Research

Ecography 35: 001–007, 2012
doi: 10.1111/j.1600-0587.2012.07724.x

Subject Editor: Nathan J. Sanders. Accepted 25 September 2012

Natural fragmentation in river networks as a driver of speciation for freshwater fishes

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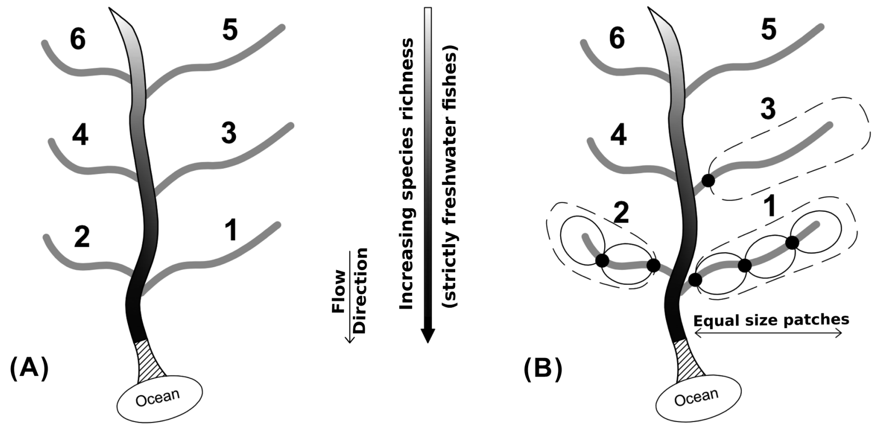
Although habitat fragmentation fosters extinctions, it also increases the probability of speciation by promoting and maintaining divergence among isolated populations. Here we test for the effects of two isolation factors that may reduce population dispersal within river networks as potential drivers of freshwater fish speciation: 1) the position of subdrainages along the longitudinal river gradient, and 2) the level of fragmentation within subdrainages caused by natural waterfalls. The occurrence of native freshwater fish species from 26 subdrainages of the Orinoco drainage basin (South America) was used to identify those species that presumably arose from in-situ cladogenetic speciation (i.e. neo-endemic species; two or more endemic species from the same genus) within each subdrainage. We related subdrainages fish diversity (i.e. total, endemic and neo-endemic species richness) and an index of speciation to our two isolation factors while controlling for subdrainages size and energy availability. The longitudinal position of subdrainages was unrelated to any of our diversity measures, a result potentially explained by the spatial grain we used and/or the contemporary connection between Orinoco and Amazon basins via the upstream Casiquiare region. However, we found higher neo-endemic species richness and higher speciation index values in highly fragmented subdrainages. These results suggest that habitat fragmentation generated by natural waterfalls drives cladogenetic speciation in fragmented subdrainages. More generally, our results emphasize the role of history and natural waterfalls as biogeographic barriers promoting freshwater biodiversity in river drainage basins.

Speciation is a key process in ecology and evolutionary biology because it generates biodiversity. The relative importance of factors contributing to diversification remains thus an active research area (Orr and Smith 1998, Losos and Schluter 2000, Rundle and Nosil 2005, Ricklefs and Bermingham 2007, Gavrilets and Losos 2009, Hortal et al. 2011). One of the earliest hypotheses advanced to explain how environmental factors could affect diversification rates was proposed by Cracraft (1982). This author hypothesized that speciation rates should increase with the number of natural barriers generating geographical isolation. Indeed, physical or climatic subdivisions of habitats limit gene flow in ways that can promote local diversification (Rahel 2007, Burridge et al. 2008, Boizard et al. 2009, Meeuwig et al. 2010). However, this fragmenting process also reduces the amount of available habitat, producing in fine smaller populations that may be subject to higher extinction rates (Fagan 2002, Morita and Yamamoto 2002, Hugueny et al. 2011).

