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An ecological trait matrix of Neotropical freshwater fishes

James S. Albert¹ , Vitor Abrahão², Daniel R. Akin¹, Jonathan G. Allen¹, Marcelo Andrade³ , Mariangeles Arce⁴, Jonathan W. Armbruster⁵, Ricardo Benine⁶, Maxwell J. Bernt⁷, Maria E. Bichuette⁸, José Birindelli⁹, Pedro Bragança¹⁰, Marcelo R. Britto¹¹, Paulo A. Buckup¹¹ , Michael D. Burns¹² , Barbara B. Calegari¹³ , Fernando G. Carvalho¹⁴, Tiago P. Carvalho¹⁵, Lilian Casatti¹⁶, Wilson Costa¹¹, William G. R. Crampton¹⁷, Robson da Costa Ramos¹⁸, Ronielson G. da Silva¹⁹, Fernando Dagosta²⁰, Joshua Egan²¹, Luis Fernández²², Jessé M. Figueiredo-Filho¹, Daniel Fitzgerald²³, João Pedro Fontenelle²⁴, Eric B. Haddad¹, Matthew Kolmann²⁵, Tomas Hrbek²⁶, Francisco Langeani²⁷, Pablo Lehmann²⁸, Rafael P. Leitão²⁹, Flávio C. T. Lima³⁰, Marina V. Loeb³¹, Carlos A. S. Lucena²⁸, Paulo H. F. Lucinda³², Nathan K. Lujan³³, Luiz R. Malabarba³⁴, Wilfredo A. Matamoros³⁵ , Bruno F. Melo¹⁰, Andre Netto-Ferreira³⁴, Carla S. Pavanelli³⁶, Fernando M. Pelicice³², Edson H. L. Pereira²⁸, Xavier Plasencia III³⁷, Marcelo Rocha²⁶, Fábio Roxo⁶, Vivianne Sant'Anna²⁸, Oscar Shibatta⁹, Veronica Slobodian³⁸ , Madlen Stange³⁹, Víctor A. Tagliacollo¹⁹, Milton Tan⁴⁰, Kevin T. Torgersen¹, Kirk O. Winemiller⁴¹ & Roberto E. Reis²⁸

The Neotropical freshwater fish (NFF) fauna constitutes the most diverse continental vertebrate assemblage on Earth, with more than 6,345 species distributed across South America, Central America, and the Greater Antilles. These species display a bewildering array of ecophysiological and behavioral traits, or *ecotraits*, used to exploit habitat and food resources across geographical, climatic, and seasonal gradients. Despite intensive taxonomic and systematic studies, the literature on ecological preferences and tolerances of NFF species is scattered and incomplete, and we have previously lacked a centralized database. Here we present the first comprehensive dataset of ecotraits for the NFF fauna using published data and expert knowledge from the community of Neotropical ichthyologists. This *ecomatrix* includes adult modal values for 42 ecotraits scored for all valid NFF species, including body size, four of habitat utilization related to water chemistry, 21 of physical habitat structure, 10 of diet (i.e. trophic guilds), and six other behavioral traits. This *ecomatrix* is a foundation for future studies on the ecology and conservation of Neotropical aquatic biodiversity.

