

Fish assemblages in temporary ponds adjacent to 'terra-firme' streams in Central Amazonia

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SUMMARY

1. The effect of habitat structural features and physicochemical characteristics of the water on the composition and richness of fish assemblages in temporary ponds near streams were examined at three spatial scales: among ponds, among streams and between drainage basins, in a 'terra-firme' (not subject to long-term flooding) forest reserve in Central Amazonia.
2. The fish assemblage in temporary ponds was composed of subsets of 18 small-bodied species widely distributed in the reserve. The assemblages had a nested subset structure, where smaller ponds contained subgroups of the species found in larger ponds.
3. Species composition and richness in temporary ponds were similar between drainage basins, although the fish assemblages in streams differed between basins.
4. Fish assemblage structure was influenced by local factors related to habitat structure, such as pond area and depth, canopy cover and hydroperiod. Physicochemical characteristics of the water in the ponds were similar between drainage basins and had little detectable effect on the structure of pond fish assemblages.
5. No correspondence was found between the composition, richness or abundance of fishes in the ponds and in stretches of the streams adjacent to the ponds. Therefore, it is not possible to predict the composition of these temporary pond fish assemblages from the fish assemblages found in adjacent streams.

Keywords: Brazilian Amazon, community structure, nested subsets, spatial scales, species composition, temporary waters

Introduction

Ponds are considered temporary if they have a predictable annual dry phase, usually in the order of 3–8 months (Collinson *et al.*, 1995). In temperate systems, temporary ponds are formed predominantly during summer and autumn (Ward, 1992). In tropical systems, such as the Amazonian forest, ponds are formed during the rainy season and the majority are temporary, but in some years may remain until the next rainy season, despite 5–6 months of low rainfall.

Fish assemblages inhabiting such temporary or permanent ponds can have dramatic effects on invertebrate community composition (Luecke, 1990; Corti, Kohler & Sparks, 1997). The importance of fish predation in maintaining tadpole diversity in ponds is well documented in temperate areas (e.g. Kats, Petranka & Sih, 1988; Hecnar & M'Closkey, 1997; Smith *et al.*, 1999; Baber & Babbitt, 2003; Baber *et al.*, 2004), and in Central Amazonia (e.g. Hero, 1991; Magnusson & Hero, 1991; Hero, Gascon & Magnusson, 1998; Hero *et al.*, 2001). However, little is known of the factors affecting fish assemblages in temporary ponds, especially in the tropics. Few studies of fish assemblages in temporary waterbodies have been undertaken in temperate areas (e.g. Williams & Coad, 1979), and they were carried out basically in wetland

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areas (e.g. Hart & Newman, 1995; Snodgrass *et al.*, 1996; Dunson, Paradise & Van Fleet, 1997; Poizat & Crivelli, 1997; Baber *et al.*, 2002). Fish may be rare in temporary aquatic systems because of the drying and the harsh abiotic conditions (Baber *et al.*, 2002).

Some species of fish, such as the rivulid annual fishes (Cyprinodontiformes), occur mainly or exclusively in temporary ponds (Costa, 1998), but most temporary-pond fish species are recruited from nearby permanent water during heavy rainfall or when streams and rivers overflow their banks. The relationship between lotic systems and flooded areas has received most attention in systems dominated by large rivers, where the flood is a predictable pulse of long duration (e.g. Goulding, Carvalho & Ferreira, 1988; Junk, Bayley & Sparks, 1989; Lowe-McConnell, 1999; Ward, Tockner & Schiemer, 1999; Drago *et al.*, 2003). In stream systems, the flood pulse is short and generally unpredictable. Despite the fact that small streams are intimately connected physically, chemically and biologically to their riparian zones (Murphy & Meehan, 1991), and that streams can serve as sources of colonists for adjacent ponds, few studies of aquatic communities have investigated both streams and temporary ponds.

Opportunities to colonise and aspects of the physical environment, such as habitat heterogeneity and physicochemical gradients, are important in structuring fish communities and are the main factors that influence species distributions at a local scale (Tonn & Magnuson, 1982; Rahel, 1984; Capone & Kushlan, 1991).

Temporary ponds in floodplain areas vary in hydroperiod and size, depending on the flood stage of the adjacent river (Drago, 1989). Kodric-Brown & Brown (1993) have shown that fish assemblages in temporary springs in Australian deserts are structured in relation to the physicochemical characteristics of the pools, and that the apparently random structure results from inadequate temporal and spatial sampling. Baber *et al.* (2002) emphasised the importance of local (e.g. depth and hydroperiod) and landscape processes (connectivity to permanent waterbodies) influencing fish assemblages in temporary wetlands in Florida, U.S.A.

It is important to know how pond assemblages are structured by the physicochemical characteristics of the ponds, because 'temporary pond assemblages' may not form a single natural management unit. If

ponds with different characteristics support different assemblages, it may be necessary to conserve a large variety of pond types to adequately represent all species. Alternatively, if the pond assemblages form nested subsets, where species-poor assemblages represent non-random subgroups of richer assemblages (Patterson & Atmar, 1986; Worthen, 1996), the conservation of a single large pond could protect more species than the conservation of several smaller ponds (e.g. Cook, 1995; Worthen, 1996; Fleishman *et al.*, 2002).

