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Biogeographic patterns of the freshwater fishes from the state of Espírito Santo, eastern Brazil

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ABSTRACT

Biogeographic studies offer valuable insights into the origin, distribution and extinction of biodiversity. As such, this study aims to identify patterns of diversity and distribution of freshwater ichthyofauna in the state of Espírito Santo, to delineate biogeographic units and to propose a hypothesis of area relationship. A database containing information on 123 fish species occurrences was compiled to conduct analyses of species richness interpolation, bioregionalization, sampling effort interpolation, endemism, and a parsimony analysis of endemism. The sampling effort in Espírito Santo is uneven, with higher representativeness of sampling sites in the highlands. Six freshwater ichthyofauna bioregions were identified, along with three major areas of increased species richness, two consensus areas of endemism and three groups of basins. The central basins of the state are characterized by a marked presence of endemic species. The southern basins also stand out as an area of endemism and density of species typical of mountainous environments, such as loricariids; they are also characterized by a significant faunal overlap with the Rio Paraíba do Sul basin. The results of this biogeographic evaluation reinforce the perception that the watersheds of the state of Espírito Santo have a diverse and characteristic freshwater fish fauna, with well-defined biogeographic units.

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Introduction

The Neotropical region figures as the most species-rich continental biogeographic unit on the planet, boasting an estimated 9,000 species of freshwater fishes, more than 5,700 formally described (Reis et al. 2003, 2016; Lévêque et al. 2008; Albert & Reis 2011; Albert et al. 2011). Brazil on its own has more than 3,500 described species (Reis et al. 2020; Froese & Pauly 2023). However, knowledge of biodiversity remains incomplete, particularly in the tropics (evidencing the Linnean and Wallacean shortfalls) (Lomolino et al. 2004; Whittaker et al. 2005; Bini et al. 2006). Though species are constantly being described in recent years, much remains unknown regarding their distributions, which are not always evident, hindering the comprehension of processes leading to speciation, dispersal, and extinction. Biogeographic studies provide valuable tools for comprehending the historical origins of this vast biodiversity (Albert et al. 2011).

The Atlantic Forest is one of the richest ecosystems on the planet, a hotspot for species conservation (Myers et al. 2000). The state of Espírito Santo, located within this biome, contains forested land and water resources, primarily in the mountainous regions of the central and southern state (Sarmento-Soares & Martins-Pinheiro 2014a; Silva et al. 2015). River basins in Espírito Santo support an unique freshwater ichthyofauna, including endemic and threatened species (ICMBio/MMA 2018; Hostim-Silva et al. 2019). The fish fauna has been the subject of several studies in the last fourteen years (e.g. Sarmento-Soares & Martins-Pinheiro 2010, 2012, 2013, 2014a, 2014b, 2017; Sarmento-Soares et al. 2012, 2017, 2018, 2022a, 2022b; Roldi et al. 2014; Silva et al. 2015; Guimarães et al. 2022), leading to the creation of a species database in museums and university collections.

This article focuses on the biogeographic and diversity patterns of the ichthyofauna and the spatial relationships of the drainages in the state of Espírito Santo. However, since the range of some basins (namely Riacho Doce, Rio São Mateus, Rio Doce and Rio Itabapoana) exceeds the state boundaries, we also

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present species records from these outer areas. For a biogeographic study of the entire Rio Doce basin, see Sarmento-Soares et al. (2022a). A previous biogeographic assessment by Camelier and Zanata (2014) examined the major rivers of the Northeastern Mata Atlantica Freshwater ecoregion, but only considered four drainages in our study area, Rio Itaúnas, Rio São Mateus, Rio Doce, and Rio Itapemirim. Therefore, the analyses conducted here explores basins that have not yet undergone biogeographic evaluation and postulates a hypothesis of area relationship among them.

Material and methods

Study area

The study area includes fourteen river basins and their adjacent micro-basins in the state of Espírito Santo, each with different dimensions (Figure 1). From north to south: 1. Rio Itaúnas plus Riacho Doce; 2. Middle and Lower Rio São Mateus; 3. Rio Barra Seca; 4. Rio Doce; 5. Rio Riacho; 6. Rio Piraquê-Açu plus Northern and Southern Aracruz microbasins; 7. Rio Reis Magos plus Serra microbasins; 8. Rio Santa Maria da Vitória; 9. Rio Jucu; 10. Guarapari plus Vila Velha, Caraís Pond and Guarapari-Anchieta microbasins; 11. Rio Benevente; 12. Rio Novo plus Iconha microbasins; 13. Rio Itapemirim; and 14. Rio Itabapoana plus Marataízes and Presidente Kennedy microbasins. The entire study area is included in the Northeastern Mata Atlantica Freshwater ecoregion (NMAF, sensu Abell et al. 2008).

The northern forest domain corresponds to the coastal tablelands of the Barreiras group (Braun & Ramalho 1980; Sarmento-Soares & Martins-Pinheiro 2020), with mild relief and rivers flowing with slow to moderate current, riverbeds composed mainly of sand or silt, a predominance of dark tea-colored water, and warm temperatures (Sarmento-Soares et al. 2009; Sarmento-Soares & Martins-Pinheiro 2014b). In the south, mountain rivers flow strongly downstream, the main riverbed has many rocks and pebbles, and the water is clear at cold temperatures. The complexity of the freshwater habitats on the slopes allows the survival of a distinctive diversity of small-sized fishes living in specific areas. The natural vegetation is composed of the Atlantic Forest, adjacent pioneer formations such as the coastal sand formations, mangroves and coastal flooded camps (Rizzini 1979; Coimbra Filho & Câmara 1996). There are some differences in the Atlantic Forest

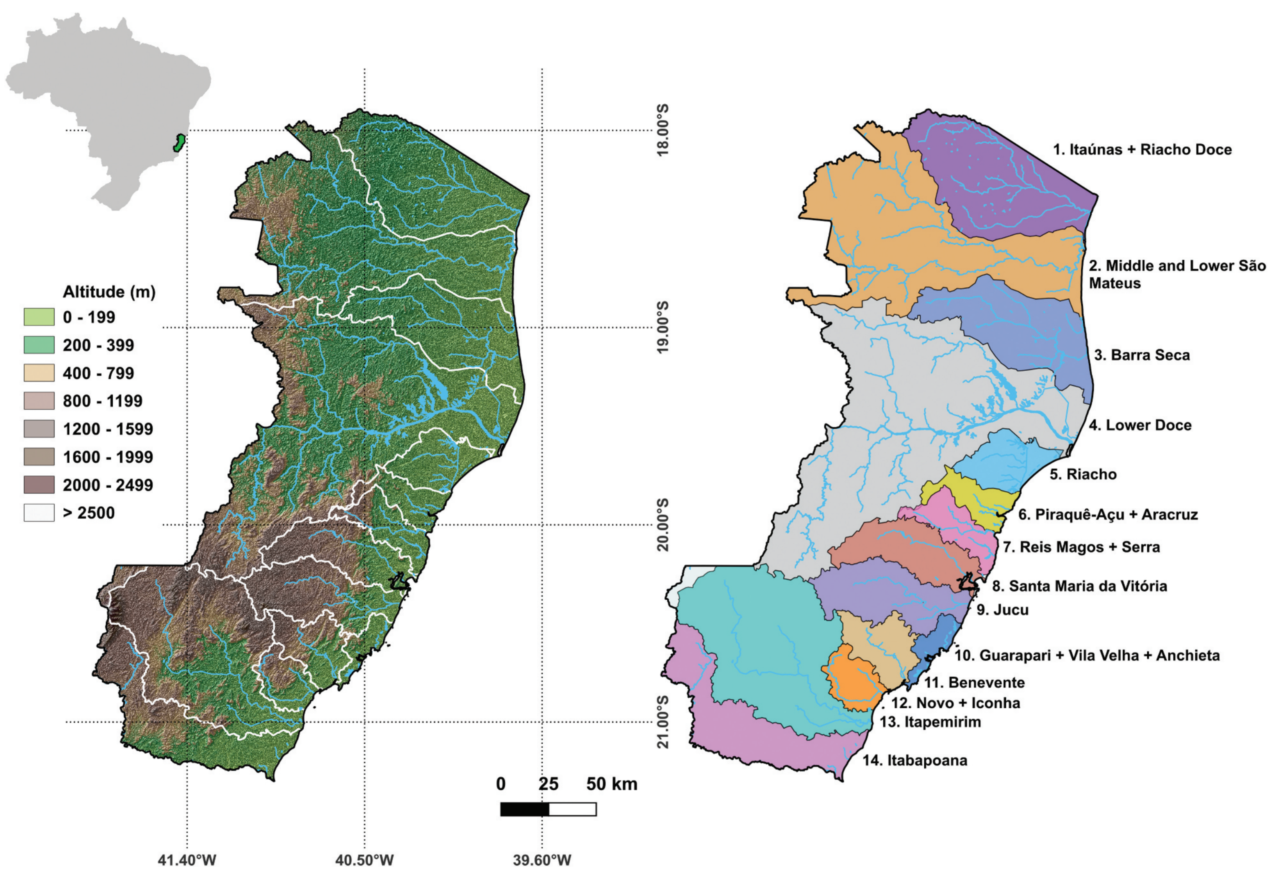

Figure 1. Hypsometric map of the state of Espírito Santo, highlighting the hydrographic basins considered in this study.

formations along the area. In the north, the dense ombrophilous forest predominates, while the south is dominated by the mixed ombrophilous forest.

