Fish composition and species richness in eastern South American coastal lagoons: additional support for the freshwater ecoregions of the world

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The relationships between fish composition, connectivity and morphometry of 103 lagoons in nine freshwater ecoregions (FEOW) between 2·83° S and 37·64° S were evaluated in order to detect possible congruence between the gradient of species richness and similarities of assemblage composition. Most lagoons included in the study were <2 km², with a maximum of 3975 km² in surface area. Combined surface area of all lagoons included in the study was 5411 km². Number of species varied locally from one to 76. A multiple regression revealed that latitude, attributes of morphometry and connectivity, and sampling effort explained a large amount of variability in species richness. Lagoon area was a good predictor of species richness except in low latitude ecoregions, where lagoons are typically small-sized and not affected by marine immigrants, and where non-native fish species accounted for a significant portion of species richness. Relationships between species and area in small-sized lagoons (<2 km²) is highly similar to the expected number in each ecoregion, with systems located between 18·27° S and 30·15° S attaining higher levels of species richness. Similarities in species composition within the primary, secondary and peripheral or marine divisions revealed strong continental biogeographic

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patterns only for species less tolerant or intolerant to salinity. Further support for the FEOW scheme in the eastern border of South America is therefore provided, and now includes ecotonal systems inhabited simultaneously by freshwater and marine species of fishes.

INTRODUCTION

The sequence of lagoons in eastern South America resembles a 'pearl necklace' along the Atlantic coast from a historical and geomorphological perspective. Just like natural pearls need a considerable amount of time to be formed by biogenic activity, South American coastal lagoons were formed during the last 120 000 to 2500 years by processes of erosion and riverine and sea-derived sedimentation, associated with several events of marine transgression and regression (Delaney, 1962; Suguio *et al.*, 1985; Barreto *et al.*, 2002; Lima *et al.*, 2013).

Lagoons of the eastern South American coastal plains have a high environmental heterogeneity, even along relatively small spatial scales (Schäfer, 1992; Esteves, 2011*a*). Closely-located water bodies may differ highly in terms of morphometry and physical and chemical attributes due to geomorphological differences of the drainage basins of which they are a part (Caliman *et al.*, 2010). In addition, coastal lagoons formed by watercourses or supplied by groundwater are predominantly fresh water, whereas those subjected to seawater intrusion are more brackish or hypersaline (Caliman *et al.*, 2010). The trade-off between marine and freshwater sources determines the salt content, which in turn can act as an environmental filter for different species of fishes with variable degrees of tolerance to salt water. As coastal lagoons are ecotones between continental and coastal waters, their fish fauna composition is derived from a mixture of freshwater and marine or estuarine species (Malabarba & Isaia, 1992; Araújo & Azevedo, 2001; Garcia *et al.*, 2003; Di Dario *et al.*, 2013). The fish assemblage in each individual lagoon is also influenced by a series of factors in addition to the biogeographic history of the region. Large-scale or global features that might influence the fish composition of coastal lagoons are, for instance, the climate conditions associated with different latitudes and El Niño and La Niña southern oscillations (Garcia *et al.*, 2003). Some relevant local-scale features that act on the species pool of different lagoons are, *e.g.* differences in morphometry, variations in hydrological connectivity, microclimate, nutrient level, biotic interactions and anthropogenic perturbations (Burns *et al.*, 2006; Di Dario *et al.*, 2013; Guimarães *et al.*, 2014).

Coastal lagoons are often highly productive systems and have provided goods for human societies in several parts of the world (Kjerfve, 1994). In South America, sandy coasts were inhabited by oyster and shell human-gathering populations about 8000 years ago. Archaeological information also indicates that native inhabitants actively promoted sandbar openings a long time before European colonization in order to increase fish capture (Dean, 1995; Esteves, 2011*b*). Most impacts which those systems are now subjected to, such as dewatering for irrigation, eutrophication by point and diffuse sources, damming, drainage and landscape cover modification, introduction of exotic species and predatory fisheries, are related with the exponential growth of human population in the coastal regions (Burns *et al.*, 2006; Menezes *et al.*, 2012).

The fish composition in coastal lagoons of eastern South America has been scientifically investigated since the first European expeditions in the 19th century (Di Dario *et al.*, 2013). To this day, however, most studies are locally restricted, *i.e.* they include only one or just a few lagoons (*e.g.* Vieira & Musick, 1994; Loebman *et al.*, 2008; Artioli *et al.*, 2009; Menezes *et al.*, 2012). Araújo & Azevedo (2001), on the other hand, summarized general patterns of fish assemblage composition in coastal marine zones, bays, estuaries and four coastal lagoons between 22° and 32° S in South America. In that study, the ecosystem area was proposed as the best predictor of local species number, supporting the classical hypothesis of the species–area relationship, in which larger areas harbour more species than smaller ones (Gleason, 1922; Rosenzweig, 1995; Amarasinghe & Welcomme, 2002). Guimarães *et al.* (2014), however, found that connectivity acts complementarily to area in predicting species richness, extending the patterns described for lacustrine systems to coastal lagoons (Bouvier *et al.*, 2009).

Abell *et al.* (2008) proposed a biogeographic scheme of 426 freshwater ecoregions (FEOW) that together cover nearly all non-marine regions of the world (FEOW). Each FEOW is 'a large area encompassing one or more freshwater systems with a distinct assemblage of natural freshwater communities and species' (Abell *et al.*, 2008). That scheme has been widely reported in the literature (*e.g.* Camelier & Zanata, 2014). A close examination of the FEOW framework on coastal lagoons is still lacking, however, probably due to underrepresentation of species from these ecosystems in most fish collections.

The present study focused on the composition of fish species in coastal lagoons across nine FEOW in eastern South America, from tropical to temperate latitudes (between 2·83° S and 37·64° S). It was tested if latitude, attributes of morphometry and connectivity, and sampling effort predict the fish species richness. It was also expected that (1) fish species richness is primarily driven by latitude, ecosystem area, and the distance to the nearest water body, but the degree of connection with sea and sampling effort may modify that relationship, and that (2) despite being inhabited by species of both marine and freshwater origins, coastal lagoons within the same FEOW are more similar in their fish composition, at least when only continental species (*i.e.* freshwater) are considered.

MATERIALS AND METHODS

Data on fish assemblages were available for 103 lagoons in nine FEOW along the eastern South American coast. FEOW delimitation and codes (IDs) are based on Abell *et al.* (2008). In a gradient from low (2·83° S) to higher (37·64° S) latitudes, the lagoons are included in the following FEOW: ID325 Parnaiba ($n = 7$), ID326 Northeastern Caatinga and Coastal Drainages ($n = 15$), ID328 Northeastern Mata Atlantica ($n = 5$), ID329 Paraiba do Sul ($n = 14$), ID352 Fluminense ($n = 3$), ID335 Tramandai-Mampituba ($n = 38$), ID334 Laguna dos Patos ($n = 19$), ID345 Lower Parana ($n = 1$) and ID347 Bonaerensean drainages ($n = 1$) (Table S1, Supporting Information). The number of lagoons in each FEOW partially reflects their abundance in the ecoregion. For example, several lagoons are located in the 700 km x 120 km coastal plain between Santa Marta Cape and Chuí Stream in southern Brazil. Man-made reservoirs were excluded, since they are relatively young compared to natural lagoons. Small-sized temporary ponds were included in the analyses due to their relevance as habitats for endemic species and to their seasonal (or perennial) connection to larger water bodies, including the sea.

COASTAL LAGOONS: GEOLOGICAL ASPECTS

The study area (Fig. 1) includes at least four of the six megadomes (cratons) formed within the context of the formation of South America (Proterozoic eon, 2×10^9 years) and the separation of South America and Africa during the end of the mid-Cretaceous ($125-110 \times 10^6$ years). During the Cenozoic (65×10^6 years to present), a series of tectonic and geomorphological events (sedimentation, erosion and weathering) changed the topography to the one seen today. This geological history created most of the current water courses of the main crystalline shield and coastal river basins, especially the large-scale patterns (Almeida *et al.*, 2000; Martin *et al.*, 2003; Ribeiro, 2006). Subsequent changes occurred due to reactivation of fault lines inside older deformation belts [Ribeira Fold Belt and Rio Paraiba Shear Zone, Araçuai Belt, Ceara Belt, Dom Feliciano Belt, as shown in Suguio & Martin (1996)].

Lagoons included in this study belong to the South Atlantic tectono-sedimentary domain, mainly created and regulated by fluvial sediment budgets, and quaternary fluvial-coastal-oceanic processes and tectonics. Exceptions are those lagoons of the lowest latitudes (ID325 Parnaiba), which belong to the Equatorial Atlantic domain and are characterized by small isolated ponds created by erosion processes and filled by drainage, largely controlled by seasonal weather and nearby forests (Suguio *et al.*, 1985).

Due to the generally shallow slope of the eastern South America coast, the distance to the sea was assumed as a potential predictor of marine water intrusions even for lagoons which are relatively distant or lacking connection with sea. The ID335 Tramandai-Mampituba differs from all the other FEOW included in the study due to its narrow coastal plain (width <20 km), whose development is limited by the escarpments of the Serra Geral plateau (Angulo *et al.*, 2006).

