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ECOSYSTEMS

Conservation Priorities for Threatened and Restricted-Range Freshwater Fishes in the Northeastern Mata Atlântica Freshwater Ecoregion, Brazil

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Abstract: In light of the growing loss of aquatic biodiversity amid the current freshwater biodiversity crisis, systematic conservation planning is crucial for developing conservation policies to establish new protected areas that effectively address the complexity of freshwater environments. This study aims to identify priority basins for conservation of threatened, near-threatened, and restricted-range endemic freshwater fish species in the Northeastern Mata Atlântica freshwater ecoregion, highlighting irreplaceable and critical locations for conservation and impact mitigation. Through spatial prioritization, three scenarios with distinct conservation features were considered: (a) 35 threatened species, (b) 118 near-threatened and restricted-range species, and (c) all 153 species. A total of 50 and 89 basins were prioritized in the first two scenarios, respectively, and 135 basins in the third scenario, with 36 classified as critical due to environmental stressors, particularly in the Rio Doce basin. Our results suggest that the current protected area network is insufficient for safeguarding most target fish species. This study presents an initial framework for prioritizing areas that can provide a basis for further, more refined assessments and to support conservation policies such as national or regional action plans, protecting basins and species.

Key words: Catchments, Endemism, Freshwater conservation, Ichthyofauna, Systematic conservation planning, Threatened species.

INTRODUCTION

Freshwater ecosystems are among the most imperiled on the planet (Dudgeon et al. 2006, Abell et al. 2007, 2008, Lévêque et al. 2008). Habitat loss and the removal of riparian forests, two major anthropogenic impacts on organisms in freshwater environments, lead to a reduction in the allochthonous resources that species rely on (Menezes et al. 2007, Lobón-Cerviá et al. 2016). These stressors, along with pollution, species introduction, and physical modification of habitats through dams and artificial channels, also directly impact species distributions and the preservation of native biodiversity and ecosystem services (Giannini et al. 2012, Azevedo-Santos et al. 2019). Additionally, emerging threats to freshwater environments, such as climate change, infectious diseases, and population imbalances of invasive species, negatively impact the biodiversity and functionality of these ecosystems (Woodward et al. 2010, Reid et al. 2019). Consequently, freshwater ecosystems exhibit the highest global extinction rates (Dudgeon et al. 2006, Turak et al. 2017, Albert et al. 2021).

Freshwater fish constitute one of the most diverse groups of vertebrates, comprising almost 19,000 described species (Fricke et al. 2025). In the Neotropical region, there are over 6,300 described species, with estimates reaching approximately 9,000 species (Reis et al. 2016, Tagliacollo et al. 2024). In Brazil, there are more than 3,600 described freshwater species, according todatabases (Froese & Pauly 2024), of which more than 290 are currently threatened (ICMBio 2018, MMA 2022). The Atlantic Forest is one of the most imperiled biodiversity hotspots on the planet, encompassing a wide variety of environments and species (Myers et al. 2000). Despite the fact that the biome features less than 5% of its original native vegetation cover, it harbors a high diversity of endemic freshwater fish species closely associated with the maintenance of riparian vegetation (Menezes et al. 2007, Abilhoa et al. 2011, Castro 2021).

The Atlantic Forest presents great heterogeneity of environments and landscapes, which is reflected in different biogeographic, evolutionary and ecological histories that have shaped groups of species and areas of endemism. In this regard, the biome encompasses the Northeastern Mata Atlântica ecoregion (NMAF, sensu Abell et al. 2008), a freshwater ecogeographic unit characterized by pronounced endemism and a substantial number of threatened fish species (Camelier & Zanata 2014, Silva et al. 2020, Vieira-Guimarães et al. 2024). The primary threats to freshwater biota in this biome include deforestation due to agricultural activities, mining enterprises, urban expansion, introduction of invasive species, pollution, and dams (Menezes et al. 2007, Abilhoa et al. 2011, Larentis et al. 2022). These factors frequently result in alterations to the habitats, environmental and biotic homogenization, followed by reduction in ecosystem services (Teresa & Casatti 2010, Azevedo-Santos et al. 2019).

Compounding this issue, many freshwater fish species in the ecoregion are particularly vulnerable, such as small-sized species with low dispersal capabilities and specialist functional traits, making them prone to local extinctions and severe population declines caused by habitat fragmentation and alterations in river flow patterns (Winemiller 1989, Ricciardi & Rasmussen 1999, Winemiller et al. 2016). This is especially true for rare, restricted-range fish species (Nogueira et al. 2010, Leitão et al. 2016). In this context, systematic conservation planning is crucial for implementing Protected Areas (PAs) to safeguard these species and mitigate impacts. Systematic conservation planning refers to the definition of complementary biodiversity priority areas that generate a protection network to achieve conservation objectives explicitly and efficiently (Margules & Pressey 2000, Pressey et al. 2007). This approach addresses aspects of biodiversity and ecosystems such as irreplaceability and vulnerability of areas and species, in addition to socio-economic frameworks (Linke et al. 2007, Frederico et al. 2021).

Despite the existence of PAs, these areas often lack optimal strategic positioning to maximize the conservation of freshwater biodiversity and its habitats. They frequently prioritize terrestrial fauna and overlook river connectivity patterns and hydrological variability, providing a poor safety net for freshwater fauna (Abell et al. 2007, Linke et al. 2007, Hermoso et al. 2011, 2016, Dagosta et al. 2020). In Brazil, several protected areas in different regions have been established with a bias towards terrestrial organisms and may be of limited value for the protection of stream fishes, and this also applies to the NMAF ecoregion (Pompeu et al. 2009, Frederico et al. 2018, Sarmento-Soares et al. 2017, Azevedo-Santos et al. 2019). Efficient systematic conservation planning must integrate terrestrial and aquatic environments, given the interdependence of these ecosystems, to maximize the protection of species, considering essential aspects for the maintenance of these ecosystems, their species and life cycles (Nogueira et al. 2010, Frederico et al. 2021).