Riverine networks represent overlooked systems offering an opportunity for testing these evolutionary hypotheses (Burridge et al. 2008). Compared to landscapes where individuals move through several dispersal routes, the movements of riverine organisms within drainage basins (i.e. strictly freshwater organisms) are restricted along the aquatic branches of the network. Then, the connectivity between organism's sub-populations strongly depends on the configuration of connections between habitat patches (Benda et al. 2004, Grant et al. 2007, Rahel 2007). As a consequence, the degree of connectivity within a river network should be an important mechanism driving speciation, extinction and immigration on evolutionary time scales. Waterfalls are natural barriers within the river network acting on the degree of connectivity and shaping the permeability and availability of habitats for populations of freshwater organisms (Rahel 2007, Cote et al. 2008). Besides decreasing colonization and increasing extinction rates, these barriers are also expected to increase speciation rates by promoting and maintaining population divergence (Losos and Parent 2009). Figure 1 depicts a river network under different configurations of habitat patches. Under a continuous river network configuration (Fig. 1A), immigration, extinction and speciation rates within subdrainages depend mostly on their size and position along the main river channel (Osborne and Wiley 1992, Oberdorff et al. 1997, Grenouillet et al. 2004, Hitt and Roberts 2012).



$$I_{1\ \&\ 2} > I_{3\ \&\ 4} > I_{5\ \&\ 6}$$
$$E_{1,3\ \&\ 5} < E_{2,4\ \&\ 6}$$
$$S_{1\ \&\ 2} < S_{3\ \&\ 4} < S_{5\ \&\ 6}$$

$$I_{1,2\ \&\ 3} = 0;\ I_4 > I_5 = I_6$$
$$E_1 > E_2 > E_3 > E_4 = E_6 > E_5$$
$$S_1 > S_2 > S_3 > S_5 > S_6 > S_4$$

Figure 1. Importance of longitudinal position and waterfalls on immigration (I), extinction (E), and speciation (S) rates (i.e. per species per unit time) in subdrainages of a hypothetical drainage basin. There is usually an increase in species richness from upstream to downstream areas (Osborne and Wiley 1992, Oberdorff et al. 1997, Grenouillet et al. 2004, Hitt and Roberts 2012) with a level off at the river mouth (when the main channel reaches the ocean; dashed region). Following island biogeography theory, (A) subdrainages close to the zone having the highest number of potential colonists should have higher immigration and lower extinction and speciation rates compared to similar subdrainages distant from this zone; large subdrainages should have lower extinctions and higher speciation rates compared to small ones. (B) This pattern changes when considering waterfalls (black dots) within the same system; immigration should be minimal and extinctions should be greater in subdrainages containing waterfalls (1, 2 and 3) compared to non-fragmented ones (4, 5 and 6), while the isolation from the species pool should promote higher speciation rates on those subdrainages that have higher number of patches (circles within subdrainages; 1, 2 and 3).

Indeed, considering that upstream subdrainages are more isolated due to the unidirectional hydrological flow, they should receive new colonists less frequently and should display greater extinction and speciation rates than downstream ones (Fig. 1A, Oberdorff et al. 2011). Compared to non-fragmented subdrainages, the presence of natural barriers along the drainage network (Fig. 1B) should greatly modify the underlying evolutionary rates. The spatial configuration and waterfall distribution presented in Fig. 1B imply differential speciation, extinction and immigration rates for the different subdrainages. These rates should depend on a combination of subdrainages size and position but also on their degree of fragmentation supposed to prevent immigration and to gradually increase extinction rates (Fig. 1B). Everything else being equal (i.e. controlling for other factors known to affect diversity), if barriers promote speciation processes, higher speciation rates should be found in subdrainages benefiting from numerous patches isolated from each other by waterfalls (see case 1 in Fig. 1B).

Here we apply the framework conceptualized in Fig. 1 to subdrainages of a large tropical and fish species-rich drainage basin, the Orinoco River in South America (Fig. 2). We hypothesize that, after controlling for environmental factors already known to influence diversity patterns, the number of continuous freshwater 'patches' within subdrainages and the position of these subdrainages along the longitudinal river gradient should be positively related to the total number of endemic fish species inhabiting these subdrainages and particularly to the number of endemics originated by in-situ cladogenetic speciation (i.e. neo-endemic species; sensu Tedesco et al. 2012).