¹University of Louisiana at Lafayette, Lafayette, USA. ²Universidade Federal da Bahia, Salvador, Brazil. ³Universidade Federal do Pará, Belém, Brazil. ⁴Academy Natural Sciences Philadelphia, Philadelphia, USA. ⁵Auburn University, Auburn, USA. ⁶Universidade Estadual Paulista Botucatu, São Paulo, Brazil. ⁷Susquehanna State University, Pennsylvania, USA. ⁸Universidade Federal de São Carlos, São Carlos, Brazil. ⁹Universidade Estadual de Londrina, Londrina, Brazil. ¹⁰American Museum of Natural History, New York, USA. ¹¹Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. ¹²Oregon State University, Corvallis, USA. ¹³Institute of Ecology and Evolution, University of Bern, Bern, Switzerland. ¹⁴Fundación Miguel Lillo, Tucumán, Argentina. ¹⁵Pontificia Universidad Javeriana, Bogotá, Colombia. ¹⁶Universidade Estadual Paulista, São Paulo, Brazil. ¹⁷University Central Florida, Orlando, USA. ¹⁸Universidade Federal da Paraíba, João Pessoa, Brazil. ¹⁹Universidade Federal do Uberlândia, Uberlândia, Brazil. ²⁰Universidade Federal da Grande Dourados, Dourados, Brazil. ²¹University of Idaho, Idaho, USA. ²²Fundación Miguel Lillo, Salta, Argentina. ²³US Fish & Wildlife Service, Washington, USA. ²⁴University of Toronto, Toronto, Canada. ²⁵Department of Biology, University of Louisville, Louisville, USA. ²⁶Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. ²⁷Universidade Estadual Paulista, São José do Rio Preto, Brazil. ²⁸Pontificia Universidade Católica Rio Grande do Sul, Porto Alegre, Brazil. ²⁹Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. ³⁰Universidade Estadual de Campinas, São Paulo, Brazil. ³¹Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil. ³²Universidade Federal do Tocantins, Palmas, Brazil. ³³Royal Ontario Museum, Toronto, Canada. ³⁴Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. ³⁵Universidad de Ciencias y Artes de Chiapas, Chiapas, Mexico. ³⁶Universidade Estadual de Maringá, Maringá, Brazil. ³⁷University of Louisville, Louisville, USA. ³⁸Universidade de Brasília, Brasília, Brazil. ³⁹Zoological Research Museum Alexander Koenig, Bonn, Switzerland. ⁴⁰Illinois Natural History Survey, Champaign, USA. ⁴¹Texas A&M University, College Station, USA. ✉e-mail: jalbert@louisiana.edu; reis@pucrs.br

Background & Summary

Biodiversity may be defined broadly as the diversity of genes, traits, species, habitats and landscapes in the biosphere^{1,2}. Estimating the species richness of a clade or region is a central task in biodiversity assessment, yet raw species counts represent only one of many biodiversity dimensions. Functional traits provide critical information for understanding community assembly, species coexistence, and biodiversity loss³. Trait-based approaches to the study of ecology and evolution illuminate how organisms interact with their environments and each other, which is essential for understanding community structure and ecosystem functioning, both now and in the future⁴. Functional traits include the ecological, life-history, morphological, physiological, and behavioral adaptations commonly used to categorize species into functional groups and guilds^{5–7}.

The Neotropics is a global center of biodiversity, including about 10% of all the world's described species of continental plants and animals^{8–10}. The Neotropical freshwater fish (NFF) fauna includes at least 6,345 valid species distributed throughout the rivers, lakes and wetlands of tropical South America, Central America south of the Trans-Mexican Volcanic Belt, and the Greater Antilles^{11–13}. This diversity represents about one-sixth (18%) of all c. 36,000 valid fish species globally, or about one in 11 (c. 9%) of all the known vertebrate species who live on the Earth today¹⁴. The NFF fauna is also the global center of diversity for genetic¹⁵, morphological^{16,17} and ecological¹⁸ diversity among freshwater (i.e., continental) fishes¹⁹. Neotropical aquatic ecosystems support the food webs of large lakes and rivers that provide a substantial fraction of the animal protein consumed by tens of millions of people^{20–22}. Recent studies have also documented the conservation²³ and evolutionary²⁴ values of the immense NFF fauna. Yet despite these many ecological and economic services, information on the natural history of NFF species has until now been scattered among hundreds of primary journal articles published in several different languages.

Among animals generally, ecophysiological traits are linked to body size, habitat utilization, trophic guilds and reproductive behaviors that inform conservation strategies aimed at preserving biodiversity and ecosystem functionality^{25–27}. With a few notable exceptions (e.g. ^{6,28,29}), most previous studies on functional trait diversity within freshwater fish faunas have used linear measurements to assess body proportions (e.g., body aspect ratio, relative eye size and gape size) as proxies for functional traits^{16,17,30–33}.

Here we present the first dataset of ecophysiological and behavioral traits (hereafter *ecotraits*) scored for all valid NFF species (available at: <https://doi.org/10.7910/DVN/WZJSNX>). These ecotraits include aspects of the integrated phenotype related to habitat and diet utilization, and behaviors related to life-history activities. The goal of this study is to characterize the range of physiological and behavioral adaptations among NFF species for utilizing and partitioning environmental and food resources in time and space, and life history specializations associated with seasonal, climatic, and elevational gradients.