Over the past two decades many studies have employed different methods to identify potential areas in different regions for the protection of aquatic fauna, using freshwater species as conservation targets (e.g., Nogueira et al. 2010, Holland et al. 2012, Carrizo et al. 2017, Frederico et al. 2018, Tognelli et al. 2019, Jézéquel et al. 2020, Epele et al. 2021, Miqueleiz et al. 2023). However, there are still gaps to be addressed in the conservation of environments in eastern basins in Brazil, especially those north of the Rio Doce basin. This study aims to identify priority areas for conservation of threatened, near threatened, and restricted-range endemic freshwater fish species in the Northeastern Mata Atlântica freshwater ecoregion. Additionally, we seek to highlight irreplaceable and critical areas that require urgent conservation measures.

MATERIALS AND METHODS

Study area

The Northeastern Mata Atlântica freshwater ecoregion extends from the Rio Itabapoana basin in the northernmost region of the state of Rio de Janeiro and the southern Espírito Santo to the Rio Japaratuba basin in northern Sergipe (Abell et al. 2008, Albert et al. 2011). The ecoregion is drained by more than 50 river basins and microbasins, in a range of distinct landscapes and phytophysiognomies (Sarmento-Soares et al. 2017). The Serra do Espinhaço, located within the eastern margin of the Brazilian Shield, acts as a significant boundary to the west, separating the NMAF from the Rio São Francisco basin ecoregion and giving rise to numerous drainage systems along its slopes (Buckup 2011). Its southern border is adjacent to the Rio Paraíba do Sul ecoregion, separated by the Rio Itabapoana basin, and the Upper Rio Paraná ecoregion, abutting the Serra da Mantiqueira, which separates it from the Rio Doce basin (Camelier & Zanata 2014, Vieira-Guimarães et al. 2024). Despite its name, the ecoregion is situated within three Brazilian biomes: Caatinga (Semi-arid) to the north and northwest, Mata Atlântica (Atlantic Forest) along the coastal and southern regions, which is the dominant biome in the ecoregion, and a patch of Cerrado (Brazilian savanna) to the west (Hales & Petry 2013).

Recent checklists report the occurrence of 305 native freshwater fish species in the NMAF, and approximately 70% of those are endemic to the ecoregion (Silva et al. 2020, Vieira-Guimarães et al. 2024). A significant proportion of the biota in northern basins of the ecoregion is shared with the Rio São Francisco basin (Camelier & Zanata 2014), while several species in southern basins are shared with the Rio Paraíba do Sul basin (Bizerril 1999, Sarmento-Soares & Martins-Pinheiro 2013).

Data compilation

Distributional data (georeferenced records) for native species occurring in the NMAF ecoregion were gathered from the literature (species descriptions and checklists), online databases (SpeciesLink, GBIF, SiBBr), and records deposited in ichthyological collections (MZUSP, MBML, MNRJ, UFBA, UFES, and UFS). The procedures for collecting, refining, and preparing species distribution data are further detailed in Vieira-Guimarães et al. (2024). The HydroBASINS hydrological database (Lehner & Grill 2013) was used to map species occurrences and designate conservation planning units. We used level 8 of the basin hierarchy, standardizing to the protocols recommended by the IUCN (2024) for delineating distribution polygons of freshwater fish (Miqueleiz et al. 2023). At level 8, the total number of basins (i.e., planning units) in the ecoregion was 728, with an average area of 695.3 km² (± 695.6 km²) (minimum area = 0.1 km²; maximum area = 4,811.1 km²; median = 467.5 km²).

Species were defined as present in a basin when occurrence records overlapped with the area of that basin (Tognelli et al. 2019). Thus, we considered that the distribution polygons of species roughly correspond to the boundaries of the basins in which they occur. Following this spatial criterion, we created distribution polygons for threatened species (ICMBio 2018, MMA 2022), near-threatened species (ICMBio 2018), and ecoregion endemics with restricted distribution, specifically those whose total range does not exceed 10,000 km² (Nogueira et al. 2010). These groups were selected due to their current or future susceptibility to extinction and their utility as conservation targets for prioritizing areas and resources (Lawler et al. 2003, Eken et al. 2004, Nogueira et al. 2010, Leitão et al. 2016).

The areas of the basins were overlapped with recent spatial data on protected areas and indigenous lands obtained from the World Database on Protected Areas (available at: www.protectedplanet.net) to calculate the proportion of territory currently protected in each basin. Indigenous lands are protected natural areas, and were included in our assessment due to their role in preventing deforestation (Soares-Filho et al. 2010, Ribeiro et al. 2018). Updated spatial data on vegetation cover for 2022, sourced from the MapBiomas platform (Souza et al. 2020, available at: brasil.mapbiomas.org), were used to calculate the proportion of remaining native vegetation relevant to ichthyofauna (e.g., forest formation, savanna formation, wetland) present in each unit. Finally, each basin was overlaid with the occurrence of hydroelectric dams (ANA 2021), a factor that strongly influences the distribution and fragmentation of freshwater fish populations and aquatic systems (Agostinho et al. 2002, Dudgeon et al. 2006, Azevedo-Santos et al. 2019).

Spatial prioritization

The software Marxan 2.4.3 (Ball et al. 2009), along with the QGIS plugin CLUZ (Smith 2019), was employed to prioritize areas based on species presence through an algorithm that identifies a set of planning units (PUs) that meet conservation targets at minimum cost (Epele et al. 2021). We considered three scenarios for area prioritization: the first scenario includes threatened species in the region; the second includes near-threatened and restricted-range species; and the third includes all species. The area of the catchments (i.e., PUs) in square kilometres (km²) was used as a proxy for cost (Moilanen et al. 2008, Tognelli et al. 2019). Basin areas with ≥ 70% overlap with protected areas were considered adequately protected and were locked into the analyses (Holland et al. 2012).

