Structure of Fish Assemblages in Amazonian Rain-Forest Streams: Effects of Habitats and Locality

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We examined fish assemblage structure in three headwater rain-forest streams in the Urubu River Basin, Central Amazonia, as it relates to habitat heterogeneity. Riffles and pools, two types of stream habitat, were defined by current, depth, and substrate parameters, adjusted for Amazonian stream characteristics. We assessed species richness, composition, and abundance as they varied between riffles and pools across three similar streams. Four riffles and four pools were identified in each stream and sampled four times during 1996 and 1997. The samples yielded a total of 856 individuals of 22 species. The most abundant species were in the families Characidae, Lebiasinidae, Helogenidae, and Rivulidae. We found an interactive influence of riffle/pool habitat and stream factors on species richness, composition, and abundance. Rain-forest stream fish assemblages are structured by both habitat and stream locality.

HABITAT heterogeneity influences distributional patterns of stream fish assemblages. This heterogeneity may occur over a wide range of scales, from drainage topography down to patch variations (Matthews, 1998). The habitats of communities in streams are variable and spatially diverse (Frissel et al., 1986). Investigations of stream fish distribution in North America have followed from the work of MacArthur (e.g., 1964), who emphasized the role of habitat heterogeneity in shaping community diversity. Gorman and Karr (1978), for example, compared fish assemblages in riffle and pool communities that differed in physical variables including substrate, depth and current. These variables predicted, to some extent, stream fish assemblages (Gorman and Karr, 1978), a finding since supported by other studies (Schlosser, 1982; Moyle and Senanayake, 1984; Gorman, 1987).

Fish distribution, richness and abundance may differ between riffles and pools (Matthews, 1998). Loricariids in Panama and cyprinids in Oklahoma, for example, appear to avoid areas where predation is more intense; thus, smaller individuals tend to occur in riffles and the larger ones in pools (Power, 1987). Pools often contain more species than riffles (Angemeier and Karr, 1984; Bart, 1989; Gelwick, 1990). Sixteen fish species were more abundant in pools than in riffles in Panamanian streams (Angemeier and Karr, 1984). A similar result was found for generalized insectivores and for insectivore-piscivores in West Virginia streams (Chipps et al., 1994). Gelwick (1990) suggested that riffles may serve as refuges for juveniles of species normally abundant in pools (Gelwick, 1990), but Bart

(1989) found that young fishes in another Ozark stream use pools.

In this study, we assess the influence of riffles and pools on the structure of Amazonian stream fish assemblages. Prior studies in Amazonia have focused on variables such as microhabitat segregation, feeding behavior, pollution and seasonality (Knöppel, 1970; Silva, 1995; Bührnheim and Cox Fernandes, 2001). The headwater geomorphology of Amazonian streams features two successive biotopes: pools, with slow current and a substrate covered mainly by deposits such as litter, detritus and driftwood; and riffles, with a fast-flowing current and mostly sandy bottom with roots, wood pieces, and occasionally small pebbles (Fittkau, 1967). In our study, we ask how species composition, richness, and abundance vary across the two types of habitat in three different streams.

MATERIALS AND METHODS

The study was conducted in three second-order streams (Horton-Strahler scale in Petts, 1994) in the Urubu River basin, Amazonas State: "Igarapé 41," "Igarapé Gavião," and "Igarapé Porto Alegre." The term "igarapé" is a northern Brazilian word for small streams or small channels between islands. Distances between mouths of our study streams varied from 7–14 km. Bührnheim and Cox Fernandes (2001) provide additional information about the location of the study streams and the geology, climate, and vegetation of the area.

During the study, water temperature ranged 22–23.8 C, conductivity 6.8–10.3 mS·cm^{-1} at 25 C, and pH from 4.1–5.29. Riffle and pool habitats differ according to current, depth, and sub-

TABLE 1. Physical Features of Habitats Obtained in October to November 1996 (I), February (II), May (III), and August to September 1997 (IV) in the Three Streams. Respectively: depth (D) in cm, current (C) in m/s^{-1}, substrate (S) in % of sand in riffles and % of litter in pools, maximum width (MW) in m, maximum length (ML) in m. Data of each four sampling habitats were pooled to obtain means by riffles and pools.

