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To cite this article: Camilo A. Roa-Fuentes & Lilian Casatti (2017) Influence of environmental features at multiple scales and spatial structure on stream fish communities in a tropical agricultural region, Journal of Freshwater Ecology, 32:1, 281-295, DOI: 10.1080/02705060.2017.1287129

To link to this article: https://doi.org/10.1080/02705060.2017.1287129

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Published online: 15 Feb 2017.

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Influence of environmental features at multiple scales and spatial structure on stream fish communities in a tropical agricultural region

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ABSTRACT
Land cover change for agricultural expansion exerts strong pressures on tropical streams. We examined the relative contributions of catchment land cover, local environmental features, and spatial patterns on stream fish communities \((n = 43)\). Explained variation in fish community structure was partitioned \((p\text{-RDA})\) between the explained fractions as follows: pure local 10%, pure catchment 1%, pure spatial 3%, and shared environmental and spatial 7%. Among the possible reasons for the lack of effect of catchment-scale variables on stream fish structure we can cite (1) weak associations between catchment-scale and local-scale features that are affecting stream fish communities, (2) major influence of past land cover on the present-day fish community structure compared to current land cover, or (3) the small variability in catchment variables \((e.g.\) homogeneous landscape) is not able to overcome the impact of local-scale variables. The best practice to improve the ecological integrity of streams would be the restoration at the catchment-scale, which is impossible for agricultural lands. In areas with intense land use for agriculture and pasture, our study indicates that restoration of riparian forests and manipulation of local conditions may be an option to reduce the impacts of anthropogenic activities on the stream fish communities.

Introduction

Every key aspect of river ecosystems, river geomorphic systems, and river chemical systems starts in headwater streams \((\text{Freeman et al.} \ 2007)\). Headwater streams provide ecosystem services from local to global, serve as ecological refuges, and supply water for human activities \((\text{Lehner et al.} \ 2011)\). Human activities commonly associated with headwater stream modification include land cover change, road construction, mining, agricultural drainage, and reservoir construction. Land cover change for agricultural expansion exerts strong pressures on freshwater ecosystems through augmented inputs of nutrients, contaminants, sediments, and modification of riparian zones \((\text{Sala et al.} \ 2008; \text{Laurance et al.} \ 2014)\). Particularly in tropical streams, land cover change is projected to have a paramount effect on biodiversity when compared with other factors, such as climate and biotic exchange \((\text{Sala et al.} \ 2008)\).

The concept of hierarchical classification of stream systems provides a useful framework for integrating the multiple scales over which ecological processes that organize stream communities are supported \((\text{Frissell et al.} \ 1986; \text{Angermeier & Winston} \ 1998; \text{Feld} \ 2013)\). An important assumption of this framework is that the structure and dynamics of stream habitat \((e.g.\) pool/riffle morphology and sequence) and biological patterns are determined by the surrounding catchment \((\text{Hynes} \ 1975;\)
Frissell et al. 1986). By considering the environmental features in a hierarchical framework, it is expected that catchment-scale variables impact the local-scale variables (i.e. at the reach-scale), which then in turn affect stream fish community structure (Fitzpatrick et al. 2001; Wang et al. 2003; Dembkowski & Miranda 2014).

Although there is a substantial number of studies that address this issue (Lammert & Allan 1999; Diana et al. 2006; Johnson et al. 2007; Cianfrani et al. 2012), including in tropical streams (Cruz et al. 2013; Casatti et al. 2015; Santos et al. 2015), the relative importance of catchment- versus local-scale factors for stream biota has remained elusive (Roth et al. 1996; Cianfrani et al. 2012). Studies addressing the issue are necessary because the assessment of catchment-stream relationships using a hierarchical classification can aid in conservation, restoration, and management of freshwater systems (Frissell et al. 1986; Cianfrani et al. 2012; Feld 2013; Dembkowski & Miranda 2014) and provides a more efficient and holistic view of these (Dembkowski & Miranda 2014).

This study addresses the relative contributions of catchment land cover, local environmental features, and spatial patterns on stream fish community structure, and discusses possible implications for management and/or restoration of streams located in heavily modified tropical landscapes. We expected that both local and catchment variables will influence the stream fish community structure since catchment variables would have indirect connections with ichthyofauna through their direct influences on local variables (Fitzpatrick et al. 2001; Wang et al. 2003; Dembkowski & Miranda 2014). We also hypothesized that spatial structure should be weak or non-significant because, as for stream organisms assessed within single, small drainage basins, environmental control prevails over spatial constraints (Heino & Mykrä 2008; Heino et al. 2015 and references therein).

**Methods**

**Study area**

The 43 stream reaches were located in the Turvo-Grande and São José dos Dourados basins in the northwest region of São Paulo State, south-eastern Brazil (Figure 1). These two basins belong to the same biogeographical province, where the fish communities have a shared evolutionary history (Géry 1969). The study area is located in the Serra Geral geological formation, presenting a relatively flat slope and plains of quaternary fluvial sedimentary nature (IPT 1999). The soil has a high erosive potential since it is composed of unconsolidated sand and clay sediments (Silva et al. 2007). The climate is tropical and hot, with two well-defined periods: a dry season with lower rainfall (28 mm mean) and cooler temperatures (21.4 °C mean) between June and September, and a wet season between December and February with higher rainfall (208.9 mm mean) and hotter (25.8 °C mean) temperatures (IPT 1999; CEPAGRI 2017).

Originally, this region was covered by semi-deciduous seasonal forest (Silva et al. 2007); however, the landscape has been fragmented since the beginning of the last century (1900) for the development of coffee crops, followed by livestock grazing (Victor et al. 2005), and more recently by sugarcane plantations (Rudorff et al. 2010). Currently, the native vegetation is restricted to less than 4% of its original area, distributed in small and unconnected fragments embedded within agricultural matrices (Nalon et al. 2008) or limited to riparian areas (Silva et al. 2007). As in other São Paulo state river basins (e.g. Corumbataí basin; Gerhard & Verdade 2016), the stream fish fauna of the study area may be considered as homogenized due to species introductions (Rahel 2002; Casatti et al. 2009), habitat destruction and simplification led by an extensive, dynamic, and long history of land cover change (Victor et al. 2005; Silva et al. 2007; Rudorff et al. 2010).

