

Local and ecoregion effects on fish assemblage structure in tributaries of the Rio Paraíba do Sul, Brazil

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SUMMARY

1. We examined the effects of physical and chemical habitat variables and ecoregions on species occurrence and fish assemblage structure in streams of the Paraíba do Sul basin, in southeast Brazil.
2. Fish and environmental data were collected from 42 sites on 26 first to fourth order streams (1 : 50 000 map scale) in three ecoregions. The sites occurred in one valley and two plateau ecoregions at altitudes of 40–1080 m and distances of 0.1–188 km from the main channel of the Rio Paraíba do Sul. Physical habitat (substratum, riparian cover, habitat types) and water quality (dissolved oxygen, pH, temperature and conductivity) variables were measured at each sampling site.
3. A total of 2684 individuals in 16 families and 59 species were recorded.
4. Ecoregion was a better predictor of the fish assemblage than the other environmental variables, according to the differences between the mean within-class and mean between-class similarities in assemblage data.
5. Differing landscape characteristics were associated with differing local variables and thereby with differing fish assemblage structures. Riffles, shrub, grass, dissolved oxygen, conductivity and temperature were closely related to fish assemblage structure.
6. Fish assemblages in sites far from the main river and at higher altitudes also differed from those near the Paraíba do Sul main channel, presumably as a result of differences in connectivity, covarying environmental factors and anthropogenic influence.
7. These results reinforce the importance of understanding how stream communities are influenced by processes and patterns operating at local and regional scales, which will aid water resource managers to target those factors in their management and rehabilitation efforts.

Keywords: fish communities, habitat, landscape, streams, tropics, watershed

Introduction

Studies of the variability of fish assemblages at stream sites located in the same river basin are fundamental to understanding the functioning of those systems

(Fialho *et al.*, 2007). Different ecoregions have been reported to have distinctly different fish assemblages (Larsen *et al.*, 1986; Hughes, Rexstad & Bond, 1987; Rohm, Giese & Bennett, 1987). Others have reported minimal ecoregional effect on the classification of fish assemblages, implying that local factors are most important (McCormick, Peck & Larsen, 2000; Van Sickle & Hughes, 2000; Herlihy, Hughes & Sifneos, 2006). There is a clear, practical interest in assessing the capability of environmental classifications for

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partitioning the within-region and between-region heterogeneity of biological assemblages sampled at multiple sites in a river basin. Such assessments aid us in deciding which, if any, environmental or geographic classifications are most helpful in predicting or modelling large-scale spatial variation in biological assemblages. Thus, comparisons of fish assemblages from different ecoregions within a river basin should increase our understanding of the relative importance of ecoregional versus local environmental factors in influencing the occurrence of species (Jackson & Harvey, 1989; Hughes, Wang & Seelbach, 2006).

Many studies have quantified the importance of local abiotic factors in determining stream fish assemblages, often emphasising the importance of habitat structure (Gorman & Karr, 1978; Grossman *et al.*, 1998; Valério *et al.*, 2007). Different fish species may show distinct preferences for these different habitats, giving rise to different fish assemblages (Chipps, Perry & Perry, 1994; Martin-Smith, 1998). Assemblage differences among habitats, such as riffles, runs and pools, have been identified (Martin-Smith, 1998; Muhlfeld, Bennett & Marotz, 2001; Eros, Botta-Dukát & Grossman, 2003). Such habitats are characterised by differences in depth, velocity and turbulence. The nature of the dominant substratum was reported to be highly correlated with fishes in some studies (Chipps *et al.*, 1994; Lammert & Allan, 1999). Additionally, species or assemblages can differ among microhabitats (Chipps *et al.*, 1994; Vadas & Orth, 2000). Compared with homogeneous habitats, complex habitats generally support more diverse fish assemblages and provide refuge from harsh environmental conditions and predators (Gorman & Karr, 1978; Schlosser, 1995).

Other studies have established the influence of physicochemistry or water quality, such as oxygen, pH, conductivity and temperature, in structuring fish assemblages (Matthews, Hough & Robison, 1992; Kilgour & Barton, 1999; Ostrand & Wilde, 2002). Furthermore, habitat structure and water quality affect each other to varying degrees and together limit the occurrence and abundance of species (Karr & Dudley, 1981; Fausch *et al.*, 2002; Pompeu & Alves, 2003).

The habitat structure and associated fish assemblage in a stream are determined by the characteristic climate, geology, geomorphology, altitude, vegetation and other features of the surrounding catchment (Frissell *et al.*, 1986). Those features also characterise and define

ecoregions (Omernik, 1987; Omernik & Gallant, 1990). Increasingly, regional environmental factors are considered primary regulators of local assemblage structure (Hughes *et al.*, 1987; Maret, Robinson & Minshall, 1997; Marsh-Matthews & Matthews, 2000; Walters *et al.*, 2003; Moerke & Lamberti, 2006; Fialho *et al.*, 2007; Valério *et al.*, 2007). Other studies have shown that the proximity of tributaries to large rivers also influences fish species richness and composition (Osborne & Wiley, 1992; Hitt & Angermeier, 2006, 2008a,b). Additionally, stream fish assemblages are determined by the local species pool, which in turn depends on its zoogeographic history (Hocutt & Wiley, 1986; Tonn, 1990), and on stream size (Fausch, Karr & Yant, 1984; McGarvey & Hughes, 2008; McGarvey & Ward, 2008).

Presumably, fish assemblages are structured by hierarchical systems of environmental filters, with regional factors having dominant effects on assemblages at broad spatial scales of analysis, and local factors playing a greater role at smaller spatial scales of analysis (Ricklefs, 1987; Jackson & Harvey, 1989; Tonn, 1990; Poff, 1997; Jackson, Peres-Neto & Olden, 2001). Ecologists generally acknowledge that at broad spatial extents (e.g. ecoregion) climatic and physiographic factors are reflected in the characteristics of streams in the region. These constraints may influence habitat structure, water quality and biological communities. Determining the relative importance of local and ecoregional factors on stream fish assemblages is necessary for understanding the main factors that limit those assemblages, those that are commonly altered by humans, and those that can be managed most effectively by humans.

