

Review article

Flowing into the unknown: inferred paleodrainages for studying the ichthyofauna of Brazilian coastal rivers

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The eastern coastal basins of Brazil are a series of small and isolated rivers that drain directly into the Atlantic Ocean. During the Pleistocene, sea-level retreat caused by glaciations exposed the continental shelf, resulting in enlarged paleodrainages that connected rivers that are isolated today. Using Geographic Information System (GIS), we infer the distribution of these paleodrainages, and their properties for the east Brazilian coast. Specifically, using elevation/bathymetric data for the largest sea-level retreats during the Pleistocene, the paleodrainages, their area and the number of contemporary basins connected by each palaeodrainage, was inferred. For the 145 inferred paleodrainages, total paleodrainage area is strongly correlated with the contemporary area encompassed by each paleodrainage, as well as with the number of contemporary basins encompassed by a paleodrainage. Differences in the continental shelf exposure along the coast affected the degree of past connectivity among contemporary rivers. With our results freely available, we discuss how paleodrainages have tremendous utility in biological studies, especially in regions with limited geologic data. With respect to the diverse ichthyofauna of the Brazilian coast, and its high endemism, we highlight how the inferred paleodrainages provide a backdrop to test hypotheses about the effect of past riverine connectivity on diversity patterns.

Keywords: Freshwater fishes, Glaciations, Pleistocene, Riverine connections, Sea-level retreat.

As bacias costeiras do leste do Brasil são formadas por uma série de rios pequenos e isolados que drenam diretamente para o Oceano Atlântico. Durante o Pleistoceno, o recuo do nível do mar causado por glaciações expôs a plataforma continental, resultando em paleodrenagens amplas que conectaram rios atualmente isolados. Usando o Sistema de Informações Geográficas (GIS), inferimos a distribuição destas paleodrenagens e suas propriedades ao longo da costa leste do Brasil. Especificamente, utilizando dados de elevação/batimetria para as maiores regressões marinhas do Pleistoceno, inferimos as paleodrenagens, suas áreas e quantas bacias contemporâneas foram conectadas por cada paleodrenagem. Para as 145 paleodrenagens inferidas, uma forte correlação é observada entre a área das paleodrenagens e a área atualmente exposta de cada paleodrenagem, bem como a quantidade de bacias contemporâneas conectadas por uma paleodrenagem. Diferenças na exposição da plataforma continental ao longo da costa afetaram o grau de conectividade passada entre os rios. Com estes resultados publicamente disponíveis, discutimos como as paleodrenagens são extremamente úteis para estudos biológicos, especialmente em regiões com dados geológicos limitados. A respeito da diversa ictiofauna da costa brasileira e seus altos níveis de endemismo, destacamos como estas paleodrenagens fornecem uma base importante para o teste de hipóteses a respeito do efeito da conectividade passada dos rios nos padrões de diversidade biológica.

Palavras-chave: Conexões entre rios, Glaciações, Peixes de água doce, Pleistoceno, Recuo no nível do mar.

Introduction

With the steep slope of mountain chains isolating the east coast from the inland (*e.g.*, Serra do Mar and Chapada Diamantina; Fig. 1), the eastern Brazilian coastal basins are a series of small and isolated rivers that drain directly into the Atlantic Ocean. As a consequence, freshwater fishes in these coastal basins have evolved in isolation with sporadic dispersal with inland basins of Brazil (Weitzman *et al.*, 1988; Ribeiro, 2006). This biogeographic history is hypothesized

to underlie the extraordinary diversity of the region, with current estimates of more than 500 valid species of freshwater fishes (Carvalho TP, pers. comm.; Fricke *et al.*, 2017; Fig. 2), many of which are endemics (95% according to Bizerril, 1994). These estimates span the basins between Laguna dos Patos and Rio São Francisco (*i.e.*, no inland basins), which is currently recognized by six Freshwater Ecoregions: Tramandai-Mampituba (335), Southeastern Mata Atlantica (331), Ribeira de Iguape (330), Fluminense (352), Paraíba do Sul (329) and Northeastern Mata Atlantica (328; Abell

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et al., 2008). However, the coastal drainages are not static. Past connections may have been formed among the isolated rivers as the physiography of the region shifted during the Pleistocene. In particular, the riverine basins that are isolated today are hypothesized to have become part of larger networks of connected rivers (Weitzman *et al.*, 1988; Dias *et al.*, 2014). That is, the formation of paleodrainages during pronounced sea level changes associated with glacial periods would have provided connections on the exposed continental shelf during sea level retreat (Fleming *et al.*, 1998; Miller *et al.*, 2011).

Although geological data provide invaluable information on how rivers may have been connected in the past, the mechanisms creating these patterns are still not fully understood (Perron *et al.*, 2012). This partially reflects the limited availability of geological data, especially among coastal drainages, and uncertainty because of the complexity of this data (for a summary of geological evidence for coastal and inland basins connections see Ribeiro, 2006). Consequently, biologists have relied upon patterns of biodiversity as a mean for identifying putative connections. For example, a generic river capture is often invoked when drainages share species pools (*e.g.*, Albert, Reis, 2011). However, relying on a pattern based on the ichthyofauna itself to make inferences about riverine connections does not allow for tests of the processes giving rise to the observed pattern (*i.e.*, there is no alternative explanations).

The availability of Geographic Information System (GIS) techniques and freely available datasets, including maps of past and present landscapes, can serve as an independent data source for inferring past connections (*e.g.*, Thomaz *et al.*, 2015; 2017), complementing traditional geologic data (Willett *et al.*, 2014). Specifically, hypothesized connections can be inferred from reconstructions of paleodrainages that would have formed during periods of low sea levels based on bathymetric data. This approach has broad applicability, given the general availability of topographic data. Moreover, it can provide detailed information for contiguous regions, in contrast to geologic data that is often limited to particular regions and given the scarcity of paleochannel data for the coast of Brazil (*e.g.*, Zalán, Oliveira, 2005; Conti, 2009; Conti, Furtado, 2009). Reconstructions based on topographic and bathymetric data for expansive coastlines like Brazil become especially appealing. With differences in the distance separating the eastern coastline from the western mountain slope (*e.g.*, Serra do Mar), as well as the width of the continental shelf (Fig. 1), the properties of paleodrainages along the Brazilian coast may also differ. Likewise, the number of currently isolated basins that became connected during the Pleistocene may also vary along the coast, possibly as a function of the width of the continental shelf.

