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Relationships Between Habitat Characteristics and Fish Assemblages in Small Streams of Central Amazonia

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Small streams with acidic, nutrient-poor waters form a dense hydrological system in Central Amazonia. However, little is known about the fish assemblages that occur in these systems. We investigated the relationships among stream size, substrate, and other physical-chemical factors and fish distributions. Fish assemblages and stream characteristics were sampled in 50-m long sections of streams at 38 sites distributed throughout the 100-km^2 florestal reserve. Forty-nine species were encountered. The mean richness was similar among sites; however, community composition was correlated with physical and chemical characteristics of the streams. The mean number of species per site ($\overline{X} = 9$) was low in relation to the total number of species recorded from the reserve (49) and in relation to the ichthyofauna that has been recorded from small forest streams near the study area. This contrasts with studies in temperate zones where strong patterns of species addition along the river continuum were found, resulting in prominent species richness gradients. The high between-site turnover in species composition and the strong habitat specificity indicate that it will be necessary to create a network of reserves to efficiently conserve the fish fauna of small forest streams in Central Amazonia.

Na Amazônia Central, pequenos riachos de águas ácidas e pobres em nutrientes constituem uma densa rede hídrica. Contudo, pouco é conhecido sobre a riqueza e abundância de sua ictiofauna. Para determinar a composição ictiofaunística existente, bem como determinar a relação entre o tamanho dos igarapés, substratos presentes nos leitos, e fatores físico-químicos e a estrutura da comunidade, nós amostramos trechos de 50-m em 38 locais distribuídos em uma reserva de 100-km^2. A riqueza média foi semelhante entre os sítios de amostragem. No entanto, a composição de espécies foi relacionada com características físicas e químicas dos riachos. O número médio de espécies por local ($\overline{X} = 9$) foi pequeno em relação ao número total de espécies encontrado na reserva (49) e em relação à ictiofauna que foi encontrada em pequenos riachos próximos à área de estudo. Isto contrasta com estudos realizados em zonas temperadas, onde um padrão muito forte de adição de espécies ao longo das bacias foi encontrado, resultando em um gradiente acentuado de riqueza de espécies. A alta troca na composição de espécies entre locais, e a alta especificidade de hábitat, indica que seria necessário criar uma rede de reservas para conservar eficientemente a ictiofauna de pequenos riachos na região.

THE Amazon basin is the world's largest freshwater drainage system and covers about 700,000 km^2 (Santos and Ferreira, 1999). It is famous for its large rivers and lakes, but also contains countless small streams that constitute one of the world's largest and densest hydrological networks (Junk, 1983). Except for some larger silt-laden rivers, with headwaters in the Andean mountains, almost all the Amazonian rivers result from the junction of small streams that drain forest areas (Walker, 1991).

In Central Amazonia, *terra firme* environments (uplands that are not seasonally flooded) are drained by streams that have acidic waters due to the presence of humic and fulvic acids. The waters are poor in nutrients and the forest canopy impairs light penetration to the stream surface, so aquatic plants are virtually nonexistent (Junk and Furch, 1985; Walker, 1995). In these oligotrophic environments, food chains are dependent on allochthonous material from the forest, such as pollen, flowers, fruits, leaves, and arthropods (Goulding, 1980; Goulding et al., 1988; Walker, 1991). However, small fishes are frequently abundant, and 20 to 50 species may occur in a single stream (Lowe-McConnell, 1999; Sabino, 1999).

Most of the ichthyofaunal studies undertaken in Amazonia have focused on the large rivers and commercially valuable species (e.g., Smith, 1979; Paiva, 1983; Ferreira et al., 1998). In order to describe the regional fish diversity, it will be necessary to have information on the poorly studied aquatic systems in the Amazon basin,

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especially the headwaters of tributaries (Menezes, 1996). It has been estimated that about 2,000 species of freshwater fish have yet to be described in South America, the great majority occurring in areas away from the large rivers and lakes (Castro, 1999). The first detailed studies on the composition and diet of the ichthyofauna of Brazilian Amazonian streams were published by Knöppel et al. (1968) and Knöppel (1970), based on collections made by E. J. Fittkau in 1965 and W. Junk in 1967. More recently, research on fish in small streams has focused on habitat use, feeding habits, and community structure (Silva, 1993; Sabino and Zuanon, 1998; Bührnheim and Cox-Fernandes, 2001).

Models of community structure and functioning of streams are largely based on patterns observed in temperate areas, such as the River-Continuum Concept (Vannote et al., 1980). This model suggests that environmental characteristics of fluvial systems vary in predictable ways, shaped mainly by the sequential processing of organic matter along a longitudinal river gradient. However, this model is not very sensitive to water chemistry, the complex biotic interactions in tropical streams (Angermeier and Karr, 1984), or the large dimension of the Amazon system (Lowe-McConnell, 1999). The major model derived for Amazonian systems, the flood-pulse concept (Junk et al., 1989), is based on floodplains of large rivers and is not directly applicable to *terra firme* streams which do not have a regular pattern of seasonal flooding. Many other models of community assembly have been proposed (e.g., Gee and Giller, 1987; Hubbell, 2001), but the lack of reliable information on fish species distribution and assemblage composition in small Amazonian streams impairs the evaluation of these models in this region.

Structural characteristics of tropical aquatic environments affect the composition of fish communities. Community structure in rivers and tropical streams has been related mainly to the size of the river (Bussing and López, 1977; Angermeier and Karr, 1984), current velocity (Bussing and López, 1977; Harding et al., 1998), depth (Angermeier and Karr, 1984; Martin-Smith, 1998; Stewart et al., 2002), predation (Greenberg, 1991; Fraser et al., 1999), and competition (Zaret and Rand, 1971; Piet, 1998). In Costa Rica (Bussing and López, 1977) and Ecuador (Galacatos et al., 1996), altitudinal gradients have been shown to influence fish community structure. Lowe-McConnell (1999) stated that fish species richness decreases towards headwaters, where physical-chemical factors, obstructions, high current velocity, and lack of refugia in the dry season may be more limiting than food availability. Although large Amazonian rivers support hundreds of species of fish, it is unknown what sustains and/or limits species richness in headwater streams. Although current velocity, physical-chemical factors, and habitat differences have been suggested to influence the distribution of species (Silva, 1995; Sabino and Zuanon, 1998; Bührnheim, 1999), none of these factors have been studied in detail in Amazonia.

