

# Effects of natural rapids and waterfalls on fish assemblage structure in the Madeira River (Amazon Basin)

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**Abstract** – Habitat connectivity is considered a central factor shaping ecological communities, and the effects of waterway barriers such as natural waterfalls on fish movements are expected to produce differing assemblage structures in riverine ecosystems. Here, we evaluate the influence of a sequence of waterfalls on the compositional dissimilarity of fish assemblages along the Madeira River, the largest tributary of the Amazon River. We found significant differences in species composition between rivers stretches located upstream and downstream of Teotônio waterfall and, to a less extent, Jirau waterfall, independently of the hydrological period. After accounting for the relative roles of local and regional factors in explaining fish compositional dissimilarity, we still observe a significant effect of the waterfalls. We conclude that these waterfalls act as natural ecological barriers limiting fish dispersal processes and discuss aspects of these ecological filters and the potential effects of two dams currently under construction in the Madeira River.

**Key words:** natural geographical barrier; fish distribution; compositional dissimilarity; white waters; dam effects

## Introduction

Connectivity, or inversely the degree of isolation, has been recognised as a fundamental factor in determining the distribution of species (e.g., MacArthur & Wilson 1967) and can be defined as the degree to which the landscape can facilitate or hinder the movement of organisms among areas (e.g., Tischendorf & Fahrig 2000). Within drainage basins, waterfalls, cascades and high gradient reaches often act as biogeographic barriers to dispersal of aquatic organisms (Rahel 2007). For instance, falls in the Snake River (Idaho, USA) have prevented upstream colonisation by several fish species (McPhail & Lindsey 1986), and stream slopes above 10% appear to prevent upstream movements for salmonids (Kruse et al. 1997). On the other hand, the suppression of natural

barriers may result in habitat invasion by species so far isolated downstream of the barrier, as recently observed for Sete Quedas Falls in the Paraná River basin (Julio Junior et al. 2009). Although it is widely recognised that these natural barriers have produced distinct aquatic biotas above and below these barriers (e.g., Rahel 2007), we are still far from a complete understanding of their influence on freshwater fish assemblages, especially in tropical aquatic environments (Böhlke et al. 1978).

In aquatic systems of the Amazon River basin, large waterfalls may disrupt connectivity and, as such, may influence the spatial structure of freshwater assemblages. The Madeira River constitutes the largest tributary of the Amazon River (Goulding et al. 2003) and presents a unique area of waterfalls with approximately 19 rapid sections along nearly 300 km,

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downstream from the mouth of the Beni River. These rapids have moderate slopes but lengths ranging from 300 to 800 m each (Goulding 1979), and in accordance with their size, could represent physical barriers for a substantial number of fish species (but see Buckup et al. 2000).

This study aimed at examining patterns of compositional dissimilarity among ten sampling sites located at the mouth of several tributaries of the Madeira River (Brazilian Amazon). Specifically, we explored the relative roles of environmental and geographical factors in explaining observed patterns of fish compositional dissimilarity. For instance, if natural waterfalls constitute strong geographical barriers for fish species dispersal, one might expect greater compositional dissimilarity in fish assemblages to be related to the presence of these natural barriers, hence overwhelming the influence of local environmental conditions in explaining assemblage patterns.

**Material and methods**

**Study area**

The Madeira River is probably the most geographically complex tributary of the Amazon Basin. In the

region where the Mamoré and Beni Rivers meet (on the border of Brazil and Bolivia), the abrupt elevation change in the transition from the Brazilian Central highlands to the Amazon lowlands results in a stretch of muddy water rapids. The rapids start 3300 km upstream from the confluence of the Madeira and Amazon Rivers, and the steepest and most important falls are situated in a 300-km river stretch between the cities of Guajará-Mirim and Porto Velho in the State of Rondônia in Brazil-Bolivia border (Fig. 1).

Nineteen rapids occur in this stretch (Goulding et al. 2003), two of which have a steep fall and high water speed: i.e., the Jirau and Teotônio waterfalls. In this stretch, the channel is variably narrow and deep, with water velocity of 0.9–1.4 m·s<sup>-1</sup> in normal (run) stretches and reaching up to 2.5 m·s<sup>-1</sup> in rapids and waterfalls. The Teotônio waterfalls result from a gorge where all the sediment-loaded turbulent waters of the Madeira River must pass.

The river channel upstream from the Teotônio waterfall is morphologically heterogeneous, cutting its way into a predominantly rocky substrate and exhibiting higher depth values (8–33 m). Downstream from the Teotônio waterfall, the rocky substrate is replaced by a sandy-muddy substrate with a shallower channel and less variation in depth (10–20 m).

