

Seasonal variation in the composition of fish assemblages in small Amazonian forest streams: evidence for predictable changes

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SUMMARY

1. The effects of seasonal inundation on the biology of fishes on floodplains of large Amazonian rivers are well studied. However, the small seasonal changes in headwater streams are generally considered to have little effect on fish assemblages.
2. In this study, we analysed seasonal changes in the species composition and abundance of fish in small Amazonian forest streams. We sampled fish with hand and seine nets in headwater streams in a 10 000 ha *terra-firme* forest reserve near Manaus, Brazil. Each stream was surveyed at the end of the 2005 dry season, at the beginning of the 2006 rainy season and at the beginning of the 2006 dry season, by means of a standardized sampling effort.
3. The numbers of individuals and species caught were higher in the dry season, but rarefaction analyses indicated that greater species numbers could have been due simply to the larger number of individuals caught.
4. Between the dry and rainy season, the direction of changes in species composition in multivariate space varied among sites, especially for quantitative (abundance) data. However, the observed variation among sites was the less than expected if the directions of change were random.
5. Fish assemblages in the second dry season were more similar to those in the previous dry season than expected if changes in species composition among seasons were random. This indicates that a general seasonal pattern in fish assemblages can be detected, despite the existence of some erratic site-specific changes.
6. Most of the species that showed large seasonal variations in density occupy temporary ponds during the rainy season, when much of the valley is inundated and pond networks form adjacent to streams. Short-duration lateral migrations to these ponds may play an important role in the seasonal fish-assemblage dynamics in Amazonian headwater streams.
7. Our results contrast with previous studies on small Amazonian streams, which have found little seasonal change in fish assemblages, and highlight the importance of the abundance of common species as an indicator of general fish assemblage structure in biological monitoring programmes.

Keywords: biodiversity assessment, community ecology, monitoring programmes, seasonality, tropical fish assemblages

Introduction

The seasonality of rainfall in Amazonia produces a gradual change in the volume of large rivers, generating an annual flood pulse closely associated with fish migrations. In the rainy season, many species make extensive longitudinal migrations upriver to reproduce, and others migrate laterally into the inundated forest to feed on fruits, seeds and terrestrial arthropods. These seasonal movements generate substantial shifts in fish density and assemblage composition throughout the year (Rodríguez & Lewis, 1997; Saint-Paul *et al.*, 2000).

In *terra-firme* (non-flooded) forests, small streams form a complex network of waterbodies, which constitute a large part of the Amazonian fluvial ecosystem. Water volume in streams does not vary gradually and predictably as observed in the large rivers but is related to the shorter and more frequent high flow events (Sioli, 1984; Walker, 1995). Local rainstorms increase the stream levels and inundate the adjacent valley for only a few hours to days at a time. During the rainy season, water from streams overflows and generates a complex system of lateral ponds which retain water for 3–11 months of the year and can maintain diverse fish assemblages, depending on pond area and hydroperiod (Pazin *et al.*, 2006).

In temperate regions, where temperature and discharge show strong seasonal variation, fish assemblages of small streams change in composition throughout the year (Gorman & Karr, 1978; Schlosser, 1982; Grossman, Dowd & Crawford, 1990; Oberdorff, Hugueny & Vigneron, 2001; Erös & Grossman, 2005). In forest streams of the Brazilian Amazon, however, seasonal changes in physical characteristics are less drastic and fish assemblages in small streams are expected to show little seasonal variation (Lowe-McConnell, 1991). Indeed, no significant differences in fish composition, species richness, or in the abundance of the more common species were detected between rainy and dry seasons in some central Amazonian small streams (Bührnheim & Cox-Fernandes, 2001). Those authors concluded, based on four surveys in 1 year in three streams of the Negro River basin, that deterministic processes are more important than environmental changes in determining the temporal stability of fish assemblages.

In a larger-scale study, Mendonça, Magnusson & Zuanon (2005) sampled 38 forest streams in Central Amazonia and showed that fish assemblage composition in headwaters changed spatially with stream size and limnological characteristics. However, no attempt was made to evaluate whether the environmental features and fish composition varied temporally. The presumed stability of physicochemical features, stream physical structure and fish assemblages has important implications for monitoring programmes and the evaluation of human impact. If seasonal or annual changes in fish faunal composition occur, they could be mistaken for human impacts, with direct implications for management plans and conservation efforts.

The central aims of this study are to test if fish assemblage composition in small Amazonian headwater streams varies between rainy and dry seasons and to evaluate the role of environmental features in changes in fish assemblages. Specifically, we tested for differences in the number of species detected, total fish abundance and assemblage composition between two dry and one rainy season, and asked whether changes in fish assemblages were related to changes in physical structure of streams and water quality between sampling occasions.

