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Biogeography of Amazonian fishes: deconstructing river basins as biogeographic units

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Biogeography of Amazonian fishes (2,500 species in vastly disjunct lineages) is complex and has so far been approached only partially. Here, we tackle the problem on the basis of the largest database yet on geographical distribution and phylogenetic relationships of Amazonian fishes, including all information available. Distributions of 4,095 species (both Amazonian and outgroups) and 84 phylogenetic hypotheses (comprising 549 phylogenetically-informative nodes) were compiled, qualified and plotted onto 46 areas (29 Amazonian and 17 non-Amazonian). The database was analyzed with PAE, CADE, BPA and BPA_0, yielding largely congruent results and indicating that biogeographic signal is detectable on multiple dimensions of fish distribution, from single species ranges to cladistic congruence. Agreement is especially pronounced in deeper components, such as Trans-Andean, Cis-Andean, Western Amazon and Orinoco basins. Results show that all major Amazonian tributaries, as well as the Amazon basin itself, are non-monophyletic and constitute hybrid sets of heterogeneous biotic partitions. Amazonian drainages should not be assumed a priori as historically cohesive areas, contrary to widespread practice. Our hypothesis allows re-evaluation of broader issues in historical biogeography, such as the predictive power of biogeographic hypotheses, the vicariant/dispersal duality, the significance of widely distributed taxa, and the need for temporal dimension in biogeographic patterns.

Keywords: Biotic dispersal, Composite areas, Historical Biogeography, Temporal congruence, Widespread taxa.

A biogeografia dos peixes amazônicos (2.500 espécies de diferentes linhagens) é complexa e até agora foi abordada apenas parcialmente. Aqui abordamos o problema com base no maior banco de dados já feito sobre a distribuição geográfica e as relações filogenéticas dos peixes amazônicos, incluindo todas as informações disponíveis. A distribuição de 4.095 espécies (tanto amazônicas como de grupos-externos) e 84 hipóteses filogenéticas (que incluíam 549 nós filogeneticamente informativos) foram compiladas e qualificadas em 46 áreas (29 amazônicas e 17 não-amazônicas). O banco de dados foi analisado a partir das metodologias PAE, CADE, BPA e BPA0, resultando em topologias amplamente congruentes e indicando que o sinal biogeográfico é detectável em múltiplas dimensões, desde a simples distribuição de peixes até em congruência cladística. A concordância topológica é especialmente pronunciada em componentes mais profundos, como as bacias Trans-Andina, Cis-Andina, Amazonas Ocidental e Orinoco. Os resultados demonstram que todos os principais afluentes amazônicos, bem como a própria bacia amazônica, não são monofiléticos e constituem conjuntos híbridos formados a partir de parcelas bióticas heterogêneas. As drenagens amazônicas não devem ser consideradas *a priori* como áreas historicamente coesas, contrariamente à prática generalizada. Nossa hipótese permite a reavaliação de questões mais amplas na biogeografia histórica, como o poder preditivo de hipóteses biogeográficas, a dualidade vicariante/dispersão, significância de táxons amplamente distribuídos e a necessidade da dimensão temporal em padrões biogeográficos.

Palavras-chave: Áreas compostas, Biogeografia histórica, Congruência temporal, Dispersão biótica, Táxons amplilocados.

Introduction

The Amazon basin is the largest hydrographic system in the world (Goulding *et al*., 2003) and covers an area of over 8,000,000 km² (Sioli, 1984). Its main river, the Rio Amazonas, has by a wide margin the largest freshwater discharge on the planet, larger than the next eight largest rivers combined (Albert *et al*., 2011). It is also the first or second longest river in the world with 6,400 km from its source in the Andean region in Peru to its mouth in the Atlantic Ocean in Brazil (Hoorn, Wesselingh, 2010; Contos, Tripcevich, 2014). As expected from its vastness, the Amazon basin is renowned for its biodiversity. As pointed out by Hoorn, Wesselingh (2010) exact figures to express this diversity do not yet exist, and estimates on the number of species are still increasing sharply, with much of the basin still unexplored or only sparsely sampled (Anjos, Zuanon, 2007).

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The Amazon basin is formed by multiple distinct physiognomies, determined by terrains of vastly different composition and geological origins, generating diverse soil kinds, vegetation and water types (*cf.* Goulding *et al.*, 2003). All those factors are related to an immensely rich and complex geomorphological history (*cf.* Lundberg *et al.*, 1998) influenced by a series of large-scale events (*e.g.*, Gondwana separation, uplift of the Andean range, course shifts of the main Amazon river, drainage capture, marine transgressions and regressions) which are not yet entirely understood. In addition, the region has been broadly stable for an extended period of time and has not been regularly subject to wide-ranging diversity-decreasing factors such as glaciations and desertification. Such historical factors imply both increased diversification rates and decreased extinction rates, resulting in extraordinary richness of the freshwater biota as seen today (Albert, Reis, 2011; Reis *et al.*, 2016).

The fish community inhabiting the Amazon basin is the largest freshwater ichthyofauna in the world, with almost 2,500 described species and a continuing parade of newly discovered taxa (Lundberg *et al.*, 2010; Reis *et al.*, 2016).That assemblage comprises myriad evolutionary lineages, resulting from the interaction of multi-layered geological patterns associated with both vicariant and dispersal agents. The Amazonian fish community includes lineages probably acquired by ancient continental connections, like Osteoglossiformes, Characiformes (*cf.* Arroyave *et al.*, 2013), Siluriformes, Cichlidae and Dipnoi, in addition to a multitude of different lineages derived from marine ancestors which invaded the Amazonian freshwater environment, such as Potamotrygonidae, Tetraodontidae, Belonidae and many others. As in most freshwater ecosystems worldwide, the Amazon basin is dominated by ostariophysan fishes with over 80% of its species being Characiformes, Siluriformes or Gymnotiformes.

At first sight, the Amazonian fish fauna seems to provide the perfect grounds for biogeographic studies. This view is based on the simple premise that freshwater fishes are limited to the water courses where they live and therefore that their history of diversification is closely linked to the processes and patterns involved in their formation. The size and complexity of the Amazonian fish fauna should amount to numerous distributional overlaps and superlative degrees of biogeographic congruence. In reality, however, the situation is much more complex. A cursory examination of available area cladograms reveals that incongruence is the rule rather than the exception. The detection of general biogeographic patterns requires a fine-grained approach where traditional concepts of freshwater areas cannot be taken for granted. Biogeographic units delimited by the physical limits of major hydrographic basins (*e.g.,* Tapajós, Xingu, Negro, Tocantins, Madeira, etc.) should be treated as hypotheses that need testing.

The puzzle posed by Amazonian biogeography has long been a matter of interest for biologists (Agassiz, Agassiz, 1868; Eigenmann, 1909; Pearson, 1937; Myers, 1947; Darlington, 1957; Menezes, 1969, 1976; Weitzman, Weitzman, 1982). However, it was only recently that attempts have been made to quantitatively analyze the problem (*e.g.*, Hubert, Renno, 2006; Albert, Carvalho, 2011; Lima, Ribeiro, 2011; Goldani, 2012). Despite their pioneering merit, all such previous efforts have limitations imposed by the density, scope or quality of the data entered and the methods employed (mostly PAE - Parsimony analysis of endemicity). Also, and more importantly, in all of them Amazonian river basins have been considered a priori as biogeographic units. As will be seen, we consider this a priori reliance to be a potential source of incongruence in biogeographic analyses of Amazonian aquatic taxa and a major obstacle to a realistic understanding of the subject.

The goal of this paper, therefore, is to provide a large-scale analysis of the biogeography of Amazonian fishes including a compilation of all the data currently available and an application of currently implementable analytical methods. To do so, we built the largest database of geographical information yet assembled for the region, which is exhaustive as far as qualified information is concerned. Our results provide a new picture of the biogeographic history of Amazonian fishes, and also bring to light a number of broader conceptual and theoretical issues related to the study of freshwater biogeography in general.

Material and Methods

Area delimitation. The Amazon basin was divided into 29 regions (Fig. 1, white circles), using as a base the division into 13 Amazonian ecoregions recognized by Abell *et al.* (2008), but refined and much subdivided, according to four criteria: 1) all drainages of considerable size are a priori considered as a separate region, independent of their tributary-order (*e.g.*, the Madeira was separated into five sub-components, the Tapajós into four, etc.; *cf.* Fig. 1); 2) whenever possible, each recognized region corresponds to the exclusive geographical distribution of two or more taxa, *i.e.*, there is evidence that it may represent an area of endemism (*sensu* Nelson, Platnick, 1981; Platnick, 1991; Harold, Mooi, 1994; Morrone, 1994; Humphries, Parenti, 1999; Linder, 2001; Szumick *et al.*, 2002); 3) the Rio Tocantins and Rio Xingu are split into upper and lower portions, in order to account for pronounced ecological and biogeographic differences along their longitudinal gradients; 4) the rivers Anapu, Pacajá, Coari, Jutaí, Ituí, Javari, Paru do Oeste and Paru were included in neighboring basins (Anapu and Pacajá in the lower Xingu, the Jutaí, Ituí, and Javari in the Juruá, the Tefé and the Coari-Urucu in the Purus, the Curuá-Paru do Oeste in the Trombetas) due to the paucity of ichthyological inventory data from those basins, both in collections and in the literature. This procedure avoids distortions in the results which might result from the large amounts of missing data in the quantitative analyses. Outgroup areas were represented by 17 regions adjacent to the Amazon (*cf.* Fig. 1, dark circles). The arid northeastern region of Brazil was not included because it lacks relevant taxa or lineages shared with the Amazon and the Rio Gurupi was included in the Capim due to a paucity of data. A total of 46 areas were included in the analyses, including both ingroup and outgroup areas.