The number of species that can maintain viable populations in a reserve depends on its size and other characteristics (Cowling et al., 1999; Saunders et al., 2002). However, the effectiveness of a reserve system also depends on how much of the regional species pool is represented in the reserves (Koleff and Gaston, 2002). It is necessary to have information on turnover of species with geographic distance or among habitats in order to optimally select areas for the reserve system (Margules et al., 2002) or determine reserve boundaries. Unfortunately, almost nothing is known of spatial turnover in Amazonian headwater fish communities.

Reserva Florestal Adolfo Ducke (RFAD) is one of the most intensively studied areas in Brazilian Amazonia (Ribeiro et al., 1999); however, there have been few ichthyological studies. A north-south central plateau separates two main watersheds in the reserve. In the western half, streams drain to tributaries of the Rio Negro; the eastern watershed is formed by streams that drain to the Rio Puraquequara, a tributary of the Rio Amazonas. It is not known whether drainage basins connected to the Amazon and Negro rivers have different fish communities.

In this study, we addressed the following questions: (1) What is the relationship between stream size and fish assemblage structure? (2) How does fish assemblage structure relate to physical-chemical characteristics of the stream? (3) How do assemblages and physical-chemical conditions vary among watersheds?

MATERIALS AND METHODS

Study area.—The study was undertaken in Reserva Florestal Adolfo Ducke (RFAD) between March and August 2001. The reserve belongs to the Instituto Nacional de Pesquisas da Amazônia (INPA) and lies on the northwest outskirts of Manaus in the Brazilian State of Amazonas, between 02°55′–03°01′S and 59°53′–59°59′W (Fig. 1). The reserve covers 10,000 ha of *terra firme* (non-flooded) rainforest.

The Manaus region is characterized by a humid equatorial climate, with mean annual temperature of 26.7 C (23.3 C–31.4 C). The mean relative humidity is 80% and mean annual

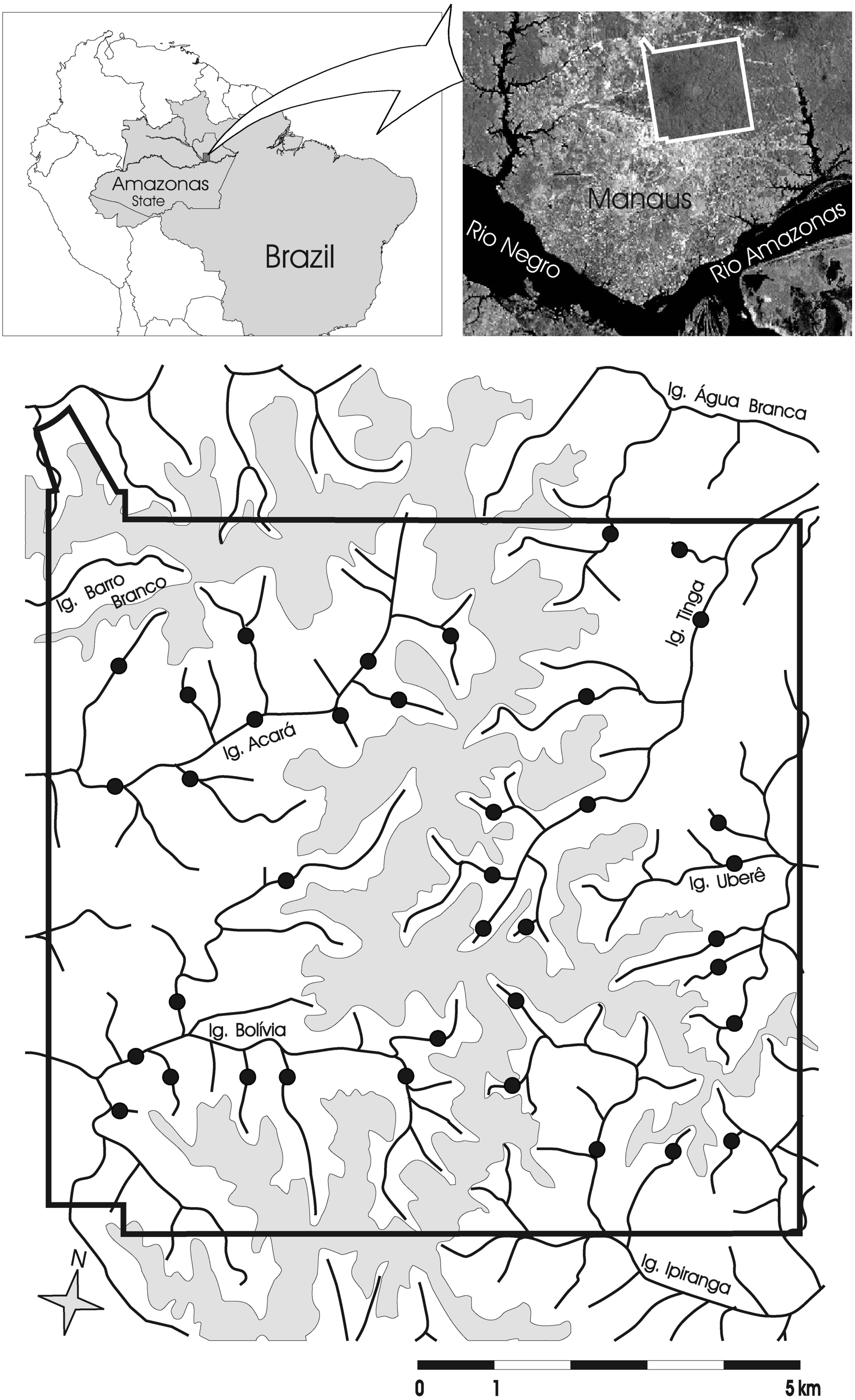

Fig. 1. Geographical location of the study area, Reserva Florestal Adolfo Ducke, near Manaus, Amazonas State, Brazil. Black circles correspond to sample sites and the shaded area corresponds to the central plateau that separates the two main drainages in the reserve (based on Landsate 5 satellite image, 1995).

rainfall is 2286 mm. The rainy season extends from November to May and the dry season from June to October (Ribeiro et al., 1999).