Methods

Study area

This study was conducted in Reserva Ducke, a 10 000 ha protected area of tropical rainforest near Manaus, Amazonas State, Brazil. This reserve is located near the confluence of the blackwater Negro River and the whitewater Amazon River, in the Brazilian Amazon (02°53'S, 59°58'W; Fig. 1). The area corresponds to site 1 of the Brazilian Long-Term Ecological Research Program (PELD), and is part of the Biodiversity Research Program (PPBio) of the Brazilian Ministry of Science and Technology (MCT). The rainfall regime in the Manaus region is characterized by a rainy season from December to May (211–300 mm mean monthly rainfall), and a dry season from June to November (42–162 mm mean monthly rainfall) (Ribeiro & Adis, 1984). The mean annual temperature in Reserva Ducke is about 26 °C (Marques-Filho, Ribeiro & Santos, 1981). The altitude varies from 40 to 110 m above sea level, and a central

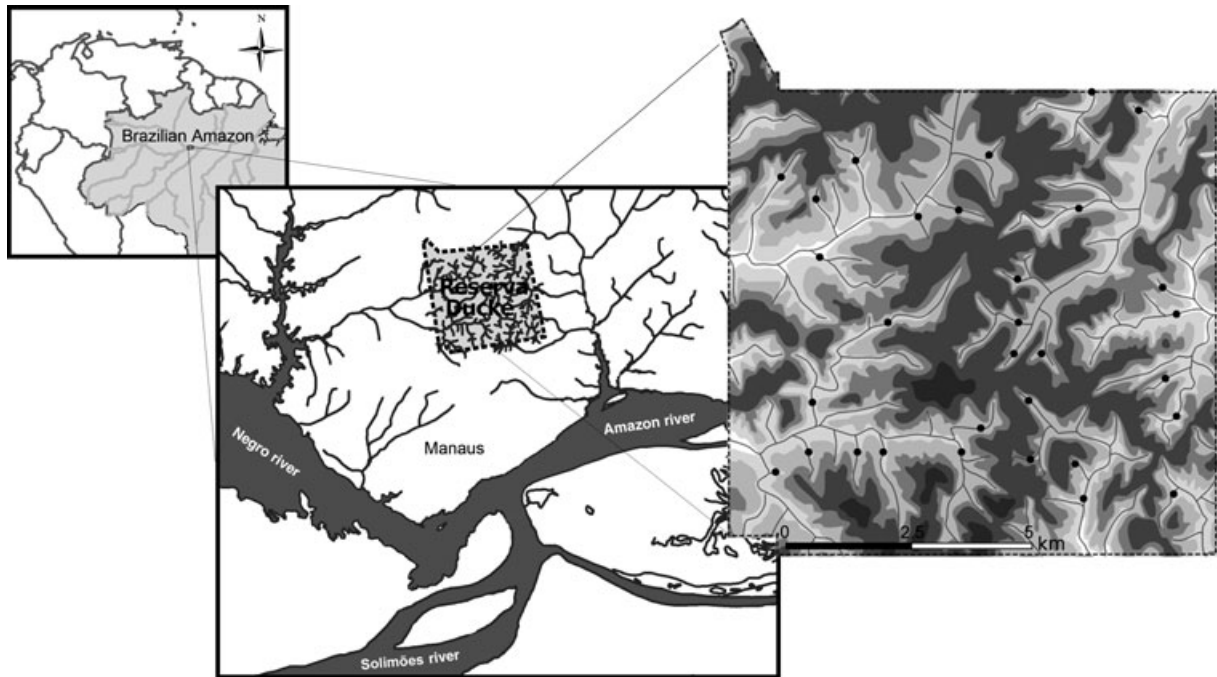


Fig. 1 Location of Reserva Ducke. The right figure shows the topography and hydrology, and the spatial distribution of 31 sampling sites (black closed circles).

plateau oriented north–south divides the Reserve into two drainage systems. On the west side, streams drain into the Tarumã Stream, a fourth-order (*sensu* Petts, 1994) tributary of the Negro River. On the east side, the water flows to the Puraquequara Stream, a fourth-order tributary of the Amazon. In the small headwater streams, the dense canopy shades the stream bed, resulting in low primary productivity (Walker, 1995) and very clear water.

Data collection

Thirty-one headwater streams were surveyed in Reserva Ducke, 16 in the Puraquequara basin and 15 in the Tarumã basin (Fig. 1). The sampling sites coincided with permanent aquatic plots established in a previous study (Mendonça *et al.*, 2005). We sampled each stream three times between September 2005 and August 2006. The first survey (September–November 2005) corresponded to the late dry season, the second survey (February–May 2006) was undertaken in the rainy season and the third survey (June–August 2006) at the beginning of the 2006 dry season. The total rainfall in Reserva Ducke between September 2005 and August 2006 was 3249 mm, with monthly mean of 196 mm in the first dry season

(September–November 2005), 393 mm in the rainy season (December 2005–May 2006) and 102 mm in the second dry season (June–August 2006) (Fig. 2).

Each sampling site consisted of a 50 m stretch of stream. The three sets of samples were collected in the same stretches, with the same equipment, number of collectors and sampling time on each survey occasion. All sampling methods followed the standardized protocol recommended by the PPBio Program (available at <http://ppbio.inpa.gov.br/Eng>).

