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Influence of environmental variables on stream fish fauna at multiple spatial scales

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Effects of environmental variables at different spatial scales on freshwater fish assemblages are relatively unexplored in Neotropical ecosystems. However, those influences are important for developing management strategies to conserve fish diversity and water resources. We evaluated the influences of site- (in-stream) and catchment-scale (land use and cover) environmental variables on the abundance and occurrence of fish species in streams of the Upper Araguari River basin through use of variance partitioning with partial CCA. We sampled 38 1st to 3rd order stream sites in September 2009. We quantified site variables to calculate 11 physical habitat metrics and mapped catchment land use/cover. Site and catchment variables explained > 50% of the total variation in fish species. Site variables (fish abundance: 25.31%; occurrence: 24.51%) explained slightly more variation in fish species than catchment land use/cover (abundance: 22.69%; occurrence: 18.90%), indicating that factors at both scales are important. Because anthropogenic pressures at site and catchment scales both affect stream fish in the Upper Araguari River basin, both must be considered jointly to apply conservation strategies in an efficient manner.

Os efeitos das variáveis ambientais em diferentes escalas espaciais sobre as assembleias de peixes de água doce ainda é um tema pouco explorado na região Neotropical. Entretanto é um assunto de extrema relevância, pois gera subsídios para definições de estratégias de manejo e conservação de ictiofauna e dos recursos hídricos. Nós avaliamos a influência de variáveis ambientais em escalas local (dentro do rio) e da paisagem (uso e cobertura do solo) na abundância e ocorrência das espécies de peixes de riachos da bacia do alto rio Araguari através da partição da variância usando CCA parcial. Um total de 38 riachos de até 3ª ordem foi amostrado em setembro de 2009. Nós quantificamos variáveis locais para calcular 11 métricas de hábitats físicos e mapeamos o uso e cobertura do solo. O conjunto de dados (variáveis locais e da paisagem) explicou mais de 50% da variação total nas espécies de peixes. Variáveis em escala local (abundância: 25,31%; ocorrência: 24,51%) explicaram levemente uma maior variação nas assembleias de peixes do que o uso e cobertura do solo (abundância: 22,69%; ocorrência: 18,90%), indicando que os fatores em ambas as escalas de estudo são importantes. Uma vez que a influência antrópica em diferentes escalas afeta as espécies de peixes em riachos da bacia do alto rio Araguari, ambas devem ser consideradas juntamente para a adoção de estratégias de conservação de uma forma racional.

Keywords: Disturbed sites, Fish assemblages, Land use, Partial CCA, Physical habitat.

Introduction

Streams are hierarchically organized and spatially nested systems (Frissell *et al*., 1986 in which conditions at smaller spatial scales are constrained by processes at larger spatial scales (O'Neill *et al*., 1989). In other words, site conditions are influenced by regional conditions (Hildrew & Giller, 1994), and different variables may act at different scales (Willis & Whittaker, 2002). Some stream processes operate primarily at regional scales, such as channel form and hydrology (Poff & Allan, 1995), but other stream conditions operate primarily at the site scale, such as habitat complexity and shade (Allan *et al*., 1997).

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The importance of the landscape to streams is associated with allochthonous and autochthonous resources and the surrounding terrestrial environment is the primary source of organic matter for many small, forested, temperate streams (Vannote *et al*., 1980; Wallace *et al*., 1997). Land use, such as urbanization and agriculture, strongly influences this linkage and changes flow regimes, temperature, water chemistry, and substrate characteristics (Schlosser & Karr, 1981; Peterjohn & Correll, 1984; Hughes *et al*., 2014). Consequently, they cause many environmental changes such as physical habitat loss, sedimentation, bank erosion and bed destabilization, contaminant loadings, canopy opening, and nutrient enrichment (Allan, 2004). Moreover, local habitat conditions are directly or indirectly affected by catchment conditions, including land use changes (*e.g*., Sály *et al*., 2011; Marzin *et al*., 2012; Macedo *et al*., 2014). Local habitat conditions are a fundamental factor for determining the structure and composition of stream biota (Schlosser, 1982; Rosenzweig, 1995; Harding *et al*., 1998; Brown *et al*., 2009). For example, fish assemblages are strongly influenced by site channel structure and hydraulic conditions, such as substrate, canopy shading, fish cover, wetted width, depth variation, and slope (Gorman & Karr, 1978; Wang *et al*., 1998; Kaufmann & Hughes, 2006). Land use changes, such as agriculture, remove riparian vegetation and decreases bank stabilization thereby increasing sedimentation. Sedimentation reduces stream depth heterogeneity, leading to decreased species diversity (Wood & Armitage, 1997; Sutherland *et al*., 2002). Therefore, those patterns and processes operating at local and regional scales play an important role in determining stream fish assemblage structure and complexity (Matthews, 1998), and both are affected by human activities.

The relative importance of catchment and site conditions to the structure of fish assemblages and the degree of anthropogenic pressure is, however, controversial. Some studies have suggested that in highly disturbed temperate catchments that are heavily dominated by anthropogenic land use/cover, the relative importance of site conditions for stream fish decline and catchment conditions prevail (Allan *et al*., 1997; Wang *et al*., 2006a), because anthropogenic pressures modify the processes that operated at different spatial scales (Moerke & Lamberti, 2006). On the other hand, in minimally disturbed temperate catchments, site conditions have greater importance (Kaufmann & Hughes, 2006; Wang *et al*., 2006b). However, contradictory results have been reported (*e.g.* Bouchard & Boisclair, 2007), including papers describing both catchment- and site-scale conditions with similar importance (*e.g.* Hughes *et al*., 2015). In addition, studies regarding the influence of environmental factors at different spatial scales on Neotropical stream biota are still scant. Understanding these relationships is an important step for taking appropriate stream conservation and management actions (Wang *et al*., 2006b). By doing so, the main drivers of impacts can be identified and rehabilitation efforts can be focused on the scales where management actions are most cost-effective.