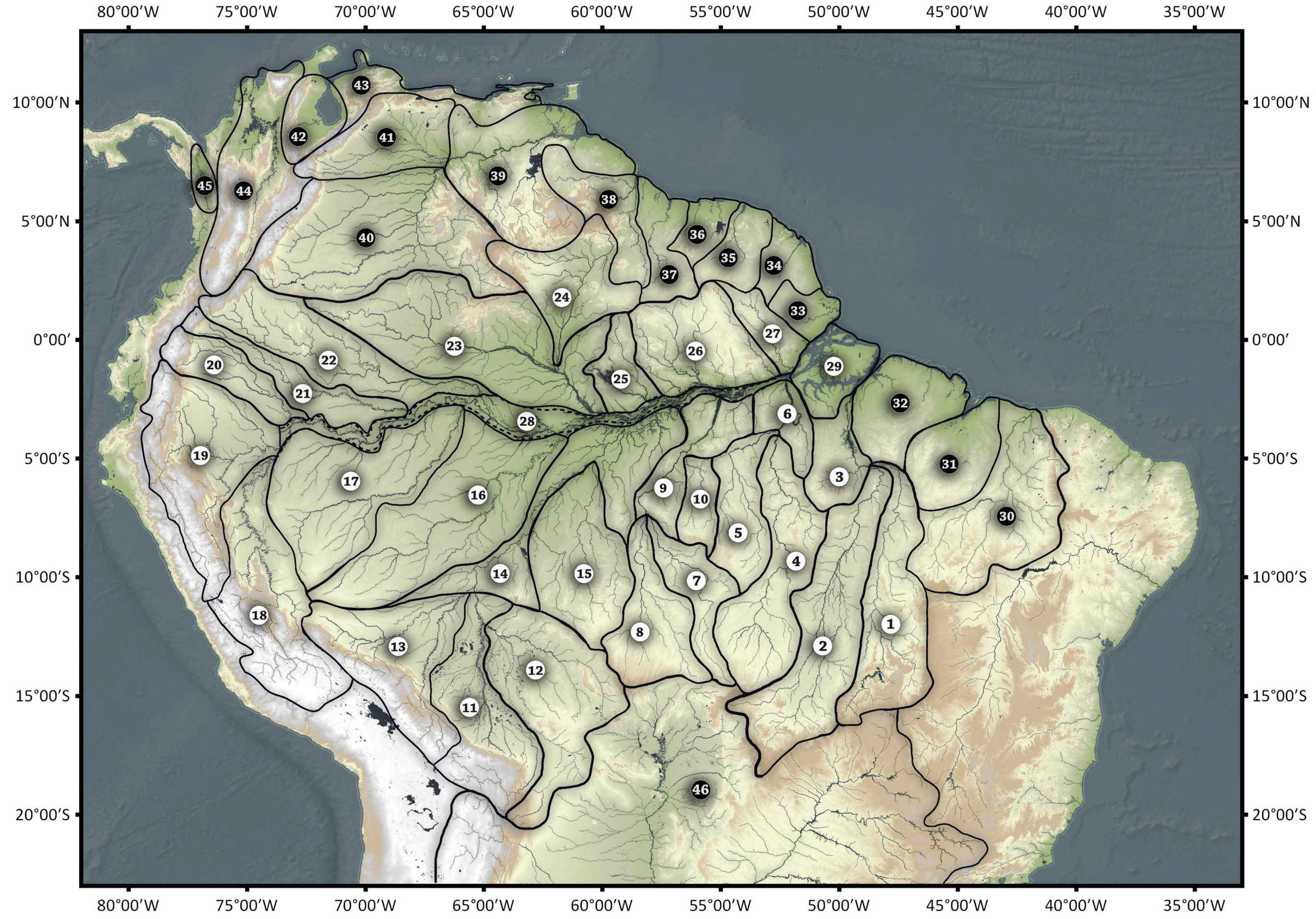

Fig. 1. Area delimitation proposed herein. White circles represent amazonian regions, dark circles neighboring areas. 1. Upper Tocantins, 2. Araguaia, 3. Lower Tocantins, 4. Upper Xingu, 5. Iriri, 6. Lower Xingu, 7. Teles Pires, 8. Juruena, 9. Tapajós, 10. Jamanxim, 11. Mamoré, 12. Guaporé, 13. Beni-Madre de Dios, 14. Middle-Lower Madeira, 15. Madeira Shield Tributaries, 16. Purus, 17. Juruá, 18. Ucayali, 19. Marañon-Nanay, 20. Napo-Ambyiacu, 21. Putumayo, 22. Japurá, 23. Negro, 24. Branco, 25. Urubu-Uatumã, 26. Trombetas, 27. Jari, 28. Amazonas main channel, 29. Amazonas Estuary, 30. Parnaíba, 31. Itapicuru-Mearim, 32. Capim, 33. Araguari-Macari-Amapá, 34. Oiapok, 35. Maroni-Approuague, 36. Coppename-Suriname-Saramacca, 37. Corentyne-Demerara, 38. Essequibo, 39. Lower Orinoco, 40. Upper Orinoco, 41. Apure, 42. Maracaibo, 43. Atlantic Coastal Drainages of Colombia and Venezuela, 44. Magdalena, 45. Atrato, 46. Paraná-Paraguay.

Database building. Individual species distributions were compiled on the basis both of direct examination of ichthyological collections and of qualified published data. Stringent criteria were applied to qualify the information incorporated into the datasets assembled herein, because the quality of such data is critical to the reliability and accuracy of results. The complete database is too extensive to be presented in the body of this paper, but is available in 10 appendices included as Supplementary Material. The collections chosen to be thoroughly examined were those with holdings most significant for Amazonian fishes, both in volume of samples and geographical coverage (**S1-2** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). Those collections were INPA, LBP, LIRP, MZUSP, MPEG, and USNM (institutional abbreviations follow Sabaj Pérez, 2016), comprising 1,769 lots directly examined for this study and verified for accuracy of taxonomic identity. Additionally, all information about the geographic distribution of Amazonian fish taxa available in the literature was critically examined, in a total of 1,524 references including taxonomic revisions, species descriptions and faunistic surveys (**S3** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni) comprising 4,176 records updated until June 2015. The final dataset includes geographical distributions for 4,095 species, including both Amazonian and non-Amazonian ones. The phylogenetic database utilized in BPA (Brooks Parsimony Analysis) and BPA$_0$ (see below) includes 84 phylogenetic hypotheses for clades with Amazonian representatives, including 951 species representing 33 families and 6 orders (**S4** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni) in a total of 549 phylogenetic nodes. The respective topologies used and their node code are provided in (**S5** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). In trees illustrated, each node was coded with a color and a name (*e.g.*, the red clade Callichthyinae indicates the node marked in red in the Callichthyinae phylogeny of Reis, 1998). The use of colors instead of numbers to cross-reference clades intends to avoid confusion with the node numbering used in original papers. Some phylogenetic hypotheses in the literature were proposed only in text, without associated trees. Those hypotheses were incorporated into the phylogenetic database, but only shown graphically when comprising more than two species. Some published phylogenetic proposals were not included for one or a combination of the following reasons: 1- insufficient species sampling, 2- doubtful species identification, 3- presence of polyphyletic species, 4- inclusion of too many undescribed taxa, 5- phylogenies for groups of questionable monophyly, and 6- phylogenies too broad to associate with meaningful biogeographic information. A list of such excluded works is provided in (**S6** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Analytical methods. Many methods have been developed to study historical biogeography, but none of them is unanimously accepted. Our choice of methods was constrained by implementation possibilities on our database, which includes 84 topologies, 549 nodes and 4,095 species (**S4** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni) rife with redundancy and widespread taxa, sometimes occurring in more than 30 areas simultaneously. We therefore chose methods which in practice can be implemented for large databases such as ours and at the same time have been demonstrated to detect some biogeographic signal. Those are presently limited to PAE (Parsimony Analysis of Endemicity), CADE (Cladistic Analysis of Distributions and Endemism), BPA (Brooks Parsimony Analysis) and BPA$_0$. Those four methods have been applied with some degree of success and their results have been shown to contain a reasonable degree of biogeographic coherence (Hubert, Renno, 2006; Ingenito, Buckup, 2007; Albert, Carvalho, 2011; Buckup, 2011; Lima, Ribeiro, 2011; Schaefer, 2011; Camelier, Zanata, 2014; Matamoros *et al.*, 2015). The use of other methods such as 3-area analysis (Nelson, Ladiges, 1991), reconciled tree analysis (Page, 1994a,b), component analysis (Nelson, Platnick, 1981) and paralogy-free subtrees (Nelson, Ladiges, 1996) would be interesting in theory, but we found that software available for their implementation cannot be reliably applied to our database, which is probably one of the largest yet assembled for any biogeographic problem. *A priori* methods apply modifications to original data in face of "exceptions" to a biogeographic pattern (*cf.* Zandee, Roos, 1987; Wiley, 1988a, 1988b; Harvey, 1992; Kluge, 1993; Farris, Kluge, 1998; Farris, 2000; Van Veller *et al.*, 2000; Lieberman, 2004) and are computationally more demanding. Although they have been successfully applied in moderately complex cases smaller than the present one (Hoagstrom *et al.*, 2014) with the help of the program LisBeth (Zaragueta-Bagils *et al.*, 2012) for 3ta with the help of paralogy free subtree analysis, they are still rarely implemented. We actually suspect that implementation difficulties partly account for the comparative paucity of published applications using those methods. Their application to our database will require implementation developments and will be the subject of a separate paper. Different methods yield results influenced by their inherent assumptions and limitations (Morrone, Carpenter, 1994). Despite such unavoidable caveats, results obtained herein are highly informative as a preliminary framework for our broad discussion on the biogeography of Amazonian fishes and the role of hydrographic basins as biogeographic units (see Discussion below).

Data on raw distribution (PAE), distribution and taxonomic categories (CADE), and distribution and phylogenetic information (BPA, BPA$_0$) were organized in matrices built with the program Mesquite - A Modular System for Evolutionary Analysis (version 3.2, Maddison, Maddison, 2017). Analyses were implemented on the basis of equal weights with the program TNT, version 1.1 (Goloboff *et al.*, 2008). In face of high degree of incongruence of biogeographic data, aggressive search options were selected in order to find the shortest topologies. Those were New Technology algorithms such as Ratchet (Nixon, 1999) which changes initial character weights to create perturbation cycles, Sectorial searches (Goloboff, 1999) which analyzes separate portions of trees, Tree-drifting (Goloboff, 1999) which compares sub-optimal topologies and Tree-fusing (Goloboff, 1999) which exchanges branches with identical composition among different topologies. Ratchet and Tree-drifting were implemented with 20 cycles and Sectorial searches and Tree-fusing with 30. Such numerous cycles are recommended for large matrices (Goloboff, 2002). The directed search aim was set at a best score of 50 times, which means that the search continued until the shortest tree was found 50 times independently, regardless of the number of starting replicas. As usual in such searches as applied to biogeography, all analyses were rooted at an all-zeros outgroup (*cf.* Cracraft, 1991; Lieberman, 2000; Van Veller *et al.*, 2000; Crisci *et al.*, 2003; Matamoros *et al.*, 2015). No specific treatment was applied to redundant distributions (areas with more than one taxon in the cladogram). Assumption A0 guided the interpretation for widespread taxa in all analyses (Van Veller *et al.*, 2000, 2001; Brooks, Van Veller, 2008) *i.e.,* shared presence of a species is regarded as evidence of common origin - incidentally one of the most contentious elements in biogeographic methods. Lineages restricted to only one basin (autapomorphic taxa or clade), albeit uninformative about area relationships, were not excluded so that the matrix is fully reflective of the database, including information on endemic taxa for each drainage (**S7-10** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Brooks Parsimony Analysis (BPA) was proposed by Wiley (1988a, 1988b) and subsequently modified by Brooks (1990) and Brooks *et al*. (2001). The method is based on the ideas of Brooks (1981) to study coevolution between hosts and parasites. It is one of the most commonly used method in historical biogeography nowadays, including several applications in freshwater fishes (*e.g.,* Albert, Carvalho, 2011; Matamoros *et al*., 2015), despite criticism in the literature (Cracraft, 1988; Platnick, 1988; Page, 1990a, 1994a, 1994b; Ronquist, Nylin, 1990; Nelson, Ladiges, 1991; Carpenter, 1992; van Welzen, 1992; Enghoff, 2000; Ebach, Edgecombe, 2001; Warren, Crother, 2001; Dowling, 2002; Ebach, Humphries, 2002; Siddall, 2004; Siddall, 2005; Siddall, Perkins, 2003; Parenti, 2007; Santos, 2007). In our analyses, the method was applied in two distinct forms, herein called BPA, its original version and BPA_0, its transformed version. The two versions differ only in the codification of absent areas. Absences are coded as missing entries in BPA, which implies agnostic premises of either extinctions, lack of records or primitive absences (**S9** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). In BPA_0, assumption A0 is applied (see Kluge, 1988), where absent areas (**S10** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni) are considered *a priori* as primitively absent and coded as “0”. Both BPA and BPA_0 were implemented herein by transforming all phylogenies into area cladograms by replacing terminal taxa for the areas in which they occur. All the data were concatenated into a single super data matrix (**S9-10** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). Synapomorphies resulting from the various analyses are available in **S11** - (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Relatively few phylogenies are available to encompass representatives of all the species-rich clades of Amazonian ichthyofauna. Given that, we decided to employ also methodologies that do not rely directly on phylogenetic data, such as CADE and PAE but which nonetheless may be discussed and tested in comparisons with results from cladistic biogeographic analyses (Porzecanski, Cracraft, 2005).