SHAPE, SIZE AND CONNECTIVITY DATA

Size, perimeter and shape (morphometry) for the 103 lagoons were measured in recent (2014) satellite images (Landsat 8, spatial resolution of 30 m). Lagoons were mapped with the isocluster module of unsupervised image classification in ArcGIS 10.2 (Esri, 2013). The small area of some lagoons hampered their visualization in Landsat 8 images, therefore those lagoons were mapped using high resolution ($\leq$5 m) images available in Google Earth. After the 103 lagoons were mapped, the Vector-based Landscape Analysis Tools (V-LATE 2.0 beta; Lang & Tiede, 2003) for ArcGIS was used to calculate the distance between each lagoon and the nearest water body, and between each lagoon and the sea. Six variables, namely area (km^2), perimeter (km), shape [$y = 0 \cdot 282\, P\, (\sqrt{A})^{-1}$, where P is perimeter and A is area], the degree of connection with sea (0, 0·5 and 1 represent none, temporary and permanently connected), and the nearest distance to a continental water body (m) and to the coastline (km) were obtained in ArcGIS 10.2 (Table S1 and Fig. S1, Supporting Information). The theoretical variation of shape is between 0, if the border of the lagoon represents a perfect circle, and infinite, for infinitely narrow and long shapes (Farina, 2006).

FISH COMPOSITION DATA AND TAXONOMY

Fish information for the lagoons included in this study derives from *c.* 20 years of studies conducted by several research institutions in Brazil, Uruguay and Argentina. Sampling varied significantly due to local features such as area, depth and habitat heterogeneity, and also the goals of the original research projects. Water depth was typically <3 m. Specimens were usually collected with standardized effort using seines (0·5 cm mesh size) and gillnets of different mesh sizes including, in some cases, multi-mesh standardized nets. In vegetated areas, sieves and fyke nets were also employed. Specimens were usually collected in 1–2 year studies, but in some larger lagoons, such as Imboassica, Rocha, Blanca and Mar Chiquita, sampling was carried out regularly over the last 15 years. Therefore, fishing effort employed was scored from 1 (1 year) to 4 (>10 years of seasonal sampling) for each lagoon (Table S1, Supporting Information). Endemic species were defined as those whose natural distributions are restricted only to one FEOW. Exotic species were defined as those whose natural geographic distribution does not include the FEOW where they were captured. Distributional data and nomenclature of species were checked using Eschmeyer's Catalog of Fishes (www.calacademy.org/research/ichthyology/catalog). There is an ongoing debate whether one
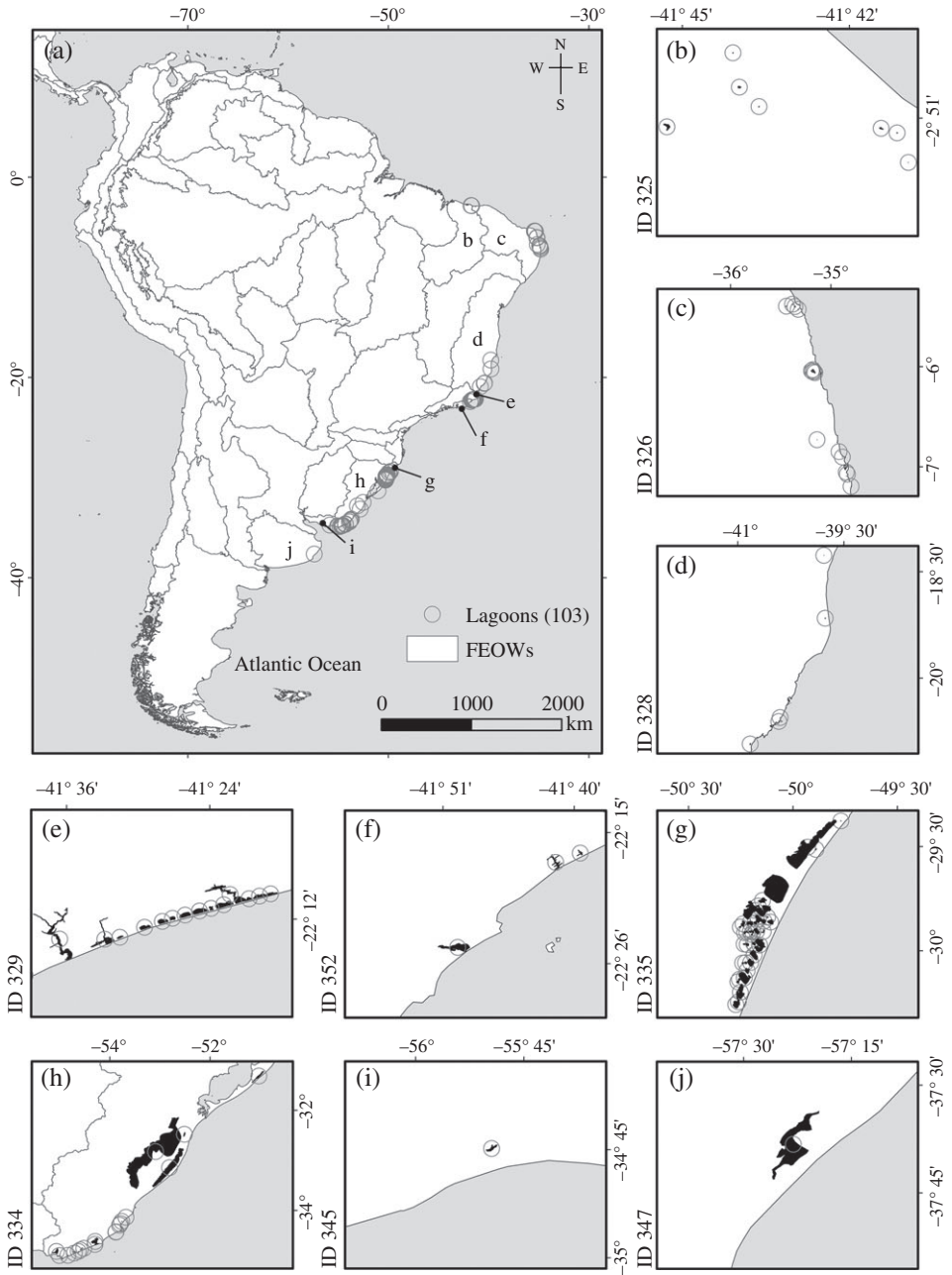
Fig. 1. (a) South American freshwater ecoregions (FEOWs) of Abell *et al.* (2008) and location of the 103 lagoons included in this study: (b) ID325 Parnaiba (*n* = 7), (c) ID326 Northeastern Caatinga and Coastal Drainages (*n* = 15), (d) ID328 Northeastern Mata Atlantica (*n* = 5), (e) ID329 Paraiba do Sul (*n* = 14), (f) ID352 Fluminense (*n* = 3), (g) ID335 Tramandai-Mampituba (*n* = 38), (h) ID334 Laguna dos Patos (*n* = 19), (i) ID345 Lower Parana (*n* = 1) and (j) ID347 Bonaerensean drainages (*n* = 1).

or two species of the coastal clupeid *Sardinella* inhabits the eastern border of South America (*e.g.* Whitehead, 1985), but growing evidence indicates that a single species, *Sardinella aurita* Valenciennes 1847, should be recognized in the region to the detriment of the apparently junior synonym *Sardinella brasiliensis* (Steindachner 1879) (Mabragaña *et al.*, 2012). That taxonomic view is therefore adopted in this paper.

Voucher specimens are deposited in the fish collections of the Campus Reis Veloso, Universidade Federal do Piauí (CZDP, Brazil), Universidade Federal da Paraíba (UFPB, Brazil), Instituto Nacional da Mata Atlântica (formerly Museu de Biologia Mello Leitão; MBML, Brazil), Núcleo em Ecologia e Desenvolvimento Socioambiental de Macaé, Universidade Federal do Rio de Janeiro (NPM, Brazil), Universidade Federal do Rio Grande do Sul (UFRGS, Brazil), Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCT-PUCRS, Brazil), Universidade Federal do Rio Grande (FURG, Brazil), Centro Universitario Regional Este (CURE-ICT, Maldonado, Uruguay), Facultad de Ciencias, UdelaR (ZVC-P, Uruguay) and Instituto de Investigaciones Marinas y Costeras (UNMdP, Argentina).

DATA ANALYSES

A multiple regression analysis was applied in order to explore the possible relationships between species richness (response variable), latitude, size, shape and connectivity of the lagoons with the nearest water body and sea, and sampling effort employed (predictor variables). A correlation matrix between the predictor variables indicated that only perimeter and area were strongly correlated ($r = 0.95$, $P < 0.01$). Therefore, perimeter was not included in the multiple regression. The contribution of each predictor variable was inferred by the respective β value. To assess the relative importance of connection with sea and sampling effort to predict fish species richness, partial correlations were also performed. Multi-collinearity among predictor variables was evaluated through the variance inflation factor (F_{VI}), whose values <10 were considered of weak influence on parameter variance (Myers, 1990). All variables were $\log_{10} x + 1$ transformed and standardized prior to analysis. Considering the lack of standardized fish sampling effort among lagoons, even though multiple gears were always used and sampling effort was scored, the analyses were restricted to a qualitative approach (Jackson & Harvey, 1997). Therefore, all the analyses used the site-species matrix containing presence or absence species data of 103 lagoons (Appendix).