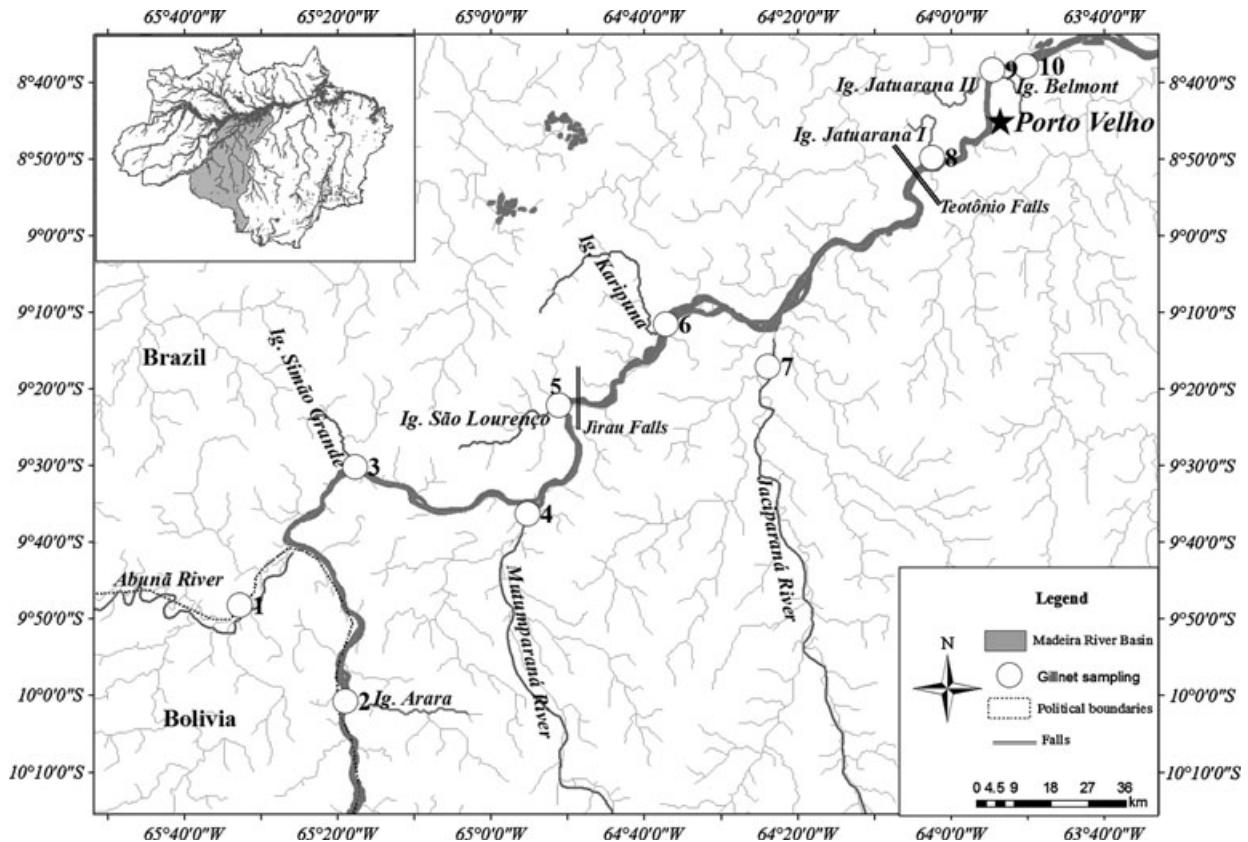


Fig. 1. Map of the study area, depicting the ten sampling stations at the confluence of the main tributaries of the Madeira River and the main waterfalls (bars). The size of bars is proportional to the importance of the waterfalls in the riverine landscape.

The tributaries along this stretch of the Madeira River are quite homogeneous, predominantly small and presenting limnological characteristics and dynamics that are typical of forest streams or *igarapés*, as named in Amazônia (cf. Torrente-Vilara et al. 2008). Floodplains are very narrow along this stretch of the Madeira River, even in periods of extreme flood (with the exception of the lower courses of the two larger tributaries: the Abunã and Jaciparaná rivers). The lower elevation and slower flowing waters downstream from the rapids stretch favour sediment deposition during the flood season, which turns the downstream stretch of the Madeira River progressively more similar to the main Amazon River floodplain.

The mean annual air temperature in this zone is 25.2 °C (20.9–31.1 °C) with relative air humidity around 85% (81–89%). The mean annual rainfall in the upstream reaches of the Madeira River is 2200 mm (1400–2500 mm·year<sup>-1</sup>), with more than 90% of precipitations occurring during the rainy season. The rainy season begins between October and December, reaches a peak in February or March and typically continues until May. The dry season starts at the end of May or early June and usually continues until the beginning of November. The annual mean amplitude of the river fluctuation level varies from 10.8 to 12.4 m (maximal amplitude between 15.4 and 21.8 m), with discharge values between 2322 and 47,236 m<sup>3</sup>·s<sup>-1</sup>, based on levels measured at the Porto do Cai n'água in Porto Velho city from 1967 to 2005 (Torrente-Vilara et al. 2008).