Here we provide reconstructions of paleodrainages using GIS technologies for the eastern coast of Brazil, and for a few basins in the northeast and south. Together they represent a significant expansion over the information to date, which is limited to a local analysis of paleodrainages (Dias

et al., 2014; Thomaz *et al.*, 2015; 2017) and of proposed paleo-connections among a set of specific Brazilian river basins (Baggio *et al.*, 2017; Lima *et al.*, 2017). We also characterize general properties of the inferred paleodrainages, including the geographic area spanned by each paleodrainage and the number of contemporary river basins associated with individual paleodrainages. This information provides insights into not only the distribution of paleodrainages and proposed past connections among the rivers that are isolated today, but also how the structure of paleodrainages differs along the coast. We discuss these findings with reference to their broad utility for studying the Brazilian ichthyofauna, ranging from studies of species distributions and diversity, to tests of how the historical connections may structure the genetic variation of contemporary fish taxa, both of which could lead to more informed conservation strategies.

Material and Methods

Geographic region. The study area includes all coastal rivers ranging from Baía de Turiaçu drainage in Maranhão State in the northeast to Laguna dos Patos basin on the board with Uruguay in the south, in Rio Grande do Sul State, an area that spans more than 5,000 kilometers (km) of the Brazilian coast. This area was selected based on the coastal and continuous freshwater ecoregions, with the exclusion of the Amazonian tributaries. In terms of freshwater fish diversity, the area is currently divided in 11 freshwater ecoregions: Laguna dos Patos (334), Tramandai-Mampituba (335), Southeastern Mata Atlantica (331), Ribeira de Iguape (330), Fluminense (352), Paraíba do Sul (329), Northeastern Mata Atlantica (328), S. Francisco (327), Northeastern Caatinga & Coastal Drainages (326), Parnaíba (325) and the eastern portion of Amazonas Estuary & Coastal Drainages (323; Abell *et al.*, 2008). The study region encompasses hundreds of currently isolated river basins that drain the Atlantic Rainforest and Caatinga biomes (Fig. 1).

Inferring Palaeodrainages. Palaeodrainages and the potential connections between contemporary river basins were estimated with ARCGIS10, using *Hydrological* tools. Four glaciation periods over the Pleistocene had the largest decreases in sea level: -123 m at 434 and 630 kya (thousand years ago), -119 m at 18 kya, and -110 m at 138 kya (Miller *et al.*, 2011). Based on these estimates, we reconstructed paleodrainages for a sea level retreat at -125 m. Topographic and bathymetric information from the General Bathymetric Chart of the Oceans (GEBCO_2014) was used at 30 arc-second resolution (*c.* 1 km; <http://www.gebco.net/>), covering from 0 degree latitude north to -40 degrees south, and -30 degrees of longitude east to -60 degrees west.

With a base contour line at -125 m created using the *Contour* tool to estimate the maximum extent of land exposed during Pleistocene, the clipped Digital Elevation Model (DEM) raster map was generated. The *Fill* tool was applied to the map to remove small imperfections, such as localized