Most of the research relating local and regional variables to fish assemblage patterns has been carried out on temperate streams. The main aim of our research was to assess stream fish assemblage structure in tributaries of a tropical river (the Rio Paraíba do Sul) to determine the degree to which ecoregions, altitude and distance from the main channel can influence local characteristics that, in turn, are associated with local fish assemblages in such streams. Specifically, we sought to determine: (i) patterns in fish assemblage structure among the sites, (ii) the relative influence of various environmental variables in classifying fish assemblages, (iii) species occurrence patterns, and (iv) relationships between species occurrence patterns and environmental variables.

We hypothesised that local habitat variables would have more influence than ecoregion in determining fish assemblages, because local habitat conditions directly affect species whereas ecoregions do so only indirectly through local environmental variables.

Methods

Study area

The Rio Paraíba do Sul flows through one of the most important industrial regions in Brazil, encompassing

Table 1 Characteristics of three ecoregions in the Rio Paraíba do Sul basin (adapted from RadamBrasil, 1983)

Ecoregion	Code	Location and characteristics
Bocaina Plateau	BP	Located in Sea Mountains (3696 km ²), a scarped mountain block at altitudes about 1800 m above sea level with mean rainfall >200 cm
Campos de Jordão/ Itatiaia Plateau	IP	Located in Meridional Mantiqueira Mountains (13 176 km ²) along the left margins of the Paraíba do Sul at altitudes between 900 and 2787 m with mean rainfall of 175 cm
Valley	V	Located in lowlands (19 592 km ²) constrained by tectonic depression and successive erosive and depositional phases, at altitudes of 0–600 m with mean rainfall of 150 cm

different ecoregions with areas of intense land use over the last four centuries. The original soils of the Paraíba do Sul basin were once very fertile, and supported a rich tropical Atlantic Forest (Figueiredo, 1999). Today only 5% of the original forest remains (on steep scarps). Most of the land is now urban or used for agriculture and cattle grazing (RadamBrasil, 1983). Along its 1080 km extent, the main channel has poor water quality, poor riparian cover, and degraded physical habitat (Pinto, Araújo & Hughes, 2006). On the other hand, several of its tributaries drain areas of low population density and human use. The main anthropogenic changes to these streams have been the conversion of the forest to pasture and the loss of riparian woody vegetation. Three ecoregions compose most of the landscape of the 57 000 km² Paraíba do Sul basin (Table 1: BP – Bocaina Plateau; IP – Campos do Jordão e Itatiaia Plateau; V – Paraíba do Sul Valley). The Rio Paraíba do Sul is formed by the junction of the Rios Paraibuna and Paraitinga, which drain the BP between 1800 and 600 m above sea level (Fig. 1). In this area, first to third order streams (1 : 50 000 map scale) join the main river and the climate is very humid. At the junction of the two rivers, the Paraíba do Sul is impounded, forming Paraibuna Reservoir. Forty kilometres downriver, another dam on the west-flowing Rio Paraíba do Sul forms Santa Branca Reservoir. The river then turns sharply towards the northeast and flows through the middle V at 500–550 m above sea level. Further downriver on the left bank, the Rio Paraíba do Sul receives several first to third order streams from the IP, which has a maximum altitude of 2500 m in an

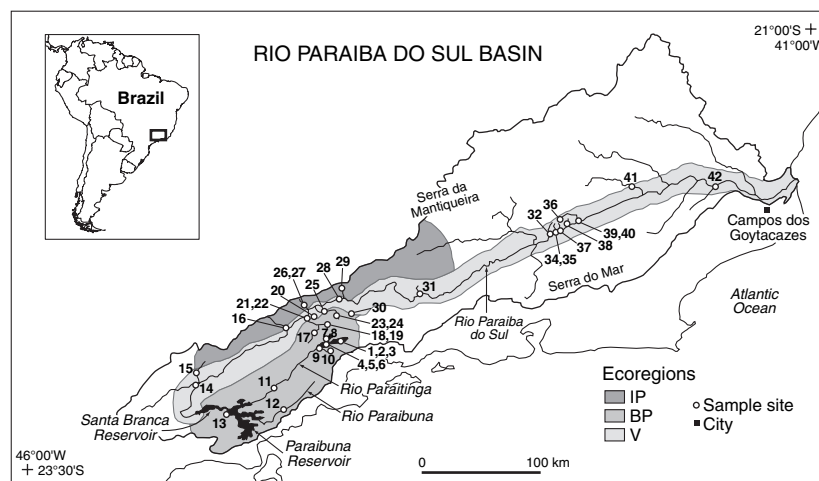


Fig. 1 Sampling site locations (1, 2, 3...42) in BP: Bocaina Plateau; IP: Campos do Jordão e Itatiaia Plateau; V: Paraíba do Sul Valley.

ecoregion with sub-humid and humid climate. On the right bank, the river again receives streams draining the BP. Further east, the river flows through the lower V (at 250–350 m above sea level), where it receives first to fourth order tributaries.

Fish sampling

We sampled 42 sites (each 100 m long and 2–5 m wide) in 26 first to fourth order streams. Sites were chosen at random from all tributary locations that were within a 100 m hike from a road. Each site, including those on the same stream, was sufficiently distant from the others to be considered independent given the home ranges of the fish species collected. Nineteen sites were located in the BP, three in the IP, and 20 in the V (Appendix S1). Fish were collected in 2002–06, in the winter dry season when stream flows are most stable (Pinto *et al.*, 2006). Four fishing methods (cast net, seine, sieve and electrofishing) were used by skilled persons in water 0.7–1.5 m deep. The level of effort of each method was determined as adequate for collecting all but exceedingly rare species (<0.05% of individuals) in pilot surveys and previous studies of this system (Araújo *et al.*, 2003). We fished with cast nets for 1 h in pools. A seine (10 m × 2 m with 5-mm mesh) was employed by two people in shallow areas for 1 h. A sieve (80 cm in diameter with 1-mm mesh) was used in macrophyte beds by one person for 1 h. Three electrofishing passes (adapted from Mazzoni, Fenerich-Verani & Caramaschi, 2000) were conducted by three people for 1 h in all mesohabitats. These different fishing methods helped to capture all the species present with a constant probability of capture across all sites for nearly all species, something that would have been impossible by using a single gear in a fixed reach. Bonar, Hubert & Willis (2009) also recommend standardised use of multiple fishing gears in warmwater streams. Following Whittier, Halliwell & Paulsen (1997), Ganasan & Hughes (1998) and Bozzetti & Schulz (2004), we pooled all fish caught by the different fishing equipment taken during each site visit into a single composite sample, thus defining the unit effort. Fish were identified to the lowest taxonomic level possible. Voucher specimens were deposited at the Laboratory of Fish Ecology, Universidade Federal Rural do Rio de Janeiro.