### Fish sampling

Owing to the difficulties of collecting fish with gill nets in the rapids, ten collection sites were established at the mouth of the ten main tributaries: five of them upstream Jirau waterfall, two between Jirau and Teotônio waterfalls and three downstream Teotônio waterfall (Fig. 1). In the Abunã and Jaciparaná tributaries, the collection sites were respectively positioned at about 20 and 10 km upstream from their confluence with the Madeira River. These sites location was motivated by the presence of human settlements close to the tributaries mouths, which represented a high risk of equipment loss or other forms of interference in the sampling procedures.

The fish fauna was sampled on six occasions, three during the flood season (October and November 2004 and February 2005) and three during the dry season (April, June and August 2004), using a set of thirteen gill nets (mesh size of 30, 40, 50, 60, 70, 80, 90, 100, 120, 140, 160, 180 and 200 mm between opposite knots) with a total catching area of 431 m<sup>2</sup> for each sample. The gill nets were exposed 24 h at each site with specimen collections carried out every 4 h. Fish specimens were transported to the laboratory and further identified to species level.

### Environmental variables

Several limnological variables were measured at the mouth of tributaries during both flood and dry seasons: dissolved oxygen (OXY/mg·l<sup>-1</sup>), water temperature (TEM/°C), pH (PH), conductivity (CON/μS·cm<sup>-1</sup>), width (WID), depth (DEP) and water transparency (TRA).

To evaluate the potential effect of each tributary (sub-basin) on fish assemblage structure, thematic maps were created on the basis of 1 km<sup>2</sup> pixels for the ten sampling sites. The delimitation and estimative area of each sub-basin were made using ArcGIS software and ArcHydro tool. A digital elevation model (DEM) generated by the Shuttle Radar Topographic Mission (SRTM) version 3 (2007, <http://srtm.usgs.gov/index.php>) of the United States Geological Survey (USGS), with a spatial resolution of 90 m, was used for the calculation of the area (ARE) and drainage extension network (DRA) of each sub-basin. Flooded area (FLO), which is an important ecological variable for the distribution of species in river–floodplain systems (Junk et al. 1989), was calculated based on the per cent cover of wetlands using radar images of the satellite JERS-1 with a spatial resolution of 100 m. The fluvial distance between sampling sites (DIS) was included to take into account its potential influence in creating compositional dissimilarities among sites (Leprieur et al. 2009). This distance was established in reference to the extreme upstream point of the studied stretch (named P1 in the analysis; Fig. 1).

The set of regional variables also included a geomorphological component, i.e., the geological age of the terrain in each sub-basin (e.g., Souza Filho et al. 1999), which is considered an important factor influencing the biogeography of species (Lundberg 1998; Lundberg et al. 1998; Wilkinson et al. 2010). This variable, expressed as a percentage of area covered, was classified into four categories: Proterozoic (PRZ), Cenozoic-Paleogene (CNP), Cenozoic-Neogene (CNN) and Quaternary (QUA) (for a description, see Heiss et al. 2003). The covering percentage of each category was estimated in the form of polygons using ArcGIS software.

### Statistical analysis

#### *Principal components analysis (PCA)*

A principal components analysis (PCA) was performed to account for the collinearity observed among the limnological (oxygen, temperature, pH, conductivity) and physical variables (width, depth and transparency) (Table 1) and to reduce the number of variables in our analyses to a set of three composite principal components that describe dominant gradients of variation in the original variables. For instance, the

first three PCA axes accounted for 80% of the total variance. The first PCA axis (hereafter  $F_{DE}$ ) accounted for 41.5% of the total variance and was highly correlated with depth ( $r = 0.93$ ), transparency ( $r = -0.89$ ) and oxygen ( $r = -0.86$ ). The second PCA axis (hereafter  $F_{PH}$ ) explained 25% of the total variance and was mainly related to pH ( $r = 0.90$ ) and conductivity ( $r = 0.94$ ). The third PCA axis (hereafter  $F_{WI}$ ) accounted for 14% of the total variance and was highly correlated with width ( $r = -0.853$ ).

*Patterns of compositional dissimilarity*

We analysed the fish species abundances under flood and dry season conditions in each tributary, including 174 columns (species) and 20 rows (10 samples in two periods). Based on abundance data, compositional dissimilarity was estimated using the Bray-Curtis dissimilarity index. A hierarchical cluster analysis (HCA) using the Ward's linkage method (Legendre & Legendre 1998) was first applied to identify patterns of compositional dissimilarity between samples. Specifically, we aimed at identifying groups of samples having markedly distinct fish faunas.

