

Trophic structure of a fish community along environmental gradients of a subtropical river (Paraitinga River, Upper Tietê River Basin, Brazil)

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Abstract This research characterized the feeding ecology of the fish community of the upper-middle course of Paraitinga River, located within the Upper Tietê River Basin, a peculiar Atlantic Forest area, regarded as a hotspot for fish conservation. Considering the several anthropogenic modifications, knowledge of the trophic structure might contribute to a better understanding of the factors that maintain the present fish community. Fish were collected with electrofishing equipment at 16 sites with different riparian vegetation, including native forest, secondary forest, pasture, and *Eucalyptus*, during the dry and rainy season of 2004/2005. Results obtained for 15 species indicated a predominance of insectivores and herbivore-detritivores along the course and an increase of total biomass, specifically of the

herbivores-detritivores at the pasture sites, which seemed to be mediated by specific habitat features, which included open canopy, high water speed, and deeper areas. Strategies of resource use indicated that 47% of total combination pairs showed high overlap, but competition seemed to be minimized through low co-occurrence, spatial segregation, and abundance of food resources. Niche width was broad for all species, with no significant differences occurring among sites, seasons, and upper and lower course. With regard to the ongoing modifications in riparian zone conditions in this area, the implications of these findings for regional biodiversity conservation are discussed.

Keywords Upper Tietê · Food habits · Niche overlap · Riparian vegetation

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Introduction

Relationships between the gradient of physical factors that occurs along fluvial systems and changes in community structure and function have been demonstrated at different levels, including patterns of species distribution associated with temporal changes in channel morphology and availability of resources (Schlosser, 1982; Paller 1994), stream size and canopy openness (Angermeier & Karr, 1983), micro-habitat segregation within a pool or riffle (Grossman et al., 1987; Langeani et al., 2005), current velocity (Meffe & Sheldon, 1988), and longitudinal changes

in community composition within a stream (Whittier et al., 1988; Mazzoni & Lobón-Cerviá, 2000; Abes & Agostinho, 2001).

Despite the extensive ongoing deforestation in tropical areas, a little information exists concerning its impacts on fish assemblages in streams, or even on the processes structuring tropical stream fish communities. Some studies have suggested an impact of deforestation on fish fauna (Angermeier & Karr, 1983; Castro & Casatti, 1997), but the mechanisms by which fish respond to potential changes in their food sources still remain unknown.

Changes in riparian canopy cover could affect communities by influencing cover, habitat, instream temperature, and primary production (Bojsen & Barriga, 2002), while litter inputs from riparian vegetation provide a major energy source for stream invertebrates (Gregory et al., 1991). Apparently, greater proportions of fish are supported by autochthonous sources of food in deforested catchments (Angermeier & Karr, 1983; Burcham, 1988), as shown by a higher density of periphyton-feeding catfishes in sites of decreased cover and a dominance of omnivorous and insectivorous Characiformes at forested sites (Bojsen & Barriga, 2002).

Within the neotropics, trophic structure of fish communities of large rivers has been relatively well studied in rivers, such as the Paraná, Amazon, and Madeira (Lowe McConnell, 1999; Goulding et al., 1988), contrasting with streams, where, despite the efforts to determine taxonomic composition of these still poorly known environments (Castro et al., 2003, 2005), more ecological information is needed.

In the State of São Paulo, the Upper Tietê River Basin represents one of the most urbanized regions, and stream environments have been adversely impacted by several anthropogenic activities that include deforestation, mining, agriculture, and industry. The study of the evolution of soil use between 1988 and 2001 in the Upper Tietê-Cabeceiras sub basin has shown that the floodplain areas were reduced by 24%, native forest by 7.7%, pasture by 9.9%, while exposed soil or mining increased 39%, indicating a reduction of original forest cover, which was substituted by forest plantations, which increased by 27.5% (Moraes et al., 2005). The Upper Tietê River Basin is also a peculiar geographic area due to physical and historical processes which resulted in a high number of endemic species, some of which are

already critically endangered (Ministry of the Environment, Normative Instruction 3, 27 May 2003 and Normative Instruction 5, 21 May 2004). Such a situation urges ecological research to enhance management options for these unique environments.

The present study focuses on the Sub-basin of Paraitinga River, one of the main tributaries of Tietê River, which has been a subject to removal of riparian vegetation in the last decades, presenting a mosaic of native forest, pasture and reforestation. Considering that such changes might be a major cause of habitat degradation, the present study was aimed to evaluate whether riparian vegetation influences species composition and diet of stream fishes and if these fish apply foraging strategies to avoid competition over the shared resources. The study also provides information that can be used to document and suggest causes for changes and future management options for similar rivers.

Study area

The Upper Tietê River Basin belongs to the Paraná River Basin and consists of the area drained by the Tietê River upstream of Pirapora Dam up to its headwaters in the city of Salesópolis, occupying an area of about 5900 km² and having an extensive urbanization which includes the city of São Paulo and most of the municipalities that integrate the Metropolitan Region of São Paulo. It is situated in the Atlantic plateau, characterized by highlands, constituted mainly by pre-Cambrian crystalline and cambro-ordovician rocks, cut by basic and alkaline Mesozoic intrusives and by coverings of sedimentary basins of São Paulo and Taubaté.

The climate in the region is within the limits of the Cbf (mild summer) and CWb (dry winter) zones according to the classification of Köppen, with total rainfalls that vary between 30 and 60 mm in the driest month (Fusp, 2000).

The Paraitinga River is one of the main tributaries of the right bank of the Tietê River, with its headwaters located at the borders of Paraíba do Sul and Upper Tietê Basins, at the Municipality of Paraibuna (SP). It runs in the east-west direction for approximately 56 km, receiving through its extension around 250 small tributaries, occupying a watershed of 225 km² (Manna de Deus et al., 2001). Since 2005, a dam of 6.6 km² has

been filled in the lower portions of the river, in order to increase water supply for the Metropolitan Region of São Paulo city (Fig. 1a).

Land use in Paraitinga sub-basin is dominated by horticulture and fruticulture (29.7%), followed by secondary forest (20.8%), wetlands (20.0%), urban area (14.0%), pasture (12.0%), reforestation (3.1%), and fragments of primary forest (0.4%) (IAC, 2006) (Fig. 1b).