Environmental variables

On the same days that we sampled fish, we estimated 19 environmental variables for each site, including site characteristics (order, altitude, distance from mainstem river, tributary mean width times mean depth), physical habitat structure (percentage of various substratum grain sizes: boulder, cobble, stone, sand and mud; percentage riparian woody vegetation; percentage of various habitat types: riffles, rapids and pools) and physicochemical variables (temperature, pH, dissolved oxygen, conductivity). Physical habitat variables were estimated visually for the entire reach. Physicochemical measurements were taken with a HORIBA W-21 multiprobe water quality meter calibrated the day before each field visit. Stream channel distances of sampling sites from the mainstem were determined from digital 1 : 50 000-scale topographic maps using CADMAPS software (Micro Map & CAD, Colorado Springs, CO, U.S.A.). Altitude was obtained with a Garmin-12 GPS unit (Garmin, Olathe, KS, U.S.A.).

Statistical analyses

We used one-way analysis of similarity (ANOSIM; Clarke, 1993) on fourth-root abundance transformations to determine whether or not major shifts in assemblage structure occurred among ecoregions (BP, IP, V), altitude groups (≥ 700 m, $510 < 700$ m, ≤ 510 m) and distances of sites from the Rio Paraíba do Sul (> 35 km, $3.5\text{--}35$ km, < 3.5 km). Analysis of similarity is analogous to univariate analysis of variance (ANOVA), which tests for significant differences among groups. Unlike ANOVA, however, ANOSIM is based on a similarity matrix rather than raw data, and significance is based on comparisons of this matrix to random permutations of the matrix (Clarke & Warwick, 1994). ANOSIM provides an *R* statistic that reflects the amount of dissimilarity associated with each factor (comparable to the *F* statistic of ANOVA). An *R*-value close to one indicates very different composition, whereas values near zero show little difference (Clarke & Warwick, 1994). This analysis tested for variations in fish assemblage structure among the ecoregion, altitude and distance groups averaged across all reaches. We calculated Bray-Curtis similarities from the proportional abundance of each taxon for every pair of sites. We then used non-metric multidimensional scaling (MDS, Primer-E Ltd., 2001)

to ordinate the assemblage similarities of those sites and to determine the number of distinct clusters based on species proportional abundances.

Classes of environmental factors are often used for reporting on, predicting or modelling groups of streams for assessment, management or conservation purposes (Pont *et al.*, 2006; Snelder, Dey & Leathwick, 2007; Paulsen *et al.*, 2008; Omernik *et al.*, In Press). To determine the relative strengths of classifications based on the taxonomic and environmental data we compared their between- and within-class similarities. We used Bray-Curtis similarities from taxon proportional abundance for sites alternatively classified for nine environmental factors: ecoregion, altitude, distance from the mainstem, predominant riparian cover, mesohabitat and type of substratum, concentration of dissolved oxygen, temperature and conductivity. We also classified the fish assemblage data (species proportional abundance, species presence/absence, family proportional abundance and family presence/absence) to assess the strength of classifications that could be expected from grouping of the sites, irrespective of environmental factors. The Bray-Curtis index of similarity was applied on taxon proportional abundance data and the Jaccard coefficient was used for presence/absence data. We used the same number of classes as there were distinct taxonomic clusters (three) to ensure that the classification-strength tests were comparable. For each alternative classification, we calculated mean within-class (W) and mean between-class (B) similarities, and two numerical estimates of classification strength (CS, or $W - B$, and M , or $B W^{-1}$) (Van Sickle, 1997). We used dendrograms to visualise the results, whereby relatively longer branches (classes in each classification) represent greater classification strength (Van Sickle, 1997; Van Sickle & Hughes, 2000). We used a permutation procedure to test whether between-class similarities were, on average, less than within-class similarities, for each classification. The statistics $CS = (W - B)$ and M were recalculated for each of 1000 randomly chosen reassignments of sites to groups of the same size as the tested classification.

We employed three additional multivariate analyses to evaluate relationships between fish assemblages and environmental variables. We used indicator species analysis (Dufrene & Legendre, 1997) to identify species characterising each class of major environmental factor examined in the preceding analysis of classification

strength. Such indicator species are those that tend to occur in all or nearly all sites within a class of sites (e.g. V), but not in other classes (e.g. IP or BP). Patterns in the abiotic environmental data were assessed by a principal components analysis (PCA; Pielou, 1984) on the correlation matrix of environmental variables. Temperature, dissolved oxygen, pH and conductivity data were log-transformed and habitat parameters expressed as percentages were arcsin square root transformed. Component loadings >0.5 from PCA were used to identify latent variables. We used canonical correspondence analysis (CCA; Ter Braak, 1986) to detect joint species distribution and environmental patterns. Statistical significance of each environmental variable was assessed by a Monte Carlo permutation test, using 1000 sample permutations. The CCA was performed by using CANOCO software for Windows, version 4.5 on fourth-root transformed data (Plant Research International, Wageningen, the Netherlands).

Results

Fish assemblage structure

We collected 2684 individuals representing 16 families and 59 species with non-natives comprising 10% of the total number of species (Appendix S2). Assemblage structure varied significantly among ecoregions

Table 2 *R*-statistic values from ANOSIM and their significance levels (1000 permutations) for pair-wise comparisons of fish assemblage structure among ecoregions (BP, Bocaina plateau; IP, Campos do Jordão/Itatiaia plateau; V, Valley Rio Paraíba do Sul), altitudes, and distances from the main channel

Ecoregions	(Global <i>R</i> : 0.50**)	d.f.	<i>P</i> -level
BP; IP	0.70**	2	0.002
BP; V	0.42**	18	0.001
V; IP	0.84**	2	0.002
Altitudes (m)	(Global <i>R</i> : 0.24**)	d.f.	<i>P</i> -level
>700; 510–700	0.04ns	12	0.14
>700; <510	0.60**	12	0.001
510–700; <510	0.15**	13	0.008
Distances from main channel (km)	(Global <i>R</i> : 0.23**)	d.f.	<i>P</i> -level
>35; 3.5–35	0.15*	13	0.01
>35; <3.5	0.47**	13	0.001
3.5–35; <3.5	0.10*	13	0.04

ns, non-significant ; d.f., degrees of freedom.