An analysis of similarity (ANOSIM) was then performed between each pair of groups defined by the HCA to test whether differences between groups were statistically significant (McCune & Grace 2002). The ANOSIM is a nonparametric procedure testing the null hypothesis of no difference between two groups of samples (McCune & Grace 2002). This test involves a dissimilarity matrix in which the distances have been converted to ranks such that the smallest distance has a rank ( $r$ ) of 1. The dissimilarity matrix was computed using the Bray-Curtis dissimilarity index based on

abundance data. The ANOSIM procedure uses the  $R$  statistic that ranges from 1 to  $-1$  (Quinn & Keough 2002).  $R$  values greater than zero indicate a greater dissimilarity between groups than within groups. When  $R$  is equal to zero, the null hypothesis is accepted. Negative values of  $R$  indicate that dissimilarities within groups are greater than among groups (see McCune & Grace 2002 for more details). Finally, the similarity percentage (SIMPER) analysis was employed to assess the relative contribution of each fish species in explaining differences in species composition among groups defined by the HCA. Specifically, the SIMPER analysis aims at determining the contribution of each species to the average Bray-Curtis dissimilarity between groups. The Past 1.95 Program (Hammer et al. 2001) was used for this analysis.

*Environmental and geographical correlates of compositional dissimilarity*

We used the Euclidean distance to quantify the difference between sample pairs for several local (i.e.,  $F_{DE}$ ,  $F_{PH}$ ,  $F_{WI}$  resulting from a PCA) and regional variables (i.e., DRA and FLO, see Table 2). We also quantified an additional geographical distance measure associated to the main waterfalls (JIR and TEO). This pairwise distance measure consisted of assigning (i) a value of one for two samples separated by a given waterfall (e.g., TEO) and (ii) a value of zero for two samples that were not separated by this geographical barrier. The hydrological period (PER; dry and flood season) was also considered because it incorporates several other nonmeasured factors that are related to environmental seasonality (see Furch & Junk 1997)

Local	PER	OXG	TEM	PH	CON	WID	DEP	TRA
P1	F	5.08	25	5.7	12.2	186	14	0.5
P2	F	2.98	25.2	5.22	7.7	30	11.6	0.8
P3	F	3.65	23.2	5.66	10.2	20	11	1.2
P4	F	4.38	24.3	5.73	9.7	18	11.8	1.6
P5	F	2.68	24.5	5.27	7.6	60	11.2	1.4
P6	F	4.06	24.9	4.8	6.4	17	7.5	2
P7	F	1.7	25.4	5.53	17.8	80	8.8	1.3
P8	F	1.16	25.9	5.15	14.3	30.3	12.9	1.7
P9	F	0.76	27.8	5.68	19.1	50	12	1.6
P10	F	1.4	28.7	6.06	38.3	50	19	0.3
P1	D	8.6	27	5.67	11.8	130	3.8	0.4
P2	D	7.9	26.2	6.44	34.9	18	2.8	0.6
P3	D	7.3	26.4	5.84	12.4	15	1.5	0.9
P4	D	7.6	28.2	5.52	7.3	30	1.1	0.92
P5	D	7.7	29.2	5.55	8.4	17	1.7	0.4
P6	D	7.6	27.3	5.64	10.4	18	1.2	0.9
P7	D	7.4	29.3	4.92	4.1	50	1.3	1.27
P8	D	9.7	26.3	5.87	9.9	15	2.2	1.9
P9	D	6.6	26	5.68	9.6	3	1.5	0.6
P10	D	6.4	26.5	6.15	40.5	8	1.5	0.5

Table 1. Physical and chemical water characteristics (local factors) measured during the flood and dry seasons at 10 sampling sites along the studied stretch of the Madeira River.

PER, hydrological period where (F) is flood and (D) is dry seasons; OXG, oxygen ( $mg \cdot l^{-1}$ ); TEM, temperature ( $^{\circ}C$ ); PH; CON, conductivity ( $\mu S \cdot cm^{-1}$ ); WID, tributary width, in meters; DEP, tributary deep in meters; TRA, water transparency measured by the Secchi disc, in meters.

Table 2. Geographical position (UTM) and summary of several regional-scale environmental variables measured from ten sampling stations located at the mouth of the main tributaries of the Madeira River in the studied stretch.