| Stream | 41 | | Gavião | | Porto Alegre | |
Habitat	Riffle	Pool	Riffle	Pool	Riffle	Pool
DI	16.5	45.5	17.0	60.6	19.2	49.5
DII	15.0	43.7	17.0	53.5	19.5	49.0
DIII	16.7	49.2	30.7	65.7	25.0	54.0
DIV	15.7	46.0	21.2	55.2	17.5	46.7
CI	0.16	0.02	0.23	0.02	0.17	0.03
CII	0.20	0.03	0.26	0.05	0.19	0.06
CIII	0.23	0.05	0.25	0.10	0.24	0.11
CIV	0.20	0.05	0.25	0.08	0.18	0.03
SI	72.5	76.2	78.7	76.2	65.0	75.0
SII	77.5	90.0	85.0	68.7	76.7	61.2
SIII	76.2	80.0	88.7	32.5	62.5	53.7
SIV	60.0	84.5	90.7	76.0	70.0	77.2
MWI	2.9	2.6	3.3	2.3	2.1	2.3
MLI	3.2	2.1	2.8	3.2	2.4	3.0

strate. Current velocity was obtained by marking the time that a styrofoam plate (10 cm × 5 cm) traveled 1.5 m on the water surface. Riffle currents were found to vary between 0.1 and 0.3 m/sec; pool currents were ≤ 0.11 m/sec. Depth was measured as the mean of 5–6 points in a line perpendicular to flow along the course, including the maximum depth point. In riffles, depth varied between 15 and 25 cm and in pools depth exceeded 35 cm. Substrate was determined through visual estimation of sand and litter quantities. Substrate in riffles was composed of at least 50% sand and pools of at least 50% litter. Litter is defined as the organic matter on the bottom of the river derived from terrestrial and aquatic vegetation.

We chose four riffle and four pool habitats along stretches of 350 m in each of the three streams, with at least 5 m separating each habitat. A total of 24 habitats were sampled, four riffles, and four pools in each stream. The areas on the streams sampled in this work are different than those of Bührnheim and Cox Fernandes (2001). Habitats with mean depths less than 15 cm were not considered here, following Gorman and Karr (1978). Current, depth, and substrate were measured during each sampling period (Table 1). Sampling was conducted during four periods: October through November 1996, February, May, and August through September 1997. The 24 habitats were resampled in each of these four periods, resulting in 96 sample points.

Fish were collected at night, between 1900

and 0300 h. The collection site was blocked with two seine nets (3 m × 2 m × 2 mm mesh and 3 m × 1.1 m × 5 mm mesh), as in Angermeier and Karr (1984), and fish were captured with a fine-mesh dipnet with the help of flashlights during 30 min in each habitat. This method is most effective in the collection of mainly diurnal fishes, for example, characins and cichlids, which stay motionless at night (Lowe-McConnell, 1964, 1987). However, this method is probably less efficient with fishes that are active at night, for example, catfish and electric fishes. In our study, the 30-min intervals of fishing were sufficient for capture of about 95% of fish located visually. To minimize interference of sampling between sites, collections were made from downstream to upstream. Fish were fixed in 10% buffered formalin and preserved in 70% ethanol.

The identification of some fishes to the species level in our collections was not definitive because some of the taxa we encountered, such as the genus *Hyphessobrycon*, need further taxonomic review. Therefore, we refer to these species as cf., meaning ''compare to'' a species that has an affinity to the name we are using. We refer to species that are apparently new, such as *Hemigrammus*, as ''sp.''

We considered sampling sites within each stream (e.g., the four riffles of Igarapé 41) to be nonindependent because of the proximity of these sampling sites. Data for each stream at each sampling period were combined into two groups, pools and riffles. Pooling makes the

species list and abundance data more complete, given the scarcity of some species (e.g., Chernoff and Willink, 2000; Norris et al., 1994; Rodríguez and Lewis, 1990). Averages of richness and abundance data were obtained by pooling the four habitat replicates of each sampling period by stream to test for stream, habitat, and sampling period effects.

Normality and homocedasticity were tested and confirmed with Shapiro-Wilks' W and Levene's tests, respectively. Variation in species richness across habitats and streams was assessed using two-way ANOVA.

We used the Jaccard coefficient of similarity, defined by the number of species in common to and unique to each sample pair, to measure the relative similarity of species composition among samples from different assemblages (Krebs, 1994). This similarity coefficient ranges from 0, no overlap of species, to 1, complete overlap. Unweighted pair-group using arithmetic averages (UPGMA) cluster analysis was used to compare species composition between riffles and pools (four replicates), with the four periods of sampling pooled.