The method of Cladistic Analysis of Distributions and Endemism (CADE) (Porzecanski, Cracraft, 2005) uses the database on species distributions in combination with data about supraspecific categories. The method is based on the premise that taxonomic hierarchy can be used as a proxy for phylogeny. This characteristic allows CADE to better distinguish ecological noise from historical information, when compared with PAE (Cracraft, 1991; Porzecanski, Cracraft, 2005). Only groups whose monophyly is not challenged in the literature were included in our database (**S4** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

Parsimony Analysis of Endemicity (PAE) (Rosen, 1988) has been severely criticized in the literature as a method of historical biogeographic analysis (*cf.* Humphries, 1989; Humphries, Parenti, 1999; Brooks, Van Veller, 2003; Nihei, 2006). Nonetheless, it has been widely employed in the biogeography of neotropical fishes (*cf.* Hubert, Renno, 2006; Ingenito, Buckup, 2007; López *et al.*, 2008; Albert, Carvalho, 2011; Buckup, 2011; Lima, Ribeiro, 2011; Schaefer, 2011). It seems certain that PAE is not efficient in recovering area relationships, since it does not utilize evolutionary data in any form. Analysis by PAE results in a dendrogram derived solely from the geographical distributions of individual species. However, it can provide testable hypotheses about the limits of areas of endemism (Morrone, 1994). Considering the widespread recent application of PAE to biogeographic data, we also felt compelled to apply it to ours (**S7** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). This allows comparisons with results from other methods and ultimately helps to better understand the significance and drawbacks of PAE.

The phylogenetic terminology applied to biogeographic trees (*e.g.*, monophyletic, sister-group, etc.) refers to topological characteristics of the trees, with no implication of properties identical to those of the same terms applied to organismic phylogenies.

Results

Analyses of our dataset by PAE, CADE, BPA and BPA_0 yielded results shown in Figs. 2-6 and **S12** (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). Upon comparison, two noteworthy features are immediately obvious. First, topologies resulting from different analyses are largely congruent. Second, they include hypothesized relationships that match some of the prevailing paradigms about historical relationships among different areas of the Amazon basin. The degree of congruence is compelling in its implication that at least part of the historical signal in Amazonian freshwater fishes is strong enough to be detected regardless of the method employed. This holds true even though some of the techniques (such as PAE) entirely disregard phylogenetic data. Although the patterns recovered may be in part due to the weight of individual species distributions, the congruence found indicates that the historical pattern left its mark even in the most superficial dimension of biogeographic information, namely individual species distributions. Large inclusive clades are particularly congruent among analyses, such as the Western Amazon, trans-Andean drainages and Orinoco basin. This shows that the strongest biogeographic signal comes from deep and therefore older patterns, whose influence on geographical distribution pervade different layers of biogeographic information. Congruence aside, it is interesting to note also that, where they differ, results including phylogenies (BPA, BPA_0) yield results more strongly reflective of currently-known biogeographic and geomorphological patterns recovered on the basis of independent evidence (*e.g.*, Western Amazon and Orinoco-Negro-Essequibo as monophyletic clades, see below).

A ubiquitous component in all analyses is the dichotomy between trans- and cis-Andean drainages. Such polarity supports the long-recognized importance of the Andean range as a biogeographic barrier, isolating trans-Andean basins from the rest of South American drainages (*cf.* Eigenmann, 1920, 1921a, 1921b, 1923; Lundberg, Aguilera, 2003; Albert *et al*., 2006; Rodríguez-Olarte *et al*., 2011). In all analyses, trans-Andean basins form a monophyletic group, with the Maracaibo basin as sister group to the clade composed of the Atrato + Magdalena. Such topology follows the sequence of the most important geological events in the Miocene, which molded the present drainage configuration in the Northwestern region of South America. The Magdalena and the Pacific Slope of Colombia were isolated from the paleo-Amazonas-Orinoco (Cis-Andean) ~12-10 m.y.a. with the formation of the Eastern Cordillera (Lundberg *et al*., 1998; Albert *et al*., 2006). Lake Maracaibo was separated from the Orinoco only 8 m.y.a. with the uplift of the Cordillera de Merida (Mullins *et al*., 1987; Hoorn *et al*., 1995; Lundberg *et al*., 1998; Albert *et al*., 2006), subsequently becoming part of the trans-Andean group. The region “Coastal Atlantic Colombian and Venezuelan drainages” includes areas both east and west of the Andean Cordilleras and cannot be characterized as either cis- or trans-Andean. Not surprisingly, that area has diverging relationships in different analyses: Cis-Andean with BPA, Trans-Andean in BPA$_0$, polytomous with Trans- and Cis-Andean clades in PAE and sister group to a Trans- and Cis-Andean clade in CADE. Such incongruence is the result expected for hybrid areas and testimony to the usefulness of the application of different methods to complex situations. One of the most discussed patterns in the distribution of Amazonian fishes is that of Upland versus Lowland Amazonian (*cf.* Eigenmann, 1909; Jégu, 1992a, 1992b; Lima, Ribeiro, 2011). Lima, Ribeiro (2011) explicitly proposed that the northern drainages of South America correspond to two monophyletic groups: a lowland clade and a upland clade. Our results, congruent in all four methods and based on more areas and many more taxa than previous studies, show topologies incongruent with the model proposed by those authors and reveal a far more complex biogeographic scenario.

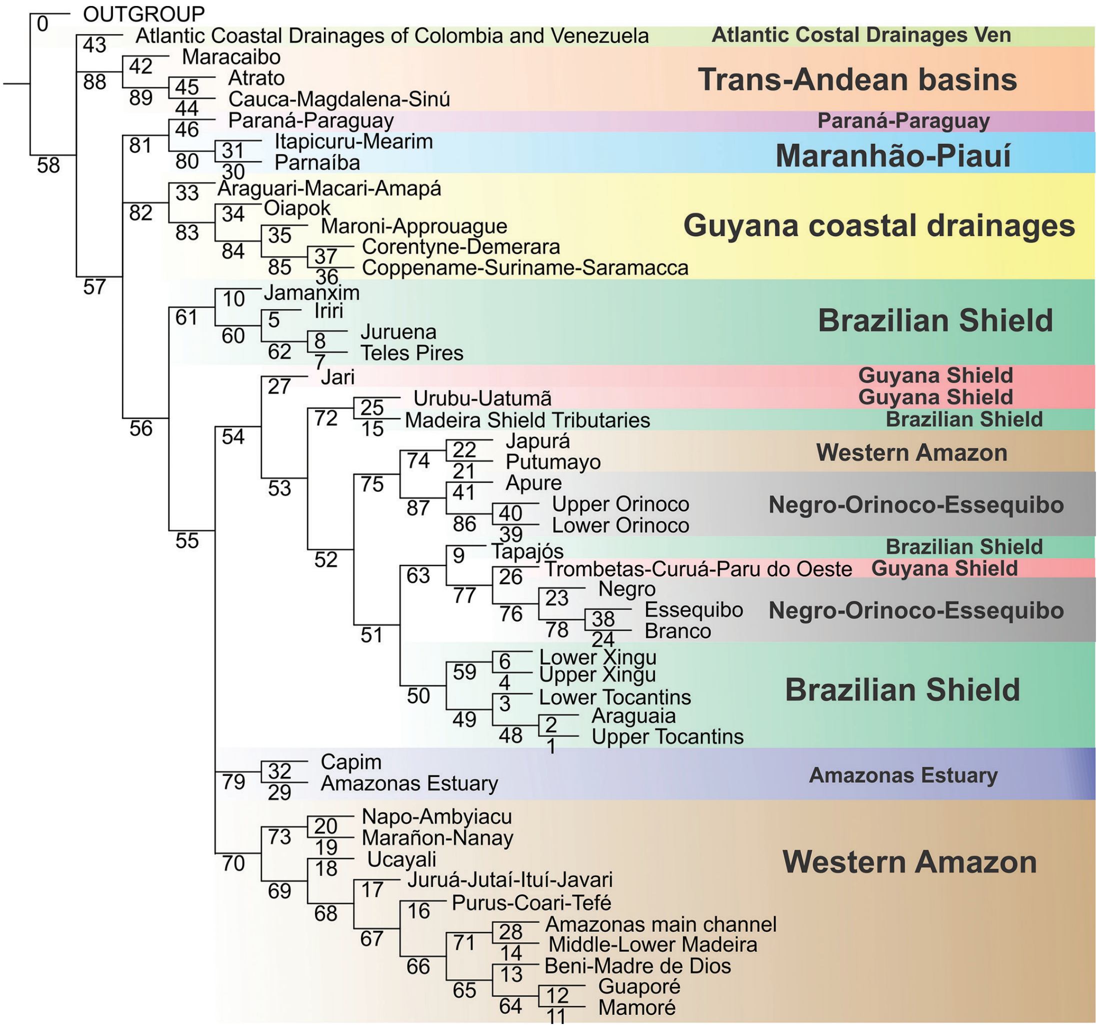

Fig. 2. Strict consensus of six most parsimonious trees obtained in PAE, built with matrix in **S7** - (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). (Atlantic Coastal Drainages Ven. = Atlantic Coastal Drainages of Colombia and Venezuela).

All of our topologies indicate the Amazon basin as non-monophyletic, confirming previous ichthyological analyses (*cf*. Hubert, Renno, 2006; Albert, Carvalho, 2011; Lima, Ribeiro, 2011). Similar conclusions were reached by authors working on other components of the Amazonian biota, such as plants (Cortés-B, Franco-R, 1997; Franco-Rosseli, Berg, 1997), other vertebrates (Cracraft, Prum, 1988; Eizirik *et al*., 1998; Marks *et al*., 2002) and arthropods (Grazia, 1997; Rodríguez, Campos, 1998; Camargo, Becker, 1999; Hall, Harvey, 2002; Morrone, 2002; Goldani, Carvalho, 2003; Nihei, de Carvalho, 2007). Basins adjacent to the Amazon, such as the Paraná-Paraguay, Essequibo and Orinoco share a large amount of taxa with the Amazon basin and even species whose closest relatives are Amazonian. In some cases, as in contacts between the Orinoco-Negro (permanent connection via Canal Cassiquiare) and Branco-Essequibo (seasonal connection Savana Rupununi) biogeographic separation between the Amazon and adjacent basins is incomplete, and still allows ichthyofaunal interchange.

The Western Amazon (=Lowland Amazon) is recovered as monophyletic in all analyses, save for the Japurá-Putumayo clade that is more closely related to the Orinoco basin in PAE and CADE. Except for part of the Rio Negro and for the Amazonas main channel downstream of the Purus Arc, the clade Western Amazon represents the spatial configuration of the Amazon Foreland basin as delimited and illustrated by Baby *et al*. (2005). The Western Amazon clade is closely related to other South American lowlands, as the Orinoco-Negro-Essequibo (BPA) and Paraná-Paraguay (BPA$_0$, CADE). Such pattern is foreshadowed in Eigenmann (1909), who noted ichthyofaunal similarities among lowlands in the Amazon, Orinoco and La Plata. A similar relationship was found by Lima, Ribeiro (2011) where the Western Amazon is the sister group to the Orinoco and that clade the closest relative to the Paraná-Paraguay.