Local	COD	LAT	LON	ARE	DRA†	DIS	FLO†	PRZ	CNP	CNN	QUA	JIR	TEO
P1	ABU	65° 32'48.9"S	9° 48'12.98"W	31527.29	5090.99	0	1155.99	1468.94	6636.38	251.72	0	1	1
P2	ARA	65° 19'6.18"S	10° 0'45.34"W	618.40	97.42	34.3	97.84	622.60	0	0	4.69	1	1
P3	SIM	65° 17'50.71"S	9° 30'12.39"W	513.47	81.03	42.8	0	527.03	0	0	0	1	1
P4	MUT	64° 55'17.93"S	9° 36'22.32"W	3334.68	588.39	71.6	106.23	1921.09	0	1131.09	383.44	1	1
P5	SLO	64° 51'13.44"S	9° 22'9.54"W	723.86	119.06	91.1	140.18	742.28	0	0.69	0	1	1
P6	KAR	64° 37'15.02"S	9° 11'32.53"W	623.89	94.36	122.4	70.31	578.48	0	61.00	0	0	1
P7	JAC	64° 23'56.67"S	9° 17'4.29"W	12163.20	2006.62	138.8	140.99	10063.55	0	2446.57	34.74	0	1
P8	JAT	64° 02'34.65"S	8° 49'49.00"W	157.29	22.57	197.8	0	29.09	0	132.04	0	0	0
P9	JTT	63° 54'41.46"S	8° 38'25.01"W	33.77	4.41	221.3	0.11	0	0	33.54	0.0079	0	0
P10	BEL	63° 50'20.51"S	8° 37'56.56"W	63.33	2.84	228.0	0.74	0	0	13.26	50.06	0	0

COD, tributary code; LAT, latitude; LON, longitude; ARE, sub-basin area (km<sup>2</sup>); DRA†, drainage extension network in km; DIS, distance from P01 (km); FLO†, flood area (km<sup>2</sup>); PRZ, Proterozoic area (km<sup>2</sup>); CNP, Cenozoic-Paleogene area (km<sup>2</sup>); CNN, Cenozoic-Neogene area (km<sup>2</sup>); QUA, Quaternary area (km<sup>2</sup>). The numbers 1 and 0 represent the position of the sampling station upstream or downstream of the Jirau (JIR) and Teotônio (TEO) waterfalls, respectively.

†Original values log transformed log<sub>10</sub> (x + 1) during analysis.

Abunã River (ABU); igarapé do Arara (ARA); igarapé Simão Grande (SIM); Mutumparaná River (MUT); São Lourenço River (SLO); Karipunas River (KAR); Jaciparanã River (JAC); igarapé Jatuarana I (JAT); igarapé Jatuarana II (JTT); igarapé Belmont (BEL).

and can result in temporal variation in the fish assemblage composition. To do this, we employed a binary distance measure. For instance, a value of one was assigned for two samples taken from the same hydrological period, whereas a value of zero was assigned for two samples that were taken from a different hydrological period. Last, we used the Manly's distance (Manly 1994) to quantify the difference in geological age between paired sub-basins (GEOL) because geological data were expressed as proportions of the total area of each sub-basin.

The significance of the relationship between compositional dissimilarity and each distance-based explanatory variable (see above) was determined using a multiple regression on distance matrices. Multiple regression using distance matrices is conceptually similar to the traditional approach, except that dependent and independent variables are represented by distance matrices. Multiple regression models using distance matrices have been successfully used in several studies (Baker 2006; Gladstone et al. 2006; Gido et al. 2009; Leprieur et al. 2009). One advantage of the method is that for each explanatory variable, the partial regression coefficients ( $\beta$ ) facilitate the comparison and ranking of their respective effects on compositional dissimilarity, while the effect caused by other variables is controlled. To overcome the problem of the lack of independence between sample pairs, the significance of standardised regression partial coefficients and multiple determination coefficients ( $R^2$ ) was evaluated using a permutation test ( $n = 999$ ; Casgrain 2001). We performed a forward selection procedure to ensure that each of the variables in the final model was statistically meaningful (Legendre & Legendre 1998; Casgrain 2001). This procedure is based on the fact that a variable should be included in the model if (i) it gives the equation with the most significant  $R^2$  and (ii)

its  $\beta$  coefficient is significant at the Bonferroni-corrected p-to-enter level ( $P = 0.05$ , see Casgrain 2001). We also showed the results of the full model including all the explanatory variables. These analyses were conducted using PERMUTE! 3.4.9 Software (Casgrain 2001).

## Results

### Fish species composition

Sampling of the ichthyofauna at the 10 collection points resulted in the catch of 5198 specimens belonging to 6 orders, 25 families and 174 species. Of these, 2294 specimens were caught during the flood season and 2905 during the dry season. The richest order was represented by Characiformes with 91 species (52.3%), followed by Siluriformes with 58 species (33.3%); the remaining orders comprised 25 species (14.4%) (see Appendix). The number of species per sample ranged from 4 to 39 with an average of 20 species (SD = 8;  $N = 60$ ).