Methods

Information sources and data extraction. The NFF ecomatrix synthesizes taxonomic and ecological information for all freshwater fishes of South and Central America and the Greater Antilles¹³ considered valid as of Dec. 2019. The study design was for project editors (JSA and RER) to build a draft version of the NFF ecomatrix by scoring taxa for all ecotraits to the genus level, and then disseminating subsets of this draft dataset by family, or subfamily in the case of the most diverse families (i.e. Characidae and Loricariidae) to each of the 55 contributing experts (Fig. 1). The edited versions of these data subsets and their associated literature references were then reassembled into the final NFF ecomatrix, which was used by the editors to conduct data analyses and prepare the final manuscript for publication. The double-headed arrows in Fig. 1 indicate two-way flows of information between the editors and other project resources and activities. Further, data compilation required more than five years, during which time many new publications became available, including about 300 new species published from 2020 to 2023, with many new ecological observations of NFF fishes. The final ecomatrix of this study is therefore presented as a starting point for continuing studies of the megadiverse NFF fauna.

Preparing the list of valid NFF species. The NFF species list includes updated taxonomic information, including synonymies, generic assignment, and missing species, for all 6,342 valid NFF species names as of Dec., 2019. This species list was compiled through an extensive review of the scientific literature by the 54 ichthyologists who serve as co-authors of this study, each with specialized knowledge of different taxonomic groups. The species list was elaborated through an extensive review of the scientific literature, which encompassed 1,286 published sources, including original species descriptions (e.g. ^{34–36}), taxonomic revisions (e.g. ^{37–39}), checklists (e.g. ^{40–42}), books (e.g. ^{19,43,44}), and online catalogs such as FishBase, SpeciesLink, and GBIF, among others. To ensure the reliability of the collected information, a verification of the taxonomic status of each species was conducted, using the Eschmeyer Catalog of Fishes as a reference⁴⁵. In this process, the spelling of scientific names was verified, synonyms were identified and corrected, and non-native species to the Neotropical region were excluded. Following this step, a preliminary list containing all compiled species was made available to collaborators for validation and refinement.

Description of the ecomatrix. Adult modal values for each ecotrait for each species were assessed by 55 experts of NFF biology, all co-authors of this study, using data from 1,294 literature references, reporting data for all 870 valid NFF genera and 32% of all valid NFF species. The NFF ecomatrix dataset is available at the Harvard Dataverse⁴⁶. The resulting ecomatrix includes 266,490 observations with 50,688 (19%) as positive observations. The NFF ecomatrix includes observations of 6,342 NFF species representing 870 genera, 97 families, and 40 taxonomic orders scored for 42 ecotraits of habitat utilization, diet, and other ecologically relevant behaviors. Species in the ecomatrix are arranged in a conventional phylogenetic sequence by Class, Order, and Family and alphabetically within genus. List of these ecotraits with brief descriptions are provided in the tables, along with

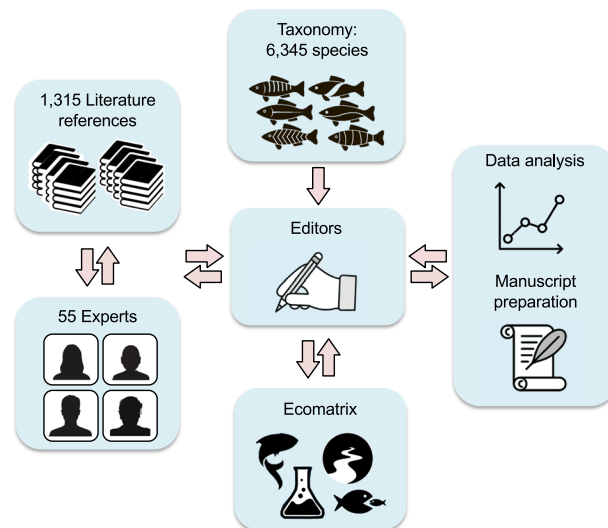


Fig. 1 Schematic overview of the study design and workflow.

the numbers of species known to exhibit these traits. To ensure consistency of scoring data collected by multiple authors using information from many different sources we employed several strategies. Ecotrait categories were delimited in advance using quantitative or qualitative values. Additional policies to ensure replicability and accuracy are described below under the section: Technical Validation: Reliability, Scoring of individual cells.