The portion of the river that was studied is located between S 23° 34' 255", W 45° 42' 407" and S 23° 31' 519", W 45° 48' 373". Different riparian conditions are found along its course, such as pasture, reforestation, and secondary and native forests. Its headwaters are surrounded by remains of Atlantic and secondary forest, the middle course with a mosaic of native forest, pasture and *Eucalyptus grandis* Hill ex Maiden plantations which extend to the lower portions of the river, where small properties with small-scale agriculture are frequent. A mosaic of runs, riffles, and pools are commonly observed within the sampled area (Table 1).

The study sites differed mainly by the degree of the anthropogenic alteration of the riparian vegetation and position along the river. Pasture and *Eucalyptus* sites, were located in the middle course, predominantly within private-property farms, where cattle are raised and where *Eucalyptus* plantations are used for charcoal production. Pasture sites differed from other sampling stations by an increase in sinuosity and higher depth, representing an area where an overflow of the river may occasionally occur during the rainy season. Native and secondary forest sites were located in the upper portion of the river, upstream of several waterfalls, inserted in an area which has been mainly used for commercial *Eucalyptus* plantations in the last decades (Fig. 1b).

Material and methods

Sampling sites and data collection

For the present study, 16 localities with different riparian conditions represented by native forest, secondary forest, pasture, and *Eucalyptus* reforestation were selected along the upper-middle course of the river, at distances that ranged between 5.5 and 28.3 km from the headwaters, comprising four sites

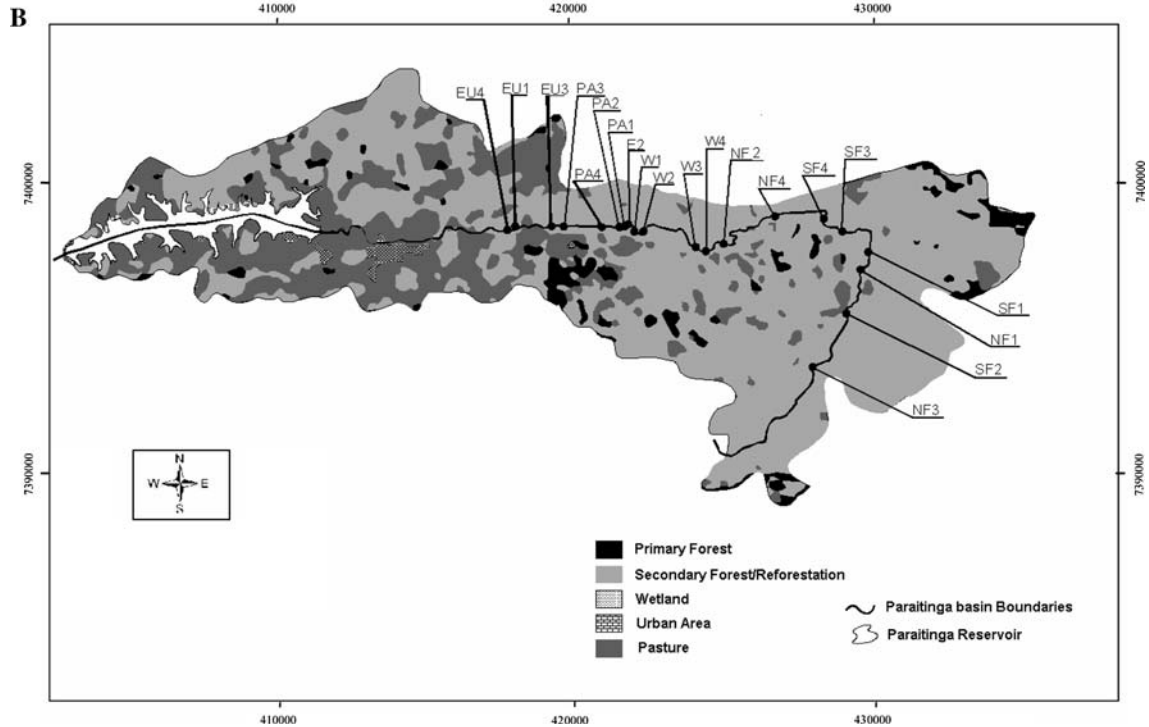
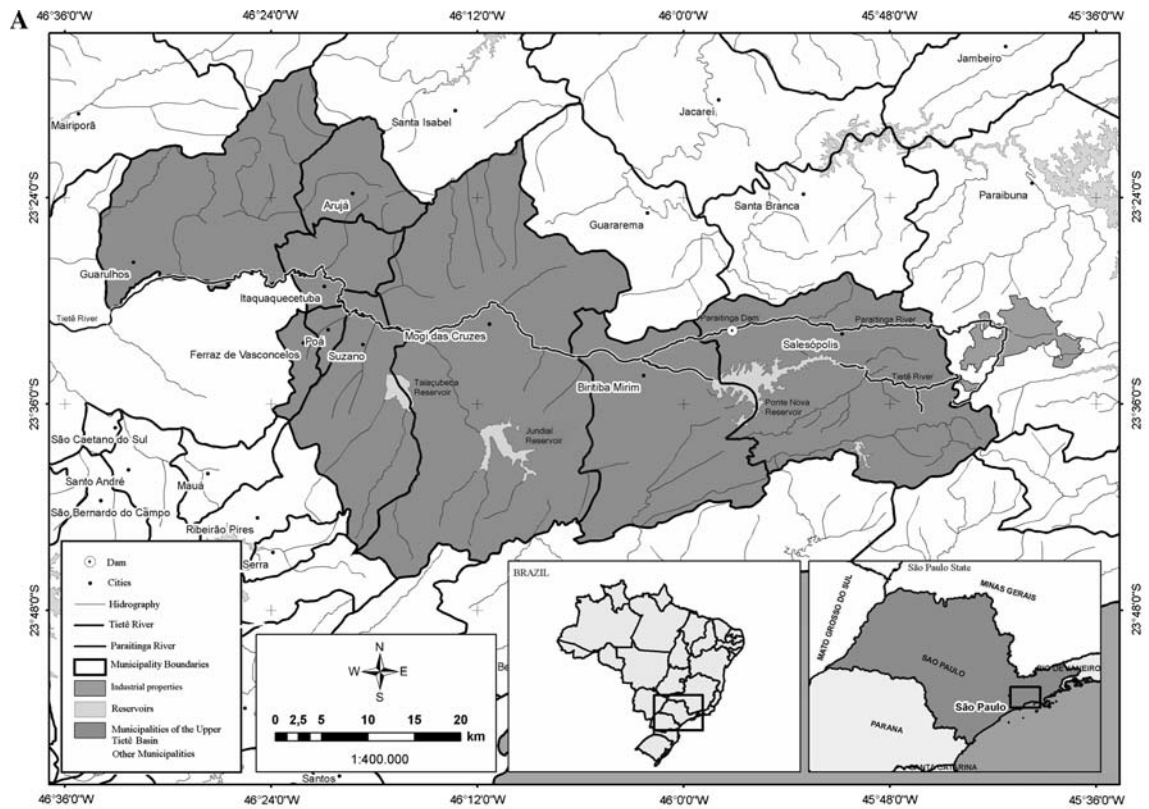
for each situation. For analysis purposes native and secondary forests were here considered "upper course," while pasture and *Eucalyptus* were considered "lower course", due to their locations along the stretch studied.

