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The importance of metacommunity processes for long-term turnover of riffle-dwelling fish assemblages depends on spatial position within dendritic network

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Abstract: Spatial position within dendritic network may determine environmental filters and connectivity with source of immigrants, influencing species composition and variation in metacommunities. We investigated how long-term turnover of riffle-dwelling fish assemblages is affected by niche- and dispersal-related processes. Multiple linear model selection resulted in four variables important to explain assemblage turnover: (i) habitat change, (ii) channel slope, (iii) dlink - a proxy for connectivity - and (iv) catchment area. These four variables were related to turnover in species abundance, while turnover in species occurrence was only related to habitat change. Models generated for each species indicated they were differently affected by niche- and dispersal-related processes. Our findings provide support for the hypothesis that metacommunity processes affecting temporal turnover of stream fish communities are dependent on the spatial position within dendritic network, but also vary among species. Our study has implications for sampling design in monitoring programs, as the degree of dissimilarities in fish communities depends not only on local habitat change, but on spatial position within the drainage network and on species particularities.

Keywords: stream, habitat change, channel slope, connectivity, dispersal

Introduction

Long-term variation in species occurrence and population density is a central theme in ecology and allows understanding and predicting how communities will behave facing particular environmental conditions (Magurran et al. 2010). Changes in species occurrence and abundance between years have been widely studied in stream ecosystems and linked mainly to variations in environmental conditions (e.g., Mykrä et al. 2011; Matthews et al. 1988, 2013). This seems to be of particular importance in stream ecosystems, as environmental conditions may be highly variable in time due to slow and continuous processes (erosion, deposition) and to episodic disturbances caused by drought and spates that lead to channel reconfiguration (e.g., Matthews et al. 1988; Grossman et al. 1998; Matthews and Marsh-Matthews 2006). However, less attention has been given to the fact that flow regime and the severity of hydrological disturbances may depend on the spatial position within a drainage network (the “Process Domain Concept”, Montgomery 1999) and that its spatial structure affects the dispersal of aquatic organisms (Hitt and Angermeier 2008; Altermatt 2013). According to the Process Domain Concept, “spatial variability in geomorphic processes governs temporal patterns of disturbances that influence ecosystem structure and dynamics”.

The importance of metacommunity theory to explain patterns and processes of freshwater assemblages in dendritic networks has received increasing attention (Altermatt 2013; Heino 2013; Heino et al. 2015). Metacommunity theory posits that local assemblages are determined by i) environmental and biotic (e.g. competition) filtering, operating at different spatial scales, ii) dispersal limitation dependent on the spatial connectivity and on dispersal abilities of species, and iii) neutral processes (Leibold et al. 2004; Heino et al. 2015). In this sense, local assemblages are recognized as open systems that are dependent on other local

communities. For instance, dispersal may influence population size and preclude local species extinctions in sub-optimal or sink patches (Leibold et al. 2004).

Metacommunity theory has been more broadly used to explain spatial patterns in species occurrence and in population abundance of local assemblages, in both terrestrial (Schmidt et al. 2008; Driscoll and Lindenmayer 2009; Myers et al. 2013) and dendritic aquatic networks (e.g. Thompson and Townsend 2006; Perkin and Gido 2012; Altermatt 2013). However, it can also address processes affecting the temporal dynamics of local assemblages (Leibold et al. 2004). For instance, metacommunity theory can be evoked to predict which communities will be more or less stable between years and over mid- to long-term periods (i.e., more than 10 years). Communities well connected in a network should receive many migrants that buffer against demographic stochasticity and allow fast recovery from disturbance events.

The hydrological regime of riverine ecosystems, including flood and drought disturbances, is probably the most important factor driving temporal variation in stream habitats and faunal composition (Poff and Ward 1989; Grossman et al. 1990; Matthews et al. 2013). Variation in flow regime can affect immigration and extinction rates of stream fishes (Taylor and Warren 2001). Due to the spatially structured geomorphologic characteristics of river basins, upstream segments of mountainous streams are expected to have steep slopes, entrenched and straight channels, to retain large substrates and to experience high stream flow energy (Rosgen 1994; Montgomery 1999; Rice et al. 2001). Also, steep channels will respond more quickly to rainfall and will produce higher and shorter peak discharges compared to streams with gentle slopes in the lower section of watersheds (Resh et al. 1988; Gordon et al. 2004; Nippgen et al. 2011). Therefore, fish assemblages in stream segments with steep channels will be subjected to strong environmental filtering owing to continuous high flow energy and to

severe hydrological disturbances caused by spates, which may influence temporal turnover of fish assemblages (changes in species occurrence and population abundance).

A second important aspect associated with the dendritic structure of stream networks is that the faunal movement is highly dependent on the connectivity between branches of the network and on how the network structure is spatially organized (Benda et al. 2004; Altermatt 2013). In contrast to dispersal in terrestrial landscapes, fish and other aquatic species are constrained to disperse through branches and confluences (or edges and vertices) of the stream network (Fagan 2002; Altermatt 2013; Altermatt et al. 2013). Two particular features of such dendritic structure are that small streams can be connected to rivers of different sizes depending on their location within the basin (central or peripheral), and within a given stream there is a longitudinal distance gradient from the connection to the mainstem channel (Fausch et al. 2002; Campbell-Grant et al. 2007). The influence of the dendritic structure of drainage networks on spatial variation in occurrence and abundance of fish species has been demonstrated (Osborne and Wiley 1992; Grenouillet et al. 2004; Thornbrugh and Gido 2010). A likely mechanism for such influence is that large rivers with increased habitat capacity act as sources of migrants, altering local richness and community structure of tributaries (Osborne and Wiley 1992). Accordingly, the distance of a stream segment from its downstream confluence with a large stream has been shown to be important for local composition of stream communities (Thornbrugh and Gido 2010). Also, centrally located stream segments are more connected to other habitat patches and to other fish populations distributed across the drainage network. Thus, isolated stream habitats in the periphery of the basin are expected to receive fewer migrants compared to more connected stream habitats in the center of the basin (Taylor 1997). Even if the extinction rates are similar between peripheral and central sites, the populations in the latter are

more likely to be ‘rescued’ from local extinction by high immigration rates. Additionally, immigration rates have been demonstrated to increase with stream size (Taylor and Warren 2001). This effect may be dependent on the combined effect of patch size and dendritic connectivity of drainage networks, which increase simultaneously in more centrally located sites (Carrara et al. 2014). Therefore, we should expect that distance from sources of colonists may lead to differences in temporal turnover of assemblages regarding species occurrence and abundance.

Considering the influences that niche- and dispersal-related processes may have on fish assemblages in dendritic networks, we investigated how long-term turnover of riffle-dwelling fish assemblages is affected by habitat change, channel slope, and spatial position within drainage network. We used habitat and slope variables as proxies for niche-related processes and spatial position variables as proxies for dispersal-related processes. We hypothesized that (1) large changes in instream physical habitat structure (i.e. changes in environmental conditions) should lead to high temporal turnover, (2) high-gradient channels should lead to high temporal turnover due to severe stochastic flood events, and (3) proximity to a large stream should lead to low temporal turnover of riffle-dwelling fish assemblages due to a high influx of downstream immigrants that dampens disturbance effects. We addressed these hypotheses using 22 stream fish assemblages sampled 13 years apart in a subtropical catchment.

Methods

Study area

This study was conducted in the Maquiné river basin (total area ca. 550 km²), an Atlantic coastal drainage located in southern Brazil between longitudes 50°05’W and 51°21’W and

latitudes 29°20'S and 29°50'S (Fig. 1). Headwaters of the river Maquiné are located on a basalt plateau (ca. 1000 m above sea level) and its final segment flows into lake Quadros (ca. 10 m above sea level). Regional climate is humid subtropical (Moreno 1961) with mean temperatures higher than 22°C in the warmest month and between 13°C and 15°C in the coldest month (Hasenack and Ferraro 1989). There is no typical dry season and annual rainfall is high (1400 mm to 1800 mm) (Hasenack and Ferraro 1989). Rain storms are common over the year (mainly in spring and summer) resulting in high-energy flash floods, which physically affect stream habitats (Becker et al. 2008). The pronounced elevation profile of the Maquiné basin and the steep and entrenched stream channels (mainly in its upper and intermediate segments), contribute to episodes of harsh hydrological conditions for the fish fauna.

Sampling sites

Fish sampling was conducted in 1999 and 2012. There were at least three catastrophic flood events in the period caused by concentrated rainfall that physically affected stream habitats: 206 mm in three days (2001), 172 mm in two days (2007) and 306 mm in three days (2008). There was more accumulated rainfall in one day in the 2008 event than in any other day between 1999 and 2012 period, exceeding the mean rainfall expected for an entire month (Appendix, Fig. A1). In fact, two of the authors (ASM, FGB) were able to visit the area immediately after the 2008 intense rains and observed a severe flood episode that caused profound channel reconfiguration in some of the stream segments, particularly those in low valley areas (< 250 m). Average monthly rainfall of the two sampling years were similar to each other (131 mm for 1999 and 123 mm for 2012) and to the average monthly rainfall of the entire 13 years sampling interval (1999 to 2012; mean = 145 mm; Appendix, Fig. A1).