Simple regressions were used to evaluate the effect of area (predictor variable) on species richness (response variable) within FEOWs. Considering that most lagoons measured <2 km^2 in area and that sampling effort and degree of connection with the sea were more similar within them, an ANCOVA was performed to explore more deeply the effect of the FEOWS (predictor categorical variable) on species richness (response variable) after controlling the effect of the area (predictor variable) within small-sized lagoons. Composition of fish assemblages was evaluated by non-metric multidimensional scaling (NMDS) using the Jaccard similarity index applied to the matrix of species presence or absence. To account for responses due to different origins and tolerance to salinity on the ordination, species matrix was split into sub-sets of species belonging to families regarded as of the primary, secondary and peripheral or marine divisions following Myers (1938). The purpose of the NMDS was to find the most parsimonious set of dimensions that could account for the location of the lagoons, so that their proximity on the ordination diagram would represent a greater similarity in the fish assemblage composition. Three FEOW (ID352 Fluminense, ID345 Lower Parana and ID347 Bonaerensean drainages) were excluded from the simple regression analyses and ANCOVA due to the low number of lagoons ($n \leq 3$). Regressions and ANCOVA were performed using Statistica (StatSoft, 2007), and NMDS were performed using PC-Ord 4.10 (McCune & Mefford, 1999) softwares. The assumption of normality of residuals (Shapiro-Wilk test) was reached in the multiple and simple regressions and ANCOVA. $P < 0.05$ was considered as the significance level.

RESULTS

The coastal lagoons included in this study were highly variable in area, ranging from just a few m^2 to 3975 km^2 (Mirim Lagoon, ID334 Laguna dos Patos). Small

lagoons of $<2\,\mathrm{km}^2$, however, comprised 73% of the studied systems and occurred in all FEOW. Large lagoons, on the other hand, are located mostly on ID352 Fluminense, ID335 Tramandai-Mampituba and ID334 Laguna dos Patos. These large-sized lagoons follow an orthogonal (Preta, Carapebus, ID329 Paraiba do Sul; Cabiúnas, Imboassica, ID352 Fluminense) or parallel (Mirim, Mangueira, do Peixe, ID334 Laguna dos Patos) orientation relative to the coastal sea line (Table I and Table S1 and Fig. S1, Supporting Information).

Coastal lagoons of the ID352 Fluminense ecoregional unit have larger values of area, perimeter and shape, and are also located near the coast, markedly differing from those of the ID325 Parnaiba, with lower values of morphometry and with an average distance of 2·5 km from the sea (Fig. S1, Supporting Information). Lagoons of the ID328 North-eastern Mata Atlantica, ID329 Paraiba do Sul, ID352 Fluminense and ID334 Laguna dos Patos, varied greatly considering the set of morphometric variables and degree of connection with sea, some of them being (mainly the largest ones) subjected to sandbar openings (Table I and Table S1, Supporting Information).

A total of 271 species of fishes was recorded when all lagoons were considered (Appendix). A large amount of variability in species richness was explained by six of the seven predictor variables (multiple linear regression, $F_{7,95} = 25{\cdot}59$, $r^2_{\mathrm{adj}} = 0{\cdot}63$, $P < 0{\cdot}01$) (Table II). Lagoons of higher latitudes, located near the coast and temporarily or permanently connected with the sea attained in general high values of species richness. The recorded species are representative of 23 orders and 66 families of Teleostei and five orders and five families of Chondrichthyes. Fourteen species were considered as exotic and 16 are endemic to a particular ecoregion: five loricariids [four species of *Rineloricaria* and *Hisonotus taimensis* (Buckup 1981)], three cichlids (*Crenicichla* and *Gymnogeophagus*), four atherinopsids (*Odontesthes*), the hypopomid *Brachyhypopomus janeiroensis* (Costa & Campos-da-Paz 1992), the pimelodid *Pimelodus pintado* Azpelicueta, Lundberg & Loureiro 2008, the pseudopimelodid *Microglanis cibelae* Malabarba & Mahler 1998, and the rivulid *Atlantirivulus jurubatibensis* (Costa 2008).

Connection with the sea accounted for most noise in the species-area curve [Fig. 2(a)]. Lagoons temporarily (Imboassica, Carapebus, do Peixe and Rocha) or permanently (Tramandai and Mar Chiquita) connected with the sea had the highest values of species richness. Significantly linear and logarithmic relationships between fish species and area were described in FEOWs with lagoons with surface area $<2\,\mathrm{km}^2$ [Fig. 2(d), (e)] and $>2\,\mathrm{km}^2$ [Fig. 2(f), (g)]. Exceptions were Parnaiba [Fig. 2(b)] and Northeastern Caatinga and Coastal Drainages [Fig. 2(c)] ecoregions, where area failed to predict species richness. At Tramandaí-Mampituba and Laguna dos Patos ecoregions, tendencies of stabilization in species number were reached at *c.* 35 species [Fig. 2(f), (g)]. The southernmost Mar Chiquita coastal lagoon had the largest number of species exclusively recorded in a single lagoon (22), a condition that might reflect its permanent connection to the sea and its location in a different (compared with more northern lagoons) biogeographic marine province (Briggs & Bowen, 2012) (Appendix).

A non-significant interaction term was obtained by testing the effect of area on species richness within small lagoons across FEOWs (ANCOVA, $F_{5,61} = 1{\cdot}95$, $P > 0{\cdot}05$). Assuming the parallelism among these relationships, the ANCOVA for homogeneous slopes evidenced that, despite the fact that species richness increased positively and linearly with the area of the small-sized lagoons (which were more similar in sampling effort), species richness is variable across FEOWs (ANCOVA,

TABLE I. The nine freshwater ecoregions (FEOW) covered in this study (ID), number of sampled lagoons, morphometry and connectivity data, species richness and ratio of species of the peripheral or marine (PER), primary (PRI) and secondary (SEC) freshwater divisions in nine FEOWs (ID) in eastern South American (values are mean ± s.d.)

	ID325	ID326	ID328	ID329	ID352	ID335	ID334	ID345	ID347
Latitudinal range	−0·03	−1·82	−2·66	−0·06	−0·13	−0·88	−3·58		
n	7	15	5	14	3	38	19	1	1
Area (km²)	0·01 ± 0·01	0·45 ± 0·44	0·26 ± 0·26	1·02 ± 1·01	1·14 ± 1·35	10·68 ± 27·62	259·84 ± 917·68	1·18	41·34
Perimeter (km)	0·24 ± 0·26	2·70 ± 2·13	4·08 ± 4·42	10·32 ± 13·21	11·26 ± 5·95	12·52 ± 18·65	64·66 ± 152·89	8·23	60·34
Shape	1·29 ± 0·23	1·41 ± 0·32	2·3- ± 1·28	2·56 ± 1·80	3·86 ± 1·72	1·46 ± 0·40	1·94 ± 1·00	2·14	2·65
Distance to the sea (km)	0·33 ± 0·32	5·17 ± 5·44	4·54 ± 6·01	0·12 ± 0·02	0·12 ± 0·02	6·62 ± 3·81	2·56 ± 4·23	2·96	2·19
Distance to the next lagoon (km)	2·56 ± 1·70	1·41 ± 1·45	4·85 ± 4·74	0·16 ± 0·22	3·31 ± 1·59	0·56 ± 0·53	2·59 ± 2·09	2·97	0·17
FEOW species richness	21	28	30	75	85	76	142	21	59
Local species richness	6·29 ± 2·87	5·60 ± 2·80	9·20 ± 6·06	13·93 ± 16·67	42·00 ± 31·80	21·37 ± 7·67	21·16 ± 20·20	21	59
PER ratio	0·14 ± 0·38	0·11 ± 0·25	0·18 ± 0·27	0·24 ± 0·18	0·52 ± 0·34	0·11 ± 0·10	0·11 ± 0·21	0·00	0·78
SEC ratio	0·26 ± 0·16	0·22 ± 0·14	0·29 ± 0·06	0·49 ± 0·20	0·20 ± 0·16	0·22 ± 0·11	0·34 ± 0·20	0·19	0·07
PRI ratio	0·60 ± 0·29	0·67 ± 0·27	0·53 ± 0·23	0·27 ± 0·17	0·28 ± 0·19	0·67 ± 0·12	0·55 ± 0·19	0·81	0·15

TABLE II. Results of the multiple linear regression ($n = 103$) between species richness and latitude, morphometric and connectivity variables and sampling effort in coastal lagoons. Variance inflation factor (F_{IV}), regression coefficient $\pm$ S.E., t-test for the adjusted coefficient, coefficients of the standardized multiple regression (β) of each predictor variable