Our survey was designed to test for differences in stream-fish faunal characteristics among seasons. We did not collect fish or environmental data during rain storms, but waited until stream volume and water turbidity returned to conditions similar to those before the rainfall event. Data on stream structure and physicochemical characteristics of the water were obtained prior to fish sampling, to avoid disturbing the substratum. Structural measures were made along four transects in each 50-m stream stretch, spaced 16 m apart. Surface water velocity was estimated by recording the time a 30 mm diameter floating plastic disc took to drift 1 m downstream and total channel width was measured. Depth was measured at nine equidistant points along each transect, and at each point we recorded the type of substratum touched by

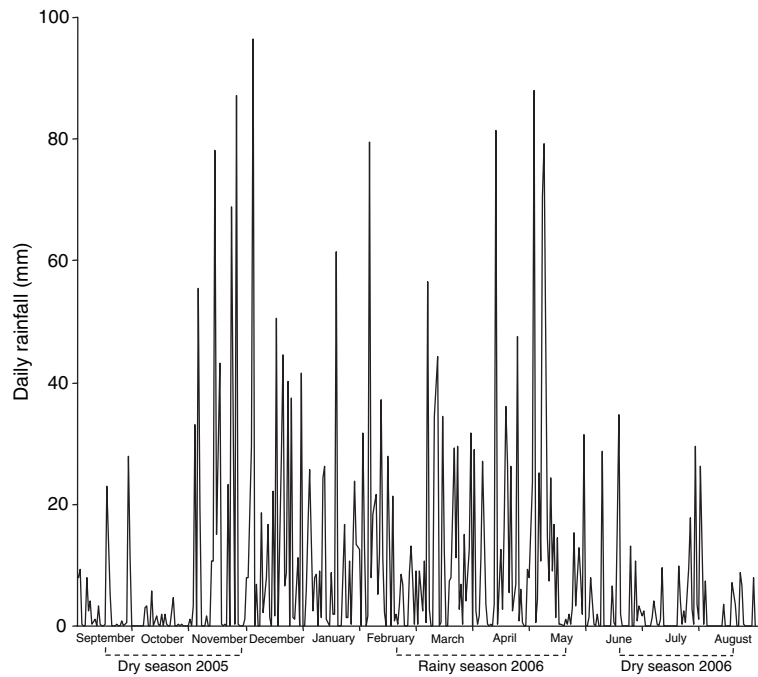


Fig. 2 Daily rainfall (in mm) between September 2005 and August 2006 registered in the meteorological station of Reserva Ducke. Dotted lines indicate the rainfall during sampling occasions.

the measuring stick. Substratum categories were sand, pebble, clay, trunk (wood with diameter over 10 cm), litter (leaves and small branches), fine litter (organic silt), roots (roots from riparian vegetation), fine roots (fine root tangles) or macrophytes (*Thurnia sphaerocephala* Hook. f. Thurniaceae) (adapted from Mendonça *et al.*, 2005). Physicochemical characteristics of the water were measured at the downstream end of the stretch, in the centre of channel and at midwater. We used a portable Aqua-Check™ Water Analyzer Operator (O.I. Analytical, College Station, TX, U.S.A.) to measure pH and conductivity and a Yellow Springs Instruments™ (Yellow Springs, OH, U.S.A.) model 58 portable oxygen meter/thermometer, for dissolved oxygen and water temperature. Humic acid concentration was determined in the laboratory by absorbance at 400 nm in a spectrophotometer Femto 700S (Femto Ind. Com. Instruments LTDA, São Paulo, Brazil), using pre-filtered water samples. For detailed sampling methods see Mendonça *et al.* (2005).

Prior to fish sampling, we blocked the 50-m stream stretch with two nets (5 mm mesh size) to prevent fish escaping; two additional nets were used to subdivide the stretch further and to facilitate fish capture. Two persons with hand and seine nets (2 mm stretched mesh) captured fish during a 2-hour period or until no fish were observed moving in the stream stretch. We retained the fish captured in a plastic box with stream

water until the end of sampling, when they were identified, counted and released. Some specimens from species difficult to identify in the field were preserved in 10% formalin and later identified using taxonomic keys or by specialists. Voucher specimens were deposited in the INPA Fish Collection (INPA 27695-27942 and 28615-28628).

Data analyses

All analyses were performed with the R statistical software (R Development Core Team, 2007) and the respective libraries used in particular analysis are cited. When variable distributions did not meet the assumption of normality we used nonparametric tests.

All the environmental variables measured were used to test for seasonal changes. To describe the substratum diversity we used Simpson's diversity index (Magurran, 1988), which considers the number and relative proportion of different substratum categories in each sampling site, according to the equation:

$$DS = \frac{1}{\sum_i^N S_i^2}$$

where S_i , the proportion of each substratum i and N , the number of substratum types in the stretch.

As there was little correlation between the physicochemical, structural characteristics and the substratum properties of streams, we conducted one nonparametric multivariate analysis of variance (np-MANOVA) for each of these variable sets to test for differences between seasons. The np-MANOVA was run using the function *adonis* provided by the *vegan* library (Oksanen *et al.*, 2007) for R.

To test for differences in fish assemblage attributes among seasons, we conducted an analyses of variance (ANOVA) on the total number of fish caught and the total number of species as dependent variables. As the number of species detected can be a function of the number of individuals caught (Gotelli & Colwell, 2001), we repeated the test based on the number of species rarefied to the minimum number of individuals caught in any stream over the three seasons.

To test for differences among seasons in the overall fish assemblage composition, we ran a np-MANOVA, both for quantitative (fish abundance) and qualitative (presence-absence) data. For quantitative data, we used the Bray-Curtis index (Faith, Minchin & Belbin, 1987) to construct the dissimilarity matrix, after dividing the number of individuals in each species by the total number of fish at each sampling site. Analysis with quantitative data favours the detection of patterns from the most abundant species, as the absolute values of differences among sites generally have greater quantitative contribution to the ordination. For qualitative data, we used the Sørensen index (Legendre & Legendre, 1998). In this qualitative ordination, the most abundant species generally contribute less to differences, as they are present in most sites.