**Site selection and land cover characterization**

For site selection, first we mapped the land cover in the São José dos Dourados and Turvo-Grande basins through the digital processing of LANDSAT-5/TM satellite images for 2004, 2005, 2007 and
2011 (221-74, 221-75 e 222-74 scenes; 30 m spatial resolution). Four classes of land cover were defined through visual estimate using Google Earth™: native forest, pasture, sugarcane, and other land cover. Second, we preselected catchments with an area between 400 and 1400 ha (first to third-order streams according to the Strahler system). Using this procedure we identified 128 catchments, from which we selected 43 reaches (from independent catchments) for study based on accessibility and landowner support. Finally, to increase the reliability of the land cover data, we re-classified land cover in each of 43 selected catchments, but this time using orthorectified aerial photographs (‘orthophotos’) with a 1 m spatial resolution (years 2010/2011). Overall, eight classes of land cover were defined using orthophotos (Table A1), but we grouped them into four broad classes: native forest, pasture, sugarcane, and other land cover.

For the digital preparation, processing, and classification of LANDSAT-5/TM satellite images and orthophotos, we used ERDAS IMAGINE 9.2 and ArcGis 9.3 software. LANDSAT-5/TM satellite images were provided by the Instituto Nacional de Pesquisas Espaciais (INPE). Orthophotos were supplied by Empresa Paulista de Planejamento Metropolitano SA – EMLASA (CLU Nº 060/14). For the sugarcane land cover class, the CANASAT project (sugarcane crop monitoring in Brazil; Rudorff et al. 2010) provided data about area location and culture of sugarcane in São Paulo State for 2012.

Fish sampling

In each stream, a 75 m-long reach was blocked using 5-mm-mesh stop nets according to standardized methods of fish collection for the region (see Casatti et al. 2009 for details). The stream reaches were sampled using a Smith Root Model LR-24 backpack electrofisher (pulsed DC, 50–990 V, 1–120 Hz, 40 A peak max, 400 W) with settings adjusted based on ambient conditions (i.e. with the quick set-up feature activated, which automatically sets output voltage,
frequency, and duty cycle) and on observations of fish behavior and recovery times. A two-pass electrofishing technique was conducted for a total of 45 minutes of standardized time in each reach. Each electrofishing pass was conducted from downstream to upstream, covering from bank to bank in order to sample all available habitats. Captured specimens were fixed in 10% formalin solution and transferred to a 70% EtOH solution. Fishes were identified to species and counted. Voucher specimens were deposited at the fish collection of the Departamento de Zoologia e Botânica da Universidade Estadual Paulista (DZSJRP 19264–19326), São José do Rio Preto, São Paulo, Brazil. Fish sampling was carried out in the dry season between July and September 2013.

**Predictor variables**

**Local-scale features**

Ten local-scale descriptors related to in-stream features, riparian physical structures, water physico-chemical properties, stream morphology, habitat composition, and heterogeneity were estimated at each reach (Table A2). We measured these descriptors following standardized protocols for the study area. These descriptors are commonly used in studies of stream fish community structure in this region (see Casatti et al. 2009).

**Catchment-scale features**

For each catchment, the proportions of native forest, pasture, sugarcane, and other land cover in the whole catchment area, as defined by the orthophotos processing (years 2010/2011), were grouped in three different sets comprising a total of 12 catchment descriptors (Figure 2 and Table A2). The definition of the sets was based on Strayer et al. (2003) as follows: catchment, which includes the land cover in the entire catchment area from each sampling site; drainage network, which comprises land cover within a 30 m buffer zone around the river network (minimum width established by the current Brazilian Forest Code); and local radius, which includes the land cover within a circle (150-m radius) centered on the sample site (adapted from Strayer et al. 2003; Figure 2).

**Spatial variables**

We considered distance between sites as network distance (i.e. the distance between sites concerned with the dispersal pathways dictated by the riverine dendritic network, Brown & Swan 2010; Altermatt 2013). The network distance between sites was calculated using Hawth’s Analysis Tool (Beyer 2004) for ArcGIS 9.3.

From the network distance matrix, principal coordinates of neighborhood matrix (PCNM) was calculated to generate spatial variables. We retained only PCNM eigenvectors with positive spatial correlation since we were mainly concerned with patterns produced by spatially contagious processes (Borcard et al. 2011). For this, we used the 'PCNM’ function from the PCNM package (Legendre et al. 2013). The threshold value used in the PCNM analysis was the minimum distance giving connected network. All analyses were carried out in the R environment (R Development Core Team 2014).

**Analytical methods**

First, we conducted a principal components analysis (PCA) to describe the main environmental gradients. The PCA was performed separately for each scale, namely, one for the local-scale and another for the catchment-scale. For PCA, environmental variables were standardized to zero mean and unit variance. Subsequently, exploratory data analysis (box-plot and quantile-quantile plots) was used to assess predictor variable normality and the presence of outliers. Since we used a linear model based on multiple linear regression (see explanation below), data transformations were
applied to (1) linearize the relationships, (2) make the frequencies of distributions as symmetric as possible, and (3) reduce the effect of outlier data (Legendre & Legendre 2012). Consequently, the logit transformation was applied to the proportion variables (Warton & Hui 2011) and for variables in other units, square root transformation was used (Table A2). Since collinearity among predictor variables should be reduced prior to RDA (Legendre & Legendre 2012), we checked for strong linear dependencies, assessed separately within each scale, using a Spearman’s correlation $\rho \geq 0.7$ as a threshold (Dormann et al. 2013). Forest in the catchment and network, pasture in the catchment and local radius, and sugarcane in the catchment and local radius displayed $\rho \geq 0.7$. We discarded forest in the catchment, and pasture and sugarcane in the local radius for the subsequent statistical analyses (Table A3). Afterward, predictor variables were standardized to zero mean and unit variance to be used in the successive analyses.