Comparisons of fish abundance were limited to species represented with more than 20 individuals in our sample, species occurring in both riffles and pools, and species occurring in more than one stream. Nonparametric tests were employed in the analysis of fish abundance because normality and homocedasticity were not achieved after data were transformed to $\ln(X+1)$. Variation between the averages of fish abundance related to the different habitats was assessed using Mann-Whitney U-tests. Kruskal-Wallis ANOVA was used to test the variation among and between streams and sampling periods.

UPGMA cluster analysis was also used to evaluate similarity, in terms of species abundance, between riffles and pools, with the four periods of sampling pooled. For this analysis, we used only species that occurred in all three streams. This cluster analysis was generated from dissimilarity matrices of normalized, root-mean-squared Euclidean distances. This distance ranges from 0 (similar) to infinity (maximum dissimilarity), the larger the distance the lower the similarity (Krebs, 1994). Statistical tests were performed on STATISTICA, and cluster analysis on SYSTAT.

RESULTS

During the period of the study, habitats exhibited slight changes in their physical parameters caused by variation in the amount of rain
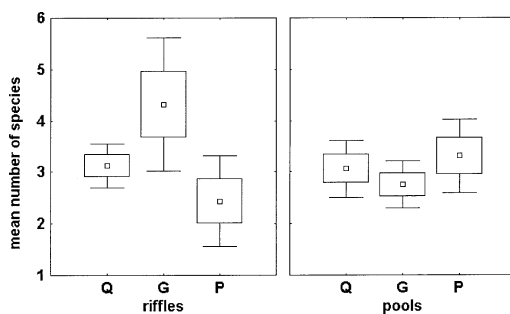

Fig. 1. Species richness in riffle and pool habitats in three streams: Igarapé 41 (Q); Igarapé Gavião (G); and Igarapé Porto Alegre (P). Rectangles encompass standard errors and error bars standard deviation.

(Table 1). Collections resulted in 856 specimens of 22 species. Riffles contained 496 specimens of 17 species and pools 360 specimens of 18 species.

There was no significant difference in species richness between riffles and pools or among streams, although there was a significant interaction between these factors (ANOVA, habitat × stream effect, $F_{2,18} = 4.95$, $P = 0.02$). The riffle habitats of Igarapé Gavião exhibited the highest mean, and variation among samples was higher there than in the other two streams (Fig. 1). Species richness of pool habitats did not vary among streams (Fig. 1). Sampling period did not have a significant effect on species richness (ANOVA, $F_{3,20} = 1.58$, $P > 0.05$).

The cluster analysis of species composition separated the pools of Igarapé Gavião from all other habitats. This separation resulted from the exclusive presence of *Hoplias* sp., *Nemuroglanis pauciradiatus*, and *Gymnotus* cf. *stenoleucus* in the pools of Igarapé Gavião. Further, the other habitats all shared three species that did not occur in Igarapé Gavião pools: the *Hemigrammus* sp., *Nannostomus marginatus* and *Aequidens pallidus* (Table 2). Pools and riffles of Igarapé 41 exhibited the most similar species composition, sharing nine species.

Species with more than 20 individuals of total abundance in our samples and found in both riffles and pools were *Hyphessobrycon* cf. *heterorhabdus*, *Hyphessobrycon* cf. *melazonatus*, *Hemigrammus* sp., *Pyrrhulina brevis*, *Iguanodectes variatus*, *Nannostomus marginatus*, *Rivulus compressus*, and *Helogenes marmoratus*. Of these species, *H.* cf. *melazonatus* did not occur in Igarapé Porto Alegre and, therefore, was not included in our CLUSTER analysis (Table 2). Four species were collected only once: *Hoplias* sp., *Microglanis* sp., *Ne-*

TABLE 2. CHECKLIST AND TOTAL SPECIMENS CAPTURED OF THE STREAM FISH FAUNA IN THE HABITATS OF THE THREE STREAMS.