To reduce the dimensionality of fish composition data and generate a visual representation of differences among sites and seasons, we ran a non-metric multidimensional scaling analyses (nMDS; Clarke, 1993), reducing the information from many species (attributes) to a small number of axes (McCune & Grace, 2002). The indices used for quantitative and qualitative ordination were the same as for the np-MANOVA.

To test whether changes between the first dry season and the rainy season were random or there was a general directional trend independent of site-specific differences, we used Rayleigh's test (Zar, 1999). We tested whether the directions of change in multivariate space represented by the nMDS axes

were random or tended to concentrate in the same direction.

To evaluate if changes in fish assemblage composition (both qualitative and quantitative data) had a seasonal tendency larger than expected by chance, we used the nMDS axes in two dimensions as predictors of fish assemblage composition. From the original nMDS site positions (first dry season), we simulated 5000 changes in composition in random directions to estimate a random position for fish composition in the rainy season, maintaining the original Euclidean distance between first dry season and the rainy season for each site. Next, we simulated 5000 changes in composition in random directions from each estimated rainy season position in order to calculate a random position for the second dry season, maintaining the original Euclidean distances between the rainy and the second dry season (for further details see Fig. 3). The null model was constrained to produce values within the observed range of values for the real community. When any simulated value was out of the original range, these values were discarded and another position was calculated. Finally, for each site we calculated the distance from the position in the first dry season to the position in the second dry season for both the observed nMDS position and for second dry season simulated positions. The proportion of mean simulated distances that was smaller or equal to the original distance was used as the probability that the observed seasonal tendency was only due to chance (null hypothesis).

The simulation procedure we used is similar to that of Ault & Johnson (1998), and we used the same statistic (the distance between the first and last sample season). However, in order to test for the whole assemblage predictability, we used the mean of the 31 site distances instead of individual site values as a measure of assemblage stability. As an alternative test of the same hypothesis, we calculated the turning angles formed by the trajectory of the transition of 2005 dry to 2006 rainy to 2006 dry seasons, as used in quantitative analysis of movement (Turchin, 1998). The proportion of mean simulated angles smaller or equal to the observed mean angle was used as an estimate of the probability of obtaining the observed mean angle under the null hypothesis. The turning angles were calculated using the R library *adehabitat* (Calenge, 2006).

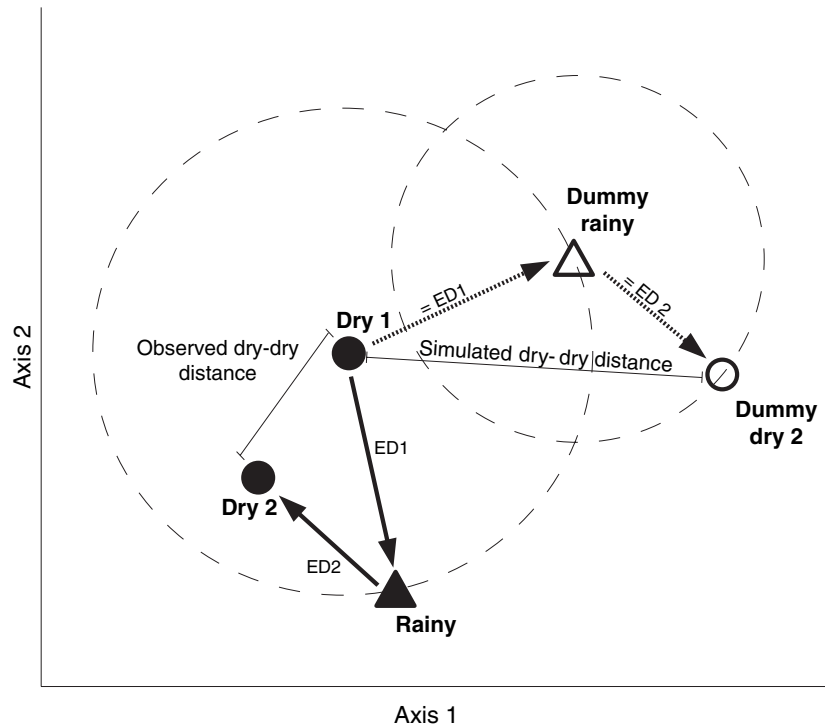


Fig. 3 Schematic representation of the simulation procedure for a sampling site. Closed and open symbols represent nMDS scores for observed and simulated data respectively. Circles represent the dry periods and triangles indicate the rainy period. The size of the circle is given by the Euclidean Distance (ED) between the seasons and its circumference indicates the possible positions of simulated values. Dry-Dry distance is the distance between the first and second dry seasons, both for observed and simulated values.

To test if differences in assemblage attributes between seasons were related to changes in environmental characteristics, the differences in fish-assemblage attributes (total number of fish species, total fish abundance and composition) were regressed against the differences in environmental characteristics. To do this, we calculated distance matrices for fish assemblage attributes and for environmental characteristics between the rainy and dry seasons. For the number of species detected, total fish abundance and environmental characteristics, we used Euclidean distances, and for assemblage composition we used Bray–Curtis and Sørensen indices, respectively, for species abundance and occurrence. We retained only the temporal portion of differences (i.e. differences between seasons for a given sampling site), discarding any differences between sites. Only the variables which showed significant differences between seasons were used to calculate the environmental distance matrix. Those were conductivity, dissolved oxygen, substratum diversity and the proportions of the substratum made up by sand and litter (Table 1). We used regressions to test the relationships between changes in the fish fauna and in the environment using two data sets, one from the 2005 dry season to the 2006 rainy season, and

other from the 2006 rainy season to the 2006 dry season.

