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Original article

Historical biogeography of fishes from coastal basins of Maranhão State, northeastern Brazil

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The Amazonian ichthyofauna is one of the most diverse in the world, yet fishes from the adjacent coastal basins of Maranhão State in Northeastern Brazil remain poorly known. We use phylogeographic, community phylogenetic and phylogenetic beta diversity methods to study the biogeographic history of fishes from the coastal basins of Maranhão State. We report a total of 160 fish species from the basins of the Maranhão region, representing a 93% increase over results of previous studies. All the fish species assemblages from Maranhão are polyphyletic, with only a few putative sister species pairs inhabiting the region. The modern watershed divides among Maranhão basins do not form substantial barriers to dispersal for freshwater fish species, and are more effectively modelled as biogeographic islands than as biogeographic provinces. In combination these results suggest that the Maranhão ichthyofauna was assembled under the influence of several macroevolutionary (extinction, dispersal) and landscape evolution processes, during the Miocene and Pliocene, as well as by the modern ecological characteristics of the region. The results indicate that the distinctive geological and climatic conditions and history of Northeastern Brazil strongly constrained the formation of aquatic faunas in coastal basins of Maranhão State.

Keywords: Biodiversity, Community phylogenetics, Paleogeography, Phylogenetic beta diversity, Phylogeography.

A ictiofauna da Amazônia é uma das mais diversificadas do mundo, mas os peixes das bacias costeiras adjacentes do estado do Maranhão, no Nordeste do Brasil, ainda são pouco conhecidos. Utilizamos métodos filogeográficos, filogenia de comunidade e de diversidade beta filogenética para estudar a história biogeográfica de peixes das bacias costeiras do estado do Maranhão. Nós relatamos um total de 160 espécies de peixes das bacias da região do Maranhão, representando um aumento de 93% sobre os resultados de estudos anteriores. Todas as assembleias de espécies de peixes do Maranhão são polifiléticas, com apenas alguns supostos pares de espécies irmãs habitando a região. As divisões modernas das bacias hidrográficas do Maranhão não formam barreiras substanciais para a dispersão de espécies de peixes de água doce, e são mais efetivamente modeladas como ilhas biogeográficas do que como províncias biogeográficas. Em conjunto, esses resultados sugerem que a ictiofauna maranhense foi montada sob a influência de vários processos de evolução macroevolutiva (extinção, dispersão) e paisagística, durante o Mioceno e Plioceno, bem como pelas características ecológicas modernas da região. Os resultados indicam que as distintas condições geológicas e climáticas e a história do Nordeste do Brasil restringiram fortemente a formação de faunas aquáticas em bacias costeiras do estado do Maranhão.

Palavras-chave: Beta diversidade filogenética, Biodiversidade, Comunidade filogenética, Filogeografia, Paleogeografia.

Introduction

Relatively little is known about the fishes inhabiting coastal rivers of Maranhão State in Northeastern Brazil, mainly due to a lack of taxonomic and ecological studies (but see Piorski *et al*., 2007, 2017; Barros *et al.*, 2011; Ramos *et al.*, 2014). Even less information has been published regarding the systematics, geographical variation and biogeography of the fishes of this region. To date no species lists have been published for the individual basins of the Maranhão region, and the region is frequently treated as a single geographic unit (*e.g.* Piorski *et al*., 1998; Rosa, 2003; Soares, 2005; Barros *et al.*, 2011; Carvalho-Costa *et al.*, 2011). The river basins of Maranhão are sometimes combined with the Parnaíba basin (*e.g.* Rosa, 2003; Ramos *et al.*, 2014) that only partially occurs in Maranhão State. The fish diversity previously reported from Maranhão rivers includes 83 species in 65 genera, 31 families and 10 orders (Soares, 2005; Barros *et al.*, 2011).

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This scarce knowledge of the Maranhão ichthyofauna is partially a consequence of the common misconception that this fauna is a subset of the lower Amazonas or Guianas rivers. Abell *et al.* (2008) contributed to this misperception by circumscribing the Maranhão region within the Amazonas Estuary and Coastal Drainages ecoregion (number 323). Depending on the approach used, the rivers of the Eastern Amazon are part of one or more distinct areas of endemism. Many studies have included the Eastern Amazon basins within the rest of Amazon (Géry, 1969; Abell *et al.*, 2008), or with Brazilian Northeastern basins (Vari, 1988). Some studies have considered these basins as independent areas (Lundberg *et al.*, 1998; Hubert, Renno, 2006; Dagosta, de Pinna, 2017).