Fish were sampled at the 16 localities during the dry season (July–August) of 2004 and wet season (January–February) of 2005 using a stationary electrofishing equipment (HONDA EX 1000 generator, 120 V, 1000 W, 60 Hz, <2.5 A, AC). At each site, three successive catches were conducted over a stretch of 50 m, following the 3-catch removal method (Zippin, 1958), resulting in a constant fishing effort (~40 min for each removal) at each locality. The equipment configuration was similar to the one used by Mazzoni et al. (2000), since its adequacy for quantitative analysis of fish populations of southeastern Brazilian streams has been considered suitable.

Fish were fixed in 10% formalin and preserved in 70% alcohol. Identifications were made at the Laboratory of Ichthyology of the State University of São José do Rio Preto (SP), and samples of each species deposited at their museum.

At each sampling site, the following variables were recorded: percent tree canopy shading, depth (m), width (m), water velocity (m s^{-1}), trunk density (%), and proportions of pools (%). Litter input was obtained using 3 trays of 0.33 m \times 0.55 m at different points of each site, which remained for 24 h. Material was then dried at 60°C for 48 h for evaluation of biomass (Henry et al., 1994). Physicochemical parameters for each site, including pH, temperature (°C), conductivity ($\mu\text{S cm}^{-1}$), total dissolved solids (mg l^{-1}), turbidity (NTU) and dissolved oxygen (mg l^{-1}) were measured with a multi-parameter water quality monitoring system (HORIBA U-22). Total phosphorus analysis followed APHA (1998).

Drift was collected in regions of high water velocity, using nets of metal frames (25 \times 25 cm) and mesh size of 350 μm , which remained at each site for 1 h. Samples were preserved in 10% formalin and returned to the laboratory for processing. Macroinvertebrates from each sample were hand picked with the aid of a dissecting microscope and weighed to the nearest microgram using a Mettler AE240 electrobalance. Biomass calculations were adapted from the abundance formula proposed by Smock (1966), which considers net dimensions, flow rate and duration of sampling.



◀ **Fig. 1** Location of Paraitinga River within Tietê-Cabeceiras sub-basin, Upper Tietê River Basin (a), and major land uses in Paraitinga watershed, indicating the sampling sites from upstream to downstream (b). SF = Secondary forest; NF = Native forest; EU = *Eucalyptus*; PA = Pasture; W = Waterfalls

Drift and litter biomass between sites with similar riparian conditions were tested using one-way ANOVA. When significant differences were detected, Tukey's test for post hoc comparisons was performed, using $p \leq 0.05$ as the level of statistical significance. Principal components analysis (PCA) (Manly, 1986), run on PC ORD v.4 (McCune & Mefford, 1999), was performed to arrange sampling sites in a minimum number of axes, after log-transformation of habitat variables.

Diet analysis

Subsamples for the most abundant species were taken, while for the remaining ones, the total number of individuals was analyzed, considering the 16 sampling sites grouped for the rainy and dry seasons. Gut contents were analyzed according to the method of frequency of occurrence and points method (Hynes, 1950), counted in a counting chamber under a stereomicroscope (25 \times), and the area occupied by each item evaluated. The total area of food items was considered the total volume (100%). Calculations of the volumetric proportion of each item were made according to the formula:

$$P_{ij} = \frac{\sum_{x=1}^N P_{ix}}{N_j}$$

where P_{ix} is the proportion by volume of item i in the gut of individual x and N_j is the number of individuals of species j .

In order to estimate the predominant food items for each species, results for frequency of occurrence and points method were combined according to the feeding index (IA_i) proposed by Kawakami & Vazzoler (1980):

$$IA_i = \frac{F_i x V_i}{\sum_{i=1}^n (F_i x V_i)}$$

where $i = 1, 2, \dots, n$ food items; F_i = frequency of occurrence (%) of a given food item; and V_i = volume (%) of a given food item.

Diet overlap among species was obtained by Pianka's overlap index which was calculated among species for which sample sizes were equal to or greater than 5, using the software ECOSIM v.5.53 (Gotelli & Entsminger, 2001) over the matrix of volume percentage:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^n p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^n (p_{2i}^2)(p_{1i}^2)}}$$

where p_{2i} is the volume of item i in the diet of individual 2 and p_{1i} is the percent volume of item i in the diet of individual 1. This index ranges between 0 (no overlap) and 1 (complete overlap). In addition, co-occurrence patterns of species pairs (% occurrence) for the 32 sites (dry and rainy seasons) were obtained, in order to determine if species were feeding on the same patch.

Trophic niche breadth was calculated according to Smith's measure, which according to Smith (1982) has good statistical properties, but is meaningless if not analysed comparatively. This index was calculated according to the formula:

$$FT = \sum \sqrt{p_i a_i}$$

where FT is Smith's niche width measure, p_i is the proportion of individuals found using resource i and a_i is the proportion of resource i of the total resources found in gut contents. The FT 95% confidence interval was calculated as follows:

$$FT \text{ 95\% confidence level} = \sin(x \pm 1.96/2 \sqrt{y}),$$

where x is the arcsine of FT and y is the total number of individuals studied.

Smith's niche breadth varies from 0 (minimal) to 1.0 (maximal), being considered a standardized measure (Krebs, 1989).

