongside the localized occurrence of less abundant species, consistent with patterns described in adjacent Orinoco sub-basins (Becerra-Infante et al., 2025). Instead of representing degraded subsets of a single regional species pool, these rivers harbor ecologically distinct assemblages characterized by spatial species replacement, particularly in the Gazaunta river, which presented the most dissimilar assemblage in the study area.

The species turnover was strongly associated with local physical habitat structure (Figure 5). Species possessing specialized benthic morphology or hydrodynamically streamlined bodies (such as *Chasmocranus rosae*, *C. dorsale*, *Dolichancistrus fuessli*, and *Creagrutus bolivari*) were positioned along faster-flowing reaches with coarse substrates, whereas taxa like *Pimelodella metae* and *Astyanax integer* associated with lower water velocities and finer sediments exhibiting a non-random distribution of species along these habitat gradients (Jackson et al., 2001; Leitão et al., 2007).

Although unmeasured physicochemical water properties (e.g., temperature, dissolved oxygen) and seasonal fluctuations may further modulate these relationships, our findings underscore the key role of physical habitat heterogeneity in driving microhabitat segregation and species coexistence (Jackson *et al.*, 2001; Walters *et al.*, 2003).

Overall, fish diversity in piedmont streams of the Humea River sub-basin is structured through spatial species turnover regulated by physical habitat heterogeneity rather than nested species loss. Because species replacement drives community dissimilarity across the landscape, conservation strategies in these systems cannot rely on protecting isolated stream reaches. Preserving regional fish diversity requires maintaining physical habitat complexity and heterogeneity (specifically variations in current velocity, channel morphology, and substrate composition) across the entire network of interconnected tributaries.

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AUTHOR CONTRIBUTIONS

VMB, and DGM contributed to the conceptualization and design of the project, participated in fieldwork and data analysis, validated the results, created visualizations, and drafted the manuscript. NFE contributed to the conceptual design, data analysis, validation, visualization, and manuscript drafting. VMB and NFE jointly supervised the work. JIM contributed to the conceptual design, participated in fieldwork, provided resources, and supervised the study. All authors contributed to reviewing and editing the manuscript.

CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

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SUPPLEMENTARY MATERIAL

Table S1. Geographic location of the 20 sampling sites and sampled area.**Tabla S1.** Ubicación geográfica de los 20 puntos de muestreo y área muestreada.

Sub-basin	River	Locality	Geographic coordinates	Area (m ²)
Humea	Gazaduje	Gazaduje River	04°35'03.4"N – 73°20'03.9"W	179.0
		Gazaduje River	04°35'07.1"N – 73°20'33.2"W	190.0
		Quebrada La Colorada	04°27'10.8"N – 73°19'31.5"W	227.3
		Gazaduje River	04°34'53.16"N – 73°19'51.14"W	241.3
	Gazaguán	Gazaguán River	04°31'50.1"N – 73°22'08.5"W	795.0
		Gazaguán River	04°31'35.3"N – 73°21'57.9"W	266.3
		Gazaguán River	04°31'32.20"N – 73°21'49.39"W	119.1
	Gazamumo	Caño Gazaine	04°27'10.8"N – 73°19'31.5"W	287.0
		Gazamumo River	04°26'43.8"N – 73°19'08.1"W	189.0
		Caño Busaca	04°30'03.4"N – 73°20'52.5"W	147.5
		Caño Gazaine	04°27'1.19"N – 73°19'21.15"W	292.5
		Gazamumo River	04°26'33.17"N – 73°18'54.62"W	257.5
	Gazaunta	Gazaunta River	04°34'20.1"N – 73°22'19.7"W	225.9
		Caño jején	04°34'41.9"N – 73°22'41.4"W	170.0
		Caño Choopal	04°34'8.84"N – 73°22'7.09"W	259.5
		Quebrada Jején	04°34'31.75"N – 73°22'28.67"W	115.0
		Quebrada Jején	04°34'31.10"N – 73°22'30.26"W	102.3
		Caño Choopal	04°24'30.1"N – 73°18'28.4"W	202.4
	Humea	Caño Choopal	04°24'20.92"N – 73°18'13.96"W	138.8
		Caño Sudio	04°24'21.47"N – 73°19'51.58"W	180.4

Table S2. Physical and compositional characteristics of the sampled locations used in the Canonical Correspondence Analysis.**Tabla S2.** Características físicas y compositivas de las ubicaciones muestreadas utilizadas en el Análisis de Correspondencia Canónica.