We evaluated the association between environmental variables and the composition of fish assemblages in 38 wadeable streams in the Upper Araguari River Basin at two spatial scales: site and catchment. We addressed the question: How much variability in the composition of fish assemblages is explained by environmental variables at the site (physical habitat) and catchment (land use and cover) scales? Because our study area has relatively high levels of human land use (Ligeiro *et al*., 2013), it is an exploratory attempt to understand how Neotropical stream fishes respond to land use/cover and to site habitat conditions.

Material and Methods

Study area and design. We conducted our study in wadeable first to third order streams in the Upper Araguari River basin, at the end of the dry season, September 2009 (Fig. 1). The Araguari River rises in the Serra da Canastra National Park, Minas Gerais, southeastern Brazil. The river is 475 km long and a major left tributary of the Paranaíba River (Baccarro *et al*., 2004), which forms the Upper Paraná River after its confluence with the Grande River. The study area was located upstream from Nova Ponte Dam (the streams flow into Nova Ponte Reservoir). The Nova Ponte hydropower plant is located in the Municipality of Nova Ponte, State of Minas Gerais (216790 S/ 7881847 E, Zone 23K) and it began operation in 1994. The total maximum volume of the reservoir is 12,792 hm^3 and the flooded area is 449.24 km^2 (Cachapuz, 2006). The Upper Araguari River has well-defined seasons: a dry season from May to September and a rainy season from October to April (Rosa, 2004). The region produces considerable amounts of soy, coffee, corn, and sugar cane and has a well-developed irrigated agriculture system. Most people live in small towns with up to 20,000 inhabitants (Ligeiro *et al*., 2013).

We randomly selected 38 sampling sites (one site per stream). Site selection followed the generalized random tessellation stratified (GRTS) sampling design according to Stevens & Olsen (2004) and Olsen & Peck (2008). This is a probability-based design in which a master sample frame is established by using a digitized drainage system map, and then the sample sites are selected via hierarchical, spatially weighted criteria. We excluded all tributaries greater than Strahler order 3 on a digital 1:100,000 scale map because our targets were wadeable perennial streams. All stream channels located > 35 km from the shore of the Nova Ponte Reservoir were excluded to reduce travel distances and limit the effect of different fish species dispersal capacities (Hitt & Angermeier, 2008). The length of each sample site was 40 times its mean wetted width, with a minimum length of 150 m (Kaufmann *et al*., 1999). Each site was subdivided into 11 equally spaced transects.