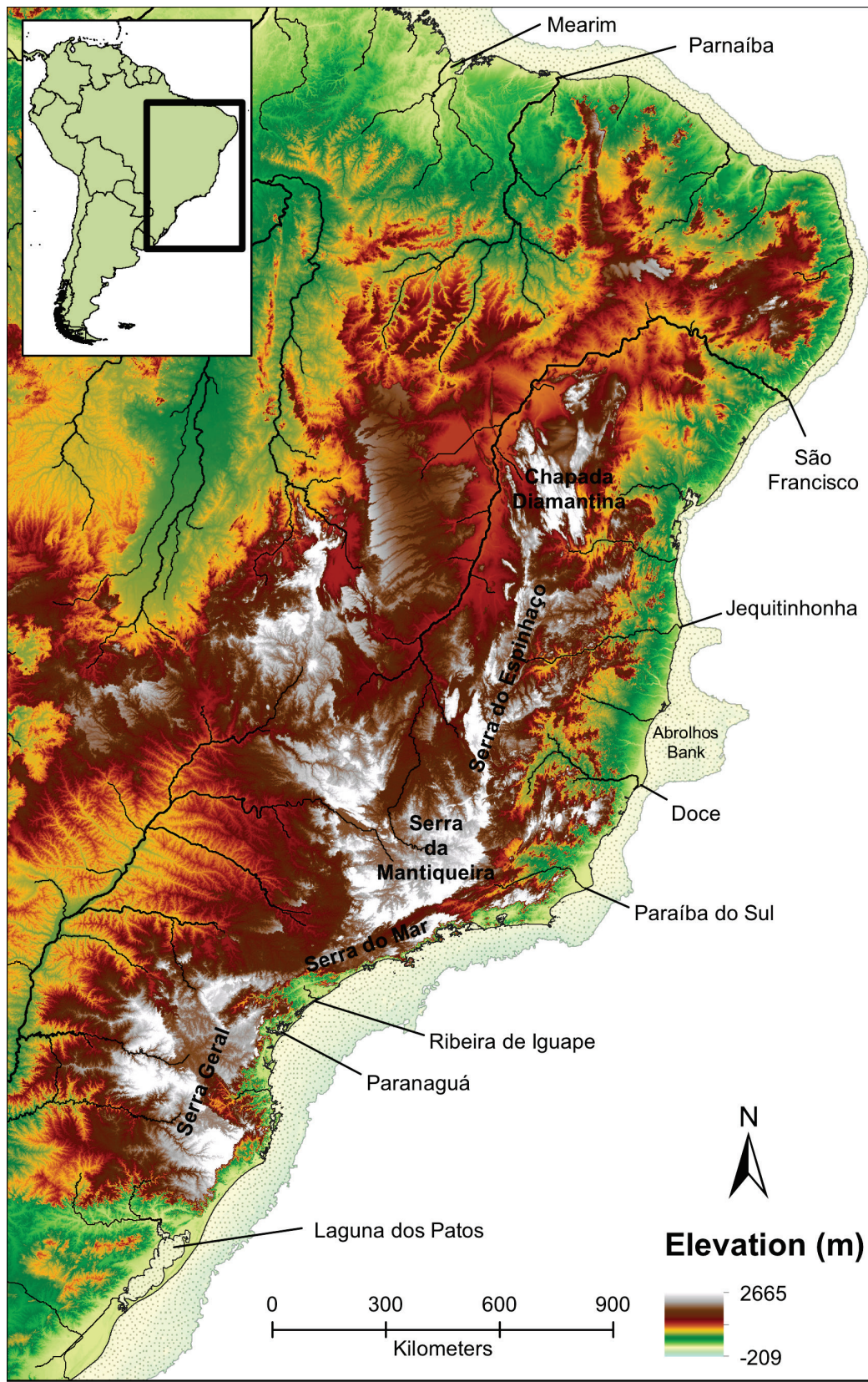


Fig. 1. Map of the Brazilian coast showing main river drainages, bays, lagoons and mountain chains. Elevation and bathymetric profile for the area highlight the isolation of the coastal basins from inland rivers by mountains, including the Serra do Mar and the Chapada Diamantina in the west. Continental shelf exposed during the Pleistocene is marked with the stippled yellow shading.