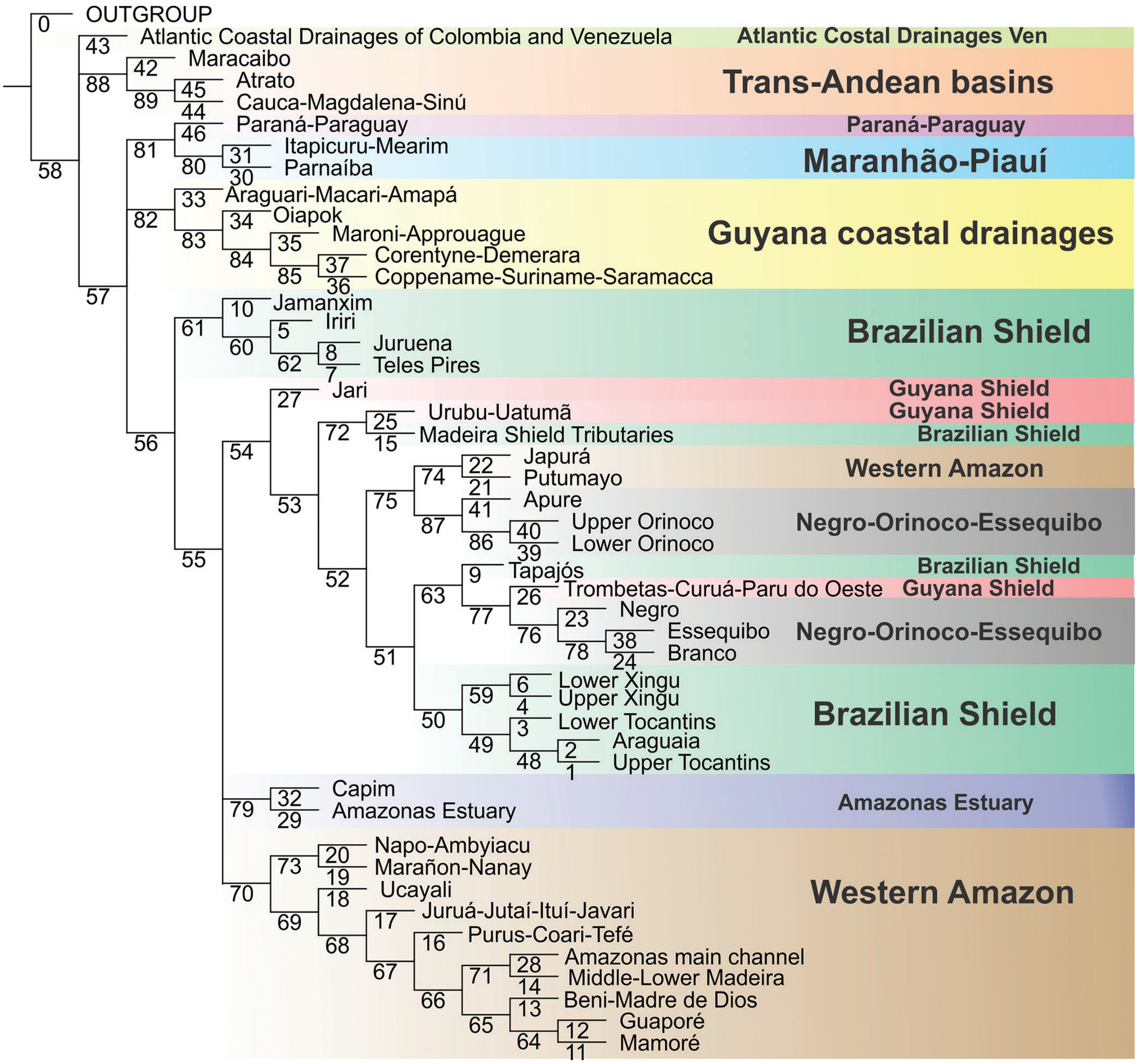

Fig. 3. Most parsimonious tree obtained in CADE, built with matrix in **S8** - (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). (Atlantic Coastal Drainages Ven. = Atlantic Coastal Drainages of Colombia and Venezuela).

In ecological terms, the Western Amazon is the main transportation route for sediments/organic matter in the Amazon, from its source in the Andean region to its mouth in the Atlantic Ocean. Therefore, it is possible that the Western Amazon is not only a historical biogeographic region, but also an ecological unit offering unique conditions for certain Amazonian species, especially those with great vagility such as species of *Brachyplatystoma* Bleeker and *Curimata* Bosc (see similar argument in Vari, 1988) and which are capable of moving throughout those basins as part of their natural life cycles (dispersion *sensu* Platnick, 1976). This is a clear example of Amazonian fish distribution being influenced both by historical and ecological causes. Of course, as noted by Ribeiro, Lima (2011), water type is itself a direct consequence of geomorphological processes and therefore also a result of the historical pattern.

According to Baby *et al*. (2005) the Amazon Foreland basin is divided by the Fitzcarrald Structural Arch into two sub-units: the Pastaza-Marañon and Beni-Mamoré basins (NAFB: northern Amazonian foreland basin and SAFB: southern Amazonian foreland basin, respectively, *sensu* Regard *et al*., 2009). All topologies obtained herein disagree with the historical monophyly of the NAFB, but corroborate that of the SAFB, a region partly corresponding to the Rio Madeira basin.

The Rio Madeira basin, in turn, is non-monophyletic in all analyses. This is a result of the close relationship between the main Amazonian channel and the Low-Middle Madeira, on the one hand, and of the position of the Shield tributaries of the Madeira (whose relationships differ among analyses) on the other. This fact corroborates the highly hybrid historical nature both of the Shield tributaries and of the Madeira as a whole. Other drainages of the Madeira basin form a monophyletic group (but whose intrarelationships differ among analyses).

Another lowland clade recovered in all analyses is the Río Orinoco. Despite the monophyly of the entire basin, there are differences of detail in their internal relationships. In BPA and BPA$_0$ the Upper Orinoco is sister group to the clade Apure plus Lower Orinoco, while in PAE and CADE, Apure is sister to the clade Upper and Lower Orinoco. Monophyly of the whole Orinoco (*i.e*., equivalent to Upper Orinoco, Lower Orinoco and Apure in our analysis) has been proposed in a BPA analysis by Albert *et al*. (2011), yet refuted in PAE analyses by the same authors and by Lima, Ribeiro (2011).

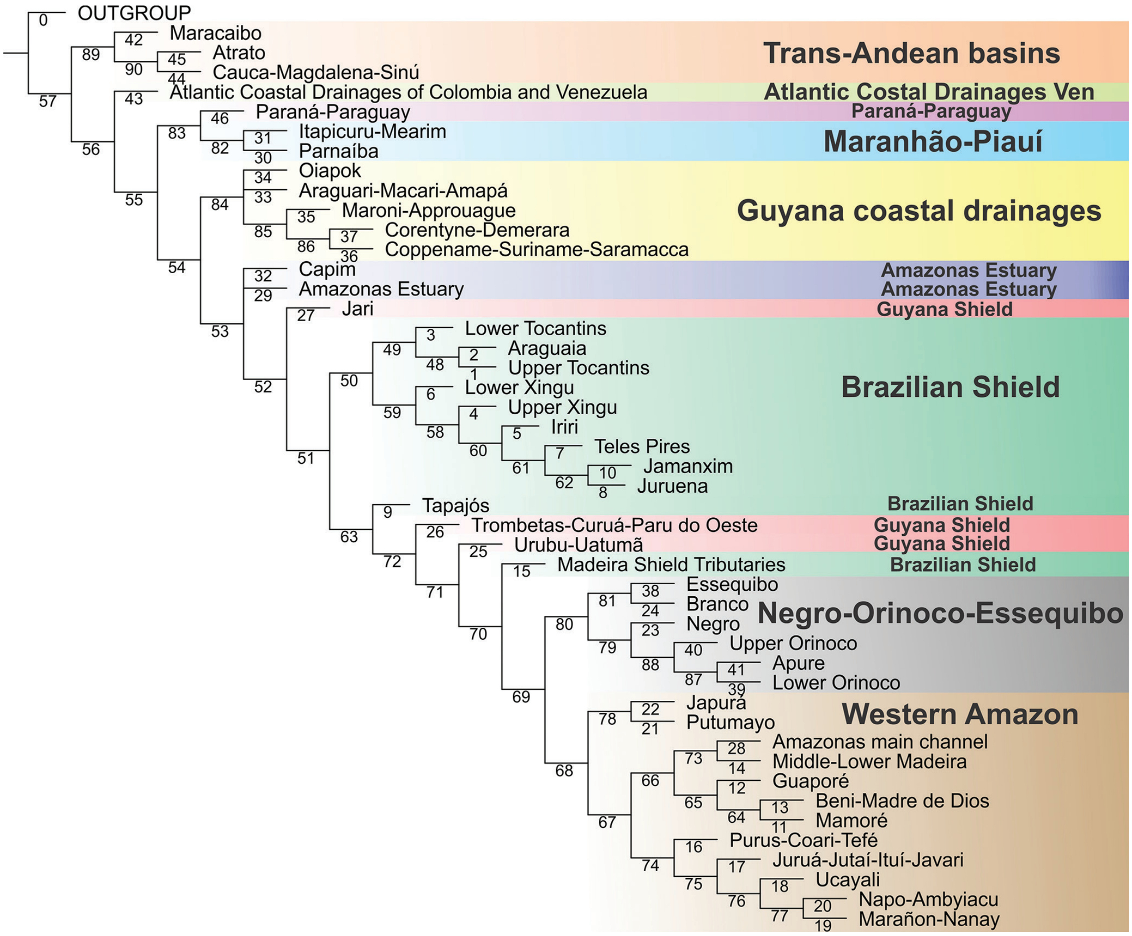

Fig. 4. Strict consensus of three most parsimonious trees obtained in BPA, built with matrix in **S9** - (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). (Atlantic Coastal Drainages Ven. = Atlantic Coastal Drainages of Colombia and Venezuela).

Finally, the Rio Branco and the Rio Negro are not recovered as sister groups in any of the analyses, despite the former being a tributary of the latter. Instead, in most topologies those two rivers are, respectively, more closely related to the Essequibo and Orinoco. Interestingly, the Negro and Branco share a miniscule number of exclusive species, with only three such cases, *Physopyxis cristata* Sousa, Rapp Py-Daniel (see Sousa, Py-Daniel, 2005), *Apistogramma gibbiceps* Meinken (see Kullander, 1980) and *Crenicichla virgatula* Ploeg (see Ito, 2013). This is remarkable in view of the massive physical connections between those basins. It is also eloquent demonstration of the inadequacy of considering physical basin delimitations as a basis for defining cohesive historical units (see section Deconstructing Amazonian hydrographic basins as biogeographic units, below).

The monophyly of Upland Amazon is refuted in all analysis, a result different from that in Lima, Ribeiro (2011). Guiana Shield basins draining into the Amazon also do not form a monophyletic group in any of the analyses and in fact is the region most highly hybridized among all those included in this study. The BPA$_0$ revealed a sister group relationship between the Trombetas-Curuá-Paru do Oeste and Urubu-Uatumã, this being the largest monophyletic subgroup of upland Amazon found in any of the analyses. Among all areas classified as Guyanan Shield, a cratonic Precambrian region, the Urubu-Uatumã is the one that drains the smaller shield area, and may equally well be classified as Lowland. Even with the Urubu-Uatumã excluded, however, remaining regions of the Guyana Shield still do not form a monophyletic assemblage. Before advancing conjectures about the historical "non-naturalness" of the region, it must be noted that its fish fauna is still quite poorly known, with few collections and therefore few species recorded. As more data on the ichthyofauna of the Guyana Shield become available, their inferred relationships may change markedly.

The basins on the Brazilian Shield draining into the Amazon, in their entirety, do not form a monophyletic group in any of the analyses. However, if one excludes the areas Tapajós and Shield Tributaries of the Madeira, the rivers of the Brazilian Shield are closely related, forming a clade in BPA and BPA$_0$ analyses. In PAE and CADE, they form two groups: one composed of the tributaries of the Tapajós plus the Rio Iriri, and another comprising the Rio Xingu drainage (except the Rio Iriri) and the Tocantins basin.