Knowledge of the structure of fish assemblages in temporary ponds, whether random, complementary, or in nested subsets, is also important for understanding the effects of fish on other taxa. Hero *et al.* (2001) suggested that fish predators are important agents in the maintenance of beta diversity in tadpole assemblages, because different tadpole species have different vulnerabilities to fish predators. Adult frogs are known to be able to use habitat-related cues to predict the occurrence of fish predators (Stauffer & Semlitsch, 1993; Takahara *et al.*, 2003), and decide where to lay their eggs. So, predictability of fish assemblages in ponds may affect the distribution and habitat use by other animal groups along the streams.

In this study, we investigated the factors affecting fish assemblage composition in temporary ponds around small forest streams in a Central Amazonian rainforest reserve, Reserva Florestal Adolpho Ducke (RFAD). The fish fauna in those streams has been studied intensively and the composition of assemblages was demonstrated to be affected by the physicochemical characteristics, size and location of the streams in the reserve (Mendonça, Magnusson & Zuanon, 2005). Accordingly, we hypothesised that fish assemblages would be affected mainly by the length of time in which the pond had water along the year, but also by morphological and physicochemical characteristics of the ponds.

Methods

Study area

Reserva Florestal Adolpho Ducke belongs to the Instituto Nacional de Pesquisas da Amazônia (INPA) and covers 10 000 ha on the outskirts of Manaus, Amazonas, Brazil. The reserve headquarters are located at the north-west corner of the reserve

(02°55' N, 59°59' W). Reserva Ducke is covered by terra-firme humid tropical forest with average canopy height between 30 and 35 m. The term 'terra-firme' refers to tropical rain forests, which are not seasonally inundated by adjacent rivers (see Pires & Prance, 1985). Altitude within the reserve varies from 40 to 120 m a.s.l. and average temperature is 26 °C, with little monthly variation. Precipitation varies from 1800 to 2800 mm per year, with a rainy season from December to May and a dry season from June to November; the rainiest months are generally March and April, with more than 300 mm of rain per month (Ribeiro *et al.*, 1999). Temporary ponds form in valley bottoms near streams and may retain water for a few days to more than 1 year.

Most streams have their headwaters within the reserve. A central plateau divides the stream systems into eastern and western drainage basins. Western streams drain to the Rio Negro (a black water river) and eastern streams drain to the Amazon River (turbid water river, with high sediment loads). Currently, the southern edge of the RFAD is in contact with suburbs, but the eastern edge of the RFAD still has connections to continuous forest.

Sampling regime

Reserva Ducke is a long-term ecological research (LTER) site and has a network of permanent plots used for long-term studies. Twenty-eight aquatic permanent plots were established in 2001, which correspond to 50 m stretches of first ($n = 15$), second ($n = 8$) and third ($n = 5$) order streams.

Within those stretches each pond ($n = 82$) was sampled four times at intervals of 2 months, starting at the beginning of the wet season (November 2002) and ending at the beginning of the subsequent wet season (October 2003).

Plots included a 50 m stretch (straight-line measurement) along the stream channel. Plot width was not standardised and corresponded to the width of the floodplain (the lowland areas around streams subject to flooding) and generally did not exceed 40 m. Floodplain width was measured at four equally spaced points along the plot, on both banks.

Pond area was measured by counting squares of a nylon grid (12 cm mesh) extended over the pond. Water depth and litter (leaves and fine twigs on the bottom of the pond) thickness were measured in the

centres of the grid squares in small ponds. In ponds larger than 3 m², depth was measured at the centre of each group of four squares. An index of pond hydroperiod was obtained from the number of sampling months in which the pond had water during the study.

Canopy cover was estimated with a concave densiometer (Robert and Lemmon Forest Densiometer, model C, Bartlesville, U.S.A.). Plots were divided in four equal stretches and measures of canopy cover were made in the center of each quarter. At each point, four readings were taken, one facing each of north, south, east and west. Canopy cover was also measured at the center of each pond.

The average width of each stream channel was calculated from the average of six equidistant measures along the 50 m stretch, including the upstream and downstream stretch limits.

Water conductivity ($\mu\text{s cm}^{-1}$), temperature (°C) and dissolved oxygen (mg L^{-1}) were measured with a portable meter (Aqua-Check™ Water Analyzer Operator, O.I. Corporation, U.S.A.). Acidity was measured with a portable pH meter (pH-30 Chek-mite, Corning Inc., NY, U.S.A.). Water characteristics were measured only once, during the first or the second sampling session.

Fish sampling

Fish were collected with scoop nets and fish traps in each pond. We searched the whole of each pond, including the litter layer, until no specimens were found in a 5–10 min interval. Because of the small sizes of most of the ponds sampled, we believe that the majority of individuals were captured in each pond.

Fishes were identified with keys for South American fishes (Gery, 1977; Kullander, 1986; Mago-Leccia, 1994; Planquete, Keith & Le Bail, 1996) and confirmed by systematic specialists at the Instituto Nacional de Pesquisas da Amazônia (INPA) and later deposited in the INPA Fish Collection.

The fish faunas in the stretches of streams adjacent to the ponds were sampled by Mendonça *et al.* (2005), using five methods. During 24 h, 12 minnow-traps and three fyke-net fish-traps were placed in each sample station and were checked at 8 h intervals. After collecting with the 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 in smaller sections and facilitate the capture of enclosed fish with hand and seine nets. An additional fyke-net and three gillnets (10 × 1 m, mesh size of 3, 5 and 6 cm) were used in third-order streams to increase the efficiency of capture. The gillnets were set during a 4 h period at each site and were checked regularly.