Ecotrait classification. The ecotrait categories used in this study for NFF species were defined using criteria developed in previous studies of Neotropical aquatic habitats, fish trophic guilds and fish behavior related to ecological functions^{18,28,47–51}. In some cases, it was necessary to modify the categories and states based on conditions observed under varied freshwater regions. For example, the ecotrait of “blackwater utilization” in this study is restricted to fishes that inhabit waters with both high organic content and low pH, which distinguishes the distinct fauna of acidophilic Amazonian blackwater rivers (e.g., Negro River, Amazonas, Brazil⁵²) from that of the darkly-coloured waters with near-neutral pH of floodplain lakes along the Amazon River⁵³, or of the Negro River of Uruguay⁵⁴. Descriptions of 26 ecotraits associated with body size, water chemistry and habitat utilization are provided in Table 1, including five associated with water chemistry, and 20 associated physical habitat structure. An additional 16 traits associated with diet and behavior are provided in Table 2. This list of ecotraits does not include quantitative data on life history traits (e.g., fecundity, survivorship, generation time), which are generally limited to commercially important species in the fisheries or ornamental fish trade, and life history data are unknown for a majority of NFF species, which represents an important knowledge shortfall^{55,56}.

Body size is a fundamental feature of the ecological phenotype in fishes and other animals, affecting metabolic rate and other physiological processes, behavior, resource utilization, locomotion and life history^{57,58}. NFF body size was assessed as the maximum recorded standard length (SL), or total length (TL) for taxa without a caudal fin, scored to four size categories: large size as 100–610 cm (2.00–2.79 log cm); medium size as 10–95 cm (1.00–1.99 log cm); small body as 2.7–9.9 cm (0.43–0.99 log cm); and miniature size as 0.9–2.6 cm (0.05–0.41 log cm). Maximum known standard or total length are highly correlated with body mass in most fishes and this a widely used metric of overall body size in fishes⁵⁹. Body size data are available for 5,400 NFF species representing 85.1% of the fauna and all the valid NFF genera. Other NFF species were scored by the editors by phylogenetic imputation based on the body sizes of their closest relatives. In several studies of NFF faunas, body size has been shown to be correlated with trophic position in predator but not prey species (e.g.⁶⁰).

The ecotraits related to water chemistry (Fig. 2A) are physiological tolerances to inhabit clearwaters with high transparency, low sediment load, low concentrations of dissolved ions, near neutral pH (5.6–8.0), whitewaters with low transparency, high sediment load, high dissolved ions, near neutral pH (5.6–8.0), blackwaters with low transparency, low sediment load, low dissolved ions, low pH (3.5–5.5), and estuarine waters located at river mouths and coastal estuaries with variable salinity values from fresh to brackish. Species commonly collected in all these habitats were scored as water chemistry generalists. Ecotraits of physical habitat structure represent physiological tolerances to distinct aspects of environmental variation at three levels of spatial scale: macrohabitat (100–1,000 m), mesohabitat (10–100 m) and microhabitat (1–10 m). Within each of these scales, habitats were characterized using environmental variables of Strahler stream order (1–5 streams and small rivers, 6–10 large rivers; Fig. 2B) as a metric for total aquatic habitat volume⁶¹. Additional mesohabitat attributes are hydrological setting (benthic channel, pelagic channel, littoral channel, floodplain; Fig. 2C), water flow (lotic vs. lentic), flow gradient (low gradient runs vs. high gradient riffles or rapids; Fig. 2D), geological setting (tectonic lakes, hypogean aquifers and caves), seasonality (annual vs. perennial), water-column position (surface, pelagic, benthic), and substrate composition (unspecified, mud/silt, sand, gravel/rocks, submerged wood, vegetation, leaf packs).