This area includes the highest elevations of the Atlantic Forest biome, such as Pico da Bandeira at 2,891 m, located on the slopes of the Caparaó Mountains in the southern state (Novo et al. 2011), and is inhabited by species adapted to torrential water environments (Sarmento-Soares & Martins-Pinheiro 2014a). The contrasting relief along the study area is reflected in its biodiversity, with different sets of endemic species between the south and the north. In the northern lowlands, a remarkable group of species inhabits the slow-flowing stream environments, in aquatic environments characteristic of coastal tableland forests (Sarmento-Soares & Martins-Pinheiro 2012).

Data compilation

We compiled records of 123 freshwater fish species (Table 1) deposited in 20 fish collections. Detailed data collection was carried out in the fish collections of MBML, MCNIP, MNRJ, MZUEL, and MZFS. In addition, records available in online databases and obtained on request from the curators of the following collections were consulted: ANSP, CZNC, FMNH, LIRP, MCP, MCZ, MZUSP, NPM, NUP, UFBA, UFRGS, UFRJ, UMMZ, UNT, and ZUEC. Institutional acronyms are available in Sabaj (2020). All records consulted here, including additional estuarine and marine species, are listed in Supplementary Material S1. Species names in these collections were approximated by using the species names available in each area. For analysis purposes, only 3,258 records with non-duplicate geographic coordinates for each species (to avoid pseudoreplication) were considered for freshwater species within the state of Espírito Santo.

We conducted fieldwork at sites visited either for the first time or as additional sampling at a historic site over a fourteen-year period, between 2004 and 2018. Standardized fieldwork was conducted using nets and hand trawls. A combination of fishing gear types was used to ensure sampling in a wide range of habitats, covering a distance of approximately 50 m and upstream where possible. Specimens were euthanized with menthol, fixed in 10% formalin and transported to the laboratory of the Instituto Nossos Riachos, and later transferred to the MBML and MNRJ collections. Taxonomic classification follows Fricke et al. (2023).

Interpolation of sampling effort

The importance of an adequate and consistent sampling effort for the detection of distribution and diversity patterns is obvious. Therefore, the density of samples in the study area was assessed by interpolating the occurrence points to generate a sampling effort map, performed in the BioDinamica library (Oliveira et al. 2019) of the Dinamica-EGO software (Soares-Filho et al. 2002). The following parameters were used: density analysis search radius = 25 km; raster size = 0.03.

Bioregionalization

The bioregionalization of the Espírito Santo ichthyofauna was performed using the Infomap Bioregions algorithm (Edler et al. 2017), which uses species distribution data (including cases of inconsistent sampling effort), an adaptive resolution method that generates a bipartite network of species and grids, and a cluster analysis to generate bioregions based on the presence of specific taxa. The following parameters were used: cell size = 0.5° to 1°; cell capacity = 10 to 100 samples; replications = 99. The remaining settings follow the program defaults.

Spatial patterns of diversity

A species richness interpolation analysis was performed to map diversity patterns in Espírito Santo, using the spline interpolation method, which smooths out potential sampling gaps by creating a continuous surface of data values, in the BioDinamica library (Oliveira et al. 2019) of the Dinamica-EGO software (Soares-Filho et al. 2002). Only records within the state boundaries were considered. The following parameters were used: raster grid size = 0.03, lambda factor = 20, minimum one sample per hexagon, using a delimitation mask of the state of Espírito Santo. The remaining settings follow the program defaults.

Areas of endemism

Endemism analyses highlight areas with congruent species distributions (Szumik et al. 2002; Goloboff 2012; Aagesen et al. 2013; Szumik & Goloboff 2015), using geographic coordinates that are transformed into presence or absence in the grid cells of consensus areas (CAs), where the resulting maps are merged to delineate endemism hotspots. The identification of endemism areas in Espírito Santo was carried out using the NDM/VNDM v. 3.1 software (Szumik et al. 2002, 2004). The NDM software calculates endemicity indices (IEs) for each species, which are summed to give an endemicity score for each area/cell on the map presented in the VNDM software. The endemicity

Table 1. Freshwater fishes of the state of Espírito Santo. We present the groups of basins where these species occur, generated by the biogeographic analysis. Species in bold are endemic to the basins of the study area. PAE = parsimony analysis of endemism.

	PAE GROUPS		
ORDER/Family/*Species*	Northern ES	Central ES	Southern ES
CHARACIFORMES			
Anostomidae			
Hypomasticus copelandii (Steindachner, 1875)	X	X	X
Hypomasticus mormyrops (Steindachner, 1875)	X		X
Hypomasticus steindachneri (Eigenmann, 1907)	X		X
Megaleporinus conirostris (Steindachner, 1875)	X	X	X
Bryconidae			
Brycon dulcis Lima & Vieira, 2017	X	X	
Brycon ferox Steindachner, 1877	X		
Brycon insignis Steindachner, 1877			X
Brycon opalinus (Cuvier, 1819)			X
Henochilus wheatlandii Garman, 1890	X		
Characidae			
Cheirodontinae			
Serrapinnus heterodon (Eigenmann, 1915)	X		
Stethaprioninae			
Astyanax microschemos Bertaco & Lucena, 2006		X	X
Astyanax scabripinnis (Jenyns, 1842)	X	X	X
Astyanax sp. aff. *A. lacustris* A	X	X	X
Astyanax sp. aff. *A. lacustris* B	X		
Astyanax sp. aff. *A. microschemos*		X	
Deuterodon giton (Eigenmann, 1908)	X	X	X
Deuterodon hastatus (Myers, 1928)	X	X	
Deuterodon heterostomus (Eigenmann, 1911)			X
Deuterodon intermedius (Eigenmann, 1908)	X	X	X
Deuterodon janeiroensis (Eigenmann, 1908)	X	X	X
Deuterodon sazimai (Santos & Castro, 2014)	X		X
Deuterodon taeniatus (Jenyns, 1842)	X	X	X
Hyphessobrycon bifasciatus Ellis, 1911	X	X	X
Hyphessobrycon eques (Steindachner, 1882)	X		
Knodus moenkhausii (Eigenmann & Kennedy, 1903)	X	X	X
Moenkhausia vittata (Steindachner, 1877)	X		
Oligosarcus acutirostris Menezes, 1987	X	X	X
Psalidodon fasciatus (Cuvier, 1819)	X	X	X
Psalidodon parahybae (Eigenmann, 1908)		X	X
Rachoviscus graciliceps Weitzman & Cruz, 1981	X		
Stevardiinae			
Mimagoniates microlepis (Steindachner, 1877)	X	X	X
Mimagoniates sylvicola Menezes & Weitzman, 1990	X		
Crenuchidae			
Characidium alipioi Travassos, 1955			X
Characidium cricarense Malanski, Sarmento-Soares, Silva-Malanski, Lopes, Ingenito & Buckup, 2019	X		
Characidium sp. 'caparaó'			X
Characidium timbuiense Travassos, 1946	X	X	X
Characidium vidali Travassos, 1967			X
Curimatidae			
Cyphocharax gilbert (Quoy & Gaimard, 1824)	X	X	X
Erythrinidae			
Erythrinus erythrinus (Bloch & Schneider, 1801)	X		
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	X	X	X
Hoplias intermedius (Günther, 1864)	X		
Hoplias malabaricus (Bloch, 1794)	X	X	X
Prochilodontidae			
Prochilodus harttii Steindachner 1875	X		
Prochilodus vimboides Kner, 1859	X	X	X
SILURIFORMES			
Ariidae			
Paragenidens grandoculis (Steindachner, 1877)	X		
Auchenipteridae			
Glanidium melanopterum Miranda Ribeiro, 1918		X	X
Pseudauchenipterus affinis (Steindachner, 1877)	X		
Trachelyopterus striatulus (Steindachner, 1877)	X	X	X
Callichthyidae			
Callichthys callichthys (Linnaeus, 1758)	X	X	X
Corydoras nattereri Steindachner, 1876	X	X	X
Hoplosternum littorale (Hancock, 1828)	X	X	X
Scleromystax prionotos (Nijssen & Isbrücker, 1980)	X	X	X
Scleromystax virgulatus (Nijssen & Isbrücker, 1980)	X		X

(*Continued*)

Table 1. (Continued).