Results

Spatial variation in environmental characteristics

Invertebrate drift biomass ranged between 0.1 and 5.8 g l⁻¹, and did not vary among sites (ANOVA, $F = 0.16$; $p = 0.92$), while litter biomass values ranged between 0 and 6.2 g m⁻² day⁻¹, differing

Table 1 Water quality and habitat structure (mean values—dry and rainy season) in the 16 sampling sites of Paraitinga River

	NF1	NF2	NF3	NF4	SF1	SF2	SF3	SF4	PA1	PA2	PA3	PA4	EU1	EU2	EU3	EU4
Width (m)	3.69	4.67	2.92	4.14	3.83	2.30	5.28	5.67	2.30	2.48	1.91	2.58	2.29	3.16	3.54	3.69
Depth (m)	0.28	0.58	0.21	0.40	0.31	0.41	0.29	0.33	0.71	0.72	0.67	0.53	1.35	0.70	0.54	0.55
Current speed (m s ⁻¹)	0.55	0.30	0.18	0.22	0.29	0.38	0.29	0.30	0.50	0.48	0.39	0.52	0.36	0.27	0.35	0.48
Canopy cover (%)	75.00	87.50	97.50	85.00	75.00	75.00	85.00	90.00	7.50	6.00	0.00	0.00	11.50	60.00	35.00	47.50
Trunk density (%)	12.65	5.37	6.02	7.91	19.35	11.33	5.84	22.74	6.43	3.98	0.00	1.32	0.00	3.42	7.85	7.65
Pools (%)	25.00	25.00	7.50	47.50	25.00	27.50	15.00	30.00	12.50	2.50	10.00	12.50	0.00	0.00	0.00	5.00
Discharge (m ³ s ⁻¹)	2.15	2.80	0.32	1.60	1.43	0.69	2.31	2.56	1.71	1.66	0.99	1.95	2.43	1.95	1.78	3.18
Temperature (°C)	16.95	16.90	17.15	19.05	16.90	16.35	18.25	17.90	16.80	17.00	17.30	17.70	17.85	19.8	18.6	20.95
Turbidity (NTU)	11.91	18.94	19.89	14.38	12.94	17.91	13.41	14.15	65.50	56.00	107.00	18.19	15.00	11.68	13.91	17.15
Conductivity (µS cm ⁻¹)	26.30	28.05	20.85	26.55	21.40	21.15	21.55	27.45	27.25	27.4	28.1	27.95	28.35	27.45	27.95	28.6
Dissolved oxygen (mg l ⁻¹)	6.86	7.10	10.08	10.58	10.42	10.38	11.11	9.78	12.4	7.67	7.95	10.47	7.77	7.46	7.3	7.41
PH	6.70	6.90	6.85	6.80	6.45	6.80	6.50	5.90	6.25	6.35	6.85	6.15	6.30	6.90	6.40	6.30
Total dissolved solids (mg l ⁻¹)	33.70	33.80	31.60	36.00	33.80	59.30	34.70	36.50	28.40	28.10	35.60	43.20	40.20	35.10	35.00	44.40
Total phosphorus (µg l ⁻¹)	72.0	64.90	22.80	79.60	108.10	36.50	82.60	86.10	46.4	49.1	106.70	62.00	76.6	89.6	74.8	71.7
Sand (%)	82.00	90.0	92.00	86.00	92.00	92.00	88.00	90.00	92.00	92.00	92.00	88.00	92.00	92.00	92.00	88.00
Clay (%)	12.00	6.00	6.00	10.00	4.00	6.00	4.00	4.00	4.00	4.00	4.00	6.00	6.00	4.00	6.00	8.00
Silt (%)	6.00	4.00	2.00	4.00	2.00	2.00	2.00	4.00	2.00	2.00	2.00	2.00	2.00	4.00	2.00	4.00

SF = Secondary forest; NF = Native forest; EU = Eucalyptus; PA = Pasture

among riparian sites ($F = 3.7$; $p = 0.02$), with significantly higher values at the secondary forest when compared to pasture sites ($p = 0.03$).

The physical and chemical parameters of water showed a little difference among sampling sites, with exception of turbidity, which showed higher values at pasture sites and total phosphorus which presented higher values at SF1 and PA3 (Table 1). PCA analysis (Fig. 2) showed that axis 1 distinguished sampling sites in relation to depth and percentage shading. Pasture and *Eucalyptus* sites concentrated on the left half of the ordination diagram and were associated with greater depth values ($r = -0.669$). On the right half, native forest and secondary forest sites were highly associated with high percentage shading ($r = 0.880$), width ($r = 0.643$), % of pools ($r = 0.615$), litter biomass ($r = 0.597$), and trunk density ($r = 0.511$). Component 2 reflected seasonal differences, with native forest and secondary forest sites of the rainy season associated with high pool percentage ($r = 0.661$), and *Eucalyptus* of the dry season with high values of trunk density ($r = -0.676$).

Pattern of trophic structure along habitat gradients

From 21 species and 1,110 fish collected during the two sampling periods, 15 species, comprising 242

individuals were used for diet analysis. According to Table 2, 53% of the species were considered insectivores, followed by herbivore-detritivores (33%), insectivore-carnivores (7%) and omnivores (7%). Adult insects from the orders Ephemeroptera, Trichoptera and Coleoptera occurred mainly in the diets of *Imparfinis piperatus* Eigenmann & Norris, 1900, *Characidium oiticicai* Travassos, 1967 and *Characidium zebra* Eigenmann, 1909. Young insects, including larvae of Chironomidae, Simuliidae, Plecoptera, Ephemeroptera, Trichoptera and Coleoptera, were identified in the diet of a few species, such as *Characidium zebra* and *Characidium oiticicai*. Since insect fragments were composed mainly of insect larvae, this also seemed to be the main food item of *Imparfinis piperatus*, *Cetopsorhamdia iheringii* Schubart & Gomes, 1959, *Astyanax paranae* Eigenmann, 1914, *Trichomycterus* sp., *Gymnotus pantherinus* Steindachner, 1908 and *Characidium cf. lagsantense* Travassos, 1947.

Insectivores were the predominant feeding guild along the studied stretch, with total fish biomass tending to increase along the river, especially from 23.8 to 26.2 km, which corresponds to the pasture zone (Fig. 3).