Methods

Biological data

We used a published data set of fish species occurrence from the Orinoco drainage basin (Lasso et al. 2004a). These authors compiled species lists for the main subdrainages (see below) from museums, taxonomic information and field work data (see references therein), providing the most updated fish species list registered for the Orinoco River basin. Only strictly freshwater species were considered in our analyses; all marine, euryhaline and introduced species were excluded based on information available in the original sources or in Fishbase (Froese and Pauly 2011). We considered 26 subdrainages of the Orinoco River basin as our sampling units: Alto Orinoco, Apure, Arauca, Aro, Atabapo, Bita, Capanaparo, Caris, Caroni, Cataniapo, Caura, Cinaruco, Cuchivero, Guaviare, Inirida, Manapiare, Meta, Morichal-Largo, Pao, Parguaza, Sipapo-Cuao, Suapure, Tomo, Venturi, Vichada, and Zuata (Fig. 2). The Casiquiare subdrainage was excluded because fish fauna exchanges with the Amazon River basin are known to frequently occur in this zone (Fig. 2, Willis et al. 2010). We registered for each subdrainage total and endemic (i.e. species unique to a single subdrainage) species richness. To guarantee that endemic species assigned to a subdrainage

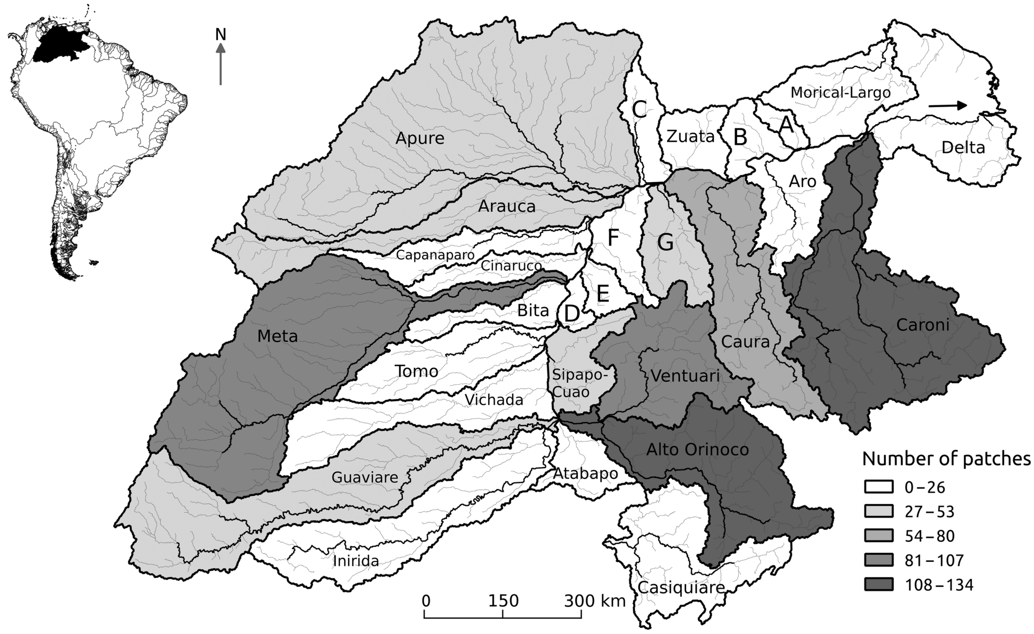


Figure 2. Number of patches within subdrainages of the Orinoco River basin. Names of small subdrainages: A = Caris, B = Pao, C = Manapire, D = Cataniapo, E = Parguaza, F = Suapure and G = Cuchivero. The arrow on the Delta region indicates the flow direction.

were not present in other South American river drainage basins, we searched for their distribution using information from Fishbase (Froese and Pauly 2011) and from the most comprehensive spatial database currently available on global riverine fish distribution (Brosse et al. 2012, Tedesco et al. 2012).

Speciation metrics

To examine the effects of the longitudinal gradient and of river network fragmentation due to waterfalls as drivers of fish speciation within subdrainages, we used first overall endemic species richness in each subdrainage as a substitute for speciation intensity. However, as overall endemic species richness may not be a good proxy to quantify speciation (Chen and He 2009, Kisel and Barraclough 2010, Tedesco et al. 2012), we further considered the number of endemic species that presumably arose from in-situ (i.e. within a given subdrainage) cladogenetic speciation (hereafter called neo-endemics, sensu Tedesco et al. 2012) as a more accurate measure of speciation intensity. To define neo-endemics we followed the method proposed by Coyne and Price (2000) considering that the presence of two or more endemic species from the same genus should reflect in-situ speciation (i.e. neo-endemic species). Finally, we applied a third speciation metric following Kisel and Barraclough (2010). Based on Coyne and Price's method, these authors quantified an index (or probability) of speciation as the number of genera with two or more endemic species divided by the number of genera with one or more endemic species (Kisel and Barraclough 2010, Tedesco et al. 2012). This last approach focuses on the ability of lineages to speciate rather than on what controls the size of radiations, which is better reflected by the number of neo-endemic species. Using only genera with endemic species also excludes lineages that have not been isolated or not been present long enough to speciate within subdrainages (Kisel and Barraclough 2010). Consequently, we excluded subdrainages for which no endemic species was recorded: Apure, Arauca, Bita, Capanaparo, Caris, Cuchivero, Manapiare, Pao, Vichada and Zuata. The index varies between 0 and 1, a value of 0 indicating no in situ speciation and a value of 1 indicating that all genera have undergone in situ speciation.