Results

The streams had clear, acid and well oxygenated waters, with low conductivity and relatively stable temperatures (Table 1). The physicochemical characteristics of the water differed between seasons (np-MANOVA: F model = 9.8; $r^2 = 0.178$; $P \leq 0.001$; 5000 permutations; Table 1). However, despite notable difference in rainfall between the seasons (Fig. 2), the variables related to stream volume (width, depth, mean flow velocity and discharge; ranges of values in Table 1) did not show significant differences among sampling seasons (np-MANOVA: F model = 2.1; $r^2 = 0.045$; $P = 0.101$; 5000 permutations).

Six substratum categories were recorded frequently: sand and pebble, fine leaf litter, coarse leaf litter, roots and woody debris. Differences in substratum properties were detected between seasons (np-MANOVA: F model = 8.3; $r^2 = 0.155$; $P \leq 0.001$; 5000 permutations), with a higher proportion of sand (ANOVA: $F_{2,90} = 29.6$; $P < 0.001$), a lower proportion of litter (ANOVA: $F_{2,90} = 14.8$; $P < 0.001$) and higher substratum diver-

Table 1 Mean (range) of environmental characteristics in the three sampling periods in Reserva Ducke streams

Environmental variables	Mean (range)		
	2005 dry season	2006 rainy season	2006 dry season
Physicochemical (F model = 9.8; $P < 0.001$)			
pH	5.11 (4.38–5.60)	4.92 (4.14–5.53)	4.97 (4.31–5.60)
Conductivity ($\mu\text{S cm}^{-1}$)*	38.6 (2.1–85.5) a	24.50 (7.6–78.6) b	43.36 (3.3–84.6) a
Dissolved oxygen (mg L^{-1})*	6.59 (4.99–7.52) a	5.01 (3.57–7.08) b	5.51 (4.51–6.56) b
Temperature ($^{\circ}\text{C}$)	24.9 (23.9–26.2)	24.5 (21.7–25.3)	24.5 (23.0–25.2)
Humic acids (Abs.)	0.017 (0.003–0.057)	0.027 (0.004–0.105)	0.022 (0.005–0.091)
Structural (F model = 2.1; $P = 0.10$)			
Width (m)	1.83 (0.85–3.28)	2.18 (0.93–5.28)	2.14 (1.01–4.63)
Depth (m)	0.20 (0.05–0.46)	0.24 (0.05–0.53)	0.24 (0.05–0.53)
Flow velocity (m s^{-1})	0.16 (0.04–0.37)	0.21 (0.05–0.39)	0.19 (0.01–0.33)
Discharge ($\text{m}^3 \text{s}^{-1}$)	0.07 (0.01–0.28)	0.12 (0.01–0.45)	0.10 (0.01–0.44)
Substrate (F model = 8.3; $P < 0.001$)			
Substratum diversity*	3.15 (1.59–4.98) a	3.93 (2.76–6.00) b	3.30 (1.55–4.95) a
Sand*	42.7 (22.2–77.8) a	27.0 (5.6–58.3) b	47.5 (22.0–77.8) a
Litter*	21.1 (0.0–44.4) a	32.1 (19.4–52.8) b	18.5 (0.0–38.9) a
Fine litter	12.4 (0.0–47.2)	16.0 (0.0–50.0)	12.1 (0.0–38.9)
Fine roots	8.5 (0.0–25.0)	12.5 (0.0–36.1)	12.5 (2.8–30.6)
Roots	5.5 (0.0–27.8)	6.9 (0.0–36.1)	3.0 (0.0–16.7)
Trunk	3.6 (0.0–13.9)	3.5 (0.0–19.4)	5.1 (0.0–19.4)
Others	1.7 (0.0–27.8)	2.1 (0.0–11.1)	1.2 (0.0–8.3)

The values for the substratum categories are presented as proportions of the total. The letters after the range in each season identify comparisons that did not show significant ($P < 0.05$) pair-wise differences among seasons (Tukey *post hoc* tests).

*Variables that showed significant differences.

Table 2 Mean and SD (range) of the fish-fauna attributes in each sampling season between September 2005 and August 2006 in Reserva Ducke streams

Fish fauna attributes	Mean \pm SD (range)			$F_{2,90}$	P -value
	2005 dry season	2006 rainy season	2006 dry season		
No. species	10.0 \pm 2.82 (5–15) a	8.06 \pm 1.94 (5–12) b	9.74 \pm 3.27 (6–18) ab	4.5	0.013
Total no. fish caught	71.35 \pm 33.70 (12–132) a	52.83 \pm 24.58 (13–104) b	75.22 \pm 33.62 (25–139) a	4.6	0.012
Rarefied species richness	9.13 \pm 2.54 (3.42–14.80) a	7.87 \pm 1.94 (3.83–12.00) b	8.16 \pm 2.18 (3.85–12.17) ab	2.7	0.072

The letters after the range in each season identify comparisons that did not show significant ($P < 0.05$) pair-wise differences in Tukey *post hoc* tests.

*Significant (ANOVA, $P < 0.05$) differences between seasons.

sity (SD index; ANOVA: $F_{2,90} = 7.5$; $P = 0.001$) in the rainy season than in the two dry seasons (Tukey *post hoc* tests; Table 1).