Treatment and data analysis

The effects of environmental factors on fish assemblage structure in temporary ponds were investigated at three spatial scales: among ponds; among streams (plots); and between the two drainage basins of the RFAD.

For among-pond analyses, a single pond in each of 25 plots was chosen randomly to be included in the analysis. For among-stream analyses, the plots ($n = 25$) were used as sampling units and the environmental variables measured in ponds in each plot were represented by means weighted by pond area. In the macro-scale analyses, we investigated differences between the two main drainage basins in environmental variables and fish species composition and richness.

Fish assemblage structure was represented by Principal Coordinates Analysis (PCoA) axes. The association matrix used in the PCoA was constructed using the Bray Curtis distance, after standardising the sites (ponds or plots, depending on the analysis) by division by the sum of individuals in the site. This procedure results in a distance that is metric and probably Euclidean (Legendre & Legendre, 1983). When used with presence–absence data, the Bray Curtis index is equivalent to the Sørensen's index (Legendre & Legendre, 1983). Ordinations were performed using abundance (quantitative) and presence–absence (qualitative) data of species in the ponds. Abundance data tend to give more weight to the most common species, because these species have larger numerical differences between plots. Presence–absence data tend to give more weight to the rare species, because the most abundant species tend to occur in all plots.

The relations between independent habitat variables and the species composition in the ponds, represented by the first three PCoA axes, were investigated by multivariate multiple regressions. To

evaluate the significance of the analyses the test-statistic Pillai's trace was used in function of its robustness (see Zar, 1999). Low tolerances (Tol. < 0.1) were used as indicating potential problems with multicollinearity (Kirby, 1993).

To determine whether the fish assemblages formed nested subsets and to quantify this pattern, we used the 'Nested Temperature Calculator' (Atmar & Patterson, 1995). This program uses the structure of a species presence–absence matrix to calculate the matrix 'temperature' (T), which can vary between 0° for a perfectly hierarchical system and 100° for a completely random system (Atmar & Patterson, 1995). One thousand Monte-Carlo simulations were used to generate random matrices, and the distributions of T -values of these matrices were used to determine the significance of the T -value for the original matrix.

To assess whether the composition of stream fish species could be used to predict the composition of fish assemblages in adjacent temporary ponds, the correlation between the between-plot association matrices (using the Bray–Curtis index) for pond fish and stream fish were calculated. The statistical significance of the correlation was calculated using 1000 permutations.

We used the PATN program (Belbin, 1992) for PCoA analyses, association matrices and Mantel test and SYSTAT 8.0 (Wilkinson, 1998) for other analyses.

Results

Pond characteristics

We sampled 82 ponds in 28 of the stream segments surveyed for ponds by Mendonça *et al.* (2005), 16 in the western drainage basin and 12 in the eastern drainage basin. The number of ponds in each plot varied from one to seven. Water physicochemical variables were measured only in 25 plots because ponds in three plots dried before the measurements could be made.

The ponds had acid waters (pH mean: 5.05, range: 3.7–6.2), with low dissolved oxygen (2.16, 1.0–3.8 mg L⁻¹), variable temperature (24.48, 22.0–26.0 °C) and low conductivity (19.22, 10.0–43.7 µs cm⁻¹). Ponds covered small areas (2.42, 0.26–9.1 m²) and were shallow (8.1, 1.25–35.0 cm).

Vegetation cover in the plots was dense, with low values of canopy openness (mean: 4.44%, range:

2.1–11.2%). The pond substratum generally consisted of clay, decomposing plant matter or sand in some ponds. The distance between the ponds and the stream was not included in the analyses because of colinearity of this variable with others, such as area and depth of ponds. In any case, this variable did not adequately represent pond isolation from the stream, because floods were frequent and allowed most species to reach most ponds. The pond hydroperiods varied from a few days to 11 months. There was no evident colinearity among the morphological and physicochemical characteristics of the pond variables included in the analyses (most tolerance values >0.4).

Distribution, composition and species richness

We found 18 fish species in the ponds, distributed in six orders and nine families (Table 1). Of these, 14 were registered in streams within plots. Characiformes, with four families and 10 species found in the ponds, was the most species-rich group. Cyprinodontiformes, represented by two species of *Rivulus*, accounted for 52% of the 1586 individuals collected. The five most abundant species (*Rivulus kirovskyi*, 43.5%; *Pyrrhulina brevis*, 12.8%; *Copella nigrofasciata*, 11.9%; *Rivulus compressus*, 8.2%; *Hyphessobrycon melazonatus*, 5.7%) represented 82% of specimens.

Table 1 Number of individuals of fish species captured in temporary ponds in different streams in the western (WEST) and eastern (EAST) drainage basins, Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil

	West		East			Total
	Bolívia	Acará	Tinga	Uberê	Ipiranga	
Characiformes						
Characidae						
<i>Hyphessobrycon melazonatus</i> Durbin in Eigenmann, 1908	65	15	7	–	4	91
Crenuchidae						
<i>Crenuchus spilurus</i> Günther, 1863	2	10	17	21	–	50
<i>Microcharacidium eleotrioides</i> Géry, 1960	7	–	–	–	–	7
<i>Poecilocharax weitzmani</i> Géry, 1965	57	–	–	–	–	58
Erythrinidae						
<i>Erythrinus erythrinus</i> (Schneider, 1801)	7	15	6	10	1	39
<i>Hoplias malabaricus</i> (Bloch, 1794)	4	7	1	2	–	14
Lebiasinidae						
<i>Copella nigrofasciata</i> (Meinken, 1952)	11	20	79	79	–	189
<i>Nannostomus cf. limatus</i> Weitzman, 1978	6	–	–	–	–	6
<i>Pyrrhulina cf. brevis</i> Steindachner, 1875	150	21	20	6	6	203
<i>Pyrrhulina cf. laeta</i> (Cope, 1872)	1	–	–	3	–	4
Perciformes						
Cichlidae						
<i>Aequidens pallidus</i> (Heckel, 1840)	13	4	–	3	–	20
<i>Apistogramma agassizi</i> (Steindachner, 1875)	4	–	4	–	–	8
<i>Apistogramma aff. hyppolitae</i> Kullander, 1982	–	–	2	18	–	20
Cyprinodontiformes						
Rivulidae						
<i>Rivulus compressus</i> Henn, 1916	27	52	16	30	5	130
<i>Rivulus kirovskyi</i> Costa, 2004	242	195	170	55	28	690
Gymnotiformes						
Gymnotidae						
<i>Gymnotus cf. cataniapo</i> Mago-Leccia, 1994	–	–	1	–	–	1
Siluriformes						
Callichthyidae						
<i>Callichthys callichthys</i> (Linnaeus, 1758)	3	1	3	1	26	34
Synbranchiformes						
Synbranchidae						
<i>Synbranchus marmoratus</i> Bloch, 1795	1	1	2	1	0	5
Total of individuals	554	322	315	232	63	1586

Of the 18 species encountered, 13 were found in both drainage basins. Three species were collected only in the western drainage and two only in the eastern drainage. These species were found in only one or two plots. The number of species per pond varied from one to 12.

The most widely distributed species in the RFAD were *R. kirovskyi*, found in 27 of the 28 plots, *R. compressus* (18 plots), *Erythrinus erythrinus* (16 plots) and *P. brevis* (15 plots).

Differences among ponds

Three PCoA axes explained much of the variance in the occurrence of fish species for quantitative ($r^2 = 0.71$) and qualitative ($r^2 = 0.93$) data. The species composition, based on abundance data, was related to pond area (Pillai trace = 0.451, $F_{3,14} = 3.83$, $P = 0.034$) and hydroperiod (Pillai trace = 0.561, $F_{3,14} = 5.96$, $P = 0.007$), but not with average depth (Pillai trace = 0.070, $F_{3,14} = 0.39$, $P = 0.760$), litter average depth (Pillai trace = 0.114, $F_{3,14} = 0.60$, $P = 0.620$), pH (Pillai trace = 0.312, $F_{3,14} = 2.12$, $P = 0.143$), conductivity (Pillai trace = 0.258, $F_{3,14} = 1.62$, $P = 0.228$), dissolved oxygen (Pillai trace = 0.139, $F_{3,14} = 0.758$, $P = 0.536$) or canopy cover (Pillai trace = 0.194, $F_{3,14} = 1.127$, $P = 0.371$).

For presence-absence data, the PCoA axes were related to hydroperiod (Pillai trace = 0.633, $F_{3,14} = 8.08$, $P = 0.002$) and tended to vary with canopy cover (Pillai trace = 0.411, $F_{3,14} = 3.26$, $P = 0.053$), but not with average water depth (Pillai trace = 0.303, $F_{3,14} = 2.03$, $P = 0.155$), pond area (Pillai trace = 0.338, $F_{3,14} = 2.39$, $P = 0.609$), litter depth (Pillai trace = 0.118, $F_{3,14} = 0.62$, $P = 0.609$), pH (Pillai trace = 0.157, $F_{3,14} = 0.87$, $P = 0.479$), conductivity (Pillai trace = 0.276, $F_{3,14} = 1.78$, $P = 0.196$), or dissolved oxygen (Pillai trace = 0.201, $F_{3,14} = 1.18$, $P = 0.352$).

The distribution pattern of the species formed a nested subset within plots [T (temperature) = 10.68°, $P < 0.001$]. Species-poor plots represented a subgroup of those with larger numbers of species. The order of plots in terms of species richness was correlated with order of plots by pond area ($r = 0.7$).

There was a clear nested pattern in the distribution of species in relation to pond area (Fig. 1a). Larger ponds (>5 m²) contained most species present in