* $P < 0.05$; ** $P < 0.01$.

($R = 0.50$; $P = 0.001$; Table 2), with three well defined groups in MDS site space and only four out of 15 BP sites clustering with V sites along axis 1 (Fig. 2). Significant differences were found for altitude

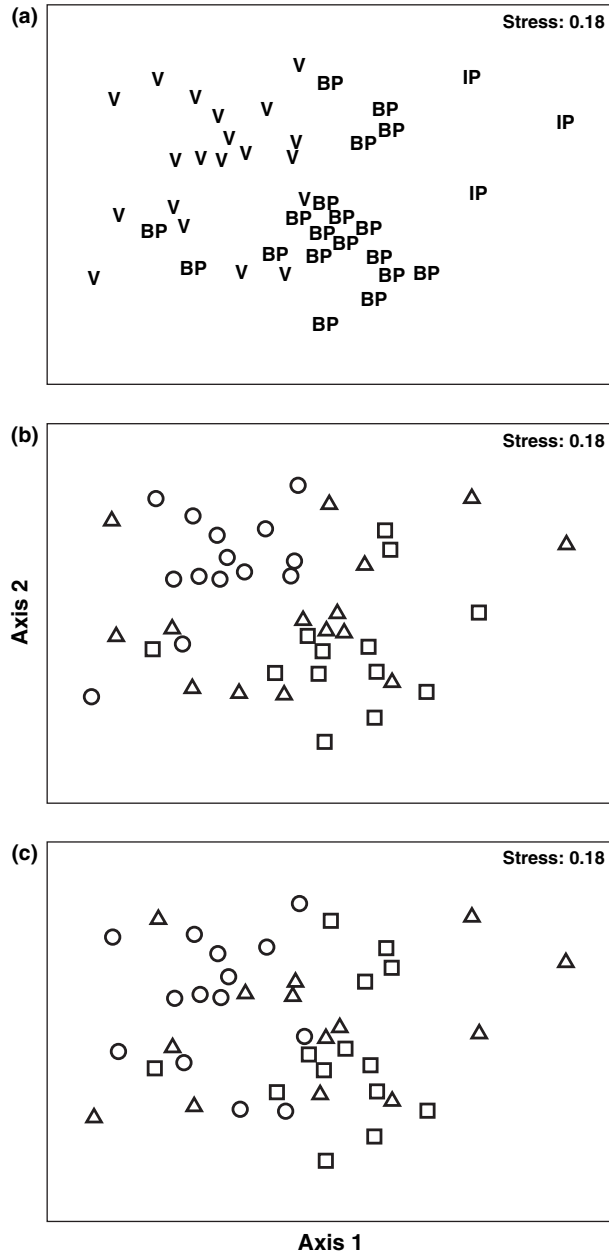


Fig. 2 MDS ordination of fish species relative abundances for sites in Rio Paraíba do Sul tributaries. (a) Samples coded by ecoregion: BP: Bocaina plateau; IP: Campos do Jordão/Itatiaia plateau; V: Valley Rio Paraíba do Sul. (b) Samples coded by altitude: □ >700 m; Δ 510–700 m; ○ <510 m; (c) samples coded by distance from the main channel: □ >35 km; Δ 3.5–35 km; ○ <3.5 km.

($R = 0.24$; $P = 0.001$; Table 2) between all group comparisons except 510–700 m versus >700 m, which showed marked overlap in site space (Fig. 2). Distance from the mainstem river separated the sites ($R = 0.23$; $P = 0.001$; Table 2), but marked overlap was observed (Fig. 2); the greatest difference occurred between sites >35 km and <3.5 km from the mainstem Rio Paraíba do Sul. Thus, the ecoregion classification discriminated the sites better than either altitude or distance classes, but the extremes in altitude or distance from the mainstem were associated with significantly different fish assemblages.

Classification strength

With the exceptions of substratum and conductivity, all *a priori* environmental classifications, as assessed by fish assemblages similarity measures, showed statistical evidence ($P < 0.05$) of greater M [ratio of overall mean between (B) – overall mean within (W) class similarity; $M = B W^{-1}$] and estimates of classification strength ($CS = W - B$) than would be seen for randomly grouped sites (Table 3). The ecoregion classification strength resembled closely that of the species presence/absence cluster (Table 3), and its dendrogram resembled that of the species abundance cluster (Fig. 3). Mean similarity dendrograms for fish

Table 3 Strengths of alternative environmental classifications for classifying fish assemblages from 42 sites in the Rio Paraíba do Sul basin

	CS	M	W	P-value
Environmental classification				
Ecoregion	0.14	0.47	0.26	0.0010
Altitude	0.08	0.67	0.23	0.0010
Distance from main channel	0.06	0.72	0.22	0.0010
Riparian cover	0.05	0.77	0.19	0.0320
Substrate	0.02	0.90	0.19	0.0500
Mesohabitat	0.03	0.84	0.19	0.0120
Dissolved oxygen	0.08	0.65	0.23	0.0010
Temperature	0.03	0.86	0.19	0.0130
Conductivity	0.01	0.95	0.19	0.3257
Taxonomic classification				
Species abundance	0.17	0.38	0.28	0.0010
Species P/A	0.13	0.40	0.22	0.0010
Family abundance	0.21	0.59	0.52	0.0010
Family P/A	0.22	0.50	0.43	0.0010

CS, classification strength; M, overall mean between-class similarity/mean overall mean within-class similarity; W, overall mean within-class similarity; Number of classes = 3; P/A, presence/absence.