We captured 6182 individuals of 53 species, 16 families and six orders (Appendix S1). Twenty-one species belonged to the order Characiformes, 15 to Siluriformes, nine to Gymnotiformes, five to Perciformes, two to Cyprinodontiformes and one to Synbranchiformes. Characiformes was also the most abundant group, comprising 76% of the total number of fish caught. Six species were highly abundant and frequent [*Hyphessobrycon melazonatus* (Durbin in Eigenmann, 1908) (15.9%), *Pyrhulina brevis* (Steindachner, 1875)

(15.3%), *Bryconops giacopinii* (Fernández-Yépez, 1950) (13.0%), *Microcharacidium eletrioides* (Géry, 1960) (11.9%), *Aequidens pallidus* (Heckel, 1840) (7.1%) and *Rivulus kirovskyi* (Costa, 2004) (7.1%)] and together they represented 70% of the fish collected. Some species were scarce and infrequent, impairing inferences about their distributional patterns. Thirty species were detected in the three sampling periods, with large differences in abundance between seasons (Appendix S1). The characid *H. melazonatus*, the crenuchid *M. eletrioides* and the rivulid *R. kirovskyi* were numerous in the two dry seasons, but much less abundant during the rainy season. *Bryconops giacopinii*, the third most

abundant species in the samples, increased in number of collected specimens throughout the study, while other species, such as *Crenuchus spilurus* and *Synbranchus marmoratus*, were mostly collected in the rainy season.

The number of species (ANOVA: $F_{2,90} = 4.5$; $P = 0.013$) and total number of fish caught (ANOVA: $F_{2,90} = 4.6$; $P = 0.012$) differed among seasons (Table 2). Tukey *post hoc* tests detected a higher number of species and total number of fish caught in the two dry seasons than in the rainy season (Appendix S2). No difference was detected in the number of species or the total number of fish caught between the two dry seasons. The effect of seasons on rarefied species richness was not statistically significant (ANOVA: $F_{2,90} = 2.7$; $P = 0.072$), though the low probability indicates a possible type II error. To test for the effect of common species on the results, we removed the six most abundant species (corresponding to nearly 70% of the total number of fish caught) and reran the analysis, resulting in non significant seasonal differences in total number of fish caught (ANOVA: $F_{2,90} = 1.0$; $P = 0.367$).

The two nMDS analyses used to reduce the dimensionality of fish composition captured 89.5% and 85.5% of the initial dissimilarity matrices, for quantitative and qualitative data respectively. There were large differences among sites within seasons (Figs 4 & 5), and np-MANOVA did not detect significant differences in composition between seasons for either quantitative (np-MANOVA: $F_{2,90} = 1.6$; $P = 0.082$) or qualitative (np-MANOVA: $F_{2,90} = 1.5$ $P = 0.106$) data. However, almost all sites changed markedly in composition from the first dry season to the rainy season and Rayleigh's test indicated that those changes were significantly more directional than expected for random changes for both quantitative ($P < 0.05$) or qualitative data ($P < 0.005$). In the second dry season, the composition tended to return to its initial composition, resulting in small distances between the two dry season scores in the nMDS plot and in acute angles (i.e. $<90^\circ$) for the temporal trajectories of individual sampling sites, in both quantitative (Fig. 4) and qualitative data (Fig. 5). The simulation procedure indicated that the tendency to return toward initial values occurred more frequently than expected for random trajectories both for quantitative ($P < 0.001$) and qualitative data ($P < 0.001$). The simulation for quantitative data without the six

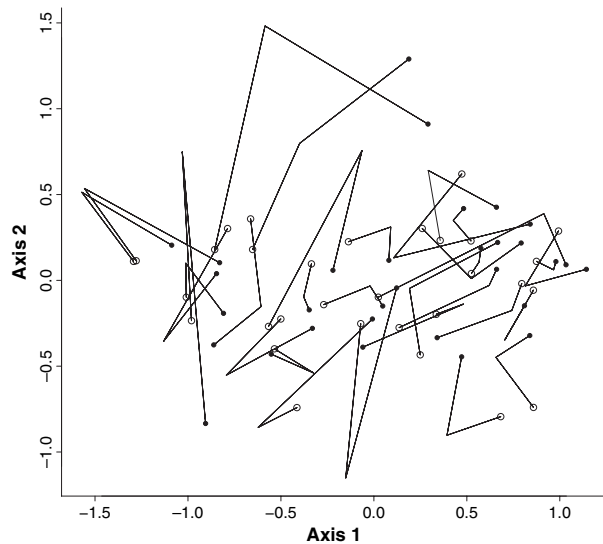


Fig. 4 Position of sampling sites in the two dimensional nMDS ordination space based on relative abundance and fish-assemblage composition (54 species and 31 sampling sites). Open circles indicate nMDS scores for sites in the 2005 dry season, the vertices indicate the 2006 rainy season and closed circles the 2006 dry season. No groups related to seasons were readily evident, although individual sites tended to return to the composition observed in the first dry season, as indicated by the short distances between dry-season scores for each site and by the acute angles. Species relative abundance refers to the number of specimens of individual species divided by the total abundance of fish at each sampling site.

most abundant species resulted in the same conclusion ($P < 0.001$). Simulations based on return angles had less power to detect changes, but gave qualitatively similar conclusions (Table 3).