ORDER/Family/*Species*	PAE GROUPS		
	Northern ES	Central ES	Southern ES
Heptapteridae			
Acentronichthys leptos Eigenmann & Eigenmann, 1889	X		
Imparfinis minutus (Lütken, 1874)	X	X	X
Pimelodella lateristriga (Lichtenstein, 1823)	X	X	X
***Pimelodella* sp. 1 sensu Sibien (2019)**	X	X	
***Pimelodella* sp. 2 sensu Sibien (2019)**	X		X
Pimelodella sp. aff. *P.harttii*		X	
Pimelodella vittata (Lütken, 1874)	X		
Rhamdia sp.	X	X	X
Loricariidae			
Delturinae			
Delturus carinotus (LaMonte, 1933)	X		
Hypoptopomatinae			
Euryochus thysanos Pereira & Reis, 2017	X	X	X
Hisonotus thayeri Martins & Langeani, 2016	X	X	X
Neoplecostomus doceensis Roxo, Silva, Zawadzki & Oliveira, 2014	X		
***Neoplecostomus espiritosantensis* Langeani, 1990**	X	X	
Neoplecostomus microps (Steindachner, 1877)			X
Otothyris lophophanes (Eigenmann & Eigenmann, 1889)			X
Otothyris travassosi Garavello, Britski & Schaefer, 1998	X	X	X
***Pareiorhaphis ruschii* Pereira, Lehmann A. & Reis, 2012**	X	X	X
Parotocinclus doceanus (Miranda Ribeiro, 1918)	X	X	X
Parotocinclus maculicauda (Steindachner, 1877)	X	X	X
Parotocinclus planicauda Garavello & Britski, 2003	X		
Hypostominae			
Ancistrus multispinis (Regan, 1912)			X
Hypostomus affinis (Steindachner, 1877)	X	X	X
Hypostomus auroguttatus Kner, 1854			X
Hypostomus scabriceps (Eigenmann & Eigenmann, 1888)	X		
Hypostomus sp. n. 'teixeirai'	X		
Loricariinae			
Harttia carvalhoi Miranda Ribeiro, 1939	X	X	
Harttia loricariformis Steindachner, 1877	X	X	X
Loricariichthys castaneus (Castelnau, 1855)	X		X
***Loricariichthys melanurus* Reis, Vieira & Pereira, 2021**			X
Rineloricaria steindachneri (Regan, 1904)			X
Rhinelepinae			
Pogonopoma wertheimeri (Steindachner, 1867)	X		X
Pseudopimelodidae			
***Microglanis minutus* Ottoni, Mattos & Barbosa, 2010**	X		
Microglanis parahybae (Steindachner, 1880)	X	X	X
Microglanis pataxo Sarmento-Soares, Martins-Pinheiro, Aranda & Chamon, 2006	X		
Ituglanis cahyensis Sarmento-Soares, Martins-Pinheiro, Aranda & Chamon, 2006	X		
Ituglanis parahybae (Eigenmann, 1918)			X
Trichomycteridae			
***Microcambeva jucuensis* Costa et al. (2019)**		X	
***Microcambeva watu* Medeiros et al. (2021)**	X		
***Trichogenes claviger* de Pinna, Helmer, Britski & Nunes, 2010**			X
Trichomycterus alternatus (Eigenmann, 1917)	X	X	X
Trichomycterus argos Lezama, Triques & Santos, 2012	X		
***Trichomycterus barrocus* Reis & de Pinna, 2022**	X		
***Trichomycterus brunoi* Barbosa & Costa, 2010**			X
***Trichomycterus caudofasciatus* Alencar & Costa, 2004**			X
***Trichomycterus gasparinii* Barbosa, 2013**		X	
Trichomycterus immaculatus (Eigenmann & Eigenmann, 1889)	X		X
Trichomycterus ipatinga Reis & de Pinna, 2022	X		
***Trichomycterus longibarbatus* Costa, 1992**		X	
Trichomycterus melanopygius Reis, Santos, Britto, Volpi & de Pinna, 2020	X		
***Trichomycterus mimosensis* Barbosa, 2013**			X
***Trichomycterus pantherinus* Alencar & Costa, 2004**		X	X
GYMNOTIFORMES			
Gymnotidae			
Gymnotus carapo Linnaeus, 1758	X	X	X
Gymnotus pantherinus (Steindachner, 1908)	X		X
Sternopygidae			
Eigenmannia virescens (Valenciennes, 1836)	X		X
Sternopygus macrurus (Bloch & Schneider, 1801)	X		
CICHLIFORMES			
Cichlidae			
Australoheros ipatinguensis Ottoni & Costa, 2008	X	X	X
Crenicichla lacustris (Castelnau, 1855)	X	X	X
Geophagus brasiliensis (Quoy & Gaymard, 1824)	X	X	X
Geophagus rufomarginatus Mattos & Costa, 2018	X		X

(*Continued*)

Table 1. (Continued).

ORDER/Family/*Species*	PAE GROUPS Northern ES	Central ES	Southern ES
ACANTHURIFORMES			
Sciaenidae			
Pachyurus adspersus Steindachner, 1879	X		
SYNBRANCHIFORMES			
Synbranchidae			
Synbranchus marmoratus Bloch, 1795	X	X	X
CYPRINODONTIFORMES			
Poeciliidae			
***Phalloceros elachistos* Lucinda, 2008**	X	X	X
Phalloceros harpagos Lucinda, 2008			X
Phalloceros ocellatus Lucinda, 2008	X	X	
Poecilia vivipara Bloch & Schneider, 1801	X	X	X
Rivulidae			
***Atlantirivulus nudiventris* (Costa & Brasil, 1991)**			X
Kryptolebias ocellatus (Hensel, 1868)	X		X
***Xenurolebias cricarensis* Costa, 2014**	X		
***Xenurolebias izecksohni* (Da Cruz, 1983)**	X		
***Xenurolebias myersi* (Carvalho, 1971)**	X		

index results from the evaluation of the total distribution of the taxon and the fit of the distribution to the area. This index ranges from 0 to 1, with the maximum value being obtained when the species has a distribution exactly equal to the area of endemism found (Sarmento-Soares et al. 2022a). The following parameters were used: cell size = 0.18°x0.18°, minimum number of endemic species = 2; minimum score for species = 0.5; minimum value of saved sets = 2.0; minimum percentage of unique species retained = 25%; flexible consensus of 10% species similarity; search repeated 100 times. The remaining settings follow the program defaults.

Area relationships

The hypotheses of interrelationships are based on the PAE method – Parsimony Analysis of Endemicity (Rosen 1988), which constructs cladograms of area affinity based on a cladistic analysis of presence-absence data matrices of taxa (Morrone 2009). The character matrix was edited using WinClada (Nixon 2002). The values of presence or absence vary from 0 to 1, where 1 is the presence of a species in this river basin and 0 is its absence. All species with a wide distribution in Espírito Santo (e.g. *Cyphocharax gilbert*, *Geophagus brasiliensis*, *Hoplias malabaricus*, *Rhamdia* sp.) were excluded from this analysis as they would be uninformative, resulting in a matrix of 83 species (Supplementary Material 2).

The PAE was conducted using TNT (Goloboff & Catalano 2016). The parsimony analysis included 14 ingroup taxa (= areas) rooted to an outgroup (a hypothetical area with zero species). A heuristic search was performed with the following parameters: Memory Max trees = 10,000; traditional search with random seed = 0; replications = 100; trees saved per replication = 100; and tree bisection and reconnection (TBR).

Results

Sampling effort

The interpolation of the sampling effort highlighted two areas with the highest density of sampling sites in Espírito Santo: the central mountainous region of the state, including the basins of the Rio Piraquê-Açu, Rio Reis Magos, Rio Santa Maria da Vitória and tributaries of Rio Doce, and the highlands of the south of the state, mainly in the headwaters of Rio Itapemirim (Figure 2). Other well-sampled areas include, to a lesser extent, the drainages of Rio Itaúnas, Rio Barra Seca, Rio Jucu, Rio Benevente, Rio Novo, and some areas of Rio Doce. A portion of the Rio São Mateus basin near the border with the state of Minas Gerais has the lowest sampling coverage in the study area.

Bioregionalization

Six bioregions were delineated in the study area (Figure 3; Table 2). Two areas are of interest: Caparaó Highlands, with an expressive presence of species from the Loricariidae family and the endemic species *Trichogenes claviger*, *Trichomycterus barrocus*, *Trichomycterus brunoi*, and *Trichomycterus caudofasciatus*; and Central Espírito Santo, which concentrates the largest number of species endemic to the state, such as *Neoplecostomus espiritosantensis*, *Trichomycterus*