		41		Gavião		Porto Alegre	
		Riffles	Pools	Riffles	Pools	Riffles	Pools
CHARACIFORMS							
Erythrinidae	*Erythrinus erythrinus*			2		1	
	Hoplias sp.				1		
Crenuchidae	*Crenuchus spilurus*		1				
Lebiasinidae	*Copella nigrofasciata*					1	2
	Nannostomus marginatus	5	6	3		7	9
	Pyrrhulina brevis	24	6	38	3	28	4
Characidae	*Bryconops inpai*	1		1			
	Hemigrammus sp.	45	38	3		25	28
	Hyphessobrycon cf. *melazonatus*	59	34	63	9		
	Hyphessobrycon cf. *heterorhabdus*	8	25	96	74		28
	Moenkhausia sp.			10	6		
	Iguanodectes variatus	9	5	14	10	5	11
SILURIFORMES							
Pseudopimelodidae	*Microglanis* sp.			1			
Heptapteridae	*Nemuroglanis pauciradiatus*				1		
Cetopsidae	*Helogenes marmoratus*	3	9	4	7	9	17
GYMNOTIFORMES							
Sternopygidae	*Eigenmannia* cf. *virescens*			1	4	1	4
	Sternopygus cf. *astrabes*						1
Hypopomidae	*Steatogenys duidae*			1	7		
Gymnotidae	*Gymnotus* cf. *stenoleucus*				1		
CYPRINODONTIFORMES							
Rivulidae	*Rivulus compressus*	13	4	3	2	6	
PERCIFORMES							
Cichlidae	*Aequidens pallidus*	2	1	1		2	2
	Apistogramma steindachneri			1			

muroglanis pauciradiatus and *Apistogramma steindachneri*.

Of the eight most abundant species only *Pyrrhulina brevis* and *Rivulus compressus* were most abundant in riffles in the three streams (Table 3, Fig. 2A–B), although the difference for *R.* *compressus* between riffles and pools for Igarapé Gavião was low (Fig. 2B). The *Hemigrammus* sp., *Hyphessobrycon* cf. *heterorhabdus* and *N. marginatus* differed significantly in abundance among the three streams (Table 3). The *Hemigrammus* sp. and *N. marginatus* exhibited low abundance in

TABLE 3. RIFFLE/POOL HABITAT, STREAM, AND SAMPLING PERIOD EFFECTS TESTED FOR THE EIGHT MOST ABUNDANT SPECIES. Probabilities from Mann-Whitney *U*-tests were adjusted using *Z*-values (* significant $P < 0.05$).