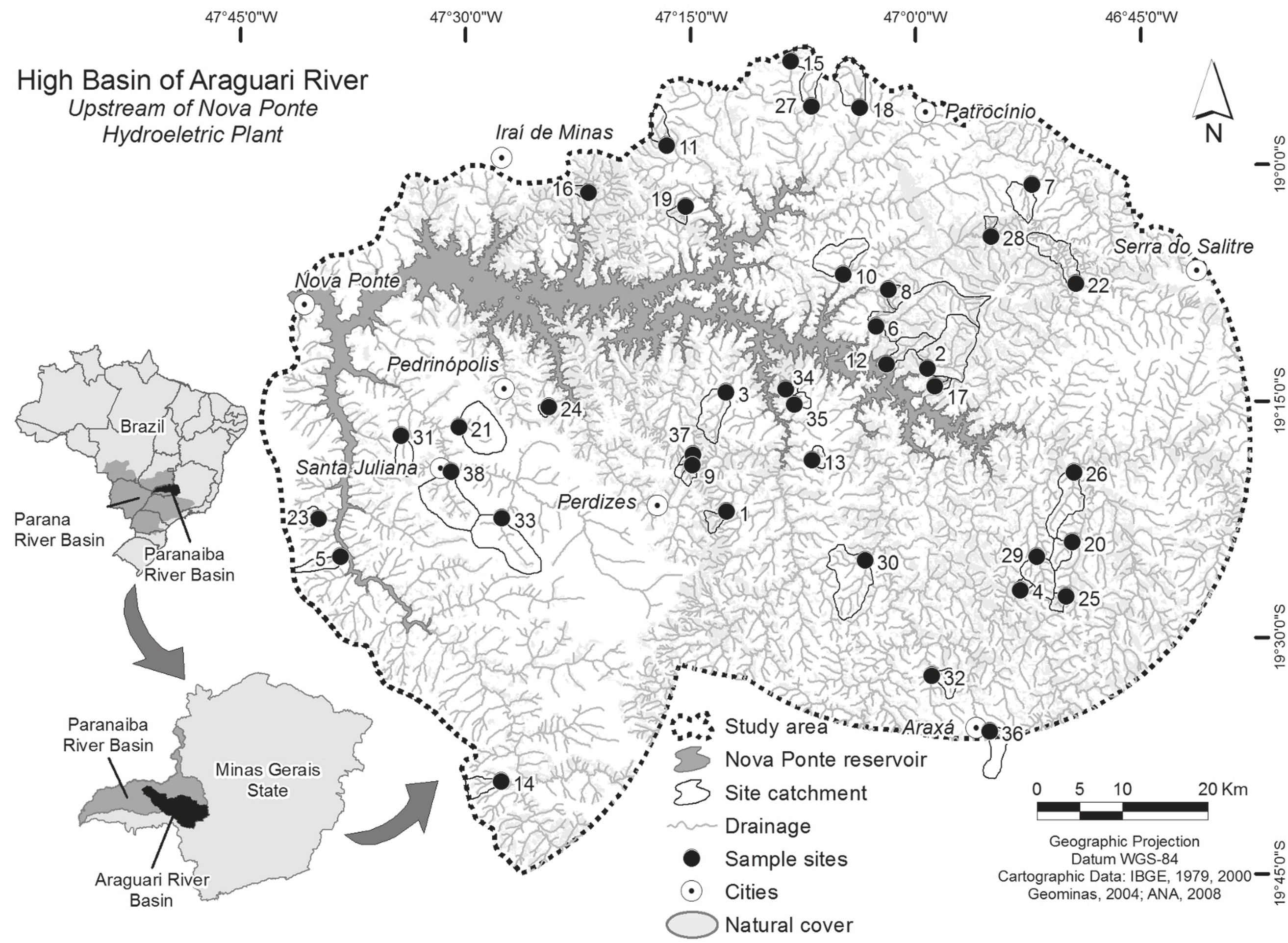

Fig. 1. Locations of the 38 randomly selected sites sampled in the Upper Araguari River basin, State of Minas Gerais, Brazil.

Site variables. At each transect, we quantified wetted width, depth, canopy cover, substrate (*e.g.* boulder, gravel, sand, wood), presence of in-stream fish cover (*e.g.* overhanging vegetation, undercut banks, macrophytes), and presence of anthropogenic activities (*e.g.* trash, pipes, roads, buildings). Between each transect, we measured thalweg depth and channel slope (with a clinometer). All variables were assessed as described in Peck *et al*. (2006) through use of pre-printed field forms that were widely used in similar studies (Hughes & Peck, 2008; Bryce *et al*., 2010; Macedo *et al*., 2014; Leal *et al*., 2016). From the site variables measured in the field, we calculated 11 physical habitat metrics according to Kaufmann *et al*. (1999) (Table 1). Site variables were log transformed to improve normality of data.

Land use and cover variables. We assessed catchment land use and cover for each site (whole catchment upstream of our sample reach) through screen digitizing of land use and land cover. We extracted catchments from the terrain model from the Shuttle Radar Topographic Mission- SRTM (USGS, 2005). Then we interpreted September Landsat TM sensor multispectral imagery (R4G3B2 false color band combination) in conjunction with fine resolution images (0.6 to 5 m spatial resolution, Google Earth data; Google, 2010). The fine resolution images provided information about the shape and texture of the elements, and the Landsat images showed specific spectral response for each land use and vegetation cover type. Then we distinguished each vegetation type through their response differences in the infrared band in multispectral imagery because their leaf structures differ considerably. Our mapping identified, and we quantified, percentages of four natural land covers: woodland savanna, grassy-woody savanna, parkland savanna, and wetland (palm swamps); and three human land uses: pasture, agriculture, and urban. We determined the extent of savanna physiognomy from tree cover or density (Sarmiento, 1984). Woodland savanna was defined by trees over 5-m tall and a total cover greater than 15%; grassy-woody savanna was defined by trees less than 5-m tall and shrubs isolated or in small groups; and parkland savanna was defined as a mosaic of savanna units including rocky fields (Sarmiento, 1984). We log transformed the variables to improve normality of data.

Table 1. Descriptions of 11 site attributes represented for acronyms according to Kaufmann *et al*. (1999).

Reach variables	Description
Xwxd	mean wetted width multiplied by depth (m^2)
Sddepth	standard deviation of thalweg depth (cm)
Xcdenmid	average values of riparian canopy cover measured with a canopy densitometer from each transect and then convert to a percentage by dividing by 17 (the densiometer maximum amount of vegetation cover) and multiplying the result by 100
PCT_FN	percentage of fine substrate (<0.06 mm, i.e., silt, clay and muck)
Lsub_dmm	$\log_{10}$ [estimated geometric mean substrate diameter (mm)]
PCT_sfgf	percentage of fine gravel and smaller (<16 mm) substrate
xfc_lwd	sum of large wood debris areal cover
xfc_brs	sum of brush and small wood debris areal cover
xfc_nat	natural fish cover. Sum of cover from large wood, brush, overhanging vegetation, boulders, and undercut banks
w1_hall	percentage of observations (11 transects x two banks = 22 observations in total) for each type of direct human disturbance (wall/dike, buildings, pavement, pipes, trash, mining activity, logging operations, pasture, row crops). Different weights were assigned for each spatial class: 1.5 to impact inside the channel or on the banks, 1.0 to impact within 10 meters from the banks, and 0.667 for impacts >10 meters from the banks. The sum of the results of all of the types of human impacts assessed at the site scale provided an estimate of local anthropogenic disturbance at the site
Xslope	water surface gradient over reach (%)

Pure spatial variables. To take into account spatial autocorrelation of the data we included pure spatial variables in our analysis. We determined the geographical coordinates (latitude and longitude) of each site in the field using a GPS. In the laboratory, the geographical coordinates (latitude and longitude) of the sites were centered on their means to reduce collinearity among terms when fitting the regression (Legendre & Legendre, 2012). Next, we calculated a matrix of spatial data, with x = longitude (centered) and y = latitude (centered), by including all terms of a cubic trend surface regression. The terms included were: x, y, x^2, xy, y^2, x^3, x^2y, xy^2 and y^3 (Legendre, 1990; Borcard *et al*., 1992). The spatial variables were log transformed.

Fish sampling. We sampled fish assemblages in an upstream direction with two hand nets made with plastic mosquito screen (1 mm mesh) attached to an 80 cm diameter hemispherical steel frame. Each site was sampled approximately for two hours (12 min in each transect), thoroughly lifting substrates and netting between each transect. The capture efficiency of this method was tested through various estimators, with efficiencies of 78-85% for both benthic and water column species (Leal *et al*., 2014). Fish were kept separately by sample site, anesthetized in a solution of clove oil, and then fixed in 10% formalin. In the laboratory, all fish were washed in tap water, preserved in 70% alcohol, and identified to the species level, according to Graça & Pavanelli (2007). Voucher specimens are deposited in the ichthyological collection of the Universidade Federal de Lavras (CI-UFLA) and in the Museu de Zoologia da Universidade de São Paulo (MZUSP). We used Hellinger-transformed fish data.