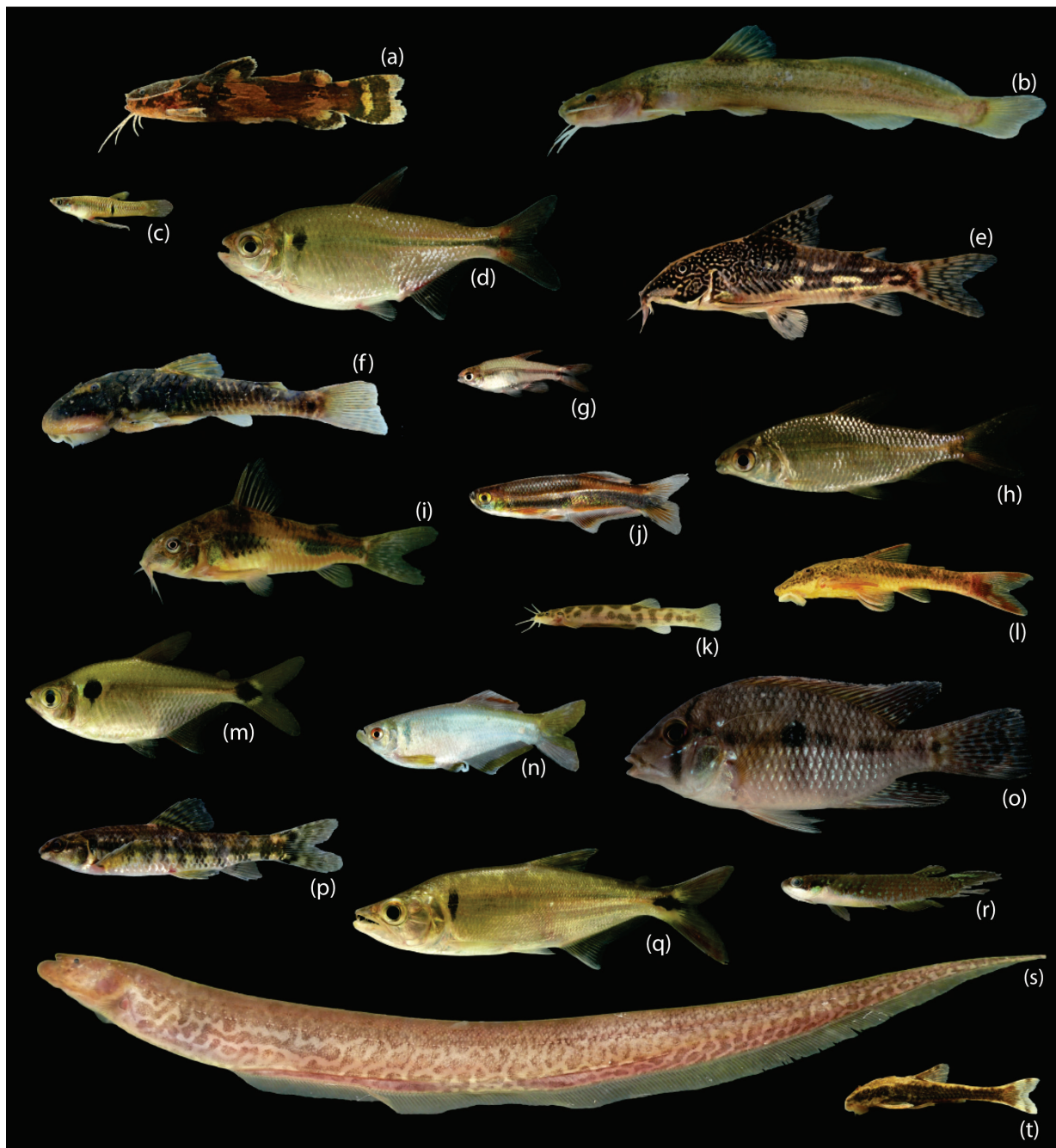


Fig. 2. Samples of some of the freshwater fish species of the Brazilian coastal drainages: **a.** *Microglanis cottoides* ((Boulenger, 1891) UFRGS 20930; 43.2 mm SL, standard length), **b.** *Heptapterus* sp. (UFRGS 20970; 89.2 mm SL), **c.** *Phalloceros* sp. (UFRGS 18596; 22 mm SL), **d.** *Deuterodon singularis* Lucena & Lucena, 1992 (UFRGS 20728; 59.6 mm SL), **e.** *Scleromystax barbatus* ((Quoy & Gaimard, 1824) UFRGS 18832; 65 mm SL), **f.** *Pareiorhaphis splendens* ((Bizerril, 1995) UFRGS 20971; 57.4 mm SL), **g.** *Spintherobolus ankoseion* Weitzman & Malabarba, 1999 (UFRGS 20923; 23.7 mm SL), **h.** *Cyphocharax santacatarinae* ((Fernández-Yépez, 1948) UFRGS 20918; 46.9 mm SL), **i.** *Corydoras ehrhardti* Steindachner, 1910 (UFRGS 20938; 50 mm SL), **j.** *Mimagoniates lateralis* ((Nichols, 1913) UFRGS 20488; 30.5 mm SL), **k.** *Trichomycterus* cf. *cubataonis* Bizerril, 1994 (UFRGS 20937; 30 mm SL), **l.** *Parotocinclus maculicauda* ((Steindachner, 1877) UFRGS 20932; 44.1 mmSL), **m.** *Probolodus oyakawai* Santos & Castro, 2014 (UFRGS 18752; 45 mm SL), **n.** *Mimagoniates rheocharis* Menezes & Weitzman, 1990 (UFRGS 20808; 54.2 mm SL), **o.** *Geophagus brasiliensis* ((Quoy & Gaimard, 1824)UFRGS 20919; 72.5 mm SL), **p.** *Characidium pterostictum* Gomes, 1947 (UFRGS 18563; 55 mm SL), **q.** *Oligosarcus hepsetus* ((Cuvier, 1829) UFRGS 18571; 65 mm SL), **r.** *Atlantirivulus* cf. *luelingi* ((Seegers, 1984) UFRGS 21033; 31.5 mm SL), **s.** *Gymnotus pantherinus* ((Steindachner, 1908) UFRGS 20928; 186 mm SL), and **t.** *Pseudotothyris ignota* Martins, Britski & Langeani, 2014 (UFRGS 20934; 33.2 mm SL). Photo credits: Tiago P. Carvalho.

depressions in the DEM, which ensures that flow is maintained among neighbouring cells in the map. Flow direction for each cell in the DEM was determined by its slope using the *Flow Direction* tool. Based on this flow direction, ridgelines were identified using the *Basin* tool, and these ridges delineated the inferred paleodrainages.

To infer the past river connections, a raster containing the total number of cells that drain to each specific cell was generated using the *Flow accumulation* tool. Each cell with more than 100 cells draining into it was used to infer the networks of streams by applying the *Stream order* function, with river order assignment following Strahler (1957). The riverine raster grids were then converted into vectors using the *Stream to Feature* tool for generating a map that can be used for analysis, as well as visualization, of inferred paleodrainages.

All files used to infer the paleodrainages and past connections, as well as the digital map of paleodrainages, are freely available at the University of Michigan archive DepBlue (Thomaz, Knowles, 2018 - dataset: <http://dx.doi.org/10.7302/Z2HH6H8P>).

Paleodrainage properties. Four properties were calculated for each inferred paleodrainage: (i) total area, (ii) contemporary land area encompassed by each paleodrainage, (iii) area of the continental shelf exposed during the drop in sea level change, and (iv) the number of contemporary river basins encompassed by each paleodrainage. Contemporary basins were estimated following the same methodology described above (excluding basins smaller than 10 km²). All summaries of area and river length were calculated using ARCGIS10.

Correlation tests were used to evaluate possible associations between different paleodrainage properties. Specifically, tests between total paleodrainage area with contemporary land area encompassed by each paleodrainage and the number of contemporary basins encompassed by each paleodrainage, as well as the area of the continental shelf of each paleodrainage exposed during sea level change, was performed using the *corr* function on R (R Core Team, 2017).

Results

We inferred 145 paleodrainages along the Brazilian coast (Fig. 3), many of which may have provided temporary past connections among 1,034 contemporary river basins that are currently isolated from each other, as well as small basins formed by a single stream. Each paleodrainage is associated with an average of 13 contemporary river basins; however, there was a wide variance in this number across paleodrainages (standard deviation, SD \pm 17; Tab. 1). For example, the paleodrainage that encompassed the most contemporary river basins is the one associated with Laguna dos Patos in southern Brazil, with 166 river basins. This large number of current basins inferred for the Laguna dos Patos paleodrainage reflects in part that the lagoon area was modelled as part of the ocean in the reconstruction. Other paleodrainages also contain a large number of contemporary river basins,

which cannot be ascribed to methodological assumptions. This includes Paranaguá estuary and one encompassing the Mearim River basin, each with 55 and 51 contemporary river basins, respectively. In contrast, there were seven paleodrainages that contain a single contemporary river basin. These paleodrainages are represented by a series of small river basins (in the past and present; Tab.1) and restricted to the northeast, occurring primarily in the Northeastern Mata Atlantica freshwater ecoregion.

The inferred paleodrainages have a mean area of 18,369 km² (SD = \pm 67,440), in contrast to contemporary basins that have a mean area of 2,246 km² (SD = \pm 24,680). However, there is a lot of variation among paleodrainages and contemporary drainages. For example, the São Francisco River, which is the largest contemporary basin, also forms the largest, and similarly sized, paleodrainage (see Tab. 1).

The total area of a paleodrainage is strongly correlated with the contemporary land area encompassed by each paleodrainage ($r^2 = 0.99$; $P < 0.0001$; Fig. 4a), as well as with the number of contemporary basins encompassed by a paleodrainage ($r^2 = 0.17$; $P < 0.0001$; Fig. 4b). Moreover, there is a significant, but weak, relationship between the contemporary land area encompassed by each paleodrainage and the area of the continental shelf exposed during the drop in sea level ($r^2 = 0.04$; $P = 0.01$; Fig. 4c).

A large variance on the width of the exposed continental shelf during the Pleistocene is observed. The continental shelf increased an average of 56 km (SD = \pm 41 km) in width during the largest sea level retreats in the Pleistocene. The width varied from a minimum of 10 km at Contas River basin up to a maximum of 191 km at the Abrolhos bank (Fig. 3).