Conservation targets for the three scenarios were defined according to the threat category of the species in accordance with the IUCN, threat status of the species as listed in ICMBio (2018), MMA (2022) and updates in ICMBio (2025). Marxan was configured to select 100% of the basins (i.e., 100% of their areas) containing Critically Endangered (CR) species, at least 75% of the occurrence of Endangered (EN) species, and at least 50% of the occurrence of Vulnerable (VU) species (Tognelli et al. 2019). For near-threatened (NT) and restricted-range species, a minimum target of 30% of their distributions was adopted, rather than selecting a number of basins (e.g., Holland et al. 2012, Tognelli et al. 2019), since many of these species have distributions limited to one or two sub-basins.

Hydrological connectivity is a significant factor in defining priority freshwater areas (Hermoso et al. 2011, 2012, Tognelli et al. 2019). By altering the boundary length modifier (BLM) values, we generate areas with varying degrees of cohesion, which affect cost and extent of protection. We tested six BLM values for each scenario (0, 0.001, 0.01, 0.1, 0.5, 1). In all three scenarios, a BLM value of 0.01 proved to be the most appropriate, as it generated more coalesced areas and fewer scattered catchments with no hydrological connectivity to others. Each scenario was run 1,000 times, and basins were classified as irreplaceable (i.e., conservation features are reduced or extinct if that site is lost, Rodrigues et al. 2006) if they were selected in all 1,000 runs (Tognelli et al. 2019). In the third scenario, basins identified as irreplaceable that have ≤ 30% native vegetation cover or large hydropower dams generating at least 30 MW of power (or both factors) were classified as critical (Nogueira et al. 2010). Basins selected that were directly affected by the Fundão tailings dam collapse in the Rio Doce basin were also classified as critical based on the known magnitude of the event and expected impacts to aquatic systems, such as deleterious physiological changes in fish species (Ferreira et al. 2020, Passos et al. 2020, Weber et al. 2020). Thus, we consider critical those selected areas that harbor target species but may be suboptimal for protection due to high-impact anthropogenic factors affecting the ichthyofauna (Tognelli et al. 2019), and that require urgent measures for damage mitigation and protection of species and habitats. The resulting maps were overlaid with the priority areas for conservation defined by the MMA (2018) for vertebrate taxa and key biodiversity areas.

RESULTS

Of the 305 native freshwater species reported for the NMAF ecoregion, 153 were considered eligible for the analyses (Supplementary Material – Table SI): 35 threatened species (13 CR, 14 EN, and 8 VU), 13 near-threatened species (NT), and 105 restricted-range endemics, hereafter RR (66 LC, 14 DD, and 25 not evaluated).

The distribution areas of the threatened species ranged between 5.7 km² and 20,731.5 km², average of 2,999.1 km² (± 3,869.6 km², median = 1,737 km²). The distribution areas of NT and RR species ranged between 279.7 km² and 9,652.2 km², average of 2,695.7 km² (± 1,883.2 km², median = 2,456.6 km²). Only 19 basins had ≥ 70% overlap with protected areas (2.6% of the total number of basins, 1.4% of the study area). Most of the catchments (674, 92.6%) have less than 30% of their area under protection, while 35 basins (4.8%) have between 30% and 70% of their territory protected. The average proportion of native vegetation cover in the basins was approximately 37% (±21.3%), with an average of 6% of protected area (±17.6%).

Conservation targets were met for all species in the three scenarios presented. In the first scenario (35 threatened species), 50 basins were prioritized, of which 47 areas (6.5% of the total planning units) were deemed irreplaceable (Figure 1, Table I), covering approximately 66,733 km² (13.2% of the total area). Most of the areas selected as irreplaceable are concentrated in the basins of the Rio Paraguaçu, Rio Doce, as well as the smaller coastal basins. Only two species (5.7% of the threatened species) were found in adequately protected basins.

In the second scenario (118 NT + RR species), 89 basins were prioritized, of which 60 (8.2%) were deemed irreplaceable (Figure 2), covering an area of approximately 106,244 km² (21% of the total area). Irreplaceable sites are primarily