Streams of the Maquiné basin are composed of riffle–pool sequences with clear and fast-flowing water and substrate composed mainly of pebbles, cobbles and boulders (Becker et al. 2008). We sampled riffle habitats with an average depth of 22 cm and average wetted width of 8.8 m (ranging from 4.0 m to 19.5 m). Catchment area of the sample sites ranged from 6.4 km² to 165.9 km², average 38.1 km² (Appendix, Tables A1, A2). Sampling sites were restricted to lower valley sections (< 250 m of elevation) and to the tributaries of the main river (Maquiné). In each stream, we selected riffle sites according to accessibility (roads) and to distance between sites (a minimum of 1 km network distance between sites).

Fish sampling

We sampled 22 riffle sites (Fig. 1) that differed in channel steepness and distance from the mainstem channel. At each site, we employed kick-sampling to capture fish along a 40-m stream riffle segment using a rectangular dip-net (80 x 40 x 40 cm with 4 mm mesh), sampling all the flowing-water micro-habitats by disturbing stream bottom. A benthic-sampler (Fisher 1987) similar to the kick-sampling procedure we used has been shown to be reliable for obtaining quantitative samples of small benthic fishes in riffle habitats. In addition, we observed that kick-sampling is efficient (compared to trawl-net, gill-net and electrofishing) for capturing fish species in riffle habitats of the study area, particularly when the focus is on riffle-dwelling specialists such as benthic species (e.g., most of loricariids; R. B. Dala-Corte and F. G. Becker, personal observation). For instance, we noted that several shocked armored catfish (loricariids) individuals get stuck among bottom rocks because of their benthic, cryptic habit and body morphology, reducing their catchability in comparison to kick-sampling (R.B. Dala-Corte, personal observation). Indeed, Champeau et al. (2009) reported that armored catfish species

were less vulnerable to electrofishing gear and may be underrepresented in electrofishing samples. Thus, although electrofishing may be more efficient than kick-sampling to sample the whole fish community, kick-sampling should be as good as electrofishing for the benthic riffle fishes in the study region. Most importantly, however, is that any potential sampling bias introduced by the chosen sampling method was standardized between the two sampling periods, as we used precisely the same sampling protocol and sampling effort.

We sampled 40-m long riffle segments because a previous assessment has demonstrated that the total number of riffle species does not increase substantially when more than 40 m are sampled (F. G. Becker, unpublished data). We were able to catch most of the species that one can find in riffles of the Maquiné river basin (25 out of 27 species) according to a previous extensive sampling effort performed throughout the whole basin (Becker 2002). We sampled each site once in the spring–summer of 1999 and once in the spring–summer of 2012. In both years, we captured fishes during low-flow periods and at least one week after rainfall events. Thus, fish catchability was unlikely to be affected by discharge variability between samples. In each site, we employed the same sampling effort in the two sampling years. Sampling performed in 2012 was supervised by the author who sampled the sites in 1999 (FGB). Most South American freshwater fishes usually live up to 5–6 years (Dei Tos et al. 2010) and, therefore, a 13-year period should be enough for at least 1 to 2 full replacements of all individuals in the population.

The fish species pool of the Maquiné basin is well known, although a few species are still not formally described (Malabarba et al. 2013), allowing us to identify individuals *in situ* during field work. Only two of the caught species have not been formally described to date (*Heptapterus* sp. and *Trichomycterus* sp.), but they were readily identifiable during field work

and thus included in the analyses. We returned all the sampled fishes to the stream site immediately after each sampling in 2012.

In order to reduce noise in statistical analyses, we removed from the data matrix those species for which kick-sampling is not an efficient method and also those species typical of other habitats (e.g. pools or stream shore aquatic vegetation), or which were only accidentally caught. After these criteria, we kept 14 species in the data matrix out of the total of 25 species captured by kick-sampling. Therefore, this study focused on benthic species that are typically found in riffle habitats. Removal of these species was based on previous studies in streams of the same basin, including electrofishing, seining and gill-nets (Becker 2002; Vogel 2012) and underwater observation (FGB and RBD, personal observation). Out of the 11 low-abundant species caught with kick-sampling and that were removed from analyses, five were among the most abundant species sampled using electrofishing (*Rhamdella zelimai*, *Crenicichla maculata*, *Astyanax laticeps*, *Astyanax douradilho*, *Rhamdia quelen*) and three were among the most abundant species caught with seine nets (*Odontostoechus lethostigmus*, *Hyphessobrycon luetkenii*, *Deuterodon stigmaturus*). These are all nektonic (*A. laticeps*, *A. douradilho*, *O. lethostigmus*, *H. luetkenii*, *D. stigmaturus*) or nektobenthic (*C. maculata*, *R. zelimai*, *R. quelen*) species. The other three species removed (*Mimagoniates rheocharis*, *Microglanis cibela*, *Phallocceros caudimaculatus*) are typical of other habitats, such as lateral backwater channels and vegetated slow water pools, and are not usually caught in riffles (Menezes and Weitzman 2009; Malabarba et al. 2013).

Local habitat variables and habitat change

In 1999 and 2012 we measured local habitat variables at five cross sections perpendicular to stream flow, and placed every 10 m along each 40-m stream segment where fish were sampled. We measured bankfull and wetted width, and depth at three equidistant points in each transect. Substrate size composition and variation were quantified by visually estimating the percent cover of five size classes of substrate at the same locations where we measured depths: 1) < 2 cm; 2) 2–7 cm, 3) 7–25 cm, 4) 25–50 cm, 5) > 50 cm. Percent cover corresponding to each substrate size were visually estimated in the following classes: 1) 1–25%; 2) 25–50%; 3) 50–75%; 4) > 75%. We used these measures to generate 13 habitat variables per site: 1–4) mean and coefficient of variation of bankfull and wetted width; 5) wetted:bankfull width ratio; 6–7) mean and coefficient of variation of water depth; 8–12) averages of percent cover for each of the five substrate classes and 13) Shannon–Wiener diversity index based on substrate classes. Differences in habitat variables between 1999 and 2012 were evaluated with paired *t*-tests, using sampled sites as blocking factor.

Based on the 13 aforementioned local habitat variables, we calculated habitat change between 1999 and 2012 for each sampling site using Euclidean distances on variables standardized by their ranges with the vegan package (Oksanen et al. 2013). Thus, habitat change was measured as the Euclidean distance based on how much a site differed in time regarding its habitat characteristics. All the statistical analyses were carried out using R Statistical Environment (R Development Core Team 2015).

Stream size, channel slope and network position

Eight variables regarding stream size, channel slope and spatial position within the drainage network were used to investigate temporal turnover of fish assemblage using species

occurrence and species abundance (Table A2). They were obtained from a digital elevation model (DEM) generated for the Maquiné basin using ArcGIS 10.2. The DEM was generated from topographic data and stream network lines available from a 1:50.000 scale digital spatial database (Hasenack and Weber 2010). These eight explanatory variables included one metric of stream size, four metrics of network position and three metrics of stream channel slope.

Stream size. To represent stream size we used square root transformed upstream catchment area, which is the cumulative catchment area (km^2) for each sampling site. Squared-transformed upstream catchment area is an indicator of discharge volume, distance from river source and channel width, and thus can be used as a stream size descriptor (Leopold & Maddock, 1953). Notice, however, that small streams can be located either in the periphery or in the center of the basin, so that catchment area does not express differences in linkage to large downstream streams (i.e., streams or rivers with greater water volume; Osborne and Wiley 1992); therefore we also calculated network position metrics for each site (see below).

Network position metrics. For each sampled stream segment we calculated the following network position metrics: downstream link magnitude, downstream order, betweenness centrality, and closeness centrality. Downstream link magnitude and downstream order of a given site are metrics that represent size of the stream after the next downstream confluence, as proposed by Osborne and Wiley (1992). We used downstream Shreve order to measure downstream link magnitude and downstream Strahler order to measure downstream order. Strahler order increases only after the confluence of two streams of same order (Strahler 1957), while Shreve order of a given network site is the sum of the number of all upstream tributaries (Shreve 1966). Consequently, stream sites with the same upstream catchment area can differ both in terms of downstream link and downstream order, depending on their spatial location

within a drainage network. For computing stream order, we follow Osborne and Wiley (1992) in not considering the most immediate downstream confluence when they were small (first order) tributaries, because of the potential influence of the larger downstream watercourse.

Betweenness centrality was measured as the number of shortest paths among all nodes that pass through a given node of interest (Newman 2010). Thus, central nodes in the drainage network will supposedly receive a high number of paths. Closeness centrality of a node was the inverse of the average length of the shortest paths from the focal node to all other nodes in the graph (Newman 2010). Betweenness centrality and closeness centrality were calculated with the igraph package (Csardi and Nepusz 2006). We used packages shp2graph (Lu 2014) and maptools (Bivand and Lewin-Koh 2014) to convert shapefiles of the drainage network and sites into igraph-class objects. Sample sites and confluences were defined as nodes. See Fig. A2 (Appendix) for a schematic representation of how network position metrics were calculated.