Category	ET#	Ecotrait	Spp.	%Spp.
Adult body size	1	Log cm SL (or TL): Large, 2.00–2.79; Medium, 1.00–1.99; Small, 0.43–0.99; Miniature, –0.05–0.41	5338	84.10%
Water chemistry	2	Clearwater: high transparency, low sediments & dissolved ions, near neutral pH (5.6–8.0)	4690	73.90%
	3	Whitewater: low transparency, high sediments & dissolved ions, near neutral pH (5.6–8.0)	1742	27.50%
	4	Blackwater: low transparency, low sediments & dissolved ions, low pH (3.5–5.5)	1185	18.70%
	5	Estuarine: Variable salinity from fresh to brackish	263	4.10%
Macrohabitat (100–1000 m)	6	Low-gradient (slope less than 2%) streams & small rivers (Strahler stream orders 1–5)	3998	63.00%
	7	High-gradient (slope more than 2%) riffles in streams & rapids in small rivers	1257	19.80%
	8	Ancient lakes, more than 10,000 ka; e.g. volcanic calderas, tectonic rifts	68	1.10%
	9	Hypogean caves & aquifers	48	0.80%
	10	Low-gradient channels & margins of large rivers (Strahler stream orders 6–10)	1561	24.60%
Mesohabitat (10–100 m)	11	High-gradient rapids of large rivers	150	2.40%
	12	Lotic (flowing) streams (English), <i>quebradas</i> (Spanish), <i>igarapés</i> (Portuguese)	4422	69.70%
	13	Lentic (standing) waters of small rivers; pools, ponds & reservoirs	539	8.50%
	14	Seasonally dry (e.g. ephemeral) aquatic habitats	302	4.80%
	15	Benthic (bottom) of large river channels	730	11.50%
	16	Pelagic (midwater) of large river channels	397	6.30%
	17	Littoral (margins) of large river channels	892	14.10%
	18	Seasonal floodplains (oxbow lakes & flooded forest) of large rivers	1051	16.60%
Microhabitat (1–10 m)	19	Benthic, unspecified	1578	24.90%
	20	Benthic, mud & silt	374	5.90%
	21	Benthic, sand	588	9.30%
	22	Benthic, gravel/rocks	1262	19.90%
	23	Benthic, submerged wood & vegetation	710	11.20%
	24	Benthic, leaf litter & packs	239	3.80%
	25	Epibenthic in water-column above bottom	2816	44.40%
	26	Epibenthic at or near surface	418	6.60%

Table 1. Descriptions of 26 ecotraits traits associated with body size, water chemistry and macrohabitat utilization. Data scored for all Neotropical freshwater fish (NFF) species. ET#, ecotrait number; total species numbers (Spp.) and proportions (%Spp.) of all NFF species scored as possessing each ecotrait.

Category	ET#	Ecotrait	Spp.	%Spp.
Diet: Trophic guild	27	Benthic microvores, small animals 0.5–5 mm	4143	65.30%
	28	Surface invertivores: Allochthonous arthropods (insects, arachnids)	218	3.40%
	29	Pelagic planktivores: Autochthonous arthropod & fish larvae	418	6.60%
	30	Benthic detritivores: Non-living decomposing organic (mostly plant) matter	205	3.20%
	31	Benthic algivores: Living algae & bacterial biofilm	1003	15.80%
	32	Folivores: Submerged plant leaves, riverweeds	57	0.90%
	33	Frugivores: Fruits & seeds	34	0.50%
	34	Piscivores: Fish tissue	527	8.30%
	35	Omnivores: Both plant & animal tissues	1317	20.80%
	36	Ectoparasites, scales & mucous	114	1.80%
Behavior	37	Potamodromous: longitudinal river migrations more than 100 km	844	13.30%
	38	Viviparous: live birth	276	4.30%
	39	Aestivation: prolonged infaunal torpor (i.e. lowered metabolic activity) & desiccation	4	0.10%
	40	Venomous: phenotypes that deliver injected toxin(s) & associated aposematic behaviors	912	14.40%
	41	Passive electroreception: sensory use of weak (mV) ambient electric fields	2685	42.30%
	42	Active electroreception & electrogenation using electric organs	261	4.10%

Table 2. Descriptions of 16 ecotraits traits associated with diet and behavior. Data format and abbreviations as in Table 1.