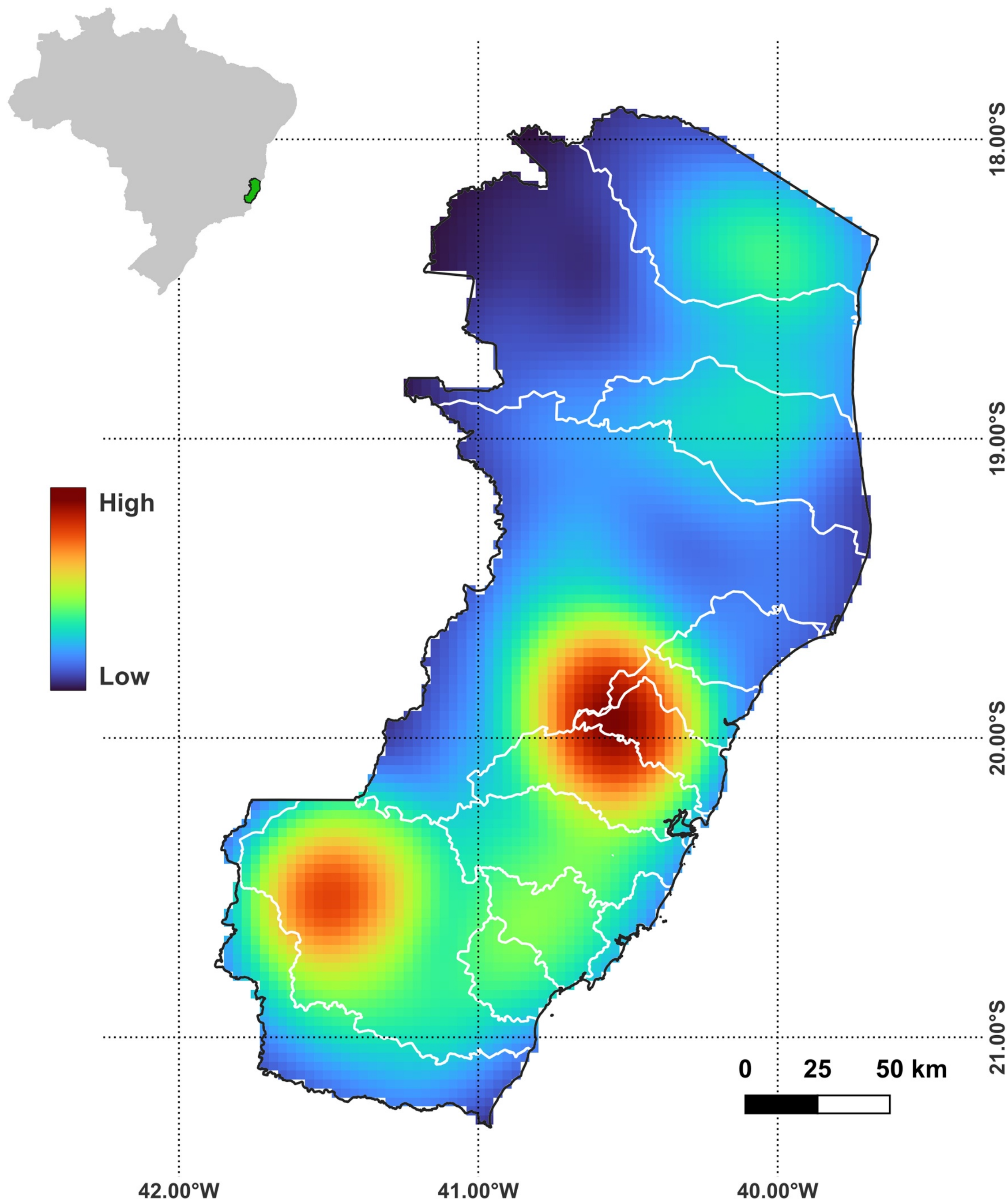

Figure 2. Sampling effort interpolation for the ichthyofauna in the state of Espírito Santo.

longibarbatus, *T. gasparinii*, *Microcambeva jucuensis*, and *M. watu*.

Spatial patterns of diversity

The species richness interpolation revealed two areas with the most significant results for this diversity index: the lower stretches of the Rio Itaúnas, Rio São Mateus and Rio Barra Seca basins, which have a high species richness shared with the southern state of Bahia; and a zone of high richness extending from the central mountainous region of Espírito Santo to the southern basins of the state, including the drainages of the Rio Piraquê-Açu, Rio Reis Magos, Rio Santa Maria da Vitória, Rio Jucu, Rio Benevente, Rio Novo, Rio Itapemirim, Rio Itabapoana and Guarapari micro-basins, as well as the tributaries of the right bank of the Rio Doce (Figure 4). Intermediate values of species richness appear in the main channel of the Rio Doce and in the Rio Riacho basin.

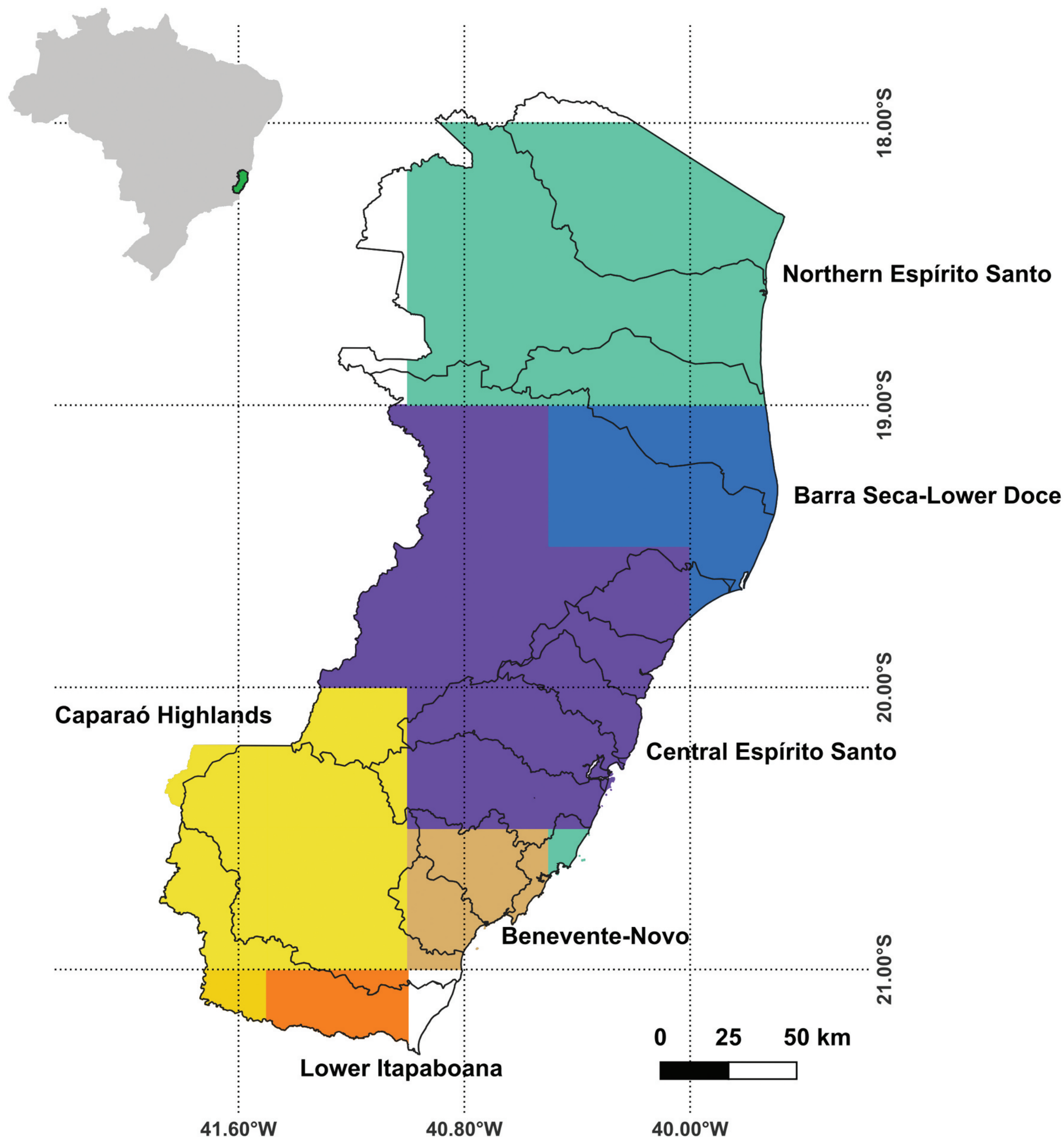

Figure 3. Bioregions of the freshwater ichthyofauna in the state of Espírito Santo.

Areas of endemism

Four areas of endemism were identified in Espírito Santo, grouped into two consensus areas (Figure 5; Table 3): CA0 in the south of the state (IEs = 2.36–2.56), covering the upper stretches of the Itapemirim and Itabapoana river basins, and defined by species such as *Trichomycterus brunoi* and *T. caudofasciatus*; and CA1 in the central region of the state (IE = 2.16), in the basins of the Rio Piraquê-Açu, Rio Reis Magos, Rio Santa Maria da Vitória, Rio Jucu, Rio Benevente and tributaries of the right bank of the Rio Doce, with indicative species such as *Phalloceros elachistos*, *Trichomycterus pantherinus*, and *Neoplecostomus espiritosantensis*.

Area relationships

The PAE presented a hypothesis of area affinity relationships based on the two most parsimonious trees, resulting in a consensus diagram (length: 163 steps, CI = 0.50; RI = 0.58, Figure 6). The consensus tree shows three groups of basins in the study area, hereafter referred to as: Northern ES clade, Central ES clade, and Southern ES clade. Detailed information on the binary matrix and taxa of the terminal groups is available in Supplementary Material 2.

Northern ES clade

The clade is composed of five drainages, from north to south: Rio Itaúnas, Rio São Mateus, Rio Barra Seca, Rio

Table 2. Bioregions of the freshwater ichthyofauna in the state of Espírito Santo. We present the basins for each bioregion, indicative species and their score in the analysis. Species in bold are endemic to basins draining the study area.