### Patterns of compositional dissimilarity

The HCA discriminated two groups of sampling localities, independently of the hydrological period: (i) the localities downstream of the Teotônio waterfall (points P8, P9, P10) and (ii) the remaining ones (Fig. 2). The ANOSIM corroborates this result by showing a significant difference in species composition between samples located upstream and downstream of the Teotônio waterfall ( $R = 0.73$ ;  $P < 0.01$ ). Among the 174 species, 67 occurred exclusively upstream or downstream from the Teotônio waterfall (see Appendix). According to the SIMPER analysis, fifteen species comprised 60% of the average Bray-Curtis dissimilarity

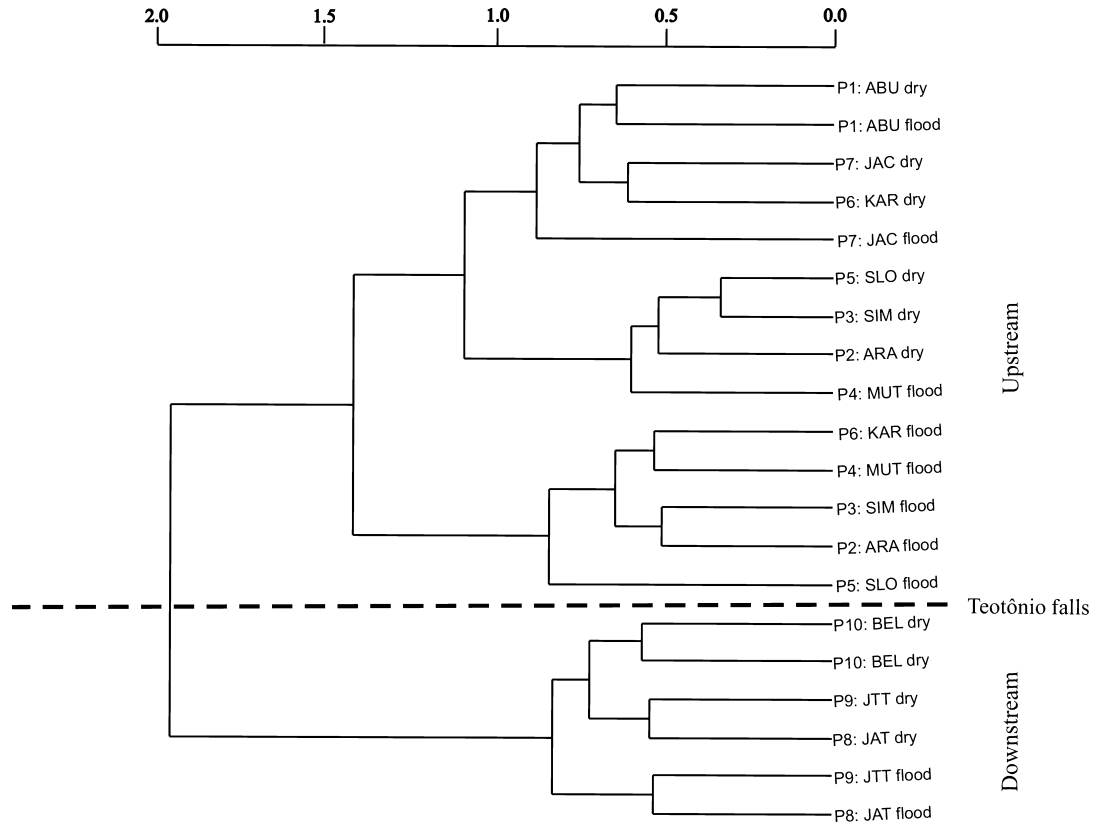


Fig. 2. Results of the hierarchical cluster analysis (Ward’s linkage method) that aims at identifying patterns of fish compositional dissimilarity for ten sampling sites. The dashed line represents the position of Teotônio waterfall in relation to the sequence of sampling stations along the studied stretch of the Madeira River.

(0.776) between samples located upstream and downstream the Teotônio waterfall (see species in bold in the Appendix): *Psectrogaster rutiloides* (11.47%), *Auchenipterichthys thoracatus* (9.33%), *Potamorhina altamazonica* (4.84%), *Acestrorhynchus microlepis* (4.50%), *Mylossoma duriventre* (4.40%), *Triportheus angulatus* (4.31%), *Hemiodus unimaculatus* (3.96%), *Sorubim lima* (2.73%), *Pimelodus aff. blochii* (2.34%), *Acestrorhynchus heterolepis* (2.30%), *Serrasalmus rhombeus* (2.18%), *Chalceus guaporensis* (2.01%), *Triportheus albus* (1.99%), *Acestrorhynchus falcirostris* (1.84%) and *Sorubim elongatus* (1.83%).

Environmental and geographical correlates of compositional dissimilarity

The complete regression model including all the explanatory variables explained 53% of the total variation in compositional dissimilarity (Table 3). Results showed that patterns of compositional dissimilarity were weakly explained by local-scale environmental conditions, especially those related to water characteristics. These results were confirmed by the reduced model resulting from a forward selection procedure, which explained 49% of the total variation

in compositional dissimilarity (Table 3). Standardised partial regression coefficients indicated that the Teotônio and Jirau waterfalls were the strongest predictors of compositional dissimilarity along the studied stretch of the Madeira River ( $\beta_{TEO} = 0.522$  and  $\beta_{JIR} = 0.433$ ). To a lesser extent, we found significant roles of river width ( $\beta_{FWI} = 0.234$ ), extension network ( $\beta_{DRA} = 0.376$ ) and hydrological period ( $\beta_{PER} = 0.207$ ) in explaining observed patterns of compositional dissimilarity.