Stream channel slope (stream gradient). We assessed the three following stream slope metrics: average slope between upstream and downstream confluences of the sampled site, average slope in a 1-km segment upstream from the sampled site, and average local slope. The first two metrics were obtained in ArcGIS 10.2 using the slope tool in the Spatial Analyst toolbox. Average local slope was obtained from field measurements of channel steepness between the five cross sections along each sampling site (see sub-section Local habitat variables and habitat change). We included stream channel slope measured at three different spatial scales because there is still little information in the literature on which scale slope should be measured to represent the influence of hydrological process on local assemblages.

Assemblage turnover and model selection

We used multiple linear model selection to evaluate three hypotheses about the influence of habitat change, stream channel slope and within-network spatial position on temporal turnover of riffle-dwelling fish assemblages. The response variable used in the models was within-site dissimilarity of assemblages between 1999 and 2012 (temporal beta diversity). We tested models using two different dissimilarity measures: 1) Sorensen dissimilarity based on species presence and absence data, to assess turnover based on species occurrence data, and 2) Bray–Curtis dissimilarity, as an indicator of assemblage change based on log-transformed species abundance data.

We generated two linear regression models, one for Sorensen dissimilarity (species occurrence) and the other for Bray–Curtis dissimilarity (species abundance) as response variables, including eight variables regarding spatial position, plus 1999-2012 changes in instream physical habitat (Table A2). We then used Variance Inflation Factor (VIF) analysis (Fox and Monette 1992) to evaluate multicollinearity in the models. Variables with higher values of VIF were removed one-by-one from the models until all remaining variables presented VIF values lower than two (Fox and Monette 1992). From the nine initial explanatory variables, two presented VIF values higher than two (betweenness centrality and downstream order) and were removed from the models (Appendix, Table A3). The remaining seven explanatory variables were kept for model selection using the second-order Akaike Information Criterion (AICc).

Reduced models with all possible combinations of the seven explanatory variables and their respective AICc values were generated with the dredge function from the MuMIn package (Barton 2014). Reduced models were ranked according to AICc differences (delta) and Akaike weights. Models with higher Akaike weights may be interpreted as being more probable given

the data (Burnham and Anderson 2002). We also estimated the relative importance of each explanatory variable by summing Akaike weights (SW) of all models in which a given predictor was included (Burnham and Anderson 2002). The validity of using SW to quantify the relative importance of explanatory variables in models has been recently demonstrated (Giam & Olden 2015). By using SW, even if a variable was not included in the best models it can be detected as important if it appeared several times in the other models. Furthermore, coefficients of the explanatory variables were standardized (beta argument in the dredge function) to make them comparable (MuMIn package; Barton 2014). Only models with delta AICc values less than two were retained. Subsequently, we included interaction terms between the most important variables (based on their Akaike weights). For example, channel slope could interact with habitat change to drive fish assemblage turnover.

Ordination and overall species variation

To best interpret the turnover of fish assemblages, we performed a Principal Coordinate Analysis (PCoA) with Sorensen (species occurrence) and Bray–Curtis (species abundance) dissimilarities using the package vegan (Oksanen et al. 2013). Species spatial position in the ordinations was proportional to their correlation with PCoA axes. We performed PCoA with 1999 and 2012 assemblage composition data.

We calculated the overall relative frequency of occurrence in the sample sites (*fr%*) and the relative abundance of individuals (*ab%*) as mean values for each species caught in 1999 and 2012. Overall differences in *fr%* and *ab%* between years were calculated as the absolute differences in these values for each species.

Individual species models

In order to assess whether fish species differed in their response to environmental variables regarding turnover from 1999 to 2012, we fitted individual models for each species. These models were performed for each one of the species that occurred at least in 10 sampling sites in 1999 or 2012 samples (9 out of the 14 studied species), using as explanatory variables only the most important variables according to SW in the overall model selection performed for assemblage turnover (see details in the sub-section above “Assemblage turnover and model selection”). The response variable in each species model was the difference in species abundance regarding an expected relationship, which indicated how much a species changed from 1999 to 2012. This was performed by fitting a linear model between 1999 and 2012 abundances for each species and using its residuals as response variables, i.e. how much the species abundance differed from expected for all sites.

Correlation between habitat variables and assemblage turnover

Posterior to model selection, we carried out an exploratory analysis to find out which instream habitat variables used to quantify habitat change were the most important variables contributing to explain the relationship between habitat change and assemblage turnover. We generated all possible combinations of the 13 instream habitat variables (from one to 13 variables) to calculate site-level habitat change (Euclidean distance). Subsequently, we tested the Pearson’s correlation between habitat dissimilarities, calculated with different combinations of habitat variables with assemblage turnover, in order to find those combinations of variables that maximized the correlation between habitat change and assemblage turnover.

Results

Instream habitat and assemblage composition

Sampling sites changed from 1999 and 2012 regarding instream habitat characteristics (Table 1). Significant differences between years were observed in the coefficient of variation of depth, in the substrate diversity and in most of the categories of substrate size. Depth and was higher in 1999 samples, while stream width and cover percentage of larger categories of substrate size increased in 2012 (Table 1).

Fourteen species of riffle-dwelling fishes were sampled at the 22 sites in the Maquiné river basin. Mean species richness per site including 1999 and 2012 data was 8.5, ranging from 5 to 11 species. One species (*Hemiancistrus punctulatus*) was sampled only in 1999, but no species occurred exclusively in 2012. Siluriformes was the richest order, with 11 species, followed by Characiformes and Cyprinodontiformes, with two and one species respectively.

The most frequent and abundant species caught for both 1999 and 2012 samples were *Rineloricaria aequalicuspis*, *Pareiorhaphis nudulus*, *Pareiorhaphis hypselurus*, *Epactionotus bilineatus* and *Characidium pterostictum* (Table 2). Overall, species that most varied in frequency of occurrence from 1999 to 2012 were *Ancistrus multispinis*, *Diapoma itaimbe* and *P. nudulus*; whereas the species that most varied in their relative abundance from 1999 to 2012 were *E. bilineatus*, *D. itaimbe*, *R. aequalicuspis* and *C. pterostictum* (Table 2). All sampled species are resident and thus turnover of the studied assemblages was not influenced by diadromous species.

Turnover of fish assemblages

We found that habitat change, i.e., local habitat dissimilarity between years, was the single important variable in the models explaining turnover in species occurrence ($R^2 = 0.23$; standardized coefficient = 0.47; Tables 3 and 4). Habitat modifications over time increased turnover of species occurrence, indicating that streams that presented more changes in local environmental characteristics also showed more variation in fish species composition (Figs 2 and 3). Interaction terms of explanatory variables were not important to explain assemblage turnover (Table 4).

Nine best models ($\Delta \text{AICc} < 2$) were selected to explain temporal turnover of assemblage based on species abundance and they included different combinations of seven explanatory variables (Table 3). Four of these seven variables were the most important to explain turnover of species abundance, since they had relative importance values greater than 0.5 and the greatest standardized coefficients (Table 4). These variables were habitat change, slope between confluences, downstream link magnitude and catchment area (Figs 4 and 5). Thus, turnover in species abundance differed from turnover in species occurrence because in addition to local habitat change, turnover in assemblages using species abundance was also influenced by channel slope, downstream link magnitude and catchment area (Table 4). Turnover of species abundance was negatively related to channel slope and downstream link magnitude and positively related to catchment area and local habitat change (Table 4).

Differences were observed in the individual response of species to the four most important variables selected to overall assemblage turnover in abundance, namely: habitat change, slope between confluences, downstream link magnitude and catchment area (Table 5). Models generated separately for each species showed some species changed more from 1999 to 2012 due to the influence of habitat change (*E. bilineatus*), downstream link magnitude (*R.*

413 *aequalicuspis*, *P. nudulus* and *E. bilineatus*), slope between confluences (*P. nudulus*) or
414 catchment area (*D. itaimbe*) (Table 5).

415 Instream habitat variables that most contributed to maximize the correlation between
416 habitat change and assemblage turnover were the combination of coefficient of variation of
417 depth and mean bankfull width for turnover in species occurrence ($r = 0.74$; Appendix, Table
418 A4); and the combination of mean depth and cover percentage of substrate size class 25 to 50
419 cm for turnover in species abundance ($r = 0.52$; Appendix, Table A5).