	F_{IV}	Coefficient $\pm$ S.E.	t	P	β
Intercept		$-3 \cdot 94 \pm 0 \cdot 45$	$-8 \cdot 69$	$<0 \cdot 01$	
Latitude (Lat.)	$1 \cdot 29$	$0 \cdot 93 \pm 0 \cdot 23$	$4 \cdot 06$	$<0 \cdot 01$	$0 \cdot 28$
Area (Area)	$1 \cdot 67$	$0 \cdot 37 \pm 0 \cdot 12$	$3 \cdot 295$	$<0 \cdot 01$	$0 \cdot 23$
Shape (Shape)	$1 \cdot 74$	$1 \cdot 72 \pm 0 \cdot 66$	$2 \cdot 60$	$0 \cdot 01$	$0 \cdot 21$
Distance to the sea (Dis.Sea)	$1 \cdot 95$	$1 \cdot 11 \pm 0 \cdot 22$	$4 \cdot 97$	$<0 \cdot 01$	$0 \cdot 42$
Distance to the next lagoon (Dist.Next.)	$1 \cdot 20$	$-0 \cdot 37 \pm 0 \cdot 26$	$-1 \cdot 46$	$>0 \cdot 05$	$-0 \cdot 10$
Connection with sea (Con.Sea)	$1 \cdot 30$	$2 \cdot 52 \pm 0 \cdot 80$	$3 \cdot 14$	$<0 \cdot 01$	$0 \cdot 22$
Sampling effort (Eff.)	$2 \cdot 20$	$2 \cdot 89 \pm 0 \cdot 71$	$4 \cdot 04$	$<0 \cdot 01$	$0 \cdot 36$
Multiple $r^2 = 0 \cdot 653$					
Adjusted $r^2 = 0 \cdot 628$					
Partial correlation coefficients (ordinal predictor variables):					
Correlation between species richness and Con.Sea					
Controlling for Eff., Area, Shape, Dist.Next., Dist.Sea and Lat.			$= 0 \cdot 38$	$<0 \cdot 01$	
Controlling for Area, Shape, Dist.Next., Dist.Sea and Lat.			$= 0 \cdot 36$	$<0 \cdot 01$	
Correlation between species richness and Eff.					
Controlling for Con.Sea, Area, Shape, Dist.Next., Dist.Sea and Lat.			$= 0 \cdot 30$	$<0 \cdot 01$	
Controlling for Area, Shape, Dist.Next., Dist.Sea and Lat.			$= 0 \cdot 26$	$<0 \cdot 05$	

$F_{6,66} = 9 \cdot 96$, $P < 0 \cdot 01$) (Table III). By comparing the adjusted means among FEOWs, species richness in lagoons of the subtropical ID335 Tramandai-Mampituba ecoregion were significantly higher than in the northernmost tropical (ID325 Parnaiba and ID326 Northeastern Caatinga and Coastal Drainages) and southernmost subtropical (ID334 Laguna dos Patos) FEOWs (Table I and Fig. 3).

Of the 271 species recorded, 142 belonged to the peripheral or marine division, 96 to the primary freshwater division and 33 to the secondary freshwater division. Families with higher number of species were the Characidae (38 species), Cichlidae (22 species), Carangidae (17 species), Atherinopsidae and Loricariidae (each with 13 species), Sciaenidae (10 species) and Gobiidae (nine species), Engraulidae (eight species) and Clupeidae, Gerreidae and Paralichthyidae (each with seven species). Within the 27 families with only one species recorded, 70% are regarded as belonging to the peripheral or marine division, 19% to the primary division (Acestrorhynchidae, Aspredinidae, Clariidae, Trichomycteridae and Hypopomidae) and 11% to the secondary division (Cyprinidae, Synbranchidae and Anablepidae) (Appendix). Ninety-seven species were reported only in one lagoon and six species occurred in >40 lagoons, and consequently, in more than one FEOW. Among those widely distributed species from the primary division are the trahira *Hoplias* aff. *malabaricus* (Bloch 1794), the characids *Hyphessobrycon luetkenii* (Boulenger 1887), *Oligosarcus jenynsii* (Günther 1864) and the curimatid *Cyphocharax voga* (Hensel 1870). Those from the secondary division are *Geophagus brasiliensis* (Quoy & Gaimard 1824) and the one-sided livebearer *Jenynsia multidentata* (Jenyns 1842). Among the species of the peripheral or marine division, the sardine *Platanichthys*
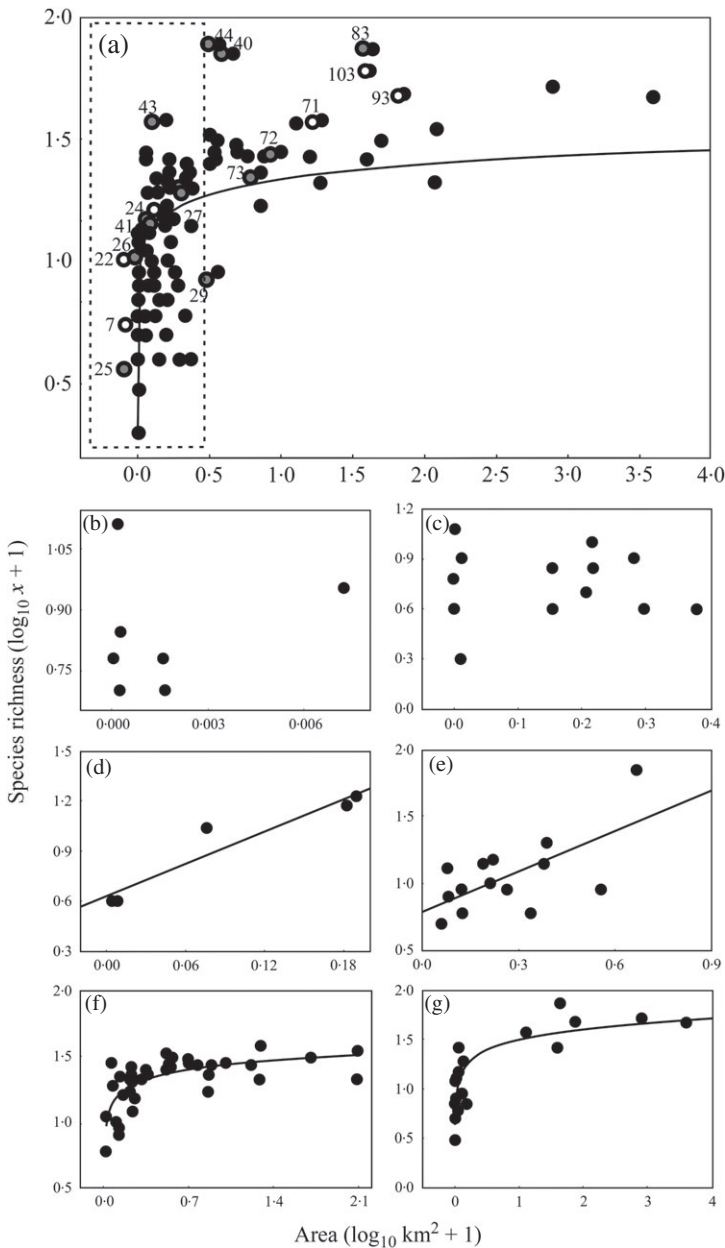
FIG. 2. Effect of area on species richness in the (a) 103 coastal lagoons included in the study and within tropical (b) ID325 Parnaíba, (c) ID326 Northeastern Caatinga and Coastal Drainages, (d) ID328 Northeastern Mata Atlantica and (e) ID329 Paraíba do Sul (e), and subtropical (f) ID335 Tramandai-Mampituba and (g) ID334 Laguna dos Patos freshwater ecoregions (FEOW) (see Table S1, Supporting Information). (a) ┌┄┄┐, includes small lagoons ($<2\,km^2$); ○, lagoons permanently connected with the sea; ◐, lagoons sporadically connected with the sea. Only FEOWs with data available for more than three lagoons are included. Scale of the x-axis varies across the scatterplots. The significant regressions were fitted by: (a) $y = 0{\cdot}72x - 0{\cdot}16x^2 + 0{\cdot}92$ ($r^2 = 0{\cdot}48, P < 0{\cdot}01$), (d) $y = 0{\cdot}63x + 3{\cdot}24$ ($r^2 = 0{\cdot}91, P = 0{\cdot}01$), (e) $y = 0{\cdot}79x + 0{\cdot}01$ ($r^2 = 0{\cdot}42, P = 0{\cdot}01$), (f) $y = 0{\cdot}57x - 0{\cdot}21x^2 + 1{\cdot}12$ ($r^2 = 0{\cdot}42, P < 0{\cdot}01$) and (g) $y = 0{\cdot}67x - 0{\cdot}13x^2 + 0{\cdot}92$ ($r^2 = 0{\cdot}71, P < 0{\cdot}01$).

TABLE III. Results of the ANCOVA ($n = 73$) for homogeneous slopes, which evaluated the relationship between species richness and area of small-sized lagoons ($<2\,km^2$). Only freshwater ecoregions (FEOW) with more than three coastal lagoons are included

	SS	d.f.	MS	*F*	*P*-value
Intercept	22·09	1	22·09	552·09	< 0·01
Area ($\log_{10}\,km^2 + 1$)	0·37	1	0·37	9·20	< 0·01
FEOW	1·52	5	0·31	7·60	0·01
Error	2·64	66	0·04		

platana (Regan 1917) (six ecoregions), the engraulid *Lycengraulis grossidens* (Spix & Agassiz 1829) (five ecoregions) and the silverside *Atherinella brasiliensis* (Quoy & Gaimard 1825) (five ecoregions), were recorded in 20–37 lagoons.