Géry (1969) reported a stronger similarity between the Maranhão and Amazon ichthyofaunas, whereas Vari (1988) considered the Maranhão ichthyofauna a hybrid of the Northeastern and São Francisco rivers, grading to the Amazon river. Lundberg *et al.* (1998) considered the Maranhão rivers a separate area, neither Amazon nor Northeastern, but a unique area, a conception followed by Hubert, Renno (2006) and Dagosta, de Pinna (2017), with some differences in the area extents of these regions. It is however necessary to emphasize that none of these studies recognized a substantial number of species present in the Maranhão rivers, the largest number being 66 species in Dagosta, de Pinna (2017).

The rivers of Maranhão State meander across a broad lowland coastal plain, a geography thought to have facilitated hydrological and faunal exchanges among the several basins through the capture of lateral tributaries and anastomosing river mouths (Huber, 1998; Wilkinson *et al*., 2006). River or headwater capture changes the flow of water from one basin to another, expanding the receiver drainage and contracting the donor drainage (Christofoletti, 1975; Oliveira, 2010). River capture has been hypothesized to help explain the observed fish species composition of the river basins of the Maranhão region (Piorski, 2010; Abreu, 2013). This continuous process, perennially connecting and separating portions of adjacent river basins, is thought to enhance biological diversity of obligate aquatic organisms, by increasing rates of dispersal and speciation, and reducing rates of extinction in some species (Albert, Crampton, 2010; Albert, Reis, 2011). Evidence for river capture in Maranhão rivers includes many elbows or abrupt changes in river courses (Piorski, 2010).

Quaternary eustatic sea-level changes are also thought to have affected the biogeography and biodiversity of river basins that drain across the Maranhão coastal plain. Successive marine transgressions (advances) and regressions (retreats) change coastlines and remodel coastal riverscapes (Dias *et al.*, 2014; Hubert, Renno, 2006; Lovejoy *et al.*, 2006). Large marine transgressions into the Marajó and São Luís sedimentary basins occurred during late Miocene and Pliocene (11.6 - 2.6 Ma). These transient marine incursions resulted in shallow coastal seas known as 'Mar de Pirabas' (Soares Junior *et al.*, 2011) and 'Gulfo Maranhense' (Ab'saber, 1960; Petri, Fúlfaro, 1983), when sea-levels were up to 15 m above modern level, and the mouths of many coastal rivers were disconnected. At times of marine regression, as at the Last Glacial Maximum (LGM) *c.* 26.5 - 20.0 ka (Clark *et al.*, 2009), sea levels were as much as 122 m below modern level, and many rivers of the Maranhão coastal plain were connected at their mouths (Costa *et al.*, 1997; Piorski, 2010).

Here we provide a comprehensive study of fishes from the coastal basins of Maranhão State, with the goal to understand how landscape evolution and historical connections among rivers drives the formation of regional fish species assemblages. We provide the most complete list of fish species from the region to date, compare species richness and composition among basins, estimate the phylogenetic diversity of these faunas, and describe the faunal similarities of these rivers with those of the Amazon basin. We report a total of 160 fish species from the basins of the Maranhão region, representing 77 newly reported species, or a 93% increase over the greatest number previously reported. We conclude that past geological events and current ecological landscapes contribute to the modern patterns of fish species distributions in this region.

Material and Methods

Ichthyofauna composition. The survey of distributions of fish species inhabiting Maranhão State (Fig. 1) was conducted through examination of museum collections of Coleção de Peixes da Universidade Federal do Maranhão (CPUFMA), data accessed through species surveys published atlases, books and catalogs (Reis *et al.*, 2003; Soares, 2005; Buckup *et al.*, 2007; Lucinda *et al.*, 2007; Soares *et al.*, 2009; Mérona *et al.*, 2010; Barros *et al.*, 2011; Lima, Caires, 2011; Claro-García, Shibatta, 2013; Ramos *et al.*, 2014; Melo *et al.*, 2016; Bartolette *et al.*, 2017; Dagosta, de Pinna, 2017; Piorski *et al*., 2017). We were unable to provide estimates of sampling completeness for these collection records, as the data necessary for rarefaction analysis are not available.

Community phylogenetic structure. Phylogenetic relationships among all 160 Maranhão fish species were estimated using a combination of published phylogenetic hypotheses following the methods of Aquino, Colli (2017). Tree estimation was conducted in three steps. 1) The robust phylogeny of Betancur-R *et al.* (2013) generated from 20 nuclear genes and one (16S) mtDNA gene, was designated as a backbone. 2) Species found in the Maranhão region but absent from the backbone were manually added as polytomies with their closest present relatives. Published phylogenies were used to establish these relationships: Mirande (2010) for Characiformes; Bockmann (1998), de Pinna (1998), Albornoz (2006), Sullivan *et al.* (2006), Chiachio *et al.* (2008), Pereira (2008), Cramer *et al.* (2011)

and Martins (2012) for Siluriformes; Hrbek *et al.* (2007) for Poecilidae; Albert (2001), Lovejoy *et al.* (2010) and Tagliacollo *et al.* (2016) for Gymnotiformes; Ilves *et al.* (2018) for Cichlidae, and Nakatani *et al.* (2011), Betancur-R *et al.* (2013) and Chen *et al.* (2013) for all other groups. 3) Species not present in the Maranhão region were pruned from the tree using Phylomatic version 3, available online (http://phylodiversity.net/phylomatic/).