River	Locality	Width	Depth	Velocity	Rock	Cobble	Gravel	Fine gravel	Sand	Silt
Gazaduje	S1-M3	64.7	1.4	1.51	3.6	3.6	46.4	28.6	17.9	0.0
	S1-M7	56.4	1.1	1.68	6.0	20.0	44.0	24.0	4.0	2.0
	S2-M6	69.6	1.2	2.01	0.0	18.5	50.0	22.2	7.4	1.9
	S2-M7	74.7	1.2	1.90	6.1	48.5	18.2	12.1	15.2	0.0
Gazaguán	S1-M11	83.6	1.5	1.95	58.9	17.9	5.1	7.7	10.3	0.0
	S1-M8	120.4	1.3	1.73	14.7	14.7	33.0	27.5	8.3	1.8
	S2-M3	73.3	1.5	1.79	0.0	35.0	25.0	30.0	10.0	0.0
Gazamumo	S1-M12	92.1	1.4	1.91	0.0	42.9	32.1	21.4	3.6	0.0
	S1-M13	56.8	1.1	1.80	0.0	13.5	35.1	13.5	16.2	21.6
	S1-M6	81.8	1.4	1.67	9.5	70.2	7.1	2.4	10.7	0.0
	S2-M12	88.1	1.2	1.38	19.1	28.6	28.6	14.3	0.0	9.5
	S2-M13	110.8	1.4	1.64	9.8	19.5	48.8	19.5	0.0	2.4
Gazaunta	S1-M10	64.7	1.17	1.81	25.5	57.5	12.8	4.3	0.0	0.0
	S1-M9	79.5	1.2	1.95	19.7	39.4	28.8	7.6	4.6	0.0
	S2-M11	49.5	1.2	1.41	17.2	27.6	13.8	41.4	0.0	0.0
	S2-M4	71.2	0.9	1.67	22.6	25.8	25.8	22.6	3.2	0.0
Humea	S2-M5	57.4	1.2	1.65	8.8	32.4	29.4	29.4	0.0	0.0
	S1-M5	65.1	1.1	1.79	28.8	11.9	11.9	47.5	0.0	0.0
	S2-M8	47.7	1.3	1.72	25.7	28.6	8.6	34.3	2.9	0.0
	S2-M9	64.5	1.2	2.06	62.1	6.9	31.0	0.00	0.0	0.0

Table S3 Species recorded in the study area by river. Abbreviations were used in figures to denote each species individually.

Tabla S3. Especies registradas en el área de estudio por río. En las figuras se utilizaron abreviaturas para identificar cada especie individualmente.