The ordination of lagoons based on the presence or absence of species of the peripheral or marine division showed a lack of geographic clustering even within closely located systems in the same FEOW [Fig. 4(a)]. When lagoons were ordinated based only on species of the secondary division, units belonging to the same and to adjacent FEOW were closer, indicating more similarities in species composition. This is the case of the lagoons of the ID328 Northeastern Mata Atlantica, ID329 Paraiba do Sul and ID352 Fluminense (mostly negative NMDS scores), and those located in the ID335 and the northernmost lagoons of ID334 (Mirim, Mangueira, do Peixe and das Flores). The high incidence of non-native cichlids in the ID325 Parnaiba and ID326 Northeastern Caatinga and Coastal Drainages, both in north-eastern Brazil, however, accounted for the absence of spatial patterns of similarity of lagoons within and between these FEOWs [Fig. 4(b)]. Higher similarities among fish assemblages were detected within
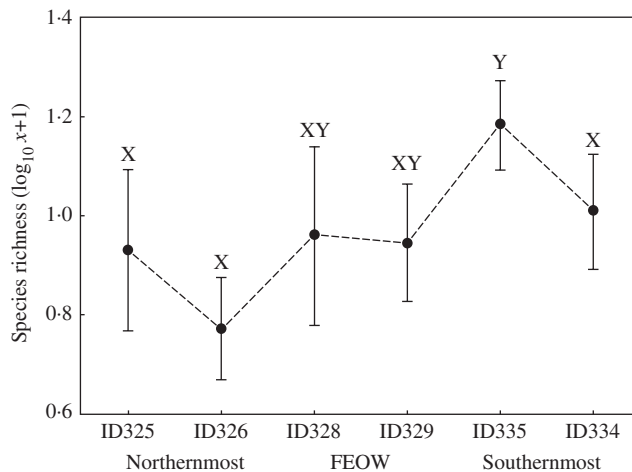
FIG. 3. Variation in species richness (adjusted mean ± 95% c.i.) in freshwater ecoregions (FEOWs) examined. Different uppercase letters indicate significant differences ($P < 0.05$) in species richness in small sized lagoons between FEOWs, after controlling the effect of area. Only FEOWs with data available for more than three lagoons are included.
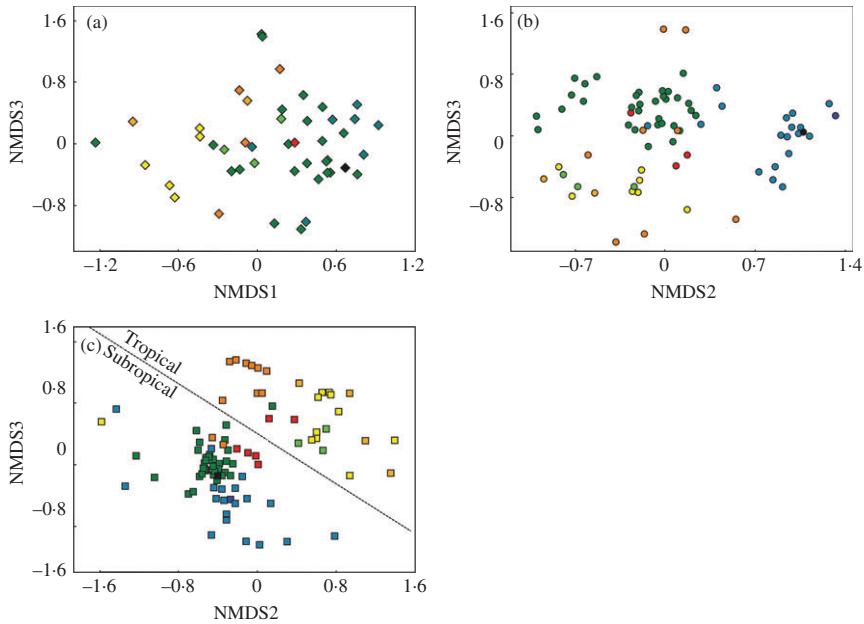
FIG. 4. Ordination of the 103 lagoons along the non-metric multi-dimensional scaling (NMDS) axes, according to similarity in composition of species of the (a) peripheral or marine, (b) secondary and (c) primary fresh-water divisions. Colours refer to the following freshwater ecoregions (FEOW) (see Table S1, Supporting Information): ■, ID325 Parnaiba; ■, ID326 Northeastern Caatinga and Coastal Drainages; ■, ID328 North-eastern Mata Atlantica; ■, ID329 Paraiba do Sul; ■, ID352 Fluminense; ■, ID 335 Tramandai-Mampituba; ■, ID334 Laguna dos Patos; ■, ID345 Lower Parana; ■, ID347 Bonaerensean drainages. The number of lagoons and stress were (a) 62 and 0·17, (b) 98 and 0·14, and (c) 99 and 0·15.

and between neighbouring FEOW when lagoons were ordinated based on species of the primary division. The ordination of the lagoons evidenced a transversal gap on the two-dimensional space formed by the axes 2 and 3 of the NMDS, which could be viewed as a transition between latitudinal zones. Lagoons belonging to tropical and subtropical FEOWs were placed above and below the line respectively, suggesting a high degree of similarity in fish assemblage composition, primarily driven by FEOW and secondarily by latitudinal gradient [Fig. 4(c)].

DISCUSSION

The present study revealed patterns of species richness and composition in fish assemblages of coastal lagoons, and adds evidence to the view that the number of species found in a given location results from processes acting at both local and larger regional scales (Kelso & Minns, 1996). In South America, lagoons associated with floodplains or along the eastern coast are mostly regarded as recent landscape elements. The relatively 'young' (in geological terms) origin of those systems might explain the absence of a substantial number of species adapted to lacustrine environments as seen in other parts of the world, including South America (Mandrak, 1995). Another consequence is that those coastal lagoons, which lie at the interface between

land and sea, have a singular, but non-exclusive faunal composition of continental and marine origins.

The 103 lagoons studied here do not totally represent the thousands of coastal water bodies along the Atlantic coast of South America, but they cover a wide latitudinal range (35°). The metrics related to latitude, morphometry, connectivity with the sea and sampling effort accounted for almost 65% of the variability in species number, suggesting that the hydrographic structure connecting the lagoons and the adjoining sea are sources for immigrants in coastal lagoons. In addition, size of lagoon is directly related to the amount of water discharge received by lentic environments on flat landscapes at the sea level (Schäfer, 1992). It is expected that lagoons connected to complex networks of streams, channels and pools, such as those located in the subtropical lower latitudes, attain larger sizes and harbour a biota mostly composed of riverine immigrants, in addition to lacustrine species less intolerant to salinity (*e.g.* species of the Cichlidae and Anablepidae). Water and fishes may wander between the continental waters and the sea, depending on the water balance or on the nature of the connection between those compartments (Briggs, 1984). Therefore, coastal lagoons resemble estuaries in that transitional and dual aspect. Another interesting feature is that, in El Niño years, which are characterized by intense rainfall in subtropical South America, the typical estuarine environment of the Patos Lagoon (Fig. 1) is literally 'flooded' by water of continental origin, with the consequence that several freshwater species disperse towards the mouth of the lagoon (Garcia *et al.*, 2003).

The classic species and area relationship was recovered among fish species and lagoons included in this study. An admittedly unbalanced sampling design limited regression fitting to only six of the nine FEOW, but results for the small-sized lagoons suggest that, after controlling for the effect of area, species richness is comparatively lower in the northern (ID325 Parnaiba, ID326 Northeastern Caatinga and Coastal Drainages) and southernmost (ID334 Laguna dos Patos) FEOWs. The range in coastal lagoon area in each FEOW was almost inversely related to the latitudinal gradient. Between 22° S and 30° S, however, the Atlantic forest hills and terraces reach the coastal area, a situation that restricts the occurrence of coastal lagoons to a narrow flatland of <20 km. The several isolated hydrographic basins of that region might explain the relative importance of species of the primary division and the higher endemism of those coastal lagoons, as is the case in several lagoons of the ID335 Tramandai-Mampituba (Appendix).

Several species of the peripheral or marine division use coastal lagoons connected with the sea for rearing and feeding, a situation that might explain the pattern of occurrence of those species in these systems. Species-level datasets, however, were zero-inflated due to the high occurrence of many occasional species across narrow and broad geographic gradients. Ordination of the 103 coastal lagoons based on their fish species composition suggests that different processes underlie the colonization and establishment of individuals in those systems, which are relatively recent elements of the landscape. In the case of species of the peripheral or marine division, stochastic events such as the attraction of coastal marine fishes inhabiting the near shore by the more brackish waters of the lagoons, might explain the lack of a spatial arrangement.

Marine biogeographic patterns (*e.g.* Spalding *et al.*, 2007; Di Dario *et al.*, 2011; Briggs & Bowen, 2012) might explain the co-occurrence of some species of fishes of the peripheral or marine division in coastal lagoons. For example, all species exclusively recorded in Mar Chiquita, Argentina, including five elasmobranchs and

the plownose chimaera *Callorhinchus callorynchus* (L. 1758) are more common in the relatively colder waters of the south-western Atlantic (Bruno *et al.*, 2013). In addition, several species recorded in coastal lagoons such as Mar Chiquita (ID347), Mirim (ID334) and Carapebus (ID329) are also present in estuaries, suggesting that these lagoons can act as transient corridors for fishes in early life-history stages, *i.e.* between the offshore spawning ground and the lacustrine and riverine nursery ground (Di Dario *et al.*, 2011; Bruno *et al.*, 2014; Mai *et al.*, 2014). This is almost certainly the case with the Carangidae, Sciaenidae and Centropomidae (Vieira & Musick, 1994; Bruno *et al.*, 2014), which may enter coastal lagoons while searching for food and shelter from predation. Other species, such as mullets (Mugilidae) enter coastal lagoons as juveniles and return to the sea before sexual maturity or as adults (Vieira, 1991; González Castro *et al.*, 2011). A few species of the peripheral or marine division, however, such as *P. platana*, *L. grossidens* and *A. brasiliensis*, are widely distributed and relatively abundant in coastal lagoons, where they spend their whole life cycle (Di Dario *et al.*, 2013; Mai *et al.*, 2014) (Appendix).