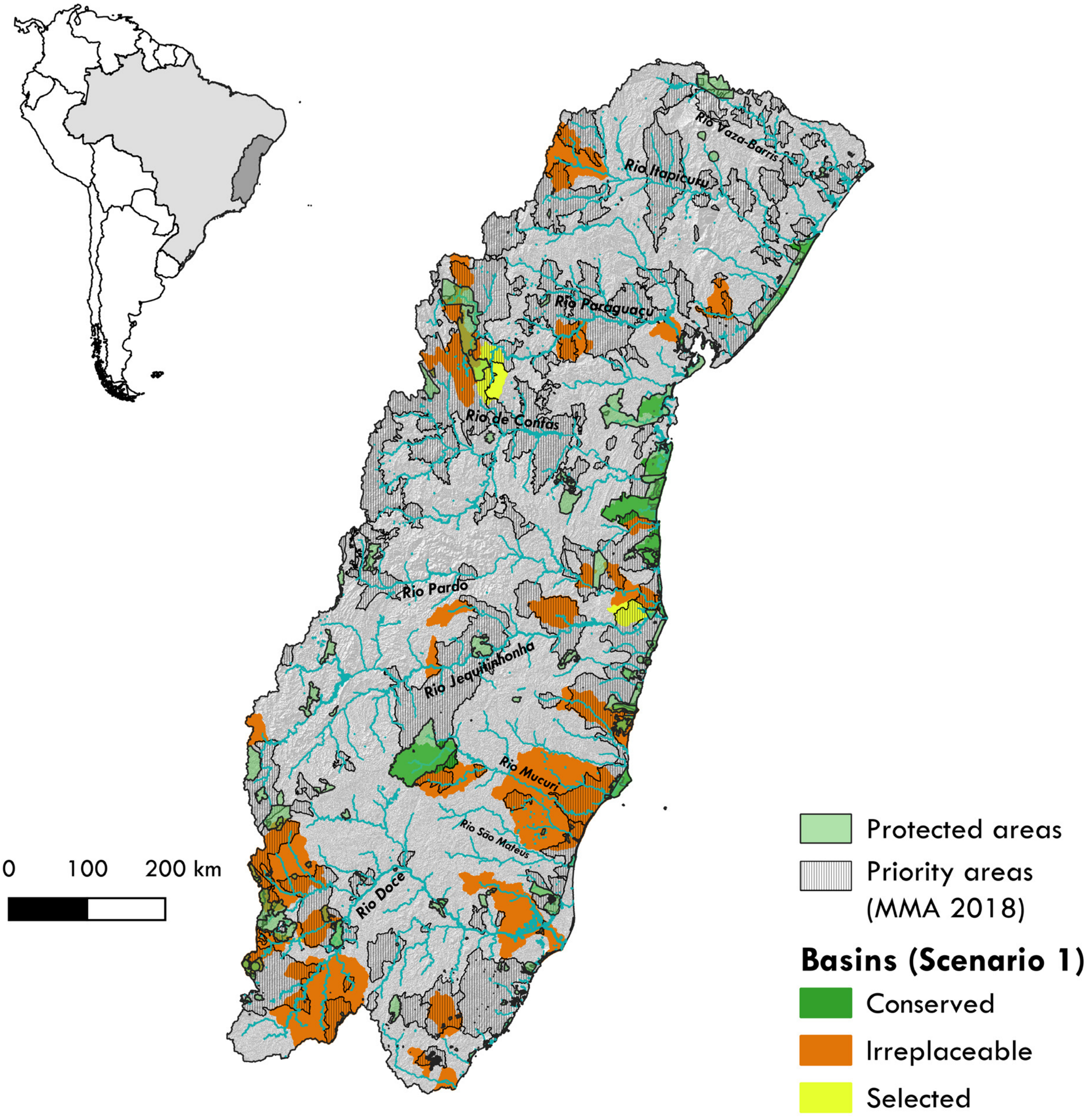

Figure 1. Priority areas for the conservation of threatened species in the Northeastern Mata Atlântica freshwater ecoregion. The map shows protected areas (in light green), priority areas for conservation acoording to MMA (2018), currently protected basins (in green), basins selected to complement the conservation of irreplaceable areas (in yellow), and irreplaceable basins (in orange).

located in the drainages of the Rio Paraguaçu, Rio de Contas, Rio Jequitinhonha, the coastal basins in the eastern part of the ecoregion, and the Rio Doce. Eight of these species (6.8%) were found in currently protected basins.

In the third scenario (153 species), 135 basins were prioritized, of which 105 (14.4%) were identified as irreplaceable, in a geographically widespread distribution across the ecoregion, and covering approximately 143,433 km² (28.3% of the total area). Among these areas, 36 (4.9%) were classified as critical, covering approximately 58,355 km² (11.5% of the total area) (Table II), primarily in the Rio Doce basin.

Table I. **Scenarios for basin prioritization in the Northeastern Mata Atlântica ecoregion. NT = Near Threatened; RR = Restricted-range.**

Scenario	No. of Species	No. of species in adequately protected basins	No. of irreplaceable basins (selected)	Basins area (km²)	Average basin area (km²)
Threatened species	35	2 (5.7%)	47 (50)	66,733 (13.2%)	1,334.7 (±1,129.5)
NT + RR species	118	8 (6.8%)	60 (89)	106,244.3 (21%)	1,193.8 (±987.3)
All species	153	10 (6.5%)	105 (135)	143,433.9 (28.3%)	1,062.5 (±1,024.8)

Ten species (6.5% of the total) were found in protected basins in this scenario.

DISCUSSION

The results of this study suggest that the current network of protected areas in the NMAF ecoregion is inadequate for encompassing the range of threatened or endemic species with limited distributions, particularly when considering only basins that are effectively protected (≥ 70% protection). There is a deficit of effectively protected basins, even in regions with a higher concentration of PAs, such as the upper Rio Paraguaçu, upper Rio Jequitinhonha and middle Rio Doce. The distribution patterns of freshwater fishes at various scales often do not align with terrestrial biodiversity. Consequently, terrestrial organisms cannot always be used as surrogates for freshwater fish conservation (Rodrigues & Brooks 2007, Darwall et al. 2011, Abell et al. 2017, Tao et al. 2023). As a result, many conservation units are not established with critical landscape factors for aquatic environments in mind, such as hydrological connectivity, dendritic networks, and regional-scale disturbances within basins (Hermoso et al. 2016, Abell et al. 2017, Tao et al. 2023). Similar findings from other studies employing different methodologies (e.g., Nogueira et al. 2010, Carrizo et al. 2017, Tognelli et al. 2019, Dagosta et al. 2020) indicate that the implementation of PAs that do not reflect the complexity of freshwater habitats is a widespread issue that contributes, among other drivers, to the progressive biodiversity loss in these environments (Abell et al. 2007, Azevedo-Santos et al. 2019).

There is a clear contradiction in this issue, since many terrestrial organisms also depend on the maintenance of aquatic environments for their survival (Abell 2002). As conservation planning should consider both aquatic and terrestrial ecosystems in decision-making, freshwater environments have been progressively incorporated into systematic conservation planning in recent years, in approaches that consider important aspects for ensuring the integrity of streams, rivers, wetlands, riparian ecosystems and their biotas (Hermoso et al. 2011, Frederico et al. 2021). The reduction in the width of riparian vegetation to be preserved along rivers, determined by the current Brazilian Forest Law, raises this pressing issue, given the consequences for freshwater biota such as losses of species and faunal homogenization (Casatti 2010).