To reduce the initial number of predictor variables we performed a forward selection procedure (Blanchet et al. 2008; Table A5). To prevent the inflation of Type I error in a forward selection procedure, a global test needs to be done prior to any variable selection (Blanchet et al. 2008). Therefore, we carried out three global tests (10,000 permutations each): one with the local-scale variables, another with the catchment-scale variables, and last one with the PCNM eigenvectors with positive spatial correlation. We also used two stopping criteria in the forward selection procedure: (1) the corrected alpha level of rejection of null hypothesis (i.e. only if the global test was significant, the corresponding set was used to continue with forward selection procedure) and (2) the adjusted $R^2$ statistic ($R^2_{\text{adj}}$) of the global test (Blanchet et al. 2008).

Finally, to identify the influence of local-scale, catchment-scale, and spatial features on stream fish community structure we performed a partial redundancy analysis (p-RDA). The p-RDA allowed the variance partitioning of the response variable (i.e. community structure assessed through the abundance of species) into fractions explained by each set of explanatory variables (i.e. local-scale, catchment-scale, and spatial features) (Legendre et al. 2011; Legendre & Legendre 2012). The Hellinger transformation was applied to the fish data prior to the p-RDA (Legendre & Gallagher 2001); however, before applying the Hellinger transformation the abundance data were square-root-transformed in order to reduce the asymmetry of the species distributions as recommended by Legendre & Legendre (2012). We used permutation procedures (10,000 permutations; $p < 0.05$) to test the partial contribution of each predictor variable set and to test the significance of

![Figure 2. Schema illustrating a hypothetical catchment representing the three different sets at which land cover was assessed.](image-url)
environmental variables assessed individually. For forward selection and p-RDA analyses, we used the ‘forward.sel’ and ‘rda’ functions of ‘packfor’ (Blanchet et al. 2008) and ‘vegan’ (Oksanen et al. 2015) packages, respectively, in the R environment (R Development Core Team 2014).

Results

A total of 3859 individuals belonging to 51 fish species, 17 families, and 6 orders were collected in the 43 stream reaches (Table A4). The first two PCA axes accounted for 46% (local-scale variables) and 59% (catchment-scale variables) of the variation in environmental features (Figure 3). Regarding the local-scale variables, PC1 represented a gradient from streams with more pools and better physical habitat conditions to streams with more grasses and unconsolidated substrate; PC2 represented streams with faster waters to wider channels (Figure 3(A)). For catchment-scale variables, the PC1 revealed the gradient from streams with more sugarcane in the catchment and forest in the network contrasting to those ones with more pasture in the catchment; PC2 separated streams with more forest and pasture in the network contrasting to those ones with other land uses (Figure 3(B)).

*Poecilia reticulata*, *Knodus moenkhausii*, *Astyanax altiparanae*, and *Aspidoras fuscoguttatus* were the most abundant species, accounting for 65% of total abundance. Overall, a small proportion of variability in fish abundance data was accounted for by the predictor variables ($R^2_{\text{Adj.}} = 0.20$, $p = 0.001$). Among the predictor variables, environmental variables were more influential than spatial variables. Explained variation in fish community structure was partitioned between the fractions as follows: pure local 10% ($p = 0.001$), pure catchment 1% ($p = 0.166$), pure spatial 3% ($p = 0.045$), and shared environmental and spatial location 7% (fraction not testable).

The environmental variables significantly related to community structure were mean depth, proportion of grasses (mostly *Brachiaria* spp.), proportion of pools, water temperature, mean width, and proportion of unconsolidated substrate (include clay, silt, and sand; Table 1). Sugarcane proportion in the entire catchment, the only catchment-scale variable retained by the forward selection procedure, was not significant (Table 1). Only one PCNM eigenvector with positive spatial correlation influenced fish community structure but its effect was weak (Table 1).

The biplot of p-RDA depicting the pure local-scale fraction effect (i.e. considering the local variables that were significantly related to community structure; Table 1) indicated that *Poecilia reticulata* and *Hypostomus cf. nigromaculatus* were mainly associated with wide and shallow sites, while

![Figure 3. Environmental gradients represented by the local (A) and catchment (B) variables in the studied sites. For variable codes, see Table A2.](image-url)
Imparfinis cf. schubarti, Rhamdia quelen, and Moenkhausia sanctaefilomenae displayed preference for deep and narrow environments (Figure 4). Species such as Gymnotus cf. sylvius and Aspidoras fuscoguttatus were associated with sites displaying high proportion of grasses, whereas the proportion of pools influenced the abundance of Astyanax altiparanae and H. cf. nigromaculatus, among others species (Figure 4).

Discussion
The objective of this study was to identify and compare local-scale, catchment-scale, and spatial determinants of stream fish communities in a highly modified tropical region. We found that local-scale variables contributed most to the total explained variability of fish community structure whereas catchment-scale and spatial features displayed non-significant or weak relationships with stream fish diversity. These results do not support our initial hypotheses that both local and catchment environmental features will explain variation in the stream fish community structure. Influences of local-scale environmental factors on the structure of stream fish communities have been recognized widely. For instance, variation in fish community structure has been associated with the addition of deeper areas (Sheldon 1968; Schlosser 1982), widespread propagation of marginal vegetation as grasses (mostly Brachiaria spp.; Casatti et al. 2009), increased extent and volume of pool habitats (Schlosser 1982), and stream width (Angermeier & Karr 1983; Lammert & Allan 1999).