The resulting tree includes the 160 species from the Maranhão region with all branches of equal length. Tree dating was estimated using the Branch Length Adjustment (BLADJ) algorithm in Phylocom 4.2 (Webb *et al.*, 2008). The pruned, dated working phylogeny used in all community phylogenetic analyses is represented in Fig. 2 and the Nexus file (**S1** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni).

To complement this working phylogeny, we next constructed a presence-absence matrix for all 160 species and each river basin studied to assess phylogenetic diversity using the R package picante 1.7 (Kembel *et al.*, 2010). We used Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD) indices to measure the phylogenetic structure of the local assemblages in each river basin (Webb *et al.*, 2002). MPD calculates the phylogenetic distances among all possible species pairs as an estimate of the phylogenetic structure of species assemblages. MNTD calculates distances between each species and its nearest neighbor in the same assemblage, capturing variations at the tip of the phylogeny (Webb, 2000). The MPD and MNTD values observed in each assemblage are then compared by z-test to a sample of 999 randomly-generated phylogenies to assess whether they diverge significantly from chance. Scores greater than 2.0 with z-test p-value <0.05 indicate phylogenetic over-dispersion, with a greater phylogenetic distance between species than expected. Values lower than -2.0 with p> 0.95 indicate that assemblages are phylogenetically clustered; *i.e.* the phylogenetic distance between them is shorter than expected on a randomly generated tree. Values between -2.0 and 2.0 indicate phylogenetic randomness, that is, the distance between species occurs at random (Cavender-Bares *et al.*, 2004). To reduce the impact of sampling effect on the results, all analyses were performed using the Standardized Effect Size (SES) algorithm available in picante (Kembel *et al.*, 2010), through 999 randomizations comparing the communities with a null model then applying a Z test.

We also used picante to calculate species richness (SR) and Faith's phylogenetic diversity (PD) (Faith, 1992). The SR index is calculated as the sum of the number of species in the studied area, without taking other indices into account, while the PD index is calculated as the sum of the lengths of tree branches for each species present in the area and thus supplied in millions of years (Ma) (Faith, 1992).

We used the PhyloSor index, which quantifies the fraction of branch lengths shared by sites (Bryant *et al.*, 2008), to assess phylogenetic beta diversity between assemblages. Phylogenetic beta diversity was calculated using the picante package to measure the degree of shared species among basins. This index was compared with two measures of geographical distance: Euclidian and Floodplains distances (*e.g.* Albert *et al.*, 2011a). Phylogenetic beta diversity between each pair of river basins was then compared to Euclidian (straight-line) and thalweg (valley-line) measures of geographical distance between those basins using a Mantel test with 99,999 permutations in ape 5.1 package (Paradis *et al.*, 2004).