420

421 Discussion

422 The hypothesis that high habitat change would lead to high turnover of communities was
423 supported. Turnover in species occurrence of riffle-dwelling fish assemblages in the 13-years
424 interval was explained only by temporal changes of habitat characteristics, with higher turnover
425 occurring at sites where physical habitat structure changed more. As well as species occurrence,
426 turnover in species abundance was explained by habitat change. Additionally, turnover in
427 species abundance was also explained by other factors that do not change with time in the
428 studied temporal scale, such as channel slope, downstream link magnitude (a proxy for
429 connectivity), and catchment area. Differences between 1999 and 2012 in channel size, depth
430 and substrate composition were the most important habitat changes explaining turnover in fish
431 assemblages. Processes of erosion and deposition, affected by regular flow and also by episodic
432 severe disturbances such as flash floods, may cause channel reconfiguration by moving substrate
433 and altering local habitat structure. Habitat change over the years may thus affect the set of
434 species capable of inhabiting the new prevailing conditions or resources, affecting population

abundance and species occurrence; a view consistent with species sorting of metacommunities (Leibold et al. 2004).

The reduced turnover of species abundance found in high-gradient sites is opposite to what we expected from our second hypothesis, which predicted that steep channels should lead to high temporal turnover due to severe stochastic flood events. Steeper channels tend to have higher flow energy and rapid response to rainfall, which will produce short and intense spates (Gordon et al. 2004; Nippgen et al. 2011). The implications for stream biota are high flow variability and harsh hydrological conditions (Resh et al. 1988), which may increase temporal variation in abundance of stream fishes (Ross et al. 1985). Moreover, flow variability has been demonstrated to be positively associated with extinction rates and negatively associated with immigration rates of stream fishes (Taylor and Warren 2001). Thus, it would be plausible to expect that stream segments with steep channels should show high assemblage changes. Despite this predicted positive relation between assemblage turnover and stream slope (as a proxy for habitat harshness), previous studies in aquatic ecosystems suggested that harsh environmental conditions may instead reduce community turnover (Chase 2007; 2010). For example, Chase (2007) found that communities in experimental ponds that experienced drought had much lower dissimilarity to each other than permanent ponds. Moreover, Chase (2010) found that community dissimilarity of producers and animals was much lower in ponds that experienced low productivity than ponds with medium or high productivities. Chase argues that niche selection may be the mechanism whereby species that could not tolerate such harsh environmental conditions were filtered out from the regional pool (Chase 2007; 2010). In contrast, in less restrictive environmental conditions, communities would be open to a large pool of colonists and thus would vary in species occurrence and abundance (Chase 2007; 2010).

Indeed, the dominant species we sampled at sites with steep channels, such as the suckermouth armored catfishes *Pareiorhaphis nudulus* and *P. hypselus*, are able to resist or avoid extremely high flows by seeking refuge among larger rocks and crevices at the stream bottom. Accordingly, we suggest that the negative relation between channel slope and turnover of species abundance was due to species sorting (Leibold et al. 2004), in which a restricted pool of species is able to maintain constant populations in hydrologically harsher (steeper slopes) environments. We highlight, however, that we measured slope in three different ways, but relationship with abundance turnover was important only when using slope between confluences, a large scale measure. Thus, the way that slope is measured may affect the detection of influence on assemblage turnover. Also we did not evaluate faunal composition immediately after hydrological disturbances, such as floods and droughts. Therefore, our results are valid for a time span of a decade and should not be extended to short periods in which assemblage turnover may be affected by episodic disturbance events (Rahel 1990).

We found that stream segments flowing directly into larger streams (i.e., sites with high downstream link magnitude) showed reduced temporal turnover in species abundance. As previously demonstrated by Osborne and Wiley (1992), downstream link magnitude was a useful proxy for size of downstream connection and connectivity within drainage network. This finding corroborates our third hypothesis, that proximity to larger streams should lead to low temporal turnover of riffle-dwelling fish assemblages, and also other studies reporting that communities living in stream segments close to confluences with main channels are more influenced by the pool of downstream immigrants (Osborne and Wiley 1992; Grenouillet et al. 2004; Thornbrugh and Gido 2010; Hitt and Angermeier 2011). The importance of spatial distance for dispersal limitation has been well demonstrated for stream ecosystems, even for

highly mobile organisms (e.g., Thompson and Townsend 2006). The influx of immigrants from downstream pools tends to be lower at isolated and peripheral sites within the drainage network (Ai et al. 2013; Miyazono and Taylor 2013). As a consequence, colonization is expected to decrease and extinction to increase at peripheral segments (Gotelli and Taylor 1999). However, our findings indicate that the effects of the potential increase in the influx of immigrants in more centrally located sites, measured as downstream stream size, was important to population abundance, but not for species occurrence. This is consistent with the experimental study of Altermatt et al. (2011), which demonstrated that local population densities of protozoa and rotifers had an increased rate of post-disturbance recovery in connected patches compared with isolated patches. In this sense, our results indicate that tributaries centrally located in the stream network (i.e. higher connectivity), and which are directly connected to the mainstem, had relatively stable abundance of riffle species over time, whereas occurrence of species was mostly determined by habitat change.

We observed that sites with large upstream catchment area presented high turnover in species abundance. We had no *a priori* expectation regarding the effects of catchment size on the turnover of stream fish assemblages. However, we included catchment size in the models because it is expected to be partially correlated with variables we hypothesized to affect assemblage turnover (Appendix, Table A3). For instance, although small streams may flow into either small or large streams, large streams necessarily flow into large streams. Nonetheless, the finding that sites with larger upstream catchment area had higher turnover are not entirely surprising, given that previous studies have observed a positive relationship between stream size and immigration rates (e.g. Taylor and Warren 2001; Miyazono and Taylor 2013). The relationship between square root of catchment area and mean discharge has been well-known to

hydrologists for decades (Leopold and Maddock 1953), and ecologists have recently used it as an indicator of stream size and volume (Gordon et al. 2004, Hughes et al. 2011). We thus suggest that large streams may function as corridors along which a temporally variable set of dispersing individuals from different species are constantly tracking suitable habitats. Large streams are not only more centrally located in the drainage network, but may present larger species pool and populations (habitat capacity), providing immigrants for restructuring local communities. Thus, the observed positive relationship between assemblage turnover and catchment area may not only reflect the influence of habitat size by itself, but the combined effects of stream size and dendritic connectivity of drainage networks (Carrara et al. 2014).

Our study was limited to riffle-specialist species; thus pool-specialists were not considered, as well as transient species that use the interface between riffle and pool habitats, most of which are nektonic species. One important implication is that the benthic riffle-specialist species sampled in our study (mostly loricariids) are commonly sedentary and/or short distance swimmers (Casatti and Castro 2006), a characteristic that may affect the immigration rates and thus the temporal turnover of fish assemblages. For example, Hitt and Angermeier (2008, 2011) observed that the most important factor influencing differences in fish species composition of centrally located tributaries (compared to isolated tributaries in the network periphery) was the influx of cyprinids with high dispersal ability from mainstem segments. Therefore, riverine species with high dispersal abilities may exert stronger influence on assemblages of tributaries near to mainstem river confluences through mass effects (Hitt and Angermeier 2011). Although our study focused on benthic riffle species, we found lower turnover in assemblages at stream sites connected to larger confluences. The studied basin is a small drainage (550 km²) in a mountainous region with large proportion of riffle habitats in tributaries and mainstem. Thus,

mainstem segments can act as potential sources of immigrants for riffle communities inhabiting adjacent tributaries. Also, mainstem segments are centrally located and can act as corridors connecting their flowing tributaries (Altermatt 2013). Distant peripheral stream segments, on the other hand, are more spatially isolated and more difficult to reach by dispersing individuals, which could influence local population dynamics (e.g. after a catastrophic event causing extinction of a local population). Hence, our study indicates that even benthic (and perhaps low-dispersing) riffle communities of tributaries near to mainstem may be more easily and frequently accessed by dispersing individuals of different species than isolated and peripheral riffle communities.

Differences in species responses to habitat change, stream channel slope, connectivity (dlink) and catchment area indicate that populations are differently affected by niche- and dispersal-related processes. For instance, connectivity may be more important to occurrence of some species for which local habitat characteristics are not very suitable. In this case, species with high dispersal abilities may have an advantage to maintain their presence in unsuitable but connected sites via immigration. Therefore, fluctuations in population abundance in mainstem or tributaries will influence species occurrence in other connected tributaries. However, our results indicate that this influence will be conditioned by how connected or how close a tributary is to a larger connection within a drainage network.

A caveat of our study is that it was limited to two sampling events with 13-years interval and does not account for seasonal and annual variation in species occurrence and abundance, and in physical habitat. Consequently, we were not able to assess multiple temporal replicates which would allow documenting the direction of assemblage changes (e.g. Matthews et al. 2013). Nevertheless, by using a long-term interval we were able to study a temporally

independent replicate (i.e. turnover of all individuals). A second issue is that a relevant proportion of the total variation in assemblage turnover was not explained by the variables used in our models. Additional likely important sources of variation are intra-annual variation in species occurrence (movement patterns), inter-annual oscillation in population abundance due to suitable breeding events, stochastic environmental variation, and also sampling error. Also, habitat change was based only on physically-based variables, e.g. substrate composition and channel size, so we did not consider other potentially important factors to assemblage turnover, such as water chemistry and streambed stability. Although not taking into account all these other potential sources of variation, our models explained a relevant amount of variation in species occurrence ($r^2 = 0.23$) and abundance ($r^2 = 0.39$ to 0.53).