Table 1. Predictor variables significantly related to fish community structure. Test based on 10,000 permutations. In bold p < 0.05.

| Predictor variable                        | Variance | F       | p      |
|------------------------------------------|----------|---------|--------|
| Mean depth                               | 0.04     | 3.91    | 0.001  |
| Proportion of grasses                    | 0.03     | 2.46    | 0.002  |
| Proportion of pools                      | 0.03     | 2.48    | 0.002  |
| Water temperature                        | 0.03     | 2.36    | 0.004  |
| Mean width                               | 0.02     | 2.07    | 0.008  |
| Proportion of unconsolidated substrate   | 0.02     | 1.80    | 0.027  |
| Proportion of sugarcane in the catchment | 0.02     | 1.42    | 0.108  |
| PCNM eigenvector 1                       | 0.02     | 2.04    | 0.010  |
| PCNM eigenvector 3                       | 0.01     | 1.25    | 0.215  |
| PCNM eigenvector 2                       | 0.01     | 0.85    | 0.656  |

Figure 4. Biplot of p-RDA depicting the pure local-scale fraction effect on stream fish community structure. Note that the biplot (scaling = 2) shows only pure effect associated with local-scale variables, excluding the effects of catchment-scale and space location. For species codes, see Table A4.
These local-scale variables are related with the vertical habitat used by fish (Sheldon 1968), availability of food resources (Angermeier & Karr 1983), and structural complexity of stream habitat (Casatti et al. 2009; Montańa & Winemiller 2010; Carvalho & Tejerina-Garro 2015). These results suggest that species’ niche differences, in terms of environmental characteristics, contribute to the variability in stream fish community structure at the spatial scale evaluated by us (Heino & Mykrä 2008). This outcome is in accordance with species sorting, the typical mechanism structuring stream communities (Heino & Mykrä 2008; Carvalho & Tejerina-Garro 2015).

On the other hand, previous studies have identified that catchment-scale variables, together with local-scale features, are also important determinants of stream fish fauna. For instance, land cover variables, as proportion of agriculture, measured at entire catchment, drainage network and local radius, influence stream fish community structure in the temperate streams (Fitzpatrick et al. 2001; Strayer et al. 2003). In tropical streams, although studies about scale-related effects are still scarce, the findings are similar to those of temperate environments. For example, in tropical agricultural landscapes both catchment- and local-scale features affected both functional and taxonomic diversity of stream fish communities (Cruz et al. 2013; Bordignon et al. 2015; Santos et al. 2015; but see Casatti et al. 2015). However, it should be mentioned that although catchment variables are important (Roth et al. 1996), in most cases local-scale variables accounted for the most variation in fish community structure (Lam-mert & Allan 1999; Wang et al. 2003; Diana et al. 2006; Johnson et al. 2007).

In our study, among the possible reasons for the lack of effect of catchment-scale variables on stream fish structure could be (1) weak associations between catchment-scale and local-scale features that are affecting stream fish communities (Heino et al. 2008), (2) greater influence of past land cover on the present-day fish community structure than current land cover (Harding et al. 1998) due to stream fish communities crossing the threshold of response to catchment modification, suggesting that post-threshold communities display a weak response to additional agricultural intensification (Balmford 1996; Fitzpatrick et al. 2001), or (3) the low variability in catchment variables (e.g. homogeneous landscape) is not able to overcome the impact of local-scale variables (Heino et al. 2007; Casatti et al. 2015).

Despite the significant effect of the environment on the stream fish community structure, its contribution was relatively low (<20% of explained variation). This could be related to the occurrence of a considerable number of less abundant and rare fish species in the data set. According to Heino and Mykrä (2008), the more prevalent these species are, the greater the amount of community structure that will not well-explained by environmental features. In addition, in communities with a high ratio of habitat generalist species, as in our study area (Casatti et al. 2009), environmental variations might not necessarily result in strong variations in local community structure (Heino 2013). Stream environments are characterized by recurrent disturbances in terms of flash floods (Heino & Mykrä 2008; Marques et al. 2013) and, in agricultural landscapes, by sporadic events of high pesticides concentration, increased water temperatures, and low oxygen concentrations (Hawkins et al. 2015). These random and spatially variable disturbances could also restrain the association between stream fishes and the environment, leading to important amounts of variation that are not accounted by environmental factors (Heino & Mykrä 2008; Heino et al. 2015).

Although spatially structured environment component could hamper the explanation of the relative importance of environmental and spatial control of community structure (Heino & Mykrä 2008), we found a weak effect of the pure spatial fraction (i.e. network distance between sites) on the stream fish community structure. This supports our hypothesis that spatial structure should be weak, as dispersal limitation will not be important at this spatial extent (i.e. within a drainage basin; Heino & Mykrä 2008; Heino et al. 2015). Weak spatial structure coupled with the absence of strong environmental influence on the community structure could suggest that the fish communities at studied sites were already homogenized. This would be related to the fact that the most sensitive species to changes in environmental features had already been extinct within the system (Brook et al. 2003). However, it should be noted that dispersal is an important determinant of stream fish population and community structure (Skalski & Gilliam 2000), and even though it is expected that it would
not influence the community structure at the spatial extension evaluated by us, data about dispersal rates and distances for majority of freshwater organisms are lacking almost completely (Bohonak & Jenkins 2003; Heino & Mykrä 2008). This obstructs the use of more appropriate divisions according with different dispersal abilities of species (Heino & Mykrä 2008). In addition, the influence of barriers built massively in agricultural landscapes (e.g. dams used by livestock; personal observation) on spatial structure is, as far as we know, still unknown. Future studies on dispersal in Neotropical stream fish will be fundamental to better understand the processes mediated by space, as studies for temperate stream fish suggest that variability in phenotypic traits is related to variability in movement behavior (Skalski & Gilliam 2000) and may explain, for example, cases of species invasions (Shigesada et al. 1995; Skalski & Gilliam 2000).

Ecological applications

The assessment of environmental features from a hierarchical perspective offers a suitable framework for integrating the multiple scales over which ecological processes organize stream fish communities (Angermeier & Winston 1998), allows identification of appropriate spatial scale(s) at which environmental features impact the freshwater systems (Feld 2013), and gives essential information to direct funds in stream and catchment restoration (Sheldon et al. 2012; Feld 2013). Results of this study reveal, in an unexpected way, that stream fish community structure in a tropical agricultural landscape was affected mainly by features operating at a single spatial scale (i.e. local scale). Therefore, local-scale variables, such as depth, proportion of grasses, proportion of pools, water temperature, width, and proportion of unconsolidated substrate could be manipulated for stream restoration purposes.