The trophic guilds are benthic invertivores (including meiovores/microvores), surface invertivores, benthic detritivores, benthic algivores, pelagic planktivores, folivores, frugivores (fruits and seeds), piscivores, omnivores (both plant and animal parts), and ectoparasites (eating scales and fins of other fishes). Many NFF species are trophic opportunists and dietary generalists, and it is not possible to identify Adult Modal Diet more finely than that of a generalized microvore⁶². Ecotraits of behavioral attributes include species with long-distance

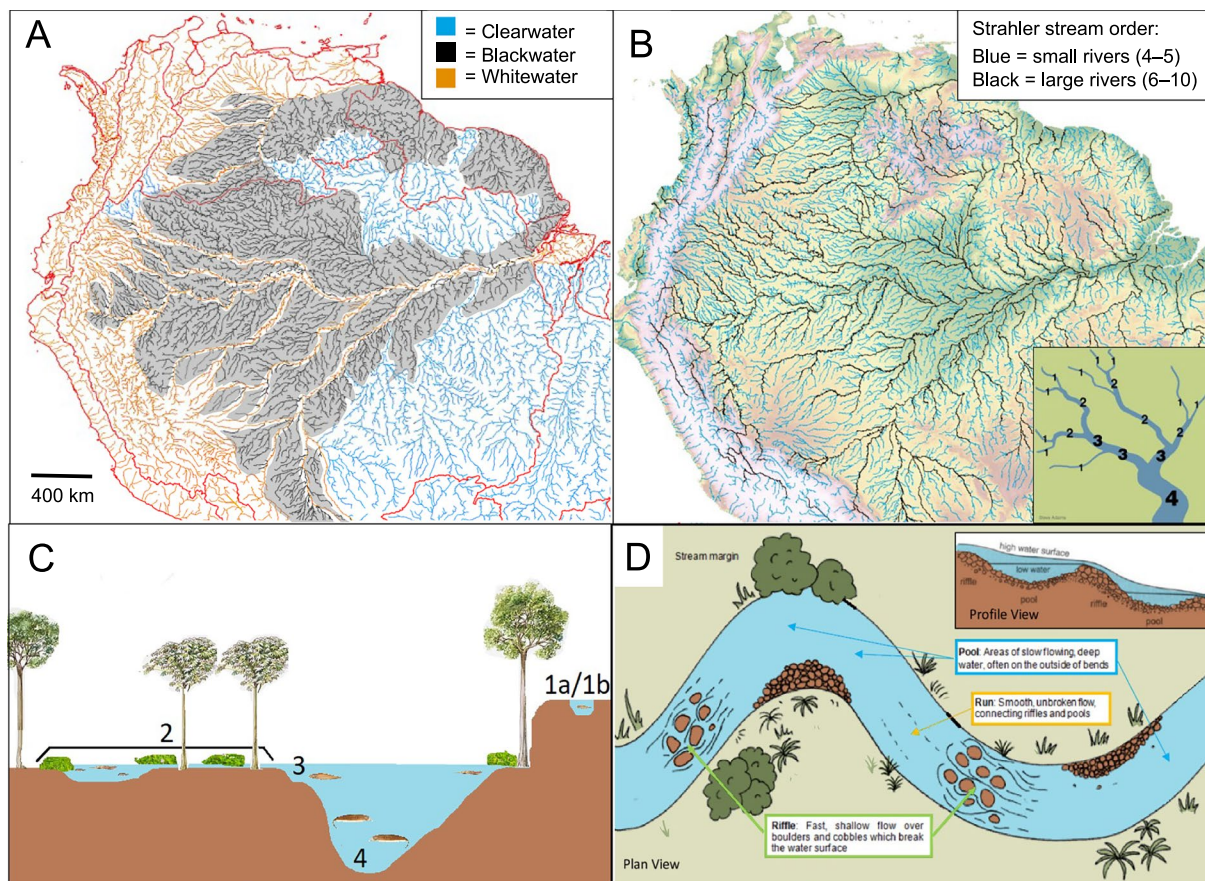


Fig. 2 Major riverscape features used to score habitats of NFF species. **(A)** Water chemistry with Amazonian rivers designated blackwater, whitewater and clearwater based on sediment flux and pH. **(B)** Stream order within the Amazonian tributary hierarchy illustrating small (4–5) and large (6–10) rivers. Inset: Strahler order with first order streams as smallest headwaters along watershed boundary. **(C)** Habitat types transverse view. 1a: Non-floodplain streams & small rivers; 1b: Non-floodplain rapids and riffles; 2: Flooded forests and floodplain lakes; 3: River margins; 4: River channels. **(D)** Habitat types plan view; profile view in inset. Note longitudinal sequence of swift shallow flow in riffles, slow deep flow in pools, and smooth unbroken flow in runs.