We found that the dynamic of stream fish communities was affected by multiple factors, including environmental filters (slope and habitat change) and the potential for communities to receive dispersing individuals (connection to larger streams). As these factors can be expected to vary throughout the stream network, our study shows the spatial position within dendritic network can affect metacommunity processes that drive turnover in stream fish assemblages. In addition, our study indicates that species differ in their response to metacommunity processes, such as habitat filtering and dispersal limitation (connectivity). These results have implications for sampling design in monitoring programs, since the degree of temporal dissimilarities in fish assemblages depends not only on local habitat change, but on spatial position of the sampled reaches within the drainage network and species particularities. Sampling design should then incorporate spatial position (e.g. downstream link) and take into account different species responses.

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References

- Ai, D., Gravel, D., Chu, C., and Wang, G. 2013. Spatial structures of the environment and of dispersal impact species distribution in competitive metacommunities. *PLoS One* **8**(7): e68927.
- Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. *Aquat. Ecol.* **47**(3): 365–377.

- 594 Altermatt, F., Bieger, A., Carrara, F., Rinaldo, A., and Holyoak, M. 2011. Effects of
595 connectivity and recurrent local disturbances on community structure and population
596 density in experimental metacommunities. *PLoS One* **6**(4):e19525.
- 597 Altermatt, F., Seymour, M., and Martinez, N. 2013. River network properties shape α -diversity
598 and community similarity patterns of aquatic insect communities across major drainage
599 basins. *J. Biogeogr.* **40**(12): 2249–2260.
- 600 Barton, K. 2014. MuMIn: Multi-model inference. R package version 1.10.0. Available from
601 <http://CRAN.R-project.org/package=MuMIn> [accessed 13 July 2015].
- 602 Becker, F.G. 2002. Distribuição e abundância de peixes de corredeiras e suas relações com
603 características de habitat local, bacia de drenagem e posição espacial em riachos de Mata
604 Atlântica (bacia do rio Maquiné, RS, Brasil). PhD Dissertation, Programa de Pós-
605 Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, São
606 Paulo, Brazil.
- 607 Becker, F.G., Carvalho, S., and Hartz, S.M. 2008. Life-history of the South American darter,
608 *Characidium pterostictum* (Crenuchidae): evidence for small scale spatial variation in a
609 piedmont stream. *Neotrop. Ichthyol.* **6**(4): 591–598.
- 610 Benda, L., Poff, N.L., Miller, D., Dunne, T., Reeves, G., Pess, G., and Pollock, M. 2004. The
611 network dynamics hypothesis: how channel networks structure riverine habitats.
612 *BioScience* **54**(5): 413–427.
- 613 Bivand, R., and Lewin-Koh, N. 2014. maptools: Tools for reading and handling spatial objects.
614 R package version 0.8-30. Available from <http://CRAN.R-project.org/package=maptools>
615 [accessed 13 July 2015].

- 616 Burnham, K.P., and Anderson, D.R. 2002. Model selection and multi model inference: a
617 practical information-theoretic approach. Springer, N.Y.
- 618 Campbell-Grant, E.H., Lowe, W.H., and Fagan, W.F. 2007. Living in the branches: population
619 dynamics and ecological processes in dendritic networks. *Ecol. Lett.* **10**(2): 165–175.
- 620 Carrara, F., Rinaldo, A., Giometto, A., and Altermatt, F. 2014. Complex interaction of dendritic
621 connectivity and hierarchical patch size on biodiversity in river-like landscapes. *Am.*
622 *Nat.* **183**(1): 13–25.
- 623 Casatti, L., and Castro, R. 2006. Testing the ecomorphological hypothesis in a headwater riffles
624 fish assemblage of the rio São Francisco, southeastern Brazil. *Neotrop. Ichthyol.* **4**(2):
625 203–214.
- 626 Champeau, T.R., Stevens, P.W., and Blewett, D.A. 2009. Comparison of fish community
627 metrics to assess long-term changes and hurricane impacts at Peace River, Florida. *Florida*
628 *Scient.* **72**(4): 289–309.
- 629 Chase, J.M. 2007. Drought mediates the importance of stochastic community assembly. *PNAS*
630 **104**(44): 17430–17434.
- 631 Chase, J.M. 2010. Stochastic community assembly causes higher biodiversity in more
632 productive environments. *Science* **328**(5984): 1388–1391.
- 633 Csardi, G., and Nepusz, T. 2006. The igraph software package for complex network research.
634 *InterJournal Complex Systems* **1695** (5): 1–9.
- 635 Dei Tos, C., Gomes, L.C., Ambrósio, A.M., and Goulart, E. 2010. An overview of freshwater
636 fish aging in South America: the science, biases and future directions. *Acta Sci., Biol. Sci.*
637 **32**(4): 323–333.

- 638 Driscoll, D.A., and Lindenmayer, D.B. 2009. Empirical tests of metacommunity theory using an
639 isolation gradient. *Ecol. Monogr.* **79**(3): 485–501.
- 640 Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic
641 metapopulations. *Ecology* **83**(12): 3243–3249.
- 642 Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to riverscapes:
643 bridging the gap between research and conservation of stream fishes. *BioScience* **52**(6):
644 483–498.
- 645 Fisher, W.L. 1987. Benthic fish sampler for use in riffle habitats. *T. Am. Fish. Soc.* **116**(5): 768–
646 772.
- 647 Fox, J., and Monette, G. 1992. Generalized collinearity diagnostics. *J. Am. Stat. Assoc.* **87**(417):
648 178–183.
- 649 Giam, X., and Olden, J. D. 2015. Quantifying variable importance in a multimodel inference
650 framework. *Methods Ecol. Evol.* In press. doi:10.1111/2041-210X.12492.
- 651 Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., and Nathan, R.J. 2004. *Stream*
652 *Hydrology: An Introduction for Ecologists*. John Wiley and Sons, U.K.
- 653 Gotelli, N.J., and Taylor, C.M. 1999. Testing metapopulation models with stream-fish
654 assemblages. *Evol. Ecol. Res.* **1**: 835–845.
- 655 Grenouillet, G., Pont, D., and Hérissé, C. 2004. Within-basin fish assemblage structure: the
656 relative influence of habitat versus stream spatial position on local species richness. *Can.*
657 *J. Fish. Aquat. Sci.* **61**(1): 93–103.
- 658 Grossman, G.D., Dowd, J.F., and Crawford, M. 1990. Assemblage stability in stream fishes: a
659 review. *Environ. Manage.* **14**(5): 661–671.

- Grossman, G.D., Ratajczak, R.E., Crawford, M., and Freeman M.C. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol. Monogr.* **68**(3): 395–420.
- Hasenack, H., and L.W. Ferraro. 1989. Considerações sobre o clima da região de Tramandaí, RS. *Pesquisas em Geociências* **22**: 53–70.
- Hasenack, H., and E. Weber. 2010. Base cartográfica vetorial contínua do Rio Grande do Sul - escala 1:50.000. UFRGS, Instituto de Biociências, Centro de Ecologia, Porto Alegre, Brazil. Available from http://www.ecologia.ufrgs.br/labgeo/index.php?option=com_content&view=article&id=123:base50krs&catid=14:download-non-visible [accessed 13 July 2015].
- Heino, J. 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biol. Rev.* **88**(1): 166–178.
- Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biol.* **60**(5): 845–869.
- Hitt, N. P., and Angermeier, P. L. 2011. Fish community and bioassessment responses to stream network position. *J. North Am. Benthol. Soc.* **30**(1): 296–309.
- Hitt, N.P., and Angermeier, P.L. 2008. Evidence for fish dispersal from spatial analysis of stream network topology. *J. North Am. Benthol. Soc.* **27**(2): 304–320.
- Hughes, R.M., Kaufmann, P.R., and Weber, M.H. 2011. National and regional comparisons between Strahler order and stream size. *J. North Am. Benthol. Soc.* **30**(1): 103–121.
- Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. *J. North Am. Benthol. Soc.* **19**(4): 573–592.

- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* **7**(7): 601–613.
- Leopold, L.B., and Maddock Jr, T. 1953. The hydraulic geometry of stream channels and some physiographic implications. *Geol. Surv. Prof. Paper* **252**: 1–57.
- Lu, B. 2014. shp2graph: Convert a spatial lines data frame object to a "igraph-class" object. R package version 0-2. Available from <http://CRAN.R-project.org/package=shp2graph> [accessed 13 July 2015].
- Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J., and Watt, A.D. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol. Evol.* **25**(10): 574–582.
- Malabarba, L.R., Carvalho Neto, P., Bertaco, V.A., Carvalho, T. P., dos Santos, J. F., and Artioli, L.G.S. 2013. Guia de identificação dos peixes da bacia do rio Tramandaí. Via Sapiens, Porto Alegre, Brazil.
- Matthews, W., and Marsh-Matthews, E. 2006. Temporal changes in replicated experimental stream fish assemblages: predictable or not? *Freshwater Biol.* **51**(9): 1605–1622.
- Matthews, W.J., Cashner, R.C., and Gelwick, F.P. 1988. Stability and persistence of fish faunas and assemblages in three Midwestern streams. *Copeia* **1988**(4): 945–955.
- Matthews, W.J., Marsh-Matthews, E., Cashner, R.C., and Gelwick, F. 2013. Disturbance and trajectory of change in a stream fish community over four decades. *Oecologia* **173**(3): 955–969.