Despite these findings, stream restoration is a major challenge for ecologists. For example, if the intention of restoration is the ecological integrity recovery, the enhancement of physical stream characteristics alone (i.e. channel reconfiguration and/or improving in-stream structural complexity) should not be the main guide for restoration efforts (Palmer et al. 2010). It is important to consider that other factors control stream biodiversity (e.g. water quality, disturbance regime, regional species pools, differences in species dispersal capacity, degraded hydrological regimes; Palmer et al. 2010 and references therein). Obviously, restoration at the catchment-scale is more effective in improving the ecological integrity of streams (Lake et al. 2007; Palmer et al. 2010), and therefore should be the first action to be considered. However, in areas like those studied herein, it is unlikely that agricultural lands would be replaced by forests in order to improve ecological integrity. Therefore, among other strategies, restoration of riparian forests plus manipulation of some local features may mitigate the impacts of anthropogenic activities in streams (Saunders et al. 2002; Palmer et al. 2010; Sweeney & Newbold 2014).

Acknowledgments

We thank to J.O. Zeni, M.C. Molina, E. Manzano and our colleagues from the Ichthyology Laboratory for their help during laboratory and fieldwork; IBILCE-UNESP for facilities; IBAMA for the collecting license (5580-1/11435); landowners for permission to conduct research on their properties; Frederico T.S. Miranda and Márcia S. Morinaga for help with land cover data; and Francisco Langeani and Fernando R. Carvalho for help with fish identification. We also appreciate the critical reading and suggestions from the two anonymous reviewers.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the FAPESP [grant number 2012/05983-0]; CNPq/TWAS [grant number 190199/2011-3]; CNPq [grant number 301755/2013-2].
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Lilian Casatti is a professor at the São Paulo State University in Brazil. Her research focus is the impact of human activities on streams. She is also interested in how to bring this information to the non-scientific public.

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References

Altermatt F. 2013. Diversity in riverine metacommunities: a network perspective. Aquatic Ecol. 47:365–377.

Angermeier PL, Karr JR. 1983. Fish communities along environmental gradients in a system of tropical streams. Environ Biol Fishes. 9:117–135.

Angermeier PL, Winston MR. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. Ecology. 79:911–927.

Balmford A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. Trends Ecol Evol. 11:193–196.

Beyer HL. 2004. Hawth’s analysis tools for ArcGIS. Available from: http://www.spotialecology.com/htools

Blanchet FG, Legendre P, Borcard D. 2008. Forward selection of explanatory variables. Ecology. 89:2623–2632.

Bohonak AJ, Jenkins DG. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett. 6:783–796.

Borcard D, Gillet F, Legendre P. 2011. Numerical ecology with R. New York (NY): Springer-Verlag

Bordignon CR, Casatti L, Pinto M. 2015. Fish complementarity is associated to forests in Amazonian streams. Neotrop Ichthyol. 13:579–590.

Brook BW, Sudhi NS, Ng PKL. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature. 424:420–423.

Brown BL, Swan CM. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. J Anim Ecol. 79:571–580.

Carvalho RA, Tejerina-Garro FL. 2015. Environmental and spatial processes: what controls the functional structure of fish assemblages in tropical rivers and headwater streams? Ecol Freshw Fish. 24:317–328.

Casatti L, Ferreira CP, Carvalho FR. 2009. Grass-dominated stream sites exhibit low fish species diversity and dominance by guppies: an assessment of two tropical pasture river basins. Hydrobiologia. 632:273–283.

Casatti L, Teresa FB, Zeni JO, Ribeiro MD, Brejão GL, Ceneviva-Bastos M. 2015. More of the same: high functional redundancy in stream fish assemblages from tropical agroecosystems. Environ Manage. 55:1300–1314. [CEPAGRI] Centro de Pesquisas Meteorológicas e Climáticas Aplicadas à Agricultura. 2017. Clima dos municípios paulistas: São José do Rio Preto [Climate of the municipalities of the State of São Paulo: São José do Rio Preto]. Available from: http://www.cpa.unicamp.br/outras-informacoes/clima_muni_559.html

Cianfrani CM, Sullivan SM, Hession WC, Watzin MC. 2012. A multitaxonomic approach to understanding local versus watershed-scale influences on stream biota in the Lake Champlain basin, Vermont, USA. River Res Appl. 28:973–988.

Cruz BB, Miranda LE, Getra M. 2013. Links between riparian landcover, instream environment and fish assemblages in headwater streams of south-eastern Brazil. Ecol Freshw Fish. 22:607–616.

Diana M, Allan JD, Infante D. 2006. The influence of physical habitat and land use on stream fish assemblages in southeastern Michigan. Am Fish Soc Symp. 48:359—374.

Dembkowski DJ, Miranda LE. 2014. Environmental variables measured at multiple spatial scales exert uneven influence on fish assemblages of floodplain lakes. Hydrobiologia. 721:129–144.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marqués JR, Gruber B, Lafourcade B, Leitão P, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 36:27–46.

Feld CK. 2013. Response of three lotic assemblages to riparian and catchment-scale land use: implications for designing catchment monitoring programmes. Freshw Biol. 58:715–729.

Fitzpatrick FA, Scudder BC, Lenz BN, Sullivan DJ. 2001. Effects of multi-scale environmental characteristics on agricultural stream biota in Eastern Wisconsin. J Am Water Resour Assoc. 37:1489–1507.

Freeman MC, Pringle CM, Jackson CR. 2007. Hydrologic connectivity and the contributions of stream headwaters to ecological integrity at regional scales. J Am Water Resour Assoc. 43:5–14.
Frisell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ Manage. 10:199–214.

Gerhard P, Verda de LM. 2016. Stream fish diversity in an agricultural landscape of southeastern Brazil. In: Gheler-Costa C, Lyra-Jorge MC, Verda de LM, editors. Biodiversity in agricultural landscapes of southeastern Brazil. Berlin: De Gruyter Open; p. 206–224.