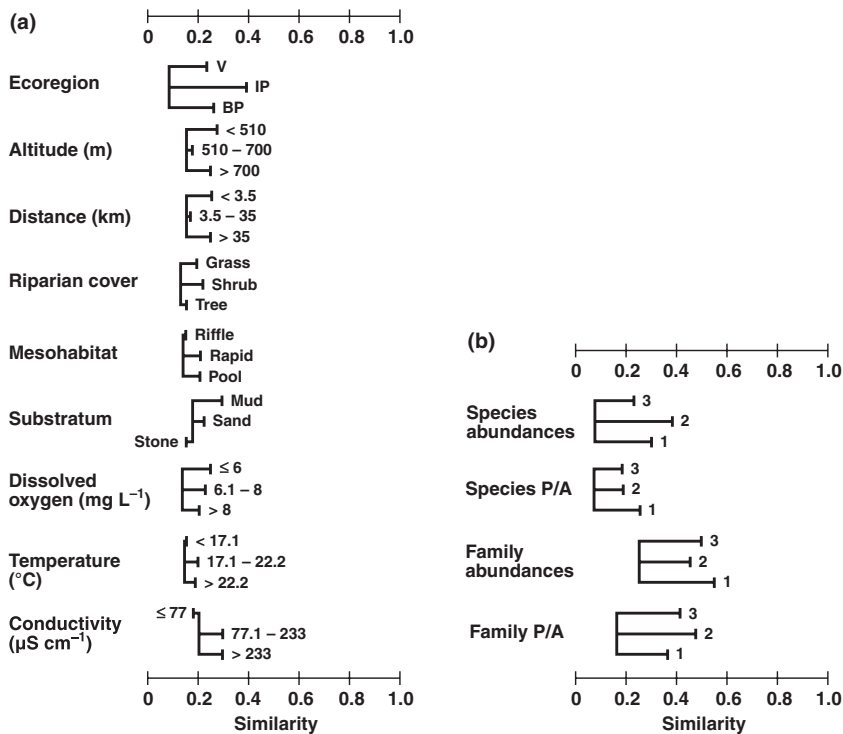


Fig. 3 Classification strength dendrogram for fish assemblages in Rio Paraíba do Sul tributaries for (a) nine environmental and (b) four taxonomic factors. The dendrogram node is plotted at the overall mean between-groups similarity and branches terminate at the mean within-groups similarity for each class. P/A, presence/absence.

assemblages showed that similarity within ecoregion was higher for the IP and PB than for the V (Fig. 3).

Regarding altitude and distance from the mainstem, within-class similarity was greatest for the extreme ranges of <510 m and >700 m, and >35 and <3.5 km respectively. However, 510–700 m and 3.5–35 km classes had within-class similarities similar to the overall mean between-class similarities of altitude and mainstem distance, respectively. Among the physicochemical measurements, dissolved oxygen had the greatest classification strength, with highest within-class similarity for concentrations of ≤6 and 6.1–8 mg L⁻¹ (Fig. 3). Based on classification strength analyses of these data, ecoregions of the Paraíba do Sul basin give the best environmental classification of the sites, with altitude, distance from the mainstem and dissolved oxygen classes yielding slightly weaker classification.

Indicator species analysis

Indicator species analysis revealed that several of the same species were indicators of ecoregion, altitude and distance from the mainstem, whereas others were indicators of only a single environmental variable

(Table 4). Regarding ecoregions, the only representative species for the BP was *Phalloceros caudimaculatus* (Hensel, 1868) ($P = 0.002$). *Trichomycterus* sp. 1 ($P = 0.001$), *Trichomycterus* sp. 4 ($P = 0.031$) and *Imparfinis minutus* (Lütken, 1974) ($P = 0.041$) represented the IP. Valley indicator species were *Astyanax bimaculatus* (Linnaeus, 1758) ($P = 0.017$), *Rineloricaria* cf. *lima* (Kner, 1853) ($P = 0.008$), and *Gymnotus* cf. *carapo* Linnaeus, 1758 ($P = 0.015$). The indicator species for altitudes >700 m were *P. caudimaculatus*, *Characidium* sp. and *Taunayia bifasciata* (Eigenmann & Norris, 1900). *Crenicichla lacustris* (Castelnau, 1855), *R. cf. lima* G. cf. *carapo*, and *A. bimaculatus* best represented the <510 m altitude group. The indicator species for site distance >35 km from the Rio Paraíba do Sul were *P. caudimaculatus*, *Characidium* sp. and *Hemipsilichthys gobio* (Lütken, 1974). *Astyanax bimaculatus*, G. cf. *carapo*, *Crenicichla lacustris*, *Characidium alipioi* Travassos, 1955 and *R. cf. lima* were the most typical species for distances <3.5 km. In general, the species representing the steeper, higher-altitude plateau sites were catfish adapted to cool, fast-flowing water (Table 4). Those adaptations included odontodes and scutes (hard bony external spines or plates, respectively) small size, slender bodies, no gas bladder and a benthic habitat

Table 4 Significant *P*-values from indicator species analysis of fish assemblages for ecoregion, altitude and distance from the main channel of the Rio Paraíba do Sul, including species autoecology

Species	Ecoregion	Altitude		Distance		Habitat	Food	Other	
		<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>				
<i>Phalloceros caudimaculatus</i>	BP	0.002	>700	0.002	>35	0.010	S	O	Viviparous, tolerates 5 °C, 1-year life span, occupies marginal slack waters
<i>Trichomycterus</i> sp1	IP	0.001	–	–	–	–	B	I	Odontodes, 150 mm S.L., slender
<i>Trichomycterus</i> sp4	IP	0.031	–	–	–	–	B	I	Odontodes, 150 mm S.L., slender
<i>Imparfinis minutus</i>	IP	0.041	–	–	–	–	B	I	Tolerates swift streams, 120 mm S.L.
<i>Gymnotus</i> cf <i>carapo</i>	V	0.015	<510	0.000	<3.5	0.001	WC	IC	Parental care, electric, air breather, 600 mm S.L., survives drying, 2-year pop. doubling time
<i>Astyanax bimaculatus</i>	V	0.017	<510	0.006	<3.5	0.016	WC	O	1.3-year pop. doubling time, 150 mm S.L., tolerates pH 5.5–7.5
<i>Rineloricaria</i> cf. <i>lima</i>	V	0.008	<510	0.000	<3.5	0.000	B	H	Odontodes, 130 mm S.L., pollution tol.
<i>Characidium alipioi</i>	–	–	–	–	<3.5	0.005	B	I	52 mm S.L.
<i>Characidium</i> sp	–	–	>700	0.001	>35	0.004	B	I	80 mm S.L., tolerates swift streams
<i>Crenicichla lacustris</i>	–	–	<510	0.041	<3.5	0.003	WC	C	Parental care, 290 mm S.L.
<i>Taunayia bifasciata</i>	–	–	>700	0.033	–	–	B	I	140 mm S.L., bony plates cover body
<i>Hemipsilichthys gobio</i>	–	–	–	–	>35	0.022	B	I	156 mm S.L., lateral scutes, tolerates swift streams