Bioregion	Basins	Most indicative species
Northern Espírito Santo	Itaúnas, São Mateus, Barra Seca	*Microglanis pataxo* (4.94) ***Xenurolebias myersi*** (4.94) *Acentronichthys leptos* (4.94) *Rachoviscus graciliceps* (4.94) *Ituglanis cahyensis* (4.94) ***Xenurolebias cricarensis*** (4.94)
Barra Seca-Lower Doce	Barra Seca, Doce, Riacho	*Paragenidens grandoculis* (18.1) *Hoplias intermedius* (18.1) *Henochilus wheatlandii* (18.1) ***Xenurolebias izecksohni*** (18.1) *Brycon dulcis* (12.9) *Erythrinus erythrinus* (12.1)
Central Espírito Santo	Doce, Riacho, Piraquê-Açu, Reis Magos, Santa Maria da Vitória, Jucu	***Trichomycterus longibarbatus*** (2.69) ***Neoplecostomus espiritosantensis*** (2.69) ***Trichomycterus gasparinii*** (2.69) ***Microcambeva jucuensis*** (2.69) ***Microcambeva watu*** (2.69) ***Phalloceros elachistos*** (2.63)
Caparaó Highlands	Itapemirim, Itabapoana, Doce	*Neoplecostomus microps* (3.87) ***Trichomycterus brunoi*** (3.87) *Hypomasticus mormyrops* (3.87) *Hypostomus auroguttatus* (3.87) ***Trichogenes claviger*** (3.87) ***Trichomycterus barrocus*** (3.87)
Benevente-Novo	Benevente, Novo, Guarapari	***Atlantirivulus nudiventris*** (13.7) *Imparfinis minutus* (13.7) *Otothyris lophophanes* (6.85) *Eigenmannia virescens* (5.87) *Characidium vidali* (5.64) *Pimelodella lateristriga* (4.79)
Lower Itabapoana	Itabapoana	***Trichomycterus mimosensis*** (32.9) *Ancistrus multispinis* (32.9) *Phalloceros harpagos* (21.9) *Ituglanis parahybae* (16.5) ***Loricariichthys melanurus*** (16.5) *Eigenmannia virescens* (14.1)

Doce, and Rio Riacho (Table 4). This group is supported by the presence of *Hypostomus scabriceps*, *Otothyris travassosi*, and *Phalloceros ocellatus*. Within the group, Rio Riacho appears as an external clade to the other basins, which are supported by the presence of *Brycon ferox*, *Characidium cricarense*, *Microglanis pataxo*, *Moenkhausia vittata*, *Pimelodella* sp. 2, and *Pogonopoma wertheimeri*. Rio Barra Seca appears as a sister-clade to Rio Itaúnas, supported by the common presence of *Ituglanis cahyensis* and *Erythrinus erythrinus*, and species such as *Euryochus thysanos, Imparfinis minutus*, and *Parotocinclus planicauda* support the close relationship between Rio Doce and Rio São Mateus.

Central ES clade

This clade consists of four basins: Rio Piraquê-Açu, Rio Reis Magos, Rio Santa Maria da Vitória, and Rio Jucu basins, and is supported by the common presence of *Characidium timbuiense*, *Euryochus thysanos*, *Neoplecostomus espiritosantensis*, *Pareiorhaphis ruschii*, *Phalloceros elachistos*, and *Trichomycterus pantherinus*. A subgroup formed by the Rio Piraquê-Açu and Rio Reis Magos basins is supported by *Parotocinclus doceanus*, *Phalloceros ocellatus*, *Trichomycterus alternatus*, and *Trichomycterus longibarbatus*.

Southern ES clade

Formed by five river basins: Guarapari micro-basins, Rio Benevente, Rio Novo, Rio Itapemirim, and Rio Itabapoana. This group is supported by *Characidium vidali, Gymnotus pantherinus*, and *Phalloceros harpagos*. The Itapemirim-Itabapoana subgroup is highlighted because it is supported by species endemic to these basins, such as *Loricariichthys melanurus*, *Trichomycterus brunoi*, and *T. caudofasciatus*.

Discussion

Taxonomic patterns

Characiformes, Siluriformes and Cyprinodontiformes are the most diverse and dominant orders of freshwater fishes in the Neotropical region (Lowe-McConnell 1999; Menezes et al. 2007), a pattern repeated in our study area. Fishes of these orders are typically smaller than 15 cm, and many of them are endemic or have a limited range. Although they do not present high

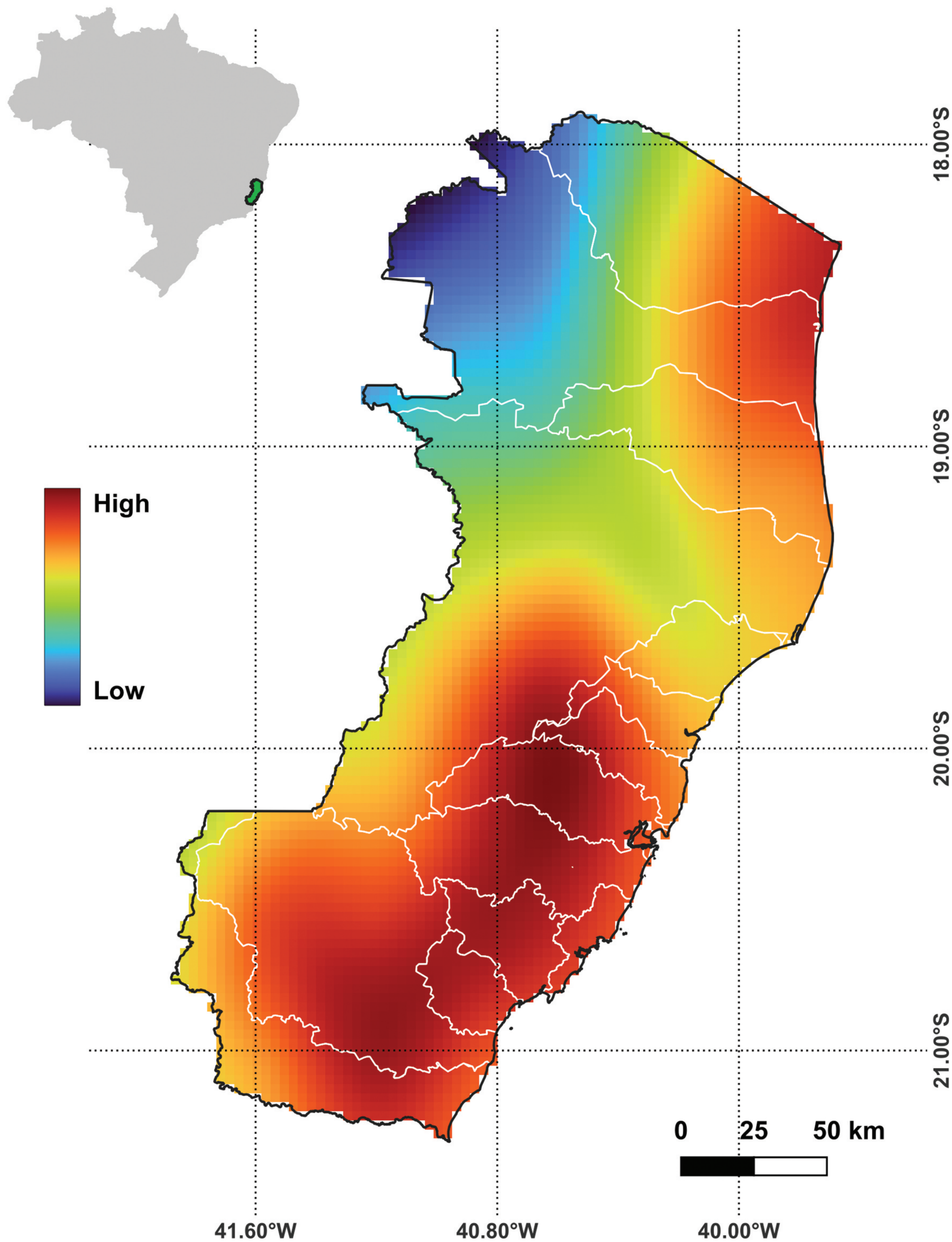

Figure 4. Interpolation of species richness from freshwater fishes in the state of Espírito Santo.

biomass, these small-sized species represent most of the biodiversity of Neotropical freshwater fishes (Castro & Polaz 2020). The proportional distribution among orders and families is also in line with what is expected for Atlantic Forest hydric systems (e.g. Langeani et al. 2007; Oyakawa & Menezes 2011), but differs from other studies considering the Northeastern Mata Atlantica ecoregion (Camelier & Zanata 2014; Silva et al. 2020), where the proportion of Characiformes species is higher than Siluriformes (vs. 35.7% and 48.8% in Espírito Santo, respectively), and the proportion of Characidae species is higher than Loricariidae (vs. the same proportion of 18.7% for both families). However, as mentioned by Camelier & Zanata (op.