Coastal lagoons are permanent habitats for several species of the primary and secondary divisions. The species composition, when only those divisions are considered, varied more substantially on a geographic (north–south) gradient, and less within each FEOW. That situation indicates a more straightforward correlation with continental biogeographic patterns and processes in each FEOW. Species of those divisions are also presumably more affected by variations in salinity, which may act as a barrier to their dispersal among different continental water bodies (Briggs, 1984). The intrusion of higher quantities of salt water into coastal lagoons, in a global warming and sea-level rise scenario, will presumably have a strong impact on the pattern of distribution and abundance of those species, especially in coastal lagoons that lack complex drainage networks, such as those in ID325 Parnaiba, ID326 Northeastern Caatinga and Coastal Drainages, and ID329 Paraiba do Sul. In addition, even though secondary productivity is often higher in saline and hypersaline systems (Kjerfve, 1994), species richness generally declines as salinity increases and only a few species are able to maintain sustainable populations in those waters (Melack *et al.*, 1997). Summing up, the FEOW framework is mostly supported by patterns of fish species richness and composition in coastal lagoons of eastern South America, indicating that this framework might be extrapolated to other types of continental aquatic habitats and should be incorporated in macro-ecological studies (Hortal *et al.*, 2014).

Another question that bears on the future of the lagoons included in this study and their species diversity is the fact that most of them are still unprotected and have been subjected to several well-documented anthropogenic impacts, some of which are: urban development (IDs326, 328 and 352), artificial sandbar opening (IDs329 and 352), water diversion to rice fields (ID334), and eutrophication by aquaculture (ID326) or by domestic sewage (IDs326, 335, 334 and 352). Lagoons Suruaca and Sucuri (ID328) are located in the tablelands, between the Espírito Santo and Bahia states, where the mild relief facilitated human deforestation and introduction of cattle and eucalyptus (Sarmento-Soares & Martins-Pinheiro, 2013, 2014). In the past, the Suruaca Lagoon drained an immense wetland of *c.* 174 000 ha, which is now reduced to a quarter of its original area. The Sucuri Lagoon, in turn, is drained by forested streams, which are characterized by dark acid waters rich in humic substances and organic debris. Man-made channels interconnecting the complex of

coastal lagoons were historically used for human transportation. The second longest artificial channel of the world is the Campos-Macaé channel, a 106 km water corridor excavated mostly by slaves in the colonial period, connecting several lagoons in the FEOWs 329 and 352 (Esteves, 2011*b*). Sadly, drastic modifications of landscape features such as those are not restricted to past centuries. In the 1970s, a conjoint initiative of the Brazilian and Uruguayan Governments resulted in the closure of a natural channel of 75 km connecting the Mirim and Patos Lagoons in FEOW ID334. That action, which would supposedly improve rice field crops in the wetlands of the Mirim Lagoon by preventing the intrusion of sea water, resulted in the extirpation of several marine and estuarine fishes from the species pool of those systems (Burns *et al.*, 2006).

The incidence of non-native species is negatively related with local species richness, and that might be relevant since invasive species are a major cause of local extinctions (Rocha *et al.*, 2014). The recently reported occurrence of the exotic common carp *Cyprinus carpio* L. 1758 in the World Reserve of Biosphere, Mar Chiquita lagoon (ID347, González Castro *et al.*, 2015), for instance, is considered as a major threat to local biodiversity. The frequency in which species are introduced to coastal lagoons, as well as the type and identity of the species, seem to be more related to the particular way a lagoon is mostly frequently used by the local population (basically, for fishing purposes). Ecologically dubious initiatives of the Brazilian Government aimed at an enhancement of fisheries production in the relatively poor freshwater bodies in north-eastern Brazil, for example, resulted in the introduction of several exotic species, including the peacock bass *Cichla ocellaris* Bloch & Schneider 1801, originally from the Amazon basin, and the Nile tilapia *Oreochromis niloticus* (L. 1758). In fact, a reduction in fish species richness of the coastal lagoons can be linked to the introduction of *C. ocellaris*, at least in ID326 (Menezes *et al.*, 2012). Interestingly, the number of invasive species is lower in lagoons south to FEOW ID326 (north-eastern Brazil). It is possible that the naturally higher species richness of those lagoons prevent the dispersal or establishment of invasive species. It is also possible that species introduced in the northern portion of Brazil, which are mostly of African and Asiatic origins, are less able to cope with the lower winter temperatures in the subtropical systems of FEOWs IDs335 to 347.

The natural conditions of the eastern coast of South America have been drastically modified by anthropogenic activities, especially in the last decades. As a consequence, the future of all lagoons in eastern South America, not only those included in this study, is highly uncertain. Results presented here indicate that coastal lagoons are peculiar ecotones that harbour a unique combination of species. Therefore, those ecosystems should be explicitly included in future strategies aimed at the conservation of fish diversity in the neotropical region.

Supporting Information

Supporting Information may be found in the online version of this paper:

FIG. S1. Relationships between attributes of morphometry of the 103 coastal lagoons across the nine freshwater ecoregions (FEOW) included in this study.

TABLE S1. The 103 coastal lagoons included in this study and respective freshwater ecoregions (FEOW), geographic position, ordinal scores of connection with sea (0; 0·5; 1) and sampling effort (1−4).

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APPENDIX Species of fishes recorded in the lagoons included in this study (x)

	E	I	Division	325	326	328	329	352	335	334	345	347
Chimaeriformes												
Callorhinchidae												
Callorhinchus callorynchus (L. 1758)			M									x
Carcharhiniformes												
Triakidae												
Mustelus schmitti Springer 1939			M									x
Squatiniformes												
Squatinidae												
Squatina guggenheim Marini 1936			M									x
Torpediniformes												
Torpedinidae												
Tetronarce puelcha (Lahille 1926)			M									x
Myliobatiformes												
Myliobatidae												
Myliobatis goodei Garman 1885			M									x
Myliobatis ridens Ruocco, Lucifora, Díaz de Astarloa, Mabragaña & Delpiani 2012			M									x
Elopiformes												
Elopidae												
Elops cf. *smithi* McBride, Rocha, Ruiz-Carus & Bowen 2010			M				x	x	x	x		
Albuliformes												
Albulidae												
Albula cf. *vulpes* (L. 1758)			M							x		

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
Anguilliformes												
Ophichthidae												
Myrophis punctatus Lütken 1852			M					x				
Ophichthus cylindroideus (Ranzani 1839)			M					x				
Clupeiformes												
Clupeidae												
Brevoortia aurea (Spix & Agassiz 1829)			M							x		x
Brevoortia pectinata (Jenyns 1842)			M						x	x		
Harengula clupeola (Cuvier 1829)			M				x	x		x		
Lile piquitinga (Schreiner & Miranda Ribeiro 1903)			M				x	x		x		
Platanichthys platana (Regan 1917)			M				x	x	x	x		x
Rannogaster sp.			M							x		x
Sardinella cf. *aurita* Valenciennes 1847			M							x		x
Engraulidae												
Anchoa januaria (Steindachner 1879)			M				x					
Anchoa marinii Hildebrand 1943			M				x	x		x		x
Anchoa spinifer (Valenciennes 1848)			M				x					
Anchoa tricolor (Spix & Agassiz 1829)			M				x					
Anchovia clupeoides (Swainson 1839)			M				x	x				
Anchoviella lepidentostole (Fowler 1911)			M	x			x					
Cetengraulis edentulus (Cuvier 1829)			M				x	x				
Lycengraulis grossidens (Spix & Agassiz 1829)			M				x	x	x	x		x
Cypriniformes												
Cyprinidae												
Cyprinus carpio L. 1758		1	S						x	x		x

Appendix Continued

	E	I	Division	FEOW ID								
				325	326	328	329	352	335	334	345	347
Characiformes												
Acestrorhynchidae												
Acestrorhynchus pantaneiro Menezes 1992	1		P						x			
Anostomidae												
Leporinus obtusidens (Valenciennes 1837)		1	P						x	x		
Leporinus piau Fowler 1941			P		x							
Crenuchidae												
Characidium rachovii Regan 1913			P							x	x	
Characidium tenue (Cope 1894)			P							x		
Characidium aff. *zebra* Eigenmann 1909			P						x			
Characidae												
Astyanax aff. *bimaculatus* (L. 1758)			P	x	x							
Astyanax eigenmanniorum (Cope 1894)			P				x	x	x	x	x	
Astyanax aff. *fasciatus* (Cuvier 1819)			P						x	x		x
Astyanax henseli de Melo & Buckup 2006			P							x		
Astyanax jacuhiensis (Cope 1894)			P						x	x		
Astyanax janeiroensis Eigenmann 1908			P			x						
Astyanax aff. *lacustris* (Lütken 1875)			P			x						
Astyanax aff. *taeniatus* (Jenyns 1842)			P			x						
Astyanax sp. 1*			P						x			
Bryconamericus iheringii (Boulenger 1887)			P							x		x
Charax stenopterus (Cope 1894)			P						x	x	x	
Cheirodon ibicuhiensis Eigenmann 1915			P						x	x		
Cheirodon interruptus (Jenyns 1842)			P						x	x	x	x
Cyanocharax alburnus (Hensel 1870)			P						x	x	x	
Diapoma terofali (Géry 1964)			P							x	x	