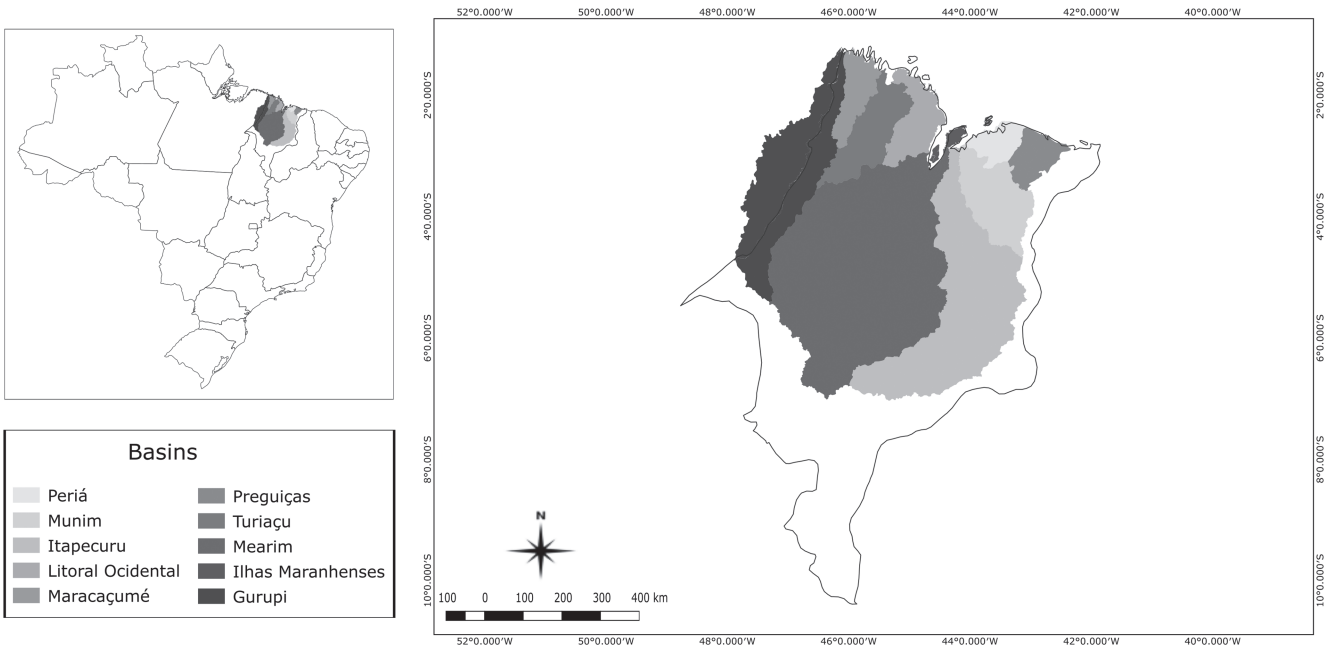

Fig. 1. Hydrographic basins of Maranhão State.

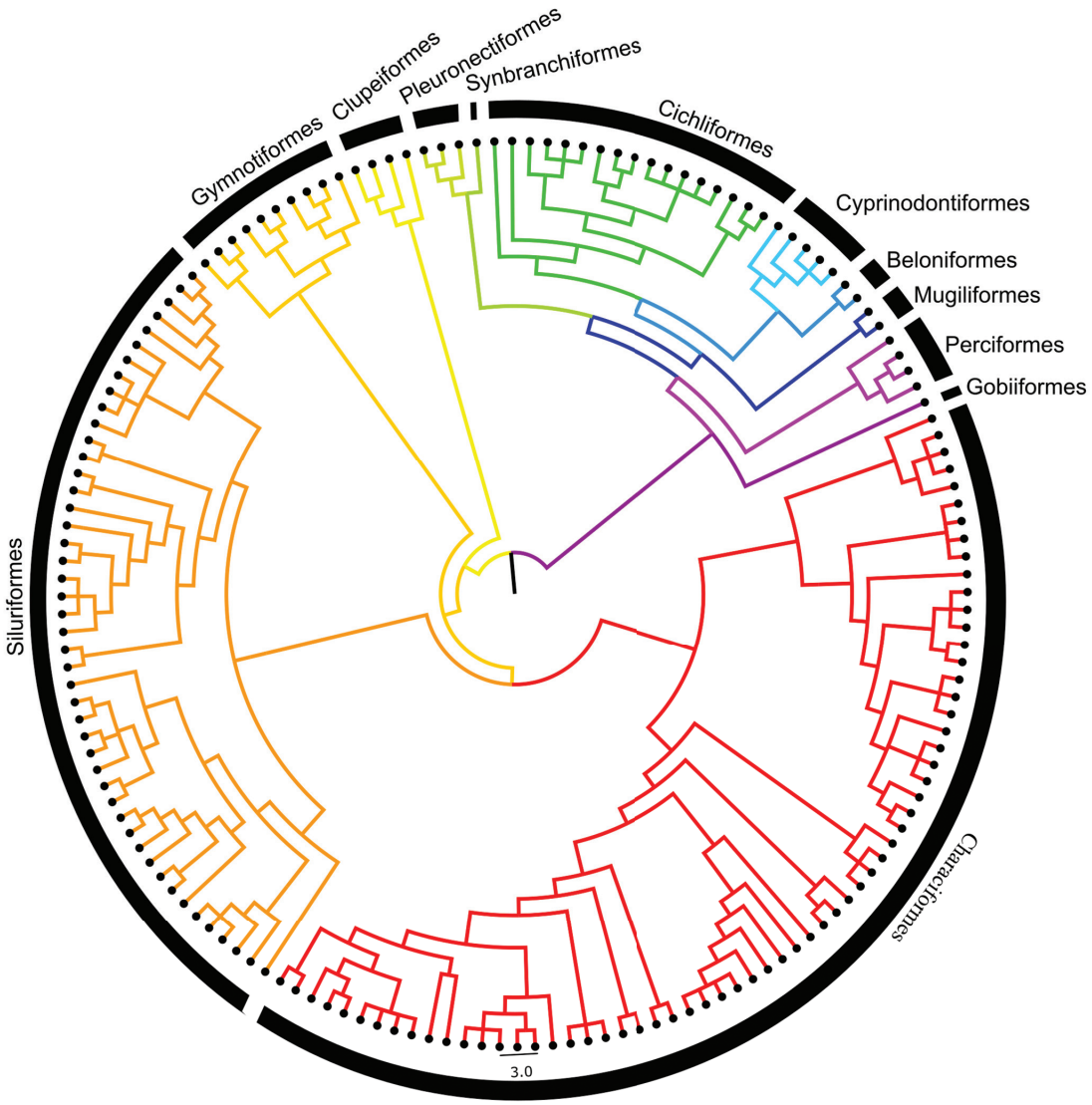

Fig. 2. Phylogenetic hypothesis generated for 160 species in Maranhão basins.