- 706 Miyazono, S., and Taylor, C.M. 2013. Effects of habitat size and isolation on species
707 immigration-extinction dynamics and community nestedness in a desert river system.
708 *Freshwater Biol.* **58**(7): 1303–1312.
- 709 Montgomery, D.R. 1999. Process domains and the river continuum. *J. Am. Water Resour.*
710 *Assoc.* **35**(2): 397–410.
- 711 Moreno, J.A. 1961. *Clima do Rio Grande do Sul*. Secretaria da Agricultura do Estado do Rio
712 Grande do Sul, Porto Alegre, Brazil.
- 713 Myers, J.A., Chase, J.M., Jiménez, I., Jørgensen, P. M., Araujo-Murakami, A.,
714 Paniagua-Zambrana, N., and Seidel, R. 2013. Beta-diversity in temperate and tropical
715 forests reflects dissimilar mechanisms of community assembly. *Ecol. Lett.* **16**(2): 151–
716 157.
- 717 Mykrä, H., Heino, J., Oksanen, J., and Muotka, T. 2011. The stability-diversity relationship in
718 stream macroinvertebrates: influences of sampling effects and habitat complexity.
719 *Freshwater Biol.* **56**(6): 1122–1132.
- 720 Newman, M. 2010. *Networks: an introduction*. Oxford University Press.
- 721 Nippgen, F., McGlynn, B.L., Marshall, L.A., and Emanuel, R.E. 2011. Landscape structure and
722 climate influences on hydrologic response. *Water Resour. Res.* **47** (12): W12528.
- 723 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson,
724 G.L., Solymos, P., Stevens, M.H.H., and Wagner, H. 2013. *vegan: Community Ecology*
725 *Package*. R package version 2.0-8. Available from: [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)
726 [project.org/package=vegan](http://CRAN.R-project.org/package=vegan) [accessed 13 July 2015].
- 727 Osborne, L.L., and Wiley, M.J. 1992. Influence of tributary spatial position on the structure of
728 warm water fish communities. *Can. J. Fish. Aquat. Sci.* **49**(4): 671–681.

- 729 Perkin, J. S., and Gido, K. B. 2012. Fragmentation alters stream fish community structure in
730 dendritic ecological networks. *Ecol. Appl.* **22**(8): 2176–2187.
- 731 Poff, N.L., and Ward, J.V. 1989. Implications of stream flow variability and predictability for
732 lotic community structure: a regional analysis of stream flow patterns. *Can. J. Fish. Aquat.*
733 *Sci.* **46**(10): 1805–1818.
- 734 R Development Core Team. 2015. R: A Language and Environment for Statistical Computing
735 [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from
736 <http://www.r-project.org/> [accessed 13 July 2015].
- 737 Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. *Am.*
738 *Nat.* **136**(3): 328–344.
- 739 Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R.,
740 Sheldon, A.L., Wallace, J.B., and Wissmar, R.C. 1988. The role of disturbance in stream
741 ecology. *J. North Am. Benthol. Soc.* **7**(4): 433–455.
- 742 Rice, S.P., Greenwood, M.T., and Joyce, C.B. 2001. Tributaries, sediment sources, and the
743 longitudinal organisation of macroinvertebrate fauna along river systems. *Can. J. Fish.*
744 *Aquat. Sci.* **58**(4): 824–840.
- 745 Rosgen, D.L. 1994. A classification of natural rivers. *Catena* **22**(3): 169–199.
- 746 Ross, S.T., Matthews W.J., and Echelle, A.A. 1985. Persistence of stream fish assemblages:
747 effects of environmental change. *Am. Nat.* **126**(1): 24–40.
- 748 Schmidt, M.H., Thies, C., Nentwig, W., and Tschardtke, T. 2008. Contrasting responses of
749 arable spiders to the landscape matrix at different spatial scales. *J. Biogeogr.* **35**(1): 157–
750 166.
- 751 Shreve, R.L. 1966. Statistical law of stream numbers. *J. Geol.* **74**(1): 17–37.

- 752 Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. *Eos Trans. AGU*,
753 **38**(6): 913–920.
- 754 Taylor, C.M. 1997. Fish species richness and incidence patterns in isolated and connected
755 stream pools: effects of pool volume and spatial position. *Oecologia* **110**(4): 560–566.
- 756 Taylor, C.M., and Warren, M.L. 2001. Dynamics in species composition of stream fish
757 assemblages: environmental variability and nested subsets. *Ecology* **82**(8): 2320–2330.
- 758 Thompson, R., and Townsend, C.R. 2006. A truce with neutral theory: local deterministic
759 factors, species traits and dispersal limitation together determine patterns of diversity in
760 stream invertebrates. *J. Anim. Ecol.* **75**(2): 476–484.
- 761 Thornbrugh, D.J., and Gido, K.B. 2010. Influence of spatial positioning within stream networks
762 on fish assemblage structure in the Kansas River basin, USA. *Can. J. Fish. Aquat. Sci.*
763 **67**(1): 143–156.
- 764 Vogel, C. 2012. Estratégias de história de vida de peixes neotropicais em diferentes tipos de
765 habitat. Master thesis, Programa de Pós-Graduação em Ecologia, Universidade Federal do
766 Rio Grande do Sul, Rio Grande do Sul, Brazil.

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Table 1. Instream habitat variables used to quantify habitat change between 1999 and 2012 for 22 sampling sites in the Maquiné river basin, Southern Brazil. CV = coefficient of variation; SD = standard deviation; p = probability of difference between years according to paired t -test.

Variables	Abbreviation	1999 Mean (SD)	2012 Mean (SD)	p
Mean wetted width	MeanWettWid	8.6 (4.7)	9.1 (4.8)	<0.001
CV wetted width	CVWettW	22.0 (10.8)	24.5 (14.1)	ns
Mean bankfull width	MeanBankWid	11.9 (6.5)	14.7 (7.2)	<0.001
CV bankfull width	CVBankW	16.6 (6.2)	15.4 (13.7)	ns
Ratio wetted/bankfull width	RatioWB	70.5 (13.9)	62.8 (15.2)	ns
Mean depth	MeanDepth	20.5 (7.0)	23.9 (5.0)	<0.001
CV depth	CVDepth	41.1 (13.0)	31.9 (7.4)	ns
%Substrate 2 cm	Subs2cm	5.8 (3.99)	1.8 (4.7)	0.014
%Substrate 2-7 cm	Subs2to7	13.5 (5.5)	10.5 (7.4)	ns
%Substrate 7-25 cm	Subs7to25	47.9 (10.9)	39.5 (11.9)	0.016
%Substrate 25-50 cm	Subs25to50	26.3 (11.1)	34.2 (11.5)	0.044
%Substrate >50 cm	Subs50cm	6.5 (6.2)	14.1 (12.3)	0.013
Shannon diversity substrate	DiverSubs	0.9 (0.1)	0.8 (0.2)	ns

ns = nonsignificant difference ($p>0.05$)

Table 2. Variation in fish species sampled in 22 riffle habitats between 1999 and 2012 samples.

Abbrev = name abbreviations; *fr%* = mean relative frequency of occurrence; *fr% diff* = absolute differences in relative frequency of occurrence between 1999 and 2012; *ab%* = mean relative abundance; *ab% diff* = absolute difference in relative abundance between 1999 and 2012.