WC, water column; B, benthic; S, sub-surface; H, herbivore; C, carnivore; O, omnivore; I, invertivore.

that resists daily freshets in the wet season. On the other hand, species characterising low slope and altitude valley sites were members of several families adapted to warm, slowly-flowing water with low and fluctuating pH and dissolved oxygen. Adaptations to such conditions included air breathing, broad pH tolerance, parental care of young, rapid population growth, a water column habitat, and large body size. Valley indicator species included herbivores, invertivore/piscivores and omnivores (Table 4).

Environmental variables

The first two PCA axes accounted for 39.4% (axis 1, 25.1%; axis 2, 14.3%) of the variance among sites (Table 5). Axis 1 was positively correlated with high percentages of grasslands in the catchment, pools, and high temperature and conductivity, and negatively with dissolved oxygen and the percentages of shrubs, trees and cobbles (Fig. 4). Axis 2 was positively correlated with sandy substratum, distance from the river, altitude and tributary size, and negatively correlated with the percentage of riffles and rocks. Sites from the IP were located on the lower left side of the diagram, corresponding to high dissolved oxygen, and high percentages of shrubs, trees, cobble, riffles and rocks (Fig. 4). On the other hand, V sites were

Table 5 Factor loadings from PCA on environmental variables for the first two axes. Component loadings >0.5 in bold

Variables	Axis 1	Axis 2
Altitude	-0.63	0.56
Distance from main channel	-0.51	0.57
Tributary size	-0.19	0.50
Width × depth	0.12	-0.13
Temperature	0.76	0.34
Dissolved oxygen	-0.63	-0.07
pH	0.45	0.34
Conductivity	0.68	-0.35
Grass	0.72	-0.05
Shrub	-0.53	0.10
Tree	-0.59	-0.18
Pool	0.68	0.12
Rapid	-0.28	0.32
Riffles	-0.43	-0.54
Boulder	-0.13	-0.77
Cobble	-0.51	0.03
Sand	0.19	0.58
Mud	0.40	0.19
Stone	0.10	0.13
Eigenvalues	4.77	2.72
% variance explained	25.1	14.3

located on the right side of the diagram, corresponding to high temperature and conductivity, low dissolved oxygen, and high percentages of grass and pools. Sites in the BP were distributed across the

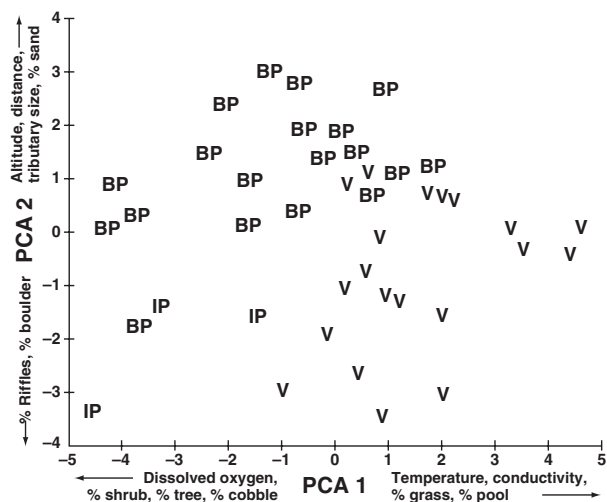


Fig. 4 PCA ordination on 17 environmental variables with sites coded by ecoregion. BP, Bocaina plateau; IP, Campos do Jordão/Itatiaia plateau; V, Valley Rio Paraíba do Sul.

upper part of the diagram, corresponding to high altitude and distance from the river, large tributary size, and high percent sand. As with the MDS ordination of fish assemblages (Fig. 2), the sites showed substantial ecoregion separation in the PCA ordination of environmental variables (Fig. 4). That separation indicates that the ecoregions differ in substratum, water quality and macrohabitats, as well as distance from the mainstem and altitude, as expected.

Fish assemblage and environmental relationships

The Monte Carlo permutation analysis within the CANOCO package indicated that only eight of the 19 variables examined were included in the CCA model ($P < 0.05$; Table 6). The first two CCA axes incorporated 42.1% (axis 1, 22.0%; axis 2, 20.1%) of the species-environment variance. Pearson correlation coefficients between environmental variables and the ordination axes (interset correlation) reflected the relative importance of each environmental variable to the fish assemblages. Axis 1 reflected altitude, number of riffles, dissolved oxygen, temperature and conductivity. Axis 2 was most strongly associated with altitude and distance from the river. Most BP sites reflected high altitudes and distances from the main channel, but IP sites were associated most strongly with high number of riffles (Fig. 5). On the other hand, V sites were located at high temperatures, grasslands and conductivity, but low dissolved oxygen, few riffles, low altitude and distance from the river (Fig. 5). The fish indicator species identified and described in Table 4 for each ecoregion (BP: *P. caudimaculatus*; IP: *Trichomycterus* sp1., *I. minutus*; V: *A. bimaculatus*, *Gymnotus* cf. *carapo*, *Rineloricaria* cf. *lima*) appear in or near the centroids of the sites for each ecoregion in Fig. 5. This suggests that the indicator species analysis and the CCA based on species and environmental data are in agreement.