Géry J. 1969. The fresh-water fishes of South America. In: Fitkau EJ, editor. Biogeography and ecology in South America. The Hague: Dr. W. Junk; p. 828–848.

Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EBD. 1998. Stream biodiversity: the ghost of land use past. Proc Natl Acad Sci USA. 95:14843–14847.

Heino J. 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biol Rev Camb Philos Soc. 88:166–178.

Heino J, Mykrä H. 2008. Control of stream insect assemblages: roles of spatial configuration and local environmental factors. Ecol Entomol. 33:614–622.

Heino J, Mykrä H, Kotanen J, Muotka T. 2007. Ecological filters and variability in stream macroinvertebrate communities: do taxonomic and functional structure follow the same path? Ecography, 30:217–230.

Heino J, Mykrä H, Kotanen J. 2008. Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. Landsc Ecol. 23:417–426.

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw Biol. 60:845–869.

Hawkins CP, Mykrä H, Oksanen J, Vander Laan JJ. 2015. Environmental disturbance can increase beta diversity of stream macroinvertebrate assemblages. Glob Ecol Biogeogr. 24:483–494.

Hynes HBN. 1975. The stream and its valley. Verh Int Ver Theor Ang Limnol. 19:1.

Johnson RK, Furse MT, Hering D, Sandin L. 2007. Ecological relationships between stream communities and spatial scale: implications for designing catchment-level monitoring programmes. Freshw Biol. 52:939–958.

Lake PS, Bond N, Reich P. 2007. Linking ecological theory with stream restoration. Freshw Biol. 52:597–615.

Lammert M, Allan JD. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ Manage. 23:257–270.

Laurance WF, Sayer J, Cassman KG. 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol Evol. 29:107–116.

Legendre P, Gallagher ED. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia. 129:271–280.

Legendre P, Legendre LFI. 2012. Numerical ecology. 3rd ed. Amsterdam: Elsevier.

Legendre P, Borcard D, Blanchet FG, Dray S. 2013. PCNM: MEM spatial eigenfunction and principal coordinate analyses. R package version 2.1-2/r109. Available from: http://R-Forge.R-project.org/projects/sedar/

Legendre P, Oksanen J, ter Braak CJF. 2011. Testing the significance of canonical axes in redundancy analysis. Methods Ecol Evol. 2:269–277.

Lehner B, Liermann CR, Revenga C, Vörösmarty C, Feyen L, Birkett P, Döll P, Endeman M, Frenken K, Magome J, et al. 2011. High-resolution mapping of the world’s reservoirs and dams for sustainable river-flow management. Methods Ecol Evol. 9:494–502.

Marques LC, Ceneviva-Bastos M, Casatti L. 2013. Progressive recovery of a tropical deforested stream community after a flash flood. Acta Limnol Bras. 25:111–123.

Montaña CG, Winemiller KO. 2010. Local-scale habitat influences morphological diversity of species assemblages of cichlid fishes in a tropical floodplain river. Ecol Freshw Fish. 19:216–227.

Nalon MA, Matto ISA, Franco GADC. 2008. Diretrizes para a conservação e restauração da biodiversidade no Estado de São Paulo [Guidelines for the conservation and restoration of biodiversity in the State of São Paulo]. São Paulo: Instituto de Botânica. Chapter 2, Meio físico e aspectos da fragmentação da vegetação [Physical environment and aspects of fragmentation of vegetation]; p. 14–21.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens HH, Wagner H. 2015. Vegan: community ecology package. Available from: https://cran.r-project.org/web/packages/vegan/index.html

Palmer MA, Menninger HL, Bernhard E. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshw Biol. 55:205–222.

R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available from: http://www.R-project.org/

Rahel FJ. 2002. Homogenization of freshwater faunas. Annu Rev Ecol Syst. 33:291–315.
Roth NE, Allan JD, Erickson DL. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landsc Ecol. 11:141–156.

Rudorff BFT, Aguiar DA, Silva WF, Sugawara LM, Adami M, Moreira MA. 2010. Studies on the rapid expansion of sugarcane for ethanol production in São Paulo State (Brazil) using Landsat data. Remote Sens. 2:1057–1076.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, et al. 2008. Global biodiversity scenarios for the year 2100. Science. 287:1770–1774.

Santos FB, Ferreira FC, Esteves KE. 2015. Assessing the importance of the riparian zone for stream fish communities in a sugarcane dominated landscape (Piracicaba River Basin, southeast Brazil). Environ Biol Fishes. 98:1895–1912.

Saunders DL, Meeuwig JJ, Vincent ACJ. 2002. Freshwater protected areas: strategies for conservation. Conserv Biol. 16:30–41.

Schlosser IJ. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecol Monogr. 52:395–414.

Sheldon AL. 1968. Species diversity and longitudinal succession in stream fishes. Ecology. 49:193–198.

Sheldon F, Peterson EE, Boone EI, Sippel S, Bunn SE, Harch BD. 2012. Identifying the spatial scale of land use that most strongly influences overall river ecosystem health score. Ecol Appl. 22:2188–2203.

Shigesada N, Kawasaki K, Takeda Y. 1995. Modeling stratified diffusion in biological invasions. Am Nat. 146:229–251.

Silva AM, Casatti L, Álvares CA, Leite AM, Martinelli LA, Durrant SF. 2007. Soil loss risk and habitat quality in streams of a mesoscale river basin. Sci Agric. 64:336–343.

Skalski GT, Gilliam JF. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology. 81:1685–1700.

Strayer R, Beighley E, Thompson LC, Brooks S, Nilsson C, Pinay G, Naiman RJ. 2003. Effects of land cover on stream ecosystems: roles of empirical models and scaling issues. Ecosystems. 6:407–423.

Sweeney BW, Newbold JD. 2014. Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: a literature review. J Am Water Resour Assoc. 50:560–584.

Victor MAM, Cavalli AC, Guillaumeon JR, Serra RF. 2005. Cem anos de devastação - Revisitada 30 anos depois [A hundred years of devastation: revisited 30 years later]. Brasília: Ministério do Meio Ambiente.