Data analysis. We used the multivariate approach "partial constrained ordination" to estimate the variation in fish species occurrence and abundance explained by environmental conditions. We used a two-step approach for variance partitioning. First, we ran a detrended correspondence analysis (DCA) to test the gradient length of species composition and then to determine the appropriate constrained ordination technique (canonical correspondence analysis, CCA, or redundancy analysis, RDA). According to Braak (1995), data with < 2 standard deviations (SD) of turnover along the first DCA axis are likely to respond linearly to environmental gradients, and RDA should be used; data with > 2 SD of turnover are likely to respond unimodally, and CCA should be used. Our two fish datasets (abundance and occurrence) responded unimodally to environmental gradients (SD > 2), so we used CCA.

We then used variance partitioning with partial CCA to partition total variation in each fish dataset (abundance and occurrence) into components explained by land use/cover (land use), site (site), and pure spatial (spatial) predictors (Anderson & Gribble, 1998; Hughes *et al*., 2015). For this, we ran twelve CCAs for each fish dataset (Table 2) to partition total variation in eight components: i) pure land use, ii) pure spatial, iii) pure site, iv) shared land use and spatial variation, v) shared land use and site variation, vi) shared spatial and site variation, vii) variation between all three components, and viii) unexplained variation. Fractions iv, v and vi were obtained by subtraction and they are not fitted variance components. The percentage of total variation explained by each constrained (Table 2, CCAs 1 to 3) or partial ordination (Table 2, CCAs 4 to 12) was obtained by the sum of canonical eigenvalues of each run divided by the sum of all eigenvalues obtained by an unconstrained correspondence analysis (CA, species data), and multiplied by 100 (Borcard *et al*., 1992). The percentage of variation in the fish data sets explained by individual variables of partial CCAs (Table 2, CCAs 6, 9 and 12) was calculated from the ratio of Lambda A (extra fit) to the sum of all eigenvalues (total inertia), multiplied by 100. These CCAs represent the percentage of total variation explained exclusively by land use dataset (CCA 6), site dataset (CCA 9) and spatial dataset (CCA 12). All analyses were run in Canoco v. 4.0 for Windows (Braak & Smilauer, 1998), down weighting rare species, with automatic forward selection of environmental variables, and 1,000 permutations using partial Monte Carlo randomization tests.

Table 2. Step descriptions of the 12 CCAs run over fish abundance and incidence datasets.

Step descriptions
(1) CCA of fish matrix,constrained by the land use matrix
(2) CCA of fish matrix, constrained by the site matrix
(3) CCA of fish matrix, constrained by the pure spatial matrix
(4) CCA of fish matrix, constrained by the land use matrix, with site variables treated as covariables
(5) CCA of fish matrix, constrained by the land use matrix, with the pure spatial variables treated as covariables
(6) CCA of fish matrix, constrained by the land use matrix, with the site and pure spatial variables treated as covariables
(7) CCA of fish matrix, constrained by the site matrix, with the land use variables treated as covariables
(8) CCA of fish matrix, constrained by the site matrix, with the pure spatial variables treated as covariables
(9) CCA of fish matrix, constrained by the site matrix, with the land use and pure spatial variables treated as covariables
(10) CCA of fish matrix, constrained by the pure spatial matrix, with the land use variables treated as covariables
(11) CCA of fish matrix, constrained by the pure spatial matrix, with the site variables treated as covariables
(12) CCA of fish matrix, constrained by the pure spatial matrix, with the land use and site variables treated as covariables

Results

We collected 4,330 individuals belonging to six orders, 14 families, 26 genera and 32 species (Table 3). We observed wide ranges in most land use and land cover variables, especially for parkland savanna (0 to 88.3%) and pasture (0 to 71.3%) (Appendix A). The site variables depicting canopy cover and percentage of fine substrates also had high standard deviations (Appendix A). The DCA analyses indicated a strong response of fish species occurrence and abundance to the environmental gradient (sampling sites), especially *Hoplias intermedius* (N=1), *Oligosarcus pintoi* (N=1), an undetermined species of Stevardiinae. (N=1), *Rhamdia quelen* (N=15) and *Poecilia reticulata* (N=6) (Fig. 2). These species were associated with site 32 (only two species sampled) and with the most urbanized site (36).

All land use and site variables were selected in all CCAs by automatic forward selection in CANOCO. Only spatial data showed collinearity between variables, leading to the elimination of some of them by the automatic forward selection. The partial CCA results indicated that >50% of the total variation in both fish datasets was explained by environmental data (abundance: 54.86%; occurrence: 51.36%) (Fig. 3). Most variation in both fish species abundance and occurrence was explained by site variables (abundance: 25.31%; occurrence: 24.51%). Among those variables, standard deviation of thalweg depth explained 4.95% of the fish species occurrences and the sum of large wood debris areal cover explained 4.07% of the fish species abundance (Table 4). Nonetheless, land use/cover variables explained nearly as much variation (abundance: 22.69%; occurrence: 18.9%). The land use variable that explained most variation in fish species abundance and occurrence was urban cover (8.96%, 8.25%, respectively) (Table 4). Little species variation was explained by pure spatial variables (abundance: 4.7%; occurrence: 3.96%) or shared environmental variables.

Table 3. Fish species collected from 38 sites in the Upper Araguari River basin, with their respective number of individuals (N) and voucher numbers. [a]Alien species; *not described species. CIUFLA, Coleção Ictiológica Universidade Federal de Lavras; MZUSP, Museu de Zoologia da Universidade de São Paulo.