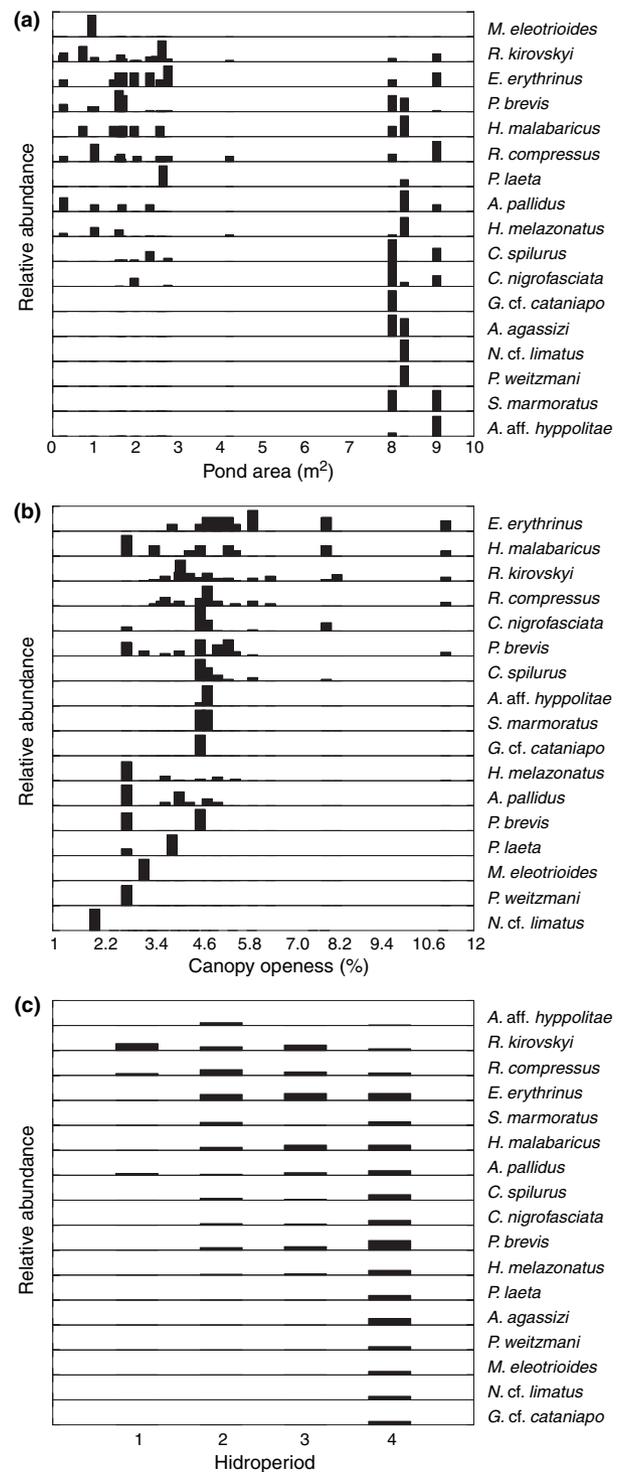


Fig. 1 (a) Relative abundance of fishes in relation to pond area and (b) canopy openness. Data are presented as relative abundance within species. (c) Number of ponds in each hydroperiod category where each species occurred. The total number of individuals varied among species (Table 1).

smaller ponds and other rare species were encountered only in these. However, there is a gap in this supposed gradient caused by a lack of ponds of intermediate area. The pattern of species distribution along the gradient of canopy cover was not clear (Fig. 1b). Most of species occurred throughout the gradient. *Crenuchus spilurus* and *E. erythrinus* were absent from closed canopy ponds. *Aequidens pallidus*, *H. melazonatus* and the rare species were recorded only from heavily shaded ponds. Ponds with larger hydroperiods contained more species (Fig. 1c). *Rivulus kirovskyi*, *R. compressus* and *A. pallidus* occurred throughout the gradient in hydroperiod.

Multiple regression was used to relate fish species richness (RIC) in ponds to the litter depth (LD), pond

area (AR), pH (PH), conductivity (CO), dissolved oxygen (OX), canopy cover (CC), hydroperiod (HY) and water depth (WD). The analysis indicated that about 84% of the variance in species richness was related to pond characteristics ($RIC = -10.1 + 0.01LD + 0.69AR + 0.97PH - 0.10CO + 0.12OX + 0.44CC + 1.98HY - 0.01WD$; $R^2 = 0.84$; $F = 8.16$; $P < 0.001$). Species richness was positively related to pond area ($P < 0.001$, Tol. = 0.59), canopy cover ($P = 0.019$, Tol. = 0.46), hydroperiod ($P < 0.001$, Tol. = 0.52; Fig. 2) and conductivity ($P = 0.021$, Tol. = 0.38), but not with the average depth ($P = 0.871$, Tol. = 0.37), litter depth ($P = 0.916$, Tol. = 0.10), pH ($P = 0.085$, Tol. = 0.38), or dissolved oxygen ($P = 0.814$, Tol. = 0.44).