The reserve is located on Cretaceous sediments from Alter do Chão formation (A. Carneiro, pers. comm.). The ridges are predominately formed by oxisols, constituted by kaolinite, iron oxide, and gipsite (Chauvel, 1981). The lowlands have predominately hydromorphic podzol sandy soils. The altitudinal variation is up to 80 m between the tops of ridges (max. ≈120 m above mean sea level) and the lowlands (min. ≈40 m above mean sea level).

We sampled first, second, and third order streams following Strahler's modification of Horton's scale (Petts, 1994), where the junction of two first order streams form a second order stream and two second order streams form a third order stream. We sampled 38 stations in 35 streams, 19 in each drainage basin (Fig. 1). Twenty-two samples were taken in first order streams, ten in second order streams, and six in third order streams. Each sample station consisted of a 50-m reach of stream.

Stream width was measured at six points (every 10 m) in each station. At each of the six points we measured depth at 10 cm intervals along a transect across the stream. Current velocity was measured at three points (every 25 m) at mid channel in the center of the water column, using a General Oceanics flowmeter, model 2030-R2, equipped with a rotor for slow current velocity.

The area at each of the six transverse sections across the stream (At) was estimated by: $At = [(Z_1 + Z_2)/2] \times l + [(Z_2 + Z_3)/2] \times l + \ldots [(Z_n + Z_{n+1})/2] \times l$, where Z_n is the depth in each point in a given transect and l is the width of the sample interval between transect points (in this case, 0.1 m). An index of mean discharge for each station was estimated as follows: $Q = Am \times Vm$, where Q = mean discharge, Vm = mean current velocity and Am = mean cross-sectional area of the stream at each of the six transects.

Environmental parameters.—Conductivity and pH were measured using a portable Aqua-CheckTM Water Analyzer Operator (O.I. Analytical). Dissolved oxygen and temperature were measured with a portable oxygen meter/thermometer (Yellow Springs Instruments, model 58). Suspended material was determined gravimetrically by the method of Meade (1985). Humic acid concentration was determined by absorbance at 400 ηm in a Milton Roy spectrophotometer, model Spectronic 301, using prefiltered water samples.

Mean canopy cover was estimated with a concave densiometer (Robert E. Lemmon Forest Densiometer, model C) at three equidistant points along each sample station. Four measurements were taken at each point, facing north, south, west, and east. Substrate was classified in one of seven categories: sand, clay, trunk (wood with diameter over 10 cm), litter (leaves and small branches), fine litter (organic silt), roots (fine roots from riparian vegetation), or macrophytes (*Thurnia sphaerocephala:* Thurniaceae). Substrate was recorded by the point quadrat method (Bullock, 1996) at each 10 cm in six transects across the stream in each station, starting 10 cm from the margin. Proportional cover was estimated as the proportion of points of each substrate type in relation to all substrate measurements in each sample station. Values obtained for environmental variables are presented as means and their respective ranges.

Ichthyofauna.—Fish were captured using five methods. During 24-h sample periods, 12 minnow-traps and three fyke-nets were placed in each sample station and were checked at 8 h intervals. After collecting with fish traps, a 50-m section of the stream was blocked with fine-mesh nets (5 mm stretched mesh size), and a mobile net was used to divide the stream into smaller sections and facilitate the capture of enclosed fish with hand and seine nets (these catches were made during daylight hours). An electric signal detector was used to locate Gymnotiform fishes hidden in debris and among roots. The detector consisted of an electric pulse amplifier and a speaker connected to two wires that were fixed to the end of a wooden pole.

Streams in the western and eastern basins, and of different orders, were sampled alternately to avoid effects of temporal variation. Samples were initially standardized for all sites. However, preliminary samples showed that the collecting methods were less efficient in third order streams. To reduce this trend, a fourth fike-net and three gillnets (10 × 1 m, mesh size of 3 cm, 5 cm, and 6 cm) were used in third order streams. Gillnets were set during a 4 hour period at each site and were checked regularly to avoid accidental capture and possible death by drowning of caimans, turtles, and semi-aquatic lizards.

Only specimens that could not be confidently identified in the field were collected. Specimens collected were killed in a 2 g/l solution of MS 222 according to guidelines of the American Veterinary Medical Association (2001), fixed in 10% formalin solution, subsequently transferred to 70% alcohol, and deposited in the INPA Fish Collection (Voucher specimens: INPA 19586-19933).

Data analyses.—Based on relative abundances or presence/absence of species, sites were ordered by Hybrid Multidimensional Scaling (HMDS) in two dimensions. HMDS analysis was undertaken using the PATN statistical package; other statistical analyses were done with SYSTAT 8.0 statistical program.

Ordinations were undertaken for quantitative (abundance) and qualitative (presence/absence) data. The quantitative data reveal patterns based on the most common species, which tend to have the greatest quantitative differences among sites. Presence/absence data tend to give more weight to uncommon species, as common species occur in most sites and therefore contribute little to qualitative differences among sites.

The presence/absence form of the Bray-Curtis index (Sorensen index) was used for qualitative data. Similarities between sites based on quantitative data were estimated using Bray-Curtis dissimilarity index on relative abundances after standardization by division by site totals. Principal Components Analysis (PCA) was used to summarize physical-chemical characteristics of the streams and produce predictor variables that were statistically independent.

''Drainage basin'' is a compound variable that may represent differences in physical-chemical characteristics, habitat diversity, disturbance characteristics, evolutionary processes, or limitations on dispersal. We tested for differences between drainage basins in physical-chemical characteristics (acidity, conductivity, temperature, oxygen concentration, amount of suspended particles, and humic acid concentration) and in fish assemblage structure using Multivariate Analysis of Variance (MANOVA). The physical-chemical characteristics (predictor variables) and the fish assemblages (dependent variables) were represented by multivariate axes (Principal Components Analysis or Multidimensional Scaling) in the multivariate inferential analyses. We included drainage basin with the axes representing physical-chemical characteristics as predictor variables in a Multivariate Analysis of Covariance (MANCOVA) to determine whether drainage basin contributed information on fish assemblage structure beyond that provided by physical-chemical factors.