Species	Abbrev	1999 (<i>fr%</i>)	2012 (<i>fr%</i>)	<i>fr%</i> <i>diff</i>	1999 (<i>ab%</i>)	2012 (<i>ab%</i>)	<i>ab%</i> <i>diff</i>
<i>Rineloricaria aequalicuspis</i>	Rae	100	100	0	42.6	33.9	8.7
<i>Pareiorhaphis nudulus</i>	Pnu	86.4	72.7	13.7	20.6	18.8	1.8
<i>Pareiorhaphis hypselurus</i>	Phy	90.9	95.5	4.6	20.9	18.6	2.3
<i>Epactionotus bilineatus</i>	Ebil	100	100	0	26.5	12.6	13.9
<i>Characidium pterostictum</i>	Cpt	100	95.6	4.4	17.9	9.9	8
<i>Diapoma itaimbe</i>	Dit	31.8	54.6	22.8	1.3	10.9	9.6
<i>Jenynsia unitaenia</i>	Jun	63.6	63.6	0	2.5	2.8	0.3
<i>Heptapterus</i> sp.	Hsp	72.7	77.3	4.6	1.8	3.3	1.5
<i>Ancistrus multispinis</i>	Amu	68.2	40.9	27.3	2.6	0.6	2
<i>Rineloricaria maquinensis</i>	Rma	9.1	13.6	4.5	0.4	0.4	0
<i>Heptapterus mustelinus</i>	Hmu	22.7	13.6	9.1	0.6	0.3	0.3
<i>Ituglanis boitata</i>	Ibo	0	9.1	9.1	0	0.3	0.3
<i>Hemiancistrus punctulatus</i>	Hpu	4.6	0	4.6	0.1	0	0.1
<i>Trichomycterus</i> sp.	Tsp	4.6	4.6	0	0.1	0.1	0

Table 3. Best linear regression models for fish assemblage turnover selected using AICc statistics ($\Delta \text{AICc} < 2$). Response variables were turnover of species occurrence (Sorensen dissimilarity) and species abundance (Bray-Curtis dissimilarity) of riffle-dwelling fish assemblage between years 1999 and 2012. Explanatory variables were channel slope, position in the network, local habitat change and stream size. Variables representing channel slope, site position within stream network, local habitat change and stream size are: slope between confluences (slope.bc); downstream link magnitude (dlink); upstream catchment area (area); habitat change (habitat); closeness centrality (centr.cl); slope 1 km upstream from the sampling site (slope.1k) and local slope (slope.loc). AICc = Akaike information criterion; df = degrees of freedom. Delta = AICc difference from the best model; Weight = Akaike weights; adj. R^2 = adjusted coefficient of determination. Only models with $\Delta \text{AICc} < 2$ are shown.

Response variables	Explanatory variables	AICc	df	Delta	Weight	adj. R2
Occurrence	habitat	-41.6	3	0.0	0.34	0.23
Abundance	slope.bc+dlink+habitat+area	-64.1	6	0.0	0.14	0.51
	slope.bc+habitat	-64.0	4	0.1	0.14	0.39
	slope.bc+dlink+area	-63.9	5	0.2	0.13	0.44
	slope.bc+dlink+centr.cl+area	-63.7	6	0.4	0.12	0.50
	slope.bc+dlink+habitat	-63.5	5	0.7	0.10	0.43
	slope.bc+habitat+slope.1k	-63.2	5	0.9	0.09	0.42
	slope.bc+habitat+area	-63.0	5	1.1	0.08	0.42
	dlink+slope.1k+area	-62.7	5	1.4	0.07	0.41
	slope.bc+dlink+habitat+centr.cl	-62.6	6	1.5	0.07	0.47
	slope.bc+dlink+habitat+centr.cl+area	-62.2	7	1.9	0.06	0.53

Table 4. Relative importance of explanatory variables based on summed Akaike weights (SW) and their average standardized (beta) coefficients resulting from all combinations of AICc models of assemblage turnover (see Table 3 for the best models). Slope between confluences (slope.bc); downstream link magnitude (dlink); upstream catchment area (area); habitat change (habitat); closeness centrality (centr.cl); slope 1 km upstream from the sampling site (slope.1k) and local slope (slope.loc). Interaction between two explanatory variables is indicated with a colon.

Response variables	Explanatory variables	Standardized coefficients	Relative importance
Species occurrence	habitat	0.47	0.78
	slope.bc	-0.12	0.26
	area	0.12	0.25
	dlink	-0.06	0.20
	slope.loc	-0.17	0.20
	slope.1k	-0.04	0.17
	centr.cl	-0.01	0.16
	slope.bc:habitat	-0.28	0.04
	area:habitat	-0.35	0.03
	dlink:habitat	-0.15	0.02
	area:slope.bc	-0.47	0.03
	slope.bc:dlink	-0.42	0.02
	area:dlink	0.26	<0.01
Species abundance	slope.bc	-0.54	0.75
	dlink	-0.49	0.66
	area	0.42	0.61
	habitat	0.37	0.57
	slope.loc	-0.34	0.25
	centr.cl	0.31	0.30
	slope.1k	-0.07	0.23
	slope.bc:dlink	-0.20	0.08
	dlink:habitat	0.06	0.03

slope.bc:habitat	-0.04	0.06
area:habitat	0.03	0.03
area:slope.bc	0.13	0.05
area:dlink	0.09	0.05

Boldface highlights the most important variables (scores > 0.5).

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Table 5. Relative importance based on summed Akaike weights (SW) and average standardized (beta) coefficients resulting from all combinations of AICc models of species abundance change. Only the four most important variables explaining overall assemblage turnover (see Table 3) were used for each species models. See Table 2 for species names abbreviations and Table 3 for variable name abbreviations.

Species	Explanatory variable	Standardized coefficients	Relative importance (SW)
Rae	dlink	0.50	0.83
	area	0.31	0.40
	habitat	0.20	0.27
	slope.bc	-0.08	0.19
Pnu	slope.bc	0.60	0.93
	dlink	0.32	0.46
	area	-0.30	0.39
	habitat	0.13	0.20
Phy	area	-0.28	0.35
	habitat	-0.16	0.23
	dlink	-0.14	0.22
	slope.bc	0.05	0.20
Ebi	dlink	0.42	0.64
	habitat	0.38	0.59
	area	0.35	0.44
	slope.bc	0.10	0.20
Cpt	habitat	-0.15	0.23
	area	0.16	0.22
	slope.bc	-0.10	0.21
	dlink	0.03	0.19
Dit	area	0.66	0.98
	habitat	-0.17	0.25
	slope.bc	-0.18	0.25
	dlink	-0.05	0.18
Hsp	habitat	0.27	0.35
	dlink	0.23	0.30
	area	0.09	0.20
	slope.bc	-0.10	0.20

Jun	habitat	0.25	0.32
	area	0.26	0.32
	dlink	0.19	0.25
	slope.bc	-0.14	0.22
Amu	area	-0.04	0.19
	dlink	0.07	0.20
	habitat	-0.05	0.20
	slope.bc	-0.03	0.19

Boldface highlights the most important variables according to SW (values ≥ 0.45).

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FIGURE CAPTIONS

Fig. 1. Sampling site location in the Maquiné river basin, southern Brazil. The hydrographic line thickness is proportional to stream size. Note the abrupt change in steep elevation within a short distance from headwater to lower valleys. Sampling was restricted to lower valley sections (< 250 m of elevation).

Fig. 2. Principal coordinates analysis (PCoA) based on species occurrence dissimilarities (Sorensen) showing turnover in fish assemblages from 1999 (circles) to 2012 (arrowhead). Arrow length is proportional to assemblage turnover and circle size is proportional to habitat change, which were the only important variables explaining assemblage turnover (AICc model selection). See Table 2 for species name abbreviations.

Fig. 3. Long-term turnover in species occurrence of riffle-dwelling fish assemblages calculated as pairwise Sorensen dissimilarity in relation to instream habitat change. Samples were obtained in 1999 and 2012, in 22 sites at the Maquiné river watershed, South Brazil.

Fig. 4. Principal coordinates analysis (PCoA) based on species abundance dissimilarities (Bray-Curtis) showing turnover in fish assemblages from 1999 (circles) to 2012 (arrowhead). Arrow length is proportional to assemblage turnover and circle size is proportional to the four most important variables explaining assemblage turnover (AICc model selection). These variables were (A) slope between confluences, (B) downstream link magnitude; (C) catchment area, and (D) habitat change. See Table 2 for species name abbreviations.

Fig. 5. Long-term turnover in species abundance of riffle-dwelling fish assemblages calculated as pairwise Bray-Curtis dissimilarity in relation to the four most important variables, according to multiple model selection. These variables were (A) slope between confluences, (B) downstream link magnitude; (C) square root transformed catchment area, and (D) habitat change. Samples were obtained in 1999 and 2012, in 22 sites at the Maquiné river watershed, South Brazil.

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Fig. 1. Sampling site location in the Maquiné river basin, southern Brazil. The hydrographic line thickness is proportional to stream size. Note the abrupt change in steep elevation within a short distance from headwater to lower valleys. Sampling was restricted to lower valley sections (< 250 m of elevation).

Fig. 1

269x210mm (300 x 300 DPI)

Fig. 2. Principal coordinates analysis (PCoA) based on species occurrence dissimilarities (Sorensen) showing turnover in fish assemblages from 1999 (circles) to 2012 (arrowhead). Arrow length is proportional to assemblage turnover and circle size is proportional to habitat change, which were the only important variables explaining assemblage turnover (AICc model selection). See Table 2 for species name abbreviations.

Fig. 2
185x169mm (300 x 300 DPI)

Fig. 3. Long-term turnover in species occurrence of riffle-dwelling fish assemblages calculated as pairwise Sorensen dissimilarity in relation to instream habitat change. Samples were obtained in 1999 and 2012, in 22 sites at the Maquiné river watershed, South Brazil.