Discussion

Large rivers in the Amazon basin, such as the Solimões, Negro and Madeira rivers, are recognised as important geographical barriers in the distribution of terrestrial fauna, as they segregate species or populations (Wallace 1852; Hellmayr 1910; Capparella 1987; Ayres & Clutton-Brock 1992; Patton et al. 2000; Hayes & Sewlal 2004). However, the manner in which rivers segregate species may differ for terrestrial and aquatic fauna. Connectivity in rivers occurs predominantly in a longitudinal direction, but also in a lateral dimension by the occupation of seasonally available aquatic habitats (the flood pulse dynamics; Junk et al. 1989; Fernandes 1997). Thus, the segrega-

Table 3. Regression of fish compositional dissimilarity against distance-based explanatory variables related to environment and geography. The full model includes all the explanatory variables. The reduced model results from a forward selection procedure (at  $P < 0.05$  after Bonferonni correction).

Variables	Complete model		Reduced model	
	Partial standardised regression coefficients ( $\beta$ )	$P$	Partial standardised regression coefficients ( $\beta$ )	$P$
<b>Local</b>				
F <sub>DE</sub>	0.225	0.322	–	
F <sub>PH</sub>	0.122	0.122	–	
F <sub>WI</sub>	0.205*	0.023	0.234*	0.008
PER	–0.004	0.984	0.207*	0.003
<b>Regional</b>				
FLO	–0.112	0.158	–	
DRA	0.476*	0.001	0.376*	0.002
GEOL	–0.243	0.107	–	
DIS	–0.397*	0.023	–0.462*	0.008
<b>Falls</b>				
Jirau	0.386*	0.001	0.433*	0.001
Teotônio	0.607*	0.001	0.522*	0.001
R <sup>2</sup>	0.530*	0.001	0.497*	0.001

Asterisks indicate significant values. See Materials and methods (Tables 2 and 3) for variable abbreviations and for more details.

tion of freshwater fauna may be defined by the different degrees of connectivity of aquatic systems (Nadeau & Rains 2007; Rahel 2007; Cote et al. 2009). The causal role of the Madeira rapids in differentiating populations upstream and downstream has been proposed for species such as the pink river dolphin *Inia geoffrensis* (Banguera-Hinestroza et al. 2010), and the giant Amazon River turtle *Podocnemis expansa* (Pearse et al. 2006). The Madeira River rapids have also been suggested to form a major barrier to migration for a number of fish species and to potentially limit the distribution of a number of other fish taxa (Goulding 1979; Hubert & Renno 2006).

In our study, the substitution of fish species upstream and downstream of the Teotônio waterfall (and more marginally of the Jirau waterfall) exceeds effects of local and regional factors known to influence fish assemblage patterns. Moreover, the boundary effect of the Teotônio waterfall was greater than effects of seasonal variations in assemblage structure, usually strongly expected in tropical systems (Goulding 1980; Lowe McConnell 1987; Junk et al. 1989).

A deeper analysis of the main fish families present in our samples reveals patterns of species substitution upstream and downstream of the waterfalls. Overall, 29 species were registered exclusively upstream of Jirau and 20 species exclusively downstream of Teotônio waterfalls, these last species being commonly found in the Amazonian lowlands (Saint-Paul et al. 2000; Santos et al. 2006; Zuanon et al. 2008). The capacity to migrate upstream requires that the fish swim faster than the water velocity, necessitating

substantial energy cost. This cost can be reduced by schooling (but see a review in Blake 2004). In this sense, Characiforms could be considered more efficient swimmers than Siluriforms (Santos et al. 2007; Makrakis et al. 2010). This may explain the higher number of species of the former group observed exclusively upstream of the rapids (15 characins vs 7 catfish species).

The slope of the Jirau and Teotônio waterfall certainly does not constitute a completely insurmountable barrier for fish (700 m from shore to shore and 10 m height of cataract, Keller 1874; Goulding 1979), especially when considering the occasional occurrence of exceptionally great river floods facilitating the upstream migration of shoals of several medium- to large-sized fishes (Goulding 1979; Howes 1998). However, it certainly reduces the upstream dispersal movements of several fish species. This is corroborated by a recent study involving the tambaqui *Colossoma macropomum* (Characidae), one of the most floodplain-dependent species of the Amazonian ichthyofauna, and which revealed low gene flow between populations upstream and downstream of the rapids stretch of the Madeira River (Farias et al. 2010). A similar pattern has also been observed recently for another Amazonian migratory species, *Prochilodus nigricans* (I.P. Farias, unpublished data).