(>100 km) longitudinal seasonal migrations, viviparity (live birth), venom injection with associated behaviours, passive electroreception with ampullary electroreceptor organs, active electroreception with electric organs and tuberous electroreceptor organs, and physiological aestivation or prolonged infaunal torpor (i.e. lowered metabolic activity) with desiccation during the low water season Fig. 3.

Data Records

Online datasets supporting this study are available at the Harvard Dataverse as: “Data matrix V2 and list of literature references for: ‘An ecological trait matrix of Neotropical freshwater fishes’”; <https://doi.org/10.7910/DVN/SBU82J>. These datasets include two files: (1) An ecomatrix of 42 ecotraits scored for 6,345 species of Neotropical freshwater fishes. (2) List of 1,294 literature references supporting data for 2,016 NFF species (32% total) representing all 870 valid genera.

Technical Validation

Reliability. The list of authenticated species names was compiled by consulting recent taxonomic reviews, and the list of valid species names available at Eschmeyer’s online Catalog of Fishes¹⁴. Valid species names exclude synonyms and were assigned to a genus name based on the most recent taxonomic revisions. The ecotrait classification was carefully designed using quantitative metrics to match freshwater habitats in all waterways of South America, Central America, and the Greater Antilles, but scored qualitatively as adult modal values to reduce error due to changes during growth or ecophenotypic variation.

Scoring of individual cells. The goal of this project is to provide the user community with a comprehensive dataset that most accurately represents current knowledge of NFF ecological diversity. The NFF ecomatrix therefore has no empty cells or question marks, and estimated trait values of some poorly known species are provided based on information gleaned from collection records and knowledge of their closest relatives. At least three experts laid eyes on every cell in the ecomatrix, including the two project editors and one or more contributing experts. Cells were scored using all available sources of information, including literature references when