RESULTS

Environmental characteristics of streams.—The streams had acidic waters (pH 3.7–4.8) with low conductivity ($\bar{X}$ = 3.7 μS/cm, range = 2.99–8.00) and relatively similar temperature ($\bar{X}$ = 24.4 C, range = 21.8–25.8). Waters were highly saturated in oxygen ($\bar{X}$ = 7.7 mg/l, range = 5.45–9.42), poor in suspended particles ($\bar{X}$ = 5.6 mg/l, range = 1.63–14.41), and had high variation in concentration of humic acids (0.014–0.624 Abs.). The streams had dense marginal vegetation (canopy cover: $\bar{X}$ = 91.0%, range = 80.4–94.5) and the bottoms of the streams were covered mainly by sand ($\bar{X}$ = 49.8%, range = 15.1–82.1) and coarse litter ($\bar{X}$ = 26.1%, range = 7.8–53.8).

The habitat variables differed among drainage basins (MANOVA: Pillai Trace = 0.778, $F_{2.76}$ = 19.15, $P = 0.025$). The habitat characteristics that differed significantly between drainage basins in individual analyses were conductivity ($\bar{X}$ = 2.99 μS/cm eastern; 4.40 μS/cm western), suspended particles ($\bar{X}$ = 6.55 mg/l eastern; 4.77 mg/l western), humic acids ($\bar{X}$ = 0.086 Abs. eastern; 0.239 Abs. western), coarse litter ($\bar{X}$ = 23.8% eastern; 28.4% western), roots ($\bar{X}$ = 8.3% eastern; 13.7% western), and trunks ($\bar{X}$ = 4.8% eastern; 7.3% western).

The first three axes of the PCA summarized 57.6% of the variation. The first component accounted for 30% of the variance in the original variables. As all variables with loadings > 0.6 on this component were associated with stream structural characteristics, this component was taken to represent stream size and associated physical changes. There was only a moderate correlation between the values of this PCA axis and stream order (r = 0.396). The second component accounted for 18% of the variance and was taken to represent water-quality characteristics of the stream. The third component accounted for only 10% of the variance, and only substrate cover of fine and gross litter had significant loadings (Table 1). The only variables not related to the first three components were temperature, dissolved oxygen, canopy cover, and % clay substrate cover and are unlikely to be informative in relation to the distribution of fish species in this system.

The fish community.—2438 individuals, belonging to 49 species, six orders, and 18 families were captured. Characiformes was the group with greatest richness and abundance values, and the 19 species in this group represented 84.3% of the total number of individuals collected. Siluriformes was represented by 11 species, Gymnotiformes by ten and Perciformes by seven species. Synbranchiformes and Cyprinodontiformes contributed only one species each. Perciformes (only Cichlids) was the second most abundant group in terms of individuals (8.3%), followed by Cyprinodontiformes (2.5%), Siluriformes (2.3%), Gymnotiformes (2.3%), and Synbranchiformes (0.1%).

TABLE 1. RESULTS OF PRINCIPAL COMPONENTS ANALYSIS (PCA) SHOWING THE VARIABLES RELATED TO PHYSICAL-CHEMICAL CHARACTERISTICS OF THE STREAMS, THEIR LOADINGS, AND PERCENT VARIANCE EXPLAINED ACROSS THE FIRST THREE COMPONENTS. Bold indicates variables with loadings > 0.6.

Variables	PCA 1	PCA 2	PCA 3
Mean current velocity	**0.745**	0.231	0.029
Discharge	**0.796**	0.473	0.140
Maximum depth	**0.863**	0.279	0.170
Mean depth	**0.876**	0.247	0.182
Mean width	**0.826**	0.387	0.209
Conductivity	0.424	**−0.716**	−0.064
Dissolved oxygen	0.316	−0.311	−0.008
Humic acid	0.447	**−0.737**	0.150
pH	−0.463	**0.708**	0.244
Suspended material	−0.236	**0.623**	−0.236
Temperature	0.250	−0.424	0.077
Sand	**0.634**	0.272	−0.260
Clay	0.184	0.254	0.474
Fine litter	−0.042	0.282	**−0.766**
Litter	0.404	0.031	**−0.685**
Macrophytes	0.179	−0.453	−0.018
Roots	**0.601**	−0.331	0.056
Trunk	**0.684**	0.111	−0.374
Canopy cover	−0.167	0.167	0.377
% Variance Explained	29.91	17.70	10.04
% Accumulated Variance	29.91	47.61	57.65

Six species had high abundances, representing 87.3% of all the collected individuals. *Hyphessobrycon melazonatus* and *Pyrrhulina* cf. *brevis* contributed 37.1% and 20.5% of the individuals, followed by *Hemigrammus* cf. *pretoensis* (7.6%), *Aequidens pallidus* (6.8%), *Erythrinus erythrinus* (5.7%), and *Bryconops giacopinii* (4.2%).

The distribution of most species was related to drainage basin. Of the 49 species collected, 24 were found in both basins, 14 were collected only in the Western basin, and 11 only in the Eastern basin (Appendix 1). On average, nine species were collected in each stream section, and the number of species collected was independent of stream discharge ($r^2 < 0.001$, $F_{1,36} = 0.001$, $P = 0.97$). Nineteen species were collected in first, second, and third order streams; seven species were captured only in first order streams, five only in second order streams, and ten only in third order streams. Rarefaction analysis indicated that the number of species captured per site was similar to the number of species estimated to be present (Mean $N_{est.} = 8.57$, SD = 2.25). The estimated number of species per site was also independent of stream size ($r^2 = 0.001$, $F_{1,36} = 0.041$, $P = 0.840$). The two axes of the HMDS analysis captured most of the variation in the original dissimilarities among sites for quantitative data ($r^2 = 0.86$) and for presence/absence data ($r^2 = 0.74$).