Environmental predictors

We used a set of environmental layers of 30-arcsec resolution (ca 1 × 1 km in the study zone) to estimate for each subdrainage variables related to isolation, energy availability and habitat size (see Supplementary material Appendix 1, Table A1 for a list of variables and sources). All these variables are known to be important predictors of total and endemic riverine fish species richness at large spatial grains and extents (Oberdorff et al. 2011). Energy availability and habitat size were measured using subdrainage mean annual net primary productivity (NPP, g carbon m^{-2}) and total surface area (area, km^2), respectively.

The degree of subdrainages isolation was estimated by using two measures acting at two different spatial extents. First, assuming an isolation gradient from upstream to downstream areas (Fig. 1), we used the distance from the confluence of each subdrainage with the main channel to the mouth of the Orinoco River (DistD) as a measure of subdrainage position along the longitudinal gradient. Second, natural waterfalls were considered as a surrogate for habitat fragmentation in each subdrainage. Based on elevation data at 3-arcsec resolution, we defined a waterfall as a slope greater than 30% between two adjacent grid cells (i.e. a difference in elevation of ca 30 m between two adjacent grid cells) along the river course (sensu knickpoints; Crosby and Whipple 2006). Since there is no consensus on which waterfall height can be considered as an insurmountable barrier for freshwater fishes, we considered such a threshold as a barrier high enough to prevent any upstream (and most downstream) fish dispersal. Then, we calculated the number of patches (continuous drainage area between two waterfalls) within each subdrainage. Assuming that small patches should prevent the establishment and maintenance of any fish population, we only considered patches having a surface area equal or greater than 13 km^2. According to Tedesco et al. (2012), this surface is the smallest area where a fish population can persist (i.e. the smallest drainage basin where a strictly freshwater fish species has been found so far).

Statistical analysis

We evaluated the effects of subdrainages' longitudinal position and fragmentation caused by waterfalls on total, endemic and neo-endemic species richness using multiple linear regression models. Area, number of patches, DistD and mean NPP values for each subdrainage were used as predictor variables in all models. When analyzing endemic and neo-endemic species richness, we added the total species richness as a covariate because this variable is known to partly explain endemic species richness (Oberdorff et al. 1999, Tedesco et al. 2012). Furthermore, in order to account for potential sampling biases present in our fish distribution dataset, we used a value ranging from one to four that broadly reflects the sampling intensity applied for each subdrainage. This last categorical variable was empirically established based on the experience and knowledge of several freshwater fish regional experts who assigned a 'sampling effort' value to each subbasin based on their own samplings and completeness of regional museum collections (Lasso et al. 2004b, p. 47); this variable was included in all models. Because the effects of fragmentation by waterfalls on species richness and endemism might vary with the location of subdrainages along the river main channel, we tested in all models the effect of an interaction term between these two variables. However, this interaction term neither produced a significant effect nor changed the effects of the other variables (results not presented). Except for the sampling intensity variable, all response and predictive variables were $\ln(x + 1)$-transformed to improve normality. To analyze the index of speciation we used a generalized linear model (GLM) with binomial distribution including all predictor variables except total richness and accounting for the number of genera having at least one endemic species. For comparative purposes, we estimated the fit (R^2) of the GLM model using null and residual deviances $[(\text{Null} - \text{Residual}) \times \text{Null}^{-1}]$. Multicollinearity in models was checked using a variance inflation factor (VIF) procedure but it revealed no strong collinearity among predictors (VIF: mean = 1.86, range = 1.23–2.97, standard deviation = 0.46).