The high levels of endemism and diversity in the freshwater ichthyofauna of the Northeastern Mata Atlântica ecoregion (Camelier & Zanata 2014, Silva et al. 2020, Vieira-Guimarães et al. 2024) can help guide conservation management policies (Pelicice et al. 2017, Tognelli et al. 2019). Like other freshwater organisms, many of these species have restricted spatial distributions

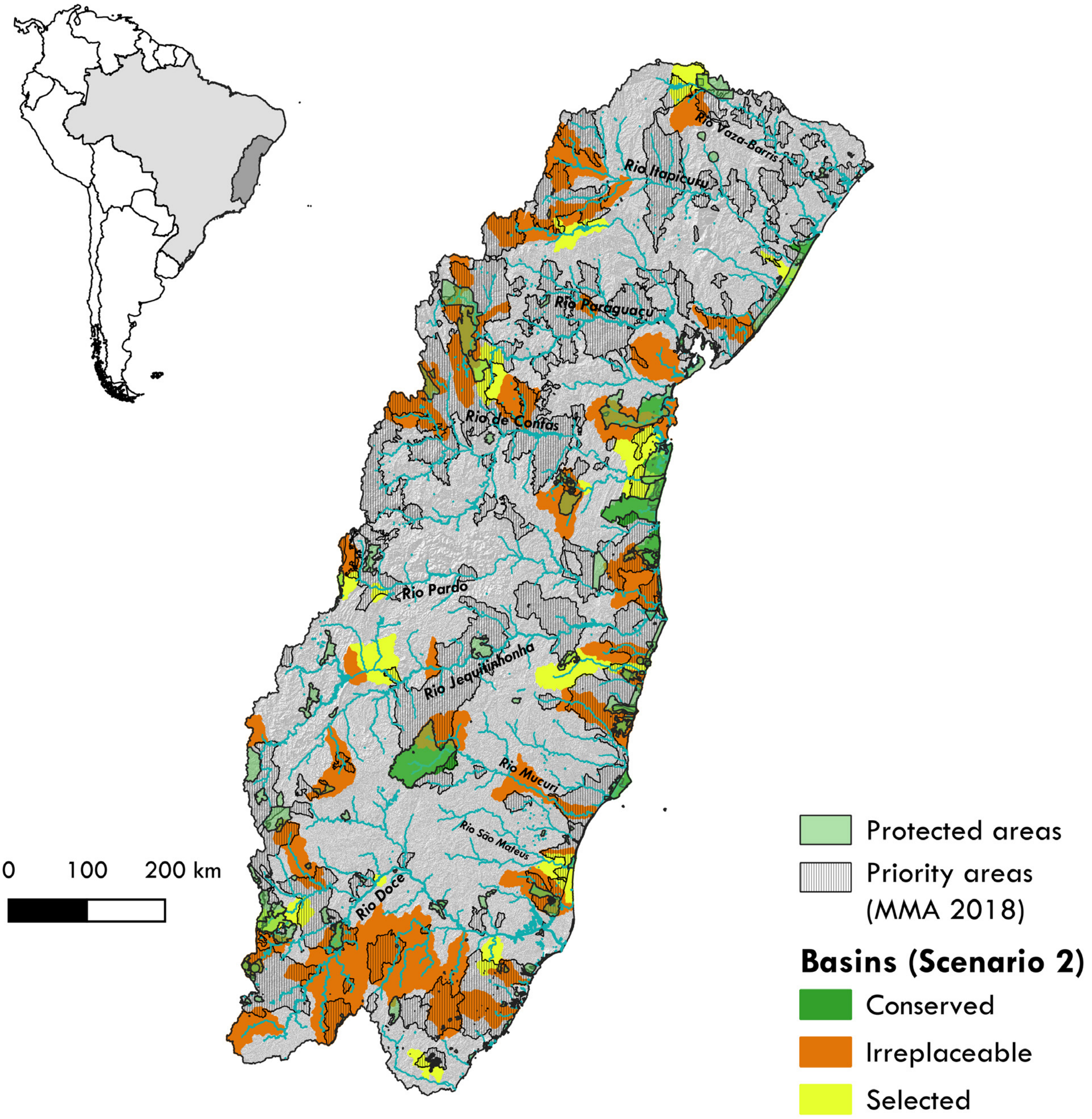

Figure 2. **Priority areas for the conservation of near threatened and restricted-range species in the Northeastern Mata Atlântica freshwater ecoregion. The map shows protected areas (in light green), priority areas for conservation acoording to MMA (2018), currently protected basins (in green), basins selected to complement the conservation of irreplaceable areas (in yellow), and irreplaceable basins (in orange).**

and limited dispersal capabilities (Myers et al. 2017). Even in regions with protected areas, such as stretches of the middle Rio Doce, the populations of these species are not adequately addressed (Sarmento-Soares et al. 2022, Costa et al. 2023). Systematic conservation planning, aimed at optimizing resources and enhancing protection networks for environments and organisms, should focus on creating protected areas that account for the presence of endemic and threatened species, as well as areas of significant taxonomic, phylogenetic, and