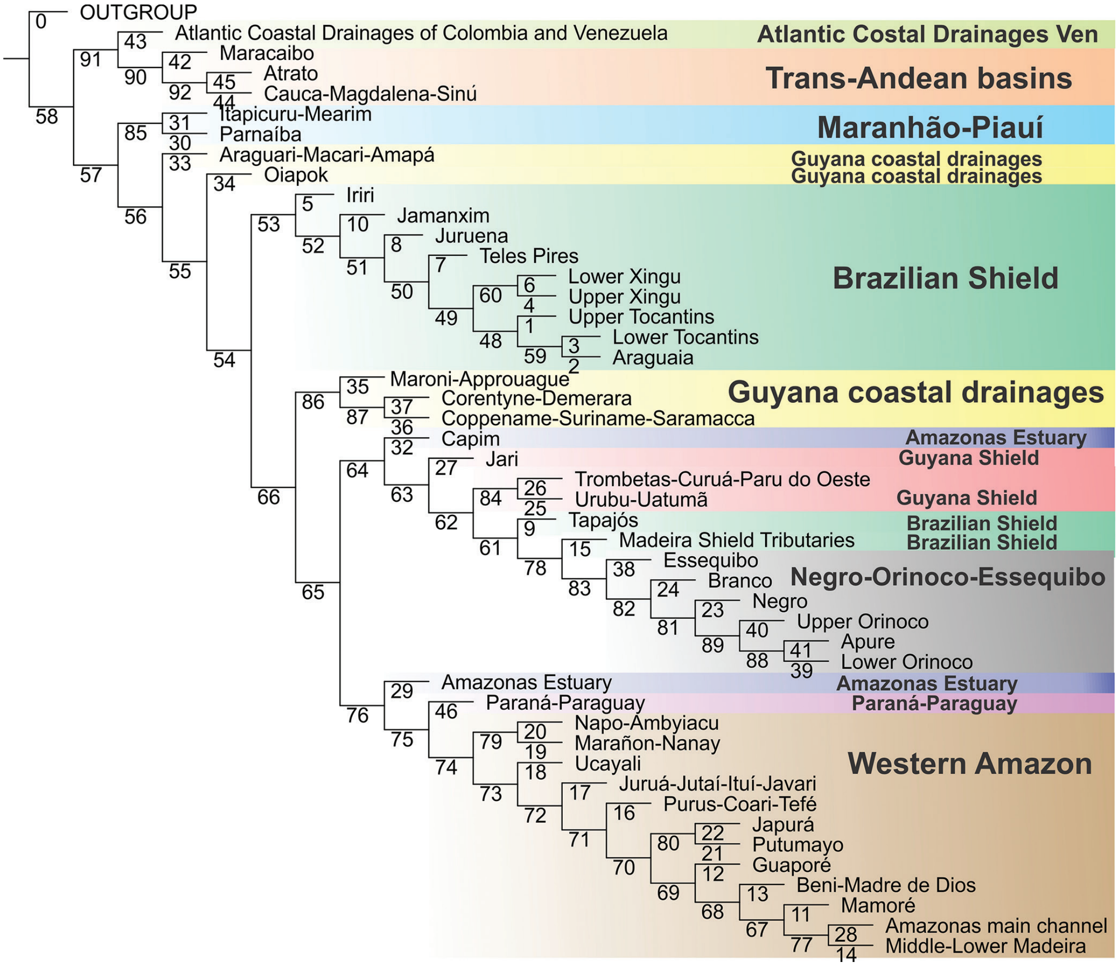

Fig. 5. Most parsimonious tree obtained in BPA$_0$, built with matrix in **S10** - (Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). (Atlantic Coastal Drainages Ven. = Atlantic Coastal Drainages of Colombia and Venezuela).

In none of the topologies obtained the Rio Tapajós basin is hypothesized as monophyletic in its entirety. The Rio Tapajós has diverging relationships in different analyses whereas the Rio Jamanxim, Rio Teles Pires and Rio Juruena form a monophyletic clade in BPA, but a polyphyletic one in BPA_0 and a paraphyletic one in PAE and CADE. In light of such results, it is clear that the Tapajós basin shows a high degree of historical hybridism.

Likewise, the Rio Xingu basin is not recovered as monophyletic in the present analyses. Although the areas Upper and Lower Xingu are sister groups in BPA_0, PAE and CADE, in no case the Rio Iriri is hypothesized as closely related to that clade. The Rio Iriri is instead related to the rivers Jamanxim, Juruena and Teles Pires (all three part of the Rio Tapajós basin) in BPA, PAE and CADE, forming a clade corresponding to the region of the Serra do Cachimbo and surrounding areas, in the northern portion of the Brazilian State of Mato Grosso and Southern reaches of the State of Pará.

In stark contrast to other large Amazonian basins such as the Tapajós, Madeira, Negro and Xingu, the Tocantins basin is recovered as monophyletic in all analyses. In BPA, PAE and CADE, the Lower Tocantins is sister group to the clade formed by the Upper Tocantins plus Araguaia, whereas in BPA_0 the Upper Tocantins is sister to the Lower Tocantins plus Araguaia.

The Guyanan Shield basins draining into the Atlantic (non-Amazonian versant) are recovered as monophyletic in BPA and PAE. In other analyses only part of that clade is recovered, because of the absences of the Araguari-Macari-Amapá and Oiapok in BPA_0 and CADE. In the latter two analyses, all or nearly all Guyana Shield basins are included in a monophyletic Amazon basin whereas in BPA and PAE the Guyanan Shield basins clade is sister to the Amazon basin, suggesting a close relationship between that region and the Amazon.

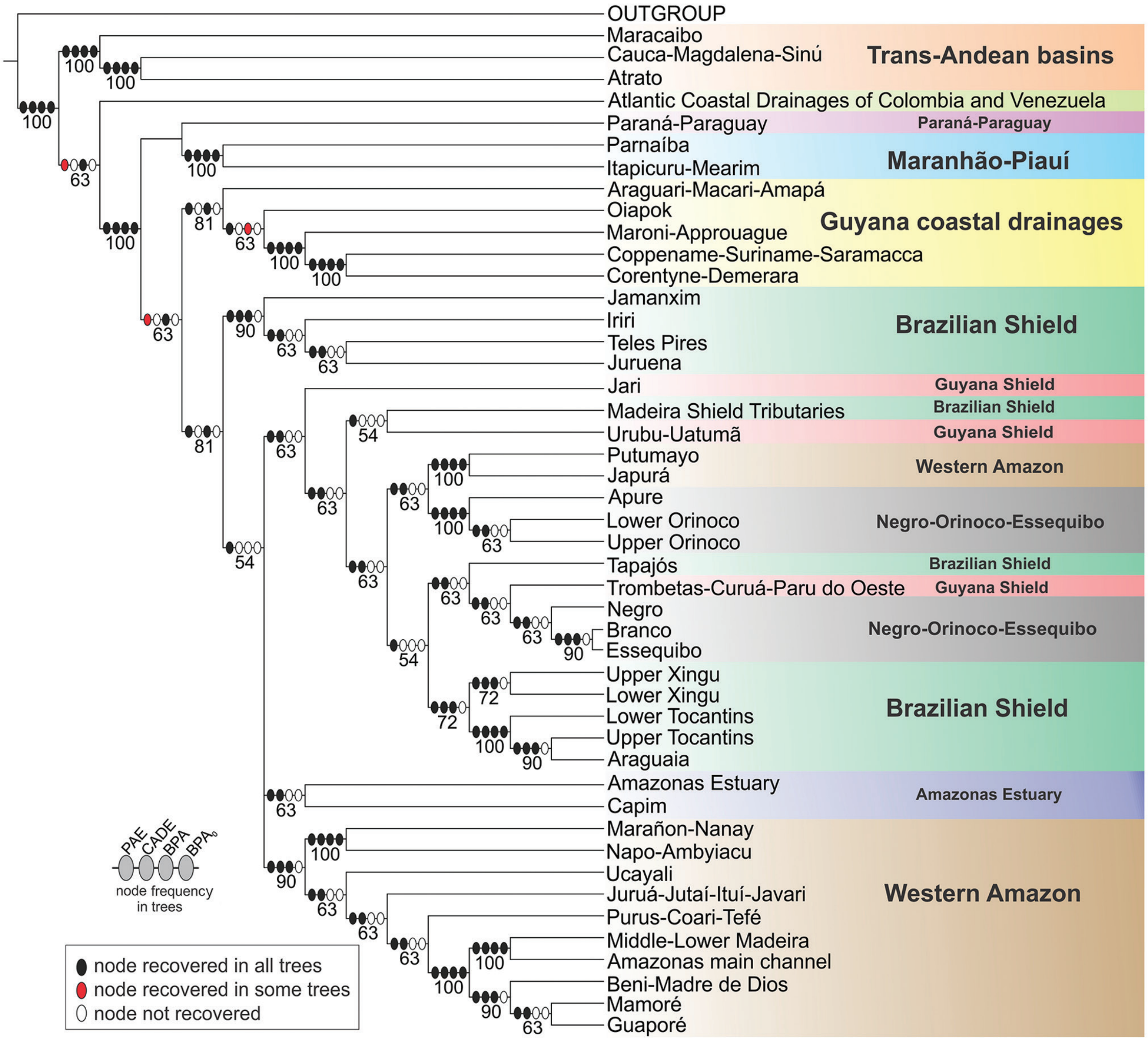

Fig. 6. Majority rule consensus tree of eleven most parsimonious trees obtained in PAE, CADE, BPA and BPA_0. Numbers below branches refer to clade frequencies in consensus.

The area Itapecuru-Mearim and the Rio Parnaíba are recovered as monophyletic in all analyses. In BPA and PAE, that clade is the sister group to the Paraná-Paraguay, a rather surprising relationship. Many papers have suggested a close relationship of the Paraná-Paraguay with the Western Amazon or with rivers draining the Brazilian Shield (*cf.* Albert, Carvalho, 2011). However, the evidence for such relationships, for example in PAE (see Fig. 2), is mostly based on the presence of species common to nearly all lowland rivers of South America (*e.g., Pygocentrus nattereri* Kner, *Pimelodus ornatus* Kner and *Sorubim lima* (Bloch & Schneider)). They are probably symplesiomorphic presences, which were optimized as synapomorphies due both to the incompleteness of data and to undesirable properties of the methods employed and their reliance on Assumption 0 (*cf.* Morrone, 2009; see Analytical Methods section for more details). Another apparent synapomorphy that might erroneously support that clade is the presence of *Moenkhausia sanctaefilomenae* (Steindachner). That species, however, is taxonomically poorly defined. A very similar morphotype occurs in the Orinoco, Amazonas and Guyana drainages, but in this case it is called *Moenkhausia oligolepis* (Günther). A taxonomic revision of the group is necessary in order to verify proper applicability of the name *M. sanctaefilomenae* and its biogeographic significance. At this time, it seems that all present evidence for linking the Paraná-Paraguay with the Itapecuru-Mearim and the Rio Parnaíba is based on questionable evidence.

The results obtained here provide an empirically solid base on which to discuss a number of broader questions related to the biogeography of Amazonian fishes and of freshwater biogeography in general. Some of those issues are addressed in sections that follow.

Discussion

Absences or presumed presences? The absence of a species in a given area may happen because of three reasons: 1) it is there, but was never sampled (pseudo-absence, Morrone, 2009), 2) it once occurred in the area, but has subsequently gone extinct, and 3) it never existed there. One valuable outcome of biogeographic hypothesis is the resulting predictive power, which permits inference of distributions that are no longer observed. A general area cladogram often distinguishes between those three kinds of absence. The present analyses reveal evident cases of pseudo-absences in poorly-sampled rivers, such as the absence of *Acestrorhynchus falcatus* (Bloch) (BPA, BPA_0) and *Hoplerythrinus unitaeniatus* (Spix & Agassiz) (PAE, CADE) in the Rio Jamanxim, considered as autapomorphic for the basin. The presence of these two species there, though still undocumented by museum specimens or the literature, has been visually confirmed by the first author during field work in the Rio Jamanxim.