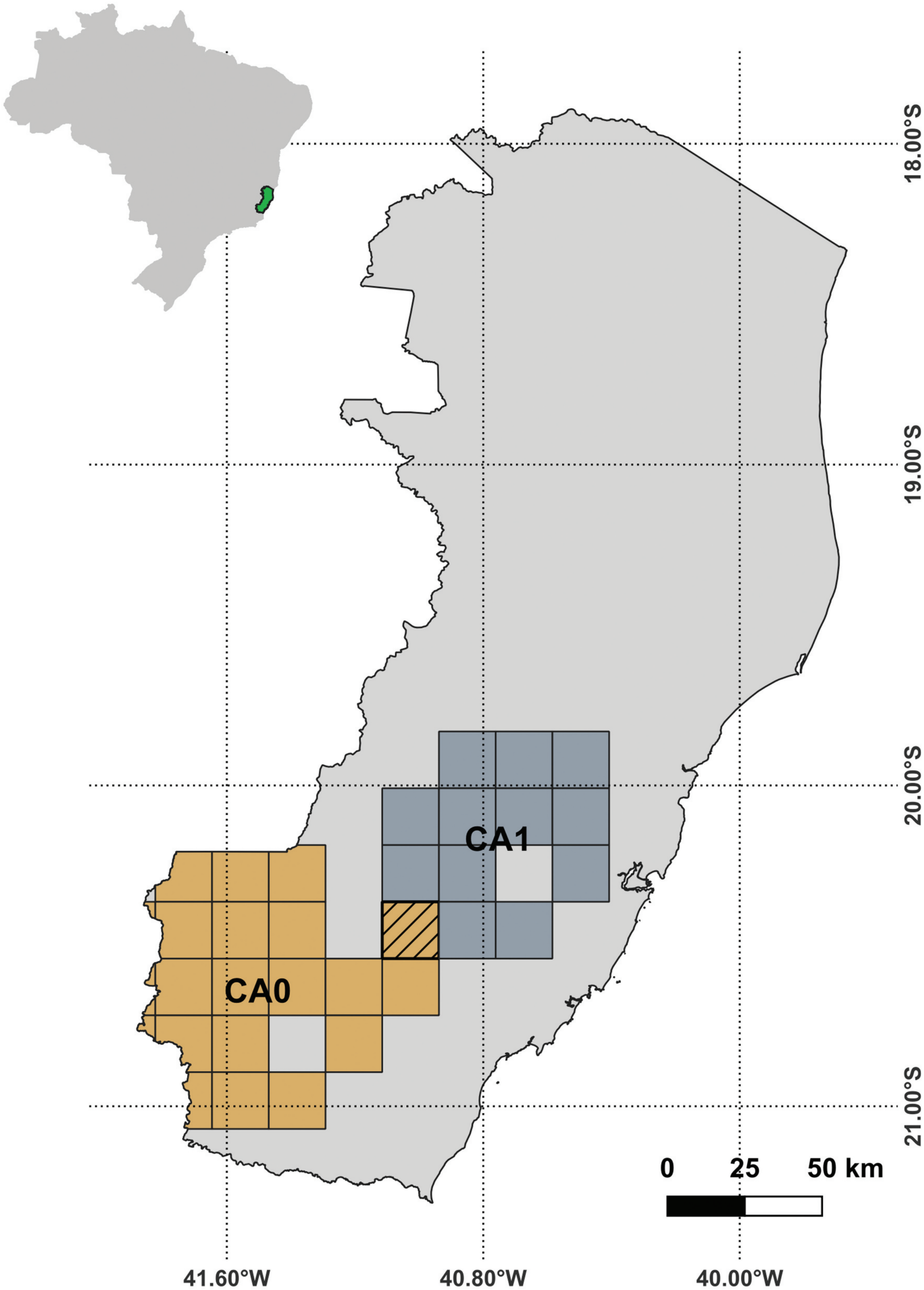

Figure 5. Consensus areas for the endemism of freshwater fishes in the state of Espírito Santo.

cit.), there is a gradual change in species composition from north to south in the ecoregion. While in the northern basins of the ecoregion there is a higher proportion of Characiformes than Siluriformes, the opposite is true for the southern drainages, especially in Espírito Santo. The total number of species in the area is comparable to that of the Rio Doce as a whole (Sarmento-Soares et al. 2022a).

Table 3. Consensus areas (CA) of endemism for the freshwater fishes in the state of Espírito Santo. We present the range of the endemicity index (IE) for the CA, drainages and indicative species with the contribution of each taxon to the endemicity index. Species in bold are endemic to basins draining the study area.

CA	IE range	Basins	Species
0	2.36–2.56	Itapemirim, Itabapoana, Doce	***Trichomycterus caudofasciatus*** (0.000–0.792) ***Trichomycterus brunoi*** (0.500–0.800) *Characidium alipioi* (0.000–0.625) *Neoplecostomus microps* (0.656–0.775) *Hypostomus auroguttatus* (0.000–0.625)
1	2.16	Piraquê-Açu, Reis Magos, Santa Maria da Vitória, Jucu, Doce	***Phalloceros elachistos*** (0.548) ***Neoplecostomus espiritosantensis*** (0.769) ***Trichomycterus pantherinus*** (0.846)

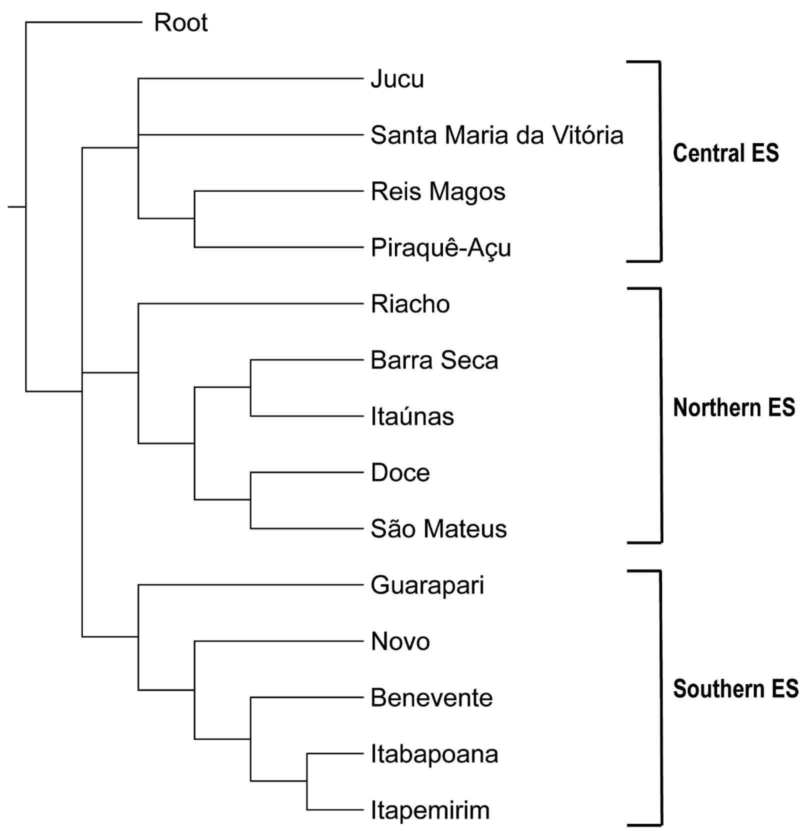

Figure 6. Consensus diagram of the interrelationships among the basins analyzed in the state of Espírito Santo.

Sampling gaps

A major problem in biogeographic and conservation studies is the lack of knowledge of all existing species (Linnean shortfall). Problematic groups, such as species complexes, can obscure the realistic recognition of biogeographic patterns in a given area. In the study area, a significant amount of the inventoried material held in collections is either in need of identification or only identified at the generic level. In order to develop more assertive conservation studies for a region, we need to overcome this problem with more taxonomic work. In spite of the increasing information regarding taxonomic and integrative revisions and new species descriptions, not all fish collections are able to keep up with the novelties in their respective databases. The lack of knowledge on the geographical distribution of species (Wallacean shortfall) creates difficulties for biodiversity conservation and hinders even the implementation of protected areas (Löwenberg Neto & Loyola 2016). Sampling efforts need to be as homogeneous as possible in the study areas.

According to Silveira et al. (2010), the low representativeness of the available data on the Brazilian ichthyofauna is an additional problem in studies on environmental impacts and fish species, especially because many studies are limited to a few basins of great interest, especially in the South and Southeast regions (Rosa et al. 2003; Langeani et al. 2009), where the most prominent research centers are located. In

Table 4. Clades generated by the PAE (parsimony analysis of endemism) and the species that support these groups.

Clades	Supporting species	Sub-clades	Supporting species
Northern ES Itaúnas, São Mateus, Barra Seca, Doce, Riacho	*Hypostomus scabriceps* *Otothyris travassosi* *Phalloceros ocellatus*	Barra Seca, Itaúnas, Doce, São Mateus	*Brycon ferox* *Characidium cricarense* *Microglanis pataxo* *Moenkhausia vittata* *Pimelodella* sp. 2 *Pogonopoma wertheimeri*
		Barra Seca, Itaúnas	*Ituglanis cahyensis* *Erythrinus erythrinus*
		Doce, São Mateus	*Euryochus thysanos* *Imparfinis minutus* *Loricariichthys castaneus* *Megaleporinus conirostris* *Parotocinclus planicauda* *Pachyurus adspersus* *Pseudauchenipterus affinis*
Central ES Piraquê-Açu, Reis Magos, Santa Maria da Vitória, Jucu	*Characidium timbuiense* *Euryochus thysanos* *Neoplecostomus espiritosantensis* *Pareiorhaphis ruschii* *Phalloceros elachistos* *Trichomycterus pantherinus*	Reis Magos, Piraquê-Açu	*Parotocinclus doceanus* *Phalloceros ocellatus* *Trichomycterus alternatus* *Trichomycterus longibarbatus*
Southern ES Guarapari, Benevente, Novo, Itapemirim, Itabapoana	*Characidium vidali* *Gymnotus pantherinus* *Phalloceros harpagos*	Novo, Benevente, Itapemirim, Itabapoana	*Astyanax microschemos* *Crenicichla lacustris* *Eigenmannia virescens* *Hisonotus thayeri* *Hypomasticus steindachneri* *Microglanis parahybae* *Otothyris lophophanes* *Pimelodella* sp. 2 *Trichomycterus alternatus*
		Benevente, Itapemirim, Itabapoana	*Glanidium melanopterum* *Imparfinis minutus* *Prochilodus vimboides* *Scleromystax prionotos*
		Itapemirim, Itabapoana	*Brycon insignis* *Characidium alipioi* *Characidium timbuiense* *Hypomasticus mormyrops* *Ituglanis parahybae* *Loricariichthys castaneus* *Loricariichthys melanurus* *Trichomycterus brunoi* *Trichomycterus caudofasciatus*

the study area, most of the sites visited by naturalist teams are located either near densely populated areas with research centers, such as the central region of Espírito Santo, close to the metropolitan region of Vitória and cities of the mountainous region, such as Santa Teresa, or close to the Caparaó mountain range, an area of increased conservation interest. The high rate of sampling in the central part of the state is mainly because of the presence of the Museu de Biologia Mello Leitão, a museum and research institute in operation since the 1940s, located in the municipality of Santa Teresa. For decades, due to the presence of natural reserves such as the Augusto Ruschi Biological Reserve and the Santa Lúcia Biological Station, this area was frequently visited by teams of naturalists (e.g. Travassos 1945). On the other hand, the interpolation results indicate that the upper stretches of the Rio São Mateus and Rio Riacho basins have a suboptimal sampling effort. In terms of geographical regionalization, the northern part of the territory, including the lower Rio Doce to the north, is significantly larger than the southern area, implying that a greater effort is required to equalize the quality of the sampling indices throughout the territory.

