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RESEARCH ARTICLE

Panbiogeographic analysis of the distribution patterns of the freshwater species of Sciaenidae (Actinopterygii: Perciformes) in the Amazon Basin

Análise panbiogeográfica dos padrões de distribuição das espécies dulcícolas de Sciaenidae (Actinopterygii: Perciformes) na Bacia Amazônica

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Resumo Sciaenidae inclui quatro gêneros (*Pachypops*, *Pachyurus*, *Petilippinis* e *Plagioscion*) e cerca de 20 espécies exclusivamente dulcícolas, distribuídas em rios sul-americanos. Neste trabalho, a distribuição de 10 espécies de Sciaenidae de água doce com ocorrência na Bacia Amazônica, pertencentes aos gêneros *Pachypops*, *Pachyurus*, *Petilippinis* e *Plagioscion*, foi analisada com métodos panbiogeográficos quantitativos. Pela análise de traços, foram encontrados três traços generalizados e seis nós biogeográficos. O centro de massa das espécies estudadas está localizado no Baixo Amazonas (Óbidos), onde ocorrem seis espécies. Os resultados sugerem que a distribuição de Sciaenidae dulcícolas da América do Sul corresponde aos eventos vicariantes associados à formação da bacias dos rios Amazonas e Orinoco e aos eventos relacionados às formações das bacias dos rios Paraná, Paraguai e Prata. O escudo das Guianas constitui uma feição geotectônica de importância na configuração dos padrões de distribuição destas espécies. Estes padrões são congruentes com os observados em outras linhagens derivadas de grupos marinhos na América do Sul.

Palavras-Chave: pan-biogeografia, análise de traços, Bacia Amazônica, América do Sul.

Abstract The Sciaenidae include four genera (*Pachypops*, *Pachyurus*, *Petilippinis* and *Plagioscion*) and about 20 species restricted to freshwater, distributed in South American rivers. In this paper, the distribution of 10 species of freshwater Sciaenidae occurring in the Amazon Basin, belonging to the genera *Pachypops*, *Pachyurus*, *Petilippinis* and *Plagioscion*, was analyzed by the panbiogeographic quantitative methods. By means of track analysis, three generalized tracks and six biogeographic nodes were found. The main massing of the species studied is located in the Lower Amazon (Óbidos), where six of the species do occur. The results of the track analysis suggest that the distribution of the South American freshwater Sciaenidae correspond to vicariant events associated to the formation of the Amazonas and Orinoco river basins and the events related to the formations of the Paraná, Paraguai and Prata river basins. The Guyanas shield constitutes an important geotectonic feature in the configuration of the distribution patterns of these species. These patterns are congruent with those observed in other lineages derived from marine groups in South America.

Keywords: panbiogeography, track analysis, Amazon Basin, South America.

Introduction

The family Sciaenidae comprises four genera (*Pachypops*, *Pachyurus*, *Petilipinnis* anf *Plagioscion*) and about 20 species restricted to freshwater, distributed in rivers of South America that drain into the Atlantic Ocean. These genera were revised and a few new species have been described in recent years, both extant (Aguilera & Rodrigues de Aguilera, 2000; Casatti, 2001, 2002a, 2002b, 2005) and fossils from Miocene deposits (Aguilera & Rodrigues de Aguilera, 2003), but the knowledge of the biogeography of the freshwater species in this family in the Amazon Basin is still very incipient (Boeger & Kitsky, 2002; Cooke et al., 2012).

In this paper, the distribution of 10 species of freshwater Sciaenidae occurring in the Amazon Basin, belonging to the genera *Pachypops*, *Pachyurus*, *Petilipinnis,* and *Plagioscion*, was analyzed using the panbiogeographic method of track analysis.

Panbiogeography, developed by León Croizat (Croizat, 1958, 1964), emphasizes the importance of the spatial (geographic) dimension of biodiversity, to provide a wider understanding of evolutionary patterns and processes, stressing the importance of the geographical distributions as direct objects of analysis. Page (1987) proposed a quantitative panbiogeographic method based on graph theory, according to which an individual track corresponds to a minimum spanning tree, which is equivalent to an undirected graph connecting all localities of a taxon, so that the sum of distances is minimal. This methodology has been employed in a number of panbiogeographic studies along the last three decades (Henderson, 1989; Craw, 1989; Craw et al., 1999).

Materials and Methods

Track analysis was performed with the programs Croizat v1.15 (Cavalcanti, 2009) and MartiTracks v0.5a1 (Echeverría-Londoño & Miranda-Esquivel 2011), using distribution data obtained from the literature (Casatti, 2001, 2002a, 2002b, 2005; Casatti & Chao, 2002; Soares & Casatii, 2000), and of the collections included in the Global Biodiversity Information Facility (GBIF, www.gbif.org), FishBase (www.fishbase.org), and FishNet (www.fishnet2.net). A total of 237 occurrence records, belonging to 10 species of freshwater Sciaenidae were included in the analysis (Table 1). Only species with at least two locality records were selected for inclusion in the analysis.