Species	N	Voucher
Acestrorhynchus lacustris (Lütken, 1875)	1	CIUFLA 0460
Apareiodon ibitiensis Campos, 1944	29	CIUFLA0461
Astyanax sp.*	476	CIUFLA 0463
Astyanax altiparanae Garutti & Britski, 2000	17	CIUFLA 0464
Astyanax aff. *scabripinnis* (Jenyns, 1842)*	1502	CIUFLA 0465
Cetopsorhamdia iheringi Schubart & Gomes, 1959	29	CIUFLA 0468
Characidium sp.*	107	CIUFLA 0469
Characidium xanthopterum Silveira, Langeani, Graça, Pavanelli & Buckup, 2008	20	CIUFLA 0471
Corydoras difluviatilis Britto & Castro, 2002	22	CIUFLA 0472
Geophagus brasiliensis (Quoy & Gaimard, 1824)	33	CIUFLA 0473
Stevardiinae *	1	MZUSP 114314
Gymnotus sylvius Albert & Fernandes-Matioli, 1999	3	CIUFLA 0474
Hoplias intermedius (Günther, 1864)	3	CIUFLA 0475
Hoplias malabaricus (Bloch, 1794)	4	CIUFLA 0476
Hypostomus sp. 1*	416	CIUFLA 0477
Hypostomus sp. 2*	12	CIUFLA 0478
Imparfinis schubarti (Gomes, 1956)	2	CIUFLA 0480
Knodus moenkhausii (Eigenmann & Kennedy, 1903)	20	CIUFLA 0481
Leporinus microphthalmus Garavello, 1989	26	CIUFLA 0483
Microlepidogaster arachas Martins, Calegari & Langeani, 2013	232	CIUFLA 0484
Neoplecostomus sp.*	46	CIUFLA 0485
Oligosarcus pintoi Campos, 1945	5	CIUFLA 0486
Parodon nasus Kner, 1859	1	CIUFLA 0487
Phalloceros harpagos Lucinda, 2008	532	CIUFLA 0488
Piabarchus stramineus (Eigenmann, 1908)	1	CIUFLA 0467
Piabina argentea Reinhardt, 1867	28	CIUFLA 0489
Poecilia reticulata Peters, 1859 [a]	27	CIUFLA 0490
Rhamdia quelen (Quoy & Gaimard, 1824)	19	CIUFLA 0491
Rhamdiopsis sp.*	28	CIUFLA 0479
Synbranchus marmoratus Bloch, 1795	1	CIUFLA 0492
Trichomycterus sp. 1*	671	CIUFLA 0493
Trichomycterus sp. 2*	51	CIUFLA 0732

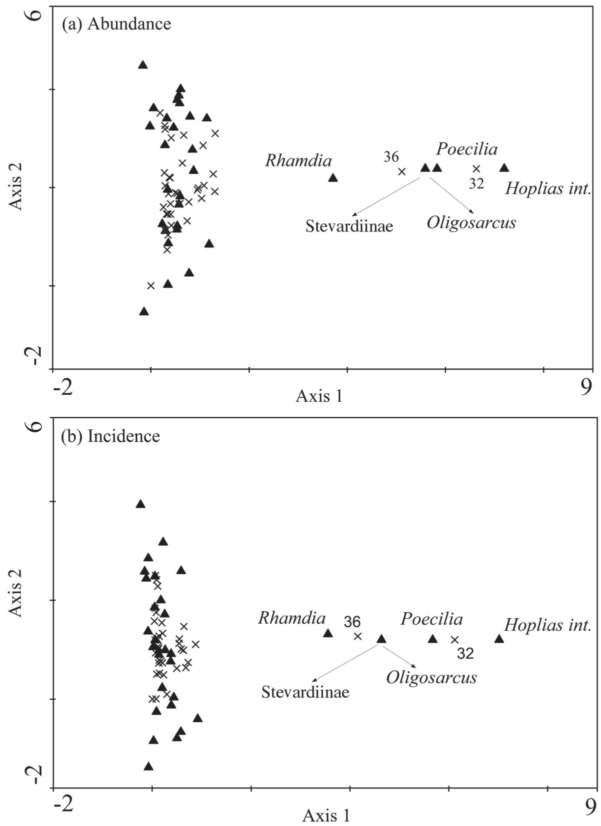

Fig. 2. Detrended correspondence analysis (DCA) of fish abundance (a) and incidence (b) along the sampling sites. The species are shown in triangle and sampling sites in X-mark.

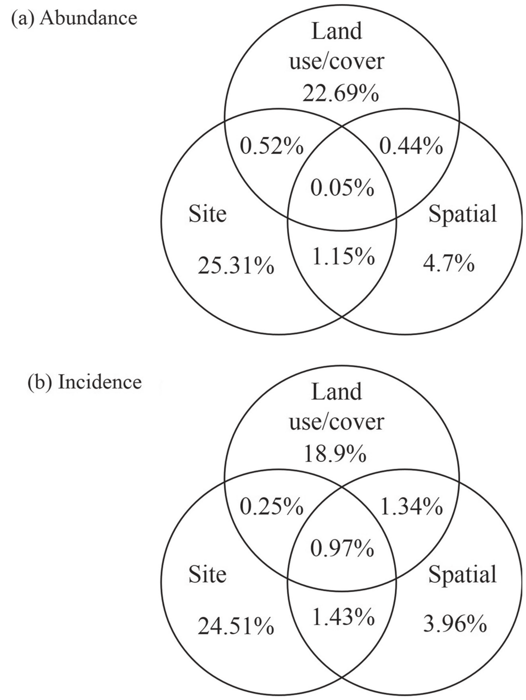

Fig. 3. Venn diagrams representing the results of the variance partitioning with partial CCA (canonical correspondence analysis): percentage of variation in fish abundance (a) and incidence (b) explained by land use and land cover, site, and spatial variables, as well as that shared between the three sets of variables in the Upper Araguari River basin, Minas Gerais. See Table 4 for a list of all explanatory variables.