Wang L, Lyons J, Rasmussen P, Seelbach P, Simon T, Wang L, Kanelh P, Baker E, Niemela S, Stewart PM. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern lakes and forest ecoregion, U.S.A. Can J Fish Aquat Sci. 60:491–505.

Warton DI, Hui FKC. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology. 92:3–10.

### Appendices

#### Table A1. Description of land cover classes.

| Land cover class       | Description                                                                 |
|------------------------|-----------------------------------------------------------------------------|
| Native forest          | Areas occupied by the different native forest found in the study area (i.e. savanna and semi-deciduous seasonal forest). |
| Herbaceous and shrub vegetation | Areas occupied by herbaceous and shrub vegetation, which also included species of cattail (Typha spp.). |
| Pasture                | Areas used for intensive and extensive livestock, also including areas covered by native grasses but to a lesser extent. |
| Sugarcane              | Areas covered with sugarcane culture (Saccharum spp.) or that showed evidences of being used for this culture. |
| Perennial culture      | Areas covered with perennial cultures (e.g. Citrus spp., Hevea spp., Coffea spp.). |
| Reforestation          | Included planted forests and restored areas with Eucalyptus spp. or Pinus spp. |
| Urban area             | Include towns and villages.                                                 |
| Other land cover       | It groups rural installations, temporary cultures, highways and exposed soil. |
Table A2. Predictor variables measured at the 43 sampling sites, Turvo-Grande and São José dos Dourados River basins at the northwest region of São Paulo State, south-eastern Brazil. Mean and standard deviation (SD) of each variable are also presented.

| Category                     | Variable                           | Unit                      | Transformation | Code | Mean ± SD |
|------------------------------|------------------------------------|---------------------------|----------------|------|-----------|
|                              |                                    |                           |                |      |           |
| **Local-scale variables**    |                                    |                           |                |      |           |
| Stream physical habitat      | Physical Habitat Index             | Absolute value            |                |      |           |
| condition                    | Mesohabitat                        | Pools                     | Proportion     | phi  | 87.56 ± 33.00 |
| Physicochemical descriptors  | Water temperature                 | °C                        | Square root    | pool | 0.20 ± 0.13 |
| Substratum                   | Unconsolidated substrate: clay, silt, and sand | Proportion | Logit       | us | 0.68 ± 0.21 |
| Stream morphology            | Mean width                         | m                         | Square root    | wid  | 1.74 ± 0.66 |
|                              | Standard deviation of width        | –                         | –              | widSD| 0.59 ± 0.25 |
|                              | Mean depth                         | m                         | Square root    | dep  | 0.20 ± 0.08 |
|                              | Mean water velocity                | m/s                       | Square root    | vel  | 0.14 ± 0.06 |
|                              | Standard deviation of water velocity| –                         | –              | velSD| 0.07 ± 0.05 |
| Marginal vegetation          | Grasses (mostly Brachiaria spp.)   | Proportion                | Logit          | gra  | 0.38 ± 0.27 |
|                              |                                    |                           |                |      |           |
| **Catchment-scale variables**|                                    |                           |                |      |           |
| Entire catchment             | Native forest                      | Proportion                | Logit          | Cfor | 0.09 ± 0.08 |
|                              | Pasture                            | Proportion                | Logit          | Cpas | 0.35 ± 0.30 |
|                              | Sugarcane                          | Proportion                | Logit          | Csug | 0.38 ± 0.34 |
|                              | Other land cover                   | Proportion                | Logit          | Coth | 0.18 ± 0.12 |
| Drainage network             | Native forest                      | Proportion                | Logit          | Nfor | 0.28 ± 0.23 |
|                              | Pasture                            | Proportion                | Logit          | Npas | 0.11 ± 0.08 |
|                              | Sugarcane                          | Proportion                | Logit          | Nsug | 0.01 ± 0.02 |
|                              | Other land cover                   | Proportion                | Logit          | Noth | 0.59 ± 0.25 |
| Local land cover             | Native forest                      | Proportion                | Logit          | Lfor | 0.25 ± 0.24 |
|                              | Pasture                            | Proportion                | Logit          | Lpas | 0.28 ± 0.28 |
|                              | Sugarcane                          | Proportion                | Logit          | Lsug | 0.18 ± 0.23 |
|                              | Other land cover                   | Proportion                | Logit          | Loth | 0.29 ± 0.23 |
| Network distance             | PCNM eigenvectors with positive spatial correlation | –                         | –              | Vi  | –         |

Table A3. Spearman’s correlation (rho) for catchment-scale features (see Table A2 for features codes). In bold, features with rho ≥ 0.7.

|       | Cfor | Cpas | Csug | Coth | Nfor | Npas | Nsug | Noth | Lfor | Lpas | Lsug |
|-------|------|------|------|------|------|------|------|------|------|------|------|
| Cpas  | -0.2 |      |      |      |      |      |      |      |      |      |      |
| Csug  | 0.1  | -0.9 |      |      |      |      |      |      |      |      |      |
| Coth  | 0.0  | 0.2  | -0.5 |      |      |      |      |      |      |      |      |
| Nfor  | 0.8  | -0.4 | 0.4  | -0.2 |      |      |      |      |      |      |      |
| Npas  | 0.0  | 0.6  | -0.5 | 0.1  | 0.0  |      |      |      |      |      |      |
| Nsug  | 0.0  | -0.2 | 0.4  | -0.2 | 0.3  | 0.1  |      |      |      |      |      |
| Noth  | -0.7 | 0.2  | -0.2 | 0.1  | -0.9 | -0.3 | -0.4 |      |      |      |      |
| Lfor  | 0.5  | -0.2 | 0.2  | -0.2 | 0.6  | 0.0  | 0.0  | 0.0  | -0.5 |      |      |
| Lpas  | -0.2 | 0.7  | -0.6 | 0.2  | -0.4 | 0.5  | -0.1 | 0.2  | -0.4 |      |      |
| Lsug  | 0.1  | -0.7 | 0.8  | -0.5 | 0.3  | -0.5 | 0.3  | -0.2 | 0.1  | -0.6 |      |
| Loth  | -0.2 | 0.1  | -0.2 | 0.3  | -0.5 | -0.1 | -0.1 | 0.4  | -0.6 | -0.1 | -0.3 |
Table A4. Fish species collected in the 43 stream reaches.