|	Mann-Whitney *U*-tests	Kruskal-Wallis analysis of variance			
	Habitat	Stream		Sampling period	
	P	$H_{2,24}$	P	$H_{3,24}$	P
Pyrrhulina brevis	0.000*	0.01	ns	0.54	ns
Hemigrammus sp.	ns	16.49	0.000*	1.14	ns
Hyphessobrycon cf. *heterorhabdus*	ns	10.79	0.004*	2.55	ns
Iguanodectes variatus	ns	4.77	ns	4.09	ns
Nannostomus marginatus	ns	6.86	0.032*	5.41	ns
Helogenes marmoratus	ns	2.45	ns	0.62	ns
Rivulus compressus	0.03*	2.71	ns	2.21	ns
Hyphessobrycon cf. *melazonatus*	ns		ns (Mann-Whitney)	7.99	0.05*
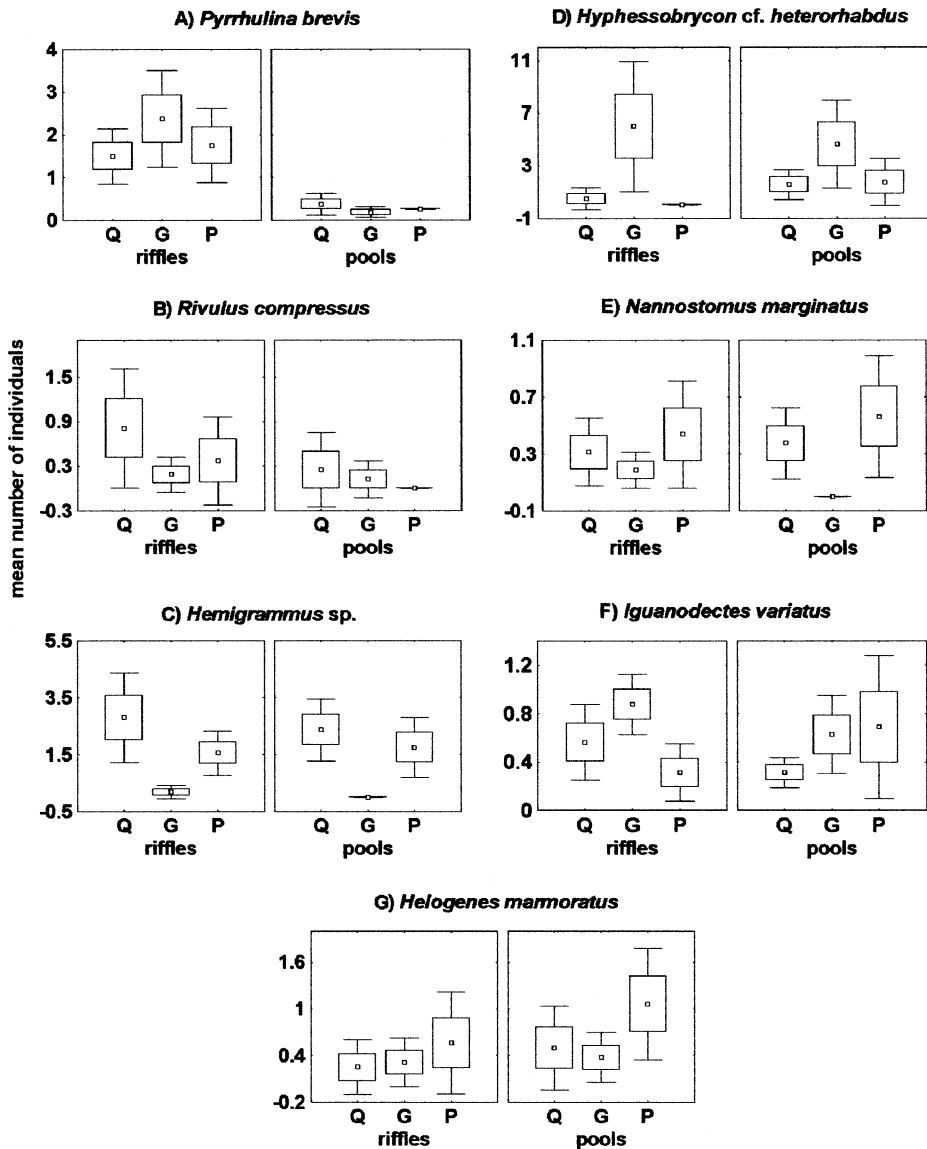
Fig. 2. Abundance of (A) *Pyrrhulina brevis*, (B) *Rivulus compressus*, (C) *Hemigrammus* sp., (D) *Hyphessobrycon* cf. *heterorhabdus*, (E) *Nannostomus marginatus*, (F) *Iguanodectes variatus*, and (G) *Helogenes marmoratus*, in riffles and pools in streams Igarapé 41 (Q), Igarapé Gavião (G) and Igarapé Porto Alegre (P). Rectangles encompass standard errors, and error bars standard deviation.

Igarapé Gavião (Fig. 2C, E). In contrast, *H.* cf. *heterorhabdus* was most abundant in Igarapé Gavião (Fig. 2C–D). *Iguanodectes variatus* and *Helogenes marmoratus* abundance was not significantly affected by habitat or stream factors (Fig. 2F–G). Only *Hyphessobrycon* cf. *melazonatus* abundance was significantly affected by the periods of sampling (Table 3), with a lower abundance in the third sampling period in Igarapé 41 and Igarapé Gavião (Fig. 3).

The cluster analysis of species abundance divided the assemblages into two main groups: habitats of Igarapé Gavião, and habitats of Igarapé 41 and Igarapé Porto Alegre. The clustering of Gavião habitats appears to be caused by the low abundance of the *Hemigrammus* sp. and the high abundance of *H.* cf. *heterorhabdus* in this stream (Fig. 2C–D). Within the other two streams, pools were separated into one cluster and riffles into another cluster. This separation
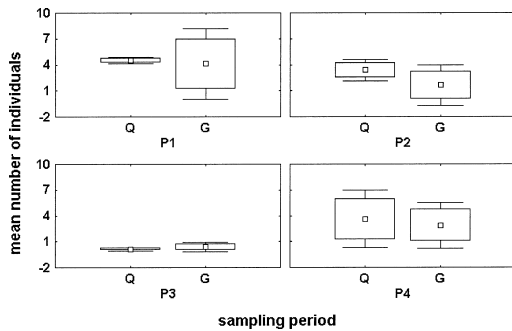
Fig. 3. Abundance of *Hyphessobrycon* cf. *melazonatus* in riffles and pools of streams Igarapé 41(Q) and Igarapé Gavião(G) in the four sampling periods (P1–P4). Rectangles encompass standard errors, and error bars standard deviation.

appears to be related to the high abundance of *Pyrrhulina brevis* and *Rivulus compressus* in riffles of both streams (Fig. 2A–B).