After building full models, stepwise procedures were implemented to determine the most important variables in each model based on Akaike's information criterion (AIC). We applied a hierarchical partitioning procedure to determine the proportion of variance independently explained by each predictor (%PV) in the models, highlighting those that most contributed to the model fit. Finally, we ensured for the absence of spatial autocorrelation in model residuals using watercourse distances, Moran's I coefficients and correlograms. All analyses were carried out in R environment (R Development Core Team) using lm, glm, step, correlog and hier.part functions from stats, pgirmess (Giraudoux 2011) and hier.part (Walsh and Mac Nally 2008) packages, respectively.

Results

There are 874 species of strictly freshwater fishes listed so far for all subdrainages of the Orinoco River basin. From this species pool, 12% (107) are considered as endemics among which 25 were classified as neo-endemic species (Supplementary material Appendix 2, Table A2). The number of patches by subdrainage is highly variable, ranging from zero (i.e. no waterfalls fragmenting a subdrainage) to 134 (mean = 29, SD = 41, Fig. 2). Alto Orinoco, Caroni and Meta subdrainages have the highest number of patches (134, 118 and 100, respectively) while Meta and Caroni have the highest endemic richness values (endemic richness: 23 and 16, neo-endemic richness: 8 and 7, respectively) and also highest number of genus containing neo-endemic species (*Apistoloricaria*, *Astroblepus*, *Bryconamericus* and *Corydoras*; *Lebiasina*, *Neblinichthys* and *Trichomycterus*, respectively).

The model explaining total species richness accounts for 28% of the variability and it identifies sampling intensity as a positive and significant predictor, while subdrainage size has a marginally significant effect. The stepwise-selected model identifies these two variables as significant predictors and confirmed that the number of patches and longitudinal gradient position (as measured by DistD) of subdrainages are unrelated to total species richness (Fig. 3A, Table 1). The model explaining endemic species richness accounts for 70% of the variability and identifies subdrainage size and energy availability (as measured by NPP) as positive and significant predictors (Table 1), while sampling intensity shows a marginally significant effect. The stepwise procedure further identifies a marginally significant effect of total richness on endemic species richness (Table 1). We found no significant effect of the number of patches (Fig. 3B) or of the longitudinal gradient position on endemic species richness.

The neo-endemic species richness model explains 21% of the variance and indicates a marginally significant positive influence of the number of patches (Fig. 3C). This tendency is confirmed by the stepwise procedure, which identifies the number of patches as the only significant predictor of neo-endemic species richness in a model accounting for 37% of total variability (Table 1). Finally, the speciation index was not significantly related to any of the predictors. However, the model having the lowest AIC value only includes the number of patches, albeit not significantly (Table 1, Fig. 3D). Whatever the models, DistD was never identified as a significant predictor. Finally, spatial