Reconstruction of paleodrainages. To understand the influence of sea-level changes in the distribution of the freshwater fishes species in this area, we estimated paleodrainage boundaries for the maximum and minimum sea level over the past 10 My based in the result from community phylogenetic structure analyze. For this we used topographical and bathymetric information extracted from a digital elevation model (DEM) GEBCO_2014 at 30 arc-second resolution (*c.* 1 km; http://www.gebco.net/) in QGIS3.2.3 using the method described by Thomaz *et al.* (2015).

These paleodrainage reconstruction shows that all nine hydrographic basins of modern Maranhão drained into just three paleodrainages at the LGM when the sea-level was 122 m below the modern level and the most areas of these basins are totally or partially submersed when the sea-level was 35 m above the modern level at 5.5 Ma (Hansen *et al.*, 2013) (Fig. 3), these results show that the sea-level changes can influence the distribution of the species in this area as well as the limits of the basins. The three paleodrainages identified for LGM are structured as follow. One of these paleodrainages included the areas of the modern Gurupi, Maracaçumé, and Turiaçu basins, and part of Litoral Ocidental basin. A second paleodrainage was formed by the modern Mearim, Itapecuru, Munim basins and part of Litoral Ocidental and Periá basins. A third paleodrainage was formed by the modern Preguiças basin and part of Periá basin.

To avoid biased results due to low species numbers we combined the basins with low species number with other basins in the community phylogenetic structure analysis. For this we used two criteria: 1) mouth connection at the LGM reconstruction and, 2) high faunal similarity (number of species shared) when the basins are connected with more than one basin at the LGM reconstruction. So, based on these criteria, the area called the "Turiaçu" corresponds here to the combined Turiaçu, Gurupi, Maracaçumé and Litoral Ocidental basins in the analyses developed in this paper.

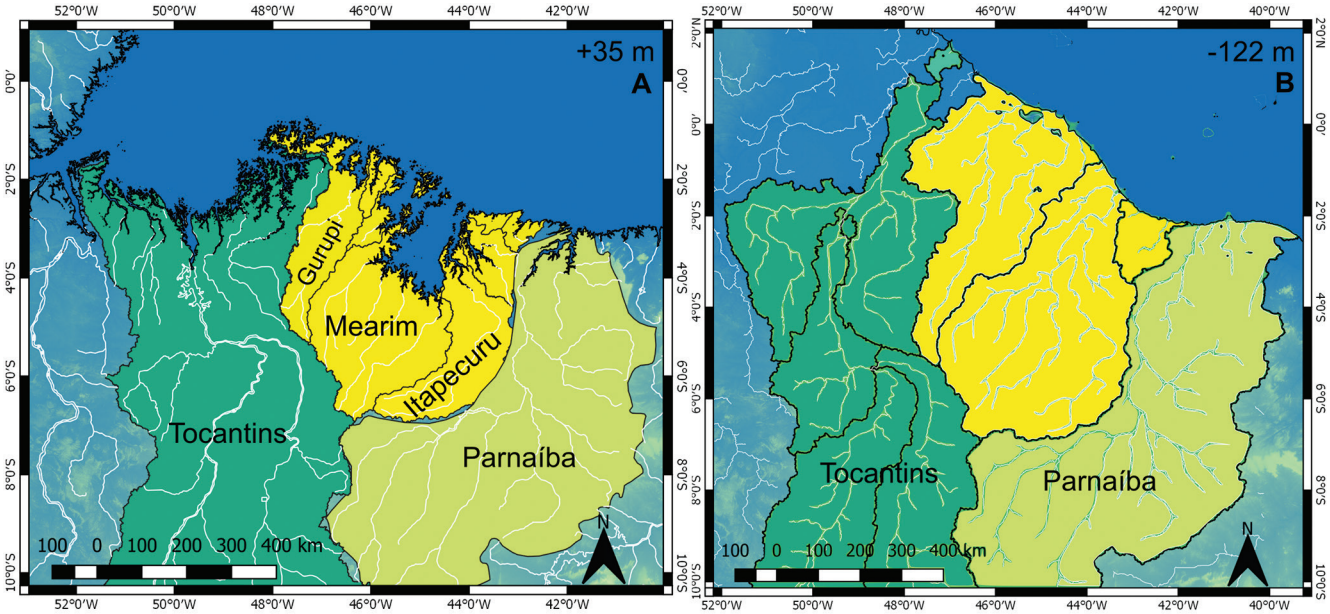

Fig. 3. Reconstruction of paleodrainages area of Maranhão. **a.** 35 m above the modern level. **b.** 122 m below the modern level. Note that all modern rivers flowed through three paleodrainages at the LGM (-122 m). Note that similarities of the fish faunas can be explained in part by past connection among the basins. These paleo-connections also justify how basins with low species richness were combined for the analyses of historical biogeography.