Table 4. Automatic forward selection results of land use and site variables for fish abundance and occurrence datasets. Bold indicates single variables that explained statistically significant variation ($p \leq 0.05$). To descriptions of site variables, see Table 1.

	ABUNDANCE				OCCURRENCE			
Variables	Lambda A	p value	F value	% explanation	Lambda A	p value	F value	% explanation
LAND USE								
Agriculture	0.10	0.64	0.82	2.03	0.06	0.69	0.66	1.98
Grassy-woodland	0.09	0.72	0.69	1.83	0.06	0.64	0.75	1.98
Parkland	0.15	0.29	1.18	3.05	0.05	0.71	0.65	1.65
Pasture	0.12	0.44	0.94	2.44	0.05	0.8	0.52	1.65
Urban	0.44	0.01	3.44	**8.96**	0.25	0.03	3.07	**8.25**
Woodland	0.17	01.7	1.34	3.46	0.06	0.7	0.61	1.98
Wetland	0.06	0.9	0.44	1.22	0.05	0.71	0.6	1.65
SITE								
lsub_dmm	0.04	0.97	0.32	0.81	0.08	0.31	1.07	2.64
xslope	0.12	0.45	0.97	2.44	0.03	0.93	0.34	1
xwxd	0.1	0.57	0.8	2.03	0.06	0.67	0.69	1.98
xfc_nat	0.1	0.53	0.77	2.03	0.06	0.41	0.82	1.98
PCT_FN	0.11	0.56	0.88	2.22	0.08	0.37	0.98	2.64
sddepth	0.12	0.37	1.04	2.44	0.15	0.04	1.84	**4.95**
xfc_brs	0.07	0.72	0.57	1.44	0.04	0.83	0.49	1.32
pct_sfgf	0.15	0.2	1.28	3.05	0.06	0.59	0.73	1.98
w1_hall	0.1	0.65	0.8	2.04	0.04	0.89	0.44	1.32
xcdenmid	0.14	0.24	1.18	2.85	0.11	0.17	1.39	3.63
xfc_lwd	0.2	0.07	1.62	4.07	0.04	0.81	0.48	1.32
Total inertia	4.91				3.03			

Discussion

The set of site variables explained more variation in our fish dataset than catchment variables. Similar results have been reported from studies in temperate regions (Wang *et al*., 2003; Johnson *et al*., 2007; Bouchard & Boisclair, 2007). We believe that our study scale contributed to this result. The different scale of study designs coupled with differences in the scale of dependency of certain process (*e.g.* organic matter input and sediment delivery) influence the contrasting results in the literature (Allan & Johnson, 1997; Wang *et al*., 2006b). Generally, one has a greater ability to detect site conditions but less ability to detect regional effects when more sites are sampled per catchment versus sampling more catchments with fewer sites in each (Wang *et al*., 2006b). We studied only the Upper Araguari River basin, in the Cerrado Domain, and many sites were located close to each other. Therefore, our scale of measurement is likely more sensitive to effects of site variables on fish assemblages.

Influence of site factors such as habitat structure on fish assemblages has been investigated extensively (Schlosser, 1982; Harding *et al*., 1998; Kaufmann & Hughes, 2006; Brown *et al*., 2009). The structure of stream fish assemblages has been related to numerous site variables, such as bottom type and cover (Angermeier & Winston, 1998), and bottom, depth, and current (Gorman & Karr, 1978). In our study, standard deviation of thalweg depth individually was the most important site variable related to fish occurrence. The standard deviation of thalweg depth is a quantitative measure of relatively flow-independent channel morphology, and it is considered an index of bottom complexity (Kaufmann *et al*., 1999). Thus, higher values are related to increased bottom complexity, with heterogeneous substrate size and hydraulic regimes, providing living space and cover for fish species with different preferences, affecting fish occurrence. For example, when fine sediment is predominant, the occurrence of habitat specialists, like benthic Loricariidae, can be negatively affected (Waters, 1995), because such species inhabit runs and riffles and are specialist benthic feeders (Terra *et al*., 2015). Furthermore, field measurements of thalweg depth are recommended for monitoring programs (Kaufmann *et al*., 1999) because the variability of this attribute can be drastically reduced by sedimentation. For fish species abundance, the site variable "sum of large wood areal cover" explained most variation. Large wood is abundant in many undisturbed stream ecosystems and plays key functions: dissipation of flow energy, stabilization of channel banks, formation of pools (Booth *et al*., 1996) and habitat for organisms (Harmon *et al*., 1986). The presence of woods influences the formation of mesohabitat features (*e.g.* pools and backwaters) and provides microhabitats (Crook & Robertson, 1999). Thus, it creates and maintains complex habitats that generally support greater biodiversity (Benson & Magnuson, 1992), and it can contribute to differences in fish abundance between streams (Angermeier & Karr, 1984). In a study of 55 stream reaches in Japan, Inoue & Nakano (2001) found positive relationships between salmon density and large wood, independently of stream size, and salmon density was higher in forest reaches than in grassland reaches. It is interesting that large wood areal cover and standard deviation of thalweg depth had low standard deviations among sites, indicating that these variables have high sensitivity to determine fish assemblage composition.

Despite the higher proportion of variation explained by site variables, land use/cover variables explained nearly as much variation. The importance of landscape conditions to create and maintain local habitat has been increasingly recognized (Allan, 2004). In this sense, human land uses are important threats to stream systems, affecting water quality, physical habitat and, consequently, changing the structure of fish assemblages in multiple ways (Allan *et al*., 1997; Harding *et al*., 1998; Lammert & Allan, 1999). Urban cover was the most important land use variable explaining fish species abundance and occurrence, and it accounted for twice the explanation of the most important site variable. Urban development changes water chemistry and physical habitat. Typically, urban streams are affected by a variety of pollutants, including domestic sewage inputs and excessive amounts of nutrients and sediments (Hughes *et al*., 2014). They are also characterized by altered flow regimes (Hughes *et al*., 2014). Consequently, channels become less stable, leading to excessive erosion and loss of stream cover and pool habitat (Wang *et al*., 2001).