To investigate which environmental variables of those differing among seasons were most closely associated with the changes in the total number of species and total number of fish caught, we regressed them on the absolute differences between two consecutive seasons (i.e. 2005 dry–rainy, rainy–2006 dry). Differences in the number of species (dry1–rainy: $r^2 = 0.06$, $P = 0.186$; rainy–dry2: $r^2 = 0.02$, $P = 0.453$) and in the total number of fish caught (dry1–rainy: $r^2 = 0.002$, $P = 0.836$; rainy–dry2: $r^2 = 0.002$, $P = 0.793$) were not related to the any of environmental variables measured.

Discussion

Although some physicochemical characteristics of the streams showed significant differences between rainy and dry seasons, variables related to stream volume

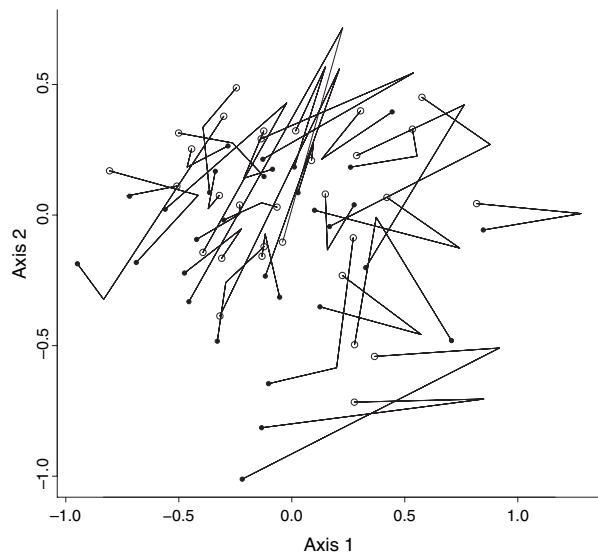


Fig. 5 Position of sampling sites in the two dimensional nMDS ordination space based on the occurrence data for fish-assemblage composition (54 species and 31 sampling sites). Open circles indicate nMDS scores for sites in the 2005 dry season, the vertices indicate the 2006 rainy season and closed circles the 2006 dry season. No groups related to seasons were readily evident, although individual sites tended to return to the composition observed in the first dry season, as indicated by the short distances between dry-season scores for each site and by the acute angles.

did not change significantly. Pristine headwater streams have dense forest cover, few or no tributaries upstream and generally sandy bottoms, features that favour a high hydrological stability throughout the year (Suguio & Bigarella, 1990). The apparent stability in channel volume occurred because we did not take measurements during, or shortly after, rainfall. In headwater streams, changes in discharge occur more rapidly in response to local rainstorms than in downstream reaches of the drainage system (Walker, 1995). During and shortly after local rainstorms,

discharge increased, the water became more turbid and turbulent, and part of the stream substratum (especially leaf litter) was relocated, which probably explains the changes in substratum composition in the rainy season. These results contradict the supposedly high physicochemical similarity between dry and rainy seasons in Amazonian headwater streams (e.g. Lowe-McConnell, 1991; Schwassman, 1992; Bührnheim & Cox-Fernandes, 2001).

The total numbers of individuals and species caught were lower in the rainy season, contrasting with previous studies of tropical headwater streams, which found higher fish abundance and species richness during the rainy season (Galacatos, Barriga-Salazar & Stewart, 2004; Casatti, 2005), and to others which detected no differences in fish-assemblage attributes throughout the year (Silva, 1995; Walker, 1995; Bührnheim & Cox-Fernandes, 2001). Despite site-specific characteristics that generated large compositional differences between sites within seasons, probably related to habitat characteristics (e.g. Mendonça *et al.*, 2005), there was an overall directional trend of composition changes between the first dry season and the rainy season. Moreover, in the second dry season the fish-assemblage composition tended to return to that in the first dry season. Previous studies may have lacked sufficient replicates to distinguish general seasonal trends from erratic site-specific changes.

In streams on steep slopes, floods might cause fish losses from the stream channel, as detected by Chapman & Kramer (1991) in a Costa Rican intermittent stream. Those authors showed that poeciliid populations were reduced up to 75% after floods and concluded that this resulted from fish mortality in drying pools, and active and passive fish movements between permanent micro-habitats and temporary pools. Franssen *et al.* (2006), studying an intermittent

Table 3 Summary of return analysis

Measure	Type of data	Original mean	Simulated mean (range)	P-value
Dry–dry distance	Qualitative composition	0.314	0.611 (0.432–0.805)	<0.001
	Quantitative composition	0.457	0.742 (0.532–0.944)	<0.001
Dry–rainy–dry angles	Qualitative composition	49.29	68.52 (47.26–93.01)	0.010
	Quantitative composition	64.23	77.75 (49.06–104.20)	0.067

Means of original measures; means (range) of simulated measures; statistical significance of simulation analysis. Dry–dry distances are the Euclidean distances between the two dry seasons in the nMDS plot. Dry–rainy–dry angles are the angles (in degrees) between the two vectors formed by the trajectories of individual sites between sampling seasons in the nMDS plots.

prairie stream in Kansas, U.S.A., reported that, due to higher connectivity, fish dispersed to intermittent reaches of the stream at high water. They suggested this as the main factor related to the temporal resilience of fish assemblages. In our study, the moderate stream slope and the absence of any relationship between changes in the fish and the environment indicate that scouring of fishes to downstream reaches and changes in microhabitats within streams were unlikely to have been important.