Individual tracks for each species were constructed by plotting on a map the occurrence localities and connecting them by minimum spanning trees. Generalized tracks were obtained by the superimposition of the individual tracks, with the areas where two or more generalized tracks intercept each other being identified as biogeographic nodes. The generalized tracks provide an objective criterion to biogeographic homology and allow to infer the existence of an ancestral biota widely distributed in the past and fragmented by subsequent vicariant events.

Species	Number of records
Pachypops adspersus Steindachner, 1879	7
Pachypops fourcroi (Lacepede, 1802)	32
Pachyurus bonariensis Steindachner, 1879	11
Pachyurus junki Soares & Casatti, 2000	3
Pachyurus schomburgkii Gunther, 1860	2
Petilipinnis grunniens (Schomburgk, 1843)	32
Plagioscion auratus (Castelnau, 1855)	20
Plagioscion squamosissimus (Heckel, 1840)	85
Plagioscion surinamensis (Bleeker, 1873)	35
Plagioscion ternetzi Boulenger, 1895	10

Table 1 – Species of freshwater Sciaenidae and number of occurrence records included in this study.

Main massings, representing sectors of geographic space with the highest concentrations of diversity, were determined by counting the numbers of species in each cell of a 1 x 1 degree grid using the DIVA-GIS Geographic Information System (Hijmans et al. 2001; www.diva-gis.org).

Results and Discussion

On the basis of the superposition of the individual tracks for each genus (Fig. 1), three generalized tracks and six biogeographic nodes were found (Fig. 2).

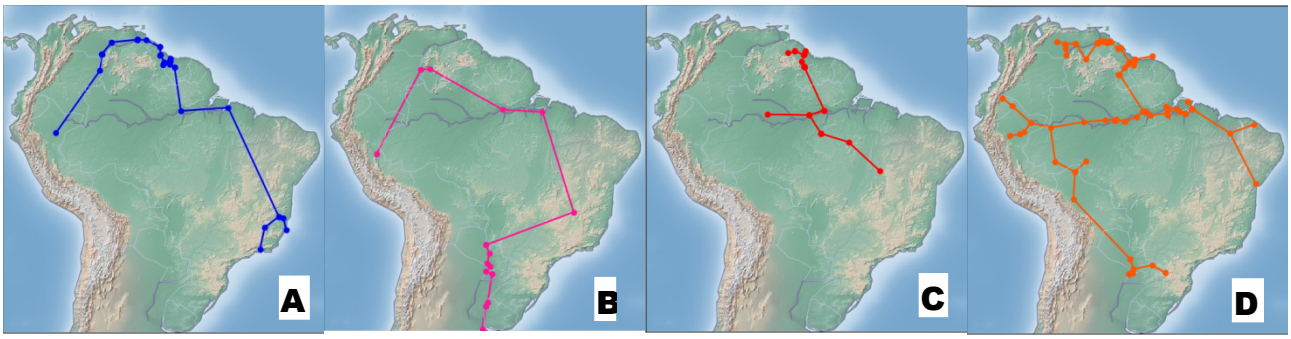

Figure 1 – Individual tracks for the genera of freshwater Sciaenidae included in the analysis (A: *Pachypops,* B: *Pachyurus,* C: *Petilipinnis,* D: *Plagioscion*).

The generalized tracks and the species that define them are: T1: *Pachyurus junki*, *Plagioscion squamosissimus*; T2: *Plagioscion auratus*, *Plagioscion ternetzi*, *Petilipinnis grunniens*; T3: *Pachypops fourcroi*, *Pachyurus schomburgkii*. The biogeographic nodes are as follows: (1) Rio

Orinoco, between San Fernando de Atabapo and Santa Barbara del Amazonas (Venezuela); (2) Rio Paragua, region of Cerro Guaiquinima (Venezuela); (3) Rio Cuyuni (Venezuela); (4) Rio Essequibo, Guyana; (5) Rio Amazonas, region of Óbidos (Brazil); (6) Rio Amazonas, region of Urucará (Brazil).