Besides the strong effect of Teotônio waterfall, we also detected a subsidiary effect of Jirau waterfall on fish distribution. The position of Jirau waterfall in the rapids stretch coincides with the boundary between two plateaus of different geological origins on the left river bank and is known to constitute a contact zone in the distribution of the frog *Allobates femorales* (Simões et al., 2004) and of two *Caiman* species (Alligatoridae; Hrbek et al., 2008). These evidences indicate that the selective barrier represented by the rapids between Jirau and Teotônio waterfalls may generate a metapopulation structure for species present in the lowlands upstream (Guaporé, Mamoré and Beni) and downstream (Central Amazon) of these waterfalls.

Besides the difficulty of overcoming the Teotônio waterfall, the effective establishment of fish populations would depend on their ability to access the few available flooded forests in that river stretch. Species adapted to floodplain environments, strongly dependent on food and shelter provided seasonally by the flooded forests and the large macrophyte stands, were rare or absent from the rapids stretch between the two waterfalls. They include several detritivorous loricariids and curimatids, some macrophyte-eating anostomids, frugivorous pacus and piranhas (Characidae: Serrasalminae) (Goulding 1980; Saint-Paul et al. 2000), species widely distributed in the Amazon lowlands including electric eels, stringrays, a few

cichlids, and many catfishes of the families Auchenipteridae, Callichthyidae, Doradidae and Pimelodidae (see Appendix). Only the piscivorous species *Acestorhynchus* cf. *microlepis* and the seed- and fruit-eating species *Myleus setiger* were restricted to (or predominantly found in) these rapids stretches. Another remarkable characteristic was that most of the few typically lowland migratory fishes found in the rapids stretch were only represented by adult specimens in poor condition (thin individuals, most often with empty stomachs and having low visceral fat deposits), indicating a lower habitat quality for those fishes (but see Hoopes et al. 2005). These evidences indicate that besides its potential effect as a barrier for some species, the nearly 100-km-long rapids stretch between Jirau and Teotônio waterfalls acts also as a strong ecological filter, restricting its occupation by many species and impairing the colonisation of upstream stretches (cf. Winemiller et al. 2008). The scarcity of aquatic macrophytes in the rapids stretch could also explain the absence or low abundance in young-of-the-year of most of these species, with a few exceptions (e.g., *Pellona castelnaeana*, *Plagioscion squamosissimus*, *Triporthus albus*, *Brycon amazonicus*; our personal observations, data not shown). Furthermore, larvae and juveniles drifting from the Bolivian Amazon and surviving the strong turbulence of the waterfalls probably do not find a suitable floodplain area that could be used as nursery habitats in the rapids stretch.

River rapids offer ideal natural sites for the construction of hydroelectric power plants. For this reason, the Brazilian government has decided to construct two large hydroelectric power plants on the Madeira River, one immediately downstream of Teotônio waterfall and one downstream of Jirau waterfall. Environmental modifications induced by dams could affect fish populations in several ways, but the most obvious negative effect is restriction of migration (Cumming 2004). Concerning this last point, our finding of clear dissimilarities between assemblages upstream and downstream Teotônio and Jirau waterfalls strongly suggests that these waterfalls already constitute natural geographical barriers for fish movements. Nevertheless, it will be particularly important, after dams construction, to avoid the blockage of migratory routes of the giant catfishes of the genus *Brachyplatystoma* and some characiform species that are supposed to regularly overcome the waterfalls (e.g., *Colossoma macropomum*, *Prochilodus nigricans*). The proposal to solve this problem is to construct an efficiently designed fish pass to allow the selective movements of such species (but see Pelicice & Agostinho 2008). A first fish pass is planned to link the lower portion of Madeira River to the stretch between Teotônio and Jirau waterfalls, and

a second one is planned to connect that stretch to the Madeira headwaters upstream Jirau.

However, dam construction can generate other impacts on the ichthyofauna. The homogenisation of environmental conditions along the Madeira River (and over the rapids stretch between Jirau and Teotônio waterfalls) as a consequence of damming will possibly result in ichthyofaunal mixing, with typically lowland fishes occupying the impounded stretches of the river and gaining a chance to access upstream areas. Moreover, the predominantly omnivorous fish assemblages that occupy the river upstream Teotônio waterfall will probably be substituted by detritivorous species, combined with an expected increase in the abundance of piscivorous fishes, as observed in other tropical dams (e.g., Gubiani et al. 2010). Habitat loss or alteration because of discharge modifications and changes in water quality and temperature, or mortality resulting from fish passage through hydraulic turbines or over spillways during their downstream migration (Bunn & Arthington 2002) foresees important impacts on fish populations as well.

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## Supporting Information

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

**Appendix 1.** Species abundance (number of collected specimens) in Madeira River stretches upstream Jirau, between Jirau and Teotônio and downstream Teotônio waterfalls.

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