Table 6 Summary of canonical correspondence analysis on species abundance and environmental variables in Rio Paraíba do Sul tributaries

	Axes				Inertia
	1	2	3	4	
Altitude	0.65	-0.57	-0.11	0.15	
Distance from main channel	0.48	-0.66	0.27	0.01	
Riffles	0.59	0.46	0.05	-0.29	
Shrub	0.42	0.23	-0.18	0.55	
Grass	-0.53	-0.08	0.01	-0.40	
Temperature	-0.66	-0.16	-0.27	0.12	
Conductivity	-0.56	0.20	-0.28	-0.28	
Dissolved oxygen	0.56	-0.08	-0.40	-0.34	
Summary					
Eigenvalues	0.44	0.40	0.28	0.26	6.47
Species-environment correlations	0.90	0.92	0.92	0.89	
Cumulative percentage variance of species data	6.8	13.0	17.3	21.3	
Cumulative percentage variance of species-environment relation	22.0	42.1	56.4	69.2	
Sum of all eigenvalues					6.47
Sum of all canonical eigenvalues					1.99

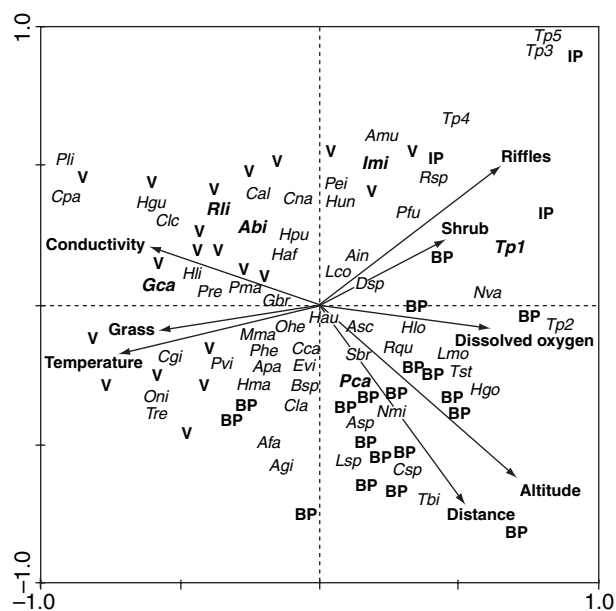


Fig. 5 CCA ordination on fish species and environmental variables with sites coded by ecoregion (BP, Bocaina plateau; IP, Campos do Jordão/Itatiaia plateau; V, Valley Rio Paraiba do Sul). The arrows indicate a factor and its direction relative to species occurrences along that environmental gradient. Species codes in Appendix S2; bold codes are indicator species from Table 4.

Discussion

All analyses (MDS, Classification Strength, PCA and CCA) performed on the fish assemblages distinguished the three ecoregions. Those analyses indicate that the plateaus and valley have different fish assemblages at this spatial extent of analysis. Also the indicator species of the three ecoregions (e.g. *P. caudimaculatus* in BP, *Trichomycterus* sp. and *I. minutus* in IP, and *A. bimaculatus*, *Gymnotus* cf. *carapo* and *Rineloricaria* cf. *lima* in V) are well adapted for the differing habitat conditions characteristic of plateau and valley ecoregions.

According to Marsh-Matthews & Matthews (2000) and Wang, Seelbach & Lyons (2006), knowing the degree to which extrinsic factors influence assemblage structure is critical for understanding assembly rules and the extent to which those rules vary with geography and environment. Maret *et al.* (1997) found little correspondence between fish assemblage patterns and ecoregions of the Snake River basin, possibly because many sites were near ecoregion boundaries or were mapped too coarsely to provide accurate geographic classifications of fish assem-

blages. Waite & Carpenter (2000) found a clear distinction between coldwater forested sites (Cascade and Coast Range ecoregions) and sites in the Willamette Valley ecoregion, attributing differences to different habitat types, altitude, slopes and water chemistry. They found that, across all ecoregions of the Willamette Basin, physical factors were most important in describing differences in fish assemblages; however, when the area of concern was confined to the Willamette Valley, water chemistry was the most important descriptor of fish assemblages. In our study, we also found the most marked difference between sites in the plateau and valley ecoregions, with the latter showing more intense land use, less natural vegetation and dissolved oxygen, and higher temperatures and conductivity than the former.

Multivariate analyses (PCA and CCA) indicated that different habitat types and physicochemical variables were associated with different ecoregions. The BP sites were characterised by sandy substratum and a high concentration of dissolved oxygen. The IP was characterised by cobble substratum, and high % riffles, % shrubs and dissolved oxygen concentration. The V had margins occupied by grasses, higher % pools and rock, high temperatures and conductivity, and a low dissolved oxygen concentration. Waite & Carpenter (2000) found a similar pattern, where altitude, slope, temperature, dissolved oxygen and other chemical variables were most strongly associated with temperate stream fish assemblages, adding that the coldwater forested ecoregion was less disturbed than the Willamette Valley ecoregion.

Ecoregions with high altitude and with sites far from the main channel (BP and IP) had better quality riparian cover (shrubs and trees) than the V ecoregion, where grasses dominated the margins. Waite & Carpenter (2000) and Maret *et al.* (1997) found that habitat and physicochemical characteristics of mountain regions were generally better preserved than in the valley regions. This is probably because higher altitude ecoregions are less accessible to humans and less suited for agriculture and urbanisation than valley ecoregions. Urban land-use was associated with low values of the index of biotic integrity for fish assemblages in streams along a forest-urban gradient (Steedman, 1988; Wang *et al.*, 2001; Snyder *et al.*, 2003; Van Sickle *et al.*, 2004; Pinto *et al.*, 2006; Grubbs, Meier & Meier, 2007). Similarly, increased

agriculture was correlated with low index of biotic integrity scores for fish assemblages, where the gradient was from natural vegetation to arable land (rowcrops) or pasture (Roth, Allan & Erickson, 1996; Wang *et al.*, 1997; Fitzpatrick *et al.*, 2001; Mebane, Maret & Hughes, 2003; Meador *et al.*, 2008).

Ecoregions (and to a lesser extent altitude, distance from the main channel and concentration of dissolved oxygen) were the most effective factors for classifying the fish assemblage in Rio Paraíba do Sul tributaries. They offer useful frameworks for examining patterns in species assemblages, where such classification factors differ distinctly. Differences among these classes arise partly because a small number of species are common in one of the classes but absent or rare in others. Fish assemblages in Rio Paraíba do Sul tributaries were more similar, on average, within ecoregions than they were between ecoregions. Omernik & Griffith (1991) reported a similar relationship for the Calapooia River, Oregon, as did Rohm *et al.* (1987) for fish assemblages of valley and mountain stream sites in Arkansas.