Significant differences in trophic guild biomass among riparian zones were found for both insectivores (one-way ANOVA; $P < 0.0001$) and herbivore-

Fig. 2 PCA plot of the 16 sampling sites considering different riparian zones and seasons. Hollow symbols refer to the dry season and solid symbols to the rainy season. TD = Trunk density

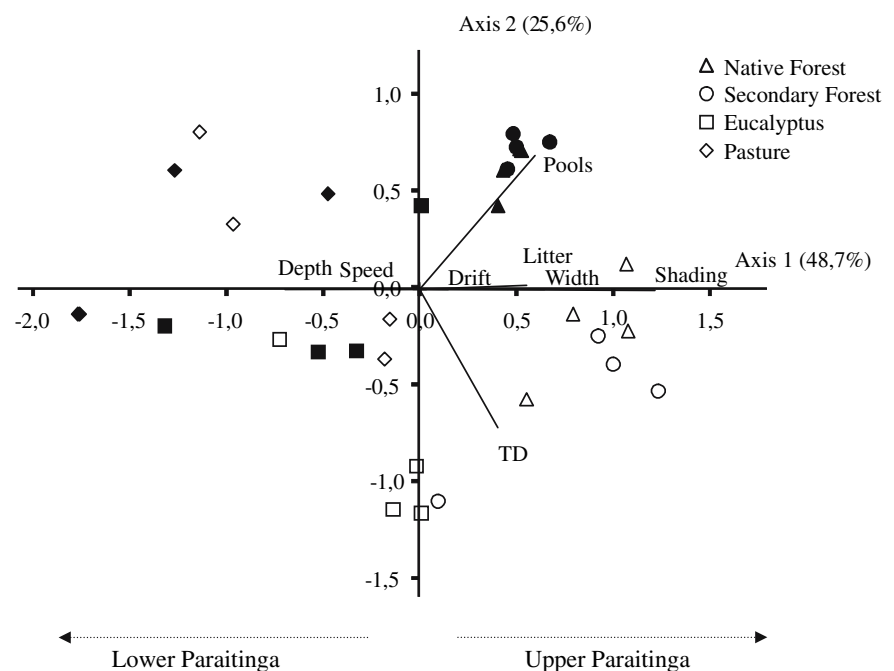


Table 2 Diet of the different species of the Paraitinga River

	Food items										Stomachs with food contents	SL (cm)	
	Algae	Young insects	Adult insects	Crustacea	Fish	Insect fragments	Vegetal matter	Organic matter	Detritus	Other			
Herbivore–detritivores													
<i>Hisonotus</i> sp. ²	0.5	0.4	–	–	–	0.6	2.4	25.4	70.8	–	–	25	2.1–5.6
<i>Phalloceros caudimaculatus</i> ³	4.9	–	–	–	–	1.6	13.2	27.3	53.0	–	–	23	2.0–5.2
<i>Pseudotocinclus tietensis</i> ²	5.9	1.0	–	–	–	1.6	3.4	22.5	65.6	–	–	27	3.4–7.6
<i>Hypostomus tietensis</i> ²	2.4	0.8	–	–	–	–	7.5	9.6	79.8	–	–	4	2.8–19.1
<i>Pimelodella meeki</i> ¹	1.7	–	–	–	–	7.1	–	4.7	86.4	–	–	2	7.2–8.3
Omnivores													
<i>Geophagus brasiliensis</i> ⁴	–	–	–	–	–	17.7	15.2	49.4	17.7	–	–	3	1.5–6.1
Insectivores													
<i>Imparfinis piperatus</i> ¹	–	4.0	0.3	–	–	72.0	1.5	22.0	0.2	–	–	25	4.3–10.9
<i>Cetopsorhamdia iheringi</i> ¹	0.02	2.1	–	–	–	48.7	3.8	35.6	9.6	0.2	–	8	7.1–9.4
<i>Asyanax paranae</i> ⁵	0.8	0.1	–	–	–	71.4	4.0	23.6	0.1	–	–	16	2.0–8.8
<i>Trichomycterus</i> sp. ⁶	–	–	–	–	–	64.7	2.3	30.6	2.4	–	–	10	3.9–13.7
<i>Gymnotus pantherinus</i> ⁷	–	0.4	–	–	–	45.2	16.9	36.8	0.7	–	–	28	5.4–26.0
<i>Characidium cf. lagosantense</i> ⁸	–	7.9	–	–	–	78.9	3.5	7.0	2.6	0.1	–	17	3.9–6.3
<i>Characidium oiticicat</i> ⁸	–	9.8	–	–	–	75.3	0.3	14.1	0.5	–	–	28	2.8–7.1
<i>Characidium zebra</i> ⁸	–	21.3	–	–	–	60.5	2.8	11.2	4.0	0.2	–	14	5.5–7.9
Insectivore–carnivore													
<i>Oligosarcus paranensis</i> ⁵	0.03	–	–	0.7	34.3	47.1	7.8	9.9	0.03	–	–	12	2.7–14.0

Item values are the feeding index (IA), which combines frequency of occurrence (%) and volume (%) of each item. Numbers in bold refer to predominant food item

Families: ¹Heptapteridae; ²Loricariidae; ³Poeciliidae; ⁴Cichlidae; ⁵Characidae; ⁶Trichomycteridae; ⁷Gymnotidae; ⁸Crenuchidae

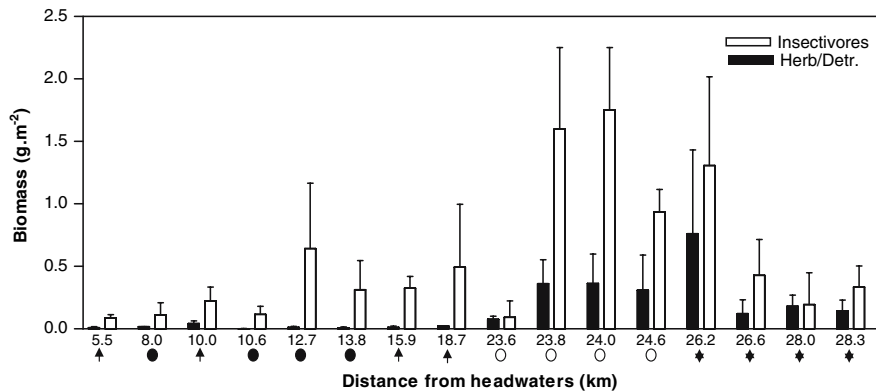


Fig. 3 Mean biomass and standard deviation (rainy and dry season) of the two predominant trophic guilds of fishes along the upper middle portion of the Paraitinga River. \blacktriangle = Native forest; \bullet = Secondary forest; \circ = Pasture; \blacklozenge = *Eucalyptus*

detritivores (one-way ANOVA; $P < 0.0003$). Insectivore and herbivore-detritivores biomass was significantly higher in pasture sites compared to the other riparian areas ($p < 0.001$), and $p < 0.01$ (herbivore-detritivores in pasture \times *Eucalyptus* sites).