Bioregions, ecoregions, provinces and their fishes

The bioregions delimited here outline part of the Mata Atlântica bioregion proposed by Dagosta et al. (2020) in their bioregionalization of the freshwater ichthyofauna of South America. Overall, the resulting areas are characterized by species endemic to Espírito Santo drainages, and certain distribution patterns emerge when analyzing species inhabiting these areas. The northern bioregions, Northern Espírito Santo and Barra Seca-Lower Doce, share part of their fauna with basins in the southern state of Bahia, between Rio Mucuri and Rio Jequitinhonha (Sarmento-Soares & Martins-Pinheiro 2012; Camelier & Zanata 2014). *Microglanis pataxo*, *Acentronichthys leptos*, *Rachoviscus graciliceps*, *Ituglanis cahyensis*, *Henochilus wheatlandii*, and *Erythrinus erythrinus* are some of the fishes common to these river basins in Espírito Santo and Bahia. The bioregion of Central Espírito Santo stands out for having a characteristic and expressive fauna of endemic species, especially in rivers flowing in the mountainous areas, such as *Trichomycterus longibarbatus*, *Neoplecostomus espiritosantensis*, *T. gasparinii*, *T. pantherinus*, *Microcambeva jucuensis*, *M. watu*, and *Phalloceros elachistos*.

The bioregions of Caparaó Highlands, Benevente-Novo and Lower Itabapoana share an expressive part of their fauna with the lower Rio Paraíba do Sul basin, in the state of Rio de Janeiro (Bizerril 1994, 1999; Bizerril & Primo 2001; Sarmento-Soares & Martins-Pinheiro 2014a). The presence of species such as *Neoplecostomus microps*, *Hypomasticus mormyrops*, *Hypostomus auroguttatus*, *Imparfinis minutus*, *Microglanis parahybae*, *Otothyris lophophanes*, *Eigenmannia virescens*, *Characidium vidali*, *Pimelodella lateristriga*, *Ancistrus multispinis*, *Phalloceros harpagos*, *Ituglanis parahybae*, and others, suggest a common biogeographic history for these drainages (Sarmento-Soares & Martins-Pinheiro 2014a). During Pleistocene glacial periods, the regression of sea levels and the extension of paleodrainages across the continental shelf possibly led to events of lateral tributary capture or basin aggregation, resulting in fauna sharing between the lower Rio Paraíba do Sul and the southern Espírito Santo basins (Sarmento-Soares et al. 2012; Thomaz & Knowles 2018). Further evidence of a possible ancient faunal sharing event in these basins is the presence of the basal taxon *Trichogenes claviger*, endemic to the Rio Itapemirim, which together with *Trichogenes longipinnis* Britski & Ortega 1983, from drainages in northern São Paulo and southern Rio de Janeiro, form the monophyletic subfamily Trichogeninae. This subfamily and Copionodontinae (genera *Copionodon* and *Glaphyropoma*, both endemic to the coastal basin of Rio Paraguaçu, Bahia) form a sister clade to all other Trichomycteridae of South America. Pattern A, as named by Ribeiro (2006), suggests a Cretaceous cladogenesis that separated the common ancestor of these subfamilies from the other trichomycterids.

These shared fish species suggest that the classification of ecoregions by watersheds proposed by Abell et al. (2008) is not fully supported, especially when considering the ecological and biogeographic relationships that involve the dispersal of species across basins that, even if currently isolated, may have been connected in the distant past (Dagosta et al. 2020). The species pool of a region is much more heterogeneous than contemporary drainage configurations allow us to perceive. In this sense, the classification proposed by Bizerril (1994), which divides the coastal basins of eastern Brazil into two biogeographic regions, the 'East Coast subprovince' and the 'Southeast Coast subprovince,' is more in line with the current species composition, especially if we consider the large distribution of fishes between the Rio Paraíba do Sul basin and the basins of southern Espírito Santo, which, according to Abell et al. (2008), belong to different bioregions. The East Coast subprovince includes the coastal basins south of the Rio São Francisco to the Rio Paraíba do Sul basin (Bizerril 1994), a region of marked endemism and isolation from the inland plateau watersheds (Menezes 1972; Buckup 2011).

Areas of increased sampling effort, richness and endemism: a congruence

The interpolation of sampling effort, by identifying the areas with a higher representativeness of records in the state, set a path that was followed by the other analyses. Of the six defined bioregional units, three are strongly supported by species with restricted distributions: Northern Espírito Santo, Central Espírito Santo and Caparaó Highlands. In turn, the interpolation of species richness points to three large areas with a higher concentration of species: the coastal areas of the Rio Itaúnas, Rio São Mateus, and Rio Barra Seca basins (= Northern Espírito Santo bioregion); and the central (= Central Espírito Santo bioregion) and southern Espírito Santo (= Caparaó Highlands bioregion) basins, in an almost contiguous area extending from the Rio Piraquê-Açu basin to the Rio Itabapoana basin. The consensus areas of endemism follow a similar pattern: CA0, including the headwaters of the Itapemirim and Itabapoana basins, as well as some tributaries of the Rio Doce (= Caparaó Highlands bioregion); and CA1, including the drainages from Rio Piraquê-Açu to Rio Jucu (= Central Espírito Santo bioregion). Although uneven sampling effort has a significant impact on the results of the analyses, the watersheds of the state have been continuously sampled and studied for almost two decades. Therefore, these congruent arrangements, supported by the presence of endemic species, suggest the existence of well-defined biogeographic units (Bizerril 1994; Ribeiro 2006) in the state of Espírito Santo.

The watersheds of northern Espírito Santo share a large part of their fauna, as already mentioned, with the rivers of southern Bahia (Sarmento-Soares & Martins-Pinheiro 2012), in the coastal tableland forest from the Rio Doce to the Rio Jequitinhonha. The basins flowing through these areas are inhabited by species endemic to this phytophysiognomy, such as *Rachoviscus graciliceps*, *Mimagoniates sylvicola*, *Ituglanis cahyensis*, as well as *Acentronichthys leptos* Eigenmann & Eigenmann 1889 (Sarmento-Soares et al. 2019), which, although not endemic, was originally described for the Rio São Mateus drainage. Other species that characterize this region of the state are the endemic rivulids *Xenurolebias cricarensis*, *X. izecksohni*, and *X. myersi*, present in ponds and temporarily flooded areas (Costa 2002) and recorded in the Rio São Mateus, Rio Barra Seca, and Rio Itaúnas drainages, respectively. *Characidium cricarense*, *Microglanis pataxo*, *Pogonopoma wertheimeri*, and two species not yet formally described of *Pimelodella* (*Pimelodella* sp. 1 and *Pimelodella* sp. 2 sensu Sibien 2019) and many others with wider ranges are other species typical of the northern basins. On the other hand, other stretches of the Rio São Mateus and Rio Itaúnas basins, close to the border with the state of Minas Gerais, present a low species richness compared to most of the study area, a result that may be attributed, among other factors, to the poor representativeness of the sampling in this region, which is concentrated closer to the coastal zones.

The basins of the central region of Espírito Santo are formed by rivers that cross the mountainous terrain that is part of the Serra da Mantiqueira complex and flow to the coastal lowlands (Sarmento-Soares & Martins-Pinheiro 2010), presenting a wide variety of environments that can support high species richness. These drainages are inhabited by most of the endemic taxa of the state, including *Neoplecostomus espiritosantensis*, *Pareiorhaphis ruschii*, *Phalloceros elachistos*, *Trichomycterus barrocus*, *T. pantherinus*, *T. longibarbatus*, *T. gasparinii*, and the recently described *Microcambeva jucuensis* and *M. watu* (Costa et al. 2019; Medeiros et al. 2021).

The landscape of the southern area is dominated to the west by the Caparaó massif and the staggered steps of Espírito Santo (Burgos et al. 2006; Sarmento-Soares & Martins-Pinheiro 2014b), which are also branches of the Mantiqueira complex and have as main basins the Rio Itapemirim and Rio Itabapoana, besides the smaller drainages of the Rio Benevente and Rio Novo. These rivers are characterized by a greater heterogeneity of available habitats, with torrential waters where species adapted to these environments live, such as the loricariids *Ancistrus multispinis*, *Hypostomus affinis*, *H. auroguttatus*, *Harttia loricariformis*, *Loricariichthys castaneus*, *Rineloricaria steindachneri*, *Pogonopoma wertheimeri*, as well as the endemic *L. melanurus*. Other endemic species in the drainages of the southern region of the state include the trichomycterids *Trichomycterus brunoi*, *T. caudofasciatus*, *T. mimosensis*, the relictual *Trichogenes claviger*, and the rivulid *Atlantirivulus nudiventris* (Sarmento-Soares & Martins-Pinheiro 2014a; Sarmento-Soares et al. 2018).