Results

Community phylogenetic structure. We report a species richness of 160 freshwater fish species distributed among the hydrographic basins of Maranhão state representing 12 orders and 39 families (**S2** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). This increases the known diversity of this region by 77 species (~93%), eight families (~26%) and two orders (20%) over all previous studies. Of these 160 species, 16 are considered endemic for this region, sometimes shared with the adjacent Parnaíba basin, and one introduced species in Brazil, *Oreochromis niloticus* (Linnaeus, 1758) originally imported for commercial purposes (Vicente *et al.*, 2014) and probably released after captive breeding. The orders with the highest number of species are Characiformes and Siluriformes, with 65 and 46 records, respectively. The families with greatest representation are Characidae, Cichlidae and Loricariidae with 24, 17 and 15 species respectively (Tab. 1). Fish species richness of Maranhão hydrographic basins is significantly correlated with basin area ($r^2 = 0.875$, $p = 0.007919$), and the species-area exponent ($z = 0.43$) value is in the range classified as "archipelagic" by Rosenzweig (2004) (Fig. 4).

The results of the MPD and MNTD analyses for each basin were not significantly different from those drawn from a random phylogeny (Tab. 2), indicating that the phylogenetic distance between species is not significantly different from what would be expected at random. This provides no evidence for either phylogenetic clustering or phylogenetic overdispersion either at the tips of the phylogeny or over its entire area.

Tab. 1. Summary of data used in analyses of Maranhão basins. Number of fish species, genera, families, areal extent, and geographic category for each basin. Numbers of taxonomic units to not sum to Total due to partially overlapping taxonomic composition of basins. 1 = ANA, 2015; 2 = NUGEO, 2016.

Basins	Category	Area (Km²)	Families	Genera	Species
Itapecuru	Lowland/Brazilian shield	54.979[1]	32	78	100
Preguiças	Lowland	6.707[2]	17	25	29
Periá	Lowland	5.395[2]	17	28	28
Munim	Lowland	15.918[2]	19	35	37
Mearim	Lowland/Brazilian shield	100.126[1]	31	70	100
Turiaçu	Lowland	88.099[1]	26	47	56
	Total	271.225	39	100	160

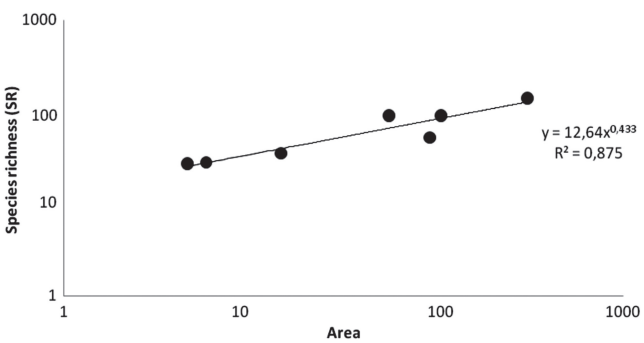

Fig. 4. Species-area relationships (SAR) for freshwater fishes of Maranhão basins. Data for 160 species.

In the analysis of PD, we recover recent colonization events and short diversification times. Taken together with the recovered SR index, this suggests that the Itapecuru and Mearim basins underwent events that caused species to diverge for a longer time than among other basins, 9.8 and 9.7 My, respectively (Tab. 2).

The results of the phylobeta diversity analysis (Tab. 3) and the other measures of geographical distance among basins (Tab. 4), showed that the basin boundaries do not constitute substantial barriers to dispersal and gene flow, and that geographic distance does not strongly hinder dispersal in freshwater fishes of this region.

Tab. 2. Summary of indices comparing species richness and phylogenetic diversity among Maranhão basins. Note these results are consistent with recent colonization events and short diversification times. PD values and species richness from Itapecuru and Mearim basins indicate older events. All basins exhibit a phylogenetically random species composition, meaning that the phylogenetic distance between clades (MPD) or sister species-pairs (MNTD) is not significantly different from what would be expected at random.