The increase in the two-dominant trophic guilds in the lower part of the river stretch studied occurred due to the restricted distribution of many species to the pasture and *Eucalyptus* sites, which included the herbivore-detritivore *Hisonotus* sp., *P. tietensis* and *P. meeki* and the insectivores *C. iheringii*, *C. lagsantense* and *C. zebra*. On the other side, few species were limited to the native and secondary forest sites, including rare species such as *Hyphessobrycon bifasciatus* Ellis, 1911.

Resource partitioning, analyzed through the calculation of inter-specific dietary overlap (Pianka's index) among species which were represented by more than eight individuals was calculated. The following pairs were compared: *Phalloceros caudimaculatus* Hensel, 1868, *Pseudotocinclus tietensis* Ihering, 1907, *Imparfinis piperatus*, *Hisonotus* sp., *Gymnotus pantherinus*, *Characidium oiticicai*, *Characidium* cf. *lagsantense*, *Astyanax paranai*, *Trichomycterus* sp., *Characidium zebra*, *Cetopsorhamdia iheringii* and *Oligosarcus paranensis* Menezes & Gery, 1983 (Table 3). Of the total combination pairs, 47% showed high overlap, which occurred mainly within detritus-consuming species and those that shared aquatic insect larvae. However, when these results are analysed in relation to co-occurrence of species, it can be observed that only a few pairs with high overlap also showed high

co-occurrence, including *P.tietensis* \times *P.caudimaculatus*, *Hisonotus* \times *P.caudimaculatus*, *Hisonotus* \times *P.tietensis*, *G.pantherinus* \times *I.piperatus*. Within species which display similar feeding tactics as the three *Characidium* species, *C. zebra* and *C. oiticicai* did not occur at the same sites, while *C. zebra* and *C. lagsantense* occurred together in 22% of them. *O. paranensis* did not show high overlap with any other species, because of its unique diet, which included the consumption of fish.

Despite the predominant use of a limited range of resources by most of the species, which consisted of organic matter, detritus or insects and plant material, niche width was broad, with no significant differences among riparian conditions, stretches, and seasons (Fig. 4).

Discussion

Trophic structure along the environmental gradient

Although four different trophic guilds were recognized within the upper-middle portion of the Paraitinga River, the contribution of omnivores and insectivore-carnivores was low and represented, respectively, by the presence of occasional species such as *Geophagus brasiliensis* Quoy & Gaimard, 1824 and *Oligosarcus paranensis*, a species which seems to occupy the lower course of the studied

Table 3 Pianka's Overlap Index calculated for each species pair based on % total volume (in bold), and percentage of sites in which species co-occurred (dry and rainy season)

	<i>P. caudimaculatus</i>	<i>P. tietensis</i>	<i>I. piperatus</i>	<i>Hisonotus</i> sp.	<i>G. pantherinus</i>	<i>C. oiticicai</i>	<i>C. lagosantense</i>	<i>A. paranae</i>	<i>Trichomycterus</i> sp.	<i>C. zebra</i>	<i>C. iheringii</i>	<i>O. paranensis</i>
<i>P. caudimaculatus</i>												
<i>P. tietensis</i>	50											
<i>I. piperatus</i>	69	44										
<i>Hisonotus</i> sp.	41	47	44									
<i>G. pantherinus</i>	66	41	38	41								
<i>C. oiticicai</i>	19	3	16	3	3							
<i>C. lagosantense</i>	25	28	28	28	22	9						
<i>A. paranae</i>	22	3	13	3	6	9	3					
<i>Trichomycterus</i> sp.	28	13	16	9	19	6	9	6				
<i>C. zebra</i>	28	28	28	28	25	0	22	0	6			
<i>C. iheringii</i>	16	16	16	16	13	0	19	0	3	16		
<i>O. paranensis</i>	22	22	16	22	16	3	9	3	0	6	3	

*Indicates overlap ≥ 0.60

stretch of the river only during the rainy season, when mature females were observed. The community was dominated by insectivores and herbivore-detritivores, with no increase in diversity of feeding guilds along the longitudinal dimension.

The low contribution of carnivores which includes species, such as *Salminus hilarii* Valenciennes, 1849 and *Hoplias malabaricus* Bloch, 1794 previously recorded for this river (Silva et al., 2006) may be explained both by the location of the sampling stations, situated in the upper-middle course, and by the existence of a recently constructed dam at the lower portion of the river, which may obstruct the passage of migratory species. Other species not collected here include two other Tetragonopteri-nae—*Astyanax bimaculatus* Linnaeus, 1758 (presently known as *Astyanax altiparanae* Garutti & Britski, 2000), and *Astyanax fasciatus* Cuvier, 1819, *Serrapinus notomelas* Eigenmann, 1915, *Cyphocarax modestus* Fernandez-Yepe, 1948, *Corydoras aeneus* Gill, 1858, *Corydoras nattereri* Steindachner, 1876 and *Hoplosternum littorale* Hanckock, 1828 (Silva et al., 2006). Obviously, the number of trophic guilds within an assemblage is limited to some extent by the diversity of the resource base available, by the number and morphological diversity of species present and the availability of prey items, as well as the degree of taxonomic resolution employed by the investigator (Pusey et al., 1995).