Discussion

The paleodrainages we inferred for the coast of Brazil using GIS technologies (Fig. 3) make specific predictions about which contemporary river basins may have experienced connections in the past. Moreover, our analyses also show how the paleodrainages vary in their respective properties (Fig. 4; Tab. 1). As such, the map and the characterizations of the relationship between the present and the past properties of paleodrainages represent an invaluable tool for biological study. Below we highlight noteworthy aspects of the paleodrainages and their distributions, as well as examples of how the results from our study can be applied to studies of the Brazilian ichthyofauna.

Paleodrainages configurations. The large number of inferred paleodrainages is quite interesting in several regards. It highlights that in addition to the notable isolation of many contemporary Brazilian river basins, there was pronounced isolation along the coast in the past as well (Fig. 3), with the properties of the inferred paleodrainages varying considerably (Tab. 1). For example, the distance of the current coast line from the mountains in the west (e.g., the Serra do Mar and Chapada Diamantina; Buckup, 2011)

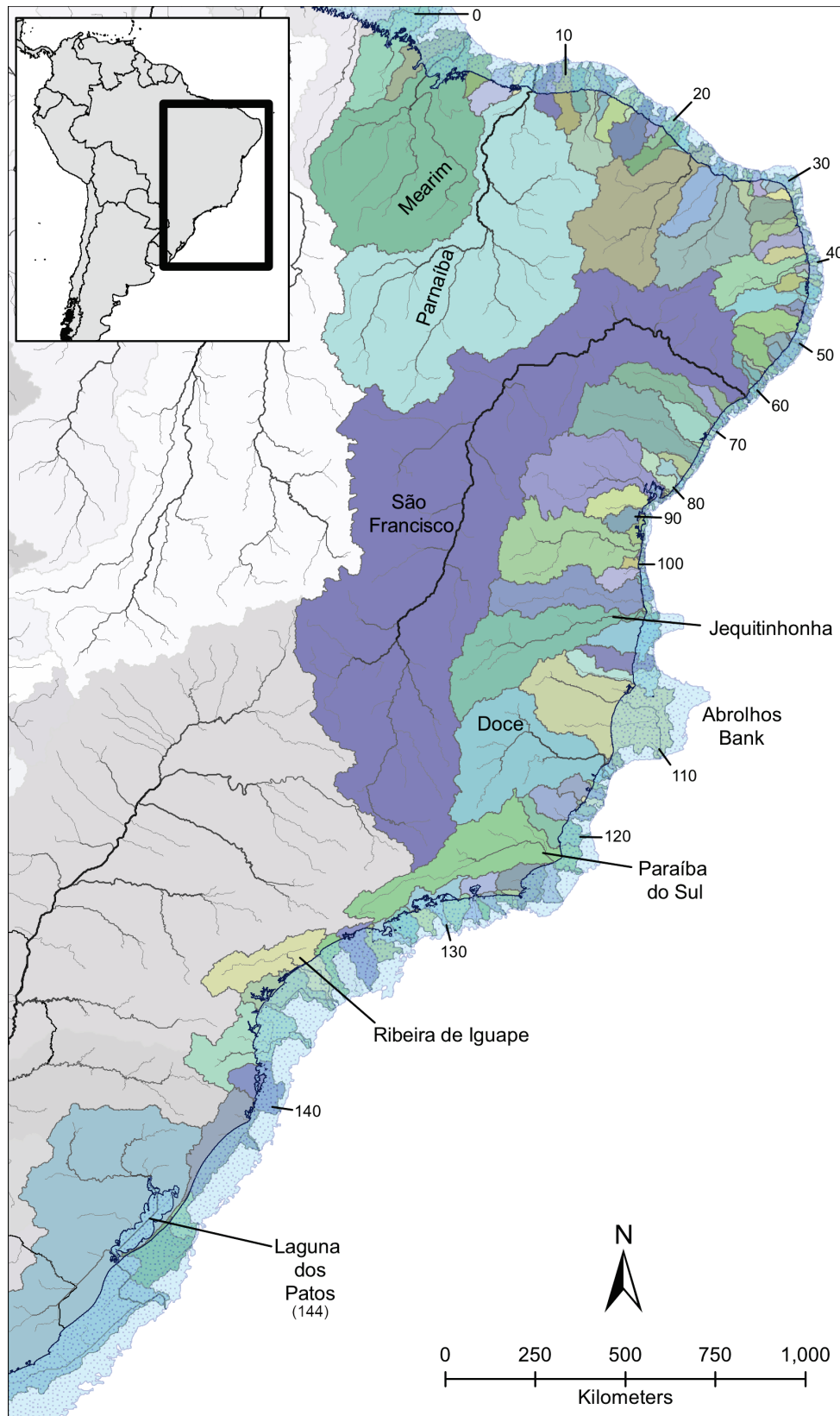


Fig. 3. Map of the 145 palaeodrainages inferred for a sea level retreat of -125 m during glacial periods of the Pleistocene; the black line marks the current coastline of Brazil. Both the area that includes the contemporary exposed land area, as well as the area of the continental shelf exposed when sea levels dropped (marked with stippling) is shown for each paleodrainage, with each paleodrainage shown in a different colour. Numbers along the coast indicate the paleodrainage ID on Tab. 1.

is larger in the north than in the south, while the width of the continental shelf exposed during the Pleistocene was larger in the south. These regional differences in the physical landscape related to the current coastal plain and the past exposure of the coastal shelf produced some clustering in paleodrainage properties, with rivers in the south becoming more connected during the Pleistocene sea level retreat in comparison to the north (Fig. 3). Independent of these regional differences, there is a significant association among paleodrainage properties in general (Fig. 4).