Basins	SR	PD (My)	ses.PD	ses.PD (p)	ses.MPD	ses.MPD (p)	ses.MNTD	ses.MNTD (p)
Itapecuru	100	9.853	-0.264	0.391	-1.211	0.120	-0.394	0.340
Preguiças	29	4.624	1.369	0.899	2.135	0.995	1.166	0.872
Periá	28	4.228	0.412	0.666	0.666	0.726	0.461	0.672
Munim	37	4.295	-1.913	0.024	-3.363	0.001	-0.938	0.190
Mearim	100	9.711	-0.721	0.242	-2.309	0.016	0.157	0.563
Turiaçu	56	6.392	-0.365	0.360	-2.456	0.013	0.080	0.545

Tab. 3. Summary of phylobeta diversity indices for Maranhão basins.

Basins	Itapecuru	Preguiças	Periá	Munim	Mearim
Itapecuru					
Preguiças	0.502				
Periá	0.546	0.697			
Munim	0.587	0.559	0.588		
Mearim	0.701	0.483	0.532	0.564	
Turiaçu	0.655	0.492	0.608	0.646	0.678

Tab. 4. Distance among Maranhão basins using three methods: phylobeta diversity (Phylosor), Euclidian distances and floodplain (*thalweg*) distances. Numbers below the diagonal are z-stat values, and above the diagonal are p-values.

Distances	Phylosor	Euclidian	Floodplain
Phylosor	X	0.192	0.053
Euclidian	2.077	X	0.461
Floodplain	12.654	5.496	X

Discussion

Ichthyofauna composition. The numbers of fish species in Maranhão are substantially higher than those reported in previously published studies (Piorski *et al.*, 1998, 2003, 2007, 2017; Reis *et al.*, 2003; Soares, 2005; Barros *et al.*, 2011). This increase in the number of species is principally due to the incorporation of the available data from CPUFMA. Among basins exclusive to the state of Maranhão, the Mearim and Itapecuru basins are the most intensively studied to date, primarily due to their being the largest basins, and therefore having a greater economic importance (Soares, 2005; Barros *et al.*, 2011). Piorski *et al.* (1998) found, for the lower region of the Itapecuru River basin, 41 species belonging to 36 genera and 13 families, while Barros *et al.* (2011) recorded 69 species, representing 65 genera, 29 families and 10 orders, in the three sectors of the basin. The larger number of species of orders Characiformes, Siluriformes and Cichliformes corroborates the existing literature, in which these groups are the most diverse for the region and for nearby basins, as well as families Characidae, Cichlidae and Loricariidae (Piorski *et al.*, 1998; Reis *et al.*, 2003; Ramos *et al.*, 2005, 2014; Buckup *et al.*, 2007; Barros *et al.*, 2011).

However, the total number of species identified for the region is greater than recent literature reports. Hubert, Renno (2006) included 33 characiforms species for the entire Maranhão endemism region, which encompasses the rivers exclusive to Maranhão and some basins in the state of Pará. In our list we recorded the occurrence of 65 characiforms, almost twice number previously reported. In a more recent work about the biogeography of neotropical freshwater fish, in which some Maranhão basins were considered, Dagosta, de Pinna (2017) built a larger database on species distribution for the Amazonian region, with approximately 5,000 species. However, and despite the efforts undertaken by the authors, they could not obtain much information on the distribution of fish in the basins of Maranhão, thus grouping the Gurupi basin with the Capim basin due to a gap in information and considering only the basins of Mearim and Itapecuru for their analysis, reaching a total of 66 species for the region.

The results described above demonstrate that the Maranhão basins has been under-sampled or even disregarded in previous studies of the fish fauna. In view of that, the present study comprises the largest database already registered for freshwater fish species from the coastal drainages of Maranhão, with a total of 160 species.

Community phylogenetic structure. The phylogenetic diversity analysis shows that the Itapecuru and Mearim basins have the highest SR and PD values, what is compatible with areas that have experienced events related to species diversification (extinction and speciation) for the longest time and present the most phylogenetically distinct species composition (Webb *et al.*, 2002). On the other hand, the other drainages have a composition of species that are closer phylogenetically, which is characteristic of areas that are newly colonized or that have been through more recent events, having less time for speciation (Wiens, Donoghue, 2004; Proches *et al.*, 2006; Davies *et al.*, 2007; Pavoine, Bonsall, 2011; Aquino, Colli, 2017).

This is also evidence that historical events, such as marine incursions in the late Miocene and Pliocene, may have left a signature on the fish species composition of Maranhão (Lundberg *et al.*, 1998; Soares Junior *et al*., 2011; Albert *et al.*, 2018). Formation of the fauna present in northern South America was greatly affected by marine incursion events (López- Fernández, Albert, 2011). The Maranhão State was strongly affected by marine incursions, as the majority of its area is below 300 m elevation (Albert, Reis, 2011). During these periods, and due to their location and size, the Mearim and Itapecuru basins were the least affected drainages in the region, being more buffered by geographic distance and topography from the paleogeographic changes that affected the other basins.