Fig. 3
101x91mm (300 x 300 DPI)

Fig. 4. Principal coordinates analysis (PCoA) based on species abundance dissimilarities (Bray-Curtis) showing turnover in fish assemblages from 1999 (circles) to 2012 (arrowhead). Arrow length is proportional to assemblage turnover and circle size is proportional to the four most important variables explaining assemblage turnover (AICc model selection). These variables were (A) slope between confluences, (B) downstream link magnitude; (C) catchment area, and (D) habitat change. See Table 2 for species name abbreviations.

Fig. 4
203x203mm (300 x 300 DPI)

Fig. 5. Long-term turnover in species abundance of riffle-dwelling fish assemblages calculated as pairwise Bray-Curtis dissimilarity in relation to the four most important variables, according to multiple model selection. These variables were (A) slope between confluences, (B) downstream link magnitude; (C) square root transformed catchment area, and (D) habitat change. Samples were obtained in 1999 and 2012, in 22 sites at the Maquiné river watershed, South Brazil.

Fig. 5

185x188mm (300 x 300 DPI)

Appendix

Table A1. Overall description of the 22 sampled sites in Maquiné river basin, Brazil. Slope between confluences (slope.bc); upstream catchment area (area); downstream link value (dlink). Large boulder = l. boulder.

Site	Mean wetted width (m)	Mean depth (cm)	Catchment area (km ²)	Slope.bc (%)	Dlink	Dominant substrates (> 20%)
1	6.0	20.4	12.6	20.2	9	cobble
2	7.9	17.0	20.4	18.3	14	cobble and pebble
3	4.8	21.0	14.0	14.4	14	boulder and cobble
4	8.1	33.9	40.6	6.2	28	boulder, cobble and l. boulder
5	19.5	22.1	81.5	9.4	39	cobble and boulder
6	4.6	20.2	7.4	15.2	39	cobble and boulder
7	4.6	15.4	11.4	8.8	39	cobble and boulder
8	12.0	23.2	15.6	19.7	11	cobble, boulder and l. boulder
9	12.8	18.0	32.8	12.3	52	cobble and boulder
10	14.5	30.5	141.6	2.3	52	cobble and boulder
11	15.0	36.8	109.7	20.4	71	cobble and boulder
12	6.9	18.8	12.4	9.0	79	cobble and boulder
13	5.8	20.5	12.9	9.0	79	cobble and boulder
14	4.0	17.7	6.4	17.2	86	cobble and boulder
15	5.5	13.4	6.5	17.2	86	Cobble
16	15.2	22.8	165.9	2.1	139	cobble, pebble and boulder
17	6.2	24.4	22.9	20.5	10	cobble and boulder
18	12.9	21.6	49.9	8.3	154	cobble and boulder
19	6.5	19.6	9.7	32.0	9	cobble, boulder and l. boulder
20	10.4	20.0	28.0	2.6	176	Cobble
21	4.9	23.3	12.4	9.6	6	cobble and boulder
22	6.7	27.3	23.2	2.3	10	cobble and boulder

Table A2. Descriptive summary of explanatory variables used in multiple regression models of turnover in species occurrences and abundances. Dorder and centr.bt were highly correlated with other variables (see Table 3) and were not used in the model selection procedure. Slope between confluences (slope.bc); slope one kilometre upstream of site (slope.1k); local slope (slope.loc); upstream catchment area (area); downstream link magnitude (dlink); downstream order (dorder); closeness centrality (centr.cl); betweenness centrality (centr.bt) and habitat change (habitat). Values in parentheses are standard deviation.

	Mean (SD)	Minimum	Maximum
slope.bc	12.59 (7.67)	2.09	32.03
slope.1k	11.42 (5.38)	1.08	19.08
slope.local	3.03 (1.32)	1.75	6.99
area	38.07 (45.40)	6.37	165.86
dlink	54.64 (49.91)	6.00	176.00
dorder	3.55 (0.91)	2.00	5.00
centr.cl	5.02×10^{-05} (1.08×10^{-05})	2.66×10^{-05}	6.48×10^{-05}
centr.bt	10459 (11850)	1263	43788
habitat	44.02 (9.83)	27.52	66.27

Table A3. Pairwise Pearson’s correlation matrix of nine explanatory variables. Slope between confluences (slope.bc); slope one kilometre upstream of site (slope.1k); local slope (slope.loc); upstream catchment area (area); downstream link magnitude (dlink); downstream order (dorder); closeness centrality (centr.cl); betweenness centrality (centr.bt) and habitat change (habitat).

	slope.1k	slope.bc	area	dlink	dorder	centr.cl	centr.bt	habitat
slope.loc	0.50	0.70	-0.51	-0.50	-0.49	-0.36	-0.51	-0.09
slope.1k		0.68	-0.29	-0.55	-0.46	-0.30	-0.19	-0.26
slope.bc			-0.41	-0.45	-0.32	-0.20	-0.34	0.08
area				0.34	0.46	0.40	0.97	0.33
dlink					0.85	0.60	0.34	-0.13
dorder						0.74	0.45	0.01
centr.cl							0.39	0.17
centr.bt								0.35

Table A4. Combinations of instream habitat variables to calculate habitat change (dissimilarity) based on Euclidean distances that maximize the correlation with fish assemblage turnover of species occurrences (Sorensen dissimilarity). See Table 1 for variable names abbreviations.

Variable combinations	Correlation (Pearson's <i>r</i>)
CVDepth	0.590
CVDepth + MeanBankWid	0.741
CVDepth + MeanBankWid + Subs2cm	0.786
CVDepth + MeanBankWid + Subs2cm + Subs2to7	0.784
CVDepth + MeanBankWid + Subs2cm + Subs2to7 + Subs50cm	0.802
CVDepth + MeanBankWid + Subs2cm + Subs2to7 + Subs50cm + MeanDepth	0.833
CVDepth + MeanBankWid + Subs2cm + Subs50cm + MeanDepth + MeanWettWid + DiverSubs	0.820
CVDepth + MeanBankWid + Subs2cm + Subs25to50 + Subs50cm + MeanDepth + MeanWettWid + DiverSubs	0.812
CVDepth + MeanBankWid + Subs2cm + Subs25to50 + Subs50cm + MeanDepth + MeanWettWid + DiverSubs + RatioWB	0.738
CVDepth + MeanBankWid + Subs2cm + Subs2to7 + Subs25to50 + Subs50cm + MeanDepth + MeanWettWid + DiverSubs + RatioWB	0.711
CVDepth + MeanBankWid + Subs2cm + Subs2to7 + Subs25to50 + Subs50cm + MeanDepth + MeanWettWid + RatioWB + CVWettW + DiverSubs	0.675
CVDepth + MeanBankWid + Subs2cm + Subs2to7 + Subs25to50 + Subs50cm + MeanDepth + MeanWettWid + RatioWB + CVWettW + DiverSubs + Subs7to25	0.640
CVDepth + MeanBankWid + Subs2cm + Subs2to7 + Subs25to50 + Subs50cm + MeanDepth + MeanWettWid + RatioWB + CVWettW + DiverSubs + Subs7to25 + CVBankW	0.479

Table A5. Combinations of instream habitat variables to calculate habitat change (dissimilarity) based on Euclidean distances that maximize the correlation with fish assemblage turnover of species abundances (Bray-Curtis dissimilarity). See Table 1 for variable abbreviations.

Variable combinations	Correlation (Pearson's <i>r</i>)
Subs25to50	0.392
MeanDepth + Subs25to50	0.522
MeanDepth + Subs25to50 + MeanBankWid	0.544
MeanDepth + Subs25to50 + Subs2to7 + CVBankW	0.585
MeanDepth + Subs25to50 + Subs2to7 + CVBankW + Subs2cm	0.603
MeanDepth + Subs25to50 + Subs2to7 + CVBankW + Subs2cm + MeanBankWid	0.605
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25	0.604
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25 + CVDepth	0.605
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25 + CVDepth + MeanBankWid	0.607
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25 + CVDepth + MeanBankWid + Subs2to7	0.596
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25 + CVDepth + MeanBankWid + Subs2to7 + Subs50cm	0.566
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25 + CVDepth + MeanBankWid + Subs2to7 + Subs50cm + RatioWB	0.514
MeanDepth + Subs25to50 + CVBankW + Subs2cm + MeanWettWid + DiverSubs + Subs7to25 + CVDepth + MeanBankWid + Subs2to7 + Subs50cm + RatioWB + CVWettW	0.405

Fig. A1. Daily rainfall from 1999 to 2012 for the studied region, southern Brazil. Data from Centro Estadual de Meteorologia do Rio Grande do Sul – CemetRS of the Fundação Estadual de Pesquisa Agropecuária – Fepagro.

Fig. A2. Schematic representation of a hypothetical network showing how network position metrics were calculated for each sampling site. Downstream order (A - Dorder) and Downstream link magnitude (B - Dlink) are based on values of downstream segment after confluences, whereas betweenness centrality and (C) and closeness centrality (D) are calculated based on the nodes. Red circle represents the network position value for a hypothetical sampling site. Values for C and D were calculated using the package igraph.