It's important to highlight that the origin and evolution of the Brazilian coastal basins have a long history that started with the Gondwana break-up. Along this time, several geological processes were responsible to form the riverine configuration that we observe today, such as uplifts, faults, fractures and river captures (e.g., Saadi, 1993; Ab'Saber, 1998; Riccomini *et al.*, 2004; Zalán, Oliveira, 2005; Riccomini *et al.*, 2010), features that also shape the distribution of the ichthyofauna in the region (for a summary see Ribeiro, 2006). Two geological mechanisms that potentially remodeled the riverine configuration along the coast that are not taken into account for the Pleistocene reconstructions inferred here are erosion and faults reactivation. Consequently, instances of river captures between adjacent basins associated with such geological phenomena are not represented in our inferred connections based on reconstruction of the paleodrainages. In the future, the application of alternative methods that model these geological processes to infer past connections could also provide valuable insights (Willet *et al.*, 2014). Nevertheless, the concordance between paleodrainages inferences based on application of GIS tool with current topographic information and reconstructions based on geological data from the literature for other portions of the world supports the merit of the approach applied here (Dias *et al.*, 2014). Likewise, a general correspondence between paleodrainage boundaries inferred from the current topography using GIS tools and that structuring of genetic variation also provide independent support for the inferred boundaries of paleodrainages (see Thomaz *et al.*, 2017).

Inferred coastal paleodrainages and studies of the Brazilian ichthyofauna. Thirty years after the proposition by Weitzman *et al.* (1988) that sea level changes may have influenced speciation and diversification processes of freshwater fishes along the Brazilian coastal drainages, paleodrainage reconstructions are increasing our understanding about the effect of Pleistocene sea level changes on Brazil's freshwater ichthyofauna. For example, fish studies have focused mostly on deeper time scales where dispersal events between coastal and inland basins predate the Pleistocene, and for which there is geological evidence for river captures (e.g., Menezes *et al.*, 2008; Ribeiro, 2006; Roxo *et al.*, 2012, 2014). Yet, without a hypothesis of river connectivity during the Pleistocene, past connections forged by sea level change have not been broadly considered as a factor contributing to observed patterns of freshwater fish

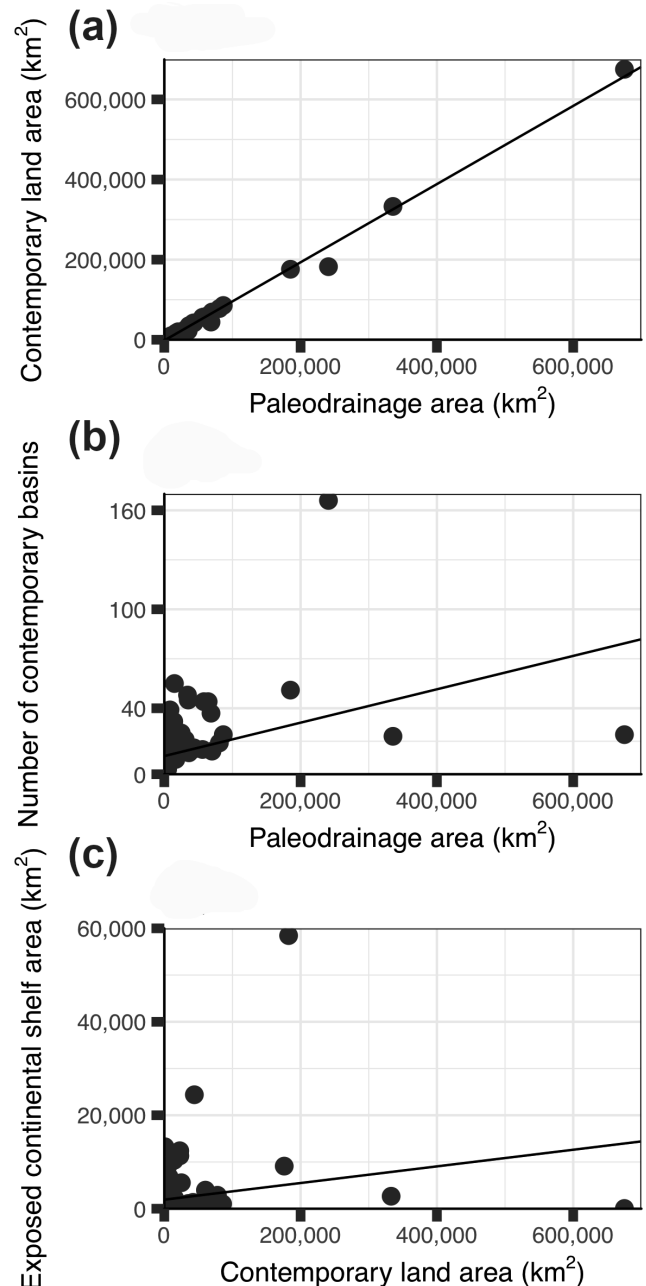


Fig. 4. Results of correlation tests: **a.** between the paleodrainage total area with contemporary land area encompassed by each paleodrainage ($r^2 = 0.99$; $P < 0.0001$); **b.** the number of contemporary basins encompassed by each paleodrainage ($r^2 = 0.17$; $P < 0.0001$); and **c.** between the contemporary land area and the area of the continental shelf exposed during the drop in sea level ($r^2 = 0.04$; $P = 0.01$). Individual values per paleodrainages are given in Tab. 1.

diversity along the coast (but see Camelier, Zanata, 2014; Carvalho, 2007; Pereira *et al.*, 2013; Torres, Ribeiro, 2008; Zamudio *et al.*, 2009).

The limited study of the role of paleodrainages in structuring the ichthyofauna of Brazil contrasts with studies elsewhere around the globe (Dias *et al.*, 2014). However,

Tab. 1. Properties calculated for each of the 145 inferred paleodrainages arranged north to south (see Fig. 3 for relative positions along coastline), which includes total paleodrainage area, the contemporary land area encompassed by each paleodrainage, the area of the paleodrainage that was exposed when sea levels dropped (*i.e.*, the corresponding areas of the continental shelf that are submerged today), as well as the number of contemporary basins that was encompassed by each paleodrainage. *Contemporary drainages with areas smaller than 10 km² were excluded (see ‘Material and Methods’ section).