More interestingly, our analyses point to other conspicuous absences which can hardly be attributed to pseudo-absences, in view of intense and overlapping collection efforts already undertaken in the respective regions which practically discard the possibility of a sampling gap. For example, some species very common throughout most of the Amazon are absent in the Rio Negro: *Acestrorhynchus heterolepis* (Cope) (BPA, BPA_0), *Semaprochilodus insignis* (Jardine) (PAE, CADE), *Curimatella dorsalis* (Eigenmann & Eigenmann) (BPA), *Anostomus ternetzi* Fernández-Yépez (all analyses), *Hemiodus microlepis* Kner (all analyses), *Jupiaba polylepis* (Günther) (BPA_0), *Pygocentrus nattereri* (PAE, CADE), *Oxydoras niger* (Valenciennes) (BPA), *Megalodoras uranoscopus* (Eigenmann & Eigenmann) (PAE, CADE), *Hemisorubim platyrhynchos* (Valenciennes) (PAE, CADE), *Pimelodus blochii* Valenciennes (PAE, CADE), and *Limatulichthys griseus* (Eigenmann) (PAE, CADE). All such cases are here hypothesized as autapomorphic absences. They are present in all other basins phylogenetically surrounding the Rio Negro (*cf.* Figs. 2-5) and optimization procedures lead to the conclusion that they were historically present in the Rio Negro but wen subsequently extinct. The causal factors for that are likely related to the extreme physio-chemical properties of the water in the Rio Negro (Sioli, 1984), which may be inimicable to certain lineages of fish (Wallace, 1889; Roberts, 1972; Kullander, 1986; Vari, 1988; Goulding *et al.*, 1988; Araújo-Lima, Goulding, 1997; Saint-Paul *et al.*, 2000; Crampton, 2011; Lima, Ribeiro, 2011). The present biogeographic hypotheses permit us to predict that the Rio Negro basin was not always hostile to those lineages as it is today and may have had a less extreme type of water earlier in its history. With time, its waters became progressively more hostile, to the point of being uninhabitable to some fish lineages, which then became locally extinct. At the same time, other lineages became endemics adapted to those particular conditions prevailing today. Such combination of extinction and local diversification resulted in the highly particular fish fauna composition of the present-day Rio Negro. Finally, we highlight that the CADE analysis also revealed two very interesting supraspecific "absence discoveries": the entire subfamily Stethaprioninae (Characidae) and the whole genus *Hypoptopoma* Günther (Loricariidae) are absent in the Rio Negro basin. Such remarkable voids had not been previously recorded in the literature, taxonomic or biogeographic. On the basis of our hypotheses, we predict that both taxa were once inhabitants of the Negro, but have subsequently gone extinct. Perhaps such extinction was caused by particular ecological conditions that at some point came to dominate the Rio Negro, such as the extremely acidic and oligotrophic waters.

Stream capture: vicariant or dispersal events? Stream capture is defined as the event when part or all of a river flow is diverted to a neighboring drainage system, as a result of unequal rates of erosion or relative tectonic movements (Bishop, 1995; Wilkinson *et al.*, 2006; Albert, Crampton, 2010; Albert, Reis, 2011, fig. 1.6; Dagosta *et al.*, 2014). The area upstream of the diversion is then separated from its original watershed and starts to drain into a new watershed.

The phenomenon of stream capture reveals unforeseen problems with the distinction between vicariant and dispersal events. Classically, those events are defined as the crossing of a preexisting barrier (dispersal; barrier is older than resulting taxa) and the origin of a barrier that interrupts a formerly continuous distribution of a taxon (vicariance; barrier is as old as resulting taxa). At first sight, a capture event may be seen as a case of dispersal, because a species or a set of species crossed a barrier that formerly existed between basins. Nonetheless, the very same phenomenon may be causing multiple lineage splits and therefore qualify as a vicariant event. Resort to the age of the barrier relative to the taxa is also ambiguous. In a stream capture event the water course change is as old as the lineages that it isolated from the original course. On the other hand, it also qualifies as a dispersal event, insofar as the former barrier crossed (between basins) is older than the lineages that it separated.

Despite the apparent ambiguity, it is possible to resolve the biogeographic nature of a stream capture event on the basis of a wider evolutionary perspective. The species carried towards another basin by stream capture were transported by agents independent of their dispersive abilities and they cannot physically return to their original drainage. At first, such event may seem like an expansion of a species' range, but the resulting isolation is an effective geographical barrier and therefore vicariant in nature. Additionally, dispersalist explanations in biogeography are usually unique in their nature, associated with single lineages or species and their specific biological dispersal abilities (*e.g.* temperature tolerance, oxygen requirements, etc.) (Croizat *et al*., 1974; Platnick, Nelson, 1978; Rosen, 1978; Brooks *et al*., 1981; Nelson, Platnick, 1981; Wiley, 1981; Wiley, 1988a, 1988b; Brooks, 1985; Kluge, 1988; Lieberman, 2000; Morrone, 2009; Wiley, Lieberman, 2011). Because stream capture events affect several unrelated lineages simultaneously (*i.e.*, all species that live in the captured stream), independently of their dispersal abilities, they are not taxon-specific in their effects.

Still, stream-capture events unquestionably combine some elements of dispersal and vicariant properties. Platnick, Nelson (1978) were the first to recognize a model were the phenomenon can be adequately categorized: biotic dispersal. The term originally coined by Platnick, Nelson (1978) had many subsequent - perhaps inadvertent - synonyms in the literature, such as geodispersal (Lieberman, Eldredge, 1996; Lieberman, 2000; Crisci *et al*., 2003; Morrone, 2009; Parenti, Ebach, 2009; Albert, Crampton, 2010; Wiley, Lieberman, 2011), mass coherent dispersal (Morrone, 2009), concerted dispersal (Morrone, 2009), predicted dispersal (Ronquist, 1997; Morrone, 2009). As defined, biotic dispersal applies to the concerted dispersal of many different elements of a biota to another area previously unoccupied by those taxa, generating cosmopolitanism or widespread taxa which may or may not experience vicariance subsequently (Platnick, Nelson, 1978; Morrone, 2009; Parenti, Ebach, 2009). As its very name implies, the main consequence of biotic dispersal is the mixing of faunas and the ensuing historical reticulation of areas (Platnick, Nelson, 1978; Morrone, 2009).

Lieberman (2000) states that cladistic biogeographers have considered vicariant processes as the only pattern-generating processes, ignoring biotic dispersal (referred to as geodispersal). We do not concur entirely with that point of view, insofar as the original idea was in fact proposed and named more than two decades before by cladistic biogeographers themselves (Parenti, Ebach, 2009). On the other hand, Lieberman (2000) is correct in drawing attention to the phenomenon, which has for a long time been largely overlooked in modern biogeographic discussions and only recently began to be taken into account (*e.g.,* Albert, Crampton, 2010; Albert, Carvalho, 2011; Albert, Reis, 2011; Albert *et al*., 2011; Roxo *et al.*, 2014). This is particularly clear in the case of fish biogeography and mostly so in neotropical fishes. Biotic dispersal has been a major factor in historical hybridization and diversity generation in Amazonian rivers. This is a consequence of the importance of neotectonic activity and resulting rearrangements in the drainage network as diversity-generating factors, both in freshwater fishes in general (Burridge *et al*., 2006, 2007; Cardoso, Montoya-Burgos, 2009; Waters *et al*., 2007) and neotropical fishes in particular (Albert, Carvalho, 2011; Albert, Reis, 2011; Albert *et al*., 2011; Lima, Ribeiro, 2011; Ribeiro *et al*., 2013; Roxo *et al*., 2014; Tagliacollo *et al*., 2015). Those observations and ensuing conclusions prompt a reevaluation of the assumption that vicariant and dispersalist events in their pure form are the best explanation for the diversification of the neotropical fish fauna. Such view is foreshadowed in Marshall, Lundberg (1996): "*Models for the evolutionary diversification of the Neotropical continental biota must therefore take into account multiple occurrences of vicariance or coalescence*". The search for a general divergent biogeographic pattern for the Amazon is nothing but a graphic simplification of a much more complex history (*cf.* Hovenkamp, 1997; Lieberman, 2000; Legendre, Makarenkov, 2002) rife with biotic dispersal. Awareness of that fact is implicitly evident in the current trend in biogeographic studies to adopt an ontology of complexity (see Cui *et al*., 2013 in comparison with Rosen, 1960; 1979 for an example). This new view is gradually replacing the traditional ontology of simplicity, as simple elegant models of the biosphere and its evolution are no longer sufficient to explain the context of diversity-generation and the processes which produce complex biotas (Brooks, 2005).

In the present analyses, biotic dispersal in the form of stream captures and its consequent faunal mixture is the most likely explanation for a multitude of cases in which tributaries are not related to their mother basins, such as Iriri, Branco, Jamanxim, Juruena, and Teles Pires. None of the five elements forms a monophyletic group with their respective hydrographic basins (the Iriri is hydrographically a tributary to the Xingu, the Branco to the Rio Negro and the remaining three to the Tapajós).

Different types of widespread fishes and their consequences to biogeography. Widespread taxa can be the result of either failure to speciate after a vicariant event or dispersal. The latter can be either random (=*jump dispersal*, *long-distance dispersal*, *sweepstakes dispersal* or *waif dispersal* Morrone, 2009), by diffusion (Morrone, 2009) or by biotic dispersal (=geodispersal). Of those, only random and diffusion dispersal can be considered as invalid in the search for historical patterns (Platnick, Nelson, 1978; Nelson, Platnick, 1981; Patterson, 1981; Rosen, 1985) because they are idiosyncratic unique events of individual lineages (Rosen, 1976) directly linked to the requirements and biological properties of single species or taxa. But not all widespread distributions are so uninformative and to ignore them *en masse* is a mistake that may obscure our understanding of many genuinely interesting biogeographic patterns that need explanation.

From the start, it is most important to be able to distinguish among the various types of widespread taxa, so that biotic dispersal events can be identified and treated properly. In the case of freshwater fishes, this is not as complex or subjective as it might appear at first. In fact, there are many such cases which are unanimously recognized among ichthyologists. Freshwater fish do not individually transpose land barriers which define hydrographic limits of their basins. So, widespread freshwater fish taxa can only be interpreted in two ways: as a result of historical hydrological patterns or as a consequence of the normal movement of species individuals in their environment that transpose basin limits by water (= dispersion *sensu* Platnick, 1976). The distinction between these two categories is linked to the vagility of species and the capability of lineages to withstand a wide variety of environmental situations (*cf*. Crampton, 2011; Crampton *et al*., 2016), with resulting broad or narrow distributions being a result of such factors in combination with historical circumstances. For example, large body-size species such as *Brachyplatystoma* spp. (Pimelodidae) have life areas which cover the entire Lowland region of the Amazon basin, undergoing reproductive migrations all the way to the Andean foothills for spawning (*cf*. Goulding *et al*., 2003). In the process, they routinely circulate through different basins. Other examples of eurytopic and broad vagility are various lineages of Characiformes such as Bryconidae, Curimatidae, Prochilodontidae, Myleinae, which descend clear water rivers to spawn at the mouth of white water rivers (*cf*. Goulding, 1980). At the other extreme are stenotopic lineages such as rheophilic species (*e.g.,* Ancistrinae, *Teleocichla* Kullander), narrowly dependent on fast flowing sectors or rapids, with highly oxygenated, high-energy waters. The ability of those species to translocate to other basins by active migrations across deep river channels is very limited or non-existent.