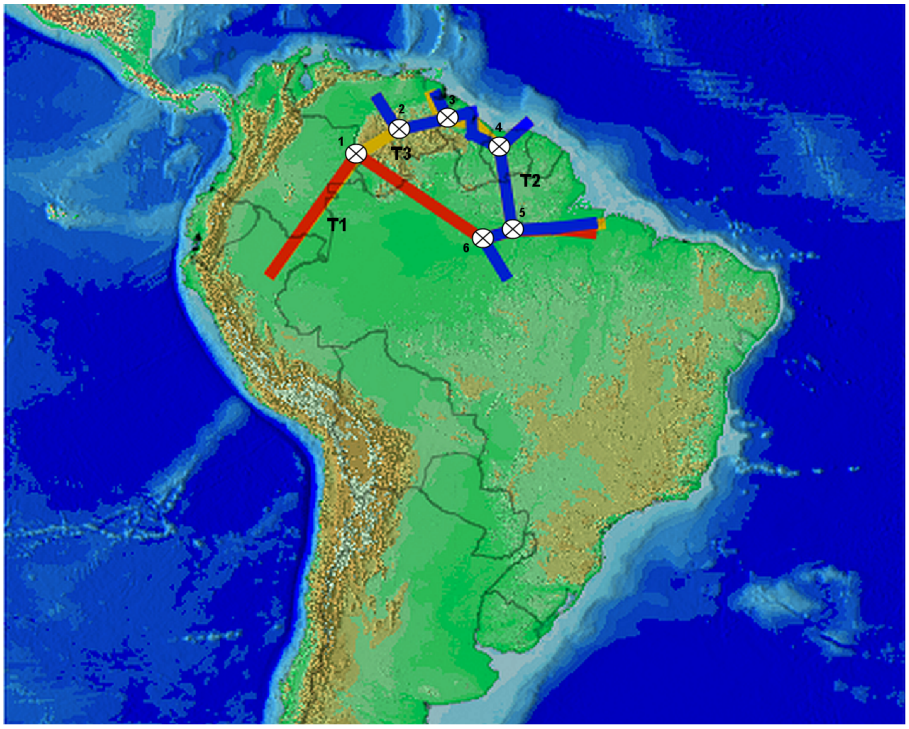

Figure 2 – Generalized tracks and biogeographic nodes found in the analysis.

These nodes closely correspond to some of those found by the panbiogeographic analysis of several groups of terrestrial animals and plants in the Amazonian subregion presented by Morrone (2000), namely Imerí (node 1), Guyana/moist Guyana (nodes 2, 3, and 4), and Várzea (nodes 5 and 6).

Pachyurus bonariensis presents a disjunct distribution, restricted to the basin of Rio da Prata; therefore this species does not contribute to any of the generalized tracks found in the analysis.

The main massing of the species of included in the present study (Fig. 3) is located in the Lower Amazon (around Óbidos, Pará, Brazil), where six of the species do occur.

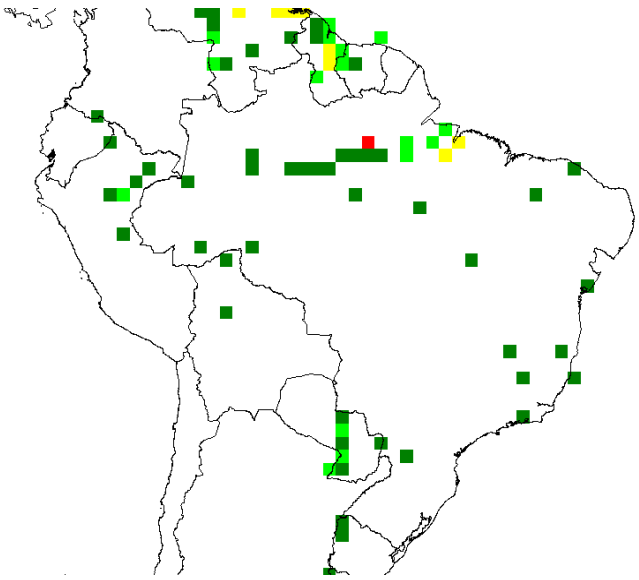

Figure 3 - Main massings (centers of diversity) of the species included in this study. Red: six species; yellow: three to four species; light green: two species; dark green: one species.

The Amazon Basin possesses the largest concentration of species of Sciaenidae and constitutes the main massing of the freshwater species in this family. Track analysis suggests that the distribution of Sciaenidae was primarily influenced by the vicariant events associated to the formation of the basins of Amazonas and Orinoco rivers, as the uplift of the Andes and marine transgressions in the north of South America (Hoorn et al., 2010) and, secondarily, to the events related to the formation of the Paraná, Paraguay, and Prata river basins. These events promoted linkages between marine and freshwater environments, especially in northern South America, and their geographic and environmental effects on the regional distribution of freshwater biotas have been well documented (Bloom & Lovejoy, 2017; Lovejoy et al., 2006). The Guyanas Shield in particular constitutes an important geotectonic feature in configuring the distribution patterns of these species, as it has already been suggested in the case of other freshwater groups occurring in the region (Lehmberg et al., 2018). These patterns are congruent with those observed for other lineages derived from marine groups in South America (sponges, mollusks, crustaceans, fishes, and aquatic mammals) and their integrated analysis by the panbiogeographic method contributes to improve the understanding of the events associated to the complex biogeographic history of the Amazon Basin.

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