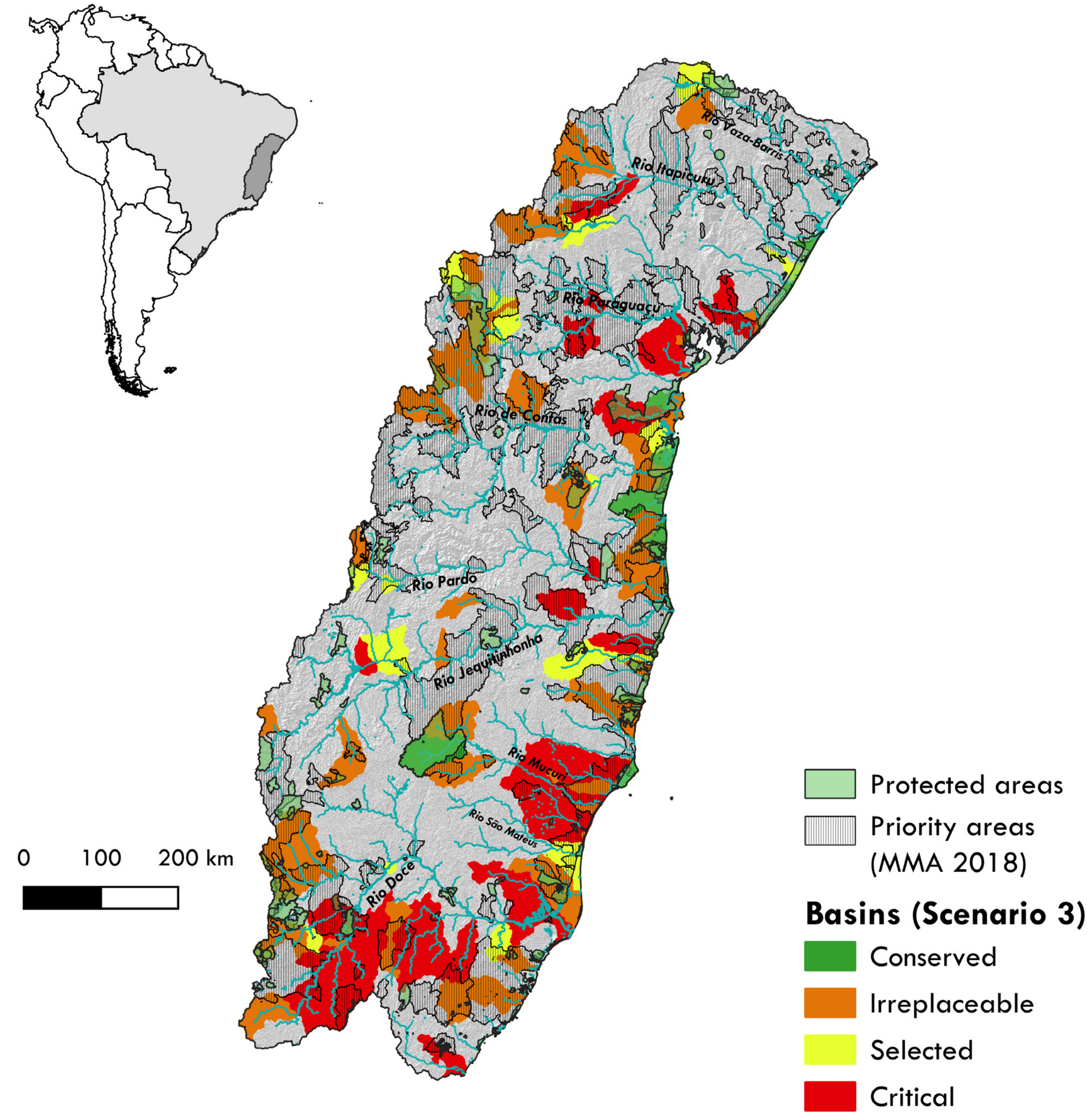

Figure 3. Priority areas for the conservation of threatened, near threatened and restricted-range species in the Northeastern Mata Atlântica freshwater ecoregion. The map shows protected areas (in light green), priority areas for conservation acoording to MMA (2018), currently protected basins (in green), basins selected to complement the conservation of irreplaceable areas (in yellow), irreplaceable basins (in orange) and critical basins for conservation (in red).

functional diversity (Fearnside 2015, Azevedo-Santos et al. 2019, Dagosta et al. 2020). Previous studies have identified several areas of contextual species richness (areas rich in species restricted to a biogeographic unit, Langhammer et al. 2007, Holland et al. 2012) within the ecoregion (e.g., Camelier & Zanata 2014, Vieira-Guimarães et al. 2024). These areas can serve as a baseline for creating effective PAs for freshwater and terrestrial fauna (Nogueira et al. 2010, Leal et al. 2020).

Table II. Critical basins for conservation in the Northeastern Mata Atlântica freshwater ecoregion. BA = Bahia; ES = Espírito Santo; MG = Minas Gerais; RJ = Rio de Janeiro.

Critical catchment	Biome	Basin, state	Area (km²)	Coordinates (centroid)	Conservation features	Environmental Stressors
Rio do Peixe	Caatinga	Rio Itapicuru, BA	1,847.7	-40.0205, -11.2641	*Cynolebias itapicuruensis* *Geophagus itapicuruensis* *Hypostomus leucophaeus* *Pimelodella itapicuruensis*	≤ 30% native vegetation cover
Rio Catu	Mata Atlântica	Rio Pojuca, BA	468.7	-38.4215, -12.1964	*Phalloptychus eigenmanni*	≤ 30% native vegetation cover
Upper Rio Pojuca	Mata Atlântica	Rio Pojuca, BA	751.7	-38.5114, -12.3394	*Phalloptychus eigenmanni*	≤ 30% native vegetation cover
Rio Jacuípe	Caatinga	Rio Jacuípe, BA	1,090.9	-38.3760, -12.5360	*Parotocinclus jacumirim*	≤ 30% native vegetation cover
Lower Rio Capivari	Caatinga	Rio Paraguaçu, BA	414.5	-40.0222, -12.3962	*Cynolebias paraguassuensis*	≤ 30% native vegetation cover
Middle Rio Paraguaçu	Caatinga	Rio Paraguaçu, BA	1,613.3	-40.1770, -12.8040	*Hypostomus jaguar* *Kalyptodoras bahiensis* *Ituglanis paraguassuensis* *Pareiorhaphis lophia*	≤ 30% native vegetation cover
Lower Rio Paraguaçu	Mata Atlântica	Rio Paraguaçu, BA	713.8	-39.0550, -12.6260	*Kalyptodoras bahiensis*	Hydropower dam ≥ 30 MW; ≤ 30% native vegetation cover
Rio Jaguaripe and Rio da Dona	Mata Atlântica	Recôncavo Sul, BA	2,779	-39.1880, -12.9420	*Aspidoras kiriri*	≤ 30% native vegetation cover
Rio das Almas	Mata Atlântica	Rio das Almas, BA	3,081.4	-39.5660, -13.6590	*Characidium samurai* *Geophagus santosi* *Gymnotus bahianus* *Leporinus melanopleurodes*	Hydropower dam ≥ 30 MW
Rio Palmeirão	Mata Atlântica	Rio Pardo, BA	444.3	-39.8520, -15.4480	*Ophthalmolebias rosaceus*	≤ 30% native vegetation cover
Ribeirão do Salto	Mata Atlântica	Rio Jequitinhonha, MG/BA	1,752.3	-40.1830, -15.8490	*Ophthalmolebias perpendicularis*	≤ 30% native vegetation cover
Rio João de Tiba	Mata Atlântica	Rio João de Tiba, BA	1,825.8	-39.43, -16.2660	*Phalloceros mikrommatos*	≤ 30% native vegetation cover
Ribeirão Piabanha	Cerrado	Rio Jequitinhonha, MG	794.2	-42.5479, -16.6164	*Microlepidogaster discus* *Trichomycterus landinga*	≤ 30% native vegetation cover
Córrego Pai Anselmo	Mata Atlântica	Rio Peruípe, BA	222.9	-39.3393, -17.6242	*Rachoviscus graciliceps*	≤ 30% native vegetation cover
Rio Peruípe tributaries	Mata Atlântica	Rio Peruípe, BA	4,221.8	-39.8958, -17.6687	*Microcambeva draco*	≤ 30% native vegetation cover