Appendix Continued

	E	I	Division	FEOW ID								
				325	326	328	329	352	335	334	345	347
Hemigrammus aff. *marginatus* Ellis 1911			P		x							
Heterocheirodon yatai (Casciotta, Miquelarena & Protogino 1992)			P							x		x
Hyphessobrycon anisitsi (Eigenmann 1907)			P							x		
Hyphessobrycon bifasciatus Ellis 1911			P			x	x	x				
Hyphessobrycon boulengeri (Eigenmann 1907)			P			x	x	x	x	x		
Hyphessobrycon igneus Miquelarena, Menni, López & Casciotta 1980			P						x	x		
Hyphessobrycon luetkenii (Boulenger 1887)			P				x	x	x	x	x	
Hyphessobrycon meridionalis Ringuelet, Miquelarena & Menni 1978			P					x	x	x	x	
Hyphessobrycon togoi Miquelarena & López 2006			P						x			
Hyphessobrycon aff. *parvellus* Ellis 1911			P	x								
Hyphessobrycon sp. 1*			P			x						
Macropsobrycon uruguayanae Eigenmann 1915			P							x		
Mimagoniates inequalis (Eigenmann 1911)			P						x	x		
Mimagoniates microlepis (Steindachner 1877)			P						x			
Oligosarcus acutirostris Menezes 1987			P			x						
Oligosarcus hepsetus (Cuvier 1829)			P				x	x				
Oligosarcus jenynsii (Günther 1864)			P						x	x	x	
Oligosarcus robustus Menezes 1969			P						x	x		
Psellogrammus kennedyi (Eigenmann 1903)			P	x							x	x
Pseudocorynopoma doriae Perugia 1891			P						x	x		

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
Roeboides sazimai Lucena 2007			P	x								
Serrapinnus heterodon (Eigenmann 1915)			P	x								
Serrapinnus piaba (Lütken 1875)			P	x								
Curimatidae												
Curimata macrops Eigenmann & Eigenmann 1889			P	x								
Cyphocharax gilbert (Quoy & Gaimard 1824)			P			x	x					
Cyphocharax saladensis (Meinken 1933)			P						x	x		
Cyphocharax voga (Hensel 1870)			P						x	x	x	
Steindachnerina biornata (Braga & Azpelicueta 1987)			P						x	x		x
Steindachnerina notonota (Miranda Ribeiro 1937)			P	x								
Erythrinidae												
Hoplerythrinus unitaeniatus (Spix & Agassiz 1829)			P	x		x	x	x				
Hoplias aff. *malabaricus* (Bloch 1794)			P	x	x	x	x	x	x	x	x	x
Prochilodontidae												
Prochilodus brevis Steindachner 1875			P		x							
Prochilodus vimboides Kner 1859			P			x						
Serrasalmidae												
Metynnis lippincottianus (Cope 1870)		1	P		x		x					
Pygocentrus nattereri Kner 1858			P	x								
Siluriformes												
Ariidae												
Genidens barbus (Lacepède 1803)			M						x	x		
Genidens genidens (Cuvier 1829)			M			x	x	x	x	x		

FEOW ID

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
								FEOW ID				
Aspredinidae												
Pseudobunocephalus iheringii (Boulenger 1891)			P							x		
Auchenipteridae												
Trachelyopterus galeatus (L. 1766)			P	x								
Trachelyopterus lucenai Bertoletti, Pezzi da Silva & Pereira 1995		1	P						x	x		
Trachelyopterus striatulus (Steindachner 1877)			P			x		x				
Callichthyidae												
Callichthys callichthys (L. 1758)			P				x	x	x	x		
Corydoras paleatus (Jenyns 1842)			P				x	x	x	x	x	
Hoplosternum littorale (Hancock 1828)			P				x	x	x	x		
Megalechis thoracata (Valenciennes 1840)			P		x							
Clariidae												
Clarias gariepinus (Burchell 1822)		1	P			x						
Heptapteridae												
Acentronichthys sp.			P				x					
Heptapterus mustelinus (Valenciennes 1835)			P							x		
Heptapterus sympterygium Buckup 1988			P							x		
Pimelodella australis Eigenmann 1917			P						x	x	x	
Pimelodella laticeps Eigenmann 1917			P									x
Rhamdia aff. *quelen* (Quoy & Gaimard 1824)			P			x	x	x	x	x	x	x
Loricariidae												
Ancistrus multispinis (Regan 1912)			P						x			
Hisonotus leucofrenatus (Miranda Ribeiro 1908)			P						x			
Hisonotus maculipinnis (Regan 1912)			P								x	

Appendix Continued

	E	I	Division	FEOW ID								
				325	326	328	329	352	335	334	345	347
Hisonotus nigricauda (Boulenger 1891)			P							x		
Hisonotus taimensis (Buckup 1981)	1		P							x		
Hypostomus commersoni Valenciennes 1836			P						x	x	x	
Loricariichthys anus (Valenciennes 1835)			P						x	x		
Otothyris lophophanes (Eigenmann & Eigenmann 1889)	1		P			x						
Rineloricaria cadeae (Hensel 1868)	1		P							x		
Rineloricaria longicauda Reis 1983	1		P							x		
Rineloricaria microlepidogaster (Regan 1904)			P							x		
Rineloricaria quadrensis Reis 1983	1		P						x			
Rineloricaria strigilata (Hensel 1868)	1		P							x		
Pimelodidae												
Parapimelodus nigribarbis (Boulenger 1889)			P							x		
Parapimelodus valenciennis (Lütken 1874)			P							x	x	
Pimelodus maculatus Lacepède 1803		1	P							x		
Pimelodus pintado Azpelicueta, Lundberg & Loureiro 2008	1		P							x		
Pseudopimelodidae												
Microglanis cibelae Malabarba & Mahler 1998	1		P						x			
Microglanis cottoides (Boulenger 1891)			P							x	x	
Trichomycteridae												
Homodiaetus anisitsi Eigenmann & Ward 1907			P						x	x		
Gymnotiformes												
Gymnotidae												
Gymnotus aff. *carapo* L. 1758			P				x		x	x		

Appendix Continued

	E	I	Division	FEOW ID								
				325	326	328	329	352	335	334	345	347
Gymnotus omarorum Richer-de-Forges, Crampton & Albert 2009			P							x		
Hypopomidae												
Brachyhypopomus janeiroensis (Costa & Campos-da-Paz 1992)	1		P				x					
Sternopygidae												
Eigenmannia trilineata López & Castello 1966		1	P									
Eigenmannia aff. *virescens* (Valenciennes 1836)			P			x			x	x		
Gadiformes												
Phycidae												
Urophycis brasiliensis (Kaup 1858)			M					x		x		x
Batrachoidiformes												
Batrachoididae												
Porichthys porosissimus (Cuvier 1829)			M						x	x		x
Mugiliformes												
Mugilidae												
Mugil curema Valenciennes 1836			M		x		x	x	x	x		x
Mugil hospes Jordan & Culver 1895			M							x		
Mugil liza Valenciennes 1836			M				x	x	x	x		x
Synbranchiformes												
Synbranchidae												
Synbranchus aff. *marmoratus* Bloch 1795			S			x		x	x	x	x	
Gasterosteiformes												
Syngnathidae												
Hippocampus sp.			M							x		

Appendix Continued

					FEOW ID							
	E	I	Division	325	326	328	329	352	335	334	345	347
Microphis lineatus (Kaup 1856)			M		x	x	x	x				
Pseudophallus mindii (Meek & Hildebrand 1923)			M				x	x				
Syngnathus folletti Herald 1942			M							x		x
Atheriniformes												
Atherinopsidae												
Atherinella brasiliensis (Quoy & Gaimard 1825)			M			x	x	x	x	x		
Odontesthes argentinensis (Valenciennes 1835)			M						x	x		x
Odontesthes bicudo Malabarba & Dyer 2002	1		M						x			
Odontesthes bonariensis (Valenciennes 1835)			M						x	x		x
Odontesthes humensis de Buen 1953			M							x		
Odontesthes incisa (Jenyns 1841)			M									x
Odontesthes ledae Malabarba & Dyer 2002	1		M						x			
Odontesthes mirinensis Bemvenuti 1996	1		M							x		
Odontesthes perugiae Evermann & Kendall 1906			M							x		
Odontesthes piquava Malabarba & Dyer 2002	1		M						x			
Odontesthes platensis (Berg 1895)			M									x
Odontesthes retropinnis (de Buen 1953)			M							x		
Odontesthes smitti (Lahille 1929)			M									x
Beloniformes												
Belonidae												
Strongylura marina (Walbaum 1792)			M				x	x				
Strongylura timucu (Walbaum 1792)			M				x	x				