Association between environmental parameters and fish assemblage structure.—Drainage basin was significantly related to ichthyofaunal composition for the ordinations based on presence/absence of species (MANOVA: Pillai Trace = 0.19, $F_{2,35} = 4.15$, $P = 0.024$). However, when this variable was included in the Multivariate Analysis of Covariance with the physical-chemical variables, there was evidence of an independent effect of drainage basin (MANCOVA: Pillai Trace = 0.16, $F_{2,32} = 3.17$, $P = 0.055$), in spite of the fact that other factors continued to have significant effects. Drainage basin was not significantly related to ichthyofaunal composition for ordinations based on quantitative data on species abundances (MANOVA: Pillai Trace = 0.09, $F_{2,35} = 1.77$, $P = 0.185$).

For quantitative data, streams of different sizes (Fig. 2a) were distinguished mainly along axis 1; however, drainage basins were not segregated in the ordination based on quantitative data (Fig. 2b). For qualitative data, streams of different sizes (Fig. 2c) were distinguished mainly along axis 2 and streams of different drainages by axis 1 (Fig. 2d).

Several factors associated with structural characteristics of the stream were highly correlated with the first PCA axis, which was significantly related to the ichthyofaunal composition of the streams for both quantitative (Multivariate Regression: Pillai Trace = 0.68, $F_{2,32} = 34.82$, $P < 0.001$) and qualitative (Pillai Trace = 0.63, $F_{2,33} = 27.62$, $P < 0.001$) ordinations. To illustrate differences mainly associated with stream size or associated factors, the abundance of each species was plotted against discharge (Fig. 3). Several species, such as *Aequidens pallidus* and *Pyrrhulina* cf. *brevis,* were found only or mainly in sites with low discharge. Others, such as *Bryconops giacopinii* and *Characidium* cf. *pteroides,* were associated with sites with high discharge rates. Many species were captured in only one or a few sites, and it was not possible to interpret their distributions in relation to environmental factors. However, some common species occurred mainly in only one of the basins (Appendix 1). For example, 103 individuals of *Bryconops giacopinii* were captured in 13 sites, but 92.3% of capture locations were in the western basin.

The second PCA axis, associated mainly with water-quality characteristics, was significantly related to the quantitative (Multivariate Regression: Pillai Trace = 0.19, $F_{2,32} = 3.82$, $P = 0.032$) and qualitative (Pillai Trace = 0.26, $F_{2,33} = 5.73$,

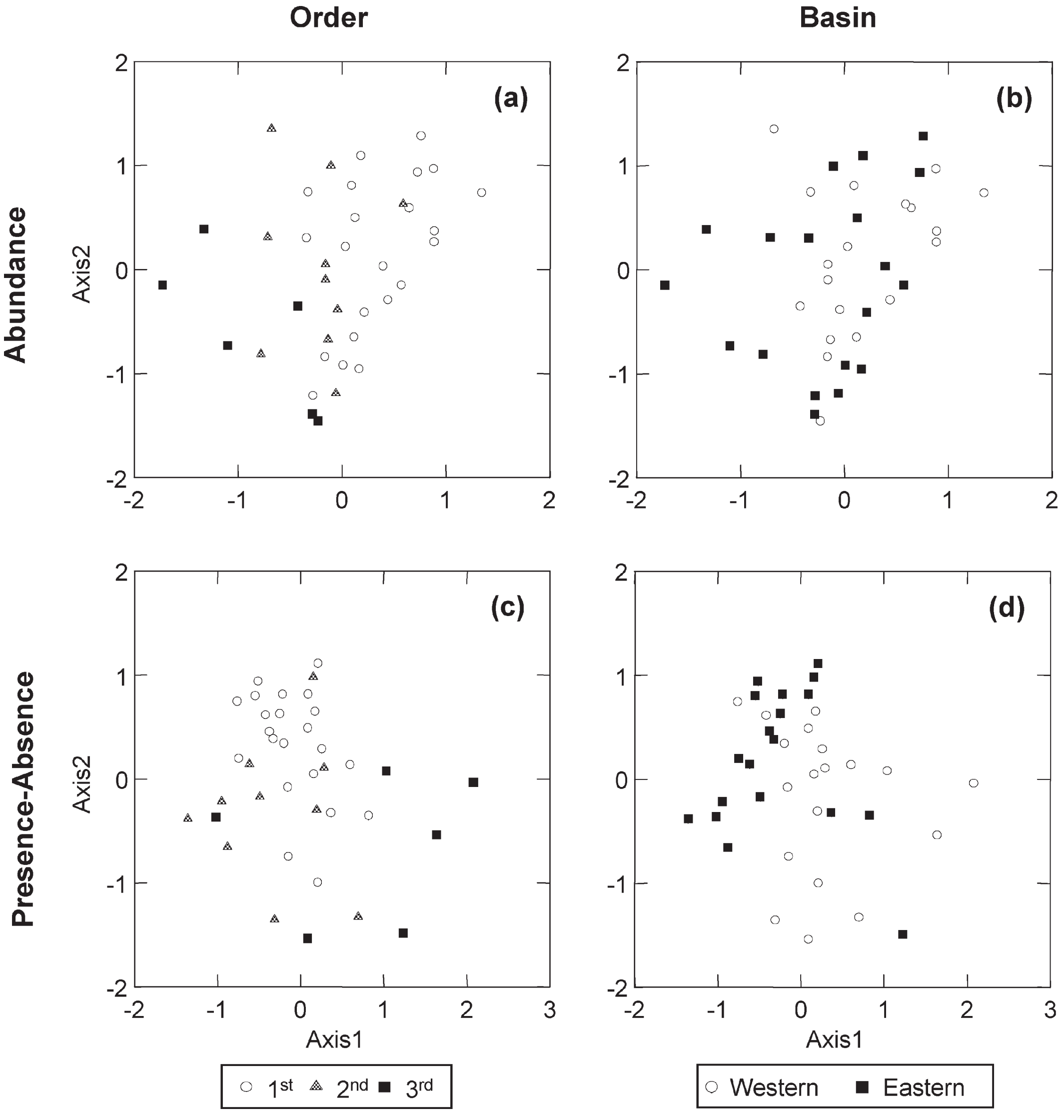

Fig. 2. Hybrid Multidimensional Scaling ordination of sites based on abundance of fish species (a and b) and presence/absence of fishes species (c and d). Each point represents fish assemblages along first, second, and third order streams (a and c) or in western and eastern basins (b and d).