Order	Family	Species	Abbreviations	Gaza-duje	Gaza-unta	Gaza-guán	Gaza-mumo	Humea	Total
Blenniiformes	Cichlidae	<i>Crenicichla geayi</i>	Cr_cal	7	0	4	10	2	23
	Poeciliidae	<i>Poecilia caucana</i>	Po_cau	0	0	0	1	0	1
Characiformes	Characidae	<i>Astyanax metae</i>	Ay_met	0	19	1	1	4	25
		<i>Astyanax superbus</i>	Ay_sup	4	13	0	1	0	18
		<i>Ceratobranchia</i> sp.	Ce_sp	3	30	49	32	0	114
		<i>Charax metae</i>	Cx_met	2	0	0	2	1	5
		<i>Creagrutus bolivari</i>	Cr_bol	7	72	2	128	55	264
		<i>Creagrutus calai</i>	Cr_cal	0	1	1	43	0	45
		<i>Hemibrycon loisae</i>	Hb_loi	1	51	0	0	0	52
		<i>Hemibrycon metae</i>	Hb_met	40	234	21	19	40	354
		<i>Knodus deuterodonoides</i>	Kn_deu	99	38	255	510	90	992
		<i>Knodus</i> sp.	Kn_sp	2	166	0	8	1	177
		<i>Odontostilbe splendida</i>	Od_spl	0	0	0	1	0	1
		<i>Astyanax integer</i>	Ay_int	0	0	2	2	0	4
	Crenuchidae	<i>Characidium cf. zebra</i>	Ch_ste	4	3	2	15	2	26
		<i>Characidium chupa</i>	Ch_chu	0	7	0	0	0	7
		<i>Characidium</i> sp.	Ch_sp	0	11	0	0	0	11
		<i>Characidium steindachneri</i>	Ch_ste	0	0	0	5	6	11
		<i>Characidium cf. boavistae</i>	Ch_boa	14	15	10	28	12	79
	Erythrinidae	<i>Hoplias malabaricus</i>	Ho_mal	0	0	0	1	0	1
	Parodontidae	<i>Parodon apollinari</i>	Pa_apo	0	23	1	15	13	52
Gymnotiformes	Apteronotidae	<i>Apteronotus galvisi</i>	Ap_gal	15	38	30	23	4	110
	Sternopygidae	<i>Sternopygus macrurus</i>	Rh_sp	0	0	0	1	0	1
Siluriformes	Aspredinidae	<i>Hoplosternon sordidum</i>	Hs_sex	3	0	0	0	0	3
	Astroblepidae	<i>Astroblepus</i> aff. <i>latidens</i>	As_lat	2	42	12	3	6	65
	Auchenipteridae	<i>Durania romani</i>	Du_rom	0	0	0	1	0	1
	Cetopsidae	<i>Cetopsis orinoco</i>	Cs_ori	2	1	3	2	5	13
	Heptapteridae	<i>Cetopsorhamdia ramirezi</i>	Cts_ram	0	1	0	0	0	1
		<i>Cetopsorhamdia orinoco</i>	Cts_ori	20	0	3	127	3	153
		<i>Chasmocranus rosae</i>	Cm_ros	7	20	43	17	2	89
		<i>Imparfinis microps</i>	Im_mic	6	0	0	0	0	6
		<i>Imparfinis robustus</i>	Im_rob	0	0	1	3	3	7
		<i>Pimelodella linami</i>	Pi_lin	9	0	0	0	0	9
		<i>Pimelodella metae</i>	Pi_lin	1	0	0	7	0	8
		<i>Rhamdia</i> sp.	Rh_sp	0	8	3	0	3	14
	Loricariidae	<i>Ancistrus triradiatus</i>	An_tri	0	1	0	15	0	16
		<i>Chaetostoma chimu</i>	Ct_chi	12	1	5	25	21	64
		<i>Chaetostoma dorsale</i>	Ct_dor	153	160	107	267	33	720
		<i>Chaetostoma formosae</i>	Ct_for	3	0	0	32	21	56
		<i>Chaetostoma joropo</i>	Ct_jor	1	0	16	0	5	22
		<i>Dolichancistrus cobrensis</i>	Di_cob	1	98	0	0	0	99
		<i>Dolichancistrus fuesslii</i>	Di_fue	0	1	0	3	0	4
		<i>Farlowella mariaelenae</i>	Fa_mar	20	2	21	8	2	53
		<i>Farlowella vittata</i>	Fa_vit	29	3	1	8	0	41
		<i>Hypostomus niceforoi</i>	Hy_nic	4	0	5	1	1	11
		<i>Lasiancistrus tentaculatus</i>	La_ten	2	0	0	0	1	3
		<i>Peckoltia lujani</i>	Pa_apo	9	0	0	1	9	19
	Trichomycteridae	<i>Ochmacanthus alternus</i>	Oc_alt	0	0	0	3	1	4
		<i>Trichomycterus</i> sp.	Tn_sp	0	5	1	5	0	11
Synbranchiiformes	Synbranchidae	<i>Synbranchus marmoratus</i>	Sy_mar	0	1	0	0	0	1