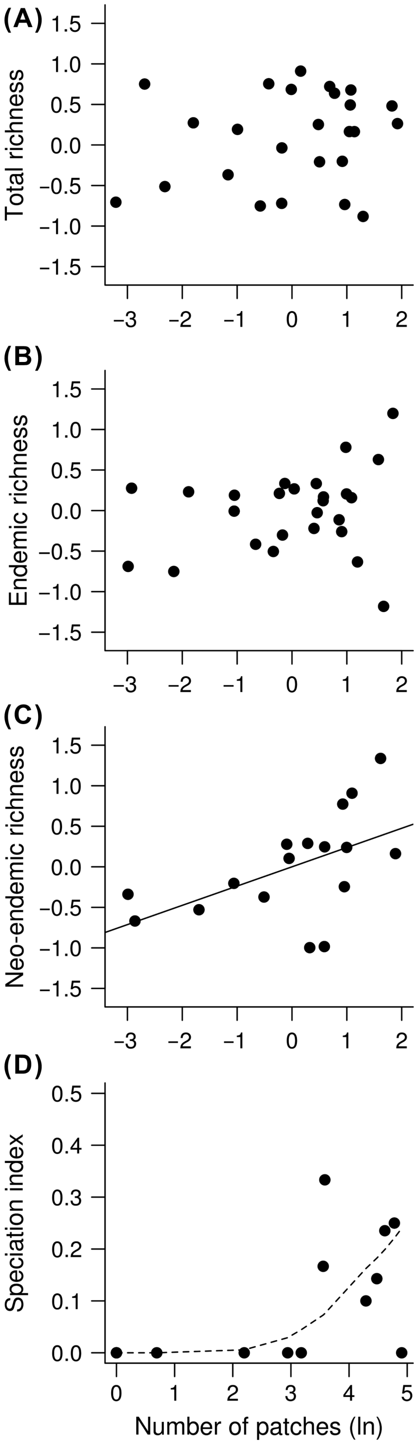


Figure 3. Partial-regression plots showing partial effects between the number of patches and (A) total, (B) endemics and (C) neo-endemic species richness extracted from full multiple linear models. Partial slopes (ß), %PV and p-values from full models are given in Table 1. (D) Relationship between the speciation index and the log-transformed number of patches. The solid line (C) represents a significant effect and the dashed line (D) shows a lowess (tension parameter = 0.6).

autocorrelation at the first distance class estimated from all model residuals shows non-significant Moran's I values (Supplementary material Appendix 1, Fig. A1).

Discussion

Habitat fragmentation has conflicting consequences on biodiversity. Theory predicts that subsequent to isolation, extinction probabilities increase in fragmented habitats where isolated populations cannot be rescued by immigrants from neighboring areas (MacArthur and Wilson 1967). Conversely, lower genetic exchanges among populations of isolated habitats enhance diversification (Gavrilets and Losos 2009, Kisel and Barraclough 2010, but see Losos 2010), promoting higher speciation rates at evolutionary time scales. Our study sheds light on the geomorphological features promoting diversification processes in a tropical species-rich aquatic realm, the Orinoco River basin. This riverine system became fully established after the rapid uplift of the Andean mountains about 7 Ma ago, a period since which some northern South American taxa (e.g. highland plants, bees, birds and rodents) have exponentially diversified producing the current outstanding biodiversity levels (Hoorn et al. 2010). Indeed, according to phylogenetic and fossil evidences, the major freshwater fish biogeographic patterns presently found in the Orinoco region probably originated during this period (Albert and Carvalho 2011).

As predicted by our schematic framework (Fig. 1), we found higher neo-endemism richness in fragmented subdrainages and a positive relationship with subdrainages fragmentation level (i.e. the number of patches created by natural waterfalls within subdrainages). Similarly, our speciation index also showed higher values in fragmented subdrainages and a clearly positive, albeit not significant, trend with fragmentation level. These findings support the hypothesis that fragmentation by waterfalls generates cladogenetic speciation within-subdrainages, a process that similarly affects highly isolated islands and lakes, where local speciation has largely contributed to an increase in endemism richness over evolutionary timescales (Heaney 2000, Losos and Schluter 2000, Barluenga et al. 2006, Seehausen 2006, Algar and Losos 2011). In our study, there was no significant relationship between overall or endemic fish richness and subdrainages fragmentation level (Fig. 3A, B). This result indicates that, even though new species may have been generated by cladogenetic processes, extinction rates could slightly overcome speciation rates, making total and endemic richness independent of the degree of subdrainages fragmentation.

Contrary to our expectations, none of our diversity descriptors was significantly affected by subdrainages position along the longitudinal gradient. This result suggests that the isolation of a subdrainage due to its position along the longitudinal river gradient is not an important factor driving diversity patterns, at least at the spatial scale applied here. This finding partly contradicts results of previous studies highlighting an increase in subdrainages species richness along the longitudinal gradient due to a longitudinal increase in the size of the species pool (Oberdorff et al. 1997). A possible explanation for this discrepancy is the existing link between the Orinoco and the Amazon River basins in the Casiquiare region (upstream region of the Orinoco River, Fig. 2). This natural waterway connecting the two river basins is considered as the Casiquiare River capture by the Negro River (Amazon basin) and acts as a

Table 1. Partial slope coefficients (ß), percentages of partitioned variance through hierarchical partitioning (%PV) and partial p-values [ß (%PV; p), respectively] from linear (total, endemic and neo-endemic species richness) and generalized linear models (speciation index) from subdrainages of the Orinoco River basin (see Methods for abbreviations). Both results from full models (using all predictors) and stepwise-selected variables (based on Akaike's information criterion) are presented. Significant p-values are given in bold.