P = 0.007) ordinations. However, the third PCA axis, associated with litter cover, was not significantly associated with fish assemblage for quantitative (Pillai Trace = 0.02, $F_{2,32}$ = 0.30, P = 0.742) or qualitative (Pillai Trace = 0.16, $F_{2,33}$ = 3.09, P = 0.059) ordinations.

Discussion

Detailed studies in Panama (Angermeier and Karr, 1984), Venezuela, Guyana, Suriname, and French Guiana (Ouboter and Mol, 1993; Hardman et al., 2002) indicate that streams of the Neotropical region have a high diversity of freshwater fishes. In Brazil, studies have been undertaken in the basins of the Alto Rio Paraná (Agostinho and Júlio, 1999), Rio São Francisco (Sato and Godinho, 1999), and the Amazon basin (Santos and Ferreira, 1999). In those areas, Characiformes dominated, followed by Siluriformes and Perciformes (mainly Cichlids). Gymnotiformes were common, while species of Cyprinodontiformes, Synbranchiformes, and other groups composed a smaller, but significant portion of the community. All these studies were focused on large rivers.

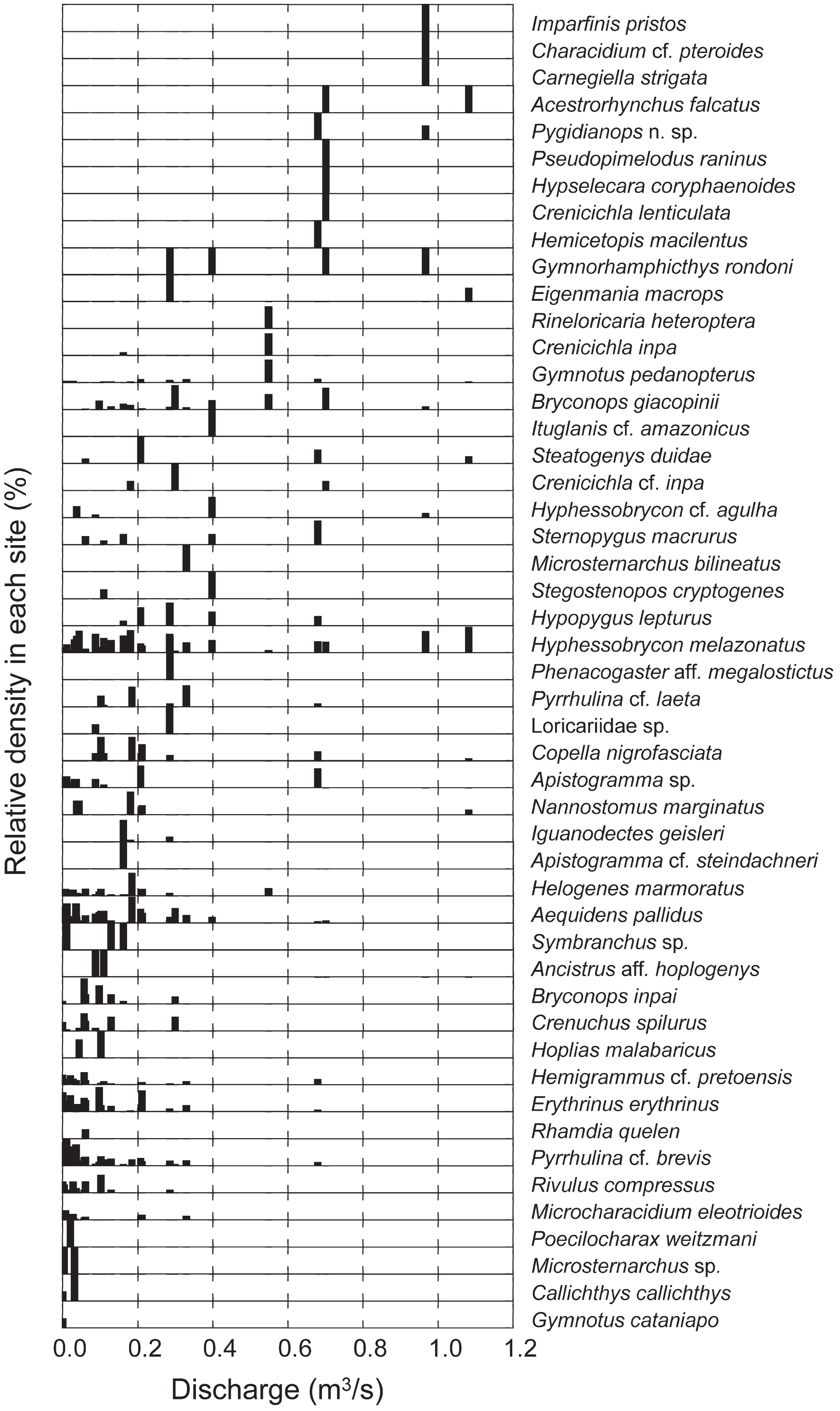

Fig. 3. Distribution of the relative frequency of capture of 49 fish species in Reserva Florestal Adolfo Ducke in relation to water discharge of streams. Total numbers of each species captured are given in Appendix 1.

In the small streams that compose the drainage basins of Reserva Florestal Adolfo Ducke, Characiformes and Siluriformes constituted more than half of the species in the fish communities. However, Gymnotiform richness was higher than that of Perciformes. This may have resulted from the methods used in this study. The use of electric discharge detectors was very effective in locating hidden Gymnotiform knifefishes, which indicates that abundances of these fishes may have been underestimated in previous studies. Siluriform richness may have been underestimated in our study because sampling was done during the day. If some Siluriform species were as deeply hidden as the knifefish, they may have gone undetected.