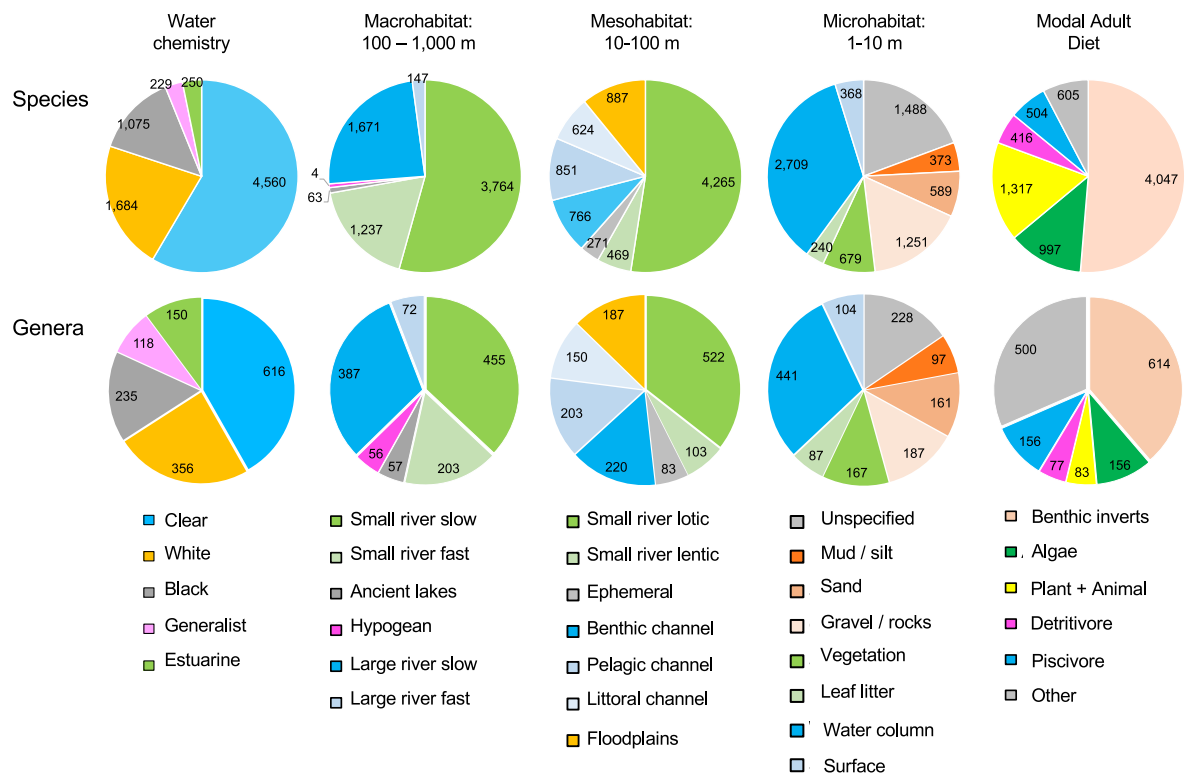


Fig. 3 Frequencies of taxa among NFF ecomatrix categories. Data for 6,345 species. Species (top row) and genera (bottom row) among each of the major ecotrait categories; see Tables 1 and 2.

available, observations of the contributing experts based on their personal knowledge from field collections and museum records, and in some cases unpublished data or consultations with other professional colleagues.

Known collection biases. Data on the species richness of the NFF fauna has several documented collection biases^{23,63}, which may also influence knowledge of fish species ecological traits. The more well-documented NFF species have larger body sizes, are exploited for fisheries with commercial value as food items or in the aquarium trade, or have other special interest to the scientific community, have broader geographic ranges, live near cities with major universities and museums of natural history, inhabit low-order streams along major roads, or high stream-order tributaries along major rivers, or inhabit places that will be affected by projects that need to obtain environmental licenses that require collections⁶⁴.

Limitations of this ecomatrix. Despite representing 42 ecotrait dimensions, a unique combination of these ecotraits does not necessarily constitute a distinct functional role or ecological niche. Some traits represent multiple functional traits depending on the habitat or diet breadth of individual species. For example, “benthic invertivores” includes fishes that consume aquatic and aerial insects, crustaceans, and molluscs, often involving distinct physiological, morphological, and behavioral phenotypes^{65–68}. Similarly, the terms “algivore”, “herbivore” and “detritivores” include species with potentially distinct modal diets as ascertained by stable isotope analysis^{69,70}. A similar logic applies to food and habitat traits where species may differ in the breadth of resource utilization seasonally or through life history^{68,71,72}. We therefore present these unique combinations not as species niches but rather as ecologically conserved clade-level (mostly super-specific) attributes.

Except for the family Poeciliidae (e.g.^{73–75}), we currently lack data regarding ecological and life history trait data for a majority of NFF taxa at the species level. This lack of information includes important data on size at onset of sexual reproduction, number and size of eggs and larvae, and reproductive lifespan⁷⁶. Other important data types with poor representation across NFF taxa include the allocation of resources to the competing ends of growth, reproduction, survivorship, maturation, growth and mortality⁷⁷.

Code availability

No specialized code was used to extract data or build the data matrix of this study.

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Author contributions

James S. Albert and Roberto E. Reis conceived the idea for this study, coordinated file sharing among the contributing authors, and served as editors to compile and proof the draft and final versions of the ecomatrix and the list of literature references. James S. Albert, William G.R. Crampton, Kirk O. Winemiller, and Roberto E. Reis developed the classification of ecotraits. James S. Albert, Kevin T. Torgersen and Roberto E. Reis performed the data analyses, prepared the figures, and wrote the first draft of the manuscript. Victor A. Tagliacollo, Fernando Dagosta, James S. Albert and Roberto E. Reis compiled and authenticated the list of valid NFF species names. All authors edited data for one or more fish families in the NFF ecomatrix, contributed references to portions of the ecomatrix, and contributed edits to the final draft of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to J.S.A. or R.E.R.

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