All these alterations drastically degrade stream ecosystems and lead to major changes in the biota even at relatively low levels of urbanization (Wang *et al*., 1997; Hughes *et al*., 2014), causing declines in fish diversity, abundance, and biotic integrity (Wang *et al*., 2000; Hughes & Dunham, 2014). However, in this study we had few samples to evaluate rigorously the influence of urban land use on site variables. Nevertheless, our results revealed the unique fish species composition of site 36, the most disturbed by urban land use. This site supported two species (*Oligosarcus pintoi* and an undetermined species of Stevardiinae) with one individual each, six *Poecilia reticulata* (also recorded at site 32), and *Rhamdia quelen* (also found at ten other sites). Degraded streams are more susceptible to invasions by alien species (Kennard *et al.,* 2004), such as *P. reticulata*. The relationship between *P. reticulata* and altered waters is documented extensively. This small-sized species has high reproductive capacity and exploits a wide variety of food resources (Koch *et al*., 2000; Cunico *et al*., 2006), persisting in highly altered systems (Araújo, 1998; Lemes & Garutti, 2002). Another species adapted to the adverse conditions of urban streams is *R. quelen*. It is omnivorous, prefers low water flow, sand or clay bottom substrate, and is resistant to high temperatures (compared with many other Brazilian species) (Gomes *et al*., 2000). However, previous studies associating *R.*

quelen with disturbed streams considered its response to physicochemical water oscillation instead of disturbed instream habitats (Casatti *et al*., 2006; Dias & Tejerina-Garro, 2010). Although *O. pintoi* lacks characteristics adapted to persistence in degraded streams, Lemes & Garruti (2002) found high frequency of the species in such systems. Here, we consider *O. pintoi* and an undetermined species of Stevardiinae as occasional species.

To conclude, we found that environmental variables at both instream and catchment spatial scales affect stream fish in the Upper Araguari Basin and must be considered jointly in effective conservation strategies with special attention to urban land use and channel morphology. One important result of our study is that environmental data explained considerable variation in both fish datasets (>50% of the total variation in species abundance and occurrence), which is superior to some previous studies (Sály *et al*., 2011; Marzin *et al*., 2012). However, there was low spatial variation in our datasets and the environmental data had, in general, low variability among sample sites. Thus, despite the relevant explained variation by environmental data, our results were strongly influenced by only two sites: one highly impacted by urban development and another with a unique composition of fish fauna. Therefore, we believe that additional research is needed to understand how different scales operate together across space and time and determine fish fauna structure.

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Appendix A. Coordinates, land use and cover (WS= woodland savanna; GW= grassy-woody savanna; PS= parkland savanna; W= wetland; P=pasture; A= agriculture; U= urban) and site variables (see Table 1) represented in percent (%) from 38 sites in the upper Araguari river basin with their respective means and standards deviation (SD).