According to Hansen *et al.* (2013), sea level oscillations caused by the glacial periods promoted a rise of up to 30 m above our current level during the Miocene, about 8 Ma, and influenced the region until the middle Pleistocene (~1 Ma), the Maranhão basins being directly affected by these variations. As all these basins empty to the sea on the modern landscape, and are strongly influenced by tidal variation, they experienced considerable impacts during various periods of sea level rise, some lasting up to 800,000 years (Lundberg *et al.*, 1998; Nores, 2004). In addition to marine incursions, geological data (Petri, Fúlfaro, 1983; Costa *et al.*, 1997) show that the reactivation of tectonic faults during the Miocene and Pliocene may have affected watershed boundaries among Maranhão basins. In combination, these climatological and geological events may have resulted in biotic exchanges among the several drainages by dispersal along the coastal plain and by headwater tributary exchanges, thereby increasing the faunal similarities between some basins.

According to Hubert, Renno (2006) some freshwater fish species may have persisted in upstream portions of the Parnaíba and Tocantins basins during marine incursions about 5 Ma. Combining this information with the PD values found for the coastal drainages of Maranhão, we propose that these upstream areas may have served as a phylogenetic refugium, as has been proposed for other geographically circumscribed regions of northern South America (*e.g.* Maracaibo basin; Albert *et al*., 2006). These upstream areas may then have served as a source area for the subsequent formation of the lowland Itapecuru and Mearim fish species assemblages. Species dispersal among these areas after marine incursion events was possibly aided by the river captures and geodispersal. These events may have occurred between the Parnaíba and Itapecuru basins, in the region of Mirador State Park, where the two basins share the longest extent of their common watershed.

Another possible area of trans-basin headwater river capture is the area between Tocantins, Mearim and the springs of Gurupi and Turiaçu, in a paleodelta (~ 2.5 Ma) located near the modern city of Tucuruí. Such a link between these basins may have provided enough connection time to promote a flow of species, even after the initial emergence of the Tiracambu mountain range at about 5.3 Ma, the main divisor of these drainages on the modern landscape (Costa *et al.*, 1997; Soares Junior *et al*., 2011).

Historical biogeography. In combination, the phylogeographic, community phylogenetic and phylogenetic beta diversity analyses of this study indicate the importance of geological events and sea level fluctuations during the late Miocene and Pliocene in the formation of Maranhão fish species assemblages. By contrast, the modern watershed borders of Maranhão basins do not appear to constitute substantial barriers to dispersal and gene flow for the freshwater fishes of this region. The species-area exponent ($z = 0.43$) of the Maranhão region is consistent with the interpretation of these basins as a biogeographic archipelago, where species richness is controlled by dispersal and extinction, and where speciation does not contribute substantially to the formation of species richness. As a result, the Maranhão basins are more effectively modelled as biogeographic islands than as biogeographic provinces (Rosenzweig, 2003; Albert *et al.*, 2011a).

These results also shed light on intra-specific genetic variation found in certain fish species in this area (Piorski, 2010; Carvalho-Costa *et al.*, 2011; Abreu, 2013; Luz *et al.*, 2015). In these studies, different species share haplotypes among the Mearim, Itapecuru and Parnaíba basins, indicating dispersal and perhaps geodispersal events (Hubert *et al.*, 2007). In the studies that includes sequences from Turiaçu basin, these samples formed a separate clade normally closer to Amazonian fish than to Maranhão fish (Abreu JMS, personal observation), an indicative of vicariance events (Hubert *et al.*, 2007). In addition, more specific analyses of taxonomic groups of the Turiaçu river indicate the occurrence of new taxa that are apparently unique to this drainage (Saraiva *et al.*, in prep; Garavello *et al.*, in prep.). The paleodrainage reconstruction plus the emergence of Tiracambu mountain (Costa *et al.*, 1997; Soares Junior *et al.*, 2011) are a reasonable explanation for the separation of the Turiaçu basin from the other basins, promoting the isolation of this area and the differentiation of the associated ichthyofauna.

Available geological data suggest that events during the Miocene and Pliocene were important time periods for the separation of Maranhão, Tocantins and Amazon basins. An

important event was the emergence of the Tiracambu range, the main divider between the Maranhão and Tocantins-Amazon drainages. At the same time, the Parnaíba basin was exposed to the same events that the Maranhão basins. These events suggest the regional fauna is relatively young, and that species may yet be colonizing the area. Speciation among populations of the several basins may be influenced by the ecological configuration of the region. The Maranhão area exhibits a singular ecological configuration, with a unique and distinctive geological and biotic history, and is more than just a transitional area between the more well-studied areas of the humid Amazon and arid Cerrado and Caatinga ecozones.

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