Table II. Continuation.

Lower Rio Mucuri	Mata Atlântica	Rio Mucuri, MG/BA	2,456.6	-40.2530, -17.8810	*Brycon vermelha* *Crenicichla mucuryna* *Delturus angulicauda* *Glanidium botocudo* *Microcambeva mucuriensis* *Mucurilebias leitaoi* *Prochilodus vimboides* *Xenurolebias pataxo*	Hydropower dam ≥ 30 MW; ≤ 30% native vegetation cover
Riacho Doce	Mata Atlântica	Riacho Doce, ES/BA	252.3	-39.7191, -18.2748	*Mimagoniates sylvicola* *Xenurolebias myersi*	≤ 30% native vegetation cover
Rio Itaúnas tributaries	Mata Atlântica	Rio Itaúnas, ES	4,811.1	-40.19, -18.2310	*Mimagoniates sylvicola*	≤ 30% native vegetation cover
Córrego São Domingos	Mata Atlântica	Rio São Mateus, ES	279.7	-39.9270, -18.5437	*Xenurolebias cricarensis*	≤ 30% native vegetation cover
Rio São José	Mata Atlântica	Rio Doce, ES	2,460.2	-40.5780, -19.0820	*Paragenidens grandoculis* *Prochilodus vimboides*	≤ 30% native vegetation cover
Rio Bananal, lagoon systems and other Lower Rio Doce tributaries	Mata Atlântica	Rio Doce, ES	2,094.4	-40.3730, -19.4670	*Paragenidens grandoculis*	≤ 30% native vegetation cover; Tailings dam collapse
Lower Rio Doce	Mata Atlântica	Rio Doce, ES	443.9	-39.9455, -19.4788	*Paragenidens grandoculis*	Tailings dam collapse
Rio Riacho tributaries	Mata Atlântica	Rio Riacho, ES	242.5	-39.9230, -19.6370	*Paragenidens grandoculis* *Prochilodus vimboides*	≤ 30% native vegetation cover
Rio Caratinga	Mata Atlântica	Rio Doce, MG	872.6	-42.1212, -19.6442	*Trichomycterus caratinguensis*	≤ 30% native vegetation cover
Rio Manhuaçu	Mata Atlântica	Rio Doce, MG	2,328.2	-41.7670, -19.6870	*Pareiorhaphis torrenticola*	≤ 30% native vegetation cover
Rio José Pedro	Mata Atlântica	Rio Doce, MG	3,625.7	-41.5850, -19.9490	*Astyanax microschemos* *Trichomycterus brunoi* *Trichomycterus caparaoensis*	Hydropower dam ≥ 30 MW; ≤ 30% native vegetation cover
Rio Guandu	Mata Atlântica	Rio Doce, ES	2,216.2	-41.1290, -19.9660	*Trichomycterus barrocus* *Trichomycterus castelensis*	≤ 30% native vegetation cover
Rio Piracicaba	Mata Atlântica	Rio Doce, MG	1,535.1	-42.8150, -19.6	*Henochilus wheatlandii* *Pareiorhaphis scutula* *Prochilodus vimboides*	Hydropower dam ≥ 30 MW
Ribeirão Sacramento and other Middle Rio Doce tributaries	Mata Atlântica	Rio Doce, MG	2,569	-42.4363, -19.7616	*Deuterodon sazimai* *Prochilodus vimboides* *Trichomycterus illuvies*	Tailings dam collapse

Table II. Continuation.

Rio do Peixe and other Middle Rio Doce tributaries	Mata Atlântica	Rio Doce, MG	1,227.7	-42.89, -20.1160	*Glanidium botocudo* *Steindachneridion doceanum* *Trichomycterus astromycterus* *Trichomycterus vinnulus*	Hydropower dam ≥ 30 MW; ≤ 30% native vegetation cover; Tailings dam collapse
Rio Matipó	Mata Atlântica	Rio Doce, MG	2,628.8	-42.3790, -20.2220	*Deuterodon sazimai* *Pareiorhaphis nasuta* *Trichomycterus tantalus*	≤ 30% native vegetation cover
Rio Casca	Mata Atlântica	Rio Doce, MG	2,524	-42.6280, -20.4980	*Pareiorhaphis nasuta* *Trichomycterus argos* *Trichomycterus brigadeirensis*	≤ 30% native vegetation cover
Rio Piranga	Mata Atlântica	Rio Doce, MG	2,527.1	-42.96, -20.6120	*Steindachneridion doceanum*	Hydropower dam ≥ 30 MW; ≤ 30% native vegetation cover
Rio Muqui do Sul	Mata Atlântica	Rio Itabapoana, ES	499.8	-41.41, -21.0220	*Brycon insignis* *Trichomycterus mimosensis*	≤ 30% native vegetation cover
Rio Preto	Mata Atlântica	Rio Itabapoana, ES	231.8	-41.2160, -21.1150	*Trichomycterus mimosensis*	≤ 30% native vegetation cover
Lower Rio Itabapoana tributaries	Mata Atlântica	Rio Itabapoana, ES/RJ	506.8	-41.0791, -21.2105	*Brycon insignis* *Loricariichthys melanurus*	≤ 30% native vegetation cover

Some of the prioritized basins in the NMAF ecoregion are repeatedly identified across scenarios and are marked as irreplaceable. This reflects the importance and specificity of the biodiversity they harbor. The concept of irreplaceability refers to the spatial options available for a particular species (Eken et al. 2004, Rodrigues et al. 2006, Langhammer et al. 2007) and, consequently, the implications of losing these often relictual environments. Numerous fish species in the ecoregion are found only in a single sub-basin or a small set of streams, making these environments irreplaceable for species conservation.