This important distinction between different forms of widely distributed fish species was foreshadowed for the first time in neotropical fishes by Eigenmann (1912): "*In this connection the word "migration" as applied to fishes needs definition. It is applied to such journeys as that of the eel to the ocean, or that of the salmon toward the headwaters, for purposes of reproduction. Such trips, although very long, probably only incidentally influence the dispersal of fishes. On the other hand, some species are natural pioneers, found always in the rivulets of the headwaters, as far up as they can get. If the headwater is advanced a few feet, they advance with it. Their migration from one system to another is not miraculous. To find such fishes on opposite sides of a low water-shed presents no mystery. If by a sudden freshet two rivulets join for but a short time, these species are present to take advantage of the temporary union, and frequently do take advantage of it. Such species usually have a very wide distribution*". In that enlightening passage, Eigenmann (1912) clearly discriminates two categories of widespread taxa: those whose distribution is the result of their great movement capabilities in life and those that achieve broad distributions by means of temporary connections among basins.

The amplitude of geographic distribution of a taxon can plausibly influence the way it will be impacted by stochastic processes to which any lineage is subjected over time. Widespread taxa are theoretically less susceptible to extinction events due to the stability provided by larger population structures, while species with narrow distributions tend to suffer higher extinction rates (*cf*. Wright, 1932, 1986). Therefore, it is expected that lineages with large vagility will tend to be less prone to extinction and more resilient over time. Naturally, the biogeographic response is influenced not only by the vagility limitations of species, but also by the geomorphology of the terrain where they live. For example, lowland basins are more prone to hydrogeological changes and more dynamic than those in shield areas (Lundberg *et al*., 1988). This implies that lowlands should have proportionally more widely distributed taxa, more cases of sympatry and lineages that are less prone to extinction. The result of those factors is that lowland rivers should have higher levels of diversity when compared to shield rivers. Thus, the Amazonian lowland can acts as "museum" *sensu* Stebbins (1974), *i.e.,* an area where species richness has accumulated as a result of low rates of extinction and the preservation of archaic lineages.

In contrast, as pointed out by Lujan, Conway (2015) even relatively small distances between patches of rapids with high energy rate may promote isolation and vicariance by increasing the universal risk of downstream export should individuals move far from a preferred microhabitat (Markert *et al*., 2010; Schwarzer *et al*., 2011). For these reasons and under the assumption that they are less susceptible to random dispersal, some authors have recently emphasized the importance of rheophilic species as good models for inferring historical biogeography. Since 70% of Amazonian fish species occur in two or more basins, there seems to be no doubt that treating widespread taxa properly is a challenge for biogeographic studies in the region. In riverine biogeography a widespread taxon may be testimony to an event of stream capture which is not simply random dispersal but instead inherently informative about the history of the biota and therefore part of the core biogeographic pattern.

Of course, that does not imply that all widespread taxa will be likewise informative and some of them are undoubtedly just widespread in the usual sense. A possible way of testing that would be to identify taxa with high proportion of migratory species (Anostomidae, Curimatidae, Prochilodontidae and Pimelodidae) and experimentally isolate their incongruence-generating impact on biogeographic analyses.

Deconstructing Amazonian hydrographic basins as biogeographic units. Wallace (1852) is widely recognized as the first author to highlight the influence of rivers in the distribution of tropical species (Lehman, Fleagle, 2006). Indeed, in the neotropical region, rivers have been proposed as biogeographic barriers for birds (*e.g.*, Remsen, Parker, 1983; Caparella, 1992; Hayes, Sewlal, 2004), reptiles (*e.g.*, Rodrigues, 1991; Pellegrino *et al.*, 2005; Passoni *et al.*, 2008), and mammals (*e.g.*, Eisenberg, 1981). While in terrestrial groups rivers are considered as effective limits in defining biogeographic units, for aquatic organisms, in contrast, rivers are considered as the conduits of taxon movements (Schaefer, Arroyave, 2010). There are exceptions in which the rivers themselves may represent biogeographic barriers for freshwater organisms (Bănărescu, 1990), such as the main channel of the Rio Amazonas serving as a barrier for highland fishes (Géry, 1962, 1969) and the highly acidic Rio Negro forming an uninhabitable desert for white-water species (Goulding *et al.*, 1988), but those are special cases.

At first glance, river basins and their fish faunas are attractive models for the recognition of historical patterns. They are well-defined isolated water courses separated by clear-cut barriers (land or oceans) mostly impassable by strictly freshwater fishes (Myers, 1947; Eadie *et al.*, 1986; Berra, 2001; de Pinna, 2006; Olden *et al.*, 2010). Such a scenario implies that extinction and speciation events are basin-specific, in turn making drainages cohesive biogeographic units. In fact, studies on neotropical fish biogeography have invariably utilized large hydrographic basins as fundamental geographical units (*cf.* Hubert, Renno, 2006; Ingenito, Buckup, 2007; Albert, Carvalho, 2011; Buckup, 2011; Schaefer, 2011; Winemiller, Willis, 2011; Lima, Ribeiro, 2011; Mariguela *et al.*, 2013; Camelier, Zanata, 2014). Of course, discrepant evidence has been known for some time, such as the existence of taxa in the same basin each associated with divergent area relationships (*cf.* Vari, 1988) and the large number of sympatric congeners, especially in the Western Amazonian lowlands. As stated by Platnick, Nelson (1978) "*it is not necessary or even expected that we find that the biota of one area belongs to only a single general pattern, or that if we find more than one, that only one pattern contributes information about the history of the areas involved*". Despite such insights, those Amazonian cases have been considered as minority exceptions which do not change the general model.

The results of our analyses, however, further bring this paradigm into question. The biogeographic topologies obtained herein (Figs. 2-7) show that large Amazonian river drainages are for the most part historically hybrid. This is the case of the Rio Negro, Madeira, Tapajós (Fig. 7) and Xingu basins and the Rio Amazonas basin itself (Fig. 8).Therefore, hydrographic basins in the Amazon may not be cohesive historical units, but rather massively reticulate physical entities, composite in their geology, biology, and time. In the following paragraphs we elaborate the arguments that undermine the basin-as-area model and deconstruct the idea of drainages as historical units.

First it is necessary to refine some subtleties related to the notion of barrier. Any species of fish has its distribution restricted by barriers operating in the present. Those are not necessarily the same barriers that caused vicariant events resulting in speciation (*cf.* Hovenkamp, 1997). There is no strict correspondence between the barriers that caused the separation of a taxon and the present-day barriers that delimit its distribution. In other words, there is no necessary relation between the historical origin of a taxon and the origin of present barriers which constrain its specific distributions today. The two may be non-identical and even entirely non-overlapping. Thus, physical barriers which delimit fish distributions cannot be considered *a priori* as identical to the historical barriers which causally determined the existence of historical units. It is particularly clear in many amazonian fishes. Fossils of *Brachyplatystoma* spp. and *Phractocephalus* indicate that the historical biogeography of these groups is related with the hydrogeological dynamics of the Western Amazon. Nowadays, these lineages occur in the Eastern Amazon because of the breaching of the Purus Arch and the formation of a transcontinental connection with the Western Amazon. In the Eastern Amazon, the distribution of these pimelodids is now limited by waterfalls (in the case of the Tapajós river basin [Eastern Amazon] these fishes are limited downstream by the Salto Augusto waterfall) that seems to have no correlation with the past diversification of these fishes.

A challenge also needs to be made on the widespread assumption that fish species distributions are basin-specific. Within individual hydrographic basins, the distribution of a fish species is determined by a combination of biotic and abiotic factors that vary longitudinally in the hydrographic network (Vari, 1988; Jackson *et al.*, 2001). Fish species are rarely or never endemic to a basin as a whole, but rather only to sections or portions of that basin (Agassiz, Agassiz, 1868; Kullander, 1986; Schaefer, Arroyave, 2010; Lima, Ribeiro, 2011). The model that basins are perfect biogeographic units would predict a plethora of taxa widely distributed in their home basin but absent in other neighboring basins. In reality, this pattern is extremely rare or non-existent among Amazonian fishes, and in fact we do not know of a single such case. If hydrographic basins somehow translate into a unique biogeographic history, that probably occurs in very restricted subregions, as microbasins etc, and hardly at the level of whole large basins as have been employed as geographical units in biogeographic analyses. As pointed out by Lima, Ribeiro (2011), the notion that river basins as historical units is so entrenched in the minds of freshwater fish systematists that identical morphotypes isolated in distinct basins are usually arbitrarily considered as different species, rather than widespread taxa.

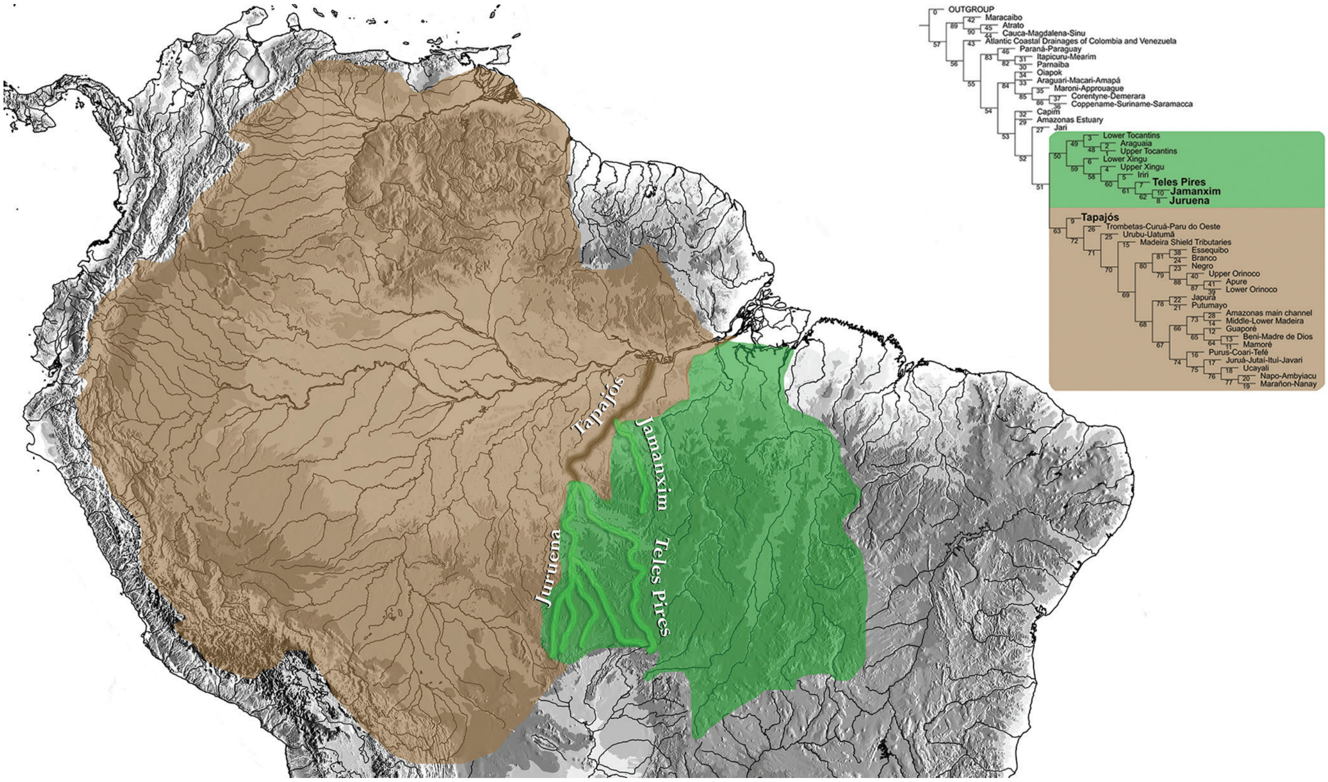

Fig. 7. Detail of the Rio Tapajós basin (thick outline) showing its composite biogeographical nature. Tributaries shown in green (Juruena, Teles Pires and Jamanxim) are related to Eastern Brazilian shield drainages, in the green area. The main channel of the Tapajós (in brown) is instead related to rivers in the brown area, composed of the Western Amazon, the Orinoco-Essequibo and most of the left tributaries of the Amazon.