DISCUSSION

Our main finding is that the structure of fish assemblages (e.g., richness, species composition and abundance) varied not only as a function of local stream habitats (pools vs riffles) but also across different streams. The interaction between habitats and streams is significant for species richness. In addition, our cluster analysis shows similar results for species composition and abundance, with a trend to group assemblages by streams as well as by habitats.

These results suggest that habitat heterogeneity is not the only factor that shapes community diversity in the Amazonian streams we sampled. These streams might carry unique characteristics that affect fish assemblage structure, even though the habitats within streams exhibited only slight variations in their physical parameters (Table 1). Closer examination of the streams might therefore provide insight into the causes of differences in assemblage structure among streams. For example, Igarapé Gavião has one extra small first order affluent upstream of the sampled areas, although it is still classified as a second order stream. This extra affluent apparently increases stream discharge, and could account for some of the distinctiveness of its fish assemblage.

We might expect to find more species in a larger stream. There are indications that species additions and replacements are related to stream size (Horwitz, 1978; Maurakis et al., 1987; Edds, 1993). Igarapé Gavião indeed exhibited a larger number of species than the oth-

er streams, although not to a statistically significant degree. In another study, we sampled these streams using multiple fishing gears, and found that Igarapé Gavião had the highest richness, with 26 species compared to Igarapé 41 (22 species) and Igarapé Porto Alegre (18 species; Bührnheim and Cox Fernandes, 2001). Four species occurred exclusively in Igarapé Gavião, in contrast to only one exclusive species in each of the two other streams (see Table 2).

The comparatively low species richness of Igarapé Porto Alegre might similarly be influenced by its unique characteristics. The lower course of this stream is situated in a fragmented forest reserve of 100 hectares, which was disturbed along its borders by logging in 1984. This location now exhibits a high second-growth forest. Perhaps this disturbance and corresponding changes in riparian vegetation downstream has had an indirect effect on assemblage structure in the stream's upper preserved course.

The number of species found in riffles versus pools varied from stream to stream. Igarapé Porto Alegre exhibited a higher mean number of species in pools compared to riffles, and compared to the pools of the other streams. By contrast, Igarapé Gavião exhibited a higher mean number of species in riffles. Igarapé 41 showed no clear difference between the two habitats. Higher richness of fish in pools may be related to greater depth and slower current (Sheldon, 1968; Angermeier and Karr, 1984; Bart, 1989). Deeper habitats are more stable than riffles, in that pools attenuate short-term changes in current, depth and substrate (Schlosser, 1982). Yet inhabitants of pools often experience higher predation and occupy riffles as refuges (Power, 1987; Gelwick, 1990; Harvey and Stewart, 1991). Although, we did not formally evaluate the effect of predators on fish survivorship, the presence of nocturnal predators such as *Hoplias* sp., *Gymnotus* cf. *stenoleucus,* and *Rhamdia quelen* (Bührnheim and Cox Fernandes, 2001) in pools in Igarapé Gavião reinforces the idea that predation might increase the number of species using riffles as refuges. Predators such as *Hoplias malabaricus*, *Gymnotus carapo*, and *Rhamdia* sp. were also noted in pools by Winemiller (1989), who concluded that prey move among habitats to avoid predators.

Spatial segregation is often related to predation risk associated with body size or microhabitat (e.g., marginal or open water; Gorman, 1987). For example, bigger fish frequently occupy deeper habitat (Power, 1987; Harvey and Stewart, 1991). Most species caught in riffles were small characins, such as *Hyphessobrycon* and

Hemigrammus, with less than 10cm in total length (Géry, 1977).

In our abundance analysis, Igarapé Gavião habitats clustered together, indicating the influence of this stream on fish assemblage structure. The great abundance of *Pyrrhulina brevis* and *Rivulus compressus* in riffles appears to determine the distinct grouping of Igarapés 41 and P. Alegre. *Rivulus compressus* was not as common as *P. brevis*, but *Rivulus* usually lives in intermittent pools along the stream edges, outside the main stream channel where we concentrated our sampling efforts (Huber, 1992). Both *Pyrrhulina* and *Rivulus* are normally found at night in intermittent small pools and riffles in central Amazonian streams.

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