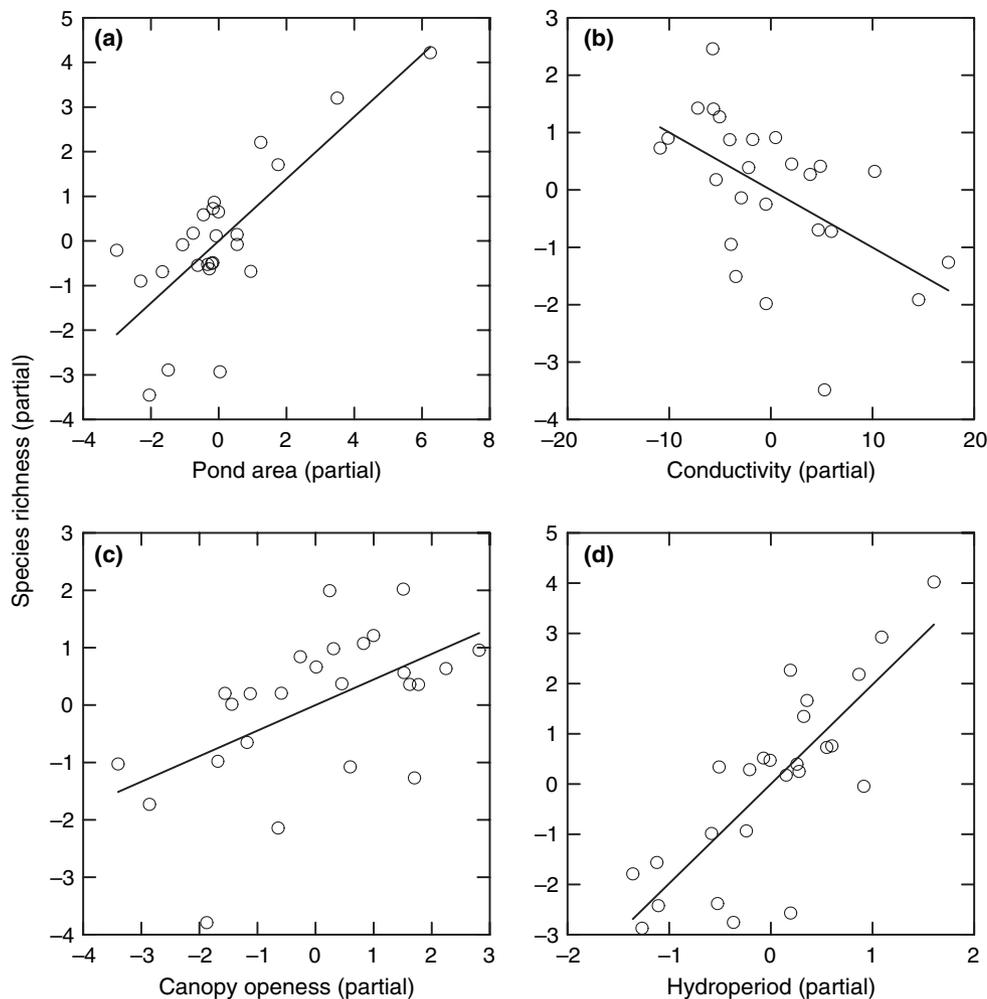


Fig. 2 Partial regressions testing the effects of pond area (a), canopy cover (b), hydroperiod (c) and conductivity (d) on fish species richness in temporary ponds. Only statistically significant relationships are shown. Average depth, litter depth, pH and dissolved oxygen included in the multiple regression did not contribute significantly to the model ($P > 0.05$ in all cases).

Differences among streams

The three PCoA axes explained much of the variation in the differences among plots for qualitative ($r^2 = 0.82$) and quantitative ($r^2 = 0.73$) data.

For abundance data, the species composition was related to pond average water depth (Pillai trace = 0.434, $F_{3,14} = 3.57$, $P = 0.042$), but not with stream width (Pillai trace = 0.168, $F_{3,14} = 0.94$, $P = 0.447$), litter depth (Pillai trace = 0.192, $F_{3,14} = 1.11$, $P = 0.378$), pH (Pillai trace = 0.094, $F_{3,14} = 0.48$, $P = 0.70$), conductivity (Pillai trace = 0.060, $F_{3,14} = 0.30$, $P = 0.826$), dissolved oxygen (Pillai trace = 0.062, $F_{3,14} = 0.32$, $P = 0.812$), canopy cover (Pillai trace = 0.143, $F_{3,14} = 0.78$, $P = 0.526$), or pond area in the plot (Pillai trace = 0.137, $F_{3,14} = 0.32$, $P = 0.545$).

For presence-absence data, the fish assemblage tended to vary with pond area (Pillai trace = 0.398, $F_{3,14} = 3.09$, $P = 0.08$), but not with other factors (multivariate multiple regression: stream width: Pillai trace = 0.285, $F_{3,14} = 1.86$, $P = 0.183$; pond depth: Pillai trace = 0.281, $F_{3,14} = 1.82$, $P = 0.189$; litter depth: Pillai trace = 0.358, $F_{3,14} = 2.60$, $P = 0.093$; pH: Pillai trace = 0.012, $F_{3,14} = 0.06$, $P = 0.981$; conductivity: Pillai trace = 0.040, $F_{3,14} = 0.19$, $P = 0.899$; dissolved oxygen: Pillai trace = 0.027, $F_{3,14} = 0.13$, $P = 0.940$; or canopy cover: Pillai trace = 0.073, $F_{3,14} = 0.37$, $P = 0.778$).

We used multiple regression to relate fish species richness (RIC) in the plots to the pond area (PA), stream width (SW), pond water depth (WD), litter depth (LD), pH (PH), conductivity (CO), oxygen (OX) and canopy cover (CC). The measured characteristics explained approximately 64% of variance in species richness ($RIC = 4.11 + 0.28PA - 0.10SW + 0.28WD - 0.39LD - 0.18PH + 0.05CO - 0.40OX + 0.13CC$, $R^2 = 0.64$, $F = 8.16$, $P = 0.015$). Species richness was positively related to total area of ponds ($P = 0.001$, Tol. = 0.64) and water depth ($P = 0.009$, Tol. = 0.64; Fig. 3), but not with stream width ($P = 0.830$, Tol. = 0.73), litter depth ($P = 0.108$, Tol. = 0.46), pH ($P = 0.826$, Tol. = 0.74), conductivity ($P = 0.905$, Tol. = 0.78), dissolved oxygen ($P = 0.601$, Tol. = 0.76) or canopy cover in the plot ($P = 0.752$, Tol. = 0.80).