| Order and families | Species and authors | Codes |
|--------------------|---------------------|-------|
| Characiformes      |                     |       |
| Parodontidae       | Apareiodon affinis  | Apaaff|
|                    | (Steindachner 1879) |       |
|                    | Apareiodon piracicae| Apapir|
|                    | (Eigenmann 1907)    |       |
|                    | Parodon nasus       | Parnas|
|                    | Kner 1859           |       |
| Curimatidae        | Cyphocharax vanderi | Cypvan|
|                    | (Britski 1980)      |       |
| Crenuchidae        | Characidium gomesi  | Chagom|
|                    | Travassos 1956      |       |
| Characidae         | Characidium zebra   | Chazeb|
|                    | Eigenmann 1909      |       |
|                    |                     |       |
| Aythyaax altiparanae| Garutti & Britski  | Astalt|
| Aythyanax fasciatus| Cuvier 1819         | Astfas|
| Aythyanax paranae  | Eigenmann 1914      | Astpar|
| Hasemaniana sp.    |                     | Hassp |
| Hemigrammus marginatus| Ellis 1911       | Hemmar|
| Hyphessobrycon eques| (Steindachner 1882)| Hypequ|
| Knodus moenhausii  | Eigenmann & Kennedy | Knomoe|
|                    | (1903)              |       |
| Moenhausia sanctaeilomenae| (Steindachner 1907)| Moesan|
| Oligosarcus pintoi | Amaral Campos 1945  | Olipin|
| Piaforma argentea  | Reinhardt 1867      | Piaarg|
| Planaltina britski| Menezes, Weitzman & Burns 2003 | Plabri|
| Serrapinnus heterodon| (Eigenmann 1915)  | Serhet|
| Serrapinnus notomelas| (Eigenmann 1915)   | Sernot|
| Acestrorhynchidae  |                     |       |
| Acesthorhynchus lacustris| (Lütken 1875)  | Acelac|
| Erythrinidae       |                     |       |
| Erythrinus erythrinus| (Bloch & Schneider| Ereyer|
|                    | 1801)               |       |
| Hoplias malabaricus| (Bloch 1794)        | Hopmal|
| Lebiasinidae       |                     |       |
| Pyrrhulina australis| Eigenmann & Kennedy| Pyraus|
|                    | 1903                |       |
| Siluriformes       |                     |       |
| Callichthyidae     |                     |       |
| Aspidoras fuscoguttatus| Nijssen & Isbrücker| Aspfus|
| Callichthus callichthis| Linnaeus 1758    | Calcal|
| Corydoras aeneus   | Gill 1858           | Coraen|
| Hoplosternum litorale| Hancock 1828      | Hoplit|
| Leptoplosternum pectorale| Boulenger 1895| Lepppec|
| Megalechis thoracata| Valenciennes 1840  | Megtho|
| Loricariidae       |                     |       |
| Hisonotus francirochai| (Ihering 1928)   | Hisfra|
| Hypostomus ancirostoides| (Ihering 1911)| Hypanc|
| Hypostomus cf. nigrmaculatus| (Schubart 1964)| Hyppnig|
| Pterygoplichthys ambrosettii| (Holmberg 1893)| Pteamb|
| Pseudopimelodidae  |                     |       |
| Pseudopimelodus manguaris| Valenciennes 1835| Pseman|
| Heptapteridae       |                     |       |
| Imparfinis cf. schubarti| (Gomes 1956) | Impsch|
| Pimelodella cf. avanhandavae| Eigenmann 1917| Pimava|
| Rhambdia quelen | (Quoy & Gaimard 1824) | Rhaque|
| Gymnotiformes      |                     |       |
| Gymnotidae         |                     |       |
| Gymnotus paraguensis| Albert & Crampton| Gympar|
| Gymnotus cf. sylvius| Albert & Fernandes-Matioli 1999 | Gmysyl|
| Sternopygidae      |                     |       |
| Eigenmannia trilineata| López & Castello| Eigtri|
| Cyprinodontiformes |                     |       |
| Rivulidae          |                     |       |
| Melanorivulus pictus| (Costa 1989) | Melpic|

(continued)
Table A4. (Continued)

| Order and families, species and authors | Codes |
|----------------------------------------|-------|
| Poeciliidae                            |       |
| Phalloceros harpagos Lucinda 2008      | Phahar|
| Poecilia reticulato Peters 1859        | Poeret|
| Synbranchiformes                       |       |
| Synbranchidae                          |       |
| Synbranchus marmoratus Bloch 1795      | Synmar|
| Perciformes                            |       |
| Cichlidae                              |       |
| Cichlasoma paranaense Kullander 1983   | Cicpar|
| Crenicichla britskii Kullander 1982    | Crebri|
| Crenicichla haroldai Luengo & Britski 1974 | Crehar|
| Geophagus brasiliensis (Quoy & Gaimard 1824) | Geobra|
| Laetacara araguaiae Ottoni & Costa 2009 | Laeara|
| Oreochromis niloticus (Linnaeus 1758)   | Orenil|
| Satanoperca pappaterra (Heckel 1840)   | Satpap|

Table A5. Results of forward selection procedure for stream fish community structure and each set of predictor variables (i.e. local, catchment, spatial). For variable codes, see Table A2. In bold \( p < 0.05 \).

| Predictor variables | \( R^2_{\text{Adj}} \) | \( p \)        | Selected variables |
|---------------------|-----------------|---------------|--------------------|
| Local               | 0.19            | \(<0.001\)    | dep, gra, pool, tem, wid, usu |
| Catchment           | 0.05            | 0.035         | Csug               |
| Spatial (PCNM)      | 0.09            | 0.001         | PCNM1, PCNM3, PCNM2 |