The South-American stream-fish fauna is composed mainly of small-bodied species (Castro, 1999), with little capacity for long migrations. In the rainy season, the high rainfall and the increase in frequency of intermittent inundations result in complex pond networks connected to streams, that become isolated as water level decline. Pazin *et al.* (2006) recorded 18 fish species from temporary ponds adjacent to streams in Reserva Ducke, of which 15 were also found in the streams (this study and Mendonça *et al.*, 2005). In our study sites, the species that showed the greatest proportional reduction in the number of individuals in the rainy season were among the most abundant species recorded by Pazin *et al.* (2006). This suggests that decreases in fish abundance in the stream channels during the rainy season may be related to lateral migrations of fishes from the stream channel to temporary ponds, in a similar way to the well documented lateral migration of fishes of large Amazonian rivers to the seasonally flooded riparian forests (Goulding, Carvalho & Ferreira, 1988; Junk, Bayley & Sparks, 1989).

Seasonal changes and fish movements

During the rainy season, hydrological fluctuations may make the stream channel environment unstable and even harsh for some species. Litter packs are an important source of food and shelter for macroinvertebrates in streams (e.g. Richardson, 1992) and some fish species in tropical streams spend almost all their life-cycle feeding on and/or sheltered in litter packs (Henderson & Walker, 1986; Sabino & Zuanon, 1998). The turbulence and high velocity caused by high discharge scours the litter packs, as has been reported for Costa Rican streams (Pringle & Hamazaki, 1997) and the associated benthic fauna (Bond & Downes, 2003). Beyond reducing food availability, the higher turbulence, velocity and water turbidity in the rainy season may make food capture more difficult for

fishes (Uieda, 1995). Thus, the increased rainfall in the wet season connects the ponds to the streams and makes them a more suitable environment for fish species tolerant of the hypoxia and highly acidic water in these habitats (e.g. *Poecilocharax weitzmani*, (Géry, 1965), *Erythrinus erythrinus* (Schneider, 1801), *Gymnotus* spp., *Callichthys callichthys* (Linnaeus, 1758).

Even when the most abundant species were removed from the analysis, the assemblage composition showed a significant seasonal pattern in the relative abundance of species. *Rivulus kirovskyi*, *R. compressus* (Henn, 1916) and *H. melazonatus* were highly abundant in the dry season, but were scarcer in the rainy season. This pattern has been reported for *H. melazonatus* by Bührnheim & Cox-Fernandes (Bührnheim & Cox-Fernandes, 2001). During the rainy season, most individuals of these species were adults captured in pools, while at the end of the rainy season, many post-larval and young specimens were caught (V.F.V. Pazin, unpubl. data), which indicates that the ponds could be the main spawning sites for these species. Two species which showed marked changes in abundance between seasons probably did not undertake lateral migrations to ponds, however. The crenuchid *M. eleotrioides* and the characid *B. giacopinini* are both species associated with running waters and were rarely or never collected in temporary ponds. Changes in their density might be related to use of instream shelters, as reported for some temperate stream fishes (Matthews, 1998), or represent differential reproductive success between spawning seasons.

The persistence of significant seasonal differences in fish assemblage composition when the most abundant species were removed indicates that other factors may have influenced habitat use by the fish species. As examples, repeated short-term occupation of recently flooded lateral ponds as foraging grounds, differential reproductive behaviour among species, or small longitudinal movements may all explain seasonal changes in fish assemblage of less abundant species.

Implications for tropical stream fish studies

Many fish species were recorded infrequently in the present study, for several possible reasons. Some species may really be rare in the study area, but for nocturnal species (such as some catfishes and knife-fishes: Lowe-McConnell, 1991) detection may be less likely during the day. Infrequently, captured species

are important in characterizing local biodiversity; however, due to their low detectability, they are often neglected in rapid assessment surveys and are thus inadequate as biological indicators of general assemblage structure. These species may be less abundant and widely distributed or of low abundance and endemic. In the latter case, special attention should be directed to factors affecting their distribution and population dynamics. The apparently rare species we recorded in Reserva Ducke streams are known to occur in other Amazonian basins (cf. Reis, Kullander & Ferraris, 2003), so are not locally endemic. Factors responsible for their low local abundance remain to be studied.

The absence of seasonality in the number of species captured per site, when we rarefied the number of species taken or removed the most abundant species, indicates that the common fish species caught more consistently in surveys confer predictability in fish assemblages along environmental gradients, such as in the physical characteristics of streams and water quality (Mendonça *et al.*, 2005), and through time. Thus, the assemblage structure based on the distribution of abundance of the more common species may be the most effective indicator for use in monitoring programmes that adopt rapid-assessment approaches in headwater streams. However, it is important to distinguish natural seasonal changes in fish assemblages from those caused by human impacts on tropical headwater streams. Although more subtle than in temperate headwater streams (e.g. Schlosser, 1982; Erös & Grossman, 2005), the clear seasonal trends in fish abundance and assemblage composition observed in the present study indicate the need to consider this factor in further studies involving headwater streams in the Amazon. Without such procedures there is a strong risk of confounding seasonal changes with long-term trends in ichthyofaunal composition, leading to inaccurate ecological conclusions and inadequate management options for biological conservation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Number of individuals of each species captured in streams at Reserva Ducke between September 2005 and August 2006.

Appendix S2. Results of the Tukey *post hoc* test for comparisons of fish attributes between the pairs of surveys.

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