Area relationships and remarks

Overall, the consensus diagram shows good support of characteristic species for the northern clade basins, with the formation of subgroups defined by two or more taxa. Rio Riacho is recovered as a basal area and is sister to all other basins in the northern clade. No species is exclusively restricted to Rio Riacho, a river basin that receives water from Rio Doce through the Caboclo Bernardo transposition channel. Many species from Rio Doce migrate to Rio Riacho through the transposition channel and vice versa. Compared to the other recovered clades (Central and Southern ES), 27 of the 83 species used in the PAE are restricted to the northern basins.

The similarity between the fauna of the Rio Doce and Rio São Mateus (together with the Rio Mucuri basin, in southern Bahia) has already been pointed out by Camelier and Zanata (2014) and Sarmento-Soares and Martins-Pinheiro (2012). The analysis also grouped the Itaúnas and Barra Seca basins in this clade, which have significant faunal similarities with the other basins in northern Espírito Santo. This is evidenced by the presence of species such as *Brycon ferox*, *Characidium cricarense*, *Microglanis pataxo*, *Moenkhausia vittata*, and *Pogonopoma wertheimeri*.

The central basins of the state are notable for the presence of a significant number of species endemic to Espírito Santo, and four of them support the formation of the clade: *Neoplecostomus espiritosantensis*, *Pareiorhaphis ruschii* (also found in the headwaters of the Rio Itapemirim basin), *Phalloceros elachistos*, and *Trichomycterus pantherinus*. On the other hand, only four of the species used in the PAE are restricted to the central basins. The Rio Jucu and Rio Santa Maria da Vitória basins featured less faunal similarity with the other basins of this group and did not form subterminal clusters. However, the Rio Jucu basin is characterized by the presence of *Microcambeva jucuensis*, an endemic species.

In the southern basins, the consensus diagram suggests that there is some heterogeneity in species composition in each area, but few species support the entire clade. Consequently, the relationships among the river basins are less consistent than in the northern area. The Guarapari micro-basins appear as an outgroup of the other basins of the southern clade. Guarapari and its neighboring small streams are composed of short, independent rivers without a proper freshwater fish fauna, and the species representation is not very well covered. Compared to the other recovered clades, of the 83 species used in the PAE, 17 are restricted to the southern basins.

The Rio Novo and Rio Benevente drainages exhibit weaker area relationships with the other drainages, as well as the Guarapari microbasins, which are mainly supported by species that are also shared with the Rio Paraíba do Sul basin. On the other hand, the sister clade formed by the Rio Itabapoana and Rio Itapemirim basins is supported by the common presence of nine species, mainly crenuchids, anostomids, trichomycterids and loricariids, as many of them live in the headwaters of these rivers, in the mountainous area of the Caparaó massif.

The PAE methodology: a comment

The vision of how species are distributed within a certain area corresponds to a key step toward biogeography studies and conservation (Humphries et al. 1995; Sarmento-Soares et al. 2022a). In this context, the recognition of patterns of endemism provides clues to prioritize the selection of areas for conservation in the Neotropical region (Crisci et al. 2003; Goldani & Carvalho 2003). Several methods have been classically used to identify and classify areas of endemism. The parsimony analysis of endemism (PAE) has historically been one of the most widely used methods for several groups of organisms (e.g. Costa et al. 2000; Goldani & Carvalho 2003; Sigrist & Carvalho 2008; Camelier & Zanata 2014; Garraffoni et al. 2017; Colli-Silva & Pirani 2019). It constructs similarity cladograms between areas using the cladistic analysis method of the presence-absence matrices of species data and supraspecific taxa. However, it is important to emphasize at this point that we used PAE only as a method to hypothesize area relationships between basins based on shared fauna, similar to what any cluster analysis would do in a less refined way. Szumik et al. (2002) criticize the use of PAE to delineate areas of endemism, suggesting that the means by which PAE delineates these areas is not adequate because of the criteria used in the analysis, a criticism supported by Casagranda et al. (2012). Other methods, such as the NDM/VNDM (Szumik et al. 2002, 2004) or, more recently, interpolations of occurrence records (Oliveira et al. 2015, 2019), are seemingly more appropriate for more in-depth recognition of areas of endemism.

Although the analysis might not be entirely suitable for delineating areas of endemic species, it is useful for drawing a number of inferences about the ecological and biogeographic history of species. Morrone (2014) reviews the methodology and compiles studies with critiques of the use of PAE and the implications of these conclusions. Peterson (2008) points out that PAE has serious drawbacks because it must use non-endemic species in order to provide overall insights, and the analysis is not suitable for artificially delineated areas. However, Morrone (2014) suggests that endemism occurs at different hierarchical levels; even if a species is not endemic to a site, it may be endemic to a larger geographic unit; the author also points out that the use of artificial areas depends greatly on the objective of the study. Non-endemic species often share the same biogeographic and ecological history as endemic species, being subject to the same processes of origin and dispersal. Furthermore, although the state of Espírito Santo is an artificial entity, its boundaries are mainly defined by the northern and southern watershed limits, which share a common geological and faunal history.

It remains challenging to estimate how the precise properties of real distributional data – or estimated distributional data – will affect the identification of biogeographic patterns (Casagranda et al. 2012). The limitations of the PAE method are obvious when there are areas of incomplete distribution (Arias et al. 2011). Otherwise, the theoretical basis of PAE can recognize areas with many species records, and in this sense, the method can be a valuable tool toward conservation planning. According to Platnick (1992), one of the fundamental questions of biodiversity conservation is currently a biogeographic question: with scarce human and economic resources, how do we determine where to invest in order to minimize biotic impoverishment? As with the PAE and other biogeographical approaches, we can identify priority sites for species conservation. Those species threatened with extinction will benefit from the use of these methodologies (as well as those of least concern). This should be a major goal of contemporary biogeography: to contribute to efficient decision making in biodiversity conservation.

Conservation issues

As the state of Espírito Santo harbors approximately 20 threatened freshwater fish species (Hostim-Silva et al.

2019), subjected to various anthropogenic impacts, the designation of priority conservation areas that concentrate a range of endemic and endangered species underscores the development of conservation-oriented public policies, even though aquatic fauna is frequently neglected in the establishment of protected areas (Sarmento-Soares & Martins-Pinheiro 2017; Azevedo-Santos et al. 2019). Species such as *Acentronichthys leptos* (CR, Critically Endangered), *Atlantirivulus nudiventris* (CR), *Brycon dulcis* (CR), *Rachoviscus graciliceps* (CR), *Trichogenes claviger* (CR), *Xenurolebias cricarensis* (CR), *X. izecksohni* (EN, Endangered), and *X. myersi* (EN), that support different biogeographic units within the state, are among the most threatened as result of habitat loss, dam construction for hydroelectric power generation, uncontrolled expansion of agriculture, among other factors (Sarmento-Soares & Martins-Pinheiro 2012, 2013; Sarmento-Soares et al. 2018).

Additionally, *Neoplecostomus espiritosantensis*, which defines the area of endemism in central Espírito Santo, was classified as Near Threatened (NT) in the latest assessment. In the southern endemic area of the state, within the Rio Itapemirim basin, Sarmento-Soares et al. (2018) propose the creation of a conservation unit to protect sensitive endangered species such as *Trichogenes claviger*, which is a target species in the Plano de Ação Nacional para a Conservação de Espécies de Peixes e Eglas da Mata Atlântica, a national policy for the conservation of Atlantic Forest freshwater fish and crustacean species (MMA – Ministério do Meio Ambiente/ICMBio – Instituto Chico Mendes de Conservação da Biodiversidade 2019). Other threatened species are covered in the Plano de Ação Nacional para a Conservação dos Peixes Rivulídeos (MMA – Ministério do Meio Ambiente/ICMBio – Instituto Chico Mendes de Conservação da Biodiversidade 2022), with emphasis on conserving fish from the Rivulidae family, which are critically endangered as a result of habitat loss, and in the Plano de Ação Territorial Capixaba-Gerais (IEF – Instituto Estadual de Florestas de Minas Gerais 2021; IEMA – Instituto Estadual de Meio Ambiente e Recursos Hídricos do Espírito Santo 2021), with a focus on threatened species in the states of Espírito Santo and Minas Gerais. These plans coordinate research and priority actions aimed at conserving species and natural environments across different regional scales, and they are fundamental for the development of management measures and public policies that safeguard species and their habitats.

Our evaluation highlights different biogeographic patterns of the 'capixaba' (natural from the state of Espírito Santo) ichthyofauna in terms of species richness, area relationships, endemism zones and biogeographic units. Three main patterns of species distribution were identified: the northern basins share a significant part of their fauna with the basins in the south of Bahia; the basins in the central part of the state are home to a significant number of endemic species and could represent a well-defined biogeographic unit; and the southern basins, in addition to presenting a distinctive fauna that includes endemic species, also share a part of their species with the lower Rio Paraíba do Sul basin. The results of this assessment reinforce the idea that, although the ichthyofauna of the state is common to other regions, the river basins of Espírito Santo have their own diverse and characteristic freshwater fish fauna. This is an unprecedented approach for the drainages of the state and we expect that it will serve as a basis for future investigations.

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