Sites	Coordinates	WS	GW	PS	W	P	A	U	xcdenmid	w1_hall	sddepth	xwxd	xslope	lsub_dmm	PCT_FN	pct_sfgf	xfc_lwd	xfc_brs	xfc_nat
1	267133 S/ 7857898 E	27,95	59,63	0	0	12,42	0	0	87,30	1,50	9,58	0,88	0,87	1,32	12,73	43,64	0,04	0,35	0,79
2	290634 S/ 7874629 E	11,54	0	81,54	0	2,39	4,54	0	74,20	0,14	29,56	2,70	0,69	0,78	0,00	70,91	0,00	0,00	0,11
3	267052 S/ 7871871 E	19,55	10,77	0	0	15,84	53,84	0	92,65	0,58	19,84	1,30	1,93	0,96	10,91	60,00	0,00	0,00	0,34
4	301543 S/ 7848716 E	27,74	8,24	0	0	38,59	25,43	0	90,11	0,73	10,76	0,38	2,51	-0,74	27,27	76,36	0,01	0,05	0,14
5	221919 S/ 7852625 E	8,26	21,51	0	0	15,55	54,68	0	85,03	1,20	8,41	0,45	1,09	0,79	0,00	50,91	0,00	0,07	0,17
6	284613 S/ 7879607 E	10,58	0	57,57	0	12,52	19,33	0	73,93	0,00	24,36	2,31	1,29	0,45	1,82	76,36	0,00	0,09	0,26
7	302881 S/ 7896183 E	9,38	0	0	0	0	90,62	0	83,56	1,93	15,32	0,76	1,02	-1,36	69,09	90,91	0,00	0,09	0,10
8	286107 S/ 7883867 E	5,84	0	88,31	0	0	5,85	0	82,62	0,48	25,87	1,27	0,97	1,57	0,00	32,73	0,01	0,06	0,50
9	263088 S/ 7863352 E	20,87	0	0	2,16	71,32	5,65	0	64,57	1,65	17,96	0,49	2,33	-0,02	36,36	69,09	0,03	0,07	0,37
10	280748 S/7885669 E	12,68	10,96	0	0	5,08	71,28	0	90,78	0,74	17,20	1,54	0,84	-0,14	14,55	87,27	0,01	0,15	0,25
11	260081 S/ 7900788 E	36,81	5,37	0	0	57,82	0,00	0	79,55	1,17	16,29	1,00	0,58	1,56	0,00	30,91	0,01	0,06	0,57
12	285892 S/ 7875125 E	8,86	0	69,18	0	0	21,96	0	71,12	0,73	31,78	1,44	1,01	0,93	0,00	52,73	0,00	0,04	0,37
13	277131 S/ 7863915 E	24,34	0	0	0	0	75,66	0	92,25	0,98	6,07	0,43	0,89	0,39	3,64	72,73	0,00	0,03	0,27
14	240730 S/ 7826308 E	23,35	3,66	0	0	19,92	53,07	0	76,07	1,07	17,33	1,01	1,45	0,76	0,00	70,91	0,05	0,05	0,47
15	274627 S/ 7910605 E	14,19	0	0	0	22,74	63,07	0	91,18	1,83	17,95	0,93	1,02	1,68	16,36	23,64	0,02	0,01	0,10
16	250949 S/ 7895246 E	21,86	22,08	0	1,10	33,25	21,71	0	48,80	1,16	8,99	0,30	1,76	-1,07	30,91	83,64	0,00	0,00	0,30
17	291479 S/ 7872603 E	18,65	0	25,10	0	0	56,26	0	98,80	1,20	15,61	0,35	1,98	1,76	5,45	43,64	0,18	0,32	0,63
18	282745 S/ 7905174 E	12,27	0	0	0	0	87,73	0	83,02	0,73	9,78	0,88	0,28	0,31	5,45	94,55	0,00	0,07	0,44
19	262337 S/ 7893610 E	14,24	34,99	0	0	6,35	44,42	0	87,83	0,36	22,37	1,14	1,47	1,68	0,00	54,55	0,05	0,33	0,58
20	307615 S/ 7854332 E	9,35	29,73	0	0	1,36	59,56	0	93,58	0,00	8,94	0,54	0,58	-0,77	14,55	76,36	0,03	0,22	0,62
21	235817 S/ 7867797 E	3,11	14,32	0	1,47	0	81,10	0	85,56	0,00	15,98	1,04	0,45	1,38	0,00	29,09	0,00	0,04	0,33
22	308006 S/ 7884630 E	19,45	24,58	16,59	0	30,91	8,47	0	87,17	1,09	10,32	0,24	1,14	0,74	7,27	43,64	0,03	0,88	1,02
23	219382 S/ 7857079 E	16,98	8,79	0	0	23,26	50,96	0	77,01	1,99	13,70	0,81	1,05	0,92	9,09	49,09	0,03	0,09	0,68
24	246327 S/ 7870163 E	11,27	0	0	0	34,72	54,01	0	85,16	0,61	9,27	0,37	0,66	0,00	0,00	90,91	0,00	0,05	0,13
25	306919 S/ 7847966 E	19,13	25,03	0	0	8,83	47,01	0	86,76	0,00	9,18	0,45	0,66	0,63	3,64	63,64	0,00	0,09	0,51
26	307823 S/ 7862520 E	13,28	14,50	0	0	12,63	59,59	0	86,23	1,86	14,08	1,52	0,60	-0,15	9,09	89,09	0,05	0,18	0,48
27	277088 S/ 7905315 E	7,92	1,86	0	0	0,00	90,22	0	87,30	1,64	11,85	0,75	0,65	0,69	7,27	56,36	0,01	0,17	0,42
28	298089 S/ 7890130 E	17,37	2,08	45,61	0	32,77	2,16	0	79,81	2,35	17,96	1,01	0,83	-0,88	54,55	100,00	0,00	0,01	0,56
29	303458 S/ 7852641 E	12,61	26,41	0	0	12,09	48,89	0	85,70	0,41	14,33	0,95	0,31	0,00	7,27	87,27	0,00	0,06	0,66
30	283325 S/ 7852176 E	11,33	8,01	0	0	3,13	77,53	0	56,28	0,33	16,03	2,34	1,07	-0,63	36,36	87,27	0,05	0,18	0,48
31	228995 S/ 7866812 E	7,08	0	0	0	4,62	88,30	0	93,32	1,88	6,18	0,31	0,78	0,63	10,91	60,00	0,00	0,05	0,48
32	291168 S/ 7838651 E	15,02	12,30	0	0	15,85	56,83	0	75,27	0,67	16,33	1,00	0,85	-0,09	14,55	69,09	0,01	0,08	0,54
33	240834 S/ 7857101 E	4,56	10,34	0	4,40	4,98	75,72	0	38,10	1,75	22,53	2,13	0,21	-1,05	52,73	89,09	0,00	0,02	0,23
34	274040 S/ 7872232 E	33,21	57,56	0	0	8,46	0,78	0	88,37	0,27	10,40	0,50	0,49	0,37	10,91	47,27	0,00	0,22	0,85
35	275081 S/ 7870412 E	14,77	5,19	0	0	18,31	61,73	0	90,24	0,47	11,76	0,47	0,99	0,22	5,45	78,18	0,01	0,10	0,31
36	297969 S/ 7832165 E	10,01	6,41	0	3,31	21,17	42,68	16,41	17,78	4,63	10,04	0,68	0,83	0,68	10,91	60,00	0,00	0,03	0,04
37	263165 S/ 7864557 E	28,97	0	0	3,54	67,49	0	0	28,74	3,45	12,34	0,46	0,47	0,42	12,73	74,55	0,04	0,06	0,50
38	234847 S/ 7862538 E	6,63	9,00	0	4,62	15,52	61,64	2,60	6,55	3,91	12,18	0,71	0,64	0,75	3,64	60,00	0,00	0,05	0,45
	Mean	15,55	11,40	10,10	0,54	16,58	45,32	0,50	76,38	1,20	14,96	0,94	0,98	0,41	13,30	65,69	0,02	0,12	0,42
	SD	8,07	14,92	24,19	1,28	18,37	29,75	2,68	21,50	1,06	6,15	0,61	0,54	0,83	16,69	20,14	0,03	0,16	0,22