Bührnheim and Cox-Fernandes (2001) reported on the fish fauna of three second order streams of the Rio Urubu drainage basin, located 40 to 80 km north of the RFAD; Silva (1995) surveyed Igarapé do Candirú, a third to fourth order stream located in the Rio Puraquequara basin, which drains the eastern watershed of RFAD. In those studies, Characiformes were also predominant, however, the number of species of Perciformes was twice the sum of Siluriformes and Gymnotiformes together. It will be necessary to undertake more studies to compare the dominance of different taxonomic groups in *terra firme* streams in Central Amazonia. However, it seems that the higher level taxonomic composition of fish communities in first and second order streams differs from that of larger rivers.

The sampling unit employed in this study was a 50-m section of stream. Within each section, there were several meanders, resulting in a mosaic of substrates, depths, and current velocities. Therefore, it is only possible to relate the community to the mean conditions, and the inferences about the habitat associations of each species are restricted to this scale. Nonetheless, some patterns are apparent. Fish species distributions were associated with stream size. Some species, such as *Microcharacidium eleotrioides, Aequidens pallidus,* and *Pyrrhulina* cf. *brevis,* occurred predominantly in small streams. Others, such as *Pygidianops* n. sp. and *Characidium* cf. *pteroides* occurred only in third order streams. Mean current velocity also was associated to the community composition. *Aequidens pallidus* and *P.* cf. *brevis* occurred mainly in sections with slow-flowing pools, *Pygidianops* n. sp. and *C. pteroides* were found in areas of strong water flow and sandy substrate, and *Microcharacidium eleotrioides* occurred only in small rapids. Some species, such as *Hyphessobrycon melazonatus, Hemigrammus* cf. *pretoensis,* and *Bryconops giacopinii,* with wide distributions, showed less preference for specific sizes of stream or flow condition.

The species composition varied among streams of different sizes and different physical-chemical characteristics. However, the number of species found per 50-m section of stream was relatively constant ($\bar{X}$ = 9, SD = 1.96), indicating substitution of species along streams. Factors associated with water quality, such as humic acid concentration and suspended particles, were related to species composition but not to richness, indicating that water quality may limit the occurrence or abundance of some species.

It is difficult to determine which physical-chemical factors were influencing the fish fauna composition, because these factors were highly correlated with each other. Streams vary in the concentration of humic and fulvic acids, as well as dissolved salts, depending on the nature and age of parent material, slope, and vegetation cover (Walker, 1995). Conditions of extreme acidity and of low conductivity can directly affect fishes since such environments influence their ionic and acid-basic regulation (González, 1996; Val et al., 1999). Several groups of fish have physiological adaptations to survive in these extreme conditions and this may explain the diversity of species assemblages in the mosaic of physical-chemical conditions (Val et al., 1999). Possibly, different species are affected by different factors, but this would require more detailed autecological or physiological studies to determine individual responses.

Oxygen and temperature are known to affect the distribution of many Neotropical fishes (González, 1996; Rincón, 1999; Val et al., 1999). However, they probably have little influence on *terra firme* stream fish assemblages, because these factors vary little at small scales in forest habitats (Rincón, 1999). In headwater streams, the small depth, high current velocity and heterogeneity in channel shape generate turbulence that results in high oxygen saturation. Relatively constant temperature is also typical of Central Amazonian streams because there is little altitudinal variation, and the dense forest cover buffers the system against diurnal fluctuations. Although litter banks are thought to be critical habitats for many species of Amazonian fishes (Henderson and Walker, 1986, 1990; Walker, 1987), litter cover did not contribute significantly to the multivariate regression model predicting fish assemblage structure.

High concentrations of humic acids in the water are thought to occur in drainages with podzol sandy soils. Soluble humic acids are adsorbed by clay minerals in oxisol soils, resulting in clear waters (Leenheer, 1980). The topographical profiles of the reserve differ between the two main drainage basins. The eastern basin is steeper, with a dominance of clay soils, while the western basin has a larger area of broad valleys with sandy soils. Those characteristics may explain the differences in physical-chemical conditions between the basins, and the resulting differences between the fish assemblages.

The major differences between the basins could be due to local stream conditions, although historical effects or different biogeographic sources may explain the occurrence patterns of some species. The western basin drains to the Rio Negro, a typical black water river, and the eastern basin drains to the Amazon River, with turbid water due to the high load of solids in suspension. The low connectivity of the two basins (≈40 km apart by water) and the very different water quality of the Negro and Amazon rivers may represent an effective barrier to some species. However, some of the species that appeared to be exclusive to one of the studied basins in RFAD have been found in peripheral streams near the Reserve associated with the other basin (pers. obs.). This strengthens the hypothesis that differences in fish assemblage structure between basins are not due solely to differences in the pool of species available for colonization. More extensive sampling, and perhaps experiments, will be necessary to evaluate the relations between habitat diversity, disturbance, evolutionary processes, and demographic processes such as dispersal, and differences in fish assemblage structure between basins. Independent of the characteristics that cause the difference between these basins, the occurrence of divergent fish assemblages indicates that they should be considered different management units in conservation plans for the reserve.

The association among stream structural characteristics, water quality, and fish assemblages results in high species turnover between sites within the reserve. Mean species richness for 50-m sections of stream was relatively low ($\bar{X} = 9$) in relation to total recorded species for the reserve ($n = 49$). Studies of fish assemblages in small temperate streams (e.g., Lohr and Fausch, 1997; Angermeier and Winston, 1998; Mazzoni and Lobón-Cerviá, 2000) have revealed similar or higher numbers of species per site, showing a strong pattern of species addition along the stream systems. Nevertheless, numbers at individual sites generally represented more than half the total number of species recorded for the drainage basin. This difference may be related to a higher degree of specialization of the tropical fish fauna along the river continuum. Species inhabiting the headwaters of tropical systems show a very strong dependence on allochthonous resources (e.g., food, shelter) provided by the riparian forest (Goulding et al., 1988; Walker, 1991; Sabino and Zuanon, 1998) that may restrict their occurrence in higher order streams. Besides, these differences may indicate a strong biogeographical effect resulting from very different characteristics of the species pools available for colonization of the streams in each region. The richer Neotropical fish fauna provides a much more diverse species pool that results in higher species turnover between streams. Also, this highly diverse ichthyofauna and the typical low abundance of most of the fish species in these oligotrophic streams can impair the understanding of local scale distributional patterns, making it difficult to separate differences in assemblage structure from sampling effects.