Id (N to S)	Area (km ²)	Contemporary land area (km ²)	Continental shelf area exposed (km ²)	Number of contemporary basins*	Major river/locality associated
0	35117	22712	12405	45	Baía de Turiaçu
1	4891	102	4790	3	-
2	13899	7112	6786	32	-
3	185098	175983	9115	51	Mearim
4	5819	2497	3322	17	-
5	9686	6801	2884	27	-
6	2367	422	1945	12	-
7	335515	332842	2673	23	Parnaíba
8	5884	3638	2246	11	-
9	1806	20	1786	2	-
10	8155	5494	2661	11	-
11	5079	2569	2510	9	-
12	17525	15329	2196	16	Acaraú
13	2064	308	1755	5	-
14	2880	1580	1300	6	-
15	7586	5909	1677	12	-
16	691	13	679	2	-
17	1531	673	858	5	-
18	11592	10066	1525	14	-
19	2626	1249	1376	9	-
20	3009	1792	1217	8	-
21	6859	5530	1329	10	-
22	2022	455	1567	8	-
23	80809	77929	2880	19	Jaguaribe
24	17787	16579	1208	15	Mossoró
25	43542	42181	1360	16	Piranhas-Açu
26	3240	2631	610	12	-
27	701	421	279	4	-
28	1916	1300	617	11	-
29	774	407	367	7	-
30	2992	1217	1776	15	-
31	2082	1519	564	10	-
32	7705	7248	457	11	-
33	122	21	101	3	-
34	688	469	219	6	-
35	6121	5806	315	11	-
36	6420	5611	810	15	-
37	4064	3658	406	10	-
38	20344	19995	349	17	Paraíba do Norte
39	267	28	239	4	-
40	299	10	289	2	-
41	1391	776	615	9	-
42	923	472	451	6	-
43	3442	2881	561	12	-
44	2203	1033	1170	13	-
45	10600	10179	421	12	-
46	1581	1025	556	4	-

Tab. 1. (continued).

Id (N to S)	Area (km ²)	Contemporary land area (km ²)	Continental shelf area exposed (km ²)	Number of contemporary basins*	Major river/locality associated
47	1717	1228	488	8	-
48	9904	8974	930	18	-
49	752	288	463	6	-
50	551	166	385	5	-
51	3488	2054	1433	11	-
52	2357	1277	1081	8	-
53	686	268	418	4	-
54	8475	7992	483	14	-
55	1117	934	182	7	-
56	290	81	209	4	-
57	162	13	149	1	-
58	1384	1201	183	6	-
59	202	24	178	2	-
60	2252	1852	400	10	-
61	488	164	324	7	-
62	351	55	296	2	-
63	675165	675112	53	24	São Francisco
64	642	102	540	2	-
65	412	40	372	1	-
66	2306	1867	438	5	-
67	311	15	297	1	-
68	3840	3605	235	4	-
69	16907	16394	513	9	Vaza-Barris
70	199	58	141	6	-
71	336	72	264	5	-
72	9148	8908	240	17	-
73	326	31	295	3	-
74	620	267	352	5	-
75	42013	41302	712	15	Itapicuru
76	3050	2604	446	11	-
77	143	52	91	5	-
78	2526	2249	278	7	-
79	107	21	85	2	-
80	4460	4366	94	16	-
81	148	83	66	4	-
82	158	110	49	5	-
83	105	63	42	5	-
84	47	29	17	5	-
85	54	32	23	2	-
86	102	15	87	1	-
87	58053	56893	1161	44	Paraguaçu
88	217	31	186	2	-
89	10068	9894	175	16	-
90	4962	4782	181	15	-
91	2912	2133	779	21	-
92	84	17	67	2	-
93	56051	55970	82	15	Contas
94	68	29	39	3	-
95	188	113	75	6	-
96	40	4	36	1	-
97	30	3	27	1	-

Tab. 1. (continued).

Id (N to S)	Area (km ²)	Contemporary land area (km ²)	Continental shelf area exposed (km ²)	Number of contemporary basins*	Major river/locality associated
98	92	28	63	3	-
99	94	14	79	2	-
100	1438	1215	222	8	-
101	5035	4877	157	10	-
102	429	129	300	5	-
103	499	195	304	5	-
104	36167	35042	1124	13	Pardo
105	715	153	562	5	-
106	70008	69178	830	14	Jequitinhonha
107	13258	8775	4483	24	-
108	9029	6970	2059	19	-
109	10314	6542	3772	13	-
110	68531	44142	24389	37	Mucuri
111	849	17	832	1	-
112	433	85	348	5	-
113	473	31	442	2	-
114	86563	85526	1037	24	Doce
115	680	233	447	4	-
116	4935	3765	1170	18	-
117	1045	163	882	6	-
118	1511	252	1259	8	-
119	9170	8166	1004	15	Itapemirim
120	9856	6501	3355	19	Itabapoana
121	64340	60362	3978	44	Paraíba do Sul
122	3940	72	3869	3	-
123	10314	5025	5289	15	Macaé/São João
124	960	612	347	6	-
125	1235	299	935	8	-
126	1892	404	1488	11	-
127	1246	58	1189	4	-
128	6509	4224	2285	27	Baía de Guanabara
129	4354	354	4000	9	-
130	8406	4922	3484	39	Baía da Ilha Grande
131	2757	85	2672	2	-
132	4801	882	3919	21	Ubatuba
133	3720	1089	2631	22	Ilhabela
134	3941	171	3771	5	-
135	10058	1760	8298	22	Baía de Santos
136	5664	1552	4112	14	-
137	30663	25100	5563	21	Ribeira de Iguape
138	14899	5649	9250	55	Paranaguá
139	34098	22782	11316	48	Itajaí
140	12137	5193	6944	27	Ilha de Florianópolis
141	24805	14444	10362	25	Tramandaí/Mampituba
142	4868	472	4396	14	-
143	14146	887	13259	19	-
144	240872	182426	58446	166	Laguna dos Patos
Mean	18369	16146	2223	13	
SD	67440	66039	5624	17	
Min	30	3	17	1	
Max	675165	675112	58446	166	

paleodrainages, as in other parts of the world, appear to be impacting the Brazilian ichthyofauna. For example, using a paleodrainage reconstruction for the southeastern coast of Brazil, it was demonstrated that paleodrainages and its properties account for most of the genetic variation and diversity observed for the characid genus *Hollandichthys* based on mitochondrial DNA (Thomaz *et al.*, 2015) and next generation sequencing data (Thomaz *et al.*, 2017). Likewise, analyses that took into consideration fluctuations on sea level suggests its role in structuring genetic divergence and demographic history of other members of the coastal ichthyofauna (Baggio *et al.*, 2017; Hirschmann *et al.*, 2017; Lima *et al.*, 2017; Ramos-Fregonezi *et al.*, 2017; Tschá *et al.*, 2016, 2017).