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
								FEOW ID				
Hemiramphidae												
Hemiramphus brasiliensis (L. 1758)			M				x					
Hyporhamphus roberti (Valenciennes 1847)			M				x					
Hyporhamphus unifasciatus (Ranzani 1841)			M					x	x			
Cyprinodontiformes												
Anablepidae												
Jenynsia multidentata (Jenyns 1842)			S				x	x	x	x		x
Poeciliidae												
Cnesterodon decemmaculatus (Jenyns 1842)			S							x	x	x
Phalloceros caudimaculatus (Hensel 1868)			S						x	x	x	
Phalloceros harpagos Lucinda 2008			S				x	x				
Phalloptychus januarius (Hensel 1868)		1	S				x			x		
Poecilia reticulata Peters 1859			S					x				
Poecilia vivipara Bloch & Schneider 1801			S		x	x	x	x				
Rivulidae												
Atlantirivulus jurubatibensis (Costa 2008)	1		S				x					
Cynopoecilus melanotaenia (Regan 1912)			S						x	x		
Carangiformes												
Carangidae												
Caranx bartholomaei Cuvier 1833			M				x	x				
Caranx crysos (Mitchill 1815)			M							x		
Caranx hippos (L. 1766)			M				x	x		x		
Caranx latus Agassiz 1831			M		x		x	x				
Chloroscombrus chrysurus (L. 1766)			M				x			x		
Hemicaranx amblyrhynchus (Cuvier 1833)			M				x			x		
Oligoplites palometa (Cuvier 1832)			M	x	x							

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
								FEOW ID				
Oligoplites saliens (Bloch 1793)			M							x		
Oligoplites saurus (Bloch & Schneider 1801)			M					x				
Parona signata (Jenyns 1841)			M									x
Pseudocaranx dentex (Bloch & Schneider 1801)			M				x					
Selene vomer (L. 1758)			M				x			x		x
Trachinotus carolinus (L. 1766)			M				x	x	x	x		x
Trachinotus falcatus (L. 1758)			M				x	x				
Trachinotus marginatus Cuvier 1832			M							x		x
Trachurus lathami Nichols 1920			M									x
Uraspis secunda (Poey 1860)			M							x		
Dactylopteriformes												
Dactylopteridae												
Dactylopterus volitans (L. 1758)			M							x		
Triglidae												
Prionotus punctatus (Bloch 1793)			M				x	x		x		
Gobiiformes												
Eleotridae												
Dormitator maculatus (Bloch 1792)			M		x	x				x		
Eleotris pisonis (Gmelin 1789)			M		x	x		x		x		
Gobiidae												
Awaous tajasica (Lichtenstein 1822)			M		x		x	x	x	x		
Bathygobius soporator (Valenciennes 1837)			M		x		x	x				
Ctenogobius boleosoma (Jordan & Gilbert 1882)			M				x	x				

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
Ctenogobius shufeldti (Jordan & Eigenmann 1887)			M									x
Ctenogobius stigmaticus (Poey 1860)			M					x				
Evorthodus lyricus (Girard 1858)			M					x				
Gobionellus oceanicus (Pallas 1770)			M				x	x		x		
Gobionellus stomatus Starks 1913			M		x							
Gobiosoma parri Ginsburg 1933			M									x
Labriformes												
Blenniidae												
Hypleurochilus fissicornis (Quoy & Gaimard 1824)			M									x
Cichlidae												
Astronotus ocellatus (Agassiz 1831)		1	S		x							
Australoheros cf. *macaensis* Ottoni & Costa 2008			S				x	x				
Australoheros facetus (Jenyns 1842)			S						x	x	x	x
Australoheros muriae Ottoni & Costa 2008			S			x						
Cichla ocellaris Bloch & Schneider 1801		1	S		x							
Cichla pinima Kullander & Ferreira 2006		1	S			x						
Cichlasoma orientale Kullander 1983			S	x								
Cichlasoma portalegrense (Hensel 1870)			S		x							
Coptodon rendalli (Boulenger 1897)		1	S			x	x	x	x	x		
Crenicichla lepidota Heckel 1840			S						x	x		
Crenicichla maculata Kullander & Lucena 2006	1		S						x			
Crenicichla menezesi Ploeg 1991			S	x	x							

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
								FEOW ID				
Crenicichla punctata Hensel 1870	1		S							x		
Crenicichla scottii (Eigenmann 1907)			S							x		
Geophagus brasiliensis (Quoy & Gaimard 1824)			S		x	x	x	x	x	x		
Geophagus parnaibae Staeck & Schindler 2006			S	x								
Gymnogeophagus gymnogenys (Hensel 1870)			S						x	x		
Gymnogeophagus lacustris Reis & Malabarba 1988	1		S						x			
Gymnogeophagus meridionalis Reis & Malabarba 1988			S							x		
Gymnogeophagus rhabdotus (Hensel 1870)			S						x	x		
Gymnogeophagus sp. 1*			S							x	x	
Oreochromis niloticus (L. 1758)		1	S	x	x							
Pomacentridae												
Abudefduf saxatilis (L. 1758)			M					x				
"Perciformes"												
Centropomidae												
Centropomus parallelus Poey 1860			M				x	x	x	x		
Centropomus undecimalis (Bloch 1792)			M	x		x	x	x				
Eleginopsidae												
Eleginops maclovinus (Cuvier 1830)			M									x
Gerreidae												
Diapterus auratus Ranzani 1842			M				x	x				
Diapterus rhombeus (Cuvier 1829)			M				x	x		x		
Eucinostomus argenteus Baird & Girard 1855			M				x	x	x	x		

Appendix Continued

	E	I	Division	FEOW ID								
				325	326	328	329	352	335	334	345	347
Eucinostomus gula (Quoy & Gaimard 1824)			M					x		x		
Eucinostomus lefroyi (Goode 1874)			M				x	x		x		
Eucinostomus melanopterus (Bleeker 1863)			M	x				x	x	x		
Eugerres brasilianus (Cuvier 1830)			M			x	x	x				
Haemulidae												
Conodon nobilis (L. 1758)			M				x	x				
Pomadasys crocro (Cuvier 1830)			M				x	x				
Lutjanidae												
Lutjanus alexandrei Moura & Lindeman 2007			M		x							
Lutjanus jocu (Bloch & Schneider 1801)			M					x				
Percophidae												
Percophis brasiliensis Quoy & Gaimard 1825			M							x		
Polynemidae												
Polydactylus oligodon (Günther 1860)			M					x				
Polydactylus virginicus (L. 1758)			M				x	x				
Pomatomidae												
Pomatomus saltatrix (L. 1766)			M					x	x	x		x
Sciaenidae												
Cynoscion guatucupa (Cuvier 1830)			M							x		x
Macrodon ancylodon (Bloch & Schneider 1801)			M						x			x
Menticirrhus americanus (L. 1758)			M							x		x
Menticirrhus littoralis (Holbrook 1847)			M						x	x		
Micropogonias furnieri (Desmarest 1823)			M				x	x	x	x		x
Pachyurus bonariensis Steindachner 1879			M					x	x	x		x

Appendix Continued

	E	I	Division	325	326	328	329	352	335	334	345	347
Paralonchurus brasiliensis (Steindachner 1875)			M									x
Pogonias cromis (L. 1766)			M							x		x
Stellifer brasiliensis (Schultz 1945)			M					x	x	x		
Umbrina canosai Berg 1895			M									x
Serranidae												
Diplectrum radiale (Quoy & Gaimard 1824)			M							x		x
Dules auriga Cuvier 1829			M							x		x
Epinephelus marginatus (Lowe 1834)			M							x		
Mycteroperca acutirostris (Valenciennes 1828)			M							x		
Sparidae												
Archosargus probatocephalus (Walbaum 1792)			M					x				
Diplodus argenteus (Valenciennes 1830)			M							x		
Stromateidae												
Peprilus paru (L. 1758)			M							x		
Stromateus brasiliensis Fowler 1906			M							x		x
Trichiuridae												
Trichiurus lepturus L. 1758			M							x		
Pleuronectiformes												
Achiridae												
Achirus lineatus (L. 1758)			M					x				
Trinectes microphthalmus (Chabanaud 1928)			M				x	x				
Trinectes paulistanus (Miranda Ribeiro 1915)			M			x	x	x				
Cynoglossidae												
Symphurus jenynsi Evermann & Kendall 1906			M									x
Symphurus plagusia (Bloch & Schneider 1801)			M							x		

Appendix Continued

Species	E	I	Division	325	326	328	329	352	335	334	345	347
Symphurus trewavasae Chabanaud 1948			M									x
Paralichthyidae												
Citharichthys arenaceus Evermann & Marsh 1900			M				x	x				
Citharichthys macrops Dresel 1885			M									
Citharichthys spilopterus Günther 1862			M					x	x	x		
Paralichthys brasiliensis (Ranzani 1842)			M					x				
Paralichthys orbignyanus (Valenciennes 1839)			M					x		x		x
Paralichthys patagonicus Jordan 1889			M									x
Syacium micrurum Ranzani 1842			M		x							
Rhombosoleidae												
Oncopterus darwinii Steindachner 1874			M							x		x
Tetraodontiformes												
Diodontidae												
Chilomycterus spinosus (L. 1758)			M					x		x		
Monacanthidae												
Stephanolepis hispidus (L. 1766)			M				x			x		
Tetraodontidae												
Lagocephalus laevigatus (L. 1766)			M					x		x		
Sphoeroides pachygaster (Müller & Troschel 1848)			M				x	x				
Sphoeroides testudineus (L. 1758)			M	x	x		x	x				

FEOW, freshwater ecoregions; E, species endemic to a particular ecoregion; I, introduced species (natural distribution does not include the ecoregion where the species was recorded). Zoogeographic origin of species indicated according to the classification of families into M, peripheral or marine; S, secondary division; P, primary division (proposed by Myers, 1938).
*Undescribed species.