Differences between drainage basins

Despite significant differences in floodplain area ($P = 0.000$, $r^2 = 0.52$) and conductivity ($P = 0.022$, $r^2 = 0.21$)

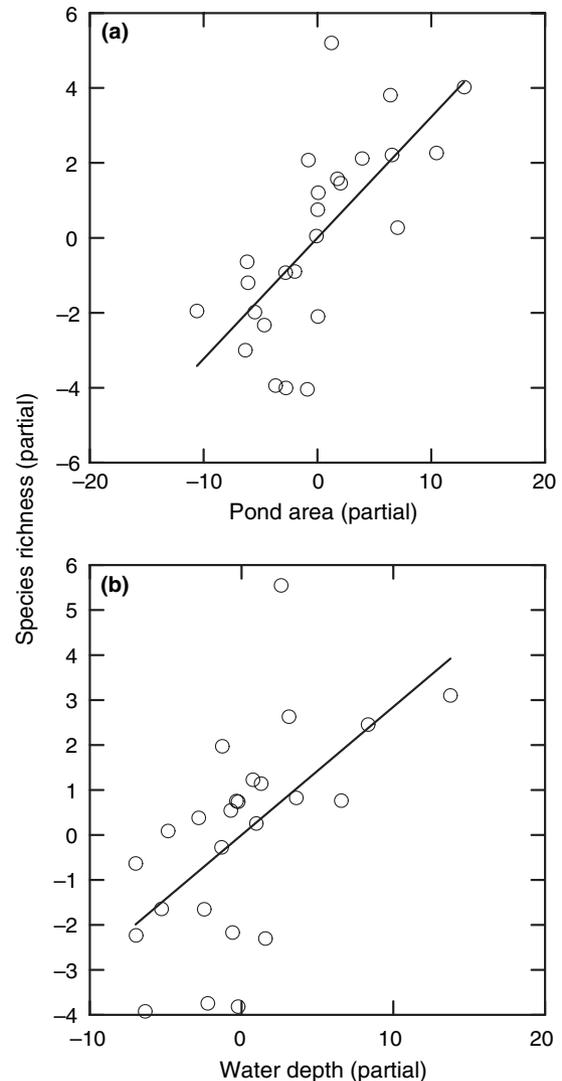


Fig. 3 Partial regressions testing the effects of pond area (a) and water depth (b) on fish species richness in plots. Only statistically significant relationships are shown. Stream width, litter depth, pH, conductivity, dissolved oxygen and canopy cover included in the multiple regression did not contribute significantly to the model ($P > 0.1$ in all cases).

in the plots between the drainage basins, the assemblage composition was not significantly different between the drainages in simple analyses using presence-absence data (MANOVA: Pillai trace = 0.167, $F_{3,21} = 1.40$, $P = 0.270$) or abundance data (MANOVA: Pillai trace = 0.173, $F_{3,21} = 1.46$, $P = 0.254$), or in analyses together with other variables (MANCOVA: presence-absence: Pillai trace = 0.193, $F_{3,13} = 1.04$, $P = 0.408$; abundance: Pillai trace = 0.159, $F_{3,13} = 0.82$, $P = 0.505$). The species richness per plot did not vary

between the two drainages in simple analyses (ANOVA: $P = 0.414$, $r^2 = 0.03$) nor when the other environmental variables were included (ANCOVA: $P = 0.535$).

Relationships between pond and stream fish assemblages

There was no significant relationship between the abundance of individuals within species in the streams, registered by Mendonça *et al.* (2005) and the abundance of these species in the ponds adjacent to those streams, when all the species found in the ponds were included in the analyses ($P = 0.999$, $r^2 = 0.218$) or only for species found in both ponds and streams ($P = 0.281$, $r^2 = 0.096$). There was no relationship between differences in composition (Bray–Curtis association) of fish assemblages in temporary ponds and differences in species composition found in the corresponding streams (Mantel test: $r = -0.001$, $P = 0.50$).

Discussion

Fish species distribution and assemblage composition

Most species found in the ponds are common and widely distributed in streams in Central Amazonia (Sabino & Zuanon, 1998; Bührnheim & Cox-Fernandes, 2001; Mendonça *et al.*, 2005). The fish assemblages that occur in ponds in Reserva Ducke are probably a group of specialised species adapted to acid waters with low levels of dissolved oxygen, which can also support the variations in the physico-chemical characteristics of the streams. Most species that occur in temporary ponds can also live in permanent ponds (Chase, 2003) and streams, but species that live in permanent waters may not persist in temporary habitats (Williams, 1996; Schneider, 1997) and some fish species are adapted to temporary wetlands (Hart & Newman, 1995).

Habitats with similar environmental characteristics, such as temporary ponds, can have dissimilar faunas because of the different probabilities of colonisation and extinction for each species. During floods, most species have the chance to disperse throughout the system. However, in RFAD, *Rivulus kirovskyi*, *R. compressus* and *P. brevis* can colonise areas beyond the direct reach of the flood area, by flipping across humid leaf litter (V.F.V. Pazin, pers. obs.). Some species of *Rivulus* can survive for 25–60 h out of

water, in humid environments (Seghers, 1978; Bastos, 1979; Huehner, Schramm & Hens, 1985). Few individuals of *R. compressus* and none of *R. kirovskyi* were found in the reserve streams. The limited use of streams by the *Rivulus* species may be associated with the presence of large predators in streams (e.g. Seghers, 1973; Fraser & Gilliam, 1992) that do not occur in adjacent ponds.

Remaining in the pond up to its complete drying does not result in the extinction of the whole fish assemblage. In the Venezuelan Llanos, at least two species of fish, an annual fish (*Rachovia maculipinnis*) and a swamp-eel (*Synbranchus marmoratus*) can survive for months in the absence of superficial water (Winemiller, 1996). In Florida wetlands, species such as *Jordanella floridae* (Cyprinodontidae) can survive dormant in wet mud (Baber *et al.*, 2002). In RFAD, *R. compressus* has been found buried in the mud and under fallen leaves in the bottom of ponds that dried 3 months earlier and probably can withstand the dry period in the ponds.

Structure of fish assemblages

The pond fish assemblage composition had a well defined hierarchical structure, in the form of nested subsets. This pattern could result from different dispersal or colonisation abilities of the species and different vulnerabilities to local extinction (Cutler, 1994; Worthen, 1996). In temporary wetlands in Florida, U.S.A., fish assemblage composition may be largely determined by colonisation, rather than by extinction (Baber *et al.*, 2002), as already demonstrated for many different taxa by Cook & Quinn (1995). Although colonisation and extinction processes may be random processes, the species assemblage we studied appear to be deterministic and highly predictable, as were the fish assemblages studied by Kodrick-Brown & Brown (1993) in Australian desert springs.

The number of species in the RFAD ponds was closely related to pond size, which indicates a hierarchical assemblage structure. According to Fleishman & Mac Nally (2001), if the species richness is correlated with area and the biota composition is nested, species richness will be higher in a single extensive area than in several smaller patches. Hence, conservation of fish assemblages may be more effective if protection is concentrated on the lower reaches of streams as these areas have more and larger ponds. However, although

we found no evidence that small ponds harbour unique communities, the conservation of headwaters (first and second order streams) is necessary to maintain conditions in the riparian areas of third order and larger streams (see Vannote *et al.*, 1980).

Relationships between environmental variables and fish assemblages

In this study, fish assemblages were related to local processes associated with water availability, such as pond area, depth and hydroperiod. Connectivity to other waterbodies influences fish assemblages in temporary wetlands in Florida, U.S.A. (Snodgrass *et al.*, 1996; Baber *et al.*, 2002). However, in RFAD the floods are frequent and link most of ponds to streams during heavy rains.

Physicochemical variables often exert strong effects on the structure of the aquatic communities (Schäfer, 1985; Allan, 1995; Dunson *et al.*, 1997). Mendonça *et al.* (2005) found significant effects of physicochemical characteristics of the water on the fish assemblages in stream stretches in RFAD. However, the physicochemical variables had little influence on the fish assemblages in RFAD pools, though these factors may affect particular species (e.g. limiting the presence of high-oxygen requiring lotic species), and conductivity was associated with species richness in pools. Olden, Jackson & Peres-Neto (2001) also found a strong association between fish community composition and factors related to lake morphology, but not water chemistry in drainage lakes in Canada.

Area exerts a strong effect in the local species composition in aquatic systems (Rahel, 1984; Taylor, 1997; Magnuson *et al.*, 1998), including temporary ponds (Ebert & Balko, 1987; Capone & Kushlan, 1991; Kodrick-Brown & Brown, 1993; Kiflawi, Eitam & Blaustein, 2003). Larger ponds in RFAD also supported larger numbers of fish species, but the reason for this is not known.

In many temporary aquatic environments, the occurrence, richness or life history traits of the species are strongly influenced by hydroperiod (Schneider & Frost, 1996; Spencer *et al.*, 1999; Baber *et al.*, 2002) and ponds that carry water for longer periods support greater numbers of amphibians species (Azevedo-Ramos, Magnusson & Bayliss, 1999; Adams, 2000), invertebrates (Schneider & Frost, 1996; Corti *et al.*, 1997; Spencer *et al.*, 1999; Kiflawi *et al.*, 2003) and

fishes (Snodgrass *et al.*, 1996; Baber *et al.*, 2002). Baber *et al.* (2004) found amphibian and macroinvertebrate assemblages strongly nested with respect to hydroperiod in temporary wetlands in southern New Hampshire, U.S.A. Ponds with longer hydroperiods may accumulate more species because of low rates of extinction and more time for colonisation. However, ponds with longer hydroperiods also tend to be the large ones, so the higher number of species could be a simple species-area effect.

Canopy cover can influence hydroperiod and the content of dissolved oxygen in temporary ponds, and affects amphibian and aquatic invertebrate distributions (Werner & Glennemeier, 1999; Skelly, Freidenburg & Kiesecker, 2002; Halverson *et al.*, 2003; Kiflawi *et al.*, 2003). Some of these authors considered that canopy openness could affect hydroperiod, but there was little correlation between canopy openness and hydroperiod in RFAD.

Differences between the fish assemblages in streams and in adjacent ponds

Drainage basins have been frequently related to differences in assemblage composition, because of geographic isolation (e.g. Angermeier & Winston, 1999; Marsh-Matthews & Matthews, 2000). However, the assemblage composition and the species richness of pond fishes were similar between the two drainage basins in RFAD. Mendonça *et al.* (2005) suggested that the two drainage basins of RFAD should be considered as distinct management units, because they have dissimilar stream fish faunas. However, the isolation by the reserve's central plateau apparently did not constitute an effective barrier for fish that exploit temporary ponds.

The fish assemblages found in the ponds did not differ between drainage basins and there was little evidence of relationships with water physicochemical characteristics. However the assemblages were related to the structural characteristics of the ponds. Assemblage structure was strongly nested, resulting in low beta diversity among RFAD ponds, in contrast to the results of Mendonça *et al.* (2005) for stream-fish assemblages in the same area. The differences in species responses to the environmental factors, as well as the strongly limiting condition of the ponds for some species, result in fish assemblages that show little relationship to the species composition found in

adjacent streams. However, more intensive studies will be necessary to determine which species are dependent on ponds to maintain viable populations in the RFAD area and for which species ponds could represent a population sink.

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