Although the inferred paleodrainages provide insights about past connections, we caution that not all connections equally influenced the Brazilian ichthyofauna. For example, differences in the slope along the coast would result in different durations of connections, and the duration of connections can impact divergence patterns (see Papadopoulou, Knowles 2015a,b). In addition, the formation of river connections does not mean that all species of fish would necessarily disperse across them. For example, an interaction between species ecology and the landscape could impact the effectiveness of past connection for dispersal (*e.g.*, differences in dispersal depending on whether the species inhabits lowland areas versus the headwaters; Hirschmann *et al.*, 2015). Consideration of species-specific effects is therefore an important biological component that needs to balance the abiotic factors that are often invoked for explaining divergence patterns (reviewed in Papadopoulou, Knowles, 2016). For example, it is possible that yet unknown river capture events might contribute to divergence patterns that do not exactly match expectations based on paleodrainage boundaries (*i.e.*, “Pattern C” in Ribeiro, 2006; Lima *et al.*, 2017) or when information about paleodrainages is lacking (Ramos-Fregonezi *et al.*, 2017). Other potential explanations could underlie these incongruent patterns, ranging from misplaced interpretations of shared lineage (*e.g.*, incomplete lineage sorting, instead of dispersal, could explain some geographic patterning of lineages, especially for Pleistocene; see Thomaz *et al.*, 2015), to taxonomic differences that influence whether and when species might have dispersed across the past connections associated with paleodrainages (Hirschmann *et al.*, 2015; Thomaz, Knowles, *in prep.*).

The small and isolated basins along the Brazilian coast have been grouped into biogeographic units based on their shared patterns of ichthyofauna distribution (Géry, 1969; Menezes, 1988; Vari, 1988; Bizerril, 1994; Abell *et al.*, 2008; Lévêque *et al.*, 2008). We note that there is a general correspondence between some paleodrainages and these proposed biogeographic areas. For example, ecoregions such as the Laguna dos Patos and Tramandai-Mampituba *sensu* Abell *et al.* (2008) show a high correspondence with the paleodrainages we inferred in these areas. Likewise, for some ecoregions, such as S. Francisco and Parnaíba, the inferred pale-

odrainages generally correspond to a single contemporary basin. Although in most cases several paleodrainages occur within a single ecoregion, the number of paleodrainages within an ecoregion varies latitudinally. For example, the south is characterized by relatively small ecoregions with fewer paleodrainages (*e.g.*, Southeastern Mata Atlantica; Ribeira de Iguape ecoregions), whereas the north is characterized by relatively large ecoregions encompassing several current and past rivers (*e.g.*, Northeastern Mata Atlantica; Northeastern Caatinga and Coastal Drainages ecoregions). Since freshwater ecoregions were proposed based on the distributions and compositions of specific groups of the freshwater ichthyofauna (*e.g.*, the genus *Trichomycterus*, several genera in Neoplecostominae and the presence of killifish; Abell *et al.*, 2008), it is still unclear if biogeographic units delineated based on select taxa will be generally representative of the entire coastal ichthyofauna. In particular, because the groups used to delineate these ecoregions are known for being small range, low dispersal and highly endemic groups, geographic distributional boundaries could differ among taxa with different ecologies. Nevertheless, analyses of endemism along the coast for a large array of freshwater fishes also presented evidence supporting the role of paleodrainage connectivity (*e.g.*, Tramandai-Mampituba rivers, and Mucuri and São Mateus rivers; Carvalho, 2007; Camelier, Zanata, 2014).

Paleodrainages properties, including the ones inferred here (*e.g.*, area and number of contemporary basins forming a paleodrainage), are known to be good predictors of species richness (Albert *et al.*, 2011; Dias *et al.*, 2014; Tedesco *et al.*, 2005). Given the differences in the properties of paleodrainages, it would be interesting to explore whether the difference in the continental shelf exposure along the coast structures the distribution and divergence patterns of ichthyofauna along the Brazilian coast. In general, currently isolated rivers are hypothesized to have been more connected during the Pleistocene in the southeast, forming large paleodrainages, relative to the northeast (Tab. 1 and Fig. 3). Therefore, the relative contribution of the past, as opposed to contemporary factors in structuring diversity might also differ. For example, although genetic structure among fish populations of southeastern rivers is largely explained by paleodrainages distributions (Thomaz *et al.*, 2015; 2017), this may be a regional phenomenon. More specifically, the contemporary northeastern river basins (encompassing the ecoregions of Northeastern Mata Atlantica – north of Abrolhos Bank, S. Francisco and Northeastern Caatinga & Coastal Drainages), not the paleodrainages, may best predict patterns of genetic divergence given the limited connectivity promoted among rivers during sea level retreat in this area (Fig. 3).

Conclusions. The inferred paleodrainages represent an application of GIS techniques with tremendous utility in biological study, with the potential to inform conservation strategies. Moreover, these inferences are particularly invaluable to regions where there is a lot of uncertainty about possible past connections among contemporary river basins

because of limited geologic data. With the incredibly diverse ichthyofauna of the Brazilian coast, and its high levels of endemism, the maps of the inferred paleodrainages provide a backdrop for researchers to test hypotheses about past riverine connectivity. The inferred paleodrainages are based on data that is independent of the biological data, allowing for test of such connections in structuring genetic variation, species divergence and distributions along the Brazilian coast. This is a significant advance over using biological patterns to simply infer past connections or possible biogeographic constraints. Lastly, for the freshwater ichthyofauna of Brazil, tests related to past distributions and possible connections among contemporary isolated river basins provides an important historical dimension for exploring evolutionary processes operating at different spatial and temporal scales that may have contributed to the diversity of freshwater fishes that inhabit coastal basins.

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