	Partial coefficients [ß (%PV; p)]			
Variables	Total richness	Endemics	Neo-endemics	Speciation index
Full models				
Waterfalls				
Ln(Npatches)	0.0918 (17.5; 0.448)	0.0932 (21.3; 0.288)	0.2376 (51.4; 0.078)	0.6686 (63.1; 0.257)
Local				
Ln(DistD)	0.0964 (1.6; 0.616)	−0.0508 (0.9; 0.711)	−0.1256 (2.7; 0.484)	−0.2248 (1.6; 0.581)
Ln(Area)	0.3983 (42.5; 0.052)	**0.3806 (28.5; 0.021)**	0.1604 (27.1; 0.477)	−0.0066 (26.7; 0.995)
Sampling intensity	**0.3557 (35.8; 0.048)**	0.2440 (8.7; 0.080)	−0.0284 (2.7; 0.910)	−0.1808 (3.6; 0.723)
Ln(Total richness)	–	0.2670 (21.0; 0.108)	0.0264 (8.3; 0.938)	–
Current climate				
Ln(NPP)	−0.1089 (2.6; 0.845)	**0.9535 (19.6; 0.024)**	−0.2118 (7.7; 0.735)	−1.0693 (5.0; 0.532)
Adjusted R^2	0.2797	0.6977	0.2066	0.5416$^{\#}$
p-values	**0.0377**	**0.0000**	0.2199	–
AIC	69.59	52.32	42.53	29.60
Selected variables (stepwise)				
Waterfalls				
Ln(Npatches)			**0.2497 (100; 0.006)**	0.6921 (100; 0.134)
Local				
Ln(DistD)				
Ln(Area)	**0.4903 (64.5; 0.004)**	**0.4392 (36.4; 0.004)**		
Sampling intensity	**0.3133 (35.5; 0.034)**	**0.2615 (8.9; 0.039)**		
Ln(Total richness)	–	0.2908 (25.3; 0.069)		–
Current climate				
Ln(NPP)		**1.1904 (29.4; 0.001)**		
Adjusted R^2	0.3402	0.7082	0.3663	0.4731$^{\#}$
p-values	**0.0032**	**0.0000**	**0.0060**	–
AIC	64.90	50.00	35.60	22.30

$^{\#}$Estimated through model deviances $[(\text{Null} - \text{Residual}) \times \text{Null}^{-1}]$.

selective corridor for fish fauna exchanges from both river basins (Willis et al. 2007, 2010, Winemiller et al. 2008). Therefore, this connection can reduce the upstream-downstream isolation gradient created by the unidirectional hydrological flow and could explain the absence of a species richness gradient along the fluvial continuum.

In addition to the prominent role of fragmentation on shaping current freshwater fish diversity and in accordance with previous findings (Oberdorff et al. 1999, Tisseuil et al. pers. comm.), our results also show positive and significant effects of subdrainages size and energy availability on endemic species richness. These relationships have been attributed to two different non-exclusive evolutionary mechanisms (Hugueny et al. 2010, Oberdorff et al. 2011): 1) larger areas are more heterogeneous, promoting in fine higher speciation rates (Losos and Schluter 2000) and 2) energy availability increases resources available for a biological community favoring in fine specialization processes (Evans et al. 2005). However, as subdrainages size and energy availability were not significantly related to our other speciation descriptors (Table 1), we suggest that habitat size or energy availability per se are not conditioning speciation intensity in our system.

To conclude, our results corroborate the assumption that speciation processes are important factors determining biogeographic diversity patterns (Losos and Schluter 2000, Chen and He 2009, Schluter 2009) by showing that speciation processes have shaped in part the regional diversity patterns of endemic freshwater fishes of the Orinoco River basin, through natural fragmentation of the aquatic networks created by waterfalls.

Acknowledgements – We thank the BIOFRESH project supported by the European Commission (FP7-ENV-2008, contract no. 226874) and the Inst. de Recherche pour le Développement (IRD, contract no. 04030047) through LMI EDIA for their financial support. MSD received a training (BSP-PCI/MCTI/CNPq/INPA no. 680.004/2009-2) and a thesis grant (Science without Borders program, MCTI/MEC) from the Brazilian government. We are grateful to B. Hugueny and Clément Tisseuil for comments on earlier versions of the manuscript and C. Jézéquel and E. X. C. Alves for assistance with GIS and mapping.

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Supplementary material (Appendix E7724 at <www.oikosoffice.lu.se/appendix>). Appendix 1, 2.