Areas repeatedly identified as irreplaceable across all three scenarios in the ecoregion include several tributaries of the Rio Paraguaçu basin, the upper Rio Itapicuru, stretches of the upper and middle Rio Jequitinhonha, portions of the Rio Mucuri, and other basins in the Tabuleiros Costeiros region, as well as several areas within the Rio Doce basin. This suggests that protecting these areas is crucial for threatened and non-threatened species (and consequently for other organisms and environments). It is worth noting that despite applying different methodologies, there is congruence between the priority areas pointed out in our evaluation and those defined by the broader MMA evaluation. Regions consistently highlighted in both assessments include the basins of the Rio Doce, Rio de Contas, Rio Paraguaçu, and smaller basins between the states of Espírito Santo and Bahia. It is also crucial to acknowledge the direct complementarity of several areas highlighted here with those previously defined, thereby amplifying the scope of potential conservation measures.

The Rio Doce basin stands out due to the significant number of critical areas, reflecting the potentially disruptive anthropogenic pressures affecting populations and habitats. The collapse of the Fundão tailings dam in 2015, which released millions of tons of toxic mining waste into the basin, has long-term repercussions for aquatic organisms (Ferreira et al. 2020, Passos et al. 2020, Weber et al. 2020, Vergilio et al. 2021, Sarmento-Soares et al. 2022). Furthermore, it is important to emphasize that other factors also contribute to the disruption of freshwater biota, such as desertification, changes in water regimes and climate change (Hofmann et al. 2021, Santos et al. 2023, Sayer et al. 2025), dams for agricultural and recreational purposes (Azevedo-Santos et al. 2024), and non-native species (Pelicice et al. 2023, Assis et al. 2024). These impacts should be also be addressed when defining priority conservation measures in the ecoregion, especially in basins north of Rio Doce (Sarmento-Soares & Martins-Pinheiro 2012, Santos et al. 2023).

While systematic conservation planning aims to prioritize areas efficiently, it must consider that not all basins have the exact conservation action costs for various reasons (Cawardine et al. 2008, Tognelli et al. 2019). Systematic planning should account for factors beyond just the area of the basins, such as socioeconomic aspects and multiple conservation targets, to maximize the pool of protected species in a given area (i.e., a true representation of local biodiversity, Margules & Pressey 2000, Nogueira et al. 2010) at the lowest possible cost. In the context of the Rio Doce basin, a broad and complex hydrographic network that supports a threatened and endemic fish fauna, Vieira (2010) suggests that subsequent evaluations are necessary in addition to identifying priority areas to define specific conservation strategies. Identifying priority areas should serve as a starting point for effective actions, whether for establishing new PAs or for mitigating impacts.

Implementing integrated watershed management policies, such as considering critical headwaters, entire rivers or basins as conservation units (Pelicice et al. 2017, Azevedo-Santos et al. 2019) and restoring degraded habitats within and around watercourses are key actions to enhance the resilience of freshwater ecosystems to environmental pressures (Hermoso et al. 2011, Sarmento-Soares & Martins-Pinheiro 2017, Azevedo-Santos et al. 2019, Tickner et al. 2020). Additionally, incorporating sustainable use practices for communities living around protected areas, such as traditional and indigenous peoples who rely on natural resources for their livelihoods, can help maintain ecosystem services while balancing social dynamics (Azevedo-Santos et al. 2019). The adoption of agroforestry systems is recently demonstrating its effectiveness in preserving forested environments and adjacent ecosystems while promoting livelihoods for indigenous and traditional populations (Ewert et al. 2013, Sarmento-Soares & Martins-Pinheiro 2017, Arroyo-Rodríguez et al. 2020, Silva et al. 2021). Furthermore, Silva et al. (2023) points to a positive citizen science initiative, where endangered catfish species *Trichogenes claviger* has become a conservation icon for a traditional community residing on the edge of a private reserve in the southern region of the NMAF ecoregion. Integrating the population into conservation efforts, in addition to other policies, could be a decisive factor in halting biodiversity losses in freshwater environments.

This study identifies priority catchments for fish conservation in the Northeastern Mata Atlântica ecoregion based on threatened, near-threatened, and restricted-range endemic species, while accounting for significant anthropogenic pressures on freshwater environments. The three target species scenarios identified irreplaceable catchments for the protection of the ichthyofauna, which must be preserved to avoid permanent loss of species. In the third scenario, 36 irreplaceable sub-basins were classified as critical due to environmental stressors, particularly in the Rio Doce basin. The most significant impact on the ichthyofauna in this regard is the loss of vegetation cover, which negatively affects habitat integrity and hydrological regimes. Our results suggest that the current protected area network might be insufficient to safeguard most target species. This assessment can support ongoing national and regional conservation action plans for species in the ecoregion, such as the National Action Plan (PAN, in Portuguese) Rivulídeos and the Territorial Action Plan (PAT, in Portuguese) Capixaba-Gerais (ICMBio 2013, Pró-Espécies 2021). It also provides a starting point for more detailed studies in each basin, considering socioeconomic, geographic, and climatic factors in the definition of new protected areas. These studies should address the complexity and specificity of freshwater systems and aim to expand the current network of protection across different regions.

SUPPLEMENTARY MATERIAL

Table SI.

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Data Availability

A comprehensive set of records considered in this study is available at the Figshare data repository: https://doi.org/10.6084/m9.figshare.23998905.