Altitude, distance from the main channel and dissolved oxygen concentration explained more of the fish assemblage differences than conductivity, substratum, riparian cover, habitat or temperature. The latter factors need additional evaluation, more accurate and precise field measurements (Hughes & Peck, 2008), and perhaps different class boundaries to improve their usefulness for classifying the fish assemblage, prediction and management. As suggested in Fig. 3, the intermediate classes of altitude and distance from the main channel had little influence on the fish assemblages, suggesting either a poor choice of classes or that a different spatial extent of longitudinal zones is needed to capture the true species pool at the stream segment scale (McGarvey & Hughes, 2008; McGarvey & Ward, 2008). Conversely, most of the above variables (but not substratum and habitat) might be better assessed and applied as continuous variables in predictive modelling (Pont *et al.*, 2006), but that would require a larger sample size than ours to avoid model over fitting (Harrel, 2001; Tabachnick & Fidell, 2001). The proximity of the main channel best discriminated fish assemblages if the sites were >35 km versus <3.5 km from the main river. Hitt & Angermeier (2008a,b) reported that sites <10 km from mainstem rivers supported more species

and demonstrated a weaker response of fish metrics to local environmental conditions than did headwater sites of a similar size. Osborne & Wiley (1992) also reported higher species richness in mainstem tributaries than in headwater tributaries of similar size. In our classification strength analyses, altitudes ≤ 510 m, and dissolved oxygen ≤ 6 mg L⁻¹ had greater classification strengths than alternative values of those two variables. Distance from source (the converse of distance from a mainstem) and altitude were important variables for predicting fish assemblage condition in European streams (Pont *et al.*, 2006) and altitude was a useful variable for classifying western U.S.A. fish assemblages (Herlihy *et al.*, 2006). Dissolved oxygen concentration has long been recognised as a key limiting factor for fishes of temperate streams (Ellis, 1937; Hynes, 1960) and 5 mg L⁻¹ is a common threshold value for temperate warm water fish assemblages. The differences in oxygen, altitude and distance among sites also partly explained why the ecoregions differ. Similarly, differences in riparian vegetation, water quality, substratum, and macrohabitat type were associated with ecoregional differences among sites (Figs 4 & 5). Thus, it is difficult to separate covarying local and ecoregional differences (Bryce *et al.*, 1999; Herlihy *et al.*, 2006).

The indicator species analysis supported our expectations concerning the occurrence of rheophilic and lentic species. The small body size of indicator species for the Plateau ecoregion (IP) enables them to hide in the interstices between rocks (e.g. *Trichomycterus* spp.) or occupy slack waters at the stream margin (*P. caudimaculatus*). The small size and frequent lack of swim bladder (e.g., *Characidium* sp.) aid them in remaining in the bottom boundary layer where velocity is low. Some (e.g. *Hemipsilichthys gobio*, *Rineloricaria* sp and *Taunayia bifasciata*) have bony plates covering their bodies, or on their opercula, which help protect them from being crushed when cobbles and boulders are mobilised during frequent freshets. Expanded pectoral fins and odontodes also aid them in maintaining position in high velocity currents while expending little energy (e.g. *Trichomycterus* spp.). Similar adaptations have been found in the majority of species that occupy riffles in other hydrographic systems (Martin-Smith, 1998; Castro, 1999; Braga, 2004; Menezes *et al.*, 2007). Martin-Smith (1998) reported that fish species occupying riffles occupied only one or two trophic guilds compared

with those living in pools. The limited dietary information available for tropical fish suggests that all riffle specialists feed on algae or aquatic invertebrates, as in temperate headwaters (McGarvey & Hughes, 2008; Ibañez *et al.*, in press). Species recorded in valley sites near the main channel were also widely recorded in the Paraíba do Sul main channel (Araújo *et al.*, 2003; Pinto *et al.*, 2006). These species generally were larger, more mobile, adapted to waters with naturally low dissolved oxygen and included species that were omnivores or generalists, as well as specialist detritivores, insectivores, piscivores, or invertivore/carnivores. Similarly, McGarvey & Hughes (2008) found greater trophic diversity of Oregon fish assemblages with increased stream size and Ibañez *et al.* (in press) also reported greater trophic diversity as stream size increased and slope decreased in temperate and tropical streams on four continents.

In conclusion, stream fish assemblages differed among Rio Paraíba do Sul ecoregions, partly because the sites also differed in altitude, distance from the main channel and local environmental factors. As expected, plateau fish assemblages were characterised by rheophilic species and those in the valley ecoregion were characterised by lentic species. Contrary to our hypothesis, local habitat variables were less important than the ecoregion in determining fish assemblages. Ecoregion, altitude and distance from the mainstem are not altered by humans, although dams or canals alter connectivity and impede or facilitate fish migrations respectively. Similarly, stream size and the proportions of riffles and pools are governed mostly by natural variations in slope, surface geology and runoff, which are typically only altered by surface mining, dams and diversions. On the other hand, though naturally varying, riparian vegetation, the percentage of fine substrata, water temperature, dissolved oxygen and conductivity are commonly altered by human land and water uses. Those latter factors can be managed, however, to achieve cooler and more oxygenated water and coarser substrata, which would favour plateau species, perhaps at the expense of valley species. However, natural differences between plateau and valley streams in the tropics are just as likely to differ in the face of anthropogenic alterations as upland and lowland streams in temperate regions. It would be wise to consider those natural differences and limitations when developing management plans and installing

pollution controls. These results reinforce the importance of understanding how stream communities are influenced by natural and anthropogenically altered factors operating at local and regional scales, which will aid water resource managers, land use planners, industries and government agencies to target factors where their management and rehabilitation efforts can be most effective.

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Supporting Information

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

Appendix S1. Sampling site locations in streams from the Paraíba do Sul basin. Sites coded by ecoregion: BP, Bocaina Plateau; IP, Campos do Jordão/Itatiaia Plateau; V, Valley Rio Paraíba do Sul.

Appendix S2. Fish species collected in Rio Paraíba do Sul tributaries from 2002 to 2006. Species are listed following Reis, Kullander and Ferraris (2003); *non-native.

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