The tropical species in this study showed greater habitat segregation than temperate species (Paller et al., 2000); however, similar habitat segregation patterns may occur in some temperate streams, where young-of-the-year segregate ecologically from adults and increase functional complexity of fish assemblages (e.g., Moyle and Vondracek, 1985). Studies of other tropical assemblages will be necessary to determine whether the pattern seen in RFAD is typical of most other tropical systems.

Reserva Florestal Adolfo Ducke appears to protect only a limited portion of the regional fauna of headwater fish. Bührnheim and Cox-Fernandes (2001) found 35 fish species in their study of the Urubu River basin, about 100 km from RFAD. Of these, only 17 were recorded in RFAD. Of the 44 species found by Silva (1995) in Igarapé Candirú, approximately 5 km from RFAD, only 10 species were captured during this study. The total number of species found in the three areas studied was similar, but the composition of species was very different, even though the areas are close to each other and belong to the same geological formation (Alter do Chão formation). The apparently high spatial turnover may result from environmental sorting, as indicated by significant effects of the physical-chemical factors in this study. However, when many species are rare, differences between studies may also result from inadequate sampling.

Recruitment limitation can reduce the effects of competitive interactions in highly diverse communities with many rare species, even when some species are competitively superior habitat specialists (Hurtt and Pacala, 1995). Species that are rare but widespread will require large or interconnected reserve systems to maintain viable populations. Therefore, independent of habitat selectivity or sampling problems, there is a need for more conservation units in Central Amazonia to conserve a representative portion of the species diversity of headwater-stream fishes. Although other forms of reserves may protect the terrestrial biota, large and connected areas are necessary to protect the stream fauna (Pringle, 2001), since these habitats are generally the first to be impacted by any form of land use.

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Appendix 1. Number of Sample Sites Where Each Species was Captured in Each Drainage Basin (Sites) and Number of Individuals Captured in each Drainage Basin (N) of Reserva Florestal Adolpho Ducke.

	Western B.		Eastern B.	
	Sites	N	Sites	N
CHARACIFORMES				
ACESTRORHYNCHIDAE				
Acestrorhynchus falcatus	1	1	1	1
CHARACIDAE				
Bryconops giacopinii	12	102	1	1
Bryconops inpai	8	22	—	—
Hemigrammus cf. *pretoensis*	9	96	2	89
Hyphessobrycon cf. *agulha*	2	8	2	8
Hyphessobrycon melazonatus	18	430	16	475
Iguanodectes geisleri	3	15	—	—
Phenacogaster aff. *Megalostictus*	—	—	1	1
CRENUCHIDAE				
Characidium cf. *pteroides*	1	3	—	—
Crenuchus spilurus	7	45	3	4
Microcharacidium eleotrioides	6	16	10	53
Poecilocharax weitzmani	1	2	—	—
ERYTHRINIDAE				
Erythrinus erythrinus	13	74	14	64
Hoplias malabaricus	1	1	1	1
GASTEROPELECIDAE				
Carnegiella strigata	1	2	—	—
LEBIASINIDAE				
Copella nigrofasciata	2	4	6	18
Nannostomus marginatus	3	8	2	3
Pyrrhulina cf. *brevis*	15	126	17	374
Pyrrhulina cf. *laeta*	—	—	5	10
SILURIFORMES				
CALLICHTHYIDAE				
Callichthys callichthys	1	1	1	1
CETOPSIDAE				
Helogenes marmoratus	14	23	8	19
Denticetopsis seducta	—	—	1	1
LORICARIIDAE				
Ancistrus aff. *Hoplogenys*	—	—	2	2
Loricariidae sp. (Juvenile)	1	1	1	1
Rineloricaria heteroptera	1	1	—	—
PIMELODIDAE				
Rhamdia quelen	—	—	1	1
Batrachoglanis raninus	1	2	—	—
Imparfinis pristos	1	1	—	—
TRICHOMYCTERIDAE				
Ituglanis cf. *amazonicus*	1	1	—	—
Pygidianops n. sp.	1	1	1	1
PERCIFORMES				
CICHLIDAE				
Aequidens pallidus	17	58	16	108
Apistogramma sp.	—	—	10	28
Apistogramma cf. *steindachneri*	1	1	—	—
Crenicichla cf. *inpa*	3	3	—	—
Crenicichla inpa	2	2	—	—
Crenicichla lenticulata	1	1	—	—
Hypselecara coryphaenoides	1	1	—	—
GYMNOTIFORMES				
GYMNOTIDAE				
Gymnotus cataniapo	—	—	1	2
Gymnotus pedanopterus	4	7	8	9
HYPOPOMIDAE				
Hypopygus lepturus	3	4	3	5
Microsternarchus bilineatus	—	—	1	1
Microsternarchus sp.	—	—	2	3
Steatogenys duidae	—	—	4	4
Stegostenopos cryptogenes	1	1	1	1
RHAMPHICHTHYIDAE				
Gymnorhamphichthys rondoni	3	5	1	2
STERNOPYGIIDAE				
Eigenmannia macrops	—	—	2	2
Sternopygus macrurus	2	4	3	7
CYPRINODONTIFORMES				
RIVULIDAE				
Rivulus compressus	3	26	11	36
SYNBRANCHIFORMES				
SYNBRANCHIDAE				
Synbranchus sp.	2	2	1	1

ERRATUM

In the figure 3 substitute:

- "*Pseudopimelodus raninus"* for "*Batrachoglanis raninus"*
- *"Hemicetopis macilentus*" for "*Denticetopsis seducta"*
- *"Symbranchus* sp.*"* for *"Synbranchus* sp.*"*