The main zonation pattern found was related to a total fish biomass increase at the lower course of the river, and an increase in the percentage of herbivore-detritivore biomass and richness of several families such as Heptapteridae and Loricariidae especially at the pasture sites. This seemed to be mediated by specific habitat features, which included open canopy, high water speed, high sinuosity, and deeper areas. Herbivore-detritivore species, such as *P. tietensis* and *Hisonotus* sp. are commonly found at or near the upper portion of the water column, in close association with subsurface structures provided by submerged branches, aquatic macrophytes, and terrestrial glass blades growing along the creek margins (Schaefer, 1998). Thus, open sites, which have a higher abundance of periphytic algae due to a lack of shading, may provide an important forage base for these species. In addition, at the pasture sites, a higher runoff from adjacent land may occur, as shown by some

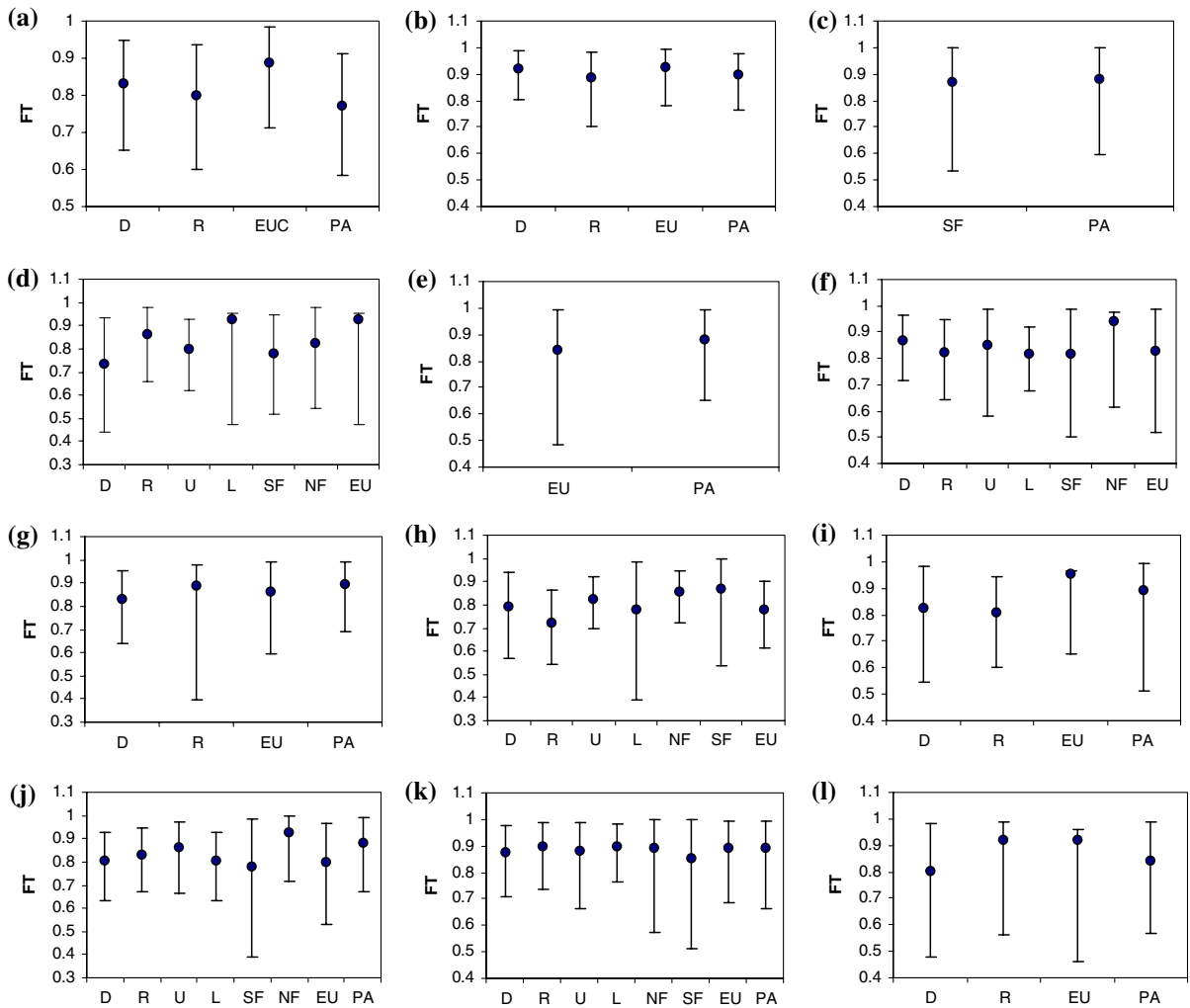


Fig. 4 Smith's niche breadth measure for the different species (means and 95% confidence intervals). 95% FT's confidence interval overlaps, provides a test to determine significant differences ($P < 0.05$) among groups. (a) *Hisonotus* sp.; (b) *P. tietensis*; (c) *Trichomycterus* sp.; (d) *A. paranae*; (e)

Oligosarcus sp.; (f) *Gymnotus* sp.; (g) *C. zebra*; (h) *C. oiticicai*; (i) *C. lagosantense*; (j) *I. piperatus*; (k) *P. caudimaculatus*; (l) *C. itheringii*. D = Dry season; R = Rainy season; U = Upper course; L = Lower course; SF = Secondary forest; NF = Native forest; EU = *Eucalyptus*; PA = Pasture

occasional increases in total phosphorus values, favoring a higher primary productivity.

Terrestrial insect consumption was occasionally recorded for species which occurred predominantly in the upper-forested sites as *C. oiticicai*, and other species with a wider distribution as *I. piperatus*, indicating the importance of riparian forest for these species. At the native forest sites, higher diversity and abundance of benthic invertebrates was found by Kreidel (2007), which may explain the predominance of insectivores that consume this resource. Invertebrates that drift from the upper forested sites may also

have contributed to support the high insectivore biomass at the lower course, since no increase in benthic invertebrates was recorded in pasture and *Eucalyptus* sites (Kreidel, 2007). The presence of physical barriers represented by waterfalls upstream from the pasture and *Eucalyptus* sites, may also account for these results, once they may obstruct the passage of schools of adult specimens of species such as *Astyanax paranae*.

Effects of deforestation on fish abundance are contradictory, since some authors have found a positive effect of deforestation on total fish

abundance (Agostinho & Penczak, 1995; Lyons et al., 1995; Harding et al., 1998), while others showed a negative impact on fish density (Toham & Teugels, 1999) in African streams. Given the different morphological features of the upper and lower zones of Paraitinga River, as shown by PCA, riparian zone influence over the fish community could not be distinguished, and seemed to be associated to other instream features as diversity of microhabitats and volume. In fact, a basic difficulty in stream studies is to distinguish between the longitudinal effects and that of deforestation (Bojsen & Barriga, 2002). Nevertheless, our results agree with other studies in Neotropical streams, which have shown that the density of periphyton-feeding catfishes (Loricariidae) increases with decreasing canopy cover (Power, 1984). Burcham (1988) called for studies of streams with similar substratum and catchment characteristics, but with different land use, to reveal that increased light availability in streams lead to a greater representation of periphyton feeders.