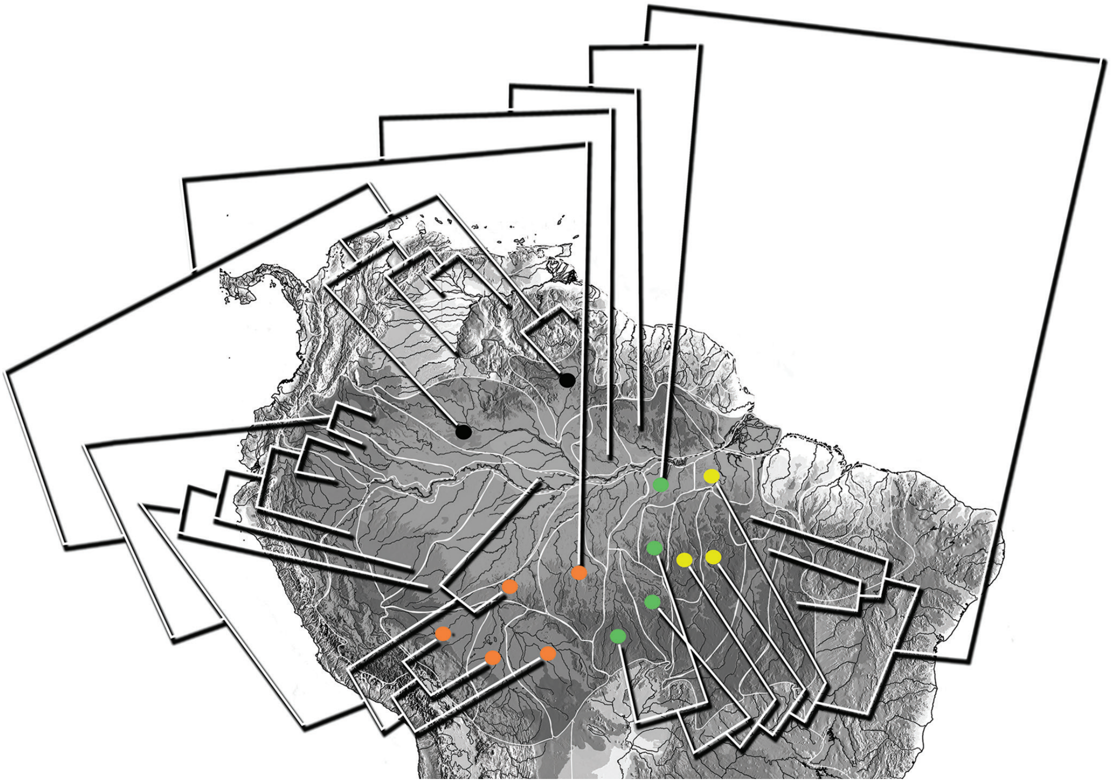

Fig. 8. Part of BPA tree (corresponding to node 51 in Fig. 4) showing reticulated relationships of some amazonian basins: Rio Negro (black circles); Rio Madeira (orange circle); Rio Tapajós (green circles); Rio Xingu (yellow circles).

Finally, and most importantly, it is necessary to challenge the idea that hydrographic basins are historically stagnant and actual instantaneous images of divergent histories. Thanks to events of biotic dispersal, areas rarely evolve in divergent fashion like taxa (Upchurch, Hunn, 2002; Brooks, 2005; Riddle, Hafner, 2006; Morrone, 2009; Sanmartín, 2012; Matamoros *et al*., 2015). There are no convincing arguments that the history of earth can be entirely represented as diverging branching diagrams (Hovenkamp, 1997) and the same can be true for the Amazonian basins and its fishes. Amazonian river drainages have evolved by numerous events of reticulation (*cf*. Hubert, Renno, 2006; Lima, Ribeiro, 2011; Ribeiro *et al*., 2013; Dagosta *et al.*, 2014). Géry (1962) was perhaps the first ichthyologist to recognize the great dynamism of South American drainages and the evanescence of their limits as biogeographic barriers to fish: "*The Characoids (at least) have shown that they can pass readily from one basin to another in a very short time, geologically speaking*" (Géry, 1962: page 67). Or, more explicitly, in Géry (1969) page 833: "*It is thus naive to believe that fresh-water fishes 'are almost inescapably confined to their own drainage system*".

The lability of historical-geomorphological limits reaches its maximum in the Amazonian lowlands, where river limits are highly movable and often blurred in the high-water season (Albert *et al*., 2011; Lima, Ribeiro, 2011). But evidence of faunistic mixing in shield rivers have accumulated in recent years as well. For the most part, they involve adjacent drainages: Tapajós and Paraguay (Shibatta, Pavanelli, 2005; Lima *et al*., 2007; Birindelli, Britski, 2009; Carvalho, Albert, 2011); Tapajós, Xingu (Campos-da-Paz, 1999; Birindelli *et al*., 2008; Menezes *et al*., 2009); Tapajós, Madeira (Netto-Ferreira, Vari, 2011; Varella *et al*., 2012); Xingu, Paraguay (Vari, 1991; da Graça *et al*., 2008; Aquino, Schaefer, 2010; Carvalho, Albert, 2011; Netto-Ferreira, Vari, 2011); Xingu, Tocantins (Zawadzki *et al*., 2008; Ingenito *et al*., 2013); Tocantins, Paraguay (Lucinda, 2005; Carvalho, Albert, 2011;); Tocantins, São Francisco (Vari, Harold, 2001; Lima, Caires, 2011; Dagosta *et al*., 2014; Freitas *et al*., 2015); Tocantins, Upper Paraná (Britski,1997; Lima, Caires, 2011); Madeira, Paraguay (Kullander, 1982; Reis, Malabarba, 1988; Kullander, 2003; Vari *et al*., 2005; Vera-Alcaraz *et al*., 2012; Ota *et al*., 2014); Madeira and Juruena (Dagosta *et al*., 2016). In all such examples, the hypothesis that ancestral populations of trans-basin taxa were once widespread in the two basins concerned can be refuted because the current watershed divide between them dates from the Precambrian and vastly predate the radiations of Teleostei in the Upper Cretaceous (c. 100-66 Ma) (Albert, Reis, 2011) and predate also the origin of the basins themselves (Lundberg, 1998). Although the Brazilian Shield is ancient, its faults and sutures were tectonically active during the Cenozoic, due to the growth of the Atlantic Ocean in the divergent margin and the subduction of the Nazca Plate (Riccomini, Assumpção, 1999; Ribeiro *et al*., 2013). Such reactivations were responsible for the great fluvial dynamism of the Brazilian Shield (Lima, Ribeiro, 2011) and offered opportunities for faunistic mixtures between neighboring basins, promoting biotic dispersal. The result is that each Brazilian Shield drainage displays species uniquely shared with each one of its neighboring basins. This means that all such basins are historically (and compositionally) hybrid. It seems certain that the ichthyofaunal composition of Amazonian basins are mosaics of divergent elements of different origins, recruited in the course of separate and differently-aged events (Hubert, Renno, 2006; Lima, Ribeiro, 2011; Ribeiro *et al*., 2013; Dagosta *et al.*, 2014).

The reticulate nature of Amazonian drainages provides exceptionally rich grounds for understanding the meaning of such entities as biogeographic units. Composite areas have long been incorporated into the horizon of possibilities in cladistic biogeography (Nelson, Platnick, 1981; Platnick, Nelson, 1984; Schuh, Stonedahl, 1986; Parenti, 1991). Still, the utilization of composite areas in biogeographic analyses has been demonstrated to be a major source of incongruence (Platnick, Nelson, 1978; Parenti, 1991), resulting in overlapping patterns (Grande, 1985) that cannot be properly understood by analytical methods available (Young, 1995; Morrone, 2009) (see below). Reticulate areas tend to result in polytomies in area cladograms (Cracraft, 1988).

Area reticulations can certainly be incorporated in branching diagrams, by means of reticulograms (Grande, 1985; Rosen, 1985; Makarenkov, Legendre, 2004; Alix *et al*., 2012), as unresolved cladograms (Grande, 1985), as different area cladograms for each historical period (Rosen, 1985) or as reticulated graphic representations (Donoghue, Moore, 2003). Regardless of such devices, hybrid areas are incorporated in biogeographic hypotheses only with difficulty (Hovenkamp, 1997; Legendre, Makarenkov, 2002) and at the cost of substantial loss or confusion of associated information.

As proposed by Parenti (1991), it is important to recognize historically reticulate areas and to avoid their use as units in historical biogeography. The results of our analyses make it abundantly clear that large Amazonian drainages are rampantly reticulate and therefore we propose that they do not be used as historical units in studies about the biogeography of the region.

With river basins deconstructed, what is left? Biogeographic areas are simply hypotheses and can be modified in light of new data, just as non-monophyletic taxa can be likewise redefined (Nelson, Platnick, 1981; Harold, Mooi, 1994; Parenti, Ebach, 2009). It is important to recognize, however, that the analogy between areas and lineages is imprecise and should not be stretched too far. No biogeographic theory predicts that areas should exist, in contrast to species and monophyletic groups, predicted by evolutionary theory (Hovenkamp, 1997). Any expectation that a general system of areas exists is contradictory with first principles of biogeography and evolutionary biology because area evolution is predominantly reticulated and do not necessarily result in naturally nested sets of categories. Therefore, if Amazonian drainages are reticulate, the simplest solution is to divide them into smaller subunits, which will less likely be hybrid. Criticism that such procedure creates an infinite regression of smaller and smaller subdivisions have been shown to be vacuous in specific cases (Parenti, 1991) and we consider that such allegations can only be tested empirically.

Alternative approaches suggest the use of temporal dimension to solve the problem of composite areas. Many biogeographers reject the incorporation of time in analyses in order to avoid untestable parameters and a potential return to purely narrative biogeographic scenarios (Morrone, 2009). Many authors, on the other hand, have underscored the importance of time scale in biogeographic research (Grande, 1985; Page, 1990b; Upchurch, Hunn, 2002; Donoghue, Moore, 2003; Nihei, 2008). They argue that ignoring the time dimension obscures the connection between biogeographic patterns and their underlying causes (Donoghue, Moore, 2003, Posadas *et al*., 2006). Page (1990b), for example, states that the addition of a temporal component increases our ability to distinguish congruence from incongruence.

Another strategy is to assume outright that river drainages are actually hybrid and rather than searching for a chimeric unified history, instead focusing on the processes involved in the formation of their biotic mosaic. Once the phylogenetic relationships of the taxa and their geographic distributions are known, it is theoretically possible to determine their age of divergence, both by phylogeographic analysis and the fossil record. Such resources allow the stratification of the composite biota in temporally congruent layers (Grande, 1985; Upchurch, Hunn, 2002; Humphries, Ebach, 2004; Wen *et al.*, 2013) and ultimately correlate them with the events responsible for the presence of specific taxa in river basins (*e.g.*, dispersal, biotic dispersal and vicariance). Parenti, Ebach (2009) suggested that an approach that separates biotas into temporally congruent slices should be applied after the search for biogeographic patterns, not before them. They argue that temporal data would not be able to alter results from biogeographic analyses and produce alternative hypotheses. In face of well-known incompleteness of the fossil record and problems in the calibration of molecular clocks, such time-slicing strategy is at present more a theoretical prospect than a practical possibility. The unification of time and space is a long-lasting challenge to biogeography (Croizat, 1964; Rosen, 1978; Nelson, Platnick, 1981; Humphries, Parenti, 1999; Knapp, 2005) and perhaps its eternal motivation. It is certain, however, that progress on the biogeography of Amazonian fishes depends on recognizing the multiple temporal facets of river basins and developing analytical tools that can deal with the problem, instead of ignoring it.

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