Strategies of resource use

The ecological niche and the partitioning of food resources have been considered a force structuring communities (Schoener, 1989). While species in stable environments might reduce competition by becoming more specialized, species in unstable environments may be unable to specialize on a specific range of resources because of frequently changing conditions (MacArthur, 1975).

The utilization of resources by the different species showed a high overlap between pairs, which may indicate abundance of resources. However, considering that only some pairs of species with high overlap values co-occurred, no evidence has been found to support the idea of food competition as an important structuring factor. May (1986) reports that even when species demonstrate high niche overlap other factors can promote coexistence, such as spatial heterogeneity and habitat complexity, combined with environmental, temporal, population, and behavioral stochasticities.

For example, *P. caudimaculatus* which overlapped with the armored catfishes *P. tietensis* and *Hisonotus* sp. at the same sites, is known to occupy shallow

regions with low current (Sabino & Castro, 1990), while *Hisonotus* sp. occurs in association with leaves and branches of submersed marginal vegetation (Casatti & Castro, 1998), a habitat also occupied by *P. tietensis*, which is commonly found in close association with sub-surface structures (Schaefer, 1998). These fishes are usually considered herbivores (Schaefer, 2003), but since detritus was consumed in high proportions and algae and vegetal matter were very low, fishes were assigned to the herbivore-detritivore guild.

Within the insectivores which co-occurred and showed high food overlap, microhabitat segregation might also occur, since *G. pantherinus* occupies the marginal vegetation and *I. piperatus* usually occurs under submersed branches (Esteves & Lobón-Cerviá, 2001). *C. oiticicai* occurred predominantly at the upper forested sites, while *C. zebra* and *C. lagsantense* were commonly found in the lower course (Pinto Lobo, 2006), indicating a clear spatial segregation. Among the co-occurring *C. zebra* and *C. lagsantense*, the sit and wait behavior employed by *Characidium*, which catch prey items at a time after visual detection (Sabino & Zuanon, 1998) may be another mechanism which helps to avoid competition.

Changes in the environmental conditions can affect prey availability, diet patterns, and costs of foraging. According to the Optimal Foraging Theory (MacArthur & Pianka, 1966), species from rich feeding areas would show a narrower food niche breadth, while those from areas with less dense and less nutritive prey would demonstrate a larger alimentary niche breadth in order to compensate for the low quality of the prey (MacArthur & Pianka, 1966; Schoener, 1971). Consequently, species living in a stressed environment would reduce their spatial niche to use only the best patches (MacArthur & Pianka, 1966).

Despite the existence of disturbed conditions, as observed particularly for the pasture sites, no significant differences in niche width calculated for the same species under the different riparian conditions were found, with fairly wide values indicating some degree of opportunistic feeding. Similarly, niche width for each species did not vary between the upper and lower course and seasons, indicating a high abundance and constant supply of resources. This constancy in resource availability may be maintained by the upper-forested patches, which seem to be an

important structural and functional parameter that contributes both with insects and detritus sources, as indicated by the similar drift biomass values among sites. According to Pomeroy (1980), the great bulk of detritus originates from plant biomass, particularly in small forest-covered streams, where terrestrial contribution may reach 99%.

In addition, as observed for other Atlantic Rain-forest streams (Esteves & Lobón-Cerviá, 2001), hydrological variations at Paraitinga River do not seem to be sufficient to produce such drastic changes in food availability as those observed in Panamanian streams (Zaret & Rand, 1971). A relative constancy of the environment, as found in rainforest streams in Sri Lanka by Moyle & Senanayake (1984) might also explain the greater importance of food items such as algae and invertebrates, which have a better chance to persist in streams that do not fluctuate so much.

These results have direct implications on species responses to habitat loss and fragmentation, since dietary habit and habitat components of niche breadth seem to be negatively correlated with sensitivity to habitat alterations, i.e., species with broad niches are less affected by habitat loss and fragmentation (Swihart et al., 2003).

Conservation aspects

Since different riparian zones were associated with specific habitat variables, the disturbance effect caused by deforestation alone could not be determined. However, considering that historical removal of riparian vegetation is a major cause of habitat degradation in streams, leading to bank erosion, sedimentation, reduction of shading from overhanging trees, and progressive reduction of habitats (Growth et al., 2003), the present-day situation in the Paraitinga River seems to reflect the habitat modifications that have occurred in the last decades, which has led to environmental degradation caused by deforestation to benefit agriculture and reforestation for commercial purposes. Thus, observed changes such as the reduction of the flooding area, as reported by local people, and the predominance of a few feeding guilds seem to reflect the presence of a pre-selected group of species which adapted to specific conditions including the potential use of the most abundant resources.

Our results seem to agree with the idea that disturbance of riparian forest restricted to small areas may constitute a minor disturbance to some fish assemblages, assuming that the watershed upstream and upslope is still largely forested (Jones et al., 1999). The literature also shows that forested riparian areas upstream of a locale can serve as refugia or sources for recolonization (Niemi et al., 1990). However, limits exist beyond which recovery will be much less likely, since upslope trees can mitigate against riparian disturbance, but only to a point (Jones et al., 1999).

Considering that the Upper Tietê reaches is one out of 23 areas in the Atlantic Forest regarded as a hotspot for fish conservation by the Brazilian Environmental Authorities (Ministry of the Environment, 2000), urgent measures to protect this area are necessary. Monitoring fish species and re-establishing natural gradients may be important measures, since according to the Ministry of Environment (2004)—Normative Instruction no 5, species such as *Pseudotocinclus tietensis*, endemic to the Upper Tietê, and *Characidium* cf. *lagosantense* are already endangered species.

Our results reinforce the importance of protecting these species and broader communities preserving insect production, especially in native forest sites, and maintaining the quality of detritus from secondary and native forests. Installing appropriate fishways to restore fish passage, and implementing protection programs for endangered habitats and species emphasizing the importance of riparian areas conservation and correct practices of soil usage are also important measures which may contribute to the maintenance of instream